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ERRATA.

Page 4, third paragraph: *Mectriocnemus* should read *Metriocnemus*.
Page 43, twelfth line from bottom: *Culicoidies* should read *Culicoides*.
Page 86, eleventh line under "Commercial Possibilities:" *Margaratifera* should read *Margaritifera*.
Page 93, Table heading: *Terrapin* should read *terrapins*.
Last column of table: Reference *b* should read *a* in all three instances.
Page 105, Legend under Fig. 81: Dash line preceding *hibernated* should be solid line.
Page 127, third line from bottom in right-hand column: *115* should read *215*.
Page 128, sixth line from bottom: *128* should read *127*.
Page 138, ninth line from bottom: Second *Exs* should read *ExS*.
Page 188, fifth line from bottom: *ptonucleus* should read *pronucleus*.
Page 193, seventh line from bottom: *anlarge* should read *anlage*.
Page 209, fifth line below table: *peridineans* should read *peridinians*.
Page 221, Last line: Colon preceding *iron* should be deleted.
Page 281, ninth line from bottom in left-hand column: *282* should read *292*.

ECOLOGICAL STUDY OF AQUATIC MIDGES AND SOME RELATED INSECTS WITH SPECIAL REFERENCE TO FEEDING HABITS.

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By ADELBERT L. LEATHERS.

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CHIRONOMIDÆ.

INTRODUCTION.

The insects belonging to the family Chironomidæ, commonly known as midges, constitute an obscure group of Diptera which, on account of their small size and inoffensive habits, have very largely escaped notice except as they may have been mistaken for mosquitoes, which they resemble only in general appearence. They are, however, very common in every community from the polar region to the Tropics. The adults are often seen on moist evenings flying in dense swarms near the ground, over sidewalks, or under trees by the roadside, and it is in this brief period of their existence, consisting of from 5 to 10 days, that they are most familiar to the general public.

Closely related to the Chironomidæ are the Orphnephilidæ, a family of semiaquatic insects as scarce as the Chironomidæ are common, the only known habitat in this country being in the environment of Ithaca, N. Y. The larval stages of the Chironomidæ, which extend over a period varying from all winter to 25 or 30 days, according to food and weather conditions, are only infrequently observed, chiefly because of the small size and secluded habits of the larvæ. They are aquatic, mainly fresh-water, insects living in burrows which they construct by fastening together the débris found at the bottom of ponds with silk secreted by their salivary glands. The great abundance of these larvæ and their relation to other aquatic organisms were the fundamental considerations that gave impetus to this study. It was hoped that an investigation of their feeding habits would give a clue to the chief adaptations which have given rise to their numerical dominance and widespread distribution.

That they do subsist in great numbers has been called to the author's attention not alone by his own observations, but by various published and unpublished works of students who have recorded them as forming an important part of the food of trout, suckers, and various other fish, and of salamanders, dragonflies, mayflies, and a variety of other predacious aquatic organisms. Herein lies the chief interest of these observations from the fish-cultural point of view, that a careful study is made of a particular group of animals which are engaged in converting vegetable detritus and other organic materials existing in fishponds into a form suitable for consumption by fish. How useful they are as a direct medium in transforming and conserving the food supply furnished by the microorganisms found in small quantities in all habitats will be shown in greater detail in the subsequent discussion.

In beginning this work the larvæ of many species were examined in order to determine their stomach contents. The organisms found were so similar, both in number and variety, to those available in a given locality that there seemed to be little or no sorting in their method of feeding. Consequently, attention was directed more to their method of capturing food than to the substances eaten, and it was here that the fundamental adaptations were found which enable the different genera and species to live in a similar environment with a minimum amount of competition. The small size of the larvæ and their great power of tiding over periods of food shortage, together with their capacity to live in habitats containing a scanty supply of oxygen, readily enable them to subsist where a larger animal would find the food supply insufficient or the environment unsuited to its manner of life.

In this study of the feeding habits the author has endeavored to associate into groups those larvæ which obtain their food in an essentially similar manner. An attempt has been made to cover the entire family. The subfamily Chironominæ has been divided into six groups, while the subfamilies Tanypinæ and Ceratopogoninæ each constitute but a single group. The number of these divisions shows in a somewhat graphic way the relative size and amount of specialization of the three subfamilies. It is to be hoped that these groups will be found sufficient to accommodate all the various species of the family, although the two consecutive seasons devoted to this work, in the absence of any considerable literature on the feeding habits of the larvæ, are all too short a time to exhaust a study involving such small and relatively obscure organisms.

This work was done in the entomological laboratory of Cornell University, under the direction of Prof. J. G. Needham, to whom the author is greatly indebted for much counsel, assistance, and encouragement in the prosecution of the work. The author wishes to acknowledge his appreciation of the assistance rendered by Prof. O. A. Johannsen in the identification of specimens, general suggestions, and sympathetic interest and encouragement in every phase of the work. He is also greatly indebted for many favors from the various members of the Department, to whom he wishes to express his appreciation for the thoughtfulness that prompted such generous cooperation.

TECHNIQUE.

In order to carry on the laboratory experiments with various chironomids it was found desirable to keep a number of living larvæ always on hand. For most larvæ very simple containers proved most satisfactory. Those that live in the manner described under Group III were brought home, together with a small mass of the débris in which they were living, and placed in shallow agateware trays. The débris containing the larvæ was usually spread out, so as not to be more than one-fourth of an inch deep, and was then covered to a depth of half an inch with tap water. After a day or so, when the larvæ were especially numerous, as a rule they used all the loose débris in constructing rather long U-shaped tubes, where they usually succeeded in maintaining themselves for weeks at a time. The shallow agateware trays were rather generally used for the various forms of larvæ that could be collected in numbers. They are especially to be recommended on account of the large amount of water surface exposed to the air, thus facilitating aeration.

In breeding the various species collected a considerable number of individual receptacles were required. In the early experiments square watch glasses with covers were used successfully. They were later discarded in favor of medium-sized test tubes. Such a tube with a cotton wool plug has numerous points of advantage over a watch glass. First, the cotton plug permits a free exchange of gases. This circulation prevents the accumulation of moisture on the inside of the test tube, so that the newly immerged fly is not so liable to be caught in a water film and drowned. Second, the cotton plug makes a very satisfactory surface to which a freshly immerged fly may cling. Third, a number of test tubes may be placed together in a slanting position, so that the water which they contain will expose a proportionally large surface to the air, thus insuring perfect aeration. Fourth, a considerable number of tubes may be placed in a tray and a uniform temperature maintained either by flowing water or by evaporation from the surface of standing water. Fifth, the data concerning the larva may be written on a small piece of paper and inserted with the cotton in the mouth of the test tube.

Mectriocnemus knabi larvæ were kept for several weeks by bringing in the leaves of the pitcher plant and placing them so that they would remain in an upright position. They were kept full by the occasional addition of small amounts of water. The larvæ were also kept for weeks at a time in petri dishes containing the water and insect remains obtained by emptying the leaves of the pitcher plant. They do not appear to be so exacting in their environmental requirements as most chironomid larvæ and can doubtless be reared in most any sort of a container.

Chironomus lobiferus were brought into the laboratory in water-soaked Sparganium stems, which were allowed to float freely in trays filled with water. In this condition the larvæ maintained themselves for considerable periods at a time. Upon removing them from their burrow they were found to adjust themselves to various artificial receptacles. The most satisfactory glass preparations for the observation of the habits of *Chironomus lobiferus* larvæ were constructed so as to give flat horizontal surfaces. This was accomplished by cementing two rectangular strips of glass cut from cover slips to either side of parallel capillary glass tubes. The size of the capillary tubes used was slightly larger than the full-grown larva.

It was found that King's "Microscopical Cement" is more satisfactory than a cement made by dissolving asphaltum in turpentine or xylol, especially when it is desired to make permanent mounts of the silken tubes. It is necessary to dehydrate rapidly in order not to dissolve this cement, but even with this defect it is more satisfactory than other cements soluble in xylol. Because of the uniform thickness and the flatness of the surfaces (fig. 26) this type of glass preparation is more satisfactory than any flattened tube the author was able to manufacture.

Ehrlich's acid hematoxlin was found to be the most satisfactory of any stain used for bringing out the silk structures. "Licht green" and "eosin" were also used but were not found satisfactory. The licht green, while staining the silk glands and the silk within the silk duct, did not stain the silk outside of the body. The eosin, while staining the silk slightly, was found unsatisfactory because of the ease with which it was removed in dehydration.

There are few animals that lend themselves more readily to a laboratory or lecture demonstration than do these stem-dwelling larvæ. They seem to differ decidedly from other chironomids, especially those that characteristically live in a mud burrow, in their reactions to strong light. Their greater tolerance of light enables one to demonstrate the silk-spinning movements and the general behavior of the larvæ by means of a stereopticon. The only requirements are that the larvæ shall have recently built a fresh, clean silk tube in a glass preparation, and that the temperature of the water be kept down to normal room temperature. The reason for requiring that the silken tube be a fresh one is that after a week or two the silk becomes much discolored by the lodgment of fine particles as well as by the deliberate attachment of masses of castings to the ends of the burrow. It is only necessary to remove the larva by a jet of water and then the tube can be removed by a needle. A few hours will usually suffice to enable them to again replace the silken tube. The temperature is easily controlled by having a specially constructed lantern slide through which a current of water can be made to pass. A type used with considerable success was constructed as follows:

Two pieces of sheet brass the size of a lantern slide were cut so as to give a symmetrically placed rectangular opening 1½ by 2 inches near their center. These two brass strips were drilled and fitted with screw bolts. Two sheets of transparent celluloid and a single sheet of rubber packing material about an eighth of an inch in thickness were punched so that the holes coincided with those in the brass plates. The rubber packing was cut so as to give a rectangular opening which coincided with that in the brass plates, and the parts were assembled in the following order: Sheet brass, celluloid, rubber packing, celluloid, and brass. Two one-eighth-inch rubber tubes were connected with the inclosed chamber by openings at diagonally opposite corners. It was found easier to make this connection through one of the sheets of celluloid than through the rubber packing material. These tubes were fused in with beeswax and their ends weighted and put into separate jars. The tube opening at the bottom of the lantern slide was used as the intake tube and the jar to which it was connected was filled with cold water. Then by gravity the water was made to flow through the chamber. Two adjustable pinchcocks were provided and the flow of water stopped while the glass preparations containing the larvæ were being placed in the chamber. Then by regulating the flow of water by means of the pinchcocks the preparation was used as long as desired. When the water had all been passed through, the jars were changed and it was sent through a second time. It was found desirable to have the water removed from the top of such a chamber on account of air bubbles which tend to accumulate when well-aerated water is heated slightly.

STRUCTURE AND FUNCTION OF HEAD OF Chironomus braseniæ WITH REFERENCE TO FEEDING HABITS.

The head of the chironomid larva, while so constructed as to be wonderfully adapted for feeding upon a large variety of foods in diverse environmental conditions, nevertheless shows a wide range of variations. These variations, while especially well marked in the subfamilies, are also to be found among the different genera and to a lesser extent within the genus. They have been taken advantage of by the systematists, who have figured the structures that best lend themselves to their purposes. Miall and Hammond (1900) and more recently Goetghebuer (1911) have made more careful studies of these structures, with special consideration of their morphology. The object in this discussion is therefore to consider the special adaptation of the mouth parts, with particular reference to their function in the feeding habits. As certain of these structures have already been treated more fully than others, only those parts whose function appears to the author to be either poorly or inadequately discussed elsewhere will be considered in great detail here.

In this study the head parts of *Chironomus braseniæ* n. sp. are figured, and an attempt is made to point out the more conspicuous differences between this species and the larger and better known species upon which Miall and Hammond (1900) worked. The most noticeable feature about the head of the larva of *C. braseniæ* is its great width relative to the length. The labrum is also unusually narrow and the head has a roughly triangular outline (fig. 10).

The labrum undergoes a remarkable amount of variation in minor details, such as the presence or absence of a thin triangular labral comb, variously arranged pectinate hairs, and paired lobular bodies. The structures located on the ventral surface of the labrum are commonly assigned to the epipharynx and consist of a three to many toothed epipharyngeal comb located on the anterior border, a thickened chitinized horseshoe-shaped area just posterior to it, within which are attached a variable number of claws or spines, and just outside of these spines a pair of peculiarly mandiblelike structures, known as premandibles (Goetghebuer) or lateral arms (Johannsen). The corresponding structures of *C. braseniæ* are peculiar in being reduced in number, larger in size, and more strongly chitinized as an adaptation to its leaf-eating habits. The function of the labrum is that of a very complexed scraping organ, and the degree of specialization of its various parts is usually found to be correlated with the nature of the food and its method of collection.

The labrum is rather less specialized in this species than in *Chironomus cayugæ* and the others included by Goetghebuer (1911) in his Group I. The pectinate hairs are fewer in number and simpler (figs. 1 and 2, *s*). The epipharyngeal comb (figs. 1 and 2, *co*) consists of three large rounded teeth with smooth inner surfaces. The horseshoe-shaped chitinous area (figs. 1 and 2, *h*) on the ventral surface of the epipharynx is in this species much less horseshoe shaped than usual. It is here represented by two chitinous bars which articulate in front with the thickened anterior border of the labrum and posteriorly with a median caudad projecting process (fig. 1) within this horseshoe area. There are four pairs of chitinous hooks (figs. 1 and 2, *e*), rather blunt in outline in *Chironomus braseniæ*, but often very much specialized and developed as minutely serrate plates. Just lateral to the posterior end of the horseshoe-shaped chitinous area are the "lateral arms" of Johannsen or "premandibles" of Goetghebuer (figs. 1 and 2, *a*). These are provided with a mesad projecting process, which loosely articulates which the central chitinous structure (figs. 1 and 2). These arms are provided with muscles and are capable of a wide variety of movements.

The lateral arms, while figured for a considerable number of species, do not seem to have been treated at all from a functional standpoint. From the author's experience it seems possible that the small size of the head and the constant activity of the larva have served to vitiate many attempts in this direction. It is easy to see from the study of a large number of dead larvæ that the arms are to be found in a variety of positions, the most frequently observed position being that found when the labrum is drawn in between the maxillæ. When the labrum is in this position, the arms project posteriorly down into the pharynx, just above the surface of the hypopharynx. When the labrum is raised somewhat, they are seen to lie just above the labium. When the labium is elevated, as in the normal feeding, the ends of the arms are farther forward.

Several times while examining the labium of living larvæ the author has observed what he considers the normal movements of these appendages. They are moved forward and toward each other when the labrum is elevated, so that their setigerous anterior margins (fig. 2, *a*) scrape the chitinous claws (figs. 1 and 2, *e*) attached within the horseshoe area, removing any food material that they may have collected. They are then swung backward in close proximity to each other as the labrum is pressed down. From these occasional observations, together with the structure of associated parts of the pharynx, it seems reasonable to conclude that the lateral arms have an important function, as they convey the food down the alimentary tract to such a level that the circular muscles of the esophagus can act upon it in the swallowing process. They would, therefore, appear to supplement the mandibles and maxillæ, which may have lost something of their primitive functions as an adaptation to their present manner of life.

The mandibles have been figured by a large number of authors, especially from the systematic standpoint. The author has tried to show in detail the method of articulation of the mandibles with the head because of the restricted movements of these appendages resulting from their method of attachment. The anterior median margins of the epicranial plate (fig. 5) carry on their inner surfaces special internal chitinous processes (figs. 4 and 5, *i*) upon which the mandibles articulate. These processes alone would give the mandibles a considerable freedom of movement. This movement, however, is somewhat restricted by the process *q* (figs. 3 and 6) and the plate *st* (figs. 4, 11, and 12). Their chief movements are consequently confined to plains approximately at right angles to each other. In this motion they oppose the labium rather than each other. The complexity of the adductor muscles, however, enables the mandibles to oppose each other when elevated. The external process of the mandible (fig. 3, *q*), which projects beyond the point of articulation out over the thickened margin of the epicranial plate (fig. 12, *pr*), adds considerable firmness and rigidity. The function of the mandibles is of especial interest, because they, next to the labium, limit the range of adaptability of the chironomids. This is especially emphasized in the discussion of the adaptability of *Chironomus braseniæ* and *C. lobiferus*.

The maxilla (fig. 11) has been the object of considerable speculation especially as regards its homologies. Mundy (1909) figures vibrissæ, which he considers as replacing the striated structures shown in figures 11 and 12, *c*. This structure Goetghebuer (1911) considers a part of the labium. The attachment of the movable parts of the maxilla is especially interesting in this connection. The structures below *p* (fig. 11) are attached to the chitinous plate *st* (fig. 11) along its outer margin. The parts marked *l* and *g* (fig. 11) are attached to the part beneath the letter *p* (fig. 11) and are capable of being folded over it. They articulate at *w* (fig. 11) and swing inward. In attempting to homologize these structures the plate *st* (figs. 11 and 12) is considered as representing the stipes, which is fused to the anterior margin of the epicranial plate *p*. Evidently *p* (fig. 11) represents the palpus and the structures below it (*p*) the palpifer; *l* and *g* represent the combined lacinia and galea and *c* the two cardos, one beneath the other.

The movements of the maxillæ are restricted by their attachment to a fixed plate outside the plane of movement of the mandibles. It seems probable that their function has been largely taken over by the labrum and especially the lateral arms. The anterior part (fig. 4, *g* and *l*) is capable of a considerable movement in a lateromedial direction and although rather thin is doubtless an important factor in the concentration of the food particles. This part of the maxilla, as well as the palpifer, carries a number of sense papillæ which doubtless have more or less well-developed taste cells, as it is easy to see that the larvæ have very acute taste organs in this part of the head. It therefore seems probable that as the function of the maxilla has decreased the maxilla itself has become very much modified.

The labium in the family Chironomidæ is very important in the determination of the larva and consequently is a familiar structure in the systematic literature. This structure is developed as a thickened plate with an anterior toothed margin. It is so closely fused with the lower surface of the epicranial plate that in many species it seems to be only a modification of the anterior border of this part of the head. This is especially noticeable in those species which show a suture between these plates in the labial region. This structure is, however, capable of being removed as a separate plate, and more complete study will doubtless show a similar arrangement throughout the subfamily. Its function is that of a scraping and cutting edge, and it is next to the mandibles in its importance in governing the range of adaptability of the species.

The hypopharynx (figs. 7 and 8) is furnished with chitinous plates *th* and a variety of spines and setæ. This anterior portion is separated from the posterior by a cavity *z* (fig. 7), which is continuous with the salivary ducts *d* (fig. 8). It is supported by a chitinous ring *f* (fig. 8). The posterior part is furnished with a large number of backward pointing setæ on its dorsal surface and is supported by a chitinous skeleton shown in figure 8, *k* and *f*. The arms (fig. 7, *k*) of the hypopharynx form a point of attachment for the upper end of the pharynx and hold this part extended.

The function of the hypopharynx is doubtless sensory to a large extent, as its rôle of guarding the entrance to the alimentary tract and the exit of the salivary ducts would naturally demand. It seems probable that the backward projecting setæ (fig. 7, *e*) at the entrance of the pharynx may also serve to disentangle the food material brought in by the lateral arms. The structure of the anterior and posterior borders of the cavity in the hypopharynx through which the silk escapes is of special interest in connection with the study of the silk structures spun both by this and other species of Chironomidæ, although the part which it plays is still uncertain.

SUBFAMILY CHIRONOMINÆ.

Group I.—Chironomus lobiferus Say.

In this first group the author wishes to consider as a type one of the chironomid larva that seems to have departed most widely from the more familiar examples. This species, however, is capable of living in a loose mud burrow and of collecting and eating its food directly from the surface of the accumulated débris about it, but this is not its most characteristic method of feeding when living in competition with other species.

HABITAT.

The burrows of *Chironomus lobiferus* may be found on floating logs, at the bottoms of ponds, or attached to stems, stumps, and other perpendicular surfaces. In these habitats the larvæ live by straining the fine particles from the water which passes through their burrows. A still more unique mode of life is shown by *C. lobiferus* in the readiness and frequency with which it penetrates the stems of aquatic plants. A list of the plants attacked includes so nearly all the submerged aquatics that it is concluded that the structure of the epidermis is the important limiting factor.

The presence of larvæ within a stem is easily recognized by two small round openings through the epidermis which they make at either end of that portion of the tissue occupied by their burrows. These openings enable the larvæ to set up a current through their burrows by throwing their bodies into an undulatory motion. In this way the larvæ are able to obtain food and carry on their respiratory processes at the same time. The general behavior of *Chironomus sparganii* Kieffer [*lobiferus*(?)] larvæ has been observed and well described by Willem (1908).

The general facts are as follows: The larvæ are found in both dead and living stems of Sparganium, in the softer tissue where the chlorophyll is lacking. They are commonly located some 8 or 10 inches below the surface of the water. In the dead and especially the well water-soaked stems of Sparganium they are to be found in abundance. Their burrows communicate with the exterior by two small openings from one-quarter to one-half millimeter in diameter. The openings are at varying distances from each other, but usually measure in a rough way the relative lengths of the larvæ, the average distances being about 15 millimeters.

The method by which the larvæ penetrate these stems seems not to have been observed nor questioned so far as the literature is concerned. In Group IV is discussed the adaptation of the head of *Chironomus braseniæ* for burrowing, and evidence is given that the penetration of the uninjured epidermis is a matter of very considerable difficulty. The larvæ of *C. braseniæ*, however, show a unique adaptation to this procedure by spinning a special silken arch by which they are able to apply pressure more advantageously to their mouth parts. This phenomenon was not seen in a considerable series of *C. lobiferus* larvæ that were kept under observation for this purpose, and it is concluded that this species has not yet developed such an adaptation.

The experiments set up for the purpose of testing out the ability of a larva to enter an uninjured stem were of two kinds: First, outdoor experiments with uninjured stems fastened together as rafts and placed among the infested stems; and, second, small sections of infested stems taken into the laboratory and placed in watch glasses, in which several larvæ removed from similar stems were placed. In the outdoor experiments the rafts were made of freshly cut stems about 2 feet long and were left to float freely in an infested portion of a pool where similar larvæ could be taken at any time during the year. These stems were observed at intervals for two months, and none showed any signs of the presence of the larvæ. In this relatively short period they showed but slight signs of decay and practically no accumulation of diatoms.

In the laboratory experiments with sections of similar stems in a more advanced stage of decay only such stems as had already been infested were used. It was soon found that the larvæ would readily accept these stems, which they usually entered by creeping into the openings at the ends. The sections cut to fit into a Syracuse watch glass could ordinarily be entered from the ends and were usually short enough to enable the larvæ to maintain their water current without penetrating the epidermis. In order to make it necessary for the larvæ to penetrate the epidermis, the cut ends were coated with melted paraffin. The result in many cases was that they simply crawled under the stems and spun their silken tubes, fastening them to the stem above and the glass below. In only one instance did a larva penetrate the stem from the side. In this case the opening was rough and jagged in outline and was located near one of the lower corners of the stem, where it seems fair to assume that the larva might have gained some advantage (by catching its posterior end under the edge of the stem) from the sharpness of the angle that would in a way compensate for its light weight in bringing pressure to bear on the mouth parts. This seems especially possible when it is observed that the claws of the posterior prolegs point forward and are capable of holding the posterior end of the body in place while the muscles of the body are used in flexing the body and holding the mouth parts of the larvæ in contact with the epidermis.

Observation on a series of stems selected at random from among a considerable number dipped up from the bottom of a pool where the larvæ were abundant showed a greater number of larvæ near the ends of the stems. In some cases a larva was so located that one end of its tube opened at the end of the stem and the other by an opening bored through the epidermis. Several stems were found to have openings along their entire length, but all were confined to what had been the inner or upper surface of the leaf where the epidermis was thinnest. In other cases the larvæ had an opening on one side of the leaf with a long vertical tube leading to its gallery which was on the opposite side, where it opened to the surface through a thickened epidermis. Old Typha stems were occasionally found with larvæ located near the broken ends, but in no case was there noticed a larval-made opening penetrating the epidermis. When the Typha stems were tested with a sharp point, the epidermis was found to be very much tougher than that of Sparganium which is most frequently inhabited by the larvæ.

The thickness and texture of the epidermis of a stem is an especially important factor, as the above observations indicate. This, however, is not the only source of evidence, but when considered in connection with the fact that two larval molts out of six examined had one of the lateral teeth of the labial plate broken (fig. 28) it becomes evident that the larvæ exert themselves to the limit in penetrating the various plants in which they construct their galleries. That the larvæ more frequently penetrate the epidermis from the inside than from the outside seems to be shown from the greater abundance of openings near the broken end of stems, and that the penetration is more easily accomplished in a small gallery, where the larva is able to brace its body against a somewhat resistant parenchymous tissue, is obvious when the nature of the larval mouth parts is understood.

These structures have been fully discussed in connection with *Chironomus braseniæ*, and it is only necessary to consider them very briefly here. The labium is used as a cutting edge and is applied at an angle of about 45° to the surface. Pressure is brought to bear upon it by the mandibles, which on a flat surface have to be widely extended in order to bring their pointed tips into use. This pressure is therefore applied very largely as a sidewise pull and has the effect of using the labium more or less like a scraper. Hence, the strength of the larva and the toughness of its labial plate are important factors limiting its attack on plant tissue.

USES MADE OF SILK.

The fact that the larva of *Chironomus lobiferus* lives as it does in a burrow which communicates with the exterior by two small openings, too small to allow the larva within to extend its body, naturally makes one curious to know how it is able to obtain food. The natural conclusion, of course, would be that it ate the plant tissue, but this is not found to be the case when the stomach content of the larva is examined. Willem (1908) observed this and stated that the stomach content was composed of organic débris analogous to that which floats in the water—"desmids, diatoms, Pediastrum, Clathrocystis, spicules of Spongilla, carapace of hydrachnids, rotifers, together with grains of sand and sometimes the fragments of plant diaphragms." The author's study of stomach contents fully corroborated the above observations, although at the time the author was not acquainted with Willem's work.

In the author's study of the behavior of the larvæ a number of burrows were cut from the stems with just enough tissue to prevent disturbing the silk lining. These preparations were placed in Syracuse watch glasses and observed under a binocular microscope. Considerable difficulty was encountered in seeing through the epidermis, so it was cut away and replaced with a cover glass. The larvæ readily readjusted themselves by making their burrows open at the ends of the section of tissue instead of up through the epidermis. In this way the behavior could be watched much more exactly, but it was not until one of the most characteristic performances, over an area where the underlying tissue had been entirely removed, was observed that a clew to the method by which the larvæ obtain their food was discovered. Willem (1908) dismisses this subject by stating that the food is removed by adhering to the walls of the burrow near the end at which it enters. The following statement, translated from the same source, seems to refer to the movement that gave this clue:

> Sometimes the larva is fixed posteriorly retracting and elongating in the act of going and coming rhythmically, its body playing the rôle of a piston for renewing the water in the tube.

This movement, so well described by Willem, the author has been able to demonstrate is concerned in the spinning of a thin conical net across the end of the burrow. This net is used to strain the floating organisms out of the water which the larva forces through it by the rhythmic undulatory motion of its body. In this process the larva clings to the silk with which its burrow is lined by means of the hooked claws on the anterior and posterior prolegs.

The current of water which is driven through the burrow by the undulating motion of the body of the larva serves the double function of bathing the branchial gills, thus renewing the oxygen supply, and of bringing in whatever particles may be floating in the adjacent water that are of use to the larva as food. The normal undulations move from the head backward, and the larva always turns about after spinning its net, so that the current is driven into the open end of the conical net. The position assumed by the larva places the caudal filaments in such proximity to the net that they are able to serve a more or less important tactile function. When the larva has maintained this current for about 10 minutes (the time element appearing more uniform than the amount of food actually present in the net at any one time), it turns about in its burrow quickly and gathers in and swallows the catch, net and all.

The net is "hauled" in a very characteristic way. The larva seizes that portion of the rim with which it first comes in contact. The mandibles, the labrum, and probably the lateral arm of the epipharynx are brought into use, and the flimsy net is torn away from the silk of the burrow and crowded down the throat of the larva by the labrum. Then the larva rotates its body and seizes the other side, which is swallowed at once. Then the remainder of the net is swallowed while the larva rotates its body first to one side and then to the other as if to wring out or twist up the net, so that it can be more easily swallowed. The conical tip of the net usually contains a considerable variety of plankton organisms ranging from bacteria, which are either stuck to the net or caught in its meshes, to crustaceans and various rotifers, which sometimes succeed in escaping but are nevertheless often captured. The entire process of "hauling" the net and eating it takes only about six seconds.

The most striking and fundamental use made of silk by *Chironomus lobiferus* is in the construction of a net by means of which the larva obtains its entire food supply. Silk has, however, other uses of very great adaptive importance even in this unusual habitat. Many burrows are found where old openings have been entirely sealed up by its use. The regular openings through the epidermis are usually made round and smaller in size by the addition of a silk margin, and the burrow itself is lined with silk which is uniformly made of such a diameter that the movements of the larva are especially effective. This ability to spin a thin, flexible, and at the same time practically water-tight lining enables the larva to adapt itself to cavities of varying sizes.

The small size of the openings at the ends of the burrow seems to be a special adaptation, for when the larvæ live under the very different conditions afforded by glass tubes they retain this same habit. It seems probable that the narrow openings increase the speed of the current and so prevent Protozoa, Crustacea, and other small organisms from swimming against it. Large particles are also prevented from entering the burrow. In case these small openings are plugged by an accumulation of particles the larva stops its rhythmic undulatory movements and suddenly throws its body into several much shorter waves which move in the reverse direction. This sets up a strong countercurrent which usually dislodges the obstruction, although the contents of the net are usually lost. In case an obstruction is not readily dislodged the larva creeps forward and brings its mandibles and labrum into play.

METHOD OF SPINNING SILK.

The method by which *Chironomus lobiferus* larvæ spin or spread out the silk used in the construction of their burrows and in the formation of the little conical nets mentioned above is very simple. The anterior pair of prolegs is the chief implement employed and so far as can be observed the only part of the body used for this purpose. The structure of these appendages takes on a new significance when function is suggested, and we at once notice the difference in structure between the anterior and posterior prolegs.

The chitinous claws of the posterior pair are widened at their base (fig. 33), are few in number, and are arranged around the front and lateral margins of the prolegs (fig. 15). The muscles of the prolegs are so arranged as to set these hooks into the silken lining of the burrow, and thus hold the larva firmly in place. The hooks point outward and are so attached that by the contraction of the muscles of the proleg they are all brought close together in the center. When extended, the hooks all move outward in different directions, with the result that the prolegs are hooked fast to the silk lining of the burrow. Their function is preeminently that of an attachment, and it is to this specialization of the posterior appendages that the anterior prolegs owe their greater freedom of movement.

The anterior prolegs are often mistaken for a part of the head because of their position just posterior to the chitinized portion of the head proper. They commonly appear as a mass of bristles radiating in all directions. From the side they appear as one, because they are always moved together and are so completely covered by relatively long spines that it is hard to see how they are attached. A sagittal view shows them to be made up of two rounded lobes separated by a narrow depression. The spines are graded in length from mere tubercles in front to long narrow hooked and barbed spines in the centre and again decreasing in size on the posterior surface. Here the short spines have rather wide bases and the tips are deeply serrate and somewhat hooked (fig. 34). The spines are obviously arranged in rows which diverge somewhat from the mid line laterally (fig. 35). The spines located near the centre of the prolegs are the best developed and are probably the most used in silk spinning. They are curved backward and hooked at their tips. Near the end there are a number of barbs on both the anterior and posterior edges. They are flattened laterally and are capable of being condensed into a very compact mass by the contraction of the muscles of the proleg. The hooks at the end of the spines point backward, and all the long spines are hooked except a few of the very outer spines, which seem to be slimmer and more hairlike.

The actual process of silk spinning is much more easily studied by observing the construction of the conical net mentioned above than in any other way. It is constructed out free from other substances and is consumed and replaced every 10 minutes night and day until the activities of the larva are slowed down by the approach of the pupal stage. The larva begins the spinning by extending its body well forward and making several fairly rapid passes with its anterior prolegs in various radial directions. These movements place the silk strands that form the attachment for the apex of the net. Then, withdrawing its body somewhat and attaching the silk to the place where these radiating strands fuse with each other, the larva retracts its body, drawing out a ribbon of silk spread by the prolegs. During this retraction the prolegs are held pointing forward at an angle of about 45 degrees with the body, and their exact use can only be surmised, but from their position and the speed of the movements it seems possible that the semifluid silk is spread either by the short spines in front or what seems more probable by the carding effect of variously hooked and serrate spines located farther back on the prolegs. When the larva reaches the end of its backward movement, the prolegs are spread and rapidly touched to the silk lining of the burrow at two nearby points. Then the forward movement is carried out. In this movement the prolegs are extended slightly forward and are more or less spread out. When the end of this movement is reached, the thread is attached either by the contact of the head or the prolegs to this central point of attachment and the process repeated. It is impossible to tell whether the head takes part in the process of attachment or not, because both the head and the prolegs are so close together at this point. It would seem probable from the small size of the apex of the finished structure that at some point in its construction the head occupying such an advanced position would be the only possible part of the body that could accomplish the attachment of the fibers. It is obvious, however, that the head does not touch the wall in the process of attaching the silk at the rim of the net, for the head is held projecting straight out and the movements of the prolegs are unmistakable.

The forward and backward movements of the body are accomplished largely through the instrumentality of the posterior prolegs. These are held attached to the silk, and the last three or four segments of the body are flexed on them as axes. On the forward movement the body is straightened and the prolegs extended forward; on the backward stroke the prolegs point backward according to the degree with which the body is flexed.

The silk net (figs. 26 and 27) is too long to be spun from one place by the simple flexing of the body. This means that it has to be spun in two sections. The overlapping of the sections gives the appearance of a continuous sheet of silk extending from the apex to the base of the net, and the original posterior attachments of the first section appear as radiating strands from the sides of the net.

The entire process of constructing the net requires less than half a minute and involves the spinning of 42 to 44 ribbons or sheets, as determined by counting the movements. When this process is completed and the larva turns about and begins forcing the water into the net, it can readily be made visible by adding a few drops of water containing powdered carmine.

The method by which the silk lining of a burrow is spun is not so easy to observe as the process of spinning a net. It takes longer, and the number of movements is so great that it is almost impossible to correlate them with any definite structure later observed. But even here, if proof were lacking that the prolegs are the one necessary factor to explain the entire process, there are structures that bear unmistakable evidence of their use. The lining, as the silk net, is spun in sections which, while not of uniform length all the way around the tube, are nevertheless approximately so.

The exact way in which the first section is constructed is not so easily understood, but from this on the process involves a considerable repetition of the method employed in the construction of the net. The body is extended and retracted in the process of attaching the sheets of silk to the first section, to each other, and to whatever support there may be available. These silken sheets are held extended by the thin branching threads of silk (figs. 36 and 37). The whole aggregation of silk sheets and threads is held under tension by silk layers attached in a spiral position. The supporting threads are then originally used as attachment fibers to hold a section of the tube extended and are later pulled into a position nearly at right angles to the lining by the tension exerted by the addition of another section. In this way the lining or tube appears slung in the centre of a cavity with numerous threads radiating in various directions (fig. 26).

SILK STRUCTURES.

The completed silk lining shows relatively little structure as far as the tube itself is concerned, but the supporting lines thrown out when the larva fastens this lining between two parallel glass surfaces are quite interesting. In studying the structure the tube is seen to be of a fairly uniform diameter and to be composed of a thick layer of silk, which shows no definite layers or strands. At intervals the silk is pulled out into conical enlargements. At these points the tube is seen to be made up of more than one layer, for the lining continues straight on leaving a space. The lining is held extended in the form of a cylinder by very interesting branched threads. These threads are often more or less sheetlike next to the tube, but divide and subdivide toward their point of attachment where they are much more widely spread out than at their origin (fig. 37). These structures show unquestionably the use of the prolegs, for it is inconceivable that such fine threads often ending in more than one plane could have been attached in any other way.

The structure of the conical net is not easily made out even under high powers of the microscope, but the addition of powdered carmine to the water passing through the net gives it such a uniform coat that the author is inclined to think the entire structure porous. At times Protozoa and other relatively large organisms are seen to be forced into one of these nets and to escape by a circuitous route, which would suggest a breach between ribbons or sheets of silk. In other cases relatively large gaps, opening directly through one side of the net, are indicated by the escape of particles. When the net is collapsed, as it always is when the larva is not forcing water through it (the condition always existing in stained material), none but the grosser structures are visible (fig. 27).

The net, as explained above, is spun in sections, but the position of the threads attached to its sides, as well as the observed behavior of the larva, shows these sections to be less regular than one might infer from the previous description. The arrangement of the net in sections in a manner similar to that of the lining of the gallery suggests the possibility of narrow slits in its surface of the same nature as those in the attachments of the tube (fig. 36). It is probable, however, that the impact of the current is necessary to open them wide enough to allow water to pass through.

The conical net is spun exceedingly thin, as one would expect from the frequence with which it is consumed and replaced. This is doubtless correlated with the speed of the movements involved in its construction. In fact, it seems reasonable to conclude that the nature of the silk rather than the psychology of the larva dictates the speed of its movements. The spinning of one part of the net upon another in such rapid succession indicates that the silk hardens very quickly on contact with the water. The quickness with which the silk hardens determines the speed at which the larva must work in order to spin silk of a given thickness. Hence, the thinner the structure the greater the speed required, because of the greater surface relative to the volume exposed. Thus it appears that the very rapid movements of the larvæ are dictated by considerations of economy in the silk used.

RELATED FORMS.

Goetghebuer (1911) in a special examination of the external structures of the larvæ of the genus Chironomus established three groups, as follows:

Group I.—Containing those species possessing two pairs of branching filaments on the eleventh segment; a thickened oval area on the labrum; an epipharyngeal comb composed of a row of regular teeth; the antennæ with five segments; and the abdominal segments of the pupa without spinose protuberances.

Group II.—Branchial filaments of the eleventh segment lacking; the median anterior piece of the labrum simple without the thickened oval area; the comb of the epipharynx not composed of a regular row of teeth; the antennæ with five segments without Lauterborn's organs; and the pupa without spinose protuberances.

Group III.—Agrees with Group II except in the presence of small granulations on the labrum of the larva and the presence of spinose protuberances on the posterior abdominal segments of the pupa.

The specimens upon which the last two groups were founded all live in the parenchyma of submerged leaves of numerous aquatic plants and are as follows: *Chironomus sparganii* Kieffer, *C. viridis* Macquert, *C. niverpennis* Fabricus, *C. tendens* Fabricus, and *C. dispar* Meigen. The list of plants in which these larvæ were found as given by Goetghebuer is as follows: *Stratiotes aloides*, *Sparganium ramosum*, *Butomus umbellatus*, and *Alisma plantago*.

In addition to this list the author has bred *Chironomus lobiferus* Say, *C. pedellus* Deger and *Tanytarsus obediens* Johannsen, from Sparganium stems, and Needham (1908) reports *Chironomus albistria* Walker from Nymphæa stems. While, of course, only the bred specimens have actually been observed to build conical feeding nets, yet the similarity of their external structures and the nature of their habitat give a considerable justification for including them in this group, especially when it is observed that *Tanytarsus obediens*, a member of another genus, possesses this habit.

A bit of information regarding the similarity of the larvæ of *Chironomus sparganii* Kieffer is contained in a paper by Willem (1908). He finds the uniform punctations of the abdominal tergites, the posterior teeth of the lateral plate of the eighth segment, and especially the peculiar process carried by certain abdominal segments would suggest *C. lobiferus* Say, the description of which was found in Johannsen's monograph. He finds his most striking difference in the fact that Johannsen says that these processes occur on all the segments, while he finds them on segments two to six only. Upon examining his own material the author finds this to be also true for *C. lobiferus* Say, as well as *C. sparganii.* Dr. O. A. Johannsen has also observed the author's material and agrees with him in the identification of this species. While it is not known how great weight this observation had with Kieffer in establishing the species *C. sparganii*, yet there is no doubt whatever that the two species will be found to resemble each other very closely, as it is difficult to find any satisfactory distinctions between them from their descriptions.

Group II.—Tanytarsus pusio Meigen.

For this group *Tanytarsus pusio* Meigen has been selected as a type, because Mundy (1909) has already studied it so completely that there is relatively little new material to be added. The only larva whose feeding habits he describes is the species given above, but he designates "Larva No. 1" and apparently "Larva No. 18" as also feeding in a similar manner. "Larva No. 18," he says, "builds a still more elaborate case, composed of long stalks to which is attached a short tube with three long arms given off at the free end. The case is not quite so opaque as that of *T. pusio* and is of a light brown color." The author has bred *T. exiguus* from similar tubes and observed its habits, which resemble very closely those of *T. pusio*, as described by Mundy.

CONSTRUCTION OF TUBE.

The following description is taken from Mundy's work (1909). The latter part is condensed from a more complete description.

> The first thing the larva does is to gather a number of particles of mud together and form them into a short strap or band passing across the body and fixed to the dish on each side. Using this band as a starting point the larva sets about building a simple straight tube closely applied to the dish and open at both ends. At first the band is merely broadened so as to cover more of the body, but soon it is shortened as well until length and breadth change places and a real tube is formed. * * *.
>
> Anchored, as it were, to the strap by its anal feet it rapidly sweeps through an angle of about 60°, touching the surface here and there with its mouth as it passes. Then, firmly grasping a particle by means of the labial armament and the anterior appendages, it powerfully contracts its body, thus drawing the particles toward the centre of operations; but not only do the above mentioned particles move, but all those touched during the sweeping movement follow in its wake, having been united together by silk threads or mucus during the first action. In this way abundance of material is collected and the building of the case proceeds rapidly.

According to Mundy (1909) *Tanytarsus pusio* and "Larva No. 1," which builds a stalk case, begin their tubes and construct them to a large extent exactly alike. When the tube of "No. 1" is 3 millimeters long, it begins to build it up horizontally, removing material from the opposite end of the old tube for this purpose. This is carried on until there is only a narrow stalk projecting up from one side of the original burrow supporting on its top end a short tube. This tube is later strengthened by the addition of saliva especially at the attachment. Then three arms are provided and the web attached.

> In strengthening an arm the larva twists its head right around it, describing thereby a complete circle, completing the forward and return movements with the greatest rapidity. [Mundy, 1909.]

Tanytarsus pusio makes a dark-brown mud tube fastened together with saliva but not lined with a distinct silk lining.

> The tube is attached for a variable length to rock or moss stem in the bed of a river, but it gradually curves away from its support, so that the anterior end projects freely in the water. This end is the widest, from which it gradually tapers toward the base.

VARIATIONS IN TUBES.

The tubes, as explained above, are composed of débris fastened securely together with silk. Taylor (1905) and Lauterborn (1905) have described other closely related larvæ, living in similar situations, that spin tubes of nearly pure silk. In texture the tubes of *Tanytarsus pusio* Meigen and *T. exiguus* Johannsen are intermediate between those of pure silk, such as are spun by *Chironomus lobiferus* when living within a stem, and those composed of a mass of débris only loosely fastened together with silk, such as are characteristic of the group that is represented by *C. cayugæ.*

The tubes figured by Mundy for *Tanytarsus pusio* are rather different in structure and proportions from those of *T. exiguus.* The substance of the tubes gives them a gray, slatey appearance that closely resembles the general color of the bottom. The arms are proportionally stouter and are represented on the sides of the burrow by elevated ridges. The tubes are as often fastened flat down to the surface upon which they rest as elevated at the end, apparently depending upon the convexity of such surfaces.

The arrangement of the tubes is not to any great extent dependent upon the direction of the current. Small stones having from 8 to 10 tubes on their undersides usually showed such a variety in the arrangement of those tubes that it would seem that free space was of more importance than the direction of the current.

Johannsen (1905) says of the tubes of *Tanytarsus exiguus:*

> During the early summer most of the cases will be found attached by the stems alone, but later in the season most of them lie flat on the rocks and are attached on one side like Simulium pupal cases.

It seems evident that this species varies considerably in the type of tube which it builds. The author's observations on this species in nature are confined to small streams which were not very rapid, and in these localities the food supply has been fairly abundant, as shown by the number and variety of the population. In such habitats the predominance of the attached type of tube would seem to indicate that the strength of the current and perhaps the food supply are the governing factors. Since the writer's observations were made both in the fall and in the spring, the effect of seasonal changes should be eliminated unless these tubes were able to persist throughout the winter, which seems improbable in most cases considering the erosion to which such small streams are subjected.

THE NET.

> The arms, as before mentioned, are connected by webs so as to form a net to retain all passing objects; but even with a high-power lens I have been unable to detect single threads. The network seems only to be made up of irregular bands of slime or mucus passing between the neighboring arms, so probably it issues from the creature's mouth in this form. [Mundy, 1909.]

NET MAKING.

> To build its net the larva proceeds as follows: Running up one of the arms for some distance it swings across to the next arm, carrying with it a thread of silk, then quickly back again, at the same time retreating somewhat into its case. This zigzag movement is repeated two or three times until the base of the arms is reached, when the whole process may be repeated over again until a sufficient number of threads have been stretched across to make a rude network which, whatever its workmanship compared with that of a spider, is at any rate good enough for its purpose and effectually stops all objects

floating by. In the case of larva No. 1 this has only to be done twice, but in *Tanytarsus pusio* from four to seven times, according to the number of arms present. From time to time the larva pulls down the net between two arms, using the labrum and thoracic feet to collect the particles together into a compact mass, which may then be used for further building operations or may be pressed into the mouth to be consumed. [Mundy, 1909.]

SILK SPINNING.

This process has not been treated in any considerable detail by Mundy except that he rightly inferred that the silk was made up of bands of slime or mucus instead of threads. The author has followed the activities of *Tanytarsus exiguus* in its silk-spinning movements and finds it a very difficult species to observe in this particular. Its chief silk-spinning activities consist of the rapid movements of its head and anterior prolegs in such close proximity to the surface that in spite of the numerous repetitions of the same movement, while applying layer after layer of silk to the rim of its burrow, the author was unable to determine that the head did not play an equally important part in this process. It was more nearly possible to distinguish the use of the prolegs in the work of reinforcing the arms. Here the most characteristic movements were upward, in which movements the head was held somewhat away from the arm as the body encircled it.

The most satisfactory movements in this process were those concerned in the construction of the web mentioned above. The specimen studied in this particular had a tube fastened to the bottom of a glass vessel. This tube had two radiating arms on which the larva spun a single thread. This web was attached to the glass as far out as the larva could reach, then to the nearest arm, and from this arm to the second and down to the glass again on the opposite side. In this process the larva in swinging from one arm to the other repeatedly struck the end with its prolegs while its head projected well beyond.

The silk is especially viscous, and the particles swept against it by the current readily stick fast. By this means the single thread spun by *Tanytarsus exiguus* was very effective in catching particles. At intervals this thread was pulled down and consumed, the labrum and maxillæ playing the important part in the process. The prolegs were not seen to be employed in the pulling down or rather pulling in of this single thread, as stated by Mundy.

ADAPTABILITY.

The *Tanytarsus pusio* larvæ were taken from flowing water and placed in dishes containing only about a quarter of an inch of water with relatively few fatalities, considering the crude methods employed in removing their burrows. The dead larvæ were removed and a small amount of organic débris added. This the larvæ raked together in masses near the ends of their burrows and consumed in what seemed tremendous amounts for such small larvæ. They simply placed their heads against one side of a mass, and by the motion of the appendages of the head alone the food was passed down their throats in a steady stream. It was apparently fastened together by the silk spun during the process of collecting it together. In this connection Mundy's observation, quoted above, on the method of collecting particles in the construction of their tubes seemed to be related phenomena.

Perhaps the most remarkable change in the behavior of these larvæ was that exhibited by a specimen which, after living a week in quiet water, suddenly found its food swept out of reach by a current. This larva in less than 15 minutes raked away a part of the rim that it had spun between the radiating arms and after reinforcing these outrakers spun a web upon them. The current was set up by a pipette operated by hand, and gave a very satisfactory means of testing the reactions of the larva, for the strength and direction of the current could be changed at will. A complete reversal in the direction of the current seemed to alter the behavior of the larva not at all in regard to its web or any other observed activity.

It would seem feasible to demonstrate the behavior of this larva in such a special lantern slide as recommended for this purpose with *Chironomus lobiferus.* The larvæ, while sensitive to a jar, do not seem to notice the light particularly, and the adhesive nature of the silk makes it possible to use powdered carmine or India ink to make the strands visible. The current recommended to keep the temperature down could be adjusted to answer for the natural flow of a stream.

Group III.—Chironomus cayugæ Johannsen.

This group is based upon a recently described species which, so far as can be judged from direct observation as well as indirect references, will prove to be one of the most widely distributed species of the family. It is on this account, as well as upon its unique habit of living in watering troughs where it is easily accessible, that *Chironomus cayugæ* Johannsen has been selected for the purposes of this study. It is a type of a very large group which is included in Goetghebuer's first group and characterized by the presence of two pairs of branchial filaments on the eleventh segment, a thickened oval area on the labrum, an epipharyngeal comb composed of a row of regular teeth, antennæ with five segments, and the pupa without spinose protuberances on the abdominal segments. The division includes most of the bigger red chironomid larvæ and is probably of greater economic importance than any other group in the family. At this point it may be of interest to recall that most, if not all, of the species of Group I under stress of circumstances adopt the habitat and behavior of this group.

HABITAT.

These larvæ are fitted by their extra branchial filaments and red blood for life in the débris at the bottom of lakes, ponds, and stagnant pools. The larvæ of the species selected as the type, while living in various other habitats, are especially common in horse troughs, having been taken by the author from troughs in Orrington, Me.; Woods Hole, Mass.; Ithaca, N. Y.; Dayton, Ohio; Greencastle, Ind.; Evanston, Ill.; and Milwaukee, Wis. The troughs most carefully studied are those in Woods Hole, Mass., Ithaca, N. Y., and Greencastle, Ind. In none of these troughs was the author able to find any other species belonging to this group represented, and it seems that by some special adaptation this species has succeeded in adjusting itself to conditions different from those common to the group. It is also found associated with *Chironomus decorus* and others in the débris at the bottoms of larger bodies of water, and it is obvious that it is not only capable of living in the same conditions as they, but, as can be shown by a simple experiment, both are able to live on the débris found in a watering trough.

It seems possible, then, that the difference may consist in such a simple adaptation as in the manner of depositing eggs. Needham (1906) has referred to the habit of *Chironomus annularis* Degeer of extruding its eggs while in flight and depositing them free in the water. Mundy (1909) has referred to the fact that *Tanytarsus pusio* eggs were found attached to leaves several centimeters below the surface. J. T. Lloyd informs the author that he has observed masses of chironomid eggs of considerable extent blown upon the shore of Cayuga Lake. The author has observed *Chironomus hyperboreus* Staeger depositing its eggs upon the surface. Some of these females were caught in flight and found to have a considerable mass of eggs ready to be deposited. On the other hand, *Chironomus cayugæ* females were observed just at dusk to light upon small stones which projected slightly above the water level and to thrust the tips of their abdomens beneath the surface of the water and there deposit egg masses attached to the stones. All the eggs taken from troughs have been found attached, and it seems possible that by this habit alone *C. cayugæ* may be especially adapted to such a singular habitat.

It is interesting to note that troughs fed from flowing streams where a considerable amount of silt is constantly present have in every case been found to contain but few or no larvæ, and it seems probable that the choking out or covering up of the food supply is the controlling factor.

Other members of this group are found in streams, ponds, reservoirs, and lakes, even at very great depths, as in Lac Leman. Here Mlle. Zebrowska (1914) found specimens designated as *Chironomus "B"* abundant to a depth of 20 meters and rare to the extreme depth of 100.

THE BURROW.

The process of building a burrow has probably been observed in this group more frequently than in any other, because the larvæ when out of their burrows are very restless and at once begin to rake particles together. The pectinate hairs and comb of the labrum and the epipharyngeal comb are used in this work. The anterior prolegs usually form the limit of the backward stroke of the head, and it is difficult to say for certain that they remove the accumulated débris; but it is clear that this débris is fastened together with silk, and it seems possible that they may be instrumental in spreading it.

When a certain amount of débris is accumulated, it is raked back by a looping of the body, so that the posterior prolegs hook into the silk that holds the particles together. When a sufficient amount has been so accumulated, the larva seizes the mass adhering to its posterior prolegs by means of its head and anterior prolegs and fastens it over the posterior end of the body in such a manner as to form a narrow band or strap, which is referred to in Group II of Mundy's description. This narrow band has the dimensions of a cross section of a burrow, and with this as a beginning the construction work consists of a direct application of building material to either side of the strap. From this stage on the behavior is the same as that observed in the ordinary lengthening of the burrow. The larva now reaches out and grasps by means of its labrum, mandibles, and prolegs a mass of débris and draws it in and puts it in place at the edge of the burrow.

Then silk is spun by the obvious use of the prolegs, as in the case of *Chironomus lobiferus*. Each addition of débris is fastened in place by silk which is attached to the older parts of the burrow and spun out and part way around this material. In this way the larvæ construct long tubes that give them protection from enemies and at the same time help support them on the surface of the soft débris where they are usually found. The tubes are often U-shaped, and thus serve to bring in fresh water from which the larvæ are able to carry on their respiration while living among decaying organisms at the bottom.

FEEDING HABITS.

The author has found it exceedingly difficult to satisfy himself that the members of this group are not really similar in habit to those included in Group I, but repeated experiment has convinced him that their habits are distinct. When a large number of these larvæ are scraped up together with a mass of the surrounding débris and then spread out in a shallow dish, they literally spin every bit of the débris into loose interwoven U-shaped burrows. When one tests the current in these burrows, the water is found to be flowing through them in a definite direction.

Methods have been repeatedly tried to get these larvæ to adapt themselves to glass tubes of the sort used so successfully with *Chironomus lobiferus*, but in no case have these experiments succeeded except when sufficient débris was present to make it possible for the larva to completely conceal itself.

Several larvæ were put upon pure sand with the hope that it would furnish protection, if that was what was desired, and at the same time fail to serve as food. The larvæ were obviously not well satisfied with their surroundings and moved about over the surface apparently in search of more suitable conditions. In removing the larvæ from their burrows a small piece of the organic débris of which their tubes are characteristically composed was left adhering to one of them. This the larva kept clinging to and trying to roll up into a burrow. The other larvæ as soon as they encountered this débris attempted to get possession of it; after a few hours they all made burrows out of sand. The current was tried by means of powdered carmine but without satisfactory results.

In another experiment several larvæ which had well-constructed tubes were removed, tubes and all, to a flat dish. These larvæ were keeping a strong current of water flowing through their burrows. After being removed they were placed in shallow water. The tubes were well separated from each other, and the bottom was lightly sprinkled with loose débris similar to that from which the tubes were constructed. After a few hours the larvæ ceased to maintain so strong a current and in most cases maintained it only spasmodically. The débris sprinkled over the surface was not disturbed even after being left over night. The current was repeatedly tested and found to be insufficient to furnish any considerable amount of food.

The tubes were then dissected under a microscope and their inner surfaces were found to be eaten full of rounded holes and enlarged in places. From this it was determined that the larva ate away the substance of its burrow from within. While the larva is in such a tube it would probably not be possible to maintain a sufficient current through the burrow to bring in much food on account of the number of openings through its wall. It seems possible, nevertheless, that the current would at times bring in and deposit substances that could be used as food. This seems especially possible, because the larvæ of Group I are known to eat and replace certain parts of the silk composing the wall of their burrows at irregular intervals.

The larvæ, on the other hand, are known to have the habit of scraping up substances to be eaten directly as food. The author has observed this behavior in the case of well-soaked pieces of cracked corn. These the larvæ seemed to have eaten exclusively, for their stomachs were full of the starch grains. The larvæ frequently reached out for some distance and unless the fragments were easily moved did not seem to attempt to drag them in. Once a piece of corn was found it was usually eaten out until nothing but the hull remained.

An examination of the débris at the bottom of the Greencastle (Ind.) troughs showed the greatest number of larvæ per square foot yet found, which by count of a smaller area was estimated to be 500 to the foot. Here an abundance of diatoms, interspersed with corn and oats brought in the mouths of the horses from a near-by livery stable, formed a layer about an inch and a half in depth. The flowing water and the undulating motion of the larvæ kept the conditions suitable to favor the development of diatoms, as was indicated by the great abundance of a relatively few species. The presence of a considerable amount of horse champings did not seem to upset the balance, as a too liberal addition of corn has been found to do in laboratory cultures. Miss Tilbury (1913) found it possible to rear the larvæ of this species from egg to adult on *Potamogeton crispus* alone. This she grated up and fed to them in small amounts.

It will be seen from the above observations that *Chironomus cayugæ* is well suited to experimental culture methods, and it seems probable that the group as a whole is equally hardy. Their large size and overlapping broods offer considerable encouragement to the hope that they may sometime be an important factor in fish culture.

Group IV.—Chironomus braseniæ, n. sp., a leaf-eating chironomid.

INTRODUCTION.

While on a lymnological trip to North Spencer, N. Y., the author's attention was called by Dr. Needham to the work of an insect larva that was cutting burrows in the floating leaves of the water shield, *Brasenia schreberi*, and to a lesser extent in the leaves of the sweet-scented water lily, *Castalia odorata*. The larvæ were found to be those of a midge of the genus Chironomus and apparently an undescribed species, although this or a species with similar habits seems to have been observed by workers in several different parts of the country. Mr. Isley, of the U. S. Bureau of Entomology, informs the writer that he has seen larvæ of this genus with similar habits in the vicinity of Washington, D. C. Dr. R. H. Pettit has referred to a species which he bred from the leaves of both *Nuphar advena* and *Nymphea odorata* in the Wild Gardens, Forest Hill, Mass. He also observed this same species at Pine Lake, Ingham County, Mich. The author has seen specimens from Fair Haven and North Spencer, N. Y. Dr. Pettit's note on an undescribed species published in the first report of the Michigan Academy of Science (1900) is the only reference the writer has found in the literature, however, to a species of Chironomus with similar habits, although the closely related genus of Cricatopus, according to a brief note by C. W. Johnson published in the Entomological News (vol.

12, p. 30) apparently contains a leaf-eating species, as Mr. Johnson states that *Cricatopus sylvestris* was bred by Prof. Smith from the leaves of *Victoria regia*. These two species, so far as the author knows, are the only ones that feed directly on living plant tissue. Other larvæ, however, are found in the large air spaces of dead and living aquatic plants, where they maintain themselves in the same way as while living in a burrow made of trash.

Dr. Pettit's note gives only a brief explanation of the nature of the damage done and a general description of the larva and pupa based on the color characters. He bred the adults and states that they belong to the genus Chironomus and are probably a new species. Since the above quoted studies are substantially in agreement with the writer's observations it would seem probable that all the above chironomid records refer to this species. The unusual food habits and other unique adaptations seem to justify a rather more comprehensive study of this species.

GENERAL HABITS.

The larvæ of *Chironomus braseniæ* from a superficial examination would appear to be true leaf miners. The straight or winding galleries are covered with a green ridge, which closely resembles the epidermis in color, and the lower epidermis is left intact. Closer examination, however, shows that the cover of the larval burrow is not the upper epidermis but rather an artificial cover made up of plant fragments fastened together with silk and moistened with a film of water which floods the entire burrow and spreads out in a thin film a little way on each side of the burrow. The larvæ can also be seen when at work to actually project their body out onto the surface of the leaf at times. They are completely immersed in the water which constantly floods their burrows, and they breathe by blood gills. Their burrows are lined with silk, which is also used in constructing the coverings of the burrows. The larvæ of the typical representatives of this genus do not carry their cases about with them as was erroneously stated in his discussion of this species by Dr. Pettit. On the contrary, this larva resembles the other members of the genus except in the method of obtaining and the nature of its food.

LIFE HISTORY.

The life history differs in several important particulars from that of the typical species of the genus Chironomus. The eggs are laid on the surface of partially submerged leaves of both the water shield and the sweet-scented pond lily (fig. 19). They are laid in strings which tend to show a double arrangement of the eggs, due doubtless to an egg coming from each ovary simultaneously. These egg strings are wound about and crisscrossed in such a way that they form a somewhat disklike mass which tends to be only one layer deep, the gelatinous coating fusing to unite the whole into a single mass. In the limited area where the eggs were found most abundantly the leaves of Castalia were selected rather more frequently than those of Brasenia, although the latter is clearly preferred by the larvæ. It seems probable that the chief factor governing the selection of these leaves is their partial submergence, as the eggs are laid on the top surface of the leaf and are unable to endure desiccation.

The young larvæ obtained from these eggs were placed on sections of Brasenia leaves and confined there in drops of water. These preparations were placed in watch glasses and the normal conditions maintained for several days. Careful observations showed no signs of the larvæ having begun burrows. They were then allowed to enter the water beneath the leaf where they lived for several weeks, but failed to develop, even though a miscellaneous supply of aquatic organisms was furnished. Several of the larvæ died and the experiment was abandoned after two months' observation.

Just how the very young larvæ maintain themselves is still undetermined. A thorough search in the early spring before the leaves of Castalia or Brasenia had reached the surface failed to reveal the presence of any of the larvæ on the roots, stems, or leaves of these, their characteristic host plants, or of any of the other near-by aquatic vegetation. From the facts that none of the small larvæ succeeded in penetrating the leaves under laboratory conditions, that only large larvæ were found in all the burrows opened, and that the burrows are of a uniform width in practically all cases, it seems probable that the larvæ do not enter the burrows before mid-larval life (figs. 20, 21, 22).

The author has been unable to make any direct observations on the length of time spent in feeding on the leaves, as the larvæ are not to be found in any of the apparently similar aquatic situations about Ithaca and when brought into the laboratory on leaves frequently leave their old burrows and start new ones. This confusion, together with the writer's inability to rear the young under laboratory conditions, forced him to use indirect means in determining the length of time spent in feeding on the leaf tissue. Late in the season a dozen leaves containing active larvæ were each labeled by pinning a square piece of paper so that a marked corner came opposite the end of the burrow. The label carried the number of the larva, and the rate of progress was measured daily. These results showed that not more than 10 days on the average would be required to construct a burrow of average length, while the larva that made the greatest progress would not have required more than seven days. Subsequent examination of these larvæ showed 100 per cent infested with a Gordian worm, so the results are doubtless inaccurate, although all larvæ that ceased burrowing after a day or two were omitted in making up the average.

The larva transforms to a pupa on the leaf where it has been feeding. The pupal chamber can often be seen at the end of a burrow 2 inches in length on the leaves of Brasenia and somewhat shorter on the leaves of Castalia. A burrow of this length represents the work as a rule of a single individual. The pupal chamber can be easily picked out because of its club-shaped appearance (fig. 24), the big portion being at the end of the burrow. The pupal chamber is, however, often completely separated from the ordinary burrow, suggesting a vagrant tendency on the part of the larva just before pupation. When separated from the larval burrow it has the same general shape and appearance as when attached. It is but little longer than the pupa and is in rough agreement with it in general outline. The pupa lies in this burrow with the head next to the large open end. When ready to transform it wriggles through this opening and the imago escapes. The pupal molt is usually left with the thoracic part projecting from the pupal chamber (fig. 24). The length of time spent as a pupa is about five days, varying considerably with the temperature and the condition of the individual pupa and the larva from which it transforms.

The adults, both males and females, were found among the bushes and underbrush along the banks, and several were shaken from the tops of trees 6 to 8 feet high. The leaves found with egg masses on them were near these trees and were shaded during a part of the day. Mating and egg laying probably takes place in the early evening, as is the habit of the family.

When infested leaves are brought into the laboratory, the adults begin to emerge in a day or so and continue to transform a few at a time until they have all completed their development. This lack of uniformity in the time of transforming is characteristic of the Chironomidæ and is an important factor in their adaptation to the dominant position that they hold in the life of the fresh waters. In the case of *Chironomus braseniæ* this adaptation makes it a worse pest.

Dr. Pettit bred his first specimens about the middle of May while at Forest Hill, Mass., and in his note before the Academy of Science he states that a second brood was seen on August 1 at Pine Lake, Ingham County, Mich. It seems probable that the term "brood" is here rather loosely applied.

PENETRATING THE EPIDERMIS.

The author has given evidence above to show that the leaf-mining method of feeding seems not to be adopted before mid-larval life, and hence is doubtless a less primitive habit than that of the young larvæ.

That this method of feeding is probably impossible for the young larvæ seems borne out by observations made upon the behavior of the half-grown larvæ in penetrating the epidermis of aquatic leaves. In attempting to induce the larvæ to start new burrows the writer removed them from their old ones and placed them on leaves where there were no unoccupied burrows. This work was for the most part rewarded only by observing the larvæ searching vainly for their original burrows. If by chance one encountered the burrow of another larva it crept boldly in, only to be met by the owner, who usually administered a sharp nip by means of its mandibles. Since the members of the genus are chiefly herbivorous and therefore for the most part peaceably inclined, the intruder usually retires quickly. It often repeats its attempt to enter the same burrow several times in succession, each time more cautiously, until it finally gives up or in some cases enters an unused part of the burrow and begins feeding. In this case it extends its burrow as a continuation of the original burrow or as a side branch, showing that it finds a decided advantage in using a burrow already started.

In case the larva gives up the attempt to enter an already formed burrow it begins a new one. The first requisite is the spinning of an arch formed of many thicknesses of silk about the size of an ordinary burrow. This, from the author's laboratory observations, is preferably located near another burrow, perhaps because of the water film that always accompanies the burrow. The larva next enters this silken arch, which is about as long as wide, turns itself on its back, and bends its head backward. This position enables the larva to brace its anterior prolegs against the underside of the silken arch and so bring pressure upon its head, which is at such an angle to the surface that the mandibles and the labrum are in contact with the surface of the leaf. In this position, with the head bent backwards a little more than at right angles, it extends its mandibles and rasps its way slowly through the epidermis. The spinning of the arch and the penetrating of the epidermis take over an hour and are doubtless severe tests on the strength of so small a larva.

Chironomids labor under greater handicaps than other gnawing larvæ in not having strong legs provided with claws for holding them in position and in not having mandibles that are opposable for cutting the tissue. Instead they have to depend upon indirect methods, of applying pressure to their mouth parts, and the utilization of their labial plates in conjunction with their mandibles for cutting the tissue.

THE BURROW.

The method of penetrating the epidermis in the beginning of the burrow is the same for the leaves of *Brasenia schreberi* as for *Castalia odorata*, but from this point on it differs markedly, due to differences in the texture of the plant. That chironomids show adaptability in their feeding habits is well shown by the differences in their burrows in *B. schreberi* and *C. odorata*, resulting from a difference in the thickness and texture of the leaves of these two plants.

We will take up first the nature of the burrow made on the leaves of Brasenia, since they are thinner, more easily penetrated, and where equally available more seriously attacked. This shows an evident selective power on the part of the larva. The writer is, however, aware that the softness of texture may be the deciding factor. When the larva has penetrated the epidermis of a leaf, it is able to bring pressure to bear more directly on the labial plate. The mandibles are hooked under the edge, and they, together with the pressure derived from the anterior prolegs, readily force the labial plate down through the epidermis. Then the larva moves a little to one side and repeats the operation. In this way the epidermis and parenchymatous tissue are removed from under the silken arch. Then the larva commences in the mid line and makes a cut as explained above from the center of the burrow to the outside edge. The larva during this operation is inverted, with its head turned backward. It next assumes an upright position, grasps the strip near its free end between its mandibles and labial plate, and pulls the strip backward, raising it upward at the same time. Then by bending its body to one side in its burrow it gets under the loose end and scrapes it clean of the green parenchymatous cells that adhere to it and fastens it in place against the silken arch (fig. 23). It next rakes this exposed area free of all the parenchymatous cells down to the lower epidermis. This removal of tissue usually results in the admission of water, probably through the mucous gland, as no openings are visible; at any rate the burrow becomes flooded and capillarity keeps it wet both inside and out.

The larva continues to cut slabs and to extend its burrow as long as it cares for food. These slabs are twisted backward and fastened in an upright position and their tips bound together with silk secreted by the salivary glands. The bottom as well as the sides and top are lined with silk. In the leaves of Brasenia the bottom and sides of the burrow have a very thin layer of silk which is closely applied to the surrounding tissue. When castings are to be extruded, the larva turns about in its burrow and the partially digested material is fastened to the arched top of the burrow by silk in such a way as to serve as sort of a porch. It is held extended by silk threads which are fastened out on the surface of the leaf. This porch or canopy serves a threefold purpose, being a shelter from the sun, a means of retaining a film of water over the area that is being excavated, and an entanglement in which the free end of the slab of epidermis becomes lodged so as to be held up while the tissue is being removed from its underside.

Later it becomes a part of the roof. Figure 23 is a diagram representing the nature of the burrow and an area with the top removed to show the general appearance of the lower epidermis, which forms the floor of the burrow.

In the case of the leaves of *Castalia odorata* the larva is obliged to bite the epidermis to pieces and remove it by sections because of its thickness. The head is applied at different angles and pieces of varying sizes are removed. Those that are small enough are swallowed and the rest are used in the construction of the sides and top of the burrow. The large spines are also removed and woven into the burrow with silk. On account of their relatively large size they greatly tax the strength of the larva. The thickness of these leaves is considerably greater than that of Brasenia leaves and the work of excavating greater. This necessitates a much greater thickness in the layer of silk making up the bottom of the burrow, especially as its bottom is at a higher level than the lower epidermis of the leaf. The castings are utilized in the same way as explained above for Brasenia, and the parenchymatous cells are eaten as food. The above changes in the method of procedure show a marked contrast to the habits of many other insect larvæ. This ability to adapt themselves to a variety of conditions has doubtless been an important factor in the adoption of their present unusual feeding habits. The pupal burrow is essentially similar to the larval burrow in structure, but is made up more largely of silk, is larger in diameter, and persists longer than the larval burrow (fig. 24).

RESPIRATION.

The larva breathes by means of four blood gills located on the posterior part of the last segment. These gills are longer and more pointed than in the species having red blood (fig. 15). The water in the burrow while small in amount is kept in circulation by an undulating motion of the body during the intervals while the larva is not feeding. The current flows from the head backward over the gills and out through the chinks in the sides of the burrow, passes forward over the surface of the leaf in thin films on either side, and again enters the open end of the burrow. The water should be well aerated, since it is exposed in thin films both to the air and to the surface of the leaf while flowing forward outside of the burrow. It is also exposed to favorable conditions for the desired exchange of gases while within the burrow, as it comes in contact with the air in the air-containing spaces of the parenchyma which is rich in oxygen and poor in carbon dioxide. That the oxygen supply is rich seems to be demonstrated by repeated accidental experiments where leaves were submerged overnight with the result that the larvæ died in the submerged leaves but lived in those on the surface.

The pupa is active and continues to aerate its burrow by occasional undulations of its abdomen. The repiratory filaments consist of several much-branched tufts located on each side of the thorax.

FEEDING HABITS.

The larvæ feed intermittently. They find an abundant food supply at hand, and the only limit set them is the rate at which digestion can be carried on. They are yellowish white in color, their blood lacking the hæmoglobin which gives the characteristic color to the other chironomid larvæ which are known as bloodworms. The green food material can be readily seen through the translucent body. It is seldom that the stomach is allowed to become more than half empty, and often the larva resumes its feeding operations when the stomach is practically full.

An attempt was made to determine the length of time that the food remained in the alimentary canal, but the small size of the larvæ and the acute discrimination in their feeding habits prevented the use of any coloring substances to mark any portion of their food. Direct observation was resorted to but proved too tedious to afford accurate data. The larvæ often withdraw from the end of their burrows and remain almost motionless for an hour or so at a time. Then they will begin feeding again, working for a half or three quarters of an hour at a time with only occasional short intermissions for the purpose of renewing their air supply by setting the water in circulation. By noting the intervals between feeding and resting it seems doubtful if the food remains in the body for more than two hours.

There is no special masticating apparatus present, and the result is that a very large per cent of the parenchymatous cells swallowed pass through the body entirely unaltered. The use of the castings for roofing material in connection with the burrow places these cells in a position which, while artificial, nevertheless offers conditions under which the carrying on of their life processes should be partially possible. These cells are held suspended in a silken mesh, bathed in water rich in the mineral salts, resulting from the digestion of similar cells, and favorably placed for the obtaining of carbon dioxide. That the covering of a larval burrow remains green for a considerable time is readily observed, and it seems possible that the larvæ have in this matter hit upon a favorable adaptation.

ECONOMIC IMPORTANCE.

The aquatic conditions of life required by *Chironomus braseniæ* larvæ confine their attacks to leaves at or beneath the surface where their burrows may be flooded with water. This requirement limits their attacks to a restricted variety of plants. The writer's observations on the injury done aquatic plants by *C. braseniæ* are confined to the one place where they occur within a reasonable distance of Ithaca, N. Y., which is Spencer Lake. Here the conditions seem to be excellently adapted to the growth of aquatic plants. The lake is shallow and *Brasenia schreberi* is the dominant plant with floating leaves, while *Castalia ordorata* is present in various parts of the lake and is next in abundance. Observations made on July 22 show a very considerable proportion of the leaves of Brasenia infested, while only one or two doubtful cases of the infestation of Castalia were observed. On October 7 the entire pond was examined, and a leaf of Brasenia which had not been injured by this larva was so rare as to make it difficult to explain how it escaped. The leaves of Castalia showed a greater percentage of infestation later in the season than at the time of the author's earlier visit, but they were not badly injured. Dr. Pettit says of the damage to water lilies:

> The pads of both *Nuphar advena* and of *Nymphea odorata* were furrowed by some miner. The pads had been badly eaten in some places and many contained living larvæ and pupæ.

CONTROL.

The injury done by these larvæ in parks and private gardens may some time become so great that methods of control will be necessary. At first thought it would not seem feasible to spray for an aquatic larva, but, as shown above, the water is kept circulating through the burrow and out on the surface of the leaf again. This use of the same water over and over, except as it is removed by evaporation and replaced by a fresh supply drawn in by capillarity through minute openings, prevents the dilution of any poison that may be added. Any arsenical spray should be effective. There is, however, an important difficulty encountered by the lack of uniformity in the rate of development of the larvæ. They are present in increasing numbers from the first of the season to late in September and infestation is taking place constantly.

Where feasible the larvæ may be destroyed in the early part of the season by draining the pond and allowing the bottom to become dry for a few days. The larvæ are unable to breathe unless immersed in water and are, therefore, easily destroyed by a relatively short period of drying. In small pools the mechanical removal and destruction of eggs and larvæ should be effective.

DESCRIPTION OF CHIRONOMUS BRASENIÆ, N. SP.

Larva.—Light green in color, the chitinized areas such as the head and claws reddish brown; antennæ slender, about three-quarters as long as the mandibles, the basal joint four-ninths of the whole length; a small spine on the apex of the basal joint and another at the apex of the second joint probably represent Lauterborn's organ. Each eye consists of two black spots in such close contact as to appear as one on superficial examination. The labrum much narrowed anteriorally, with a few setæ and four pectinate hairs. The epipharynx with three blunt teeth on its anterior border, the usual chitinized horseshoe area laterally compressed with the usual pectinate setæ, a posteriorly projecting median process and the two lateral arms articulate with the posterior margin of this area. The lateral arms also have dorsally projecting portions for the attachment of muscles. They are furnished with a median projecting membraneous flap. Maxilla with short palpus, several setæ, and two mesad projecting lobes. Mandibles with blackened teeth, the two median and outermost teeth not much blackened. Labrum with blunt-pointed margin, the teeth with rounded outline. Posterior prolegs with bilobed claws. Anal blood gills long and somewhat pointed. The posterior dorsal tufts of setæ are each placed upon a papilla, which is about as broad as long (fig. 15). There is also a pair of setæ just dorsal to the anal gills. Length, 7 millimeters.

Pupa.—Light green in color, the chitinized parts somewhat infuscated. Respiratory organs consist of a pair of tufts of white filaments. Dorsal surface of the second to sixth abdominal segments with a well-developed anterior band of brown setæ, the second and third segments with a posterior row of coarse spines, the entire surface covered with minute setæ, which are slightly smaller on a few irregularly placed areas, thus giving the surface a slightly mottled appearance. The lateral fin of the eighth segment with the usual set of four filaments and a brownish slightly toothed chitinized portion seen best in the pupal molt (fig. 16). The caudal fin has the usual fringe of filaments. Length, 5 millimeters.

Male.—Head, proboscis, palpi, and basal joint of antennæ yellow, tubercle slightly developed, eyes black. Antennal shaft and verticils brown. Antennæ with 14 joints, the terminal two-thirds as long as the rest of the antennæ. Pronotum projecting laterally, but not reaching the level of the mesonotum dorsally. Mesonotum greenish yellow, translucent, somewhat pruinose; vittæ of a light buff color; scutellum and halteres yellow; metanotum and sternopleura buff colored. Wings white, longitudinal veins and cross veins not infuscated. Cubitus forking distinctly beyond the cross vein; third and fourth veins ending about equally distant from the apex of the wing. Abdomen light green, densely clothed with long yellow hairs. Segments without distinct fascia. Hypopygium as in figure 17. Legs whitish, fore tarsus not bearded, second and third joints densely bearded for their entire length. Tibial comb darkened on all legs; basal segments of fore tarsus more than one-half longer than the tibia, proportions as 47 : 30. Pulvilli well developed, empodium, narrow. Length, 4 millimeters.

Female.—Antennæ yellow, apical joint slightly infuscated, seven jointed; posterior margins of the abdominal segments with a narrow whitish fascia. Otherwise like the male. Length, 3.5 to 4 millimeters.

Group V.—Trichocladius nitidellus Malloch.

To this group belong those larvæ which feed directly and apparently by preference on filaments of Spirogyra. *Trichocladius nitidellus* Malloch, a species described in 1915, is the only species that the author has thus far found which properly belongs here, although Lyonet (1832) described the habits of a species which obviously belongs to this group. Miall and Hammond (1900) state that this species has been rediscovered and studied by T. H. Taylor. They give in considerable detail the habits and behavior of this larva based on Taylor's observations. But it seems to the writer that there is a considerable difference between the two species and that the larva studied by Taylor agrees more nearly with that of *Trichocladius nitidellus*, which the author has studied, than with that observed by Lyonet. This difference will be more readily understood after the feeding habits of Trichocladius have been outlined.

FEEDING HABITS.

The description of the habits of this group has been well given by Miall and Hammond (1900, p. 11–17) based on Taylor's studies. *Trichocladius nitidellus* differs only in a few details. Filaments of Spirogyra are eaten exclusively by the older larvæ. There seems to be some selective ability exercised in the choice of filaments when more than one species of Spirogyra is present. This selection favors the smaller filaments. The larva often seizes a filament near the middle and forces the loop down its throat two fibers abreast. The same thing is often done with the larger filaments, and only occasionally are they bitten off completely. In this respect the author's observations differ from those of Taylor, who says: "A filament of Spirogyra is seized by the mandibles and bitten in two."

Taylor also states: "The labrum beginning at one end of the filament draws it into the gullet by a stroking action." The labrum is not so well adapted to meet the requirements of this method of feeding as the lateral arms which are located on the epipharynx. This will become more obvious when it is understood that the filaments are only crushed a little between the mandibles and possibly also between the labrum and the labium. This leaves the filaments in so natural a condition that when evacuated they immediately straighten out into their original shape. The stroking action of the labrum on a smooth filament, it would seem, is a far less effective method of forcing such a filament down into the stomach than the contact on either side by a well-developed pair of lateral arms which can be swung through an especially wide angle due to their position on the underside of the labrum. The movements of the lateral arms are so correlated with those of the labrum that the apparent stroking action observed by Taylor might well have been misinterpreted. The correctness of this line of reasoning has been confirmed by the author by direct observation with the low power of the compound microscope on a larva which was feeding with the ventral side up.

Digestion in *Trichocladius nitidellus* as in *Chironomus braseniæ* is incomplete, many cells appearing to be unaltered in the course of their passage through the body.

THE BURROW.

The burrow, as far as the author has been able to observe, is quite variable. In the older species it is made up of filaments of Spirogyra which have already passed through the body, as Taylor has also observed. In the case of the very young larva the burrow seems to be made up of dark-colored débris due to a different type of food eaten by the young larva. It is found to be made up of organic débris in which diatoms figure very largely. The writer is not sure at what stage the larvæ begin to feed upon Spirogyra, but it is certain that specimens not more than one-fourth the size of the mature larvæ do feed upon Spirogyra. These larvæ have been observed to drag their burrow after them in a manner similar to that described by Lyonet. His observations when translated are approximately as follows:

> Its activity in transporting itself from one region to another is very great and its behavior is peculiar. It extends its head for this purpose, seizes in its teeth all objects which it encounters, retiring quickly without relaxing its hold. The claws of the anterior prolegs hook themselves into the object seized by the teeth, loosening them it elongates itself again in order to seize some more distant object and draw itself forward.

Taylor does not seem to have noticed this habit, for he states under the heading of "locomotion":

> As the case is not fixed the larva can travel without leaving it. It does not creep like a caddis larva, but jerks itself forward by a few powerful undulations, in which the flexible case participates.

The older larvæ, however, according to repeated observations made on *Trichocladius nitidellus* both in the laboratory and out of doors, show so wide a range of behavior that it is impossible to confirm or disprove any of the above statements. Larvæ of this species found living on the algæ near the surface in a watering trough were placed in watch glasses and fed diatomaceous débris, which they ate and from which they constructed tubes in no way different from those characteristic of *Chironomus cayugæ*, as described above. Others, fed on a scant amount of Spirogyra, built no tube at all. About 30 larvæ were found at the bottom of a small pool clinging to an old and partly decayed table leg. These had no tubes. It is not difficult to find all intermediate stages between the attached, the free tube, and the larvæ without any tubes.

The food supply seems to be a controlling factor in the nature of the tube built. Since the larva lives on Spirogyra by preference, it eats away all the filaments in its immediate vicinity unless they are very abundant and closely matted. In that case it selects out the filaments which it prefers and simply extends the case. When the food becomes scarce, the larva is able to feed upon whatever débris it finds available, and when feeding in this manner it constructs the tube characteristic of larvæ feeding in this manner.

Taylor's observation upon the use of evacuated Spirogyra filaments in the construction of the tube is quite correct for *Trichocladius nitidellus*, as is also his observation of the use of silk to fasten the fragments together. "Fibrous structure," which Taylor saw only "faintly," was not noticed.

The larva carries on its respiration in the usual way, but since it habitually lives in a well-aerated environment it lacks hæmoglobin in its blood and simply takes the color of the food contained in its stomach. Such larvæ characteristically have much better-developed tracheal systems than those provided with hæmoglobin. This fact, together with Taylor's drawing (Miall and Hammond, 1900, p. 15, fig. 8), which shows a well-developed tracheal system, tends to corroborate his identification to the genus Orthocladius to which all the species of Trichocladius were formerly referred.

The available literature on the feeding habits of all the Orthocladius larvæ is so limited that it is impossible to tell whether any considerable number feed upon different filamentous algæ or not. It seems probable that the specimen observed by Taylor and assigned to this genus is either identical or closely related to *Trichocladius nitidellus*.

Group VI.

This group or subdivision of the Chironominæ is erected to include several species known to live throughout the larval stage without building any semblance of a tube. Since there are several genera represented by these forms which have relatively little more in common than their free living manner of life, the author has divided them into subgroups based upon the structure of their mouth parts and the nature of their habitats.

Group VI: Subgroup A.—Metriocnemus knabi Coquillett.

These larvæ are quite unique in their habitat, food, and manner of life. They were apparently first studied in the larval condition by Knab (1905), who made a number of observations on the larvæ and pupæ. He found them in the pitchers of the pitcher plant (*Sarracenia purpurea*), and, so far as known, the larvæ are not found in any other habitat. Although confined apparently to a single limited habitat, they are evidently widely distributed, for Knab found them at Westfield, Springfield, and Wilbraham, Mass., and at Cedar Lake, Ill. The writer has found them at McLean, N. Y., and they are doubtless to be found wherever *Sarraccnia purpurea* occurs.

> The larvæ of the present species live at the bottom of the water-filled leafcups of *Sarracenia purpurea*, burrowing in the closely packed débris composed of the fragments of decomposing insects. Evidently their food is from this source. [Knab, 1905.]

HEAD STRUCTURES.

The head structures for this subfamily have already been discussed, but this particular species and doubtless the entire genus (for the larval stage of very few are known) show decided modifications in their mouth parts. These modifications are well adapted to the present mode of life of the larvæ.

The labrum has the usual epipharyngeal comb well, though not strongly developed. It also has the labral comb well developed, very wide, and finely toothed. The usual hooks, pectinate hairs, and spines are present, but somewhat modified. The pectinate hairs are here quite broad at their tip and furnished with a straight and uniformly toothed margin. There are two pairs of these pectinate hairs, which, together with the other spines and processes, make quite a formidable and closely set array of scraping implements. The labium is, on the whole, not very different from the one figured for *Chironomus braseniæ* except in the number and relative lengths of the teeth. In *Metriocnemus knabi* the teeth of the labium are of nearly uniform length.

The maxillæ are quite remarkably different. The inner mesad projecting portion has a number of long close set spines which lie in the same plane as the labium and doubtless are of great assistance in supplementing it and the hypopharynx in their scraping action. The basal portion labeled for *Chironomus braseniæ* is in *Metriocnemus knabi* narrower and less firmly united to the epicranial plate. The fan-shaped structure marked *c* (figs. 11 and 12) is entirely lacking in this species.

The hypopharynx is long and well supplied with short, blunt processes. Its margin lacks the chitinized plates shown for *Chironomus braseniæ* and is obviously specialized as a delicately sensitive scraping structure. Its general appearance is that of a soft and somewhat flexible tonguelike structure covered with processes that are doubtless tactile in function. The epipharynx is provided with the usual pair of lateral arms which are here similar but less strongly developed than is the case with *Chironomus braseniæ.*

FEEDING HABITS.

Knab's remark that the larvæ burrow among the fragments of decayed insects and evidently obtain their food from this source is true as far as it goes. It leaves one in doubt, however, as to the actual food of the larvæ. Several times the author saw larvæ with broad chitinous bands around their bodies, evidently segments of insects' legs. Other observations have shown the larvæ with considerable parts of their bodies extending into these narrow insect appendages where the larvæ were apparently feeding. This would lead one to think that the larvæ feed upon the decaying tissues found there. This is doubtless true, for they are quite adaptive in their habits; but from other observations it would seem that they were, perhaps, even here feeding indirectly on the insect structures by devouring the large numbers of bacteria that in turn break down the insect tissues. This conclusion has been reached after considerable experience with these larvæ under artificial conditions.

Larvæ were removed from the pitcher plants and placed in petri dishes, together with the insect débris in which they were living. They were found to be perfectly well fitted to live in this manner. It was also found that they could live on beef broth, smoked beef, and decaying plant material. It is obvious, therefore, that insects are not the only source of food for these larvæ.

The question at once arises, Why is this species found so universally in the pitcher plant and nowhere else if it can live upon so wide a range of food? The answer is obviously given in the adaptation of this larva to a particular kind of food. In this adaptation the mouth parts are doubtless most fundamental. As explained above, they are fitted with a number of combs, spines, and fingerlike processes. The structure and length of the hypopharynx also indicate that it, too, is used as a delicate scraping organ, which is of prime importance in assembling the scattered bacteria. In this connection the presence of well-developed silk glands in close association with the hypopharynx suggests the possible function of their secretion in assembling the bacteria upon which the larva largely subsists.

That the larvæ prefer bacteria to the more solid tissues can be observed by their behavior in a petri dish, where they move about in a very characteristic manner. The head is carried at an angle of about 45° to the bottom, and the anterior prolegs are the chief organs of locomotion. They alternate with the head in supporting the body and are provided with about three rows of strong coarse spines. The larva moves along by a rapid alternate depression of the head and backward stroke of the anterior prolegs. The posterior prolegs are little used, and the larva curves its body up first on one side and then on the other, thus aiding the head and anterior prolegs in their forward movement. The larvæ always move forward, and the spines on the inner border of the maxillæ and hypopharynx are doubtless of prime importance in collecting the fine organisms, in correlation with this progressive method of feeding.

The pitcher plant seems to be the chief natural environment where such food substances are available. While its inner surface is covered with closely placed spines which all point inward, it nevertheless offers a favorable environment to such small larvæ, for they are able to move about among these spines and collect the bacteria and mold spores which accumulate there. That these larvæ may find conditions at least imperfectly suited to their method of feeding in other environments would seem to simplify the explanation of their distribution. The swamps are widely separated, and the pitcher plants are not numerous, and if a few larvæ could live in other environments the distribution would be more readily accounted for.

Group VI: Subgroup B.—Orthocladius sp. (?)

These larvæ have not been bred, but are abundant and will doubtless be found to be one of the common species. They are found in flowing streams about Ithaca and were collected the first part of June among the débris resulting from the disintegration of Cladophora. They were at that time very numerous, but the writer has been unable to find them on several occasions during the last of July and the first part of August. As forms found in flowing water are hard to rear, none of those taken early in the season were reared.

LARVAL CHARACTERS.

The larvæ are bluish green in color and have several rows of coarse black claws both on the anterior and posterior prolegs. The caudal filaments are placed on very small short papillæ, and the filaments themselves are very short, scarcely extending beyond the anal gills. The head parts are rather stout (figs. 29 and 30), and the fan-shape membranes are entirely absent.

The larvæ apparently do not make use of their well-developed silk glands for the purpose of building tubes. It seems probable that they would not be so well developed unless they had some important function. The author has concluded therefore that their development is correlated with the nature of the food eaten.

FEEDING HABITS.

The larvæ creep about on the surface of submerged stones and even out of the water where the rocks are only moist. A very noticeable feature in the behavior of these larvæ is the frequency with which they turn over. This habit of rolling over every few minutes while creeping over moist stones seems to be an adaptive measure. The upper portion of the body would become dry and the surface film would break away from the larva if it were not for the frequent moistening of the entire surface of the body. This revolving of the body about on its long axis the larva accomplishes by bending its head and the first two or three segments of its body off to one side, then, by relaxing the underneath muscles and stressing the upper muscles, this angle is made to revolve about the body until the larva again reaches an upright position.

These larvæ feed upon the organic débris to be found on the ledges in flowing water. Those whose stomach contents were studied had eaten Cladophora almost exclusively, and both the cell contents and the cell walls could be recognized. There were also a few diatoms, several filaments of Oscillatoria, and a few spherical cells, possibly of Aphanocapsa sp. The well-developed silk glands are doubtless used by the larvæ as digestive glands, and their development may be due to the coarse organic nature of their food.

Group VI: Subgroup C.—Prodiamesa sp.

The genus Prodiamesa was established by Kieffer in 1906. In the "Genera Insectorum" he refers six European species to this genus, and the writer has found only one South American species which has subsequently been referred to it. There is therefore no record of the occurrence of the species of this genus in this country. The species upon which these observations are based has been bred, and, from the larval mouth parts figured by Kieffer and Thienemann (1908), it is found to resemble *Prodiamesa præcox* very closely. The adult description, however, does not agree with that of *P. præcox*, and it seems probable that it will be found to be a new species.

The larvæ are yellowish white with reddish-brown heads and brownish claws on the prolegs. They, as well as the larvæ of the genus Diamesa, are characteristically found in flowing streams. The larvæ of Prodiamesa were found burrowing through the coarse débris that had accumulated in a roadside watering trough which was fed by a rapidly flowing stream from a near-by hillside. The trough was nearly full of sticks, grass, and leaf mold in various stages of decay, and it was through this rather loosely aggregated material that the larvæ were seeking their food.

BODY STRUCTURES.

This genus as represented by the writer's material (which is essentially in agreement with the larva of *Prodiamesa præcox*) is structurally quite similar to the burrowing forms. This is especially true of the anterior prolegs which are made up of several rows of fine spines. The branchial gills of the eleventh segment are absent in this genus. The caudal filaments are well developed.

MOUTH PARTS.

The most characteristic modifications in the mouth parts are to be observed in connection with the maxilla, the hypopharynx, and another structure the homology of which has not yet been satisfactorily established.

The maxilla is capable of a great deal of free movement, as the basal portion (as in the other species in this group) is not fused to the adjacent epicranial plate (fig. 31). Its inner mesad projecting process (fig. 31, *l*) is provided with numerous fingerlike processes resembling those observed in *Metriocnemus knabi*. The hypopharynx also suggests that of *M. knabi* and doubtless shows a close generic relationship.

The structures referred to above as not having their homologies well established are those to be found on the ventral side of the head (fig. 32, *c*), and suggest at once the fan-shaped membrane which the writer has labeled *c* in figure 11. Mundy (1909) has observed and mentioned these structures. He also gives a figure (Pl. V, fig. 18) and states that it is his opinion that the long filaments which the author has shown in figure 32 doubtless fuse and form the fanlike membrane which is so characteristic of the genus Chironomus. The author has been unable to establish the connection between these structures and the articulation of the maxilla shown in figure 11 and is therefore doubtful about their identity. The other mouth parts are very similar to those given for *Chironomus braseniæ* and therefore need no special mention.

FEEDING HABITS.

The feeding habits, judging from the food found in the stomach, involve a process of selection. The larvæ, as indicated above, creep along through the trash at the bottom of streams and consume whatever they encounter that seems most edible. Those examined had a considerable quantity of plant fragments and some soft, brown unrecognizable substance in their alimentary canal, but no diatoms were found. It was suggested by Mundy that the vibrissæ on the ventral side of the head of this larva might serve as the vibrissæ on the sides of a cat's head. It seems probable to the writer that their function is a tactile one. They doubtless enable the larva to distinguish the different substances which are more or less edible and in this way supplement the more delicate sense structures within the head of the larva.

The group as a whole contains larvæ with mouth parts that allow greater freedom of movement, especially in connection with the maxillæ, than in any of the other groups. Associated with this modification of the maxillæ is the entire lack or slight development of the fanlike membrane on each side of the labrum. The hypopharynx seems to be developed as a more efficient organ of sense and doubtless serves an important function in the selection of the food. The other structures of the head are in general similar to those characteristic of the previously discussed groups. It seems probable from the structure of the mouth parts that this is the more primitive group, as Goetghebuer has also suggested. The free-living habits of the larvæ seem also to supplement this conclusion.

SUBFAMILY TANYPINÆ.

This subfamily contains seven genera, and at least 45 species are known to occur in North America; but in spite of the number of known adults the author has failed to find any considerable literature bearing on the larval habits. Fr. Meinert (1886) made a number of observations upon a Tanypus species which he figures. These observations have been followed quite closely by Miall and Hammond (1900) and Johannsen (1903). This literature while good as a general treatise fails to give any very adequate idea of the feeding habits beyond the statement that the larvæ are predacious. Miall and Hammond, however, state:

> Bloodworms are preyed upon by many aquatic insects as well as by fishes. Caddis worms, Perla larvæ, Sialis larvæ, and Tanypus larvæ devour them greedily. A number of empty heads of the bloodworms may often be seen in the stomachs of a single Perla or Tanypus larva.

The behavior of the larvæ belonging to this subfamily is quite similar for the members of the group but very different from that of the larvæ of the other subfamilies. The Tanypinæ differ from the Chironominæ in the length and structure of the head and the function and arrangement of the mouth parts. The anterior prolegs are less strongly developed in Tanypus and are capable of being entirely retracted, so as not to give even a protuberance on that part of the body. The posterior prolegs are more strongly developed, are longer, and are furnished with claws of greater length than those of the Chironominæ. In other respects they differ less from the Chironominæ in appearance than in structure. They are not all nearly colorless, as Miall (1895) states, but there are a few which are blood red in color. These differ in their behavior as will be explained below. They also differ from all the aquatic members of the subfamily *Ceratopogoninæ* in the possession of both anterior and posterior prolegs.

In his study of this group the author has observed as many different species as he could find, but his chief attention has been given to *Tanypus carneus*, *T. hirtipennis*, *T. monilis*, and *T. dyari*, which have also been bred in the course of this work.

Tanypus hirtipennis differs from the other species mentioned in having red blood with which is correlated a burrowing habit. The presence of hæmoglobin in the blood seems to enable this species to live in a less well-aerated environment in the same way that it does in the case of certain members of the subfamily Chironominæ. They do not build tubes as so many of the true bloodworms, however, but simply prowl around pushing their inquisitive heads here and there among the organic débris at the bottom. On this particular point Meinert (1886) states that the Tanypus larvæ construct tubes where they remain concealed. Dr. Johannsen tells the writer that in no case has he observed them to behave in this manner. Since the salivary glands are much smaller in proportion to the rest of the body, since the larvæ live upon tube-dwelling larvæ, and since the pupæ are active like those of Culex, it seems probable that they are only found in tubes where they have gone in pursuit of their normal food. This also seems most likely from the fact that the Tanypus larvæ when disturbed flap themselves out of the tube or débris where they are, as readily as otherwise, which is not the case with the tube-building larvæ. This species, except for its adaptation to a lower level where it is more protected from bottom-crawling enemies as well as impeded in its locomotion, differs but little from the surface-dwelling forms.

Tanypus carneus is perhaps the best representative of a surface-dwelling member of this subfamily. It is slim, has a head about three times as long as wide, and its anterior proleg is long and slim and shows its double nature only toward the tip, where it is divided into two rounded branches provided with a few rather delicate claws. This proleg is capable of being completely withdrawn and thus adapts the larva to life among filamentous algæ where it seems most at home. The long posterior prolegs enable the larvæ to glide along snakelike through the filaments. When an enemy approaches, they are able to withdraw by a backward flexing of these prolegs and the posterior end of the body. Their behavior when sufficiently stimulated resembles that of the crayfish. So rapid is their movement that whether their prolegs catch on any solid particles or not they shoot backward far out of danger. When at rest on the débris beneath the surface, the stimulation of their caudal setæ causes them to give a little flip to their bodies which brings their heads almost exactly at the point where their posterior ends had been. This power to rapidly right about face, while especially characteristic of all the Tanypinæ, is not confined to this subfamily, but is a common reaction in all free-living species of the Chironominæ.

The author's chief justification for considering the feeding habits of this entire subfamily together is the similarity in the structures of the head and the mouth parts. The figures and the discussion of these parts found chiefly in systematic works have misinterpreted the homology of these parts. On this account, as well as the fact that the mouth parts in this group are of prime importance in any discussion of their feeding habits, they will be discussed in considerable detail.

MOUTH PARTS.

The hypopharynx of the larva of the subfamily Tanypinæ has commonly been called the labium. But it seems probable from figures 42 and 43, *th*, that what has hitherto been called the labial plate is really an especially well chitinized anterior border of the hypopharynx. Its strong development is here associated with its very much greater functional importance in this species. The strong muscles attached to this part of the head swing the plate upward and backward, the entire chitinized framework of the hypopharynx taking part in this movement. The toothed border of the upper chitinized bar also serves a similar scraping and cutting function (figs. 42 and 43, *hy*). The labium proper is double and has been labeled hypopharynx. From its position it seems more properly called the labium, and its double nature finds a partial counterpart in the labium of *Chironomus digitatus* Malloch (Malloch, 1915, pl. 30, fig. 13).

In the latter species the central part of the labium is a large rounded light-colored process, while the two sides are black and toothed in a manner very similar to the two-toothed areas in the Tanypinæ. The central area appears to be homologous to the "labial papillae" of Malloch, 1915 (pl. 25, figs. 4 and 9; see also fig. 41 in this work). This centrally arranged flap is soft and muscular and has a band of roughened scales on its dorsal surface. The mandibles are opposable and very pointed. They are also able to be used in opposition to the labium. In *Tanypus dyari* they are furnished with a row of seven lateral teeth (fig. 41, *md.*), the first of which is especially well developed in practically all species, as is the case in *T. dyari*. It seems possible that this long-pointed tip, together with the first well-developed tooth, are structures homologous to the double tip so common in the Chironominæ, which is frequently mentioned as of specific value.

The maxilla in the Tanypinæ (fig. 40) is very different from the homologous structure in the Chironominæ. Here instead of being attached to a flattened plate (figs 11 and 12) it is capable of a considerable movement. It consists of a flattened appendage with a roughly circular chitinous supporting structure made up of several partially fused sclerites (fig. 40). This freedom of movement and increased functional importance of the maxilla have an important bearing on the freedom of the movement of the mandible, as one can readily appreciate who is familiar with the restricted movement of the latter in the genus Chironomus due to the fusion of the maxilla to the sides of the head. Correlated with this freedom of movement of the maxilla one is able to note that the mandibles may be employed either above or below the maxilla. The anterior portion of the maxilla (fig. 40) is furnished with a large number of thin plate-like processes which doubtless have a tactile function.

The labrum (fig. 39) is thin and but slightly developed compared to the labrum in the Chironominæ. It is furnished on its anterior border with several processes apparently possessing sensory functions. These processes seem to be of more or less specific value and may sometime be of use, as this group is lacking in really good larval characters of systematic value. The chitinous processes (*cp*) may be homologous to the lateral arms of the hypopharynx of the Chironominæ.

The head structure of Tanypus is quite unique, being developed for a special manner of life, and the constant recurrence of this structure throughout the group, together with the great similarity in the habits of these species, seems to abundantly justify the placing of all the species in one group. From the ventral side of the head one is able to distinguish longitudinally arranged muscles which are attached at one end to the chitinous framework of the hypopharynx and at the other end to the posterior border of the head. From the dorsal surface, however, one sees a very different muscular arrangement. Here the muscles in the anterior part of the head radiate anteriolaterad from the mid-dorsal line, and in the posterior part of the head they radiate posterior-laterad from this same mid-dorsal line. Here in the center of the head is an area which doubtless serves as a sort of pump and to which are attached long muscles which radiate anteriorly and posteriorly. This pump is a structure present throughout the subfamily so far as the author has observed.

Another unique feature of the head is the presence of retractile antennæ, which Meinert (1882) has figured and described in detail. He does not seem to have observed their functional significance, however, but considers them only from the standpoint of their anatomy and homology. It will, therefore, be sufficient to state that the antennæ are withdrawn into the head capsule itself where there are special chitinous sheaths to receive them. They are withdrawn by special well-developed muscles and are said to be extended by blood pressure. They are of great functional importance in that they enable the larvæ to actually measure the distance from their prey. A few easily made observations enable one to see how constantly they are used. The larvæ prowl about with their antennæ partially extended, and upon encountering an active object they withdraw them as they approach, thus keeping in touch until near enough to seize the object.

FEEDING HABITS.

The larvæ are all predacious as far as the author has been able to determine, although it is very difficult to actually observe them feeding. Numerous studies of the stomach contents of the larvæ have shown such an array of diatoms and desmids as to entirely mislead one looking for proof of their predacious habits. Meinert (1886) states that he has observed a living Simocephalus in the intestine of a Tanypus larva, while Miall and Hammond (1900) have apparently observed indubitable evidence that they were predacious on bloodworms from the presence of the heads of these larvæ in their stomachs.

It was not, however, until the author had starved a *Tanypus carneus* larva for a week that he was able to observe the actual feeding habits. This larva when put in a dish containing a number of large Cyprididæ would apparently strike at them when they came in contact with its head. The striking seemed to be a more or less involuntary reaction, for when the nature and size of these crustaceans were discovered they were allowed to go uninjured. One of these crustaceans was killed and placed near the head of the hungry larva, but it was left undisturbed until movement was imparted to it by the aid of a needle. From repeated observations it seems apparent that the larvæ of this subfamily will not touch anything which is not moving. When movement was imparted artificially to dead pyschodid larvæ they were attacked, but before the skin was broken the larva abandoned them. When tried a day or so later on this larva it would not touch it, thus showing that decaying or dead material is not eaten even when the larva is very hungry, a fact in decided contrast with the behavior of a number of Chironomus larvæ, especially *Chironomus lobiferus*. The Tanypus larva to which was offered a freshly killed crustacean, however, ate it readily. It nevertheless showed a preference for small recently hatched bloodworms. These were swallowed whole and were apparently uninjured, as they were capable of moving for a time after being swallowed.

The method of attack and the defensive attitude of the larvæ of this subfamily were well shown in an encounter which occurred between two larvæ which the author was keeping on short rations preparatory to making observations on their feeding habits. The larvæ were of different species, one having a smaller and longer head than the other. The encounter was a head-on collision, each apparently striving to defend itself. They were taken under the compound microscope and their behavior observed. The head of the smaller larva was apparently not much within that of the larger one, but it was easy to see that the muscles within its head were being sucked toward the anterior tip of the head. The result was that the smaller larva was killed, although it was not consumed nor were any of the muscles of the head actually sucked out. The survivor, although unprovided with food from any other source, left its victim undisturbed as a result, doubtless, of its lack of movement.

An observation on *Tanypus carneus* well illustrates the function of the head as a sucking organ. A specimen that had been without food for four or five days was placed in a watch glass with a very active bloodworm (Chironomus sp.?) which was about the same size as the Tanypus larva. The Tanypus larva attacked the bloodworm just back of the head, employing its sharp mandibles to hold the larva. Very soon a reddish color could be observed in the head of the attacking larva, showing that it was beginning to suck the blood of the other. Then the alimentary canal was cut off, probably by the mandibles, and with its contents (diatoms, etc.) sucked into the body of the Tanypus. This left only the collapsed body wall of the larva to be consumed. This was accomplished by the use of the same powerful sucking apparatus. The body wall was drawn into the mouth while the hypopharynx rasped a hole through it, then the continued squeezing and sucking action of the head removed the muscles of the body wall. This method of treatment was repeated on different parts of the body until finally all the muscles of the body wall were removed. In this case the head was not swallowed and the muscle fragments of the bloodworm were in such a broken state that they would almost defy identification.

Miall and Hammond have remarked on the presence of red coloring matter in the body of Tanypus larvæ which they consider due to the bloodworms they have eaten. It is easy to confuse a natural red color with the color due to the food eaten, but a little experience will enable one to see a difference in the intensity of the color that is unmistakable.

The silk glands (fig. 44) are small and egg-shaped in general outline. Their ducts fuse some little distance posterior to their opening, which is situated just dorsal to the anterior border of the hypopharynx. The shape, relative size, and transparency of these salivary glands, together with the very different functions of the head and mouth parts in the Tanypinæ, at least suggest that their function is more exclusively that of a digestive gland than it is in the Chironominæ.

The alimentary canal is developed rather differently in the Tanypinæ than in the Chironominæ. Miall (1895) figures the alimentary tract for *Tanypus maculatus* but does not label the parts. In comparing these structures with the drawings of the alimentary canal of Chironomus sp.? given by Miall and Hammond the croplike enlargement so easily distinguished in the Tanypinæ (fig. 44, *cr*) is represented only by a narrow esophagus. The cardial chamber (fig. 44, *c*) is narrow and sharply marked off, and its surface is covered with longer coeca than in the Chironomus, but, on the whole, not so very different from it. The stomach proper (fig. 44, *st*) is proportionally shorter and of less functional importance. The remainder of the alimentary canal is quite similar in both subfamilies.

The food is retained in the crop (fig. 44, *cr*) part of the alimentary canal when first consumed and is constantly being stirred about by a peristaltic motion. When specimens are starved for a considerable time, the food is retained in this part of the alimentary tract often for the greater part of a week, which would seem to indicate its relative importance.

The peritrophic membrane, if present, is very thin and inconspicuous. The author has been unable to discover its presence by gross dissection and has consequently concluded that in this respect the Tanypinæ are decidedly modified as a result of their carnivorous habits. From the length of time that the diatoms are retained in the alimentary canal it would seem probable that they also are as well digested as they are in the stomach of the Chironominæ. As stated above, the digestion in this latter group is quite incomplete and any comparative statement must be relative in its nature.

It will be clear from the above considerations that the fundamental structures of this subfamily are closely correlated with its peculiar manner of life. It seems probable that this subfamily represents a more primitive type of insect than those included in the Chironominæ. This conclusion is based not alone on the free-living active behavior of the larvæ, but also upon the pupæ, which resemble the pupæ of Culex in their manner of life, as well as upon the primitive venation of the wings of the adults.

SUBFAMILY CERATOPOGONINÆ.

This is a widely distributed group. Many of the adults are known as blood-sucking insects, some attacking other insects exclusively and some turning their attention to the higher animals including man, while others appear not to take any food in the adult condition.

In the larval condition their habits are also variable. Guérin (1833) found the larvæ of *Ceratopogon geniculatus* Guérin and *C. flavifrons* Guérin under the bark of dead trees in a humid environment. Dufour (1845) found larvæ of a species which he identified as *Ceratopogon geniculatus* Guérin in decomposing onions. Perris (1847) found the larvæ of *Ceratopogon brunnipes* Perris in decomposing mushrooms at the base of a poplar tree. He also found *Ceratopogon lucorum* Mirgen in a heap of decomposing elm leaves and succeeded in rearing them indoors in this same material Laboulbène (1869) found the larvæ of an unidentified species of Ceratopogon in the ulcers or injured places in elm trees where they were living in what Dufour (1845) calls "la marmelade de l'Orme." These larvæ were reared and the species named *Ceratopogon dufouri* in honor of Léon Dufour by Laboulbène. Long (1902) found *Ceratopogon brumalis* Long in great numbers on the underside of nearly dry cow dung. He also found several hundred larvæ of all ages on the undersurface of a piece of moist rotting elm wood. He found similar larvæ and pupæ in the nests of the common foraging ants (*Eciton coecum*). The larvæ of *Ceratopogon specularis* Coquillett were found by Long to live gregariously in cow dung. Larvæ of *Ceratopogon stenomatis* Long were found by Dr. W. M. Wheeler in an ant nest, where they were moving about in the refuse heaped up by the ants in certain portions of their nests.

The larvæ of *Ceratopogon taxanus* Long (Long, 1902) were found beneath the bark of old dead trees in moist places or on the underside of very damp rotting wood. The only other habitat so far as known where the larvæ are commonly found is a strictly aquatic one. This latter environment according to Johannsen (1905) is occupied by the species having smooth wings. An examination of Malloch's (1915) keys, which cover only the Illinois species of this subfamily, shows 4 genera and 22 species with hairy wings to 9 genera and 72 species with smooth wings. It would appear, therefore (granting the supposition that smooth wings and aquatic habitat for the larvæ are correlated characters), that the greater number of the species are aquatic, but so few species are known in the immature stages that it is impossible to say whether the greater number undergoes development in water or in some more distinctly terrestrial environment.

BODY STRUCTURES.

The bodies of the aquatic larvæ are long and tapering, and their heads are proportionally longer and slimmer than those of the semiaquatic and terrestrial forms. The aquatic larvæ are entirely devoid of walking appendages, and the only external body structures that link them up with their near allies are the caudal filaments. These have either been considered homologous with claws of the posterior prolegs or left without any attempt at a comparison. In a permanent preparation of the larva of a Culicoidies sp.? the author has discovered that these filaments are arranged in two groups (figs. 45 and 48), which clearly suggest that they are homologous with the caudal filaments of the Chironominæ. Several authors have suggested that these structures, since they can be made to point either forward or backward, function as locomotor appendages. This observation is apparently correct. The great relative size and length of these caudal filaments seem to be functional modifications, for they are sense organs in other genera of the family.

The semiaquatic species (fig. 49) found in the sap flows of injured elms here at Ithaca, N. Y., resembles the one described by Laboulbène (1869), which he named *Ceratopogon dufouri*. These larvæ differ from the aquatic forms in having only poorly developed caudal setæ and in the presence of very short and contractile posterior prolegs, which are fused together and provided with a circle of hooked claws (fig. 50). This form was not bred, but from the mouth parts it seems possible that this is a mycetophilid and not a chironomid at all.

The typically terrestrial forms have well-developed anterior and posterior prolegs. Perris's (1847) observations on *Ceratopogon brunnipes* and *C. lucorum*, together with a study of the aquatic species already mentioned, would indicate a series of intermediate stages between those with both anterior and posterior prolegs and those without either. The author has indicated one stage of this series above. The first stage has caudal filaments which replace the posterior prolegs. The other stages are represented by the two species described by Perris. The first, *Ceratopogon brunnipes*, he found in decaying mushrooms at the foot of a poplar tree. Of this species he says the anterior prolegs are deeply dilobed and each lobe is furnished with a few claws. These are completely retractile, but those of the posterior prolegs are not. The other species, *Ceratopogon lucorum*, he says, appears to have a proleg formed of two pieces united by a suture, each of which is feebly bilobed. The exterior lobe is bare, and the inner lobe is furnished with fine spines. The last species, found in decaying elm leaves, resembles the typically terrestrial forms in general; besides possessing both anterior and posterior prolegs it has a spiny body.

In considering the terrestrial nature of these larvæ Laboulbène (1869) says that stigmates certainly exist but that he has not been able to count the openings. His opinion that they really do exist seems to be due to his observations on the arrangement of the tracheæ. The authors quoted in regard to the variety of habitats occupied by the larvæ of the Ceratopogoninæ all emphasize the humid condition of the habitat, and in the absence of any direct observations on the presence of spiracles it seems probable that in this respect at least the group is a unit.

HEAD STRUCTURES.

To understand the feeding habits of any insect, the structure of the mouth parts lends an important clue. This is equally true of the mouth parts of the larvæ of the Ceratopogoninæ. The frequency with which the early students complain of the difficulties of such a study is a sufficient justification for a somewhat incomplete consideration of these structures here.

In the aquatic larvæ Culicoides sp.?, probably *C. guttipennis*, the head is long and slim, about four times as long as wide. The antennæ, so conspicuous and useful in the other subfamilies, are here very slightly developed, scarcely reaching to the anterior border of the head. Their location (fig. 45) on the dorso-lateral border of the head, together with their slight development, fits them to serve as a sense organ with only a very limited function. This slight development of the antennæ is characteristic of the entire subfamily and is doubtless associated with the nature of the food consumed.

The mandibles, in Culicoides sp.?, possibly *guttipennis*, are quite characteristic structures (figs. 46, 47, *md*). They are so hinged as to be capable of being extended beyond the head and are opposable. They are also often observed within the head with their tips pointing backward, showing that they have a wide range in their movements. The fact that the mandibles are capable of being swung through such a wide angle shows that they are doubtless very essential to the feeding habits of the larvæ.

The larvæ resembling Laboulbène's larvæ which the author found in the sap flows on elm trees about Ithaca have mandibles with teeth resembling those on the typical

Chironomus mandibles (fig. 51). These were used by the larvæ for the purpose of locomotion. They move alternately, and the head is tipped down slightly, so that their motion in a dorso-ventral direction enables them to function as feet. In this species the anterior prolegs are entirely lacking, and the larva moves by a gliding eel-like motion aided by the mandibles, which also help to clear the way. A similar function of the mandibles in Culicoides sp. is suggested (figs. 46 and 47).

The labium has several times been figured showing a strongly chitinized central tooth and in some species a single pair of lateral points on the otherwise smooth, somewhat thickened lower margin of the head. This central tooth appears to be the hypopharynx. Its probable function as a piercing organ would doubtless be suggested to everyone by its shape.

The epipharynx in Culicoides sp. seems to be located near the middle of the head and, so far as it is possible to tell from drawings, what the author considers as the epipharynx (figs. 46 and 47, *ep*) is what has been called the hypopharynx by Malloch (1915). Its function seems to be that of a strainer or comb, coupled doubtless with a tactile function.

The ventral half of the head seems to be fitted with long muscles which doubtless operate the mouth parts. The dorsal half of the head posterior to the epipharynx seems to be filled with radiating muscles, as described in the case of the Tanypinæ, which doubtless serve a similar function, namely, that of a pump or sucking organ.

FEEDING HABITS.

Culicoides (*guttipennis?*) larvæ, which were under observation for some time, were extremely hard to observe while feeding. The only case actually seen was that of a larva feeding within the dead body of a pupa. This pupa was of the same species as the larva. When observed, the body of the larva was thrust deep into the nearly empty shell. The larva was revolving its head and first two segments about, and of course could not bring pressure upon its mouth parts because of its lack of prolegs. It seems probable that the mandibles came into use at this time, as they are the only mouth parts adequate to the purpose. It was impossible to observe the activity of the mouth parts on account of the thickness of the chitinous wall.

The author's experience in trying to study the stomach contents of these species is exactly parallel to that of Miall and Hammond (1900), who were unable to identify the small particles occasionally found in the stomach. According to these same authors "The digestive system is straight and simple and apparently adapted to the wants of a carnivorous animal."

From the obvious specialization of these aquatic larvæ, as shown by their relatively great length and slight breadth, it seems fair to assume that they are adapted to an environment where they are able to reach food inaccessible to thicker and more chubby larvæ. During the winter larvæ of an aquatic species were found deep in various decaying stems, especially those of Typha and Sparganium. The following summer the writer was unable to find them in connection with these stems, but by dipping up masses of floating green algæ in the same pool he found them in considerable numbers.

What then is the nature of the food upon which the larvæ of the Ceratopogoninæ live? It seems probable that larvæ living under decaying bark, in rotting onions, among decaying elm leaves, or under cow dung would have but little choice in the food which they obtain, especially when we learn that these larvæ do not burrow but simply wiggle and creep along through the moist and semifluid portions of their environment. That they in all probability live on decaying organic matter, together with the bacteria and mold which are always present in such substances, seems obviously a case of necessity. That an aquatic environment offers a greater opportunity for larvæ adapted to such a life to select their food is readily seen from the study of even a limited habitat.

The fact that aquatic larvæ kept in confinement will eat animal material is well shown by the observations mentioned above of a larva found eating the tissue of a dead pupa of its own kind. Their presence among filamentous algæ suggests that they may also eat out the protoplasmic contents of the larger filaments. It seems probable that various other organisms might become entangled in these filaments and be used as food by these larvæ.

In conclusion, it may be said that the larvæ of this group as a whole show a specialization of the mouth parts which fit them to live on soft substances. The various habitats in which the larvæ are found seem to bear testimony to the organic nature of the food consumed. The uniform failure of all attempts at microscopic analysis of the stomach contents of these larvæ suggests the structureless nature of the food taken. It seems apparent, therefore, that, since all decomposing organic matter offers a very similar food supply, the larvæ of this subfamily are capable of adapting themselves to a wide range of food substances. The humidity more than any one other factor doubtless limits this adaptability, since moisture not only aids decay, thus making hard inedible substances available as food, but also serves as a factor of prime importance from the standpoint of respiration to a larva lacking spiracles.

SUMMARY.

In the following groups the author has tried to show the more striking differences in the feeding habits of the Chironomidæ. In each group the mouth parts and general behavior have been made use of in determining the feeding habits. The stomach contents have been depended upon only as a confirmation of activities actually observed, thus avoiding several errors in connection with the predacious forms. The family as a whole shows a wide range of structural variations and a wider range, if possible, of special adaptations.

In Group I the larvæ, although somewhat variable in habits, can and do live to a very considerable extent upon bacteria, Protozoa, diatoms, small Crustacea and other free-floating aquatic organisms, which they strain from the current driven through their burrows by means of delicate silken nets.

In Group II the larvæ utilize the natural flow of the stream and subsist on the plankton organisms found there. The individuals of this group are usually very numerous, but as Group I consists of forms characteristic of quiet water, Group II does not compete with it.

Group III contains the greater number of the typical Chironomus larvæ, known as bloodworms. They are found wherever any considerable accumulation of diatoms and plant débris occurs. In laboratory experiments they were found to be able to subsist for considerable periods upon a very scanty supply of food material. Thus, we find them to be a group capable of utilizing and conserving whatever amount of diatoms, algæ, and plant débris may chance to fall upon the bottoms of fresh-water ponds. Their large size and overlapping broods indicate their possible importance to fish life and in fish culture.

Group IV contains an aberrant species that feeds directly upon floating aquatic leaves and is noteworthy chiefly for its direct injury to those plants.

Group V contains at least one species (*Trichocladius nitidellus*) that promises to be of considerable importance, as it is able to subsist entirely upon filamentous algæ, chiefly Spirogyra.

Group VI includes a number of free-living forms that occupy somewhat unique habitats but constitute a group of minor importance.

The entire subfamily Tanypinæ consists of predacious forms, which as a group apparently do not contribute anything of economic importance to the Chironomidæ as a whole. They, however, do occasionally feed upon small Crustacea and the more rapidly moving diatoms and in this way help to counteract their otherwise well-merited position as an economically undesirable group, from the standpoint of the fish-culturist.

The subfamily Ceratopogoninæ are scavengers as a group and as such fulfill a useful function.

From the consideration of these rather arbitrary divisions, as well as the natural subdivisions of this large family, it becomes evident that there is a wide range in the adaptations of its different members. Some of these adaptations are of generic value, while others seem to vary within the genus, as in *Tanytarsus obediens*, which is included in Group I, although the other members of the group belong to the genus Chironomus. In a similar manner the red color of the larvæ seems to occur with little or no relation to the genus or subfamily but is rather more closely associated with the nature of the environment.

It is obvious from the above that the family has become specialized for different habitats. While the author has tried to point out what seems to be the behavior normally characterizing each group, it is easily apparent from a few observations that the great adaptability of all these species when under the stress of adverse conditions reduces them to what is probably the primitive habit of the group, namely, that of direct feeding on the débris about them.

The degree of departure from the primitive method of feeding, however, varies considerably. In the Tanypinæ we have a form that is strictly predacious, while in the Ceratopogoninæ we have a form that is adapted to live on dead and even decaying organic matter. The latter group seems to be about as abundantly represented in semiterrestrial environments as in those that are strictly aquatic, and it is this group that doubtless contains the most or perhaps the least primitive representatives of the family. The Tanypinæ doubtless come next and then the Chironominæ.

In the Chironominæ it would seem that from direct feeding by the use of silk to attach together the particles fed upon the use of silk in entangling particles in a stream would be but a simple step. Then, from this beginning an artificial current, made necessary by the poor supply of air, might readily lead up through a series of stages, from the entanglement of particles in the lining of their burrows to the present highly specialized silk net, which characterizes Group I.

The small size of these larvæ and their adaptability to such a wide range of habitats enable them to take possession of an environment where the food supply would be insufficient for a larger form with similar food requirements. It is this factor that seems most readily to explain the wide range and great numerical dominance of the family. It is this fact, too, which seems best to account for their numerous enemies among the aquatic animals.

ORPHNEPHILIDÆ.

This family is included here because of its close kinship with the Chironomidæ, as shown by the structure of the adult. It is also of considerable interest on account of the unique and little known habits of the larva, which lives on the surface of ledges covered by only a thin film of water (fig. 38) and breathes by means of a trachea, rendering it entirely unable to live submerged for any considerable time. As might be inferred from these two conditioning factors this family is not likely to occur in many parts of the country. That it is really scarce is well illustrated by the fact that the record for the family in this country prior to 1916, so far as known, was based on three specimens found by Dr. O. A. Johannsen at Ithaca, N. Y. Dr. V. L. Kellogg (1902) states that he has examined specimens of every family of the Nematocera except Orphnephila. References in the literature to this family are so infrequent as to make it almost unknown except to a specialist in Diptera. Thienemann (1909), however, found and described the larva which he obtained from mountain streams in Europe. His paper considers the nature of the habitat, the distribution, and the method of locomotion of the larvæ of *Orphnephila testacea.* According to Kellogg (1905, p. 327) this species is the only one representing the family in this country and as far as the author is aware the only species known, if the American and European forms are actually identical.

The three adult flies found by Dr. Johannsen referred to above were taken in sweeping for insects, and none were taken in a manner to reveal the whereabouts of their immature stages. It was therefore a very pleasant surprise to the author to accidentally run across the habitat of this most unique semiaquatic insect in the environment of Ithaca, the only place in this country where this species is known to occur.

As the interests of the author centered about the ecology of the species, especially as it concerns the feeding habits of the larvæ, he several times attempted to take specimens into the laboratory that the necessary conditions of their environment might be more readily studied. Several of these attempts were failures because the larvæ were drowned while en route, but by lining test tubes with moist cheesecloth it was found very easy to carry any number of the larvæ considerable distances under perfectly normal conditions.

HABITAT.

While Thienemann's description is in substantial agreement with the writer's own observations, it seems best to summarize the conditions under which the larvæ were found.

The horizontal strata of the rock, so characteristic of all the gorges and "hanging valleys" in the environment of Ithaca, together with the usually rather irregular vertical cleavage, frequently gives rise to a stair-stepped bottom to the streams that enter the deeper valleys. The only habitat in which these larvæ were found was on a series of "giant steps" (fig. 38), where a small stream spreads out over these broad and nearly horizontal stones in its precipitous descent to the valley of Six Mile Creek. Here the larvæ were found rather more frequently on the vertical than the horizontal surfaces of the ledges. They also seemed to select those parts of the rocks which were free from any vegetable growth, a selection probably closely correlated with their method of locomotion.

That the larvæ are unable to live on the surface of any other than perfectly quiet water was discovered by repeated attempts, as above stated, to carry living larvæ home in bottles half filled with water. The result was nearly 100 per cent fatalities. This does not mean that they can not move over quiet water, for they are very much at home in such conditions; but as soon as the surface film rises above the ventral third of the body, which is distinguished by being somewhat flattened and white in color, the result is total submergence. Total submergence is, of course, only fatal in larvæ which breathe by means of tracheæ and have no special means of escaping from the water. The larvæ of Orphnephila do breathe by tracheæ, and, while they are very well adapted to move rapidly on the surface of moist ledges, their very peculiar sidewise movement of the body is not at all suited to locomotion beneath the surface film. In fact, they depend very largely upon the surface film which holds them so closely in contact with the rock's surface that with the claws of their anterior and posterior prolegs they are able to anchor one end while the other is being swung around in a horizontal plane. This zigzag sidewise movement is sufficiently rapid to enable them to move four or five times as fast as a chironomid can crawl and gives them the appearance of being very sprightly.

This poor adaption to an aquatic environment is one of the factors that doubtless makes for their infrequent occurrence, next to the nature of their habitat, which is of itself rather unique. In several laboratory experiments in which the author attempted to duplicate natural conditions the larvæ were observed leaving the moist stones upon which they had been placed and voluntarily subjecting themselves to the current which swept them over the edge of the dish. So far as it is possible to judge, the same thing is liable to occur in nature, and the results are doubtless fatal, for the bigger streams are constantly agitated by swirls and cross currents which would submerge and drown the larvæ.

In order to try to eliminate the nonessentials in the environment of the larvæ, the author began searching for suitable methods of rearing them in captivity. At first an experiment, referred to above, was set up in which rocks taken from the natural habitat were placed in a tray through which a stream of gently flowing water was maintained. The result was that the larvæ allowed themselves to be carried over the edge and were lost down the sink spout. At Dr. Johannsen's suggestion a cheesecloth pocket was used and resulted in the successful completion of the transformation of some five or six adults.

This pocket was made by placing a double thickness of cheesecloth over the top of a wide lamp chimney and pressing it down so that it would hang in a conical sort of a pocket. This was covered with two thicknesses of cheesecloth after the larvæ and a fair supply of food had been placed within. Then both the cover and the pocket were made fast by successive coils of white thread, which were wound about so tightly that the larvæ were unable to creep out between the layers of the cheesecloth. The pocket was moistened by water which was kept dripping slowly over its surface. To insure the more uniform distribution of the water to all parts of the receptacle, a mass of cotton wool was placed on the cheesecloth cover. That this sort of an artificial environment seemed to meet their every need was demonstrated by the fact that the larvæ lived under these conditions for several weeks with very few fatalities, even though the water ceased dripping several times for a number of hours, thus causing a considerable drying out. The pupæ, which seem never to have been found in nature, were observed to be located in a fold in the pocket where the water supply was more uniform and where greater security of position was doubtless possible.

The author was unable to find a pupa out of doors even after he had bred the pupæ in an artificial environment. The larvæ, while quite abundant in the one habitat in which the author succeeded in finding them, either do not live to transform to pupæ in any considerable numbers or else they possess some unusual habits which entirely escaped the writer's notice, for repeated search for pupæ in the most likely places and at such widely separated intervals was made that it does not seem possible that they could have been abundant in the environment occupied by the larvæ. That the pupa can live under the same conditions in which the larvæ are found is amply demonstrated by the author's laboratory experiments, where upwards of 50 per cent of the nearly mature larvæ transformed to adults. Another source of information which seems to corroborate the notion that the pupæ are not abundant was the fact that repeated sweeping over these rocks and in the adjoining region failed to give even a single adult specimen. The eggs so far as is known have never been found, and nothing is known of the mating habits of the adults.

FEEDING HABITS.

The feeding habits of Orphnephila are no less unique than its other environmental adaptations. Let us first take up the structure and arrangement of the mouth parts, as a knowledge of their nature and position is fundamental to all ecological considerations.

Thienemann (1909), as mentioned above, has figured the more commonly observed mouth parts of Orphnephila, but the separate drawings give no adequate notion of the relative position of each part. The author has found it necessary to draw the mouth parts as they appear in position and then for the sake of comparison several of them separately. The assembled mouth parts (figs. 53 and 54) show that the mandibles, instead of moving from the outside inward toward the mid line, as described in the case of the chironomids, are so hinged as to move outward from the mid line when in use for the purpose of scraping food from the rocks. This arrangement of the mandibles in Orphnephila, so far as the author is aware, is unique among Arthropoda. Correlated with the mandibles are the maxillæ which are furnished with a border of spoon-shaped plates which are opposable to the mandibles. This arrangement makes their function as collecting baskets, for gathering in the particles scraped free from the stones by the mandibles, quite obvious. The rods shown in figure 54, *rd* are supporting structures which fuse with the clypeal plate and extending beneath the mandibles form a partial support for the articulation of the maxillæ. The very marked development of the labrum suggests at least its probable function, and while the writer has not been able to observe this particular mouth part in use it is probably brought into play in connection with the mandibles in such a way as to scrape an intermediate area not touched by them.

The rather narrow labrum is provided with a considerable number and variety of spines at its terminal end and, together with the somewhat similarly clothed hypopharynx, is doubtless instrumental in collecting the food scraped loose by the labrum, as well as in the removal of the food particles assembled by the maxillæ (*fig. 53, lb*).

The food itself consists almost exclusively of diatoms, and as the number of kinds of diatoms in such streams is few and as those found on exposed ledges where the larvæ feed are even less varied the variety is not great. Figure 57 shows a typical selection of the food from the stomach of one of these larvæ. The many unique features in the habits of this insect seem to limit its life and activities to a very restricted environment to which it seems but poorly adapted, if the infrequent capture of adults and the evident scarcity of pupæ can be taken as criterions. From the above observations it might readily be considered as a species which had only recently acquired the aquatic habit.

EXPLANATION OF FIGURES.

CHIRONOMUS BRASENIÆ.

FIG. 1.—Ventral aspect of the epipharynx; a, lateral arm; co, epipharyngeal comb; e, chitinous claws; h, horseshoe-shaped chitinized area; p, lateral process; s, pectinate hairs; t, thickened border of the labrum; x, chitinous process.

FIG. 2.—Lateral view of the strongly chitinized structures somewhat diagrammatic; p, lateral process; s, setæ and pectinate hairs; u, clypeus; (other structures as above).

FIG. 3.—Lateral aspect of the mandible (md); j, pectinate setæ; q, external process; m, portion of the adductor muscle and its thickened exteria; v, extensor muscle.

FIG. 4.—Median aspect of the left side of the head; c, cardo (position indicated); g, galea; i, internal chitinous process; j, pectinate setæ; l, lacinia; la, labium; m, adductor muscle; md, mandible; p, maxillary palpus; st, stipes; u, clypeus; v, extensor muscle; w, center of articulation of the galea and lacinæ.

FIG. 5.—Ventral aspect of a portion of an epicranial plate; i, internal chitinous process; r, antenna; u, clypeus.

FIG. 6.—Dorsal aspect of mandible; j, pectinate setæ; o, articular surface of mandible; q, external process.

FIG. 7.—Dorsal aspect of hypopharynx; b, posterior lobe; c, backward pointing setæ; k, arm or chitinous process; th, chitinous plate; z, exit of the salivary ducts.

FIG. 8.—Dorso-ventral aspect of the hypopharynx; d, salivary duct; f, chitinous ring; k, arm or chitinous process; th, chitinous plate.

FIG. 9.—Antenna, lateral aspect; l, Lauterborn's organ; n, sensory spine.

FIG. 10.—Ventral view of the head; c, cordo; d, salivary duct; e, epicranial plate, la, labium, md, mandible; mx, maxilla; r, antenna; u, clypeus.

FIG. 11.—Lateral aspect of the maxilla; c, cardo or striated membrane; g, galea, l, lacinia; p, palpus; pf, palpifer; st, stipes; w, center of articulation of the galea and lacinia.

FIG. 12.—Lateral aspect of a portion of the epicranial plate; c, cardo or striated membrane; la, labium; pr, chitinous process limiting the movement of the mandibles; st, stipes.

FIG. 13.—Ventral aspect of the anterior margin of the labium.

FIG. 14.—Labium of young larva.

FIG. 15.—Posterior segments of the larva; b, branchial gills; ca, caudal filaments; c, claws.

FIG. 16.—Lateral fin on the 8th segment of the pupa; ca, chitinized area.

FIG. 17.—Hypopygium of the imago, dorsal aspect.

FIG. 18.—Wing.

FIG. 19.—Portion of an egg mass.

FIG. 20.—Tracings of the larval burrows in the leaves of Brasenia.

FIG. 21.—The same as fig. 20.

FIG. 22.—The same as fig. 20.

FIG. 23.—Diagrammatic drawing of the larval burrow greatly enlarged; a, silk supporting threads; b, section of the epidermis cut out by the larva; c, canopy composed of larval castings; d, epidermal slab used as the sides of the larval burrow; e, edge of epidermis and the underlying parenchyma; f, vein of the leaf; g, mucus gland.

FIG. 24.—Pupal chamber on the leaf of *Castalia odorata;* c, idioblast; p, anterior portion of pupa molt.

FIG. 25.—Cross section of a *Castalia odorata* leaf showing its general structure; a, stomata; b, upper epidermis; c, idioblast; d, lower epidermis; e, air space.

CHIRONOMUS LOBIFERUS.

FIG. 26.—Diagram of a glass preparation showing the position occupied by the larva in its burrow; lc, lower glass; nt, conical net; t, glass tube; u, upper glass; v, larva.

FIG. 27.—Diagram of the contracted conical net.

FIG. 28.—Broken labial plate.

ORTHOCLADIUS SP.

FIG. 29.—Labium.

FIG. 30.—Mandible.

PRODIAMESA SP.

FIG. 31.—Maxilla; ar, articular process; c, vibrissæ; l, lacinia; la, labium; p, palpus; st, stipes.

FIG. 32.—Ventral aspect of a portion of the head; ar, articular process; c, vibrissæ; la, labium.

CHIRONOMUS LOBIFERUS.

FIG. 33.—Claw of posterior proleg.

FIG. 34.—Spines of anterior proleg; a, serrate spine; b, c, hooked spines; d, hairlike spine.

FIG. 35.—Left anterior proleg; a, hairlike spines; b, hooked spines; c, serrate spines.

FIG. 36.—An enlarged silken holdfast attached to a glass surface; g, a process on the side of a larval burrow.

FIG. 37.—Silken network between two larval burrows (g, h); i, interlacing silk fibers.

ORPHNEPHILA AMERICANA.

FIG. 38.—View of habitat where larvæ were found, west bank of Six Mile Creek, Ithaca, N. Y.; F, water level of the main stream; l, ledges kept moist by water flowing in a small stream shown just above; w, water flowing over ledges.

TANYPUS DYARI.

FIG. 39.—Labrum; ch, chitinous plate; cp, chitinized process; se, sensory process.

FIG. 40.—Chitinous structures of the maxilla; l, lacinia; p, palpus.

FIG. 41.—Ventral aspect of the head; hy, hypopharynx; la, labial papilla; md, mandible; mx, maxilla; p, maxillary palpus; r, antenna.

FIG. 42.—Dorsal view of the labium and hypopharynx; ar, articular plate; cb, chitinous band; hy, hypopharynx; la, labial process; lp, lateral hypopharyngeal process; pr, sensory process; th, chitinous plate of the hypopharynx.

FIG. 43.—Lateral view of the same.

FIG. 44.—Dorsal view of the entire larva; br, branchial gill; c, cardiac chamber; cr, crop or proventriculus; g, salivary gland; m, malpighian tubule; r, retractile antenna; st, stomach or ventriculus.

CULICOIDES SP.

FIG. 45.—Dorsal view of entire larva; f, caudal filaments; g, branchial gills.

FIG. 46. Lateral view of the head; d, salivary duct; ep, epipharynx; ey, eye spot; hy, hypopharynx; la, labium; lb, labrum; md, mandible; mx, maxilla.

FIG. 47.—Ventral view of the head; structures the same as shown in fig. 46.

FIG. 48.—Dorsal view of the posterior end of the larva considerably enlarged; f, caudal filaments; ff, accessory caudal filaments; g, branchial gills. Larva from sap flow in elms resembling *Culicoides hieroglyphicus*.

FIG. 49.—The entire larva, dorsal view; ch, chitinous rod.

FIG. 50.—Posterior end of the same greatly enlarged; c, caudal processes; g, branchial gills; s, setæ resembling caudal filaments.

FIG. 51.—Mandible.

ORPHNEPHILA TESTACEA.

FIG. 52.—Side view of entire larva showing characteristic color pattern.

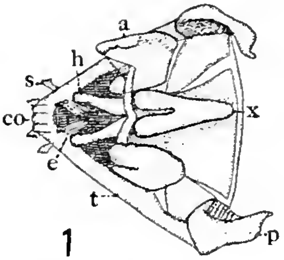
FIG. 53.—Side view of the head and proleg; ey, eye spot; la, labium; lb, labrum; md, mandible; mx, maxilla; pr, proleg; r, antenna; sp, spines.

FIG. 54.—Frontal view of the head; cl, clypial plate; la, labium; lb, labrum; md, mandible; mx, maxilla; rd, rod attached to the mandible.

FIG. 55.—Ventral aspect of the mandible.

FIG. 56.—Dorsal-lateral aspect of the hypopharynx.

FIG. 57.—Miscellaneous diatoms from the stomach of Orphnephila.



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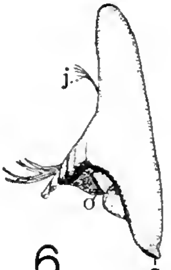

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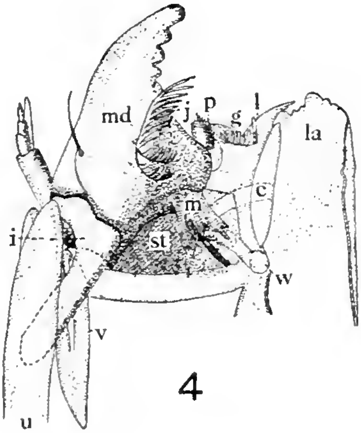

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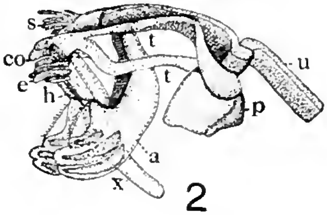

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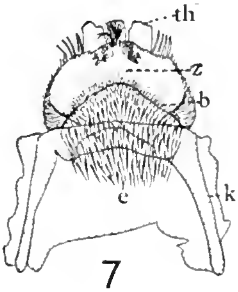

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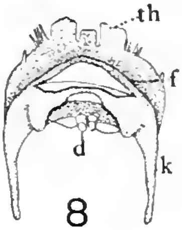

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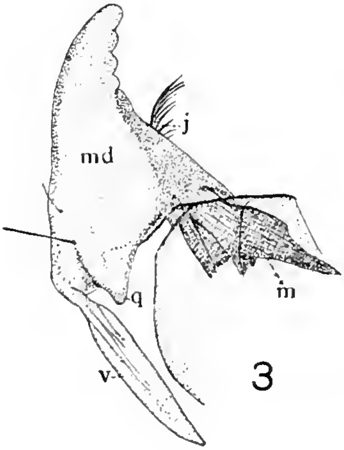

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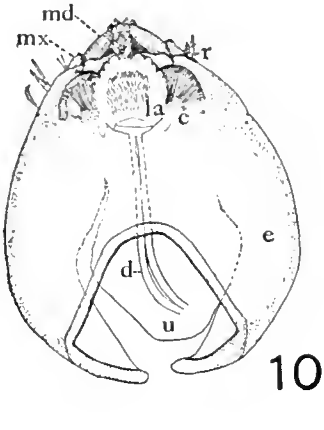

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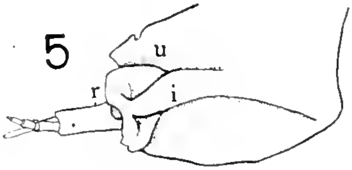

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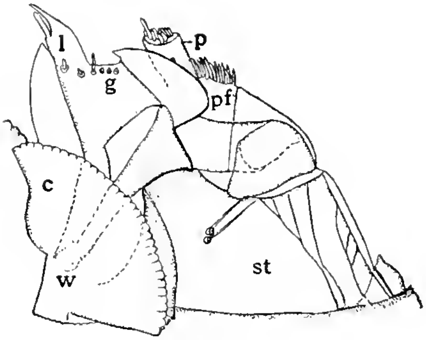

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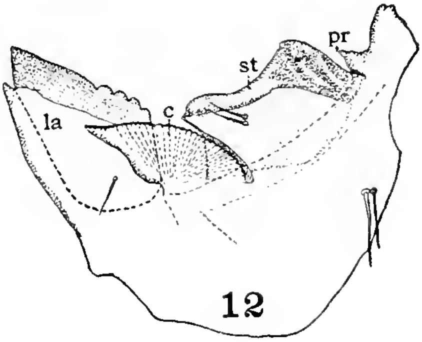

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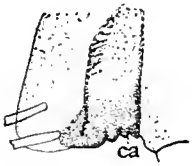

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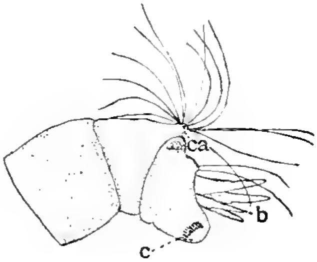

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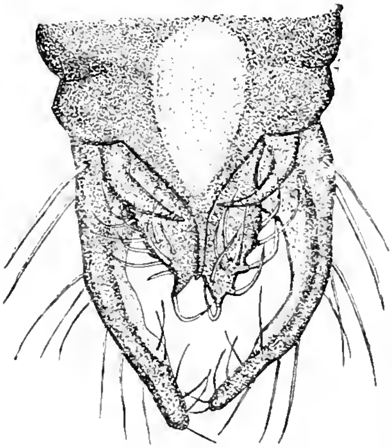

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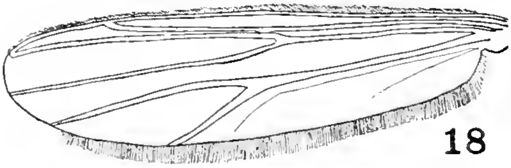

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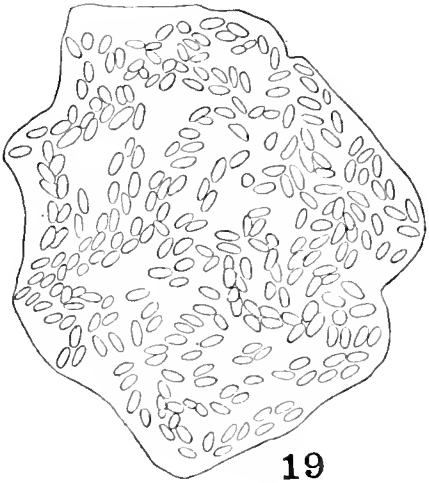

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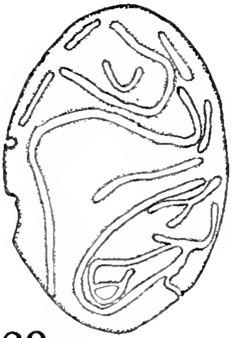

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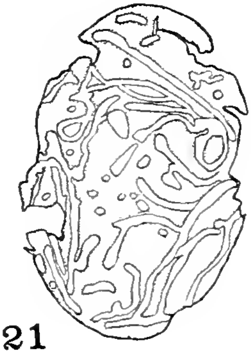

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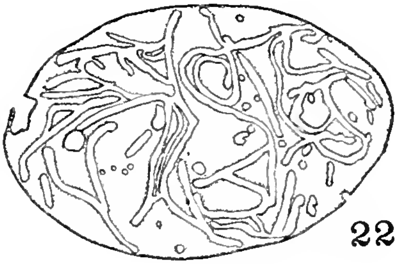

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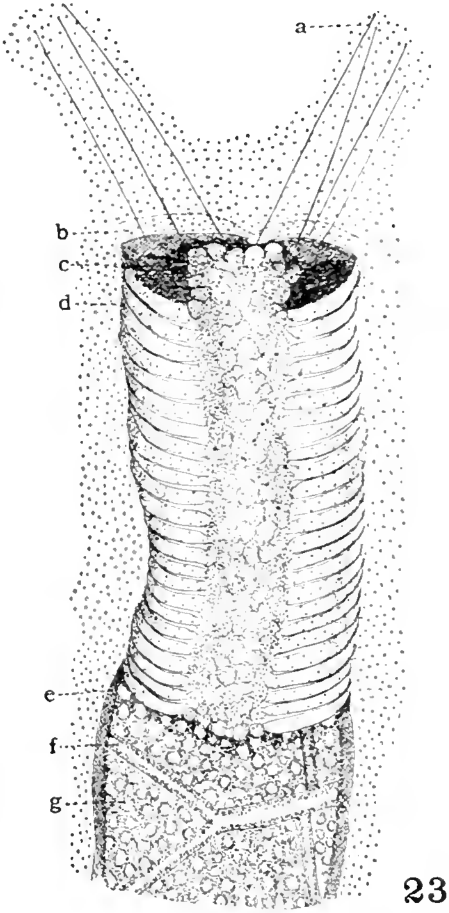

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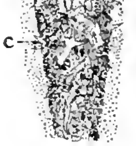

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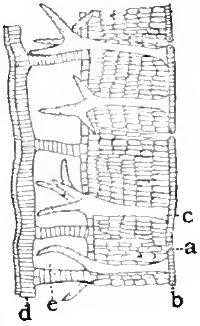

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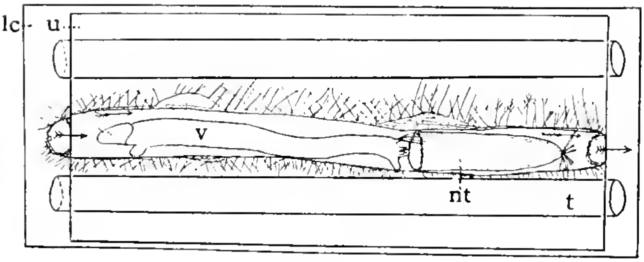

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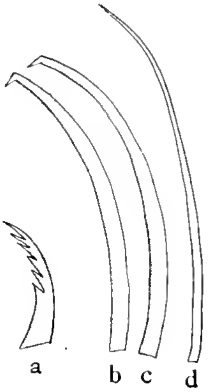

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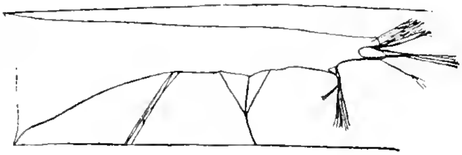

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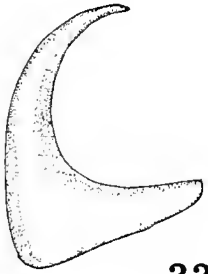

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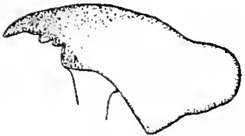

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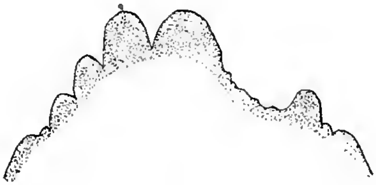

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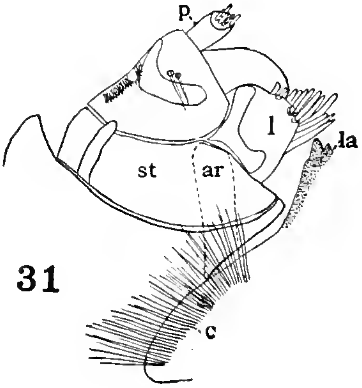

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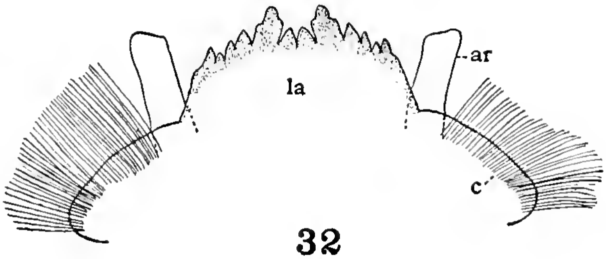

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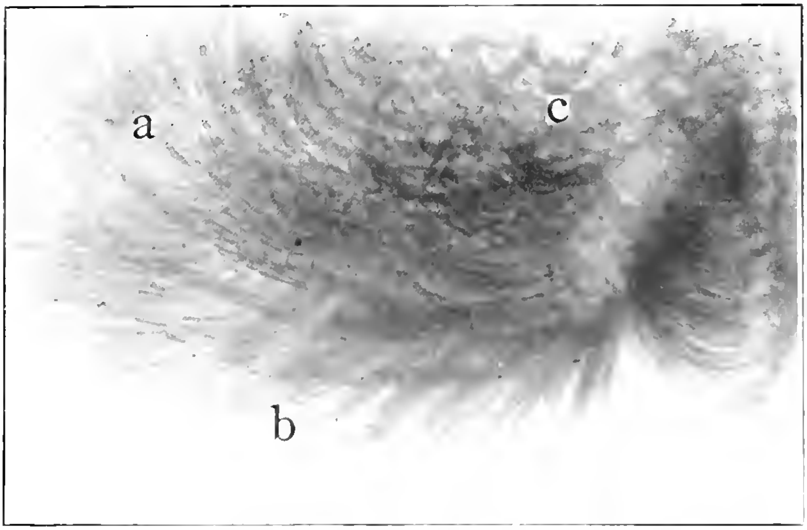

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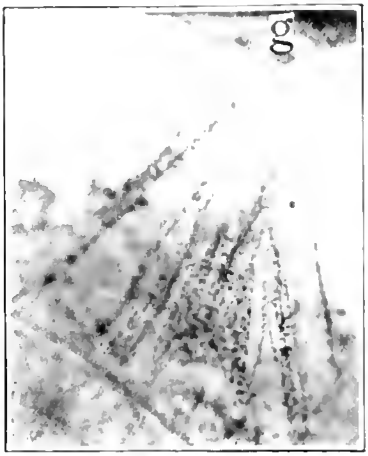

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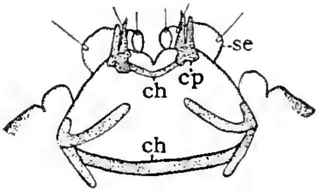

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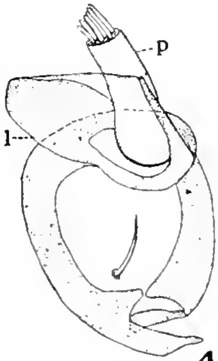

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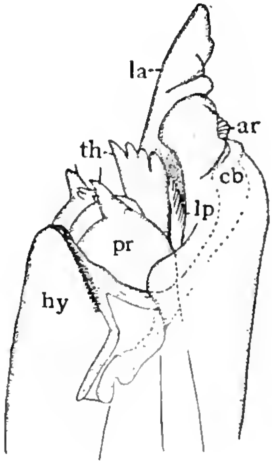

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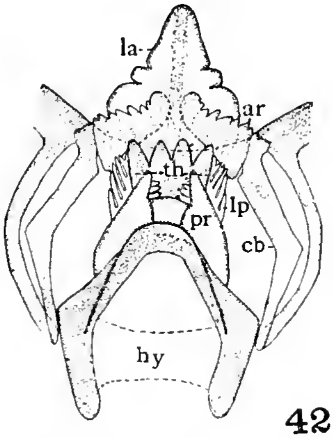

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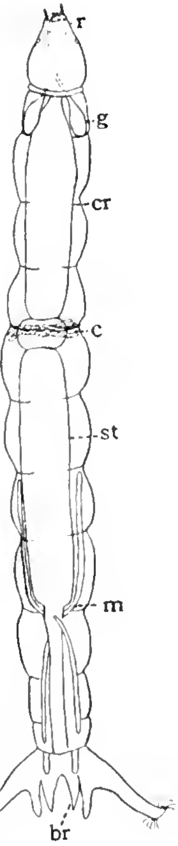

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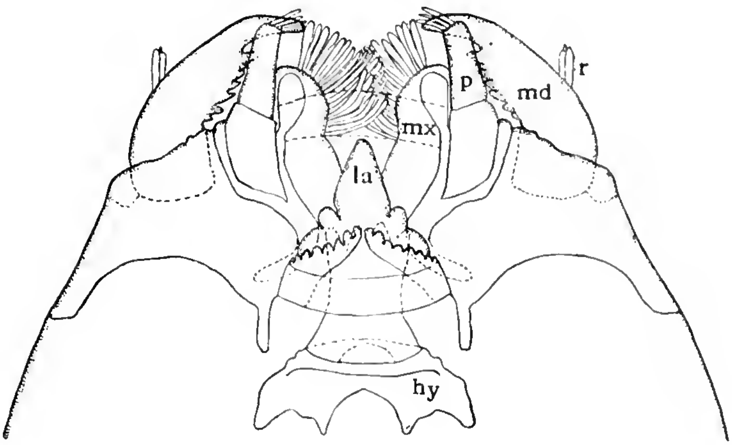

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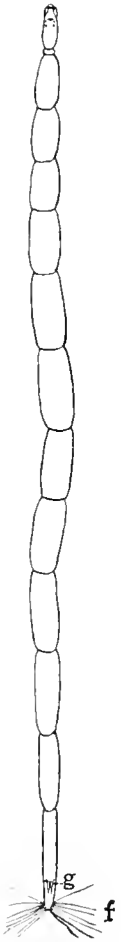

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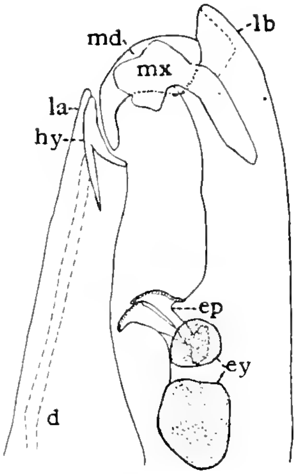

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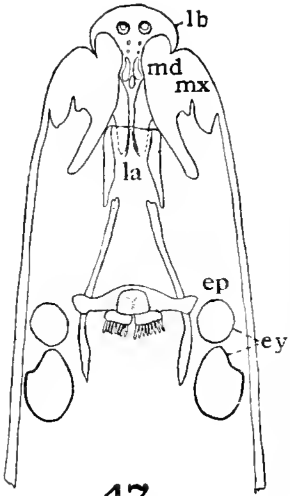

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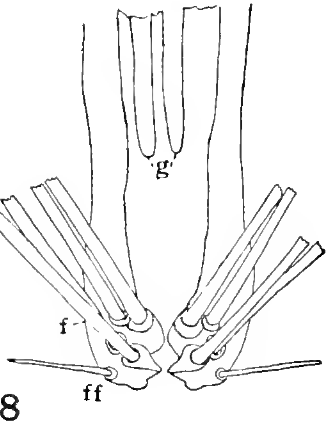

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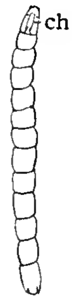

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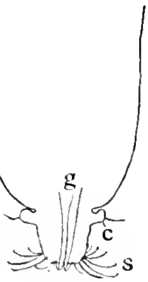

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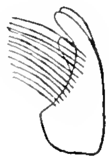

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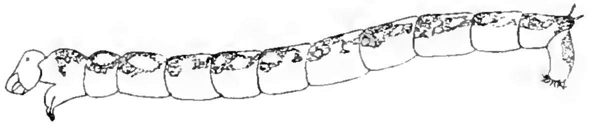

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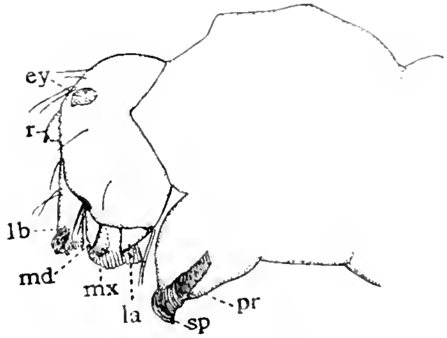

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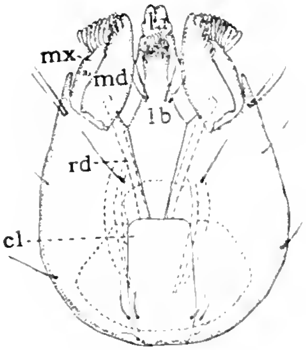

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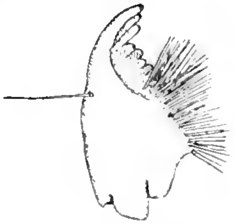

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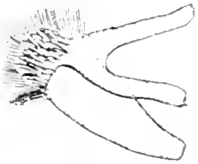

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EXPERIMENTS IN THE CULTURE OF FRESH-WATER MUSSELS.

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INTRODUCTION.

The coming of fresh-water mussels to a position of commercial importance in America resulted in a special demand for information as to methods of propagating them. In response to this demand the U. S. Bureau of Fisheries undertook an extensive investigation of the commercial fresh-water mussels. This led to the adoption of a method of propagation that promised effectively to increase the supply of mussels. This method, briefly, is the infection of suitable fish with the young mussels in the parasitic stage. These fish are then released to spread the mussels at large under natural conditions. The investigations have been continued for the purpose of extending the application of the methods now in use, the testing of new methods, and to secure more complete information on the life history of the mussels used in pearl-button manufacture.

Since Leydig's (1866) discovery that the young fresh-water mussels are parasitic on fish, many attempts have been made to raise them in captivity. No particular difficulty has been experienced in carrying certain species through the parasitic stage, but up until the time of the present investigation there seem to have been no records of the rearing of these under observation through what is called the juvenile stage.

In aquaria, either balanced or supplied with running water, they did not seem to thrive. Even in tanks out of doors supplied with water from their usual habitat the results were negative. The majority apparently at the very beginning of their free life were eaten by predacious forms, or, if by chance they escaped these enemies, they continued their existence dwarfed. Something in the environment was unfavorable to them.

Among European investigators who have attempted to rear young mussels are the following, with the results attained as to time carried under culture: F. Schmidt (1885), 4 weeks; C. Schierholz (1888), 4 to 5 weeks; W. Harms (1907), 7 weeks; and Karl Herbers (1913), about 2 months, or to a size of 3.13 millimeters.

In America we have the following records of artificially reared mussels. Lefevre and Curtis (1912) found a young mussel two years after a plant had been made in a tank. Similar results were attained at the U. S. Fisheries Biological Laboratory at Fairport, Iowa. In this case two mussels, *Lampsilis ventricosa* (Barnes), were obtained in a pond one year after a recorded plant had been made. In these two instances no observations of the mussels were made in the period between the planting and finding of the mussel at an advanced stage of development. A. F. Shira (report in MS.) reared the Lake Pepin mucket in a balanced aquarium to a size of 4.4 millimeters.

As a part of the general plan mentioned above, the experiments described in this paper were carried on to test the possibilities of artificial culture of mussels from the earliest stages up to the mature adult. The studies were carried on at the U. S. Fisheries Biological Laboratory at Fairport, Iowa, under the direction of Dr. R. E. Coker, in charge of the investigations upon the fresh-water mussels, and later under A. F. Shira, his successor. The author wishes to acknowledge here courtesies extended and assistance rendered in the conduct of these studies to the Crerar Library, of Chicago, for use of their excellent facilities; to Bryant Walker, Detroit, Mich., for assistance in determination of mussels; to Caroline Stringer, Omaha, Nebr., and Ruth Higley, Grandview, Iowa, for determination of Rhabdocœls; to Prof. Edwin Linton, Washington, Pa., for assistance in the determination of Turbellaria; and to Prof. F. B. Isley, Fayette, Mo., for suggestions of methods.

METHODS AND PLAN OF INVESTIGATION.

After some little experimental study of developing mussels it was realized that there must be some vital deficiency under artificial conditions to account for the many failures in attempts to raise mussels. It seemed that a promising line of attack in solution of the problem would be to find some way which would depart from the natural habitat only so far as the necessity of mechanical control demanded. To rear at least one brood of the young seemed to be an objective of prime importance. Success in this would answer some unsolved questions as to growth, as well as furnish a starting point for more artificial methods if these were desirable. In our situation, where we take the mussels from the Mississippi River, the most practicable solution that offered itself was a floating crate containing baskets made of wire cloth of sufficient size to hold the fish and of a mesh small enough to retain the miscroscopic mussels.

A crate held at the surface accommodates itself to the frequent rise and fall of the river, is convenient of access, and removes the young mussels from many of their enemies prevalent at the bottom. Another advantage of a surface location is the fact that the precipitation of silt there is at a minimum. The first crate used (fig. 74) was constructed

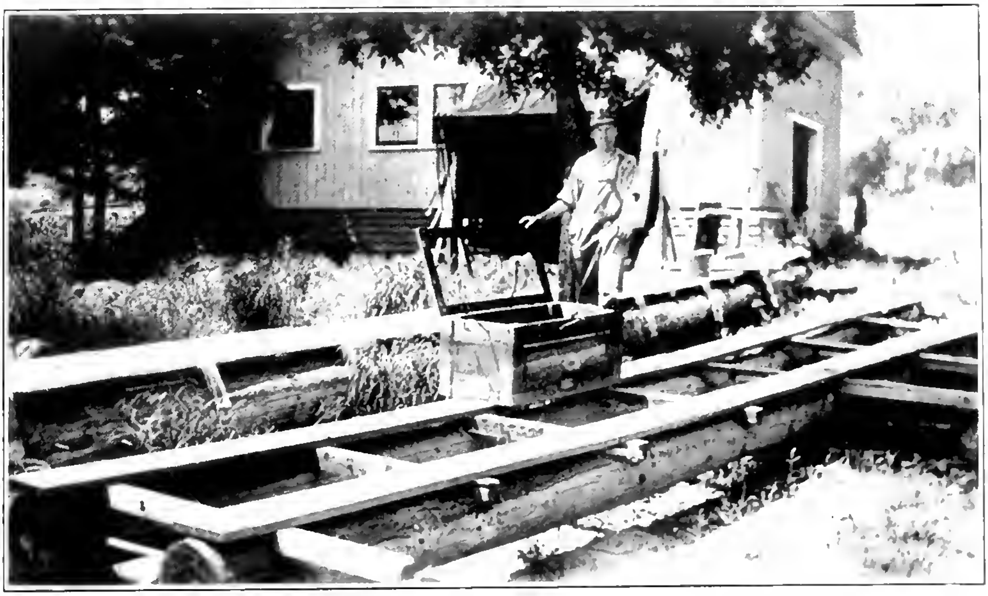

FIG. 58.—Improved float employed in experiments in mussel culture showing one of crates on "deck" opposite its berth.

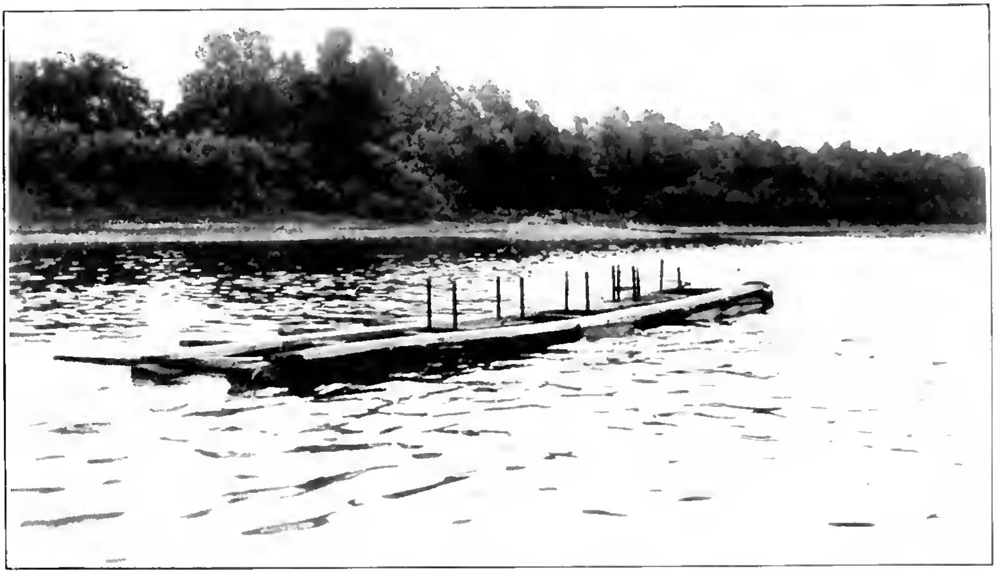

FIG. 59.—Same float as in fig. 58 anchored in the river showing three crates in position supported by adjustable iron hangers which are visible above the float.

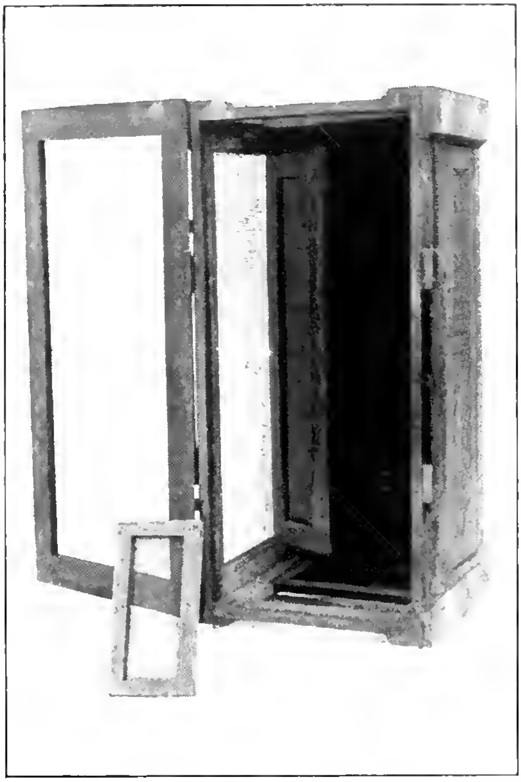

FIG. 60.—A crate of improved pattern showing outer screens of ¼ inch mesh and inner detachable screens of copper cloth, one of which is completely removed and the other turned in to show manner of insertion. Infected fish are held in the crates until the parasitic mussels are shed. The copper cloth prevents the escape of the mussels in the early minute stages.

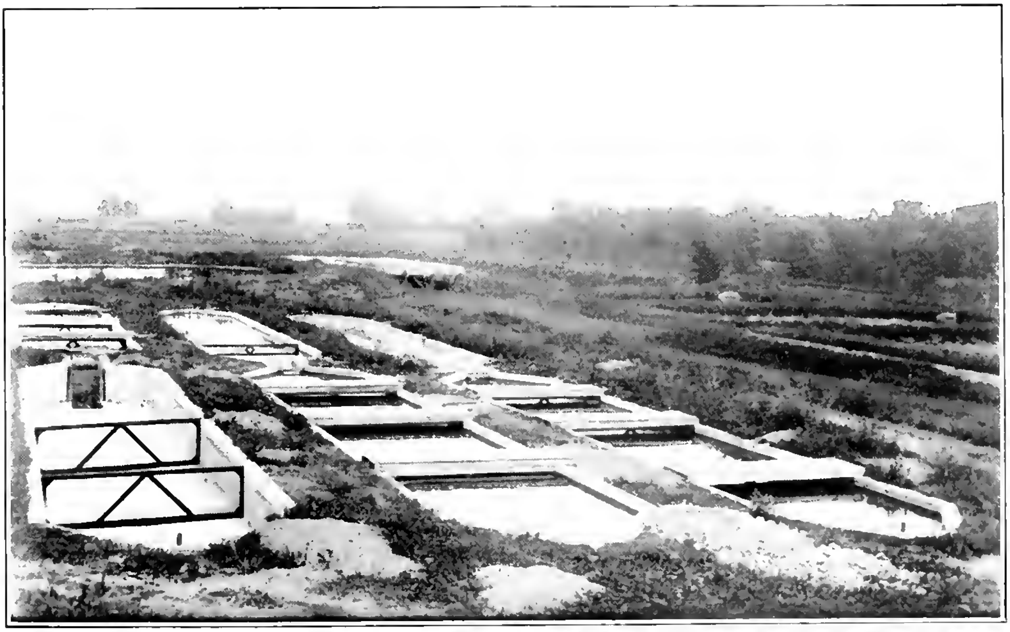

FIG. 61.—Concrete ponds used for mussel culture experiments. In the dry pond on the left is shown the method of dividing into smaller units by means of screens. Bridges are shown over the two ponds on the right. These furnish shade for the fish and prevent their jumping over the screens as well as serving the purpose of bridges for the operators when seining the fish. Earth ponds and shed-covered troughs appear in the background.

from a floating fish car to which were added barrels to give greater buoyancy. Four baskets (fig. 75) of rectangular shape, 1½ by 2¼ feet, were made to fit inside. These consisted of a framework of galvanized iron attached to a bottom tray of the same material, both of which were painted with two or three coats of asphaltum to prevent corrosion. On the frame was stretched copper cloth 100 meshes to the inch. In the baskets were placed the fish infected with mussels. In order to reduce the length of time necessary for retaining the fish in such narrow confines, they were not placed in the crate until a few days before the end of the parasitic period of the mussels and were removed as soon as the mussels were shed. Plants of the following species of mussels were made from time to time: The washboard, *Quadrula heros* (Say); the mucket, *Lampsilis ligamentina* (Lamarck); Lake Pepin or fat mucket, *L. luteola* (Lamarck); the yellow sand-shell, *L. anodontoides* (Lea); and the pimple-back, *Quadrula pustulosa* (Lea).

Modifications of the floating crates were introduced from time to time with a view to improvement of conditions for both fish and mussels and economy of operation. The latest form of float (figs. 58 and 59) adopted is made from two cedar telegraph poles held apart by crossbeams, 4 by 4 inches, at a distance sufficient to suspend lengthwise seven crates having dimensions 3½ by 1½ by 1½ feet. The crossbeams are placed at 4-foot intervals, and to them are bolted strap-iron hangers by means of which the crates are suspended. On the crossbeams over the telegraph poles are nailed 2-inch planks, 10 inches wide, forming a walk on each side the full length of the float. From this walk two operators can conveniently raise the crates in which the infected fish are placed. A float of this form was devised to protect the crates from wave wash and to give greater stability in stormy weather, when a shorter and smaller float would be tossed about.

The crates or baskets (fig. 60) in the improved type are constructed of cypress lumber, being made as light as the demand for strength permits. The bottom or floor is made of matched lumber and tight enough to prevent the escape of the microscopic mussels. The superstructure consists of a framework, on the outside of which is nailed galvanized screen of one-fourth-inch mesh. Fitted inside of the frame and outer screen are the inner screens, which consist of wooden frames to which copper cloth is fastened with copper tacks. The inner screens are removable, held in place by buttons or other locking devices. The removable screens are so provided with overlapping strips as to give a joint sufficiently tight to prevent escape of the small mussels. In the use of removable wire screens the following objects were in view: It facilitated the cleaning of the copper cloth and provided an opportunity to enlarge the mesh of the screens as the mussels increased in size, thus giving them a freer flow of water and economizing the higher-priced fine-meshed copper cloth. The use of wood instead of metal as employed in the first baskets provided distinct and obvious advantages. Metal was objectionable wherever the young mussels might come in contact with it, was less durable, and was more expensive. Metal cloth could not be dispensed with entirely, because other fabrics will not last under water. The increase in size of the crates or baskets was of marked advantage in providing more room for the fish, thus permitting use of greater numbers with less mortality.

The whole assembly of float and crates provided a convenient and economical means of operation greatly improved over the first crates, in which the raising of the much smaller baskets was necessarily done from boats and in comparison was awkward and difficult. The improved float because of its form is more readily towed and handled in the current than the very much smaller floats first constructed and may be easily drawn out of the river by a team of horses when necessary, as for winter quarters.

Other methods were employed in the investigation and, in a way, carried parallel for comparison to test the possibilities of the equipment already installed at the biological laboratory at Fairport. These were aquaria and indoor tanks and troughs, cement ponds, and earth ponds. Each of these was supplied with running water except in the case of special experiments with balanced aquaria. The water for the most part was taken from a reservoir receiving its supply by pump from the Mississippi River. Thus the water was, as a rule, practically unmodified. In some experiments with balanced aquaria filtered river water was used in order to eliminate the predacious animals which prey on the early stages of the mussels. For the same purpose, as well as to reduce the amount of sedimentation in river water, specially devised settling tanks were employed for supplying aquaria.

The cement ponds (fig. 61) were of reinforced concrete 50 feet long, 10 feet wide, and averaging 2¼ feet deep, having perpendicular sides and constructed for the temporary retention of fish. An accumulation of mud and a specially prepared bottom of gravel, together with an abundance of water plants, furnished conditions which proved suitable for some of the most delicate species of fish. It was assumed that these conditions were as suitable to the needs of the mussels as they could be made under the circumstances.

The earth ponds were from 41 to 61 feet long and 24 feet wide, varying in depth from 4 inches at the intake pipe to 4 feet at the well. An abundance of water plants furnished food and shade for the fish. The cement and earth ponds as compared with the floating crate do not so readily furnish the means for frequent observations of early stages. In using them it was planned to test their possibilities of rearing clams by a comparison of older juveniles grown in them. Thus the probable disadvantage of frequent disturbance necessary in making observations on younger juveniles would be avoided.

Plants of young mussels were made from infected fish in each of the culture devices mentioned. A modification of the cement pond was used in one instance for the purpose of securing a current comparable in rapidity to that to which the river mussels are accustomed. A flow of 50 gallons per minute was supplied to a trough 16 inches wide by 12 inches deep by 50 feet long, giving a current of 0.1 mile per hour. This is by no means equivalent to the 2 to 3 miles per hour of the Mississippi, but was planned to imitate the conditions of the river more closely than that of the ponds in which the flow is inappreciable.

OBSERVATIONS ON GROWTH OF JUVENILE MUSSELS.

In this investigation studies upon growth have been made with a view to securing data upon general conditions as well as upon the more specific methods of rearing under artificial environments. The species tested were chiefly heavy-shelled river mussels, which include most of those that are considered of commercial value, as distinguished from the thin-shelled pond-dwelling forms. The latter apparently offer no particular difficulties. The most complete results were obtained from a species which selects a habitat somewhat intermediate between these extremes, in that it dwells in lakes and

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Lake Pepin mucket, *Lampsilis luteola* (Lamarck), at various stages from young to adult.

FIGS. 62 and 63.—An adult gravid female, age about three years. Natural size. The right shell (fig. 63) has been removed to expose the viscera. At *m* is shown the marsupium in which the young are carried from the egg to the glochidial stage. Mussels grown under control in the experiments here described equaled this one in size at the age of first breeding, two years and three months.

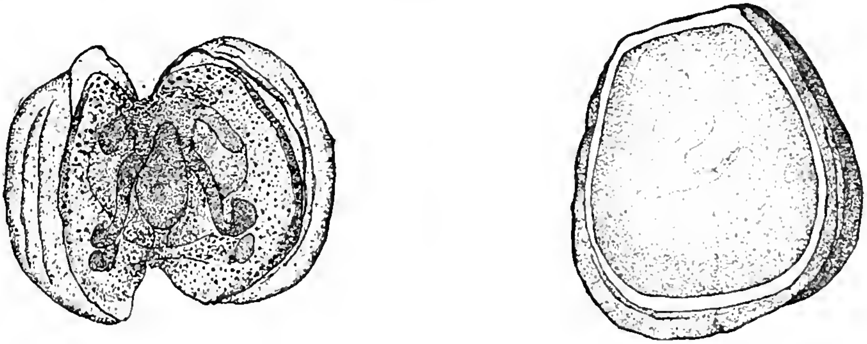
FIG. 64.—Glochidia or parasitic stage in the young as they appear on leaving the parent mussel. One with valves open may be seen at the middle left margin of the field. Photomicrograph, × 27.

FIG. 65.—Gill filaments of a black bass infected with the glochidia of *Lampsilis luteola* 14 days after infection. Photomicrograph, × 27.

FIG. 66.—Left to right: Young mussels of one, two, three, four, five and one-half months of age, respectively. Natural size.

the quieter waters of rivers. This was the Lake Pepin mucket, *Lampsilis luteola* (Lamarck). In this mussel a surprising amount of growth took place during one season. The other species fared less well, in some cases apparently surviving only a short period. Since satisfactory positive results were attained with *L. luteola*, the experiments with this species furnished a basis for comparison of the methods in reference to their influence on growth. As the results with this species may have been largely due to inherent qualities, a short account of its natural history and development seems desirable.

The Lake Pepin or fat mucket, as it is generally called, has a shell of excellent quality and possesses a good reputation as a pearl producer. It is probably the most widely distributed of the fresh-water mussels used commercially. Simpson (1900) gives its distribution as follows: Entire Mississippi drainage southwest to the Brazos River, Tex.; St. Lawrence drainage; entire Dominion of Canada east of the Rocky Mountains. The author has found it under the most varied conditions—from those of the marshy slough of a small creek to the deep waters and wave-beaten beaches of the Great Lakes. These observations would indicate that the form is adaptable to widely varying environment and would, perhaps, explain its thriving condition in this experiment where other species fared less well.



67 **68**

FIGS. 67 and 68.—A young mussel one to three days after leaving the fish, in outward form like the original glochidium but internally (that is, inside the shell) showing organs developed. Drawn with a camera lucida. × 140. 67.—Ventral view with valves apart, from specimens stained and cleared. 68.—Side view; a narrow growth of the new definitive shell may be seen bordering the glochidial shell.

This species belongs to the bradytictic group called winter breeders. The glochidia are produced in the late summer or fall and are carried through the winter in the distended marsupial gills (see fig. 62) of the female. The glochidia (fig. 64) are favorable for infection, because their comparatively large size makes it easy to follow the progress of infection (fig. 65) and subsequent shedding. Unfortunately, the number of glochidia produced is relatively small.

The gravid mussels for this experiment were obtained in Lake Pepin, Minn., about May 15, 1914, and shipped to Fairport, Iowa, by express. On May 21 ripe glochidia were taken from three of the live mussels for the experiment. Some dozen different species of fish were infected and of these, six proved susceptible and carried the young mussels through their metamorphosis. Before the young mussels began to be shed eight infected largemouth black bass were placed in basket No. 2 of the floating crate. Some very rough weather followed, tossing the crate about in such a way as to make the conditions severe for the fish and killing five of the eight. On June 10, 20 days from the date of infection, most of the young mussels were found to have been shed from the three remaining fish. On the same date shedding was found to have taken place from infected fish placed in the cement ponds and aquaria. The time of shedding for the earth ponds was not observed.

The young mussels were secured at this early stage from the aquaria. At the time of shedding there is apparently no growth of shell beyond that of the original glochidium, but the young mussel (see fig. 67) internally has for the most part the organs of the adult in contrast with the simple structure of the larval glochidium. Growth of the shell begins at once (see figs. 67 and 68), as shown, and in the figure a narrow border of the new shell is already visible.

GROWTH IN FLOATING CRATES.

Two weeks after obtaining the plant of young mussels from the bass, evidence that they were thriving in the crate was obtained. A small sample of sediment from the bottom revealed some half dozen or more. These had already a considerable growth of shell, the largest having an increase in surface of at least three times the size of the original glochidium (see fig. 69).

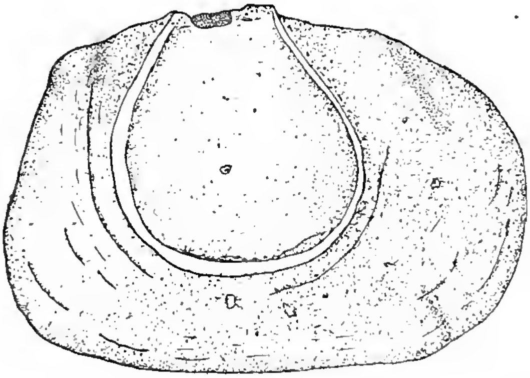


FIG. 69.—A juvenile mussel 15 days after the beginning of free-living stage, or about two weeks older than that of figure 68. View of right side. Drawn with a camera lucida. × 140.

At various intervals throughout the summer and autumn the author readily obtained specimens, making observations on rate of growth and preparing material for studies of development. Figure 66 shows individuals illustrating the amount of growth from month to month. The last examination was made about November 20, when the whole plant in the basket (fig. 75) was photographed under water. Later they were removed from the mud, a census was taken, and more photographs were made (fig. 70). After completing such observations as were feasible upon the whole plant of living mussels they were returned to a crate and placed in a pond to spend the winter.

The series shown in figure 66 represents about the average[1] growth from month to month. These, with the exception of the third, were removed from the basket on the dates given in Table 1, page 69. By inspection it is obvious that the rate of increase in growth as represented by these is not uniform throughout. This is due partly to the fact that in some cases small numbers only were removed at a time. In this way the average size was not secured in each instance. In one case only was a voluntary selection possible, and this was the last, made from several of nearly equal size. The specimen in the series for the second month (fig. 66, second from left) was probably smaller than the average. It will be noted that by months the increase is much more rapid at first, so that the rate is a decreasing one.

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[1] These were selected at random in most cases and so probably approximate the average.

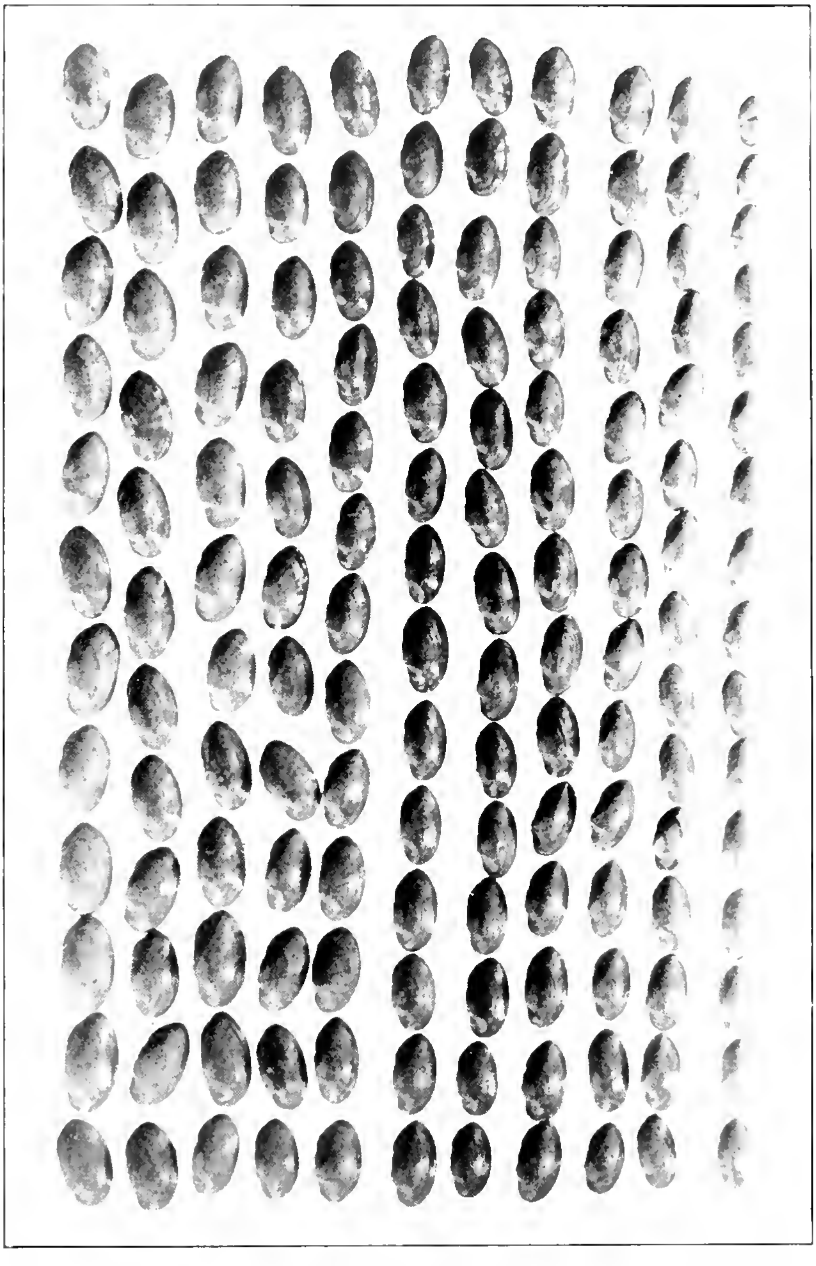

FIG. 70.—The contents of one propagation basket at the end of a season's growth of five and one-half months. The mussels were of microscopic size when shed in the basket by the fish. The arrangement in series shows the amount of variation at this age under the prevailing conditions. Reduced to five-twelfths natural size.

TABLE 1.—INCREASE IN LENGTH OF JUVENILE MUSSELS IN A FLOATING CRATE DURING THE GROWING SEASON OF THE FIRST YEAR, 1914.[1]

Date collected.	Length.	Increase in length.		Date collected.	Length.	Increase in length.	
	Mm.	*Mm.*	*Per cent.*		*Mm.*	*Mm.*	*Per cent.*
June 10	0.25			Sept. 12	22.3	9.3	71.5
July 18	4.2	3.95	1,580.0	Oct. 10	27.2	4.9	21.9
Aug. 17	13	8.8	209.5	Nov. 24	32	4.8	17.6

[1] The mussels measured were taken at random, with the exception of the last one, which was selected as the maximum.

The length of 32 millimeters at the close of the season (1914) is one hundred and twenty-eight times that of the original juvenile at the beginning of free life. This certainly compares favorably with the total length of 3 millimeters reported by Herbers (1913), which was the largest in his culture of juveniles, while the mussels in the experiment of which this paper treats were still alive and vigorous at the end of the season. Figure 70 is a photograph of the contents of a basket at the end of the season reduced to five-twelfths natural size. The mussels range in size from 32 to 15.5 millimeters. The variation is considerable, but it should be noted that less than 27 per cent are under three-fourths of the maximum size. The last mussel in the series, and one of the smallest, is deformed, probably restricted in growth by lodging in a crevice. Two more small mussels were found when the mud was passed through a sieve. Of these one measured 14.1 millimeters and the other the remarkably small size of 6.9 millimeters. The latter was living at the time of removal from the river. These few cases of dwarfing are doubtless due to lodgment in unfavorable locations—under crowded conditions—in the basket.

During the last month, from October 20 to November 20, a record of growth was taken to determine to what extent growth takes place as the water temperatures fall. Measurements of 10 mussels from the basket were taken. After marking and measuring each they were returned to the crate. The results are presented in Table 2, following which are given the water temperature averages, maximum, minimum, and range for the period. It will be seen that the growth for the period was very slight.

TABLE 2.—INCREASE IN LENGTH OF JUVENILE MUSSELS IN A FLOATING CRATE DURING THE LAST MONTH OF THE GROWING SEASON, 1914.

Specimen number.	Length.		Increase in length.	Specimen number.	Length.		Increase in length.
	Oct. 20.	Nov. 20.			Oct. 20.	Nov. 20.	
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
1	23.3	23.4	0.1	7	25.4	25.8	0.4
2	24.0	24.2	.2	8	23.3	23.6	.3
3	24.2	24.5	.3	9	29.4	29.7	.3
4	25.2	25.5	.3	10	23.5	24.0	.5
5	21.3	21.3	.0				
6	29.0	29.0	0	Average			.24

WATER TEMPERATURE FOR PERIOD OF MEASURED GROWTH.

	°F.
Average:	
For 11 days, Oct. 20 to 31	54.9
For 10 days, Nov. 1 to 10	50.9
For 10 days, Nov. 11 to 20	43.2
For whole period, Oct. 20 to Nov. 20	49.2
Maximum for whole period, Oct. 20 to Nov. 20	60
Minimum for whole period, Oct. 20 to Nov. 20	32
Range for whole period, Oct. 20 to Nov. 20	28

On consulting the temperature averages the assumption is natural that such growth as occurred took place before the temperature fell.

It is obvious that for the whole period (Oct. 20 to Nov. 20) growth was much less than in the warmer months. Compare the maximum of 0.5 millimeter for the period with the growth of 4.9 millimeters shown in Table 1 (p. 69) for the period from September 12 to October 10. The desire to secure these records resulted in the postponement of the date for removal from the river until a time dangerously late. On the night of November 19 ice floes bore down on the crate. Only by the rarest good fortune was the whole plant saved. The ice instead of destroying the crate or carrying it away landed it on shore, where the mussels were extricated without injury. A count of mussels grown in the basket follows:

Alive in basket Nov. 20	172
Dead in basket Nov. 20	6
Removed from basket June 25 to Oct. 30	45
Total living for season	217

As the original plant from the three surviving bass was an estimated 2,400 juveniles, it would give a survival of something better than 8⅓ per cent. The mortality would be indicated by the difference in the figures of the original plant and the final crop.

Observations upon growth were continued during the second and third summers. The results of measurements taken from month to month on marked mussels are indicated in Table 3. In figure 71 is plotted the increase of growth per month for 18 months, with the graph of the average water temperature. The data are taken from observations on mussel No. 3 in Table 3, as the record for this mussel is the most complete. Absence of growth from November to the middle of April, though not shown in the table, was observed and is supplied in the graph. Lack of observation for May, 1915, is supplied from another brood of the same age giving an approximation to the true figure sufficiently close for our purpose. This would give the following increases in millimeters for each month: May, 1.7; June, 6.1; July, 9.1; August, 7.1; September, 3.9; October, 1.5; May (1916), 1.9. The growing season seems obviously to be correlated with the rising temperature of summer. In a general way, doubtless, it is dependent upon the phytoplankton, and the plankton is controlled to a large degree by the temperature (Kofoid, 1903, p. 572, par. 18).

TABLE 3.—GROWTH OF MUSSELS IN A FLOATING CRATE IN THE SECOND AND THIRD YEARS.

Specimen.			Length in millimeters.										Weight in grams, Oct. 6, 1916.
Number.	Sex.	Mark.	Apr. 19, 1915.	June 10, 1915.	June 22, 1915.	July 22, 1915.	Aug. 21, 1915.	Sept. 25, 1915.	Oct. 26, 1915.	May 31, 1916.	Aug. 15, 1916.	Oct. 6, 1916.	
1	....	I	31.6	....	....	....	....	....	....	....	....	....	....
2	Female	II	30.6	....	36.9	48.5	53.9	57.5	53.8	....	72.0	[1] 71.8	53.5
3	Female	III	27.5	35.3	35.3	44.4	51.5	55.4	56.9	58.8	....	74.6	67.0
4	Male	IV	21.7	....	29.3	39.6	46.9	51.8	52.7	55.5	....	74.9	49.6
5	Female	V	25.1	....	....	47.0	52.4	57.4	....	59.6	....	73.0	57.8
6	....	VI	29.5	....	....	....	....	....	....	....	....	....	....
7	Male	VII	26.4	33.4	....	....	51.5	55.7	55.9	58.2	....	78.8	56.5
8	Female	VIII	21.1	27.7	29.1	....	43.4	....	....	51.6	....	69.6	57.6
9	Female	IX	24.1	30.7	....	41.9	47.2	....	51.1	52.7	....	65.0	44.6
10	Male	X	26.0	....	....	....	51.4	55.8	....	58.6	....	80.0	61.6

[1] No growth indicated here. Decrease perhaps due to breaking of periostracum.

The second summer yielded one individual measuring 62.8 millimeters (2.47 inches) in length, the maximum, and many over 55 millimeters (2.16 inches) in length. From one of these were cut 16-line buttons 2 lines thick (see fig. 72). Although this is not a favorable size for cutting, the fact that the shell in two seasons' growth is almost suitable for commercial use is of significance and far exceeds expectation.

Growth during the third summer, when the adult stage was attained, determined by the first breeding, reached a maximum length of 85 millimeters, weight 63.1 grams, in the male, and a length of 77 millimeters, weight 66.5 grams, in the female (gravid). Length, average male 79.1 millimeters, average female 71.5 millimeters. The growths of the 1915 brood during their second summer compared with that of the 1914 brood for their second summer show a very striking difference. Although the 1915 brood began the second summer very much smaller, averaging 11.6 millimeters in length, compared with 25.7 millimeters for the 1914 brood, at the end of the season the former had increased 475 per cent while the latter had gained only 212 per cent.[2] This disparity in growth brought the brood of 1915 to a size—their second year—equal to that of the 1914 brood at the end of their second year in the face of a large handicap.

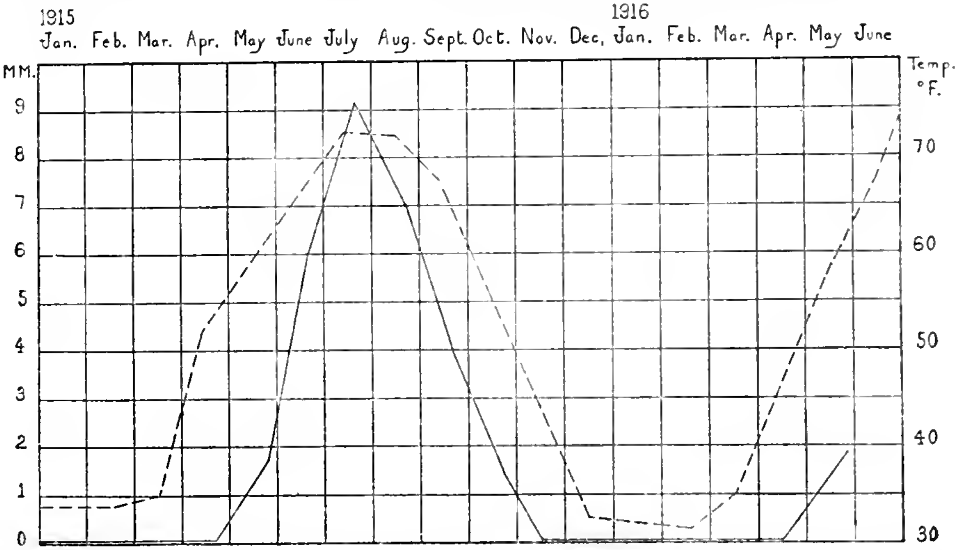

FIG. 71.—Growth of a fresh-water mussel in relation to temperature: — — —, mean monthly water temperature (F.) in the Mississippi River at Fairport, Iowa; ———, monthly increase in growth of a fresh-water mussel in its second year, in millimeters. Zero represents the line of no growth and the coordinates represent the increase for each month taken separately. (See p. 70.)

This difference may be ascribed to difference in season which is, perhaps, the simplest explanation. The summer of 1916 had higher water temperature, higher water stages, and less wind than usual. Flood stages, generally speaking, have been found unfavorable to plankton production as determined by Kofoid in the Illinois River (Kofoid, 1903). The rapid growth this season occurred on falling stages but at an unusually sustained high level. As this high level was not due to local precipitation, it would seem that the conditions were consistent with (an assumed) high plankton production at the point of observation. The absence of wind as an important cause of turbidity would be favorable to the feeding of mussels.

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[2] The small size of the 1915 brood was due to a late planting and partly, doubtless, to a less favorable growing season.

Another explanation of this difference is the possibility of the existence of an inherent controlling factor in growth, whereby an average growth may be obtained by the end of the second year. That is, in the case of a small first year's growth there would be compensative additional growth the second year. This phenomenon is not of uncommon occurrence in organisms. Barney (1922) in studies of growth in terrapins finds "runts" selected in 1913 in 1917 exceeding in growth larger selected individuals of 1913.

A plant of yellow sand-shell, *Lampsilis anodontoides* (Lea), was not as successful in numbers, but yielded three juveniles which survived the summer, and the largest attained a size of 8.3 millimeters in 6 months. The second summer it attained a length of 41 millimeters and a weight of 5.8 grams.[3]

GROWTH IN AQUARIA, TANKS, AND TROUGHS.

A plant of juveniles from two bass, *Micropterus salmoides*, and one calico bass, *Pomoxis sparoides*, was obtained in a rectangular glass aquarium. The young were readily found within a day or two after their escape from the fish, but later than this only shells of the earliest stages could be found. It is possible that the absence of growth in this instance was due to the destruction of the young mussels by enemies to be mentioned later.

Another test of the possibilities of aquaria was made by placing in them rapidly growing mussels taken from the floating crate at a more advanced stage and comparing their growth with the growth of mussels remaining in the crate. The growth in millimeters and the increase is shown in Table 4. While in the aquarium the same individuals were measured each time, the measurements of growth in the crate were not based upon particular mussels, but upon different examples taken as representative of the lot. Observations were made in this way, because the recovery of marked mussels in the crate entailed danger of too much disturbance to the whole plant.

TABLE 4.—COMPARATIVE GROWTHS OF JUVENILE MUSSELS IN AQUARIUM AND IN FLOATING CRATE.

Place of growth.	Length in millimeters.		Increase in millimeters Aug. 17.	Place of growth.	Length in millimeters.		Increase in millimeters Aug. 17.
	July 27.	Aug. 17.			July 27.	Aug. 16.	
Aquarium	6	7	1	Floating crate	(6)	13	7
	5.5	Lost.	....		(5.5)	12.8	7.3
	3	4.2	1.2		(3)	10.1	7.1

The figures, although only approximate, are sufficiently accurate to represent fairly the great difference in growth that has been shown in many experiments in other ways. The total growth from the beginning of the juvenile stage, June 10 to August 17, is 7 millimeters for the largest of three mussels placed in the aquarium for three weeks, while it is 10.1 for the smallest of three taken from the crate on the same date. This gives a difference of 3.1 millimeters where the influence of the aquarium is exerted only for the relatively short period of three weeks.

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[3] Attention is called to the employment of the garpikes, *Lepisosteus osseus* (L.) and *L. platostomus* Raf., as hosts for the mussels in this experiment. These are the only fish found of many tested which will carry the glochidia of this mussel (Howard, 1914b).

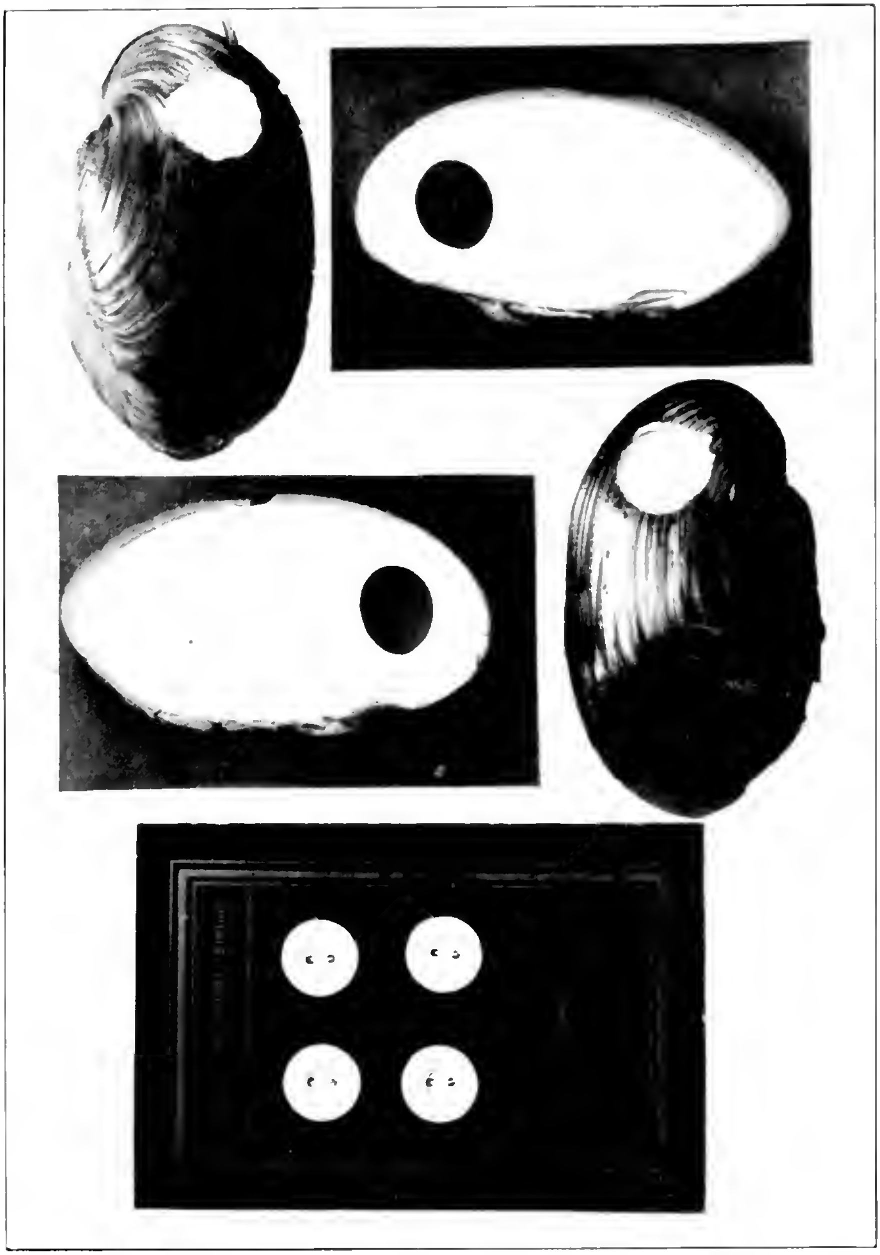

Fig. 72.—Mussels at the age of one year and four months, and buttons cut from them. These mussels were the product of artificial infection and rearing by the crate method. Photographed by J. B. Southall.

Young mussels of various sizes from one-half inch up placed in tanks and aquaria indoors at various times have shown a negligible amount of growth. Likewise, negative results have been secured in plants of young mussels made in the following types of aquaria indoors supplied with flowing river water which was unmodified so far as known: Wooden tanks or troughs, tanks and troughs lined with galvanized iron painted and unpainted, and cement tanks and troughs. Two systems of water supply have been tried. In one the river water was pumped direct, in the other it was pumped first into a reservoir, from which it was distributed by gravity flow. Later results seemed to indicate a difference to be discussed below under cement ponds.

In order to eliminate the destructive turbellarians and other predacious forms that might be introduced with the water, balanced aquaria, large and small, filled with filtered river water were tried. Here, too, the mussels survived for only a short time.

More recent experiments in rearing young mussels in a type of container of comparatively small dimensions have been conducted with considerable success, first by F. H. Reuling (1920) at Fairport and later by the author and others. The conditions were so different from those of the experiments just described that they should throw light on controlling factors in the development of juveniles. Their convenient size made them admirably suited for experimental purposes where a considerable number of units are required. The equipment consisted of galvanized-iron troughs 14 by 8 inches by 8 feet, painted with asphaltum. The troughs were protected from the sun by a shed roof of wood; otherwise they were uninclosed. (See center background of fig. 61.)

The water supply was derived from the surface of a pond containing vegetation. This arrangement yielded water of comparative clarity even when the river supplying the pond was turbid. The point of intake at the surface probably insured a minimum of animal enemies, such as Turbellaria, which might prey on the mussels. Additional precautions were taken against enemies by further straining through ordinary cloth and later close-meshed metal fabric.

Broods of *Lampsilis luteola* and some one-half dozen *L. ligamentina*, the river mucket, were reared in these troughs the first summer. In 1919 successful results were secured with three species approximately as follows: Yellow sand shells, *L. anodontoides*, 2,000; Lake Pepin mucket, *L. luteola*, 3,000; the river mucket, *L. ligamentina*, 500.

The dwarfing effect observed in aquaria and tanks indoors is a condition the causes of which have not been entirely determined. There is reason to suppose that reduced light and excessive precipitation of silt are possible factors, assuming that the water supply is the same as that of the river, ponds, or out-of-door troughs. Any such assumption is unwarranted, however, until comparative determinations of water conditions and contents have been made. Lack of growth suggests that the plankton, supposedly the principal food of the mussels, or other elements are for some reason wanting. The following evidence indicates the nature of some of these constituents which conceivably may be lost in part from water standing in reservoirs.

Detritus, including dead organic matter, forms a considerable proportion of the food of mussels, according to A. F. Shira and Franz Schrader. (Coker, Shira, Clark, and Howard, 1921, pp. 88 and 93.) Wilson and Clark (1912), in the examination of the stomach contents of river mussels, find a proportionally small amount of plankton combined with what is apparently a larger quantity of nonliving organic and inorganic material appearing like the mud in which the mussels are embedded when in their natural habitat. Mussels are supposed by some to act as scavengers in consuming sewage. The evidence indicates, however, that, as a rule, they flourish better in waters of natural purity. (Linnville and Kelly, 1906.) It seems not unlikely that mussels may derive considerable nutriment from substances in solution. Churchill's (1915) experiments on the absorption of fat by mussels seem to support such a view.

Consideration of the finely balanced conditions found necessary for the welfare of other lamellibranchs, including marine clams, to the growth of which considerable study has been given, removes any wonder at negative results with fresh-water mussels that have been subjected to highly artificial environments of aquaria and tanks. Complete success in the use of aquaria and such more or less artificial containers can hardly be expected until the factors of growth and their control are more thoroughly understood.

GROWTH IN CEMENT-LINED PONDS.

The cement ponds (see p. 66 and fig. 61), because of their location, size, and shape, were found very convenient in the experimental work for temporary holding of fish. The perpendicular sides permitted of ready subdivision by screens and easy control of fish, such as removal, transfer, etc. For the planting and culture of juvenile mussels, however, their usefulness is still somewhat a question. Many unsuccessful trials led to the assumption that the cement bottom and sides presented an environment unnatural and unsuited to the life of the mussel; but later results seemed to indicate that by proper control of conditions in them fair results might be obtained.

Variations in bottom were tested, together with changes in depth and flow of water, in order to take into account the special needs of given species so far as known. The kinds of bottom employed were gravel, sand, mud or loam, and the uncovered cement. The gravel, sand, or loam were evenly distributed 1 to 3 inches deep over the cement. In addition to this a greater or less deposit of silt always accumulated from the water, the maximum precipitation occurring at the end where the supply pipe entered.

The plants of juveniles were made from their fish hosts with the following species of mussels: *Lampsilis luteola*, *L. ligamentina*, *Quadrula plicata*, and *Q. pustulosa*. After one plant of *L. luteola* on mud bottom at the end of the growing season in November, 1914, an examination was made to determine the results as to growth. The whole bottom contents of the pond were passed through a sieve of 3-millimeter mesh. Two mussels only were present out of a plant of several thousand. These measured only 11.4 and 15.3 millimeters, respectively, and the appearance of their shells gave evidence of unfavorable conditions. Many tests with the different species were made on a bottom of sand or mud.

Another variation tried was the narrow cement pond in which large plants of the pimple-back mussel, *Quadrula pustulosa*, were made. In these ponds, as has been described (p. 66), a current of water over gravel and sand was kept up during the growing season. There was no opportunity for fish to disturb them, as the host fish (channel cat, *Ictalurus punctatus*) were removed as soon as the mussels had been shed from their gills.

Absolutely negative results were obtained from these experiments, as no trace of mussels could be found in screenings from a series of sieves in which the minimum mesh was 2 millimeters. (There is no doubt that the presence of any mussels approaching normal growth of two seasons would have been revealed by this search.) In these ponds normal aeration of the water and sunlight were more certainly provided for than in tanks and aquaria indoors.

In contrast with these results, largely negative, was a plant of *Quadrula pustulosa*, in which the outcome was more satisfactory. In one pond, in its first year used—i. e., the first year the cement was submerged (1913)—infected fish were placed in the lowest division—i. e., nearest the outlet and farthest away from the inlet pipe. This division was reserved for channel catfish for the purpose of simplifying the history of this section in case any results were obtained. The pond as a whole was employed as a stock pond. A continuous supply of water was kept up summer and winter with a view to giving any mussels that might be obtained opportunity to reach a size that could readily be found.

During four years the water was drawn down only a few times. On these occasions the lowering of the water was not allowed to an extent that would be injurious to any mussels that might have started. Only a cursory examination was made for mussels that might have reached a size to be readily detected. Purposely the treatment of this pond was varied from that accorded to the other ponds which, one or two years after plants had been made, were subjected to close inspection by sieving of the bottom soil. Had the same regimen been followed in this case the young mussels would certainly have been found even the first year, and it was an odd chance that the mussels prospered in this one pond where the "let-alone policy" was carried out. As this policy was different from that accorded to all ponds only in respect to the second to fourth years of growth it had no particular bearing upon the question as to how a set was obtained the first year. In seeking an answer to this question we may find a clue by considering wherein the conditions differed from the other ponds.

In respect to two features, or rather a combination of two (possibly more, of course), the conditions here seem to have been unique for this type of pond. In the first place the division in which the catfish were held was practically free of bottom soil, there being an exceedingly thin layer only, if any, on the cement. In the second place, this division was farthest removed from the intake pipe, around which there was considerable subaquatic vegetation, with the result that the water reaching the lower end of the pond was comparatively free of silt which had been unloaded in the upper division. It is pretty certain that juveniles of many species in the earliest stage can not thrive where silt is precipitating rapidly, and it is quite probable that certain species of Naiades, like some marine pelecypods, require a clean bottom and possibly a hard substratum. It is somewhat difficult to avoid silt precipitation in ponds supplied with water pumped from a turbid river. In this case the form of the pond, the vegetation, and the position of the mussels presumably brought about the result.

Another probable factor in the successful "set" was the "newness" of the water supply system and the consequent nonestablishment of predacious species which are found under usual pond conditions. Rhabdocœls are abundant in the ponds but not in the river water. Since the reservoir which supplies the ponds was filled first only the previous fall and this pond was filled for the first time a few days before the plant was made, it seems likely that rhabdocœls and similar enemies had not yet become established. The number of successful sets observed in the case of newly established ponds (see earth ponds) leads to the conclusion that this factor of "newness"[4] may be very important.

In Table 5 below are given the measurements of 10 of these shells, including the largest and smallest. There is given the increase per year as indicated by the winter rest line.

TABLE 5.—GROWTH OF 10 MUSSELS QUADRULA PUSTULOSA, DURING FOUR YEARS IN A CONCRETE-LINED POND.

Specimen number.	Yearly growth in millimeters.				Total length in millimeters.
	1913	1914	1915	1916	
1	4.3	6.2	6.2	5.3	22
2	4.6	7.2	6.8	5.6	24.2
3	5	6.1	5.8	5.7	22.6
4	4.8	3.6	6.4	3.2	18
5	4.3	3.8	5	4.5	17.6
6	4.5	6.1	5	4.7	20.3
7	4	6.5	5.5	4.5	20.5
8	4.8	6.9	5	4	20.7
9	4.4	5.3	4.4	2.3	16.4
10	3.7	4.6	5	2.3	15.6
Average	4.44	5.63	5.51	4.21	19.79

The largest mussel of this series reared in a pond is considerably smaller than a mussel of about the same age grown in the river, as shown by the following figures: Pond grown, length, 24 millimeters; weight, 1.9 grams. River grown, length, 28 millimeters; weight, 4.6 grams. The retarding effect of the artificial conditions is obvious enough in this comparison, where the advantage of selection is all in favor of the pond-grown shell and in which the river-grown shell is a few months younger.

In the summer following the discovery of this "set" of juveniles experiments were carried out to determine if the results could be repeated. The conditions as to bottom and clarification of water and source of water supply were made to coincide as closely as possible with those of the successful "set." In one respect only as far as known was there a difference, namely, in regard to the factor of "newness" or absence of pond conditions. The water was taken from the same reservoir which, having been in use four years, had in a measure acquired the characteristics of a standing body of water. This difference was realized, but it seemed best to make use of the established system of supply as long as its suitableness was not disproved. Three species of mussels were used and several plants made with each. These species were *Lampsilis ligamentina*, *L. anodontoides*, and *L. luteola*. The results were negative except with *L. luteola*, which, as indicated elsewhere, is not a typical river mussel and has yielded successful sets in almost all instances under the conditions prevailing in the ponds at the Fairport laboratory. These results would seem to indicate at least that the conditions provided were not decisive factors in the one successful set of *Quadrula pustulosa*, and that possibly the one factor in question, namely, the water supply, is the one which was responsible for success or failure.

A review of the results attained in this type of pond, with its successful plants among the failures, holds out some hope still for the solution of the problems of rearing the true river mussels. The line of procedure indicated would seem to be the provision of a water supply direct from the river and a rigid exclusion of established pond condi-

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[4] The condition of the water supply before typical pond conditions have time to develop

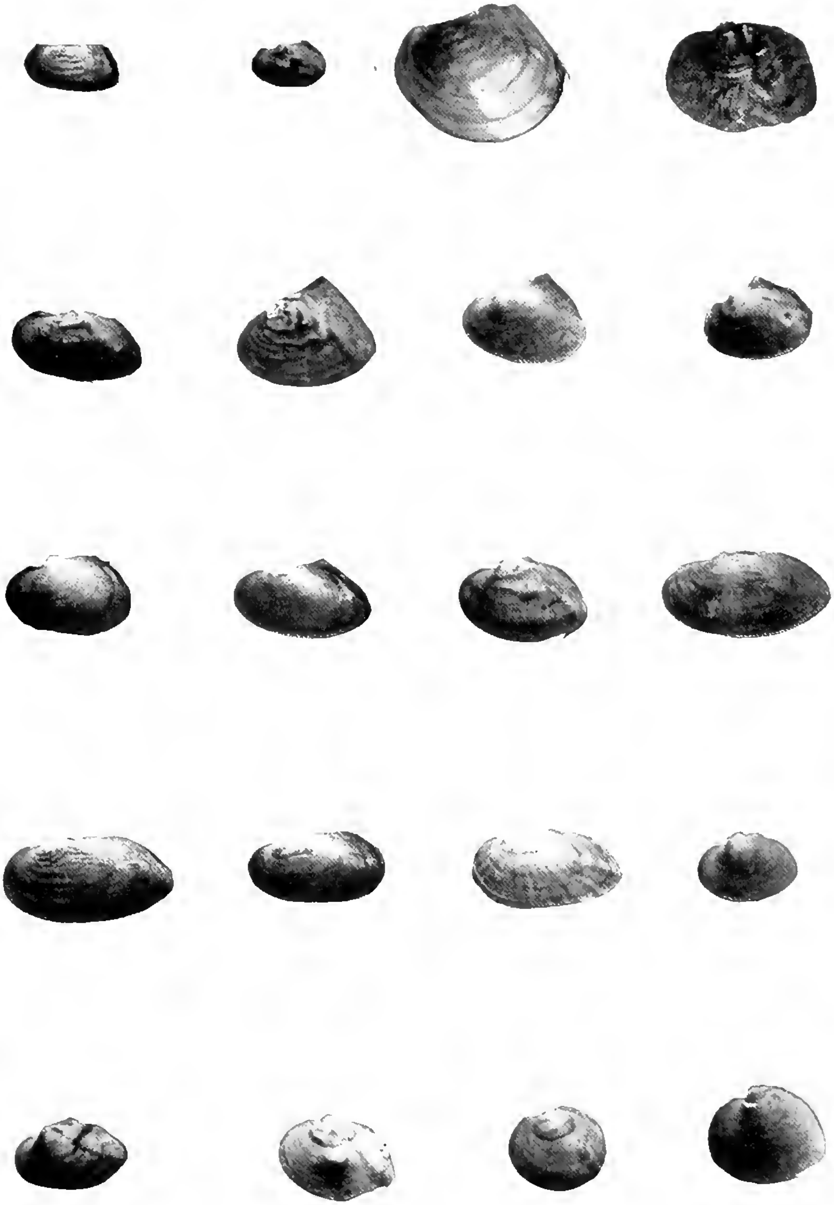

FIG. 73.—Juveniles of 20 species of mussels found in the artificial ponds at the U. S. Fisheries Biological Station within two years from the time of construction of the ponds. All reproduced natural size excepting the two right-hand figures in top row which are reduced one-half. (Photographed by J. B. Southall.) Reading from left to right these mussels are:

Top row: *Anodonta imbecillis*, *Anodonta corpulenta*, *Anodonta suborbiculata*, *Arcidens confragosus*.
Second row: *Strophitus edentulus*, *Symphynota complanata*, *Lampsilis alata*, *Lampsilis laevissima*.
Third row: *Lampsilis capax*, *Lampsilis gracilis*, *Lampsilis ventricosa*, *Lampsilis luteola*.
Fourth row: *Lampsilis subrostrata*, *Lampsilis parva*, *Lampsilis ligamentina*, *Obovaria ellipsis*.
Fifth row: *Plagiola donaciformis*, *Obliquaria reflexa*, *Quadrula plicata*, *Quadrula undulata*.

tions. It should be possible to maintain such conditions by thoroughly cleaning the walls and bottom each season and, so far as possible, excluding pond plants and animals during the critical period when the young mussels are escaping from their hosts.[5]

GROWTH IN EARTH PONDS.

A large plant of *Lampsilis luteola* was made in an earth pond in 1914 from crappie of two species, *Pomoxis annularis* and *P. sparoides*, and the sunfish, *Lepomis pallidus*. The following spring an examination of the bottom yielded some eight mussels, the largest 24 millimeters in length, the smallest 12. The growth was not as great as that in the floating crate, but compared favorably. The number surviving, however, compared with the thousands introduced into the ponds by means of the fish, was disproportionately small.

In lowering the water level of the pond there were found a few sheepshead, *Aplodinotus grunniens*, whose presence was quite unexpected and contrary to the plan of the experiment. As this is a mussel-eating fish, its presence might explain the disparity in numbers of the young mussels. Fortunately, a smilar plant was made the same season by the fish-cultural staff at the suggestion of the director. Since the pond was larger and the total number which was recovered was greater, it will better represent the results by the pond method.

A number of black bass were infected with *Lampsilis luteola* in the fall of 1913. In the spring they were placed in one of the large earth ponds, 0.843 acre in extent, used for propagation. The following November (1914), when the pond was drawn, some 60 mussels were picked up from the bottom. In the spring of 1915 more were recovered, making a total of 150. These were examined and measured. They had attained about the same growth as the mussels in the floating crate. The largest measured 35 millimeters in length, the smallest 15.5.[6] The greater length would be explainable as due to the longer growth period; having been on the fish during the winter, they would in all probability have completed their parasitic development some time before June 10, the date on which the plant in the floating crate was made. As compared with the small pond, the size doubtless contributed to the maintenance of more favorable conditions. We have in such a body of water conditions closely approaching the habitat of *L. luteola* in nature. Whether the distinctively river-growing mussels would thrive in such a pond in the absence of a current has not yet been satisfactorily determined. However, the fact that, in spite of many failures with some of these species, a few of these (represented in fig. 73) have been found in the ponds, for the most part of unintentional or sporadic occurrence (see Coker, Shira, Clark, and Howard, 1921, p. 105), leads one to believe that favorable results might be obtained by a proper control of conditions.

GROWTH IN PENS.

Recently a device was employed by Roy S. Corwin (1920) at Lake City, Minn., which gave very satisfactory results with the Lake Pepin mucket. A box 10 by 10 feet square and about 8 inches high was surmounted by chicken wire and the whole

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[5] Experiments planned to conform as closely as equipment permitted to the conditions proposed were carried through the season of 1919. Precipitation of silt occurred in large quantity, which doubtless accounts for failure to secure a plant of river mussels. A plant of lake mussels (*L. luteola*) was obtained.

[6] Measurements of these mussels after a second summer's growth, Dec. 1, 1915, give for the largest a length of 65.6 millimeters. From two of these were cut 16-line buttons 2 lines thick. (See footnote, p. 71.)

sunk in a protected part of Lake Pepin. In the pen thus made it was possible to retain a considerable number of fish carrying heavy infections. At the end of the season the wooden bottom was floated to the surface, and an examination revealed a total of 11,000 small mussels as reported. This is to date the greatest quantity production of mussels yet attained in an inclosure. This method has several obvious good features for situations in which it may be employed. It approaches natural conditions more closely than the other methods described. The suitable depth for both fish and mussels is more readily obtained than in a crate, as well as more ample range in other directions. It seems doubtful if it can be used in a river where the current would remove the young mussels or the silt deposit cover them too rapidly.

This season (1920) a test of the device is being made in the growing of river mussels in the Fox River, where the mucket mussel (*Lampsilis ligamentina*) is abundant and apparently thriving, since young mussels are readily found. The water of this stream is clear so large a part of the time that a protected location devoid of current should prove suitable. It is difficult to see how such a pen could be employed in a turbid river like the Mississippi, since at points devoid of current the precipitation of silt would bury the young mussels. The habitat of juvenile mussels in the Mississippi has been found to be a current-swept gravel bottom, always clean despite the almost constant presence of mud-laden waters.

STRUCTURE AND DEVELOPMENT OF JUVENILE MUSSELS.

The rearing of these mussels through the juvenile stage presented for the first time the opportunity to determine the structure at almost any age and processes of development during this period in the life history of fresh-water mussels. The investigations by Herbers (1913) and Harms (1909) have recounted in detail the development during that period for the Anodontas, Margaritanas, and Unios. In these cases, however, the juveniles were obtained for the most part free in nature, and therefore their age could not be given with certainty. As no detailed account has been published for the development of the large and valuable group of mussels included under the Lampsilinæ, the description of complete development in these would be a distinct contribution to our knowledge of mussels. However, because of other features demanding more attention at the present time, the intention of this paper is to mention only a few prominent points in the development, reserving the detailed account for another publication.

Upon beginning free life the shell of the young mussel, as has been stated above, is that of the larva. When closed, therefore, no striking difference between the young mussel and the glochidium is noticeable. Like the glochidium, it is for the most part colorless and transparent. If, however, the young mussel is alive it soon extends its foot, and in its use quickly demonstrates it to be an organ well developed for the purposes of locomotion. The foot is somewhat cleft at the apex, so as to give a bilobed appearance, and is clothed with cilia, all of which are in rapid motion during extension. On smooth surfaces like glass it has the power of adhesion, a property apparently not held in the adult, at least not to the same extent. By means of this organ the young mussel is able to move about rapidly. These peculiarities in the foot of the early juvenile are soon lost, and during the first month the foot assumes the characteristic form of this organ in the adult.

The gills are in the form of papillæ, of which at this stage there are three or four on each side of the foot, the longest being anterior, since it is the oldest or first developed (see figs. 67 and 68). They are long, slender processes slightly recurved at the ends. These increase in number with age and later become united to form the continuous lamellæ of the inner gill. The outer gills become visible between the first and second month or at a length of between 3 and 5 millimeters. Schierholz's (1888) determination of the time as the second and third year for Anodonta and third and fourth for Unio has been shown by Herbers (1913) to be incorrect for Anodonta, and will probably be found to be rather late for Unio.

Other prominent features in the youngest juveniles are the liver and the adductor muscles. The liver, because of its dark color, becomes quite prominent before the young mussel leaves the fish. It furnishes in this manner a ready index for the degree of development when examined alive. The adductor muscles also become conspicuous, but in another way. Because of their form and an index of refraction higher than that of the surrounding tissues they appear as bright spots. The stomach and intestines seem to become functional at once, the latter at first with a few turns comes gradually to the tortuous condition in the adult. The heart and kidney can not readily be made out in whole mounts. Herbers (1913) by sectioning finds their development pretty well advanced in *Anodonta celensis* at a length of 2.59 millimeters, corresponding to the second month in *Lampsilis luteola.*

The mantle is a direct derivative of the same organ in the glochidium. The coming of free life marks a change in its function. Where in the glochidial and parasitic periods (in this species) no increase of shell occurs, in the juvenile stage a phenomenal growth takes place. Beginning as a delicate microscopic membrane lining the glochidial shell, it increases with the growth of the mussel until, as we have seen, it is increased in size thousands of times in a single summer and eventually produces the heavy shell, the protective armor of the grown mussel.

The shell of juveniles up to the second month has two features that are characteristic of this early period. In consistency it is like horn, being transparent and less hard than later, when it becomes calcareous. The surface is uneven owing to a series of regular and relatively high undulations, knobs, etc., which are characteristic for each species (fig. 73). These are designated as "umbonal sculptures" by conchologists in describing the adult mussel, in which they are not infrequently found well preserved.

A structure to which special attention is called is the byssus, an organ that is characteristic of the juvenile stage in certain groups of fresh-water mussels. It consists of a hyaline thread produced by the byssus gland located on the ventral and posterior median edge of the foot. The first instance of it observed in the present culture was at an age of about 38 days, when the smallest of the mussels collected had a length of 4 millimeters (other cultures 1.9 millimeters). In this same species in nature the author has seen it present at a size of 2.8 millimeters. In juveniles of *Quadrula heros*, at an age of a few days, there is apparent a tough mucous-like secretion that serves to anchor the young mussel. Near the end of the growing season byssi were found on mussels of over 1 inch in length. The strength and caliber of the threads are appropriate to the size of the mussel. When the mussels were removed from the water at a temperature near that of freezing on November 20, attachment by byssi was not noted. However, the circumstances of their removal from the river rather than the change in temperature may have caused them to become detached. An examination in March of the following spring revealed the byssus present in most of the individuals, and it was present until June 10, after which date it could no longer be found. The disappearance at this time near the middle of the season's growth requires some explanation. It comes at the beginning of the period of most rapid growth, which is, perhaps, a decided physiological change, although very gradual, coming as it does after two months of spring growth. The observations to be recounted of a byssus in adult mussels would lead one to expect the persistence of the byssus under favorable conditions. On August 14, 1914, the author found an adult *Plagiola donaciformis* on a byssus, and later E. A. Martin showed the author a still larger individual. The byssi in these cases were strong enough to support the weight of the mussels. In this species (*Plagiola donaciformis*), then, we find the byssus habit not confined to the juvenile stage.

The development of the reproductive glands in fresh-water mussels was clearly made out by Herbers (1913) in Anodontas and Unios. He was able to distinguish early stages of the glands in Anodontas of 5.7 millimeters length. The maturity of these organs would mark the adult stage. In collecting various species of mussels in the field one occasionally discovers remarkably small individuals breeding. As these are so uncommon they are undoubtedly examples of precocity and exceptional.

The author has not found gravid individuals of *Lampsilis luteola* under what was apparently the third year. In the cultures here described sexual differentiation in secondary characters appeared the second summer. Modifications of the gills to form the marsupia appeared in the female, together with the corresponding fullness of the shell over that organ. The males were marked by the more pointed posterior portion of the shell. In the middle of August of the third summer the first gravid mussels were found. This, the first observed date of breeding, was 2 years, 2 months, and 24 days from the date of implantation of the glochidium. All females as far as examined were found to be gravid, which indicates that breeding is general at this age. The glochidia were mature in some individuals on August 14 and near maturity in others, which from the date of last observation would fix the time of ovulation as July.

Mature glochidia from these mussels were taken and an implantation obtained on a number of fish. The first free juveniles after metamorphosis were obtained in 10 days, others remained as late as the 18th day, a rather long period of shedding. The juveniles obtained represent the second generation of mussels, but the life cycle was completed when glochidia were obtained, as that was the stage with which the experiment began.

HABITS AND HABITAT OF JUVENILE MUSSELS.

The juvenile or postparasitic period begins with the release of the young mussels from encystment on the host. Because of the small size of mussels at this stage information regarding their habits and environment must depend largely upon studies under conditions of control or experiment. Obviously, it is entirely impracticable to count on finding them thus early in nature. The watching of the process of separation from the host has been found practicable only by making cuttings of infected gills from living fish and by examinations under the microscope. The first sign of the change is a repeated opening and closing of the shells. This is followed by extension of the foot, the movements of which become gradually more vigorous until this remarkably motile organ sweeps an arc in the plane of the valves included by the three sides of the mantle cavity (the anterior, posterior, and ventral opening of the shell).

The cases observed by the author took several hours, but under the conditions of observation the difficulties are greater than when normal in the living host. There seems to be an adhesion of the shell to the host's excised tissues that is due, very likely, to coagulation. In some cases the process was so prolonged that, before escape was effected, considerable decomposition of the host tissue was apparent. The juveniles, therefore, exhibited a remarkable resistance to the products of decay toxic to most animals.

The free juvenile under conditions of observation appears at times very active. In moving from place to place the foot is extended a distance fully equal to the length of the shell, becomes fast to the glass or some object, then contracts, bringing up the remainder of the animal. This is repeated again and again, thus accomplishing a kind of creeping motion which carries the small organism across the field of the microscope in a suprisingly rapid manner. The presence of cilia all in rapid motion upon the foot and edges of the mantle add to the effect of vigorous vitality.

It seems probable that the young mussels do not move about much if they find a suitable bottom. Time and again the author has looked for them on trays set on the bottom of the aquarium to catch them as they fall from the hosts, but all in vain before washing off the sediment. When this accumulated sediment in which they were lying was removed, they could be seen, and after being left for a few minutes without disturbance they would extend the foot and begin the migration reactions mentioned above. Often one finds considerable débris adhering to their shells. In one species delicate hair-like processes were observed. A covering of bottom sediment doubtless serves as a shield from enemies.

The mortality at this age is very high as may be seen by the number of empty shells and the scarcity of live mussels a few days after the beginning of free life. Their chief enemies, so far as noted under cultural conditions, are very small rhabdocœls, turbellarians that are extremely abundant during the summer in the water as it comes from the reservoir. These swarm over the bottom of the aquaria, and examples may readily be found through the transparent body walls of which may be seen the mussels they have eaten. These have been observed in both the glochidial and early juvenile stages.

The species of Turbellaria as determined by Caroline Stringer were *Microstomum* sp., *Stenostomum leucops*, and *S. tenuicauda*. Specimens of the Microstomum were preserved with the young mussels still inclosed in their relatively capacious intestines. Another enemy which it has been possible "to arrest with the goods still on him" is a small chætopod, apparently Chætogaster. Neither of these worms is more than 0.4 millimeter wide, so that after the mussel attains three weeks' growth it must be safe from their ravages.

The food of the very young juveniles seems to be similar to that of the adult; i. e., at least in part, microscopic plants and animalcules taken in through the incurrent siphonal aperture. In small juveniles one can watch these as they enter. The author once observed a considerable deposit of excreta containing the skeletal remains of such forms as diatoms. This débris was lying in a heap outside beneath the excurrent siphonal opening.

The floating crate method furnished an unusual opportunity for the study of living juveniles after the first two weeks, but as it was the first successful trial, for fear of disturbing the plant, the occasions for raising of the baskets were reduced to a minimum. Such incidental notes as were taken while tending the cultures may be of interest, inasmuch as so few observations have been made upon the habits and habitat of the juvenile Naiad.

In relating observations upon the habits of the culture attention is directed to the conditions prevailing during the experiment. The arrangement of the crate and baskets is described under Methods, page 64. (See also figs. 74 and 75.) The crate, being placed in the river channel, received a current of 2 to 3 miles per hour. In the individual baskets when at the surface no current could be detected. The fineness of the mesh was chiefly responsible for this. Much of the time, however, owing to a slight sinking of the crate, water to the depth of an inch flowed over the top. Thus the mussels, although probably never in a continuous current comparable to that in the river, received a constant renewal of the water supply. A gathering of the mussels at the sides of the basket was very marked. This might be construed to indicate that they found there conditions more favorable than at other points. Doubtless at the bottom of the basket the freshest supply would be at the outer edges. During a greater part of the summer flood conditions prevailed in the river, so that the content of suspended silt was very high. The checking of the current on reaching the baskets resulted in the deposit of this silt at the rate of over 1 inch per week. This is considerable when the conditions are considered. Thinking this might bury the young mussels, the silt was removed weekly by washing through the sides of the basket. Later this regimen was abandoned, being considered too violent and an unnecessary disturbance for the minute mussels. At the end of the season in November the silt in the bottom had accumulated to a depth of 3 inches. This sedimentation, however, covered a long period, most of which was not in time of high water.

The first collection of *Lampsiles luteola* from the crate numbered 7 at an age of 15 days. Three of these were built into the mosaic tube of a caddisfly larva, and of these three, two were still alive. The larva finding a scarcity of sand grains and similar building material had evidently made use of the mussels. The predacious worms mentioned above as so abundant and destructive of mussels were not found in the crates. They are apparently a bottom species, and thus the position of the crate on the surface forestalls their ravages. One of the most conspicuous species associated here with the mussels was the larvæ of the Ephemerid mayflies. As they are vegetarian they could be destructive of young mussels only in a competitive way, but ordinarily in crate culture they would not develop in time to be troublesome. The presence of these and like insect forms is doubtless due to the development of eggs deposited by the adult insects in the crate itself. Some other forms observed were numerous Hydra and Polyzoa, together with the free-swimming forms which make up the plankton of the main river.

The byssus was first observed in mussels of 38 days. The attachment was to such objects as could be found in the mud at the bottom of the baskets, some on the filaments of Cladophora and other algæ growing in the basket. One was found attached to the tarsus of a dead spider. The byssus increased in diameter and length with the growth of the mussels. When the latter were large enough to be readily seen, it was surprising

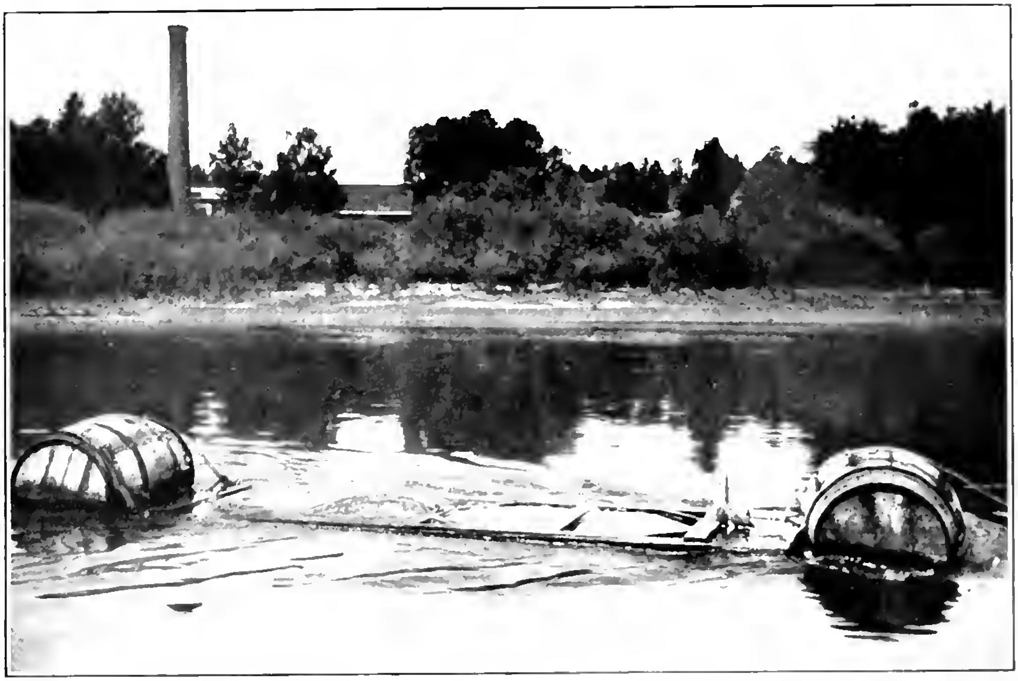

FIG. 71.—A floating crate containing four baskets (cf. fig. 72) in which were placed the fish infected with glochidia. The first successful attempt to rear mussels was made in this device.

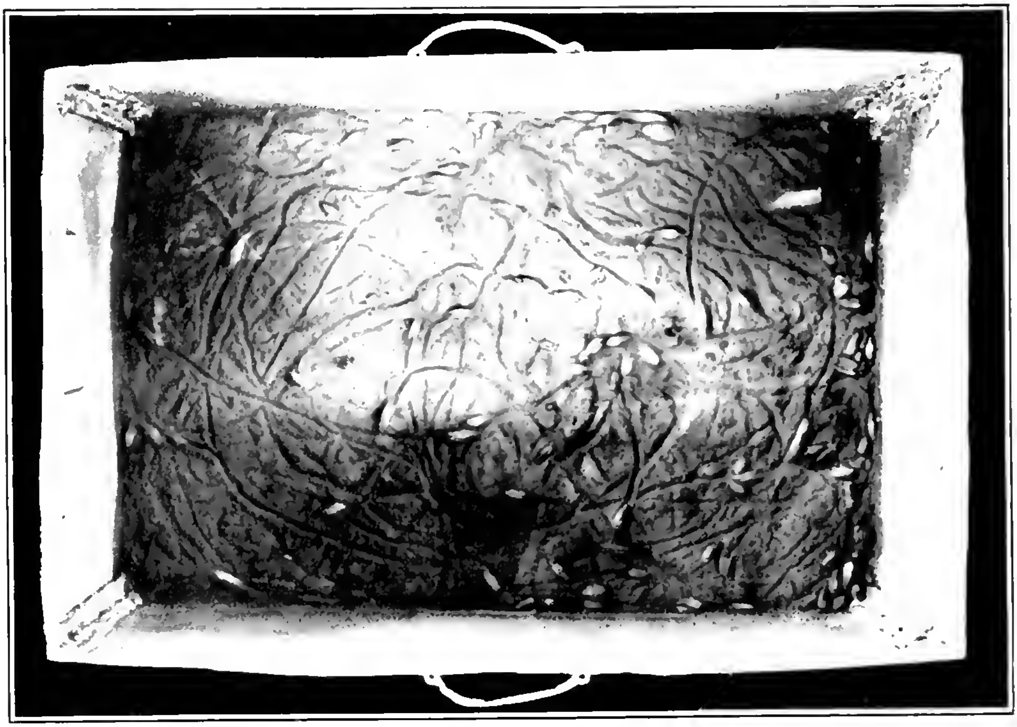

FIG. 72.—One of the propagation baskets with the bottom still submerged and photographed from directly above. Owing to disturbance of the water supply the young mussels, as shown by their trails, have migrated considerably. Such migrations apparently do not occur under ordinary conditions. Reduced to two-ninths natural size.

to find that they, like adult mussels, were usually buried in the mud, a small portion only of the posterior end of the shell reaching the surface. In fact, the only exception observed was in a case of interference with the water supply coming to the mussels, a discussion of which will be taken up later. No evidence of migration, by tracks or other signs, was seen. It would seem, therefore, that for this species when on a mud bottom the byssus would serve chiefly as an anchor for emergencies and would not frequently be called into service (cf. Isely, 1911). A change of position in the mud was noted when, owing to the presence of a small catfish that had escaped from another basket, the mussels burrowed deeper.

At the time of removing the mussels from the river for the winter the basket containing the brood of *Lampsilis luteola* was placed in a tank and the fresh supply of water cut down; then the mussels began to migrate, as can be seen by their tracks in the photograph (fig. 75). When the water was entirely drawn off, those on the surface fell over and closed their shells.

Altogether by observations for such brief periods the author did not note a varied number of locomotor reactions. The fact is, mussels when thriving and undisturbed seem to be comparatively inactive. Experimentally, doubtless, there would be a varied number of reactions depending upon the variety of stimuli applied. At present in our campaign to preserve the mussels and to increase their numbers we are particularly interested in the reactions manifested under natural conditions. We have some evidence of adaptations to depth of water and migration determined by river stages. There are indications also that some breeding reactions are influenced by light, others by temperature, chemical action, etc. The reactions of mussels when caught on sand bars by receding water vary with the species. The hieroglyphics of their wanderings under these conditions are sometimes very elaborate.

The discovery that the parasitism of mussels is limited in some species to one or a few species of hosts suggests the possibility of specific reactions in these by means of which the infection of the host is insured. (Howard, 1914a, Conditions of Infection in Nature, p. 39). This particular phase of their habits did not come within the range of this investigation, but it is suggested that in these ecological relations of parasitism the student of animal behavior may find that the ordinarily inactive fresh-water mussel will furnish a varied and interesting subject for study.

DISCUSSION AND APPLICATION OF RESULTS.

In considering the results of the foregoing experiments attention is directed particularly to those which seem applicable immediately to the campaign for mussel conservation.

Prof. J. L. Kellogg (1910) points out that there can be practically no conservation without culture or cultivation. Extinction has been the unvaried fate of useful forms, plant or animal, where the natural supply has been depended upon. In the more primitive human societies all food is obtained from the public domain, but civilization, with increase of population, has survived by assigning individual property rights from the public domain, thus encouraging and making cultivation possible. To give an example in a field closely allied to that of fresh-water mussels, this principle has been strikingly illustrated in the history of the oyster and clam fisheries. Those States, as Rhode Island and Connecticut, which framed laws encouraging the culture of oysters increased immensely their production, while a constant decrease was observed where the natural reefs were depended upon without sufficient encouragement to cultivation (Massachusetts Commissioners of Fish and Game, 1907).

This may be an extreme view, but it has been often true. It may be said, on the other hand, that although game protection (of fish, birds, and mammals) has been so frequently only a name in America, there are cases known to all where wild species have thrived under efficient protection combined with restocking in cases of depletion. Past efforts in the conservation of mussels have been largely confined to this limited type of protection. The work has consisted in "artificial propagation" (definition of which follows) and a certain amount of protection by law instituting open and closed seasons to fishing. The closing of certain streams for a number of years, thus creating preserves, has been advocated. Further assistance to nature in recovering from the effects of depletion is suggested in a system of culture, including protection and planting like that employed in restocking with fish.

The experiments here described furnished practically the first positive data contributing to the development of a system for the culture of fresh-water mussels. It seems worth while to consider whether cultural methods, which the present investigations indicate to be quite feasible, might add anything to the methods now in use. In using the term culture we distinguish from propagation.

ARTIFICIAL PROPAGATION.

Artificial propagation as it has been applied to mussels is a method which, as indicated above, has been employed by the Bureau of Fisheries some eight years past. The larval mussels are brought in contact with and allowed to infect the host fish, which are then released to spread the mussels under the usual conditions prevailing in nature.

In the effort to secure increased production of mussels this artificial infection has the following advantage: Whereas in nature the number of mussels which succeed in finding lodgment upon a fish is, as a rule, comparatively small, by artificially bringing parasite and host together the fish is made to carry a much greater number than would otherwise succeed in finding a host. Thus, the number of mussels reaching the juvenile stage is increased.

The place of shedding of the young mussels from the fish is to a large extent doubtless a matter of chance. As among marine clams probably those only survive which fall on, or subsequently reach, a favorable bottom. These considerations are largely responsible for the present investigations in the effort to supplement artificial propagation.

THE CULTURAL METHOD.

The cultural method as suggested by the present experiments would consist in carrying protection through the second critical period in the life of the young mussel and in planting in favorable localities the mussels obtained.

PROTECTION.

In almost all successful attempts at rearing animals or plants protection in critical stages is the important factor. An example from fish culture is the raising of trout. In agriculture the plant or animal is placed under the best environment attainable and protected from destructive forces of all kinds at all stages until used. If finally consumed for human use, provision is made to insure the perpetuation of the stock. In nature the dominant animals are the mammals which apply the principle of protection in the care of their young. Likewise among plants, those lines that have adopted this economy have attained dominance.

By the "artificial propagation method" the young mussel is carried through one critical event (infection) only. Liberation from the host and the early juvenile stage are equally if not more critical. Evidence showing this has been given above, and corroborative of this is the following testimony of Prof. Kellogg (1910) regarding the corresponding stage in the soft clam:

> Probably not even the swimming stage is more critical for Mya than this period of creeping which is of longer duration. It is exposed to numerous enemies and has little defense against them, for its transparent shell is still very thin and brittle.

Lefevre and Curtis (1912, p. 192) say regarding this stage of fresh-water mussels:

> It is to be supposed that only a very small proportion of individuals thus liberated would succeed in reaching maturity, as they would be exposed to the same destructive agencies as are encountered under natural conditions.

The results attained in the present investigation seem to indicate that a culture carried at least through the early juvenile stage and possibly to the adult stage would be economically practicable. In the floating crate method and the ponds[7] we seem to have found methods of protection. The proportion of survivals (8 plus per cent) in the crates is apparently greater than from those raised in the ponds (according to the best records we have) and doubtless can be greatly improved upon. Compared with the number under analogous conditions in nature it is tremendous. For example, Prof. Möbius (1877) finds that a young oyster has $\frac{1}{1045000}$ of a chance to survive and reach maturity. The same is true among practically all forms in which the young are early exposed to the vicissitudes of a free life. In the culture of sea clams the operator is dependent for planting upon such seed clams as are obtainable from a purely natural and thus somewhat uncertain supply. There is this decided advantage in operations with fresh-water mussels, that the necessary glochidia can be obtained with practical certainty as long as adult mussels last.

Protection at other than the two critical periods mentioned would be included in a complete system of culture. During the parasitic period it would consist in the proper care of the host fish. It may be noted that the fish when infected demands reasonable care, as the attaching glochidia cause a certain amount of laceration of the gills which subjects the fish to possible infection from fish mold (saprolegnia) and doubtless to some exposure from bacterial invasion.[8]

Culture for the adult mussels consists in providing the best environment for growth as well as economical means of protection and recovery. Experience has shown that other things being equal more rapid growth and development of heavier shell occurs in flowing water than where a current is lacking. (For other factors, see "Habitat," p. 94, Coker, Shira, Clark, and Howard, 1921.)

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[7] The recent results described under troughs and pens have yielded even larger percentages.

[8] *Bacterium columnaris* Davis has caused considerable mortality in experimental work at Fairport.

PLANTING.

The planting of mussels in nature by dropping from the host fish, although conceivably controlled to a certain extent by natural factors favorable to the mussel (Howard, 1914a, p. 39), is doubtless for the most part a haphazard process. Those which fall on unfavorable bottom must perish, and there is every reason to believe that successful mussel beds are the results of a precise combination of conditions at a given place. The investigations on sea clams and oysters show that myriads of the young develop to a given stage only to die if they are not on a suitable bottom. Great accumulations of these young clams on unsuitable ground may be saved by transplanting. When so employed in cultural operations, they are designated as seed clams.

In the case of fresh-water mussels an artificial planting likewise would doubtless be more economical of mussels—at least than the planting in nature by fish allowed to go at large. In restocking either privately controlled or publicly owned waters the general procedure that suggests itself is to rear the young mussels to an age of 2 or 3 months or more and then to release them on bottoms that are known to be favorable.

COMMERCIAL POSSIBILITIES.

If the natural supply is not maintained by the means described and the price of shells continues to advance, there will possibly come a time when the rearing of mussels by a complete system of culture will become commercially profitable for individuals and privately owned corporations, whereas now carried out only by Government agencies.[9]

A few experiments have been made to test the palatability of fresh-water mussels. Incomplete and inexhaustive as these tests have been they have yielded encouraging if not completely satisfactory results. Reports of edible species have been received. The use of the mussel for food in addition to the present use of the shell alone would aid greatly in making the culture of mussels commercially profitable. The successful culture of the marine mother-of-pearl shell (*Margaratifera* var. *maxatlantica*) has been described by Dr. C. H. Townsend (1916). Señor Gaston J. Vives, on Espiritu Santo Island, in the Gulf of California, reared these shells on a scale commercially profitable.

The development of an industry of this nature in the culture of fresh-water mussels might be dependent upon the acquirement of property rights on river bottoms suitable for rearing mussels. Precedents for such allotments of water-covered areas are familiar in the leases for oyster beds on our sea coasts. However, the experiments thus far carried out indicate that the culture of mussels may differ to this extent from that commonly employed in America [10] for edible oysters, in that mussels can more conveniently be grown in crates or containers of some sort rather than on open bottom. This is true at least because of the potential migratory nature of the mussel as compared with the sessile habit of the oyster; i. e., it is necessary in the former case to provide for a possible loss of a plant by migration. However, that the recovery of fresh-water mussels may be comparatively easy under some conditions is the testimony of Prof. Isely (1914). He

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[9] The possible alternative is the practical extermination of the mussel through excessive fishing either for the mussel itself or its host fish, or both. There have been well-known examples in history of complete extermination of useful species.

[10] In the more intensive cultivation of oysters and clams in Europe containers called ponds, which are in the nature of sluiceways through which flowing water is conducted, have been extensively employed.

was successful in finding a very large percentage of marked mussels months and even over a year after planting. It will be noted that his work was done in small rivers where collection was possible by wading during low water.

Solution of some of the problems still unsolved can doubtless be more directly and economically reached by further investigations of the life history and habitat of mussels and especially of the early juvenile stage. A few of the recent studies along these lines not mentioned in the foregoing pages follow: Allen (1914, 1921) has made a study of the food of lake and river dwelling species. Baker (1916, 1918) has made extensive ecological investigations in Oneida Lake. The author has had the opportunity of making an ecological survey of a portion of the Mississippi River, where mussels are abundant. A report is in preparation putting forth the results of this study of conditions controlling the development of mussel beds and the growth of mussels under such an environment. In general, much more detailed information is required concerning the various elements in an environment favorable to the mussel (see Coker, Shira, Clark, and Howard, 1921), including water content, as substances in solution and in suspension, both food and gases; temperature variations; depth and flow; amount of light; and kind of bottom.

That the conditions favorable to juveniles sometimes differ from those for adults has been indicated. If this is the case, as it is well known to be for many animals, a more complete knowledge of the requirements of the critical postparasitic stage in mussels will certainly contribute to their culture. Perhaps the most pressing problem is the securing of a complete knowledge of their enemies and means of combating these. There are still some commercial species for which the appropriate host is yet undetermined, and in most cases where the host has been determined practically nothing of the manner of infection and like ecological relations is known. The solution of these problems is difficult because dependent upon the observation of phenomena occurring in a medium different from our own. In the case of river mussels this medium owing to turbidity is not readily penetrated by sight. In spite of such difficulties, however, we must agree with Lefevre and Curtis (1912) that among invertebrate animals the Unionidæ, for the variety in economic and scientific interest of the problems they present, are scarcely excelled.

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FURTHER NOTES ON THE NATURAL HISTORY AND ARTIFICIAL PROPAGATION OF THE DIAMOND-BACK TERRAPIN.

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INTRODUCTION.

There appears to have been sufficient progress made in the experimental work on the artificial propagation of the diamond-back terrapin, *Malaclemmys centrata*, at the United States Fisheries Biological Station, Beaufort, N. C., since 1915 to warrant the drawing up of a report covering such information on this subject as has been collected to date and has remained unpublished. In Economic Circular No. 5, revised, of the U. S. Bureau of Fisheries,[1] the results of observations up to and including 1915 are cited with methods outlined for construction of pens, selection of brood stock, care of eggs, young, and adults, and some notes on the growth of the terrapins. Much information has been collected since that time by continuing observations on many of the same terrapins considered in the 1917 report and also through further studies with different purposes begun in more recent years.

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[1] Hay, W. P., Artificial Propagation of the Diamond Back Terrapin. Economic Circular No. 5, revised. U. S. Bureau of Fisheries, Washington, 1917.

The terrapin propagation study has been directed since its beginning by several investigators. Originally Dr. R. E. Coker gave his attention to its possibilities and prepared a report of his results for the North Carolina Geological and Economic Survey.[2] At the same time Prof. W. P. Hay began similar investigations in Chesapeake Bay. In 1909 these were transferred to Beaufort, where Dr. Hay took charge of the experimental work and continued giving it his direction from 1909 to 1915. During this time H. D. Aller planned and carried out the feeding of yearling terrapins during the winter in a warmed nursery house. Lewis Radcliffe relieved Mr. Aller in 1912 and was later followed by S. F. Hildebrand. Some of the material herewith discussed is from experiments begun by the two last-named investigators, but left unfinished because of their removals from Beaufort. The present paper is based on the unorganized notes of each of the above-mentioned investigators and also on the systematic observations carried on under their supervision by Charles Hatsel, the terrapin culturist stationed at Beaufort, N. C., since the experimental work was begun. The large share of credit for the continuity and the accuracy of the observations of the entire experimental terrapin propagation project is due Mr. Hatsel for his exceptionally careful, energetic, and faithful work. The writer has had the direction of the experiments since the fall of 1919. B. J. Anson has assisted in organizing and tabulating the data discussed in this paper and J. B. Southall has prepared the graphs.

BROOD STOCKS OF THE EXPERIMENTAL FARM.

The terrapins of the original brood stock, which are either the parents or grandparents of all the Carolina terrapins that are held in captivity and under observation at the Beaufort station, were purchased in two lots, the so-called "original lot of North Carolina breeders" and the "second lot of North Carolina breeders." To these was added later, but kept separate, a number of adult Texas terrapins as brood stock. The production in eggs and young throughout the years of captivity of these terrapins is herewith tabulated (Table 1) and shown in graphic form (fig. 76).

TABLE 1.—RECORDS OF BREEDING STOCKS OF TERRAPINS IN CAPTIVITY AT BEAUFORT, N. C.

Stock and year.	Males.	Females.	Eggs.		Young.		Per cent eggs hatched.
			Number.	Rate per female.	Number.	Rate per female.	
Original stock:							
1909	23	44	12	(?)	12	(?)	(?)
1910	23	44	288+	6.5+	288	6.5	(?)
1911	[a] 18	43	598+	13.9+	598	13.9	(?)
1912	18	43	688	16.0	538	12.5	78.1
1913	18	43	732	17.0	610	14.1	88.3
1914	18	39	736	18.8	594	15.2	80.7
1915	18	39	922	23.6	836	21.4	90.6
1916	18	39	921	23.6	813	20.8	88.2
1917	18	39	722	18.5	639	16.3	88.5
1918	18	39	[b] 757	[b] 19.4	[b] 675	[b] 17.3	[b] 89.1
1919	[a] 23	39	[b] 834	[b] 21.3	[b] 757	[b] 19.4	[b] 90.7

[a] Five males taken from this lot for experimental purposes in 1911 were returned to it in 1919.
[b] Estimated.

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[2] Coker, R. E. The Cultivation of the Diamond-Back Terrapin. Bulletin No. 14, the North Carolina Geological Survey. Raleigh, 1906.

TABLE 1.—RECORDS OF BREEDING STOCKS OF TERRAPIN IN CAPTIVITY AT BEAUFORT, N. C.—Con.

Stock and year.	Males.	Females.	Eggs.		Young.		Per cent eggs batched.
			Number.	Rate per female.	Number.	Rate per female.	
Second stock:							
1911	45	70	....	....	....	....	....
1912	45	70	649	9.0	583	8.3	89.8
1913	45	70	673	9.4	600	8.6	90.0
1914	45	70	745	10.4	724	10.2	97.1
1915	45	70	958	13.4	876	12.5	91.3
1916	29	64	871	13.6	783	12.2	89.8
1917	29	63	[a] 973	[a] 15.4	805	12.7	[b] 82.7
1918	28	63	[a] 731	[a] 11.5	[a] 670	[a] 10.6	[b] 93.0
1919	27	50	[a] 773	[a] 15.4	[a] 702	[a] 14.0	[b] 90.8
1920	[b] 50	89	1,172	[c] 13.1	1,133	[c] 12.7	96.6
Texas stock:							
1912	[d] 32	34	127	3.7	101	2.6	79.5
1913	[d] 29	34	292	8.5	281	8.2	96.2
1914	[d] 29	34	412	12.1	376	11.0	91.2
1915	[d] 29	34	399	11.7	366	10.7	91.7
1916	[d] 12	25	421	16.8	383	15.3	90.9
1917	[d] 12	25	497	19.8	439	17.5	88.3
1918	[d] 12	25	([e])	([e])	([e])	([e])	([e])
1919	5	11	270	24.5	247	22.4	91.4
1920	5	11	138	[c] 12.5	134	[c] 12.1	97.0

[a] Estimated.

[b] The 1920 record represents the combined production of the original and the second brood stocks. The penning together of individuals of both stocks made it impossible to ascertain the production of either stock.

[c] Decrease in production probably due to destruction of eggs by rats.

[d] This record for males includes five Carolina original stock males used in hybridization studies.

[e] Records for production not obtained on account of storm which destroyed egg beds and washed many small and adult terrapins from their inclosures.

ORIGINAL CAROLINA BROOD STOCK.

Considering the original or first lot of breeders it will be noted that highest egg production occurred in 1915 and that since then the egg rate per female, with exactly the same number of females laying, has diminished by from three to five eggs. The percentage hatched has varied but slightly. This, however, would be reasonably expected with the same number of males on hand and the number of eggs to be fertilized somewhat less. In view of the fact that egg production has fallen off since the 1916 production and remained under that high mark now for four years through 1920, it seems probable that the period of maximum egg production in this brood has passed. However, the slight increase during 1918 and 1919 perhaps means that the brood may still reach greater egg production than its maximum egg record of 1915. Still beneath the maximum mark, it may also indicate that certain females are about to reach maximum production while others have passed this point. The heavy falling off in recorded egg production in 1920 (see figures for 1920 under second stock in Table 1) was due to the depredations of rats which dug up many nests and destroyed hundreds of eggs before control methods were effective. The 1920 figures, therefore, do not represent the possible egg production and hatch, for the record of eggs laid would doubtless have been very much higher had it not been for the destruction caused by the rats.

The average size of the females of this lot in 1911 was 154 mm.[3] Considering what is known of the history of some of the individuals of this lot since 1902, their size then and their growth since, it appears probable that at the time of their measurement in 1911 they averaged close to 20 years of age. The estimated age of these terrapins is

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[3] Approximated from measurements recorded in inches.

arrived at from a knowledge of their size at the time of their purchase and of the number of years during which they have been captive in the experimental pens. They were all adults at the time of their purchase, and the approximation of their age must be quite accurate. From the knowledge that it takes at least much longer than nine years for hibernating terrapins to reach an average length of 142 mm. (see Table 3) and that after the length 142 mm. is reached the average annual growth increment is not more than 1.5 mm., it appears reasonable that the age of the terrapins of this brood was at least 18 years in 1911 (the year of measurement).

	Years.
To reach average length of 142 mm.	9
To grow from 142 to 154 mm. (the 1911 average length)	9
From 1911 to 1921	10
Total average age in 1921	28

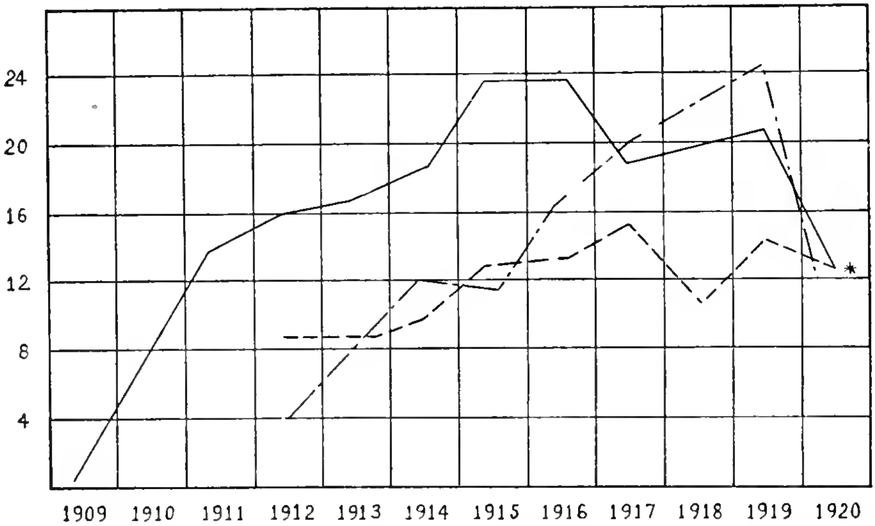

FIG. 76.—Egg production per female in original and second Carolina and Texas brood stocks. ———, Original Carolina brood stock; — — — —, second Carolina brood stock; —·—·—·, Texas brood stock; * combined egg production per female of original and second Carolina brood stocks. Marked decrease in egg production probably due to destruction of eggs by rats.

Inasmuch as maximum recorded egg production for this lot occurred in 1915, we may presume, then, that maximum egg production occurs about the twenty-fifth year of a terrapin's life. The actual maximum production of young, however, would, of course, depend on the presence of sufficient males among the breeding stock.

SECOND CAROLINA BROOD STOCK.

The second lot of North Carolina breeders, with average measurement of 141 mm.[4] in 1911 and probable average age of 9 years, has shown, with the exception of the years 1918 and 1920, a general increase in egg production since the beginning of its laying. The 1918 record showed a dropping off in egg production of 2.1 eggs per female. The reason for this decrease is problematical, but the exceptionally severe winter of 1917–18 and the following late spring, with its resulting longer hibernation period and its retard-

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[4] Approximated from measurements recorded in inches.

ing influence on normal spring feeding and growth in the terrapins, may possibly be the causes of the decreased productiveness, though a similar decrease is not found in the egg production of the original brood stock. The 1920 decrease shown in Table 1 is due in part to the destructiveness of the rats above referred to and probably also to a very late spring, the first eggs being laid on May 17, a rather late date. Many of the brood terrapins, however, did not lay their first eggs of the season until the middle of June, more than a month after the usual first egg-laying date. In 1917 certain of the females of the second lot of breeders were set aside for experimental purposes, and this had a tendency toward diminishing the actual number of young produced, while the experiments yielded information which is of value from other aspects and will be discussed later. Because of this experimental work the figures for "young" in the table are estimates and are included only tentatively in the 1918 and 1919 records. The mixing of part of the first lot with the entire second lot of breeders in 1918 and 1919 made it necessary also to estimate the number of eggs laid by both these lots, and these records have been so noted.

The estimation was possible in view of the fact that a considerable proportion of the original brood stock was not mixed with the second brood stock. The method followed to obtain the estimated records was this. One lot of the original brood stock (lot A) was held in a separate pen during the year, and from the egg and young production of this lot was computed an average egg and young production for the entire original brood stock. From this computation it was possible, then, to figure the production of those terrapins (lot B) of the original brood stock which had been penned with the second brood stock. The egg and young production of the entire second brood stock (lot C) was ascertained by subtracting the egg and young production of lot B from the total egg and young production of lots B and C combined, lot B plus lot C representing the mixed lots of brood stock.

In 1920 the terrapins of the first and second lots of breeders were so mixed that it was impossible to estimate at all accurately the egg production of either lot, and for this reason the egg production and hatch of these broods for 1920 are combined. The combined egg and young production record, though lower than that of either lot in the preceding year, is not significant, however, because of the heavy egg destruction caused by rats.

TEXAS BROOD STOCK.

The Texas brood stock, with average length in the spring of 1920 of 177 mm.[5] and probable age of 30 years, has shown an increasing productiveness annually since its first laying in confinement until 1920, when doubtless, as above, the decrease in the egg and young production record was due to destruction of eggs by rats. In 1919 from 11 adult females of this stock which had been used in hybrid studies with Carolina males there were obtained 270 eggs, or 24.5 eggs per female. In 1916 all but 12 of the Texas terrapins were returned to Texas. The 12 that remained were the finest and largest females of the original Texas lot, and the exceptional egg production of the 11 mentioned above may be due to this fact. It is understood that when the entire Texas brood stock was at Beaufort the average number of eggs produced per female was lower than for either of the Carolina lots.

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[5] Approximated from measurements recorded in inches.

It is noteworthy in this connection that this maximum production for the Texas stock is greater than that of the Carolina breeders. The maximum records of the two stocks are as follows: Carolina, egg rate, 23.6; young rate, 21.4. Texas, egg rate, 24.5; young rate, 22.4.

The excessively cold winter of 1917–18, which apparently slowed down output among the second brood stock of Carolina terrapins, did not effect any retardation in the productiveness of the Texas stock. The heavy decrease in recorded productiveness of this brood stock in 1920 is due to destruction of eggs by rats, as in the case of the first and second lots of Carolina breeders.

RATIO OF SEXES AND FERTILITY.

The number of males in a given stock of brood terrapins in each of these experimental lots has been about one-third to one-half the number of females present. There appears to be a negligible difference in the rate of young hatched per female in the different broods with differing percentages of males present. A normal hatch appears to be about 90 per cent of the eggs laid, no matter how great a number of males may have been present. It is needless to say that scarcity of males would, of course, increase the number of infertile eggs laid. This percentage of infertile eggs is much larger at the beginning of the laying period (fig. 79) of the terrapins and at the beginning of captivity (Table 1).

The cause of the high infertile egg rate among terrapins which have laid for the first time under our observation and have been penned with male terrapins of exactly their age throughout their lives may be found in the fact that possibly the males do not reach sexual maturity as early as the females. This is indicated in a study of certain lots of terrapins experimented with during 1919. Seventy-eight female terrapins of the 1914 brood which had never laid fertile eggs, due to the fact that males had never been penned with them, were separated into two equal lots which were kept in separate pens. With one lot of 39 females were placed 3 males of the original brood stock at least 25 years old; with the other lot were placed three 5-year-old males of the 1914 brood. This division of the lot and introduction of males occurred on the same day in early spring, so that there might be plenty of opportunity for fertilization to occur before the egg-laying period arrived. The production was as follows:

	Females.	Males.	Age of of males (years).	Eggs laid.	Eggs hatched.	Per cent fertile eggs.	Per cent infertile eggs.
Pen 9	39	3	5	245	54	22.0	78.0
Pen 19	39	3	25	187	152	81.2	18.8

It is suggested from these data that males of 5 years are less potent than much older ones and that maximum fertility may not be expected where young males, just reaching sexual maturity, are used.

In reviewing the entire matter of the most desirable numerical relation of males to females in this species, it should be pointed out that mating among terrapins is promiscuous. Copulation in one year may mean the production of fertile eggs for more than that year alone. To cite a case under our observation, in 1914, 10 females of the second lot of Carolina breeders which had been producing young were set aside in a separate pen without males. With no further association with males, these terrapins laid fertile eggs each subsequent year until and including 1918. The record of egg production and hatch of these 10 terrapins through 1918 is as follows:

	Eggs.	Young.	Per cent infertile eggs.		Eggs.	Young.	Per cent infertile eggs.
1915	129	128	0.7	1917	130	39	70.0
1916	110	102	12.0	1918	108	4	96.2

In the spring of 1919, 5 males were introduced into this lot, and the fall production was 137 young from 146 eggs. From this experiment it appears that female terrapins may retain live spermatozoa in a healthy condition after a single copulation as long as four years, and under such conditions some eggs laid even in the fourth year may be fertile. It is apparent also that fertilization may occur immediately after copulation.

In further consideration of the proper ratio of sexes for maximum fertility we have the records of several domestic broods (Table 2) which, it happens, have contained fixed ratios of males per 100 females throughout their existence. This set of observations includes lots in which the males number 5, 9, 12, 24, 32, and 50 per 100 females, and the records give some suggestion of what may possibly be the most desirable ratio of males to females to produce maximum fertility.

TABLE 2.—SEX RATIO AND FERTILITY OF THE DIAMOND-BACK TERRAPIN IN CAPTIVITY

Egg-laying year.	Males.	Females.	Males per 100 females.	Eggs laid.	Per cent fertility.	Egg-laying year.	Males.	Females.	Males per 100 females.	Eggs laid.	Per cent fertility.
1909 hibernated brood:						1910 winter-fed brood					
First	8	4	200	96	77.8	First	10	140	8	12	100.0
Second	8	4	200	118	63.5	Second	10	107	9	348	83.3
Third	2	4	50	98	73.4	Third	10	107	9	572	78.6
Fourth	2	4	50	119	95.7	Fourth	10	104	9	606	90.5
Fifth	2	4	50	138	94.7	Fifth	9	103	8	952	75.4
Sixth	2	4	50	140	89.2	Sixth	9	103	8	298	45.9
1910 hibernated brood:						1911 winter-fed brood:					
First	5	89	5	38	97.4	First	10	82	12	8	100.0
Second	5	89	5	260	82.4	Second	10	82	12	7	0.0
Third	5	89	5	452	93.2	Third	10	82	12	470	94.1
Fourth	5	89	5	640	75.0	Fourth	10	82	12	682	93.5
Fifth	5	89	5	421	61.2	Fifth	10	82	12	583	84.6
1910 selected brood:						Sixth	10	82	12	621	88.8
First	8	25	32	27	81.5	1912 winter-fed brood					
Second	8	25	32	418	74.0	First	18	43	24	177	91.4
Third	8	25	32	529	91.2	Second	18	43	24	188	85.1
Fourth	8	25	32	526	95.5						
Fifth	8	25	32	678	91.5						
Sixth	8	25	32	467	95.7						

In viewing the records of these broods it is necessary to bear in mind that maximum fertility does not occur in the first year of laying in any brood unless there happens to be laid only a very few eggs which may have, by chance, become fertilized. Accepting 90 per cent as normal fertility, it will be noticed that this per cent of fertility was reached in the 1910 hibernating brood in the third year of laying, and that this brood contained only 5 males per 100 females. However, in the following year, when there were about 200 more eggs laid, the per cent of fertility dropped to 75. The fifth year, though showing a decrease in fecundity in the terrapins, shows another considerable lowering of percentage fertility. A similar drop in the per cent of fertility is also found in the fifth and sixth years of laying of the 1910 winter-fed brood after it had reached at least 90 per cent fertility in previous years. It was accompanied in the fifth year by an increase of 346 eggs to be fertilized. The 1911 winter-fed brood in its fifth year of laying also showed a decreased fertility of approximately 9 per cent, with an increase of 301 in number of eggs to be fertilized. Even with a smaller number of eggs by 362 to fertilize in its sixth laying year there was only a 4.2 per cent increased fertility, 12 males being present throughout the observations.

To be compared with these records there are the 1910 selected brood and the 1912 winter-fed brood. These contained, respectively, 32 and 24 males per 100 females. The lot with 32 males per 100 females has yielded better than 90 per cent fertility now for the past four years, even though the egg production with the exception of the last year has increased yearly during this period. This is an especially good record in view of the fact that the egg rate in this lot in 1919 averaged 27.1 per female. The 1912 winter-fed brood, with 24 males per 100 females, has laid but twice, and it is needless to say the record of these first two years may not be indicative of the future record of this group. However, the egg production was very large for the first laying year, and the percentage of fertility of the eggs in this case may be of considerable comparative value. This record is the highest of our observations for percentage of fertility in the first year where there has been substantial egg production. It will be noted, however, that with an increase of egg production in the second year the percentage of fertility declined to 85.1 per cent.

The 1909 brood, in which there are half as many males as females, has given during the past three years a high record. There is no doubt that there are more than enough males in this lot, since the 1910 select brood has a record equally as good in percentage of fertility and contains only 32 males per 100 females.

From our table and this discussion it seems warranted to conclude that after the brood has established a substantial egg-laying record a 90 per cent fertility may be obtained with from 24 to 32 males per 100 females. The record of the 1911 hibernated brood is good with only 12 males per 100 females. This record may be influenced, however, by the fact that appreciable egg laying in this brood was relatively late, coming in the ninth year, and thus much more time for copulation was available with but very slight utilization of the spermatozoa.

GROWTH.

Many data at hand concerning feeding and growth and their bearing on the development and functioning of the sexual organs of the terrapin are of value to the commercial terrapin culturist. The several annual broods, the offspring of the original and second lots of breeders, have had chosen from them certain numbers of individuals which have received varying treatments, the results of which can be compared to advantage.

The effect of hibernation on the growth of the small, newly hatched terrapin is considerably different from that of winter feeding in a warmed nursery house. Whereas the hibernated terrapin grows none during the winter, the fed terrapins may make considerable growth. The food used and the temperature at which the terrapins are kept appear to be the factors most influencing growth in the nursery house. The heating plant employed at Beaufort is merely a large coal-burning sheet-iron stove. The radiation from this stove causes the water of those boxes closest to the stove to remain at high temperature throughout the day and night, while those farther away are not so thoroughly and continually kept at as high a temperature. These feeding boxes closest to the stove always contain the largest terrapins in the spring, while those at the greatest distance from the stove contain the smallest. This indicates the desirability of having a heating system which radiates its warmth equally and in constant and considerable quantity. To the commercial culturist a heating system of this kind is of prime necessity. The effect of winter feeding other than in its bearing on actual growth—that is, in causing earlier arrival at sexual maturity—will be indicated in certain of the annual brood studies. This is another valuable consideration for the commercial grower of terrapins.

What growth may be expected of winter-fed terrapins, compared with those that are allowed to hibernate, is well suggested in the records of the 1910 and 1911 broods, lots of which received these treatments, respectively. The fed lots at any age are generally about 1 year's growth in advance of the hibernating lots, and in some cases much more. This difference in growth in 2 and 3 year old terrapins is from about 10 to 20 mm. The difference between the average lengths of the lots diminishes as they pass the fourth year. From this time on the variation averages about 10 mm. and remains thus constant through the ninth year, if not longer (Table 3, fig. 77).

TABLE 3.—GROWTH OF WINTER-FED VERSUS HIBERNATED TERRAPINS.

Age in years.	Season of measurement	1910 and 1911 broods combined.					
		Winter-fed.			Hibernated.		
		Number.	Measurement in millimeters.		Number.	Measurement in millimeters.	
			Total.	Average.		Total.	Average.
1	Spring	97	[a] 3,006	30.9	98	[a] 2,738	27.9
	Fall	95	4,467	47.0	89	3,833	43.0
2	Spring	125	7,067	56.5	190	7,980	42.0
	Fall	182	14,392	79.0	182	10,976	60.3
3	Do	183	16,667	89.9			
4	Spring				175	15,807	90.3
	Fall	81	9,315	115.0	78	8,260	105.8
5	Do	209	26,556	127.0	168	19,486	115.9
6	Do	132	17,277	130.8	167	20,560	123.1
7	Do				156	20,347	130.4
8	Do	201	29,692	142.7	167	22,757	136.2
9	Do	126	17,984	142.7	89	12,147	136.4

[a] Measurement of plastrons.

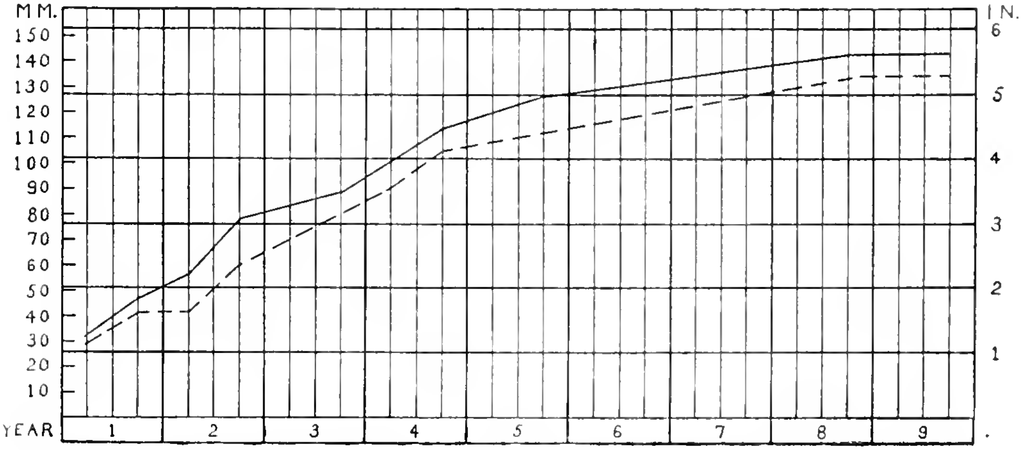

FIG. 77.—Average growth of winter-fed and hibernated terrapins. Curves based on combined records of growth of winter-fed and hibernated lots of the 1910 and 1911 broods. ————, Winter-fed; – – – – – – – hibernated.

ATTAINMENT OF SALABLE SIZE.

The relation of age and growth to salability is of importance to the prospective terrapin farmer, and for this purpose a table has been prepared showing the number and per cent of terrapins of the 1910 winter-fed and hibernating lots reaching the 5 and 6 inch lengths at given ages (Table 4). The rate of growth of the terrapins in captivity is heavily retarded between the 5 and 6 inch lengths.

TABLE 4.—ATTAINMENT OF MARKETABLE SIZE BY FEMALES OF 1910 BROOD.

Age in years.	Six inches.				Five inches.			
	Winter-fed.		Hibernated.		Winter-fed.		Hibernated.	
	Number.	Per cent.	Number.	Per cent.	Number.	Per cent.	Number.	Per cent.
4	....	....	....	....	32 in 81	39.5	....	....
5	2 in 127	1.5	....	....	67 in 127	52.7	14 in 90	15.5
6	8 in 133	6.0	....	....	90 in 133	60.2	34 in 89	38.2
7	....	[a] 10.0	1 in 78	1.2	....	[a] 71.0	45 in 78	57.6
8	20 in 129	15.5	2 in 89	2.2	108 in 129	83.7	75 in 89	84.2
9	25 in 129	20.3	4 in 89	4.4	123 in 129	95.3	85 in 89	93.2

[a] Estimated.

It will be noted that in the fifth year only 1.5 per cent of the winter-fed brood had reached the 6-inch length. In the sixth year 6 per cent of the brood had reached that length. The figures in the table appear small when a mere hundred terrapins are considered. To multiply them several times, however, changes them to the exact meaning they would have for the terrapin farmer—not merely to multiply them by the number of hundreds in the one brood alone, but to multiply them also by the number of broods which contain individuals that are reaching the 6-inch mark.

In the fifth year it appears that 52.7 per cent of the terrapins of the winter-fed brood has reached the 5-inch mark. Although the price paid for 5-inch terrapins in the market is not nearly so much as that for 6-inch, it is evident that selling when the 5-inch mark is reached may have its value from a commercial viewpoint. It means a quicker turning over of the money invested and possibly a better business proposition when large numbers of terrapins are considered. For example, a terrapin farmer may rear from the eggs possibly 15,000 or more terrapins per year. Eliminate one-half (a much too large percentage) for death rate during the five years. Now, in the fifth year, 3,750 terrapins will have reached the 5-inch mark. This is approximately 300 dozen, which, sold at $20 per dozen, bring $6,000. The market for 6-inch terrapins would have to be especially good to make the two or three years' extra keeping of them pay. However, the market for 6-inch terrapins generally pays double the amount paid for 5-inch terrapins, and there is the possibility that the raising of terrapins to the 6-inch length is the more desirable business proposition, especially when it is remembered that there will be an increasing number of broods producing 6-inch terrapins after the enterprise has been carried for a few years, not to mention the increasing young production.

CULLING.

Each brood of newly born terrapins contains a great many which, when held in a warm nursery house, will not eat, or, if they do, do not make any growth. They serve only to bring down to a lower figure the average annual growth increment of the lot.

If, however, one selects the largest grown three-quarters of each lot, the average growth increment for 1-year-olds is much increased. To indicate this point, a concrete example will best serve the purpose. There were 1,004 terrapins of the 1916 hatch placed in the nursery house in November, 1916. During the following winter 500 or more of the same brood were allowed to hibernate, while the larger lot was fed. In May, 1917, the average length of the 1,004 was 39.2 mm. The best grown three-quarters, or 780 terrapins, had an average length of 42.9 mm. The largest 200 terrapins of this lot averaged 54.7 mm. in length. To be compared with this lot there was still the unchanged fall average measurement of the hibernated terrapins, 28.1 mm.

From this discussion it appears that it would be economical to cull the young, poorly grown terrapins, either to force-feed them, liberate them because of their relative costliness in handling, or to sell them as soon as possible after they reach the 5-inch length in order that all the fast-growing characteristics of the brood stock may remain unmixed and protected against contamination with slow-growing individuals.

Present knowledge of the relative growths of first-year "runts" and first-year "selects," however, indicates that discarding or too strict culling of "runts" at the end of the first year is not entirely economical, since it has been learned that terrapins of poor first-year growth often reach in the fourth or fifth year equal length with their "select" brothers. It would doubtless be profitable to destroy very early any yearlings that show symptoms of disease unless effective remedial and prophylactic treatments are available.

WINTER FEEDING.

In view of the fact that in some locations favorable for terrapin culture fresh food may not always be available or may cost excessively, experiments have been carried on to learn the relative value of fresh and salt food in its assimilability and its growth-producing value. For this purpose one lot of newly hatched terrapins with an average length of 28 mm., 662 in number, was fed oysters, while another lot of the same age and average length, 613 in number, was fed salt fish. It appears from the following tabulation that the fresh-fed terrapins thrive much better than the salt fed:

Treatment	Number of terrapins.	Average length, September, 1916.	May, 1917.			
			Average length.	Maximum length.	35 millimeters or more.	Average length of 100 best.
		Mm.	*Mm.*	*Mm.*	*No.*	*Mm*
Salt-fed	613	28.0	29.9	40.0	34	34.2
Fresh-fed	662	28.0	33.8	51.0	228	42.7

The maximum length of any terrapin under our observation kept through one winter and until the following May in the nursery house is 81 mm.[6] The greatest length of a winter-fed terrapin at approximately 2 years of age (measured in September) is 104 mm.,[6] or slightly more than 4 inches. The offspring of domestic stock appear to do better in captivity than those of "wild" stock (fig. 78). From measurements

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[6] These measurements are taken on the lower shell, following the commercial method of measuring a terrapin 81 mm. ≎ 3¼ inches; 104 mm. ≎ 4⅛ inches.

taken in the autumns of 1919 and 1920 the following information on this point was brought to light:

Offspring of—	Number.	Age in years.	Treatment.	October, 1919.		Average length in millimeters, October, 1920.
				Average length in millimeters.	Maximum length in millimeters.	
"Wild" stock	95	3	Fed one winter	65.3	87	66.8
"Domestic" stock	99	3	do	74.4	116	76.5

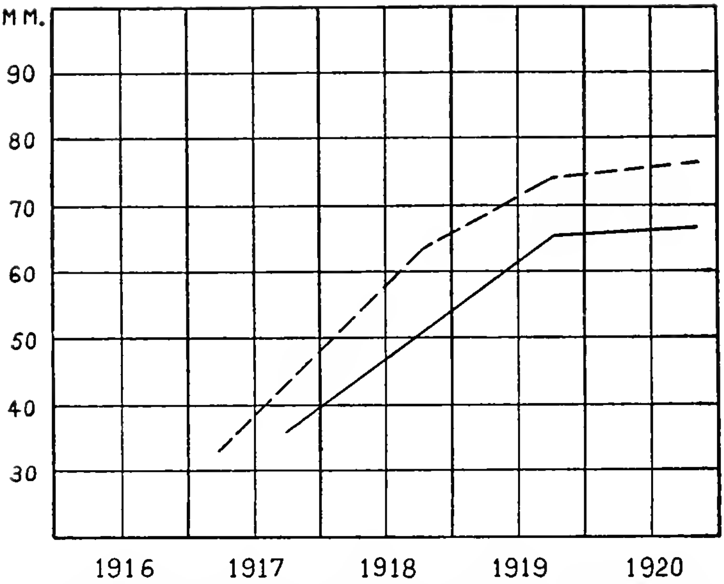

FIG. 78.—Growth of 1910 offspring of domestic and wild parentage. Each lot was fed one winter and selected for large size in the fall of 1917. — — —, Offspring of 1909 domestic stock; ————, offspring of original Carolina wild brood stock.

SPACE REQUIREMENT.

The 1917 brood had two lots of 100 each chosen from it in 1919. One of these lots, with average measurement of 52.5 mm., was placed in a large so-called fish pool which measured 38 by 24 feet. The other lot with average measurement of 60.1 mm. was placed in a small pen with dimensions of 29 by 12 feet. Observations on the growth of the two lots have been as follows:

Treatment.	Square feet per terrapin.	Number of terrapins.	Average length in millimeters.		Increased length in millimeters, May to October, 1919.	Average length in millimeters, Oct. 5, 1920.	Increased length in millimeters, October, 1919, to October, 1920.
			May, 1919.	Oct. 23, 1919.			
Closely confined	3.6	100	60.1	66.6	6.5	70.3	3.7
Wide range	9.3	100	52.5	60.9	8.4	72.2	11.3

A conclusive statement of space requirement or of the value of extensive running ground is not warranted from this single set of observations. It is of significance, however, that the greater growth has occurred in two successive years in the larger pool. This may have been due, nevertheless, as much to the fact that the terrapins were smaller in this pen than in the "close-confinement" pen and may have just reached or were in a stage of rapid growth, whereas the other group may have passed that same period. That plenty of space has a tendency to increase fecundity in the terrapin is suggested by the 1909 brood. These terrapins, held in a pen 32 by 5 feet for six years, have had a very large average yearly egg production per female. This pen provides each terrapin with approximately 26.6 square feet of ground. The exceptionally high laying record of these terrapins may be due, in part, to the large space and uncrowded condition of their pen. Their size, of course, is large, but abundant space may be a contributing factor in causing increased productiveness.

1909 BROOD.

This brood, the first terrapins hatched in captivity in the Beaufort pens considered in this paper, consisted of 12 individuals—8 males and 4 females. Several of the males of this lot have been used in other experiments, and since 1915 there have been only 2 males with the 4 females under observation. They have been kept during this time in a small pen which, however, is large enough to support many more terrapins than these 6. This 1909 lot has hibernated each winter since its birth and shows what is probably a normal growth and development for terrapins held in captivity. The first eggs from the females of this brood were laid in 1915 (fig. 79) when the terrapins were 6 years old. The egg rate per female in that season was 24. Yearly since then there has been an increase, until in 1919 the egg rate reached 32.2 per female. This 1919 egg production was accompanied by a hatch of 30 young per female and represented at that time the best record observed at Beaufort for average egg production and hatch. In 1920, how-

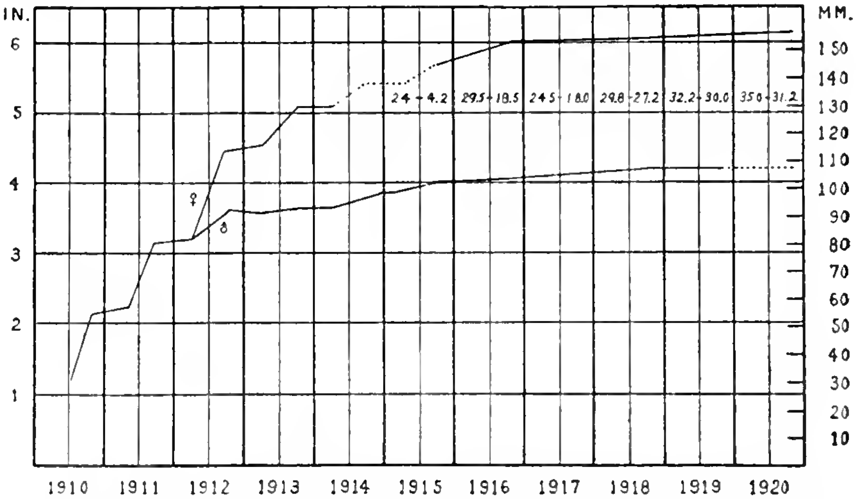

FIG. 79.—Growth of 1909 brood of original Carolina brood stock. Egg production and hatch per female per year expressed, respectively, by figures on the curve. This brood has always had but four females. · · · · ·, Estimated.

ever, the brood surpassed its best record again by laying 140 eggs, of which 125 hatched, giving an average egg record of 35 per female and an average hatch of 31.2 young per female. There were 16 nests found in 1919 and 19 in 1920, indicating quite conclusively that all females of the 1909 brood laid at least four times and that three of them laid five times in 1920. Growth after the seventh year is small, but it is attended by increasing fecundity. The cause of the high percentage of infertile eggs in the first year of laying of this brood may be due to the fact that the males of the brood were not mature. However, the following year the larger part of the eggs by far was fertile.

1910 BROOD.

Two lots of the 1910 brood were set apart in the fall of 1910, one fed the first winter, the other allowed to hibernate. A comparison of the average growth of these two lots indicates that the first lot, winter-fed, by average measurement, arrived at the 5-inch mark and to egg-laying one year before those that hibernated, and also that the egg-laying began at a higher rate and continued higher than that of the hibernated group (fig. 80). In early spring (1915) 8 males and 25 females were selected for size from the fed lot and kept in a separate inclosure. Their egg production in the second year of their laying was 16.7 per female, a much greater productiveness than was made either by the ordinary lot of fed terrapins from which the selected individuals were chosen or by the lot of hibernating terrapins three years later in 1919.

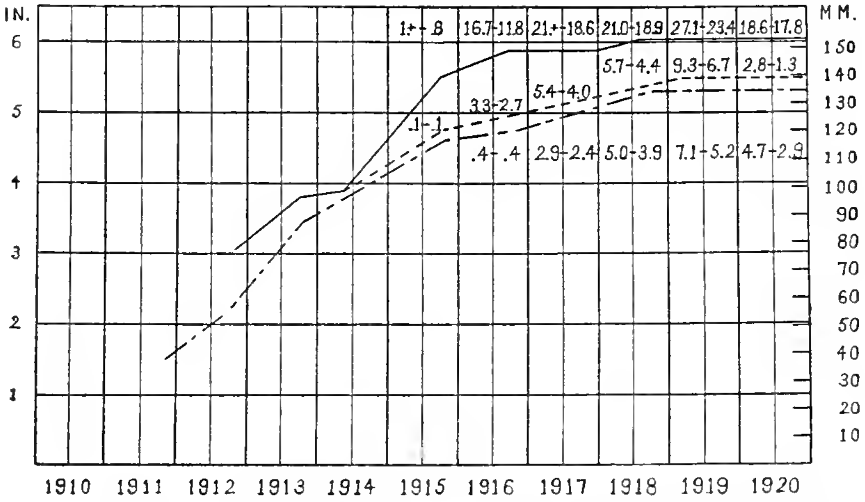

FIG. 80.—Growth of 1910 brood of original Carolina brood stock. Egg production and hatch per female per year expressed, respectively, by figures on the curves. ————, Fed two winters and selected for large size in the spring of 1914; — — — —, fed one winter; —·—·—, hibernated.

These facts indicate that for the commercial terrapin culturist it would pay more in a series of years to hold the largest and fastest growing stock as breeders rather than to pick here and there for his commercial sales. He could hold such brood stock over a long period of years and feel certain that maximum production would not come before at least 15 or 20 years. He would know, also, that the egg production of his breeders was as large as could be obtained. Thus, each year a certain number of the best grown females of 3 years or older could be chosen to be held as the established brood stock.

The balance could then be used as salable stock whenever their size was great enough to make them marketable. This would tend, then, to the selection by the terrapin farmer of his best producers and fastest growers and in the course of years lead to a race of quick-growing, large-framed, and highly productive terrapins.

1911 BROOD.

The 1911 brood has consisted of two lots of terrapins, one fed two winters and hibernating thereafter, the other hibernating each winter. The average growths of these two groups differ about 12 mm. at any season of any year. The tendency, however, as age increases, is toward a diminishing of this difference in the average growths. The evidence brought to light in the 1910 brood that winter feeding tends toward earlier productiveness is borne out in this brood also. In the fed lot the first egg laying occurred in the fourth year, probably by only one female. Substantial output occurred in the sixth year with an egg rate of 5.2 per female. The first production of the hibernating lot occurred in the seventh year, but this was negligible—0.2 egg per female. The second egg laying in the hibernating stock was likewise small, the rate per female being 2 eggs. This only further points out the desirability of winter feeding. It indicates, also, when the results are compared with the 1910 brood lot which was fed only one winter, the futility and extra cost of feeding terrapins more than one winter. It appears that the 1910 winter-fed brood has shown that egg production and growth from one year's winter feeding is much more desirable than the same from two years' winter feeding when selection is not made of the brood stock.

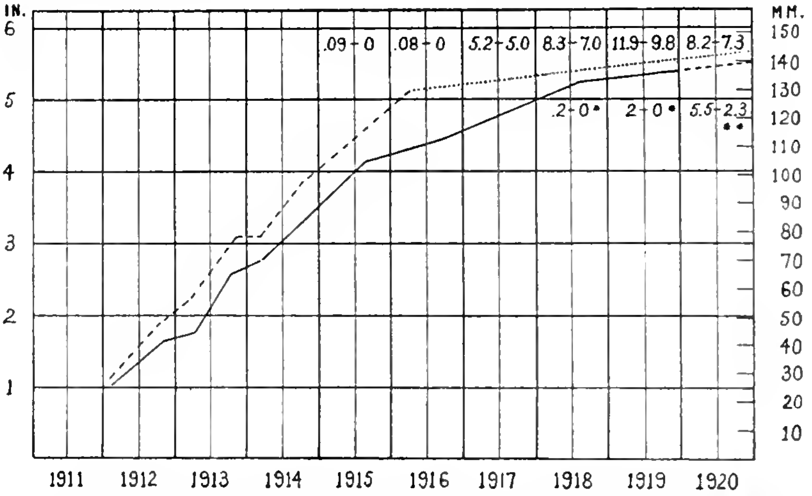

FIG. 81.—Growth of 1911 brood of original Carolina brood stock. Egg production and hatch per female per year expressed, respectively, by figures on the curves. ————, Fed two winters; - - - - - -, hibernated; ·········, estimated; * no males in this lot previous to this year; ** fertility modified by experimentation.

It may be added in this general connection that winter feeding does not tend toward the development of weaker adults nor necessarily to animals more susceptible to disease. It is true that young terrapins in the nursery house are subject to disease, and there is occasionally considerable mortality from this cause. It apparently kills many of those that would probably die from inherent weakness at best. There are many terrapins which suffer an attack of the disease in question and again recover their well-being. The subject of mortality among the young terrapins is discussed on page 108.

It is of interest to note in further discussion of feeding two winters and its lack of advantage to the culturist the fact that, from average measurement, the hibernated terrapins reach the 5-inch mark approximately one year and one-half after those fed two winters. Referring again to the 1910 brood, the lot fed one winter reached the 5-inch mark two years before the 1910 hibernating group. It may then, perhaps, be that two winters' feeding may slow down growth rather than hurry development. It will be noted, too, that egg production in the 1910 brood lot fed one winter is negligibly different as regards the year of substantial egg production from that of the 1911 lot fed two winters

1912 BROOD.

The 1912 brood was fed the first winter and allowed to hibernate each winter thereafter. In the spring of 1914 there was made a selection of 100 each of the smallest and largest grown terrapins of the stock. These two lots were kept separately, and their growth and egg production to 1920 have been observed. The lot selected for large size after the first two years did not exhibit as unusual growth as it had in the first winter, while the "runts" after 1915 showed relatively much faster growth. Their average length in 1917 was about 10 mm. greater than the lot which had been chosen originally for its early rapid growth. Both lots produced eggs in the same year (1919) when they were 7 years old. It is of interest to note in this connection that the "runt" group averaged 2.3 eggs per female, while the "selects" averaged 1.6 eggs per female.

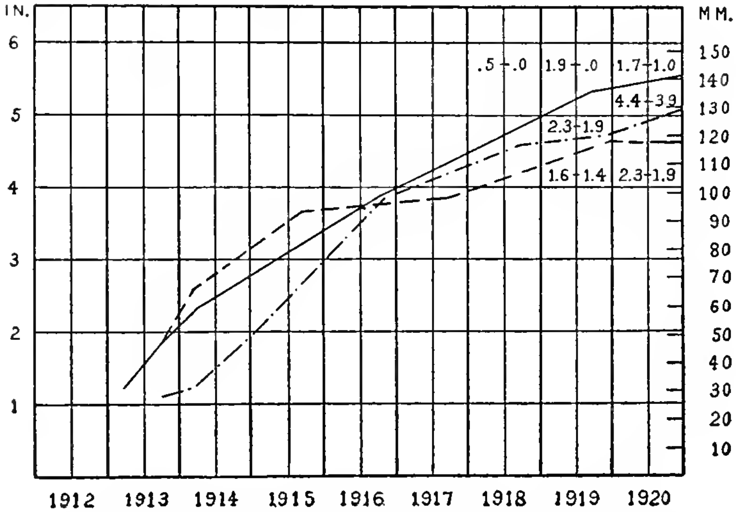

FIG. 82.—Growth of 1912 broods of original Carolina and Texas brood stocks. Egg production and hatch per female per year expressed, respectively, by figures on the curves. ————, Offspring of Texas brood stock, fed one winter; — — — —, offspring of Carolina brood stock, selected from winter-fed lot for large size October 1, 1913; ·—·—·—·, offspring of Carolina brood stock, selected from winter-fed lot as runts October 1, 1913.

It is suggested, then, from this brood stock that selection with a view toward early attainment of salable size or early and increased egg production took place at too young a stage in the development of the terrapins to be of any advantage to the terrapin culturist. A comparison of this 1912 study in the effect of selection with that of the "selects" of the 1910 brood emphasizes this point. Selection for size occurred in the 1910 brood when the terrapins were 4 years old. The egg production from these "selects" was especially large. In the 1912 lot the egg production is not above normal for either group of terrapins fed one winter and remaining unselected. Selection as early as the second year is premature, since the terrapin at that age has not reached one-half its adult size, and there may be many influences after the second year to retard growth in what then appears as an exceptionally healthy and rapidly growing terrapin.

The Texas brood of 1912, numbering 24 in 1916, 1917, and 1918, and 14 from 1919 to 1921, has shown greater average growth and produced eggs in 1918, a year earlier than the Carolina terrapins of the same age. The possible earlier arrival of the offspring of Texas stock at sexual maturity may be hereditary in character. All the antecedents of this Texas stock were from the marshes of Texas, where the longer growing and laying season with the very limited hibernation period would normally tend toward the occurrence of an earlier maturing animal than would be found in nature in North Carolina. This early maturing characteristic may have become inherent in the Texas stock.

1913 BROOD.

The 1913 brood was originally divided into two lots—one hibernated while the other was fed. Of the fed lot the largest 100 terrapins were selected for further study. These selected individuals at 6 years of age did not average 4½ inches, though, of course, there were some over 5 inches in length in the lot. Neither had they laid any eggs. There was, however, in the seventh year a small production of eggs and young in this stock. Their slowness of growth can not be well

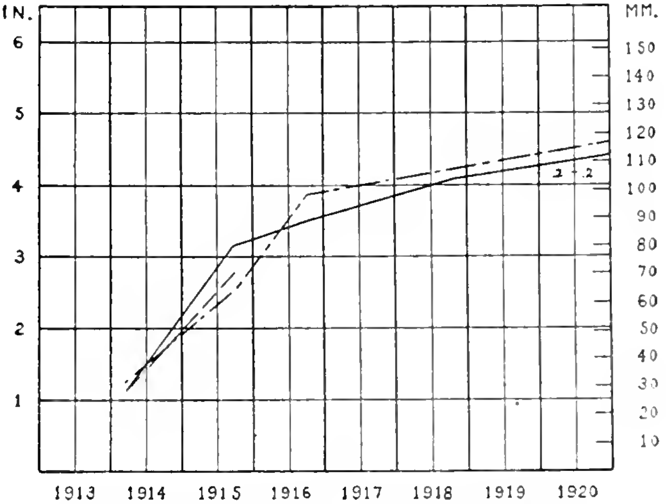

FIG. 83.—Growth of 1913 broods of original Carolina and Texas brood stocks. Egg production and hatch per female per year expressed, respectively, by figures on the curve. ————, Offspring of Carolina brood stock, selected for large size in the spring of 1914; — - — - —, offspring of Texas brood stock, fed one winter; — — —, offspring of Texas brood stock, hibernated

accounted for. The severe winter of 1917–18 may have retarded their development somewhat, but the retardation in the average growth curve occurs before that winter. It seems only further evidence that selection of the large terrapins at the beginning of the second year does not necessarily mean that those terrapins will be the largest or best producers in the fifth or sixth year; that, as has been well shown in the 1912 "selects" and "runts," selection of brood stock as early as the second year is premature. The Texas brood of 1913 does not show normal growth. Its average growth has, however, been better than that of the Carolina brood which received the same treatment. No eggs have been laid by the Texas stock. It may be that the retarded average growth curve of the Texas stock is due to the fact that a number of the larger terrapins of this lot were lost in a heavy storm in the summer of 1918. This would also explain the late egg laying of this group.

1914 BROOD.

This lot of Carolina terrapins selected in the spring of 1915 from those terrapins that had been fed during the previous winter has not shown more than ordinary growth and did not produce eggs during 1919, the fifth year of its life. In 1920, the sixth year, however, there was a small production of eggs. Early selection and the brood's later retardation in average growth, which has been evidenced in lots previously discussed, is further borne out here. The Texas brood of 1914 has been rather insignificant, inasmuch as it consisted of only five terrapins in 1919, the others having been shipped to Texas. These five averaged somewhat larger than the Carolinas of the same stock, but had not produced eggs up to 1920. To make room for other experimental lots they have been shipped to Texas to be liberated.

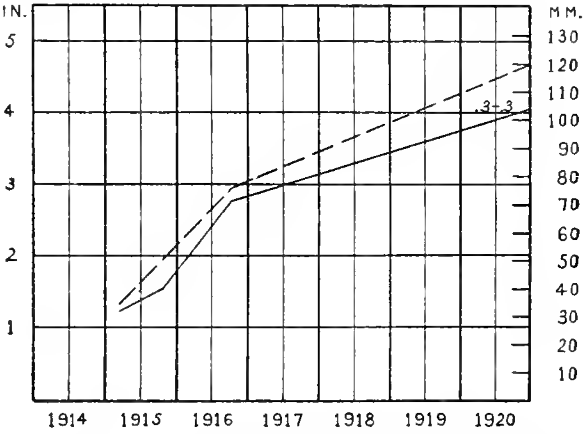

FIG. 84.—Growth of 1914 broods of original Carolina and Texas brood stocks. Egg production and hatch per female per year expressed, respectively, by figures on the curve. ————, Offspring of Carolina brood stock, selected for large size in the spring of 1915; — — —, offspring of Texas brood stock, selected for large size in the spring of 1915.

MORTALITY.

As has been pointed out in the report of 1917 mortality among adult terrapins is very small. It does not amount to more than one-half of 1 per cent. In the young the mortality runs higher, especially if the terrapins are winter-fed. The death rate among young terrapins hibernating the first year after birth is, however, very small. There may be an increase during the year following, but it is negligible. The death rate in the nursery house, however, is a matter of importance, though in certain years it is small. The cause of heightened mortality in the winter-fed individuals is a disease, rather cancerous in nature, which attacks the head, flippers, and especially the tail of the terrapin. The disease rots off the tail and spreads to the body proper, probably affecting the spinal cord and causing paralysis and death. Often terrapins become blind or unable to eat because of the disease. Its cause is unknown, though it probably is due to a microorganism. The disease seems most virulent to those nursery boxes which are best heated or in the sun, while those which remain throughout the cold season in the shade or at a considerably lower temperature than the others do not suffer so high a death rate. The disease does not attack the weak and small terrapins alone, but often kills some of the best grown. The kind of food used seems to have no connection with the prevalence or the virulence of the disease. Antiseptic washes and thorough cleanliness in the house and boxes apparently have some advantages, but the disease will prevail even when the most scrupulous care is taken. Possible value of antiseptic treatments seems to be borne out to some extent in the table on page 110. Treatments have been with potassium permanganate solution applied to the nursery boxes at intervals of a day or every few days. The solution is poured into the boxes and thrown upon the sides, allowed to remain some time, and then drawn off. Early in the fall before young terrapins are housed a thorough treatment with formalin or copper sulphate solution is given the boxes and walls of the house. The floor, being sand, is treated with lime.

The first year that any antiseptic was used in the nursery house was 1915. In 1914 the percentage of mortality among terrapins housed for the winter was 29. In 1915, with the disinfecting treatments being used, the mortality dropped to 5 per cent. However, this drop in mortality rate may have been due to causes other than the use of the disinfectants, for since 1915 there has been a continued high mortality rate even though disinfectants have been used regularly.

Apparently the infecting organism can live in either salt, brackish, or fresh water, as the disease, once started, spreads when the water in the nursery boxes is changed from fresh to salt, or vice versa. Certain terrapins that are attacked recover after several weeks, but the majority die. What possibly is another symptom of the same disease, or perhaps another disease altogether, is the so-called "softening of the shell" among the young terrapins. It is found among the terrapins that make no growth and is due, perhaps, to faulty absorption of the yolk sac or to possible infection of the body wall during this process. Such infection could be readily conveyed to the internal organs and destroy the health of the terrapins so affected. The "softening of the shell" symptom is always accompanied by loss of the power of growth and sometimes by the loss of pigment in the carapace or by a deadened appearance of the entire shell. Terrapins that develop this latter symptom rarely live. The offspring of the Texas stock are as susceptible to the disease as those of the Carolina. Hybrids (Carolina-Texas cross) are none the less susceptible to the disease.

From a study of the winter-fed terrapins during the winter of 1919–20, it is suggested that high temperature and direct sunlight on the nursery boxes in which are held the several lots of yearlings are correlated closely with the prevalence of the disease. It appears that the greatest mortality occurred in those boxes closest to the stove and in such locations in the nursery house that direct sunlight fell upon them. Greatest growth also occurs in those terrapins held closest to the heater, and therefore there appears to be a direct relation between rapid growth and increased prevalence of the disease. The mortality of winter-fed terrapins, as it has occurred during the period from November of one year to March of the next since 1912, is as follows:

MORTALITY OF WINTER-FED TERRAPINS.

Year.	Number fed.	Mortality.		Year.	Number fed.	Mortality.	
		Number.	Per cent.			Number.	Per cent.
1912	546	40	7	1916	2, 126	227	10
1913	569	41	7	1917	2, 038	554	27
1914	1, 771	522	29	1918	([a])		
1915	1, 493	87	5	1919	2 937	529	18

[a] All terrapins of the 1918 brood were liberated.

SUMMARY.

The egg production and the hatch of the original and second Carolina and of the Texas brood stocks during their captivity at Beaufort have been reviewed. It appears that the probable average age of individuals of the two Carolina brood stocks in 1921 is 28+ and 18+ years, respectively. Egg production in domestic terrapins has occurred as early as the fourth year. In terrapins fed one or two winters egg production generally begins in the fifth or sixth year. In hibernating terrapins it rarely occurs before the seventh year. Egg production immediately after penning is small but increases to normal in about the third year of captivity. At least for the first six years of sexual maturity, probably for much longer, it is greater among the fed terrapins of a certain brood than among those of the same brood allowed to hibernate. It is estimated that maximum egg production occurs when a terrapin is approximately 25 years of age.

Terrapins in captivity have been observed to lay as often as five times in a single season. Average annual egg productions as high as 23.6 and 24.5 per female have been recorded for the original Carolina stock and the Texas brood stock, respectively. The maximum average annual egg production of any female under observation has been 35 eggs; the maximum hatch per female, 31.2 young. This record was obtained in 1920 from the 1909 offspring of the "wild" stock.

Rats, because of their burrowing into lately made nests and destroying large numbers of eggs, are serious enemies of the terrapin.

The proper numerical relation of males to females for maximum fertility is not known exactly, and it is difficult to ascertain it accurately in view of the habit of promiscuous mating among terrapins. One mating, moreover, may give rise to fertile eggs for four years thereafter; that is to say, the life of the spermatozoon in the female after copulation may be at least four years. A 90 per cent hatch, which appears to be normal, can, however, be obtained among well-matured terrapins when the number of males is one-third the number of females. This average percentage of hatch is not increased by the presence of a larger proportion of males. It appears from the study of certain of the domestic broods that while egg laying is small a maximum fertility may be obtained, but not always, from broods in which there are 5 to 12 males per 100 females. However, when egg production is substantially increased it appears that there must be more males to obtain maximum fertility. Broods in which the males numbered 24 to 32, respectively, per 100 females produced a normal fertility, even though egg production was large. It seems warranted, then, to conclude that from 24 to 32 males per 100 females are necessary in order to obtain a 90 per cent fertility when the females of a brood average perhaps from 12 to 24 eggs per season. Males are apparently a year slower than the females of the same brood in coming to sexual maturity.

The growth of terrapins from birth to their maturity is recorded. The increasing number and percentage of individuals of a given brood reaching the 5 and 6 inch lengths, the marketable size of terrapins, as age increases has been pointed out. In the sixth year 60 per cent of a given winter-fed lot reached the 5-inch length and 6 per cent the 6-inch length. In the seventh year of a given hibernated lot 57 per cent of the brood reached the 5-inch length and 1 per cent the 6-inch length.

A large number of each brood of winter-fed terrapins will have reached the 5-inch length by the fourth year. In the fifth year the average winter-fed terrapin will pass the 5-inch mark. Winter feeding not only hastens growth but quickens development of the sex organs and influences toward greater fecundity at an earlier date than occurs among terrapins allowed to hibernate. Offspring of domestic terrapins appear to do as well in captivity as the offspring of "wild" stock. The maximum growth for any terrapin raised in captivity under observation has been 81 mm. for one year's and 104 mm. for two years' development. Small terrapins seem to make faster growth when fed oysters than they do when fed salt or fresh fish. Adults make good growth when fed fresh fish.

Selection of brood stock should not occur before the third year, preferably later. Selection for this purpose should be of the largest individuals of a brood, since there is a positive correlation between size, age, and fecundity. Earlier selection than in the third year is undesirable, since rapid-growing 1 and 2 year old terrapins often have their growth retarded in the following years and at the fifth year are no larger and no more productive than those terrapins which were poorly grown in the first two years.

It appears that the more space allowed terrapins in captivity the greater will be their growth within certain limits. Plenty of space may also have a bearing in its possible influence on increased egg production.

Mortality among yearling terrapins fed in a warmed nursery house during the winter varied from 7 to 29 per cent from 1912 to 1919. Mortality among the adult terrapins, as has been pointed out in another publication, is about one-half of 1 per cent. There is no doubt that many more than one-half of the young terrapins of any brood will live in captivity to attain a salable size. Yearling Texas and Carolina terrapins and the hybrids of these stocks seem to be equally susceptible to a disease, probably bacterial, which has killed many young terrapins in the nursery house at Beaufort. Disinfecting treatments of the nursery house and boxes have not proved to be a consistent control of the disease.

❧

NOTES ON HABITS AND DEVELOPMENT OF EGGS AND LARVÆ OF THE SILVERSIDES MENIDIA MENIDIA AND MENIDIA BERYLLINA.

By SAMUEL F. HILDEBRAND,
Assistant, U. S. Bureau of Fisheries.

Contribution from the U. S. Fisheries Biological Station, Beaufort, N. C.

INTRODUCTION.

The present paper embodies the results of observations made on eggs, larvæ, and adults of the silversides *Menidia menidia* and *Menidia beryllina*. All observations were made on living or fresh material, in the immediate vicinity of the Fisheries Biological Station, Beaufort, N. C., and they extend over a period beginning in April, 1914, and ending in August, 1916.

The eggs used in this work were artificially spawned and hatched in the laboratory. The descriptions and drawings are offered with the view of affording means of identifying the eggs and larvæ with the adult. The two closely related species under consideration are compared and contrasted in order to show likenesses and differences in their habits and development.

Menidia menidia, SILVERSIDE.

ADULTS.

This fish belongs to the family Atherinidæ, the silversides, which are elongate shapely fishes with a silvery lateral stripe. Most of them are of small size, inhabiting fresh or salt water of temperate or tropical latitudes, and they usually run in large schools. The genus Menidia may be distinguished from related genera by the strongly curved premaxillary, the narrow bands of teeth on the jaws, the short lower jaw, which is included in the upper when the mouth is closed, the rounded abdomen, and the smooth, firm scales. There are only two species of the genus known from North Carolina waters. The present species may be distinguished from *Menidia beryllina*, the other species, by the larger size, by the longer anal fin, which consists of one spine and 21 to 26 soft rays, by the more posterior position of the dorsal fins, and by the black peritoneum.

This species is exceedingly abundant in the vicinity of Beaufort, N. C., inhabiting both salt and brackish water, and it is the only fish which occurs in large numbers in the shallow waters throughout the winter. Large schools may be seen along the shores of Pivers Island during the coldest days, when practically all other fishes have migrated to deeper water or to a warmer latitude.

It was learned from the examination of large collections that the ratio of males to females is about equal. It so happens, however, for unknown reasons, that at times a school which consists almost wholly of females is taken, and again the reverse is true. The females are constantly somewhat larger than the males, their average length being about 100 millimeters, with a maximum length of 123 millimeters. The average length of the males is about 89 millimeters, with a maximum length of 112 millimeters. The food of this species consists of small fish, crustaceans, algæ, and diatoms.

SPAWNING.

Spawning occurs from early spring to late summer, ripe or nearly ripe fish having been taken by the writer during March, April, May, June, July, and August. Eggs of several sizes are present in the ovaries at one time. When one lot is spawned, the eggs of the next lot are large enough to be seen with the unaided eye. The presence in the ovaries of several different sizes of eggs at one time strongly suggests that spawning occurs more than once and perhaps several times during the season. An average-sized female produces as many as 500 eggs at one time, and the eggs can easily be hatched artificially. The writer has hatched them during cool weather by merely placing them in a shallow glass dish at the time of fertilization and leaving them undisturbed and without change of water until the young fish appeared; but when the weather is warm an occasional change of water is essential.

The eggs are deposited in shallow water along grassy shores, where large schools of fish collect for this purpose. Capt. Charles Willis,[1] a resident of Morehead City, N. C., found a very large school of silversides spawning among eelgrass, in shallow water near Morehead City in May, 1915. The eggs were attached to the vegetation in clusters and became exposed at ebb tide. He then collected and preserved about a quart of the eggs, together with several specimens of the fish which he later exhibited to the author.

EGGS.

The eggs of this species are approximately 1¼ millimeters in diameter and are slightly heavier than sea water. Their form is spherical when spawned, and they remain so until hatched. The eggs to the unaided eye appear to be separate when first spawned, but as soon as exposed to water, opaque threads of considerable length become visible at the upper pole of the egg. If the water is agitated, the threads become visible more quickly than they do in quiet water; likewise the eggs appear to become attached to objects in the water or to each other more quickly. The addition of the sperm, too, seems to hasten the formation of the opaque threads. A microscopic examination, however, showed that the eggs are delivered in a transparent gelatinous mass, consisting of more or less definite strands, but, as already indicated, the mass does not become opaque and definitely threadlike until exposed to the elements. The strands again become transparent after they have been exposed for a somewhat variable period of time, and then they are elastic like rubber and of very remarkable strength. It was necessary to use glassware and glass apparatus for incubating and handling the eggs, as they readily adhered to all other materials with which they were placed in contact.

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[1] Capt. Willis was employed for several seasons by Mr. Russell J. Coles in the latter's investigations of the fishes of Cape Lookout. It was through this employment that Capt. Willis's interest in the natural history of fishes was stimulated.

It is obvious, then, that the purpose of these gelatinous strands is to afford ready means by which the eggs may attach themselves to vegetation or other objects in the water. It is likewise apparent that because of this provision the parents spawn in places where there is an abundance of vegetation.

The eggs are yellowish green, as seen in a mass with the unaided eye, but when seen singly under magnification they are semitransparent, and the slight greenish pigment appears to be in the individual granules of the yolk. It is also seen that what appeared to the unaided eye to be a single thread by means of which the egg becomes attached is really a bundle of very fine strands of uniform size. A large fat globule, occupying a central position, is always present, and smaller globules, from a few to several in number, are variously distributed. There is a perceptible space between the egg membrane and the vitelline membrane which varies in width. It is broadest at the germ disk and narrowest opposite this point; that is, the yolk sphere occupies the upper part of the egg sphere (fig. 85).

EMBRYOLOGY.

The protoplasm becomes concentrated after fertilization has taken place at the lower pole of the egg, forming a cap on the yolk of the egg. This mass of protoplasm is the blastodisk. The first cleavage plane cuts the blastodisk parallel with the axis, passing through the upper and lower pole of the egg (fig. 86). The second is at right angles to the first (fig. 87). Cleavage in these eggs is quite regular (fig. 88) and proceeds rapidly in a relatively high temperature, but it is much retarded in a relatively low water temperature; for example, the stage represented in figure 89 was reached in about six hours in a water temperature of 84° F., but in a water temperature of about 40° F. the time required to reach the same stage was approximately 48 hours.

The outline of the blastoderm on the yolk after an advanced cleavage stage is reached is only indistinctly visible, and the development can not be clearly observed. Within 12 hours after fertilization with a water temperature of 84° F., or within about 60 hours with the temperature of the water at approximately 60° F., the outline of the embryo, however, may be seen (fig. 90).[2] It is curved with the periphery of the egg and is somewhat less opaque than the remainder of the blastoderm.

Within 24 hours after fertilization with a water temperature of about 84° F., or within approximately four days with a water temperature of about 60° F., the embryo is distinctly formed and has about 12 somites. It now extends at least half the distance around the periphery of the egg, and only one large fat globule remains (fig. 91).

Two days after fertilization with a water temperature of 84° F., or about seven days with a water temperature of 60° F., the heart begins to pulsate and large blood vessels may be seen traversing the yolk. The blood at first contains relatively few corpuscles, which flow slowly, but their number and speed increase rapidly with the development of the embryo (fig. 92). Soon after circulation is well established large dark-green or brownish chromatophores appear on the yolk and smaller ones on the embryo. The embryo by this time has fully encircled the egg and is segmented throughout and capable of considerable movement, the tail being partly free. The period of incubation is about 16 days in a water temperature varying from 40 to 60° F.

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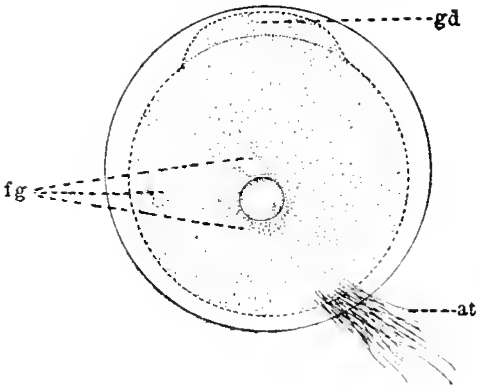
[2] The author's attention was called to an irregularity in this figure by Dr. Albert Kuntz, who kindly examined the illustrations and read the manuscript, suggesting that an abnormal egg was probably studied, as the outline of the advancing blastoderm should be regular and not broken as shown in the figure.



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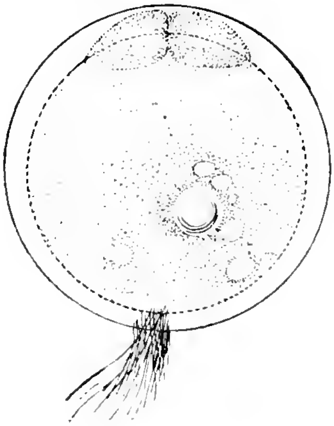

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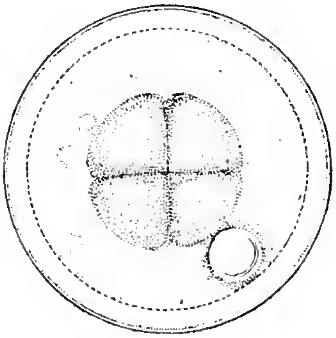

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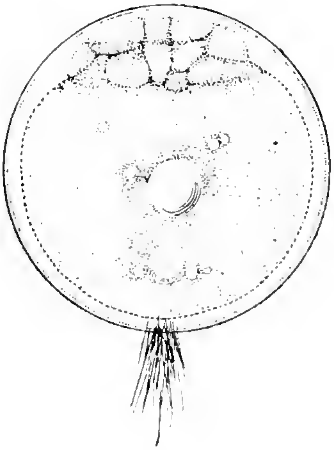

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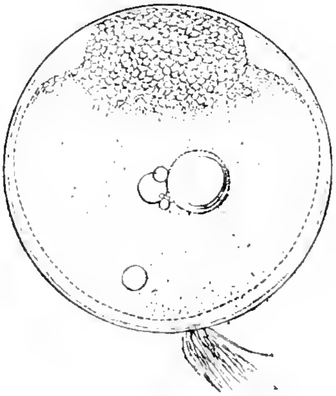

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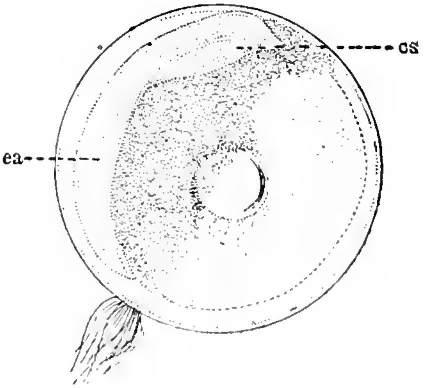

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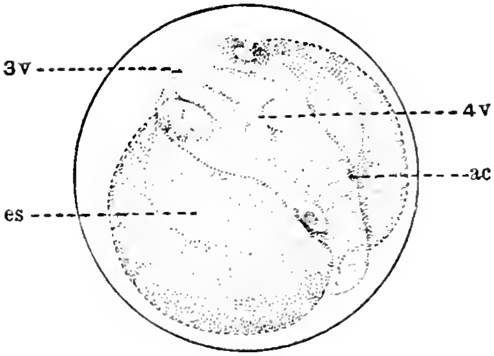
Egg of *Menidia menidia.* × 34. (Drawn by Mrs. E. B Decker.)

FIG. 85.—Egg shortly after fertilization at, adhesive threads; gd, germinal disk; fg, fat globules.
FIG. 86.—Egg in 2 cell stage.
FIG. 87.—Egg in 4 cell stage, surface view.
FIG. 88.—Egg in 32-cell stage, with 11 cells visible in side view.
FIG. 89.—Egg in advanced cleavage stage.
FIG. 90.—Egg in stage showing first outline of embryo:[3] ea, embryonic area; cs, cleavage space. (The blastoderm appears to project above the yolk of the egg more prominently in some eggs than in others.)



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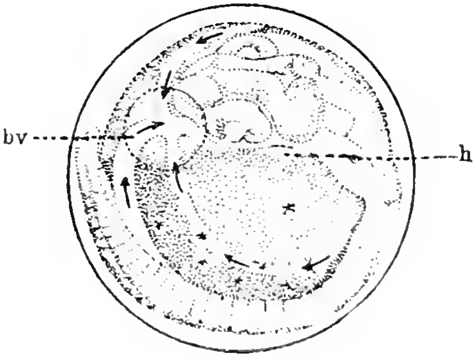

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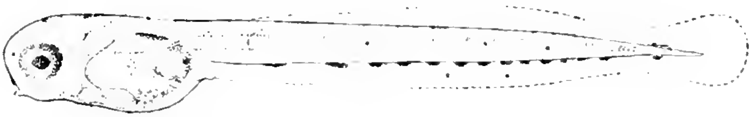

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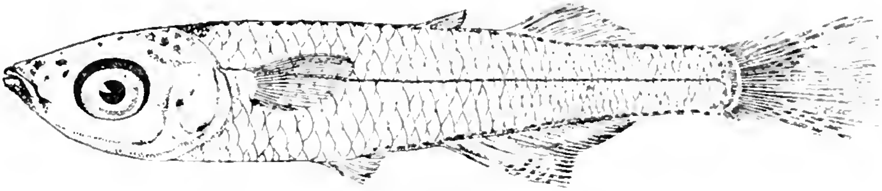

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Menidia menidia. (Drawn by Mrs. E. B. Decker.)

FIG. 91.—Surface view of egg 2 days after fertilization, water temperature, 82° F. es, embryonic shield; 3v, third ventricle of the brain; 4v, fourth ventricle; ac, auditory canal. × 37.

FIG. 92.—Egg slightly more advanced than fig. 91, showing large blood vessels (bv) transversing the yolk, arrows indicating the direction of the flow; h, heart. × 37.

FIG. 93.—Newly hatched larva. × 20.

FIG. 94.—Young fish, 13 mm. in length. × 9.

LARVÆ.

The newly hatched larva is approximately 5 millimeters in length. Considerable coiling, obviously, is necessary in order that a fish of this length may be contained within an egg only 1.25 millimeters in diameter. The larvæ are very slender, having an extremely long tail. They are very active, but for want of proper food or other causes they lived only a short time (usually about three days) in the aquarium after hatching. The yolk is completely absorbed by this time, but no important structural changes are evident. The newly hatched fry are highly transparent, only a few yellowish-green pigment spots being present. A few large spots occur on the upper surface of the head and a row of smaller ones along the base of the ventral fin fold. Circulation, due to the transparency of the newly hatched fish, can be nicely observed with a low power of the microscope. The blood may be seen flowing through the aorta to the tail, then curving sharply and returning through the caudal vein. One large blood vessel is still evident on the small yolk yet remaining. The vertical fins appear as continuous folds, surrounding the entire caudal portion of the body (fig. 93). Swimming appears to be accomplished by the very rapid vibration of the tail. The young fish has assumed practically all of the characters of the adult when it reaches a length of 13 millimeters, and it is then easily recognized (fig. 94).

Menidia beryllina, SILVERSIDE.

ADULTS.

This fish differs from *M. menidia* in the smaller size, in the shorter anal fin, which consists of 16 to 19 soft rays, in the more anterior position of the dorsal fins, and in the pale silvery peritoneum. It is much less abundant than *M. menidia*, and it inhabits only fresh and brackish water in the vicinity of Beaufort, N. C., although it is reported from salt water from other localities. It is fairly common in the mullet pond and in the fresh or brackish water creeks along the inland waterway and above the "narrows" in Newport River.

The females, as in the foregoing species, are somewhat larger than the males, reaching an average length of about 61 millimeters and a maximum length of 72 millimeters, while the males reach an average of only about 55 millimeters and a maximum length of 65 millimeters. The ratio of the males to the females appears to be about equal. The food of this species consists of small fish, small crustaceans, diatoms, and algæ.

SPAWNING.

This fish, as does *M. menidia*, spawns throughout the summer, or from March to September. The author has taken ripe or nearly ripe fish during March, April, May, June, and July, but the small size of the young taken during October and November indicates that it spawns as late as September. This species also selects shallow water with an abundance of vegetation for its spawning ground. It is quite evident that this fish, as does *M. menidia*, spawns several times during one season, for it has ova of several sizes in the ovaries at one time, and when one lot of eggs is ripe those of the next largest size are big enough to be plainly visible with the unaided eye.

DEDUCTIONS CONCERNING THE AIR BLADDER AND THE SPECIFIC GRAVITY OF FISHES.

By HARDEN F. TAYLOR,
Chief Technologist, U. S. Bureau of Fisheries.

The function of the air bladder in fishes has been a subject of discussion since the time of Aristotle, all manner of uses having been suggested for it—flotation adjustment, sense organ, manometer, barometer, respiration reservoir, sound producer, steering device, and the like. The most obvious function is that having to do with adjusting the equilibrium of the fish in water, and, knowing as we do the bewildering diversity of modification of most other organs among the thousands of species of fishes which are known, it is not at all surprising that the air bladder has also been adapted to perform many functions other than the principal and obvious one. For a brief description of the air bladder of fishes and a discussion of its functions see Tower (1902), Goodrich (1909), and Günther (1880).

It is not necessary in the present connection to consider the various secondary functions of the air bladder. The mere fact of its presence necessarily affects the specific gravity of fishes, and it is on this point that this discussion centers.

The specific gravity of the fat-free substance of salt-water fish (including backbone, but not the head and viscera) can be shown to be about 1.076. For the present purpose that figure will be taken for the whole fat-free fish. Full sea water has a specific gravity of about 1.026. A 10 kg. fish, fat-free and exclusive of air bladder or other spaces, would have a volume of $\frac{10000}{1.076}=9293$ cc. In order to be in equilibrium with sea water of the specific gravity mentioned, it should displace $\frac{10000}{1.026}=9746$ cc. An air bladder or other space of $9746-9293=453$ cc. is necessary to give the fish the required displacement. For water of increasing salinity, from pure fresh water to most concentrated sea water, the following table shows the corresponding air-bladder volume necessary to float each 10 kg. of fish whose specific gravity is 1.076:

Specific gravity of water.	Volume of air bladder.	Pressure in air bladder, millimeters mercury.	Specific gravity of water	Volume of air bladder	Pressure in air bladder, millimeters mercury.
	Cc.			*Cc*	
1.000	706	760	1.020	511	1,030
1.005	657	817	1.025	463	1,159
1.010	608	882	1.026	453	1,188
1.015	559	959	1.030	416	1,289

This table shows that if fish live in and are adjusted to fresh water and if they travel seaward it will be necessary for the air bladder to become smaller. In those fishes in which the air bladder is closed (as in all the Acanthopteri, or spiny-rayed species, which are typically marine) the volume may presumably be reduced by resorption of some gas in the blood and the discharge of it into the sea, or the gas volume may be compressed, in which case the pressures developed in the air bladder corresponding to the various salinities are shown in the table in terms of millimeters of mercury, the assumption being made that when the fish is adjusted in fresh water its air-bladder pressure is 1 atmosphere (760 mm.). In nearly all the teleost fishes, except the spiny-rayed fishes, the air bladder is provided with a pneumatic duct connecting either with the alimentary canal or with the exterior. Presumably, excess of gas may be expelled through this duct. Some of our most important species, such as salmon, shad, and herring, have this duct.

If the fish lives in and is adjusted to sea water and travels in the direction of a diminishing salinity gradient, the conditions are entirely different, for in this case a migration toward fresh water will demand an enlarging air bladder. If, however, the air bladder is at 1 atmosphere when the migration begins, then the pressure must become less than 1 atmosphere, or a partial vacuum must be established in the air bladder, which seems quite improbable. As an alternative to this we may suppose the gas to be absorbed into the blood from the surrounding sea water and discharged into the air bladder. Apart from the physicochemical and physiological difficulties involved in this gas transference against pressure, it is obvious that the mere pumping of gas into the air bladder will be without influence on the specific gravity of the fish if it merely develops pressure and will be effective only in so far as it actually expands or stretches the fish to a larger size. This method of reducing specific gravity appears quite as improbable as the method that would involve a partial vacuum. Unless some other means is found the fish will have to maintain itself afloat by constant muscular effort if it goes to water of a lower salinity.

The specific gravity of a fish varies with the amount of fat present in the tissue. In fact, Bull (1896, 1897) investigated the possibility of determining the fatness of fish quickly and simply by determining the specific gravity of the fish, and his results, while not altogether satisfactory, are promising. The foundation of this work is, of course, the fact that the specific gravity of fish fat or oil is less than 1 (usually about 0.925), while that of fat-free substance is greater than 1 (about 1.076), that is, fats float on water, while fat-free fish substance sinks. When amounts by weight (W_1 and W_2) of two substances of different specific gravities (S_1 and S_2) are combined, the resultant specific gravity of the whole (S_{1+2}) is given by the formula[1]:

$$S_{1+2}=\frac{W_1+W_2}{\frac{W_1}{S_1}+\frac{W_2}{S_2}}=\frac{S_1S_2(W_1+W_2)}{W_1S_2+W_2S_1}.$$

On a percentage basis (where $W_1+W_2=100$):

$$S_{1+2}=\frac{100\,S_1S_2}{W_1S_2+W_2S_1}.$$

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[1] The formula for this relation given by Bull (1897, p. 641), $\frac{Ff+Tt+Vv}{100}$, is in error. In this formula F and f, T and t, V and v are, respectively, the weight and specific gravities of fat, dry susbtance, and water

EGGS.

The eggs of this species are not quite spherical when first spawned, and they are somewhat smaller than those of *M. menidia*, their greatest diameter being approximately 0.75 millimeter. The action of the eggs after spawning, with respect to adhering to objects in the water, is identical in the two species; but under magnification it is seen that in the present species the gelatinous threads are comparatively few in number, and one of them is always much enlarged (fig. 95), while in *M. menidia*, as already shown, they are very numerous and of uniform size. The eggs of the two species appear to be identical in all other respects

EMBRYOLOGY.

Nothing essentially different from *M. menidia* in the embryology of this species was noted (figs. 95, 96, and 97). The eggs hatched in a water temperature varying from 78 to 82° F. on the eighth, ninth, and tenth day after fertilization.

LARVÆ.

The newly hatched larvæ are approximately 3.5 millimeters in length, or 1.5 millimeters shorter than the newly hatched larvæ of *M. menidia*, and it is only in size that they can be readily distinguished from the latter (fig. 98). Therefore, what was previously stated with respect to the larvæ of *M. menidia* also applies to the present species. The development of the young fry, too, appears to be identical, except that in the present smaller species the development with respect to size is proportionately slower, although from field observations it is evident that maturity is reached just as early.

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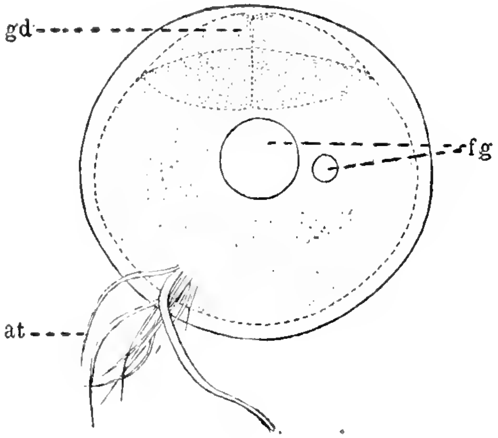

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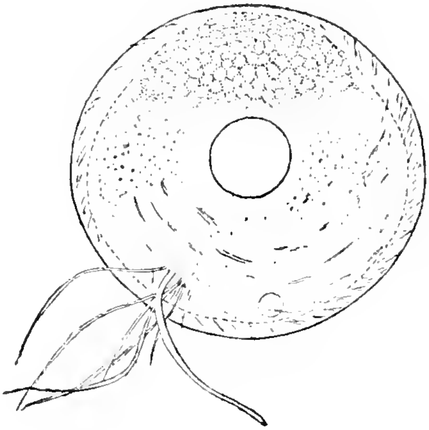

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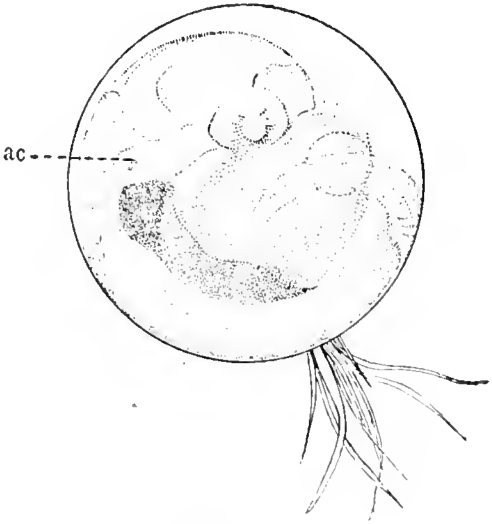

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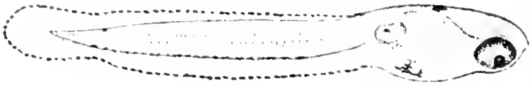

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Menidia beryllina. (Drawn by Mrs. E. B. Decker.)

FIG. 95.—Egg in 2-cell stage. at, adhesive threads; gd, germinal disk; fg, fat globules. × 67.
FIG. 96.—Egg in advanced cleavage stage. × 67.
FIG. 97.—Egg 2½ days after fertilization, water temperature 82° F.: ac, auditory canal. × 67.
FIG. 98.—Newly hatched larva. × 22.

Calculating the specific gravities of a fish on the two figures assumed above (0.925 for fat, 1.076 for fat-free substance), we have the following specific gravities of fish with increasing percentage of fat:

Per cent of fat.	Specific gravity of fish.	Per cent of fat.	Specific gravity of fish.
0	1.0760	14	1.0519
2	1.0726	16	1.0486
4	1.0692	18	1.0453
6	1.0656	20	1.0419
8	1.0621	22	1.0385
10	1.0587	29.34	1.0260
12	1.0553	46.55	1.0000

Thus, a fish which increases in fat content diminishes in specific gravity. At 29.34 per cent fat the fish without air bladder would be in equilibrium with sea water and at 46.55 per cent fat (if it were possible) would float in fresh water without air bladder.

How does the air bladder react to those changing specific gravities? As the fish grows fatter the air bladder must occupy less and less space, as shown in the following table. This table begins with a 10 kg. fish without fat and shows how the air bladder must change as the fish adds fat, so that each weight has the percentage of fat indicated, the other constituents of the fish remaining constant.

Fat in fish (per cent).	Total weight of fish	Specific gravity of fish substance.	Volume of solid fish substance.	Displacement necessary to float fish in sea water, specific gravity=1.026.	Air bladder volume necessary.
	a	b	$c=\left(\frac{a}{b}\right)$	$d=\left(\frac{a}{1.026}\right)$	$c-d$
	G		*Cc.*	*Cc.*	*Cc*
0	10,000	1.0760	9,293	9,740	453
2	10,204	1.0726	9,513	9,945	432
4	10,416	1.0692	9,741	10,152	411
6	10,638	1.0656	9.983	10,368	385
8	10,869	1.0621	10,233	10,593	360
10	11,111	1.0587	10,495	10,829	334
12	11,363	1.0553	10,767	11,075	308
14	11,628	1.0519	11,054	11,323	279
16	11,904	1.0486	11,351	11,602	251
18	12,195	1.0453	11,666	11,880	220
20	12,500	1.0419	11,997	12,183	186
22	12,820	1.0385	12,335	12,495	160
29 34	14,152	1.0260	13,793	13,793	0

These figures demonstrate clearly that as the fish becomes fatter the specific gravity of the fish substance diminishes and the necessary air-bladder volume becomes smaller and smaller. Thus, in a fish of 22 per cent fat (which is not uncommon in herring and salmon) the fish would be in equilibrium with sea water (specific gravity = 1.026), with scarcely more than a third (160 cc.) as much air-bladder volume as would be required for a fish free from fat. At 29.34 per cent fat the fish would be in equilibrium with sea water without an air bladder. Thus, fat can take the place of the air bladder and make the latter unnecessary.

We saw above that a fish must find some means of increasing its displacement if it is to migrate from salt water to fresh water and not sink. With the several increments of fat the fish would be in equilibrium with water of the specific gravities shown below without any change of air bladder volume of 453 cc. per 10 kg. body weight.

Per cent of fat.	Specific gravity of water.
0	1.0260
2	1.0239
4	1.0217
6	1.0193
8	1.0171
10	1.0158
12	1.0127
14	1.0097
16	1.0084
18	1.0062
20	1.0040
22	1.0025
25.3	1.0000

It appears from these figures that a fish living at sea and accumulating fat would find itself more at home physically in fresher water without the necessity of enlarging the air bladder. May this not be the influence which directs salmon and shad from salt water to the mouths of rivers? Indeed, it seems unavoidable to conclude that such difficulties in navigation as are introduced by 20 per cent and more of fat must have a profound influence on the movements of the fish. The changes that take place in composition of salmon have been extensively studied. The fluctuations of body composition of the salmon at different stages of the life cycle were studied by Miescher-Ruesch (1880), Paton (1898), Greene (1914, 1919), and those of the herring by Hjort (1914).

Briefly, the career of the Atlantic salmon at sea is as follows: Two or two and one-half years getting its growth, developing muscle and bony tissue (a period obviously of high body specific gravity), then in the third year the accumulation of much fat, whereupon the fish moves to fresh water in the fourth year, when the spawning migration is performed. The large accumulation of fat is consumed in the development of the reproductive organs and in supporting the fish during the journey in fresh water when no food is taken. We do not know so much of the shad as we do of the salmon, but what information we have agrees in a general way with the above.

Apparently, therefore, the fish can not well go into fresh water before a sufficient quantity of fat has been accumulated, because of difficulties in keeping afloat. After the fish has accumulated the fat there would seem to be a strong influence directing it to fresh water.

There is another possible means of overcoming the excessive buoyancy of fat in sea water. That is, the fish may descend until the pressure of the water, by reducing the volume of the air bladder, reduces the displacement of the fish to the necessary extent. This reduction of displacement, with increase in specific gravity, must always occur, in any event, when a fish containing an unprotected air bladder descends. The deeper the fish goes into the water the more easily it descends, the excess weight of the fish becoming greater and greater. If the fish begins to rise, the excess weight over displacement, which must be overcome by muscular exertion, becomes less. The effect to be realized from this cause depends, however, on the volume of air bladder present when the fish is at the surface, for, obviously, when, say, 500 cc. of gas is compressed to 250 cc., a greater difference in specific gravity will result than when 100 cc. of gas is compressed to 50 cc., though the same amount of pressure would be required in either case. Therefore, in a fish whose air bladder had been reduced (if such reduction really occurs) in response to accumulating fat, the effect on specific gravity of diving would be correspondingly reduced.

In the following table there is shown for the several percentages of fat the corresponding depth to which a fish must descend in fresh and salt water, respectively, so that the pressure of the water would equalize the displacement by compressing the air bladder. There is also given the excess weight in grams over the displacement which the body of a 10 kg. fish would acquire by diving 10 m. in water whose density is 1.026 if the fish is in equilibrium at the surface.

Per cent fat.	Depth for equilibrium, fresh water.	Depth for equilibrium, sea water, specific gravity=1.026.	Load in excess of displacement, 10 meters depth.	Per cent fat	Depth for equilibrium, fresh water.	Depth for equilibrium, sea water, specific gravity=1.026.	Load in excess of displacement, 10 meters depth.
	Cm	*Cm.*	*G.*		*Cm.*	*Cm*	*G.*
0	....	....	253	12	486	474	158
2	50	49	. .	14	644	628	......
4	105	102	211	16	831	810	130
6	182	177	. .	18	1,094	1,066	......
8	266	259	186	20	1,582	1,542	96
10	368	358		22	1,881	1,833	......

The air bladder is present in the great majority of fishes. In the Selachii it is absent, in the teleosts it is generally present, although the Heterosomata or flatfishes, Xiphias, the swordfish, Menticirrhus, all the Alepocephalidæ, and a few other families or genera are without air bladders. In all the spiny-rayed fishes (which are typically marine) the air bladder when present has no outlet duct in the adult fish. Any reduction in volume of the air bladder must therefore be accompanied, at least temporarily, by pressure. The pressure might be relieved by absorption of gas into the blood. It does not seem at all unlikely that the varying salinities of ocean water guide such fishes as the mackerel, tuna, herring, bluefish, sharks, and many others. Temperatures, oxygen and CO_2 content, plankton, and other food supply have been studied as directing influences, but it is difficult in every case to show what the immediate effect of the influence is on the fish. In the case of specific gravity the direct effect is obvious and unavoidable.

It would be exceedingly unsafe to make assumption as to what method the fish uses to maintain itself in equilibrium with the water. We know from the work of Tower (1902) and others that the composition of the gas in the air bladder of fishes varies. It contains more and more oxygen with increasing depths, so that fishes taken from great depths have nearly pure oxygen in the air bladder. It was shown that the air bladder very probably performs an important respiratory function. Certainly the loading into the blood stream or the removing therefrom of large quantities of gas could not possibly fail to have a profound effect on the physiological functions of the fish even if fatal embolisms did not occur.

The following conclusions are drawn:

1. Fish on migrating from water of low salinity to that of high salinity may adjust specific gravity by reducing the size of air bladder. In the reverse direction there is no apparent means for voluntary adjustment.

2. As a fish puts on fat its body specific gravity diminishes, *pari passu*, and in proportion to the amount of fat present (*a*) its navigation in salt water is more difficult; (*b*) fresher water is better suited as a physical medium. Until a certain amount of fat is accumulated migration from salt to fresh water must be difficult or impossible.

3. Reduction of volume of air bladder may possibly be effected by (*a*) resorption of gas from bladder to blood and expulsion through gills; (*b*) direct expulsion of gas through pneumatic duct (except in Acanthopteri); (*c*) diving, whereby hydrostatic pressure reduces the volume. The effect produced by diving a given depth is proportional to the absolute volume of the air bladder.

4. Diminishing specific gravity consequent upon increasing fatness probably constitutes a strong directive influence governing the movements of fishes, both marine and anadromous.

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FIG. 97.—Sea mussels growing on a wharf pile at Vineyard Haven, Marthas Vineyard, Mass. Closely associated with the shellfish are hydroids, sea anemones, sea pork, and sea squirts. Two small fish (cunner) are in the act of browsing on the shellfish. A jellyfish and squid are shown to the right of the colony. (Photograph of a model on exhibit at the American Museum of Natural History, New York. Photograph by courtesy of the American Museum of Natural History.)

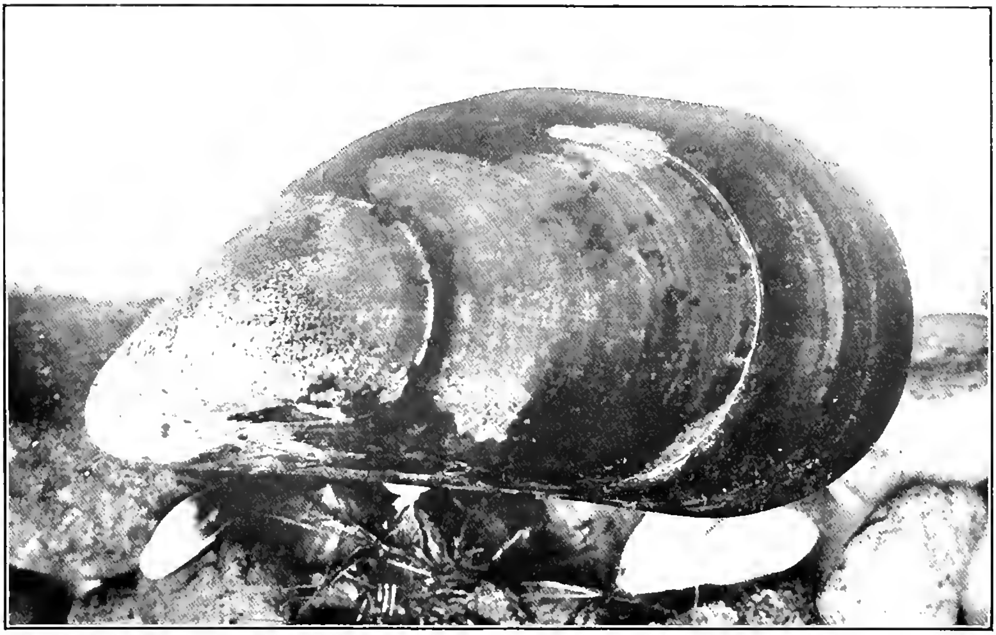

FIG. 100.—The sea mussel *Mytilus edulis* Linnaeus, showing foot distended and attachment by byssus.

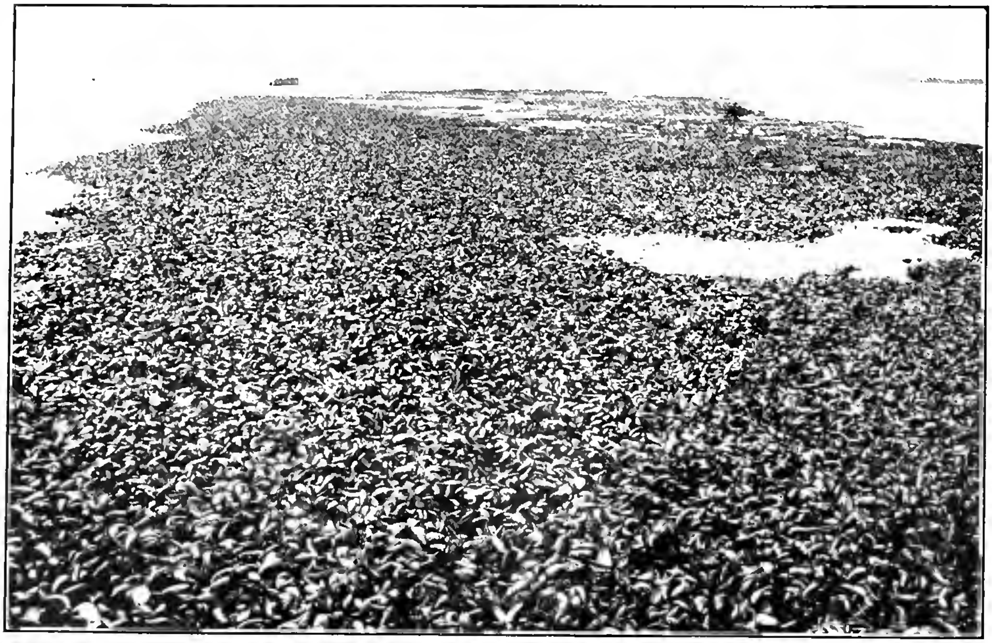

FIG. 101.—A bed of sea mussels in Menemsha Pond, Marthas Vineyard, Mass., exposed at low tide. Each square yard of surface is covered with more than a bushel of the shellfish.

BIOLOGY AND ECONOMIC VALUE OF THE SEA MUSSEL
Mytilus edulis.[1]

⁂

By IRVING A. FIELD, *Late Professor of Biology in Clark University and Special Investigator, U. S. Bureau of Fisheries.*

⁂

Contribution from the U. S. Fisheries Biological Station, Woods Hole, Mass.

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[1] After this report was completed and submitted to the Bureau but before it could be published Dr. Field's untimely death occurred in February, 1921. Consequently there was no opportunity for the author to review the final editorial corrections or to read the proof. The report was submitted to the faculty of Clark University, Worcester, Mass., in partial fulfillment of the requirements for the degree of doctor of philosophy.

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INTRODUCTION.

The object of this report is to present as completely as possible the facts known concerning the biology and economic importance of the sea mussel *Mytilus edulis* Linn. and the possibilities of developing a mussel fishery in the United States. In a previous paper (Field, 1911) the food value of the sea mussel was demonstrated to be equal to or greater than that of any other commercial shell-fish on our coast, and the mussel beds of our eastern and western coasts were shown to constitute one of our great undeveloped marine food resources. The importance of this sea mussel as a valuable source of food supply was considered so great that a more exhaustive study of the life history, distribution, and the commercial possibilities of utilizing the species was considered advisable. The results of this investigation show the possibility of adding to our food supplies millions of pounds of wholesome flesh food annually.

The material entering into this report is based upon the review of an extensive literature verified and supplemented by a series of investigations carried on during seven summers for the United States Bureau of Fisheries at its biological station at Woods Hole, Mass., and by a reconnaissance of the mussel beds on a limited portion of the north Atlantic coast. A considerable portion of the work was done in the biological laboratories of Clark University.

SYSTEMATIC AND ECONOMIC RELATIONS OF MOLLUSKS.

The term mussel, as generally used, applies to either of two groups of bivalve mollusks one of which is restricted to salt and brackish waters, the other to a fresh-water habitat.

The marine species belong to the genus Mytilus and other allied genera of the family Mytilidæ. On our eastern coast there are five species of this family representing three genera, the most important of which is the common sea mussel, *Mytilus edulis* (fig. 100, opp. p. 128), which ranges from the Arctic Ocean to Cape Hatteras. The horse mussel, *Modiolus modiolus*, is next in importance, ranging from the Arctic Ocean to New Jersey. *Mytilus hamatus*, the hooked mussel, is found from Chesapeake Bay southward and on the Gulf coast. *Modiolus demissus* (*Modiola plicatula*), the plicated mussel, is a shallow water form found from Maine to Georgia. *Modiolaria nigra* is a northern form which inhabits the deeper waters from the Arctic Ocean to Cape Hatteras.

On our western coast the family is likewise represented by three genera and five species. *Mytilus edulis* occurs from the Arctic Ocean to San Francisco. *Mytilus californianus* is common on the California coast. *Modiolus modiolus* and the straight horse mussel, *Modiolus rectus*, are also present on the California coast. *Modiolaria nigra* occurs from Arctic waters to San Francisco. The marine mussels are characterized by a byssus which is secreted from a gland located at the base of the foot.

The fresh-water mussels belong to the family Unionidæ represented by Unio, Anodonta, Quadrula, and other allied genera. They are particularly common in most of the rivers of the central United States. They secrete no byssus in the adult stage.

The phylum Mollusca comprises a great variety of forms; but there is a close relation between all the groups, which are merely modifications of the same type. It includes the chitons, Amphineura; snails, Gastropoda; mussels, clams, oysters, scallops, etc., Lamellibranchia; and the nautilus, devilfishes, and squids, Cephalopoda.

The characteristic feature of these animals is a ventral, muscular foot which usually serves for locomotion, but is much modified according to habit. The body is soft and moist and usually more or less covered with a shell which is generally either univalve or bivalve; the shell is secreted by a glandular fold of skin called the mantle. The shell often consists of three layers; an outer thick, tough portion, or periostracum; a middle prismatic layer, which is much thicker; and an inner mother-of-pearl, or nacreous layer, which is sometimes brilliantly iridescent. The adult forms show no sign of segmentation and the body cavity is more or less obliterated. The pericardium represents the chief portion of what is left of the true body cavity. Communication between the pericardium and the exterior is established through the nephridia. The respiratory organs consist of gills except in a few species, chiefly terrestrial, which possess a sort of lung. It is probable, also, that the mantle plays an important part in respiration. The nervous system consists of three ganglionic centers with connectives located respectively in the head, cerebral ganglion; in the foot, pedal ganglion; and on either side of the œsophagus, visceral ganglia. Sense organs of touch, sight, smell, and equilibrium may be present in the head region. In the development of the Mollusca segmentation of the egg is unequal and the larvæ pass through a free-swimming or trochosphere stage which is also the characteristic larval stage of the Annelida. There is also a probable relationship with the Polyzoa.

In distribution, we find the Mollusca occupying, in a general way, the whole surface of the earth at all latitudes and altitudes. They are found in the polar, temperate, and tropical regions; in the ocean; along the seashore; on land; and in fresh-water lakes, ponds, and streams. Certain snails of the suborder Stylommatophora have been found in mountains at a height of 15,000 feet; abyssal mollusks have been taken from a depth of 2,800 fathoms. There are pelagic species which are distributed over the surface of the sea, some live on the floating seaweed, while others descend many thousands of feet from the surface. It is within the Tropics, however, both on land and in the sea, that the Mollusca are most abundant both in numbers and varieties.

Protective markings of a striking nature are characteristic of many mollusks. Most of the pelagic species are colorless or tinged with blue. The nudibranchs, which are found on the floating sargassum weed, are beautifully marked with yellow and brown like the weed itself. Other species are green or red in color, similar to the algæ on which they live. The shellfish which live in the great depths beyond the reach of the faintest ray of light are characterized by thin, colorless shells, a highly developed tactile sense, and the absence of visual organs.

The length of life and age of attaining sexual maturity vary considerably for different mollusks. Mytilus reaches the adult stage in one year. The fresh-water mussels, Anodontidæ, do not reach sexual maturity until they are 5 years old. Some mollusks, nudibranchs, and the cephalopod, Rossia, appear to live for one year only, while others, as Mytilus and the oyster, may live 10 or more years; the periwinkle, Littorina, has been known to attain an age of 20 years in captivity, and the Anodontidæ, which are remarkable for their long life, may reach an age of 25 or 30 years.

The Mollusca is an old group whose fossil representatives are found in all Paleozoic deposits upward. As a group it has met the changing conditions of the world most successfully, as is clearly demonstrated by its present abundance and wide distribution. More than 28,000 living Mollusca have been described up to the present time, more than half of which are Gastropoda.

The economic importance of the Mollusca is very great indeed. The group includes species of negative as well as of positive value. In the former class may be mentioned the so-called shipworm, *Teredo navalis*, a boring lamellibranch whose habits are extremely destructive to the bottoms of wooden ships, to wharf piles, and to other submerged wooden objects, which are riddled by its borings. To prevent the destructive inroads of the shipworm it is necessary to incase the bottoms of wooden ships with a metal sheath and to coat such wooden objects as spars, buoys, etc., with verdigris paint periodically every six months.

Among the gastropods are found many voracious species armed with rasping organs against which few shellfish are safe. They prey upon many species valuable to man, such as oysters, clams, scallops, mussels, etc., by boring holes through their shells and literally eating them alive. The destructive ravages of these snails on the commercial species of mollusks amount to many thousands of dollars yearly. The Cephalopoda are also carnivorous animals of very active and voracious habits. They dart into the schools of young fishes and feed upon them in great numbers. Young lobsters and other small crustaceans often fall prey to them.

Molluscan species of positive value to man are numerous and represent every class except the Amphineura. Most of the cephalopods are good to eat and are utilized extensively as food in some countries. Although not used as such in the United States, there is no reason why they should remain a neglected food product. Squid is the most valuable bait known in the cod fisheries and for this reason often brings fancy prices. When abundant it is used for fertilizer. The cuttlefish furnishes the cuttle bone which is used as a food for canary birds, and formerly its inky secretion was sold as India ink or sepia, which was used for drawing purposes.

The gastropods include species of food value, as, for example, the large, edible snail of Europe, the periwinkle, *Littorina littorea*, which is eaten by the ton in London, but, as yet, remains unknown as a food in this country. The abalone of our western coast is beginning to be appreciated as a food through the influence of the Chinese, who have developed the fishery into a business worth many thousands of dollars annually. Its shell is remarkable for its great beauty and was formerly used by the Indians for making their money. In Europe it is used for making buttons, studs, and buckles and for decorating purposes.

The class Lamellibranchia is the most important of all from the commercial standpoint. It includes the oyster, which furnishes the most valuable fishery of the nation, the receipts from this source alone amounting to one-third the total income derived from all the fisheries of the United States. The flesh of the oyster constitutes a most delicious morsel, and the shells are used in the construction of roads, as a food for poultry, as fertilizer, and as cultch for starting new oyster beds. About 25,000,000 bushels of oysters are utilized in the United States annually. Other valuable edible lamellibranchiate species are the clams Mya and Venus, which have made the New land clam-bake famous throughout the land, and the scallops, which are popular in every hotel and restaurant of our northeastern coast.

The fresh-water mussels of our inland waters furnish pearls of rare value and shells especially adapted for the button industry and for the manufacture of articles of much beauty. So great has been the demand in recent years for the important species that the resources have been greatly depleted. Fortunately, however, the United States Bureau of Fisheries has been able to take up the problem, and, by the application of scientific methods, it is now propagating mussels to provide for the increased demand.

Not only do the lamellibranchs yield products of commercial value, but in their daily functions they perform a service which has never been estimated in dollars and cents. Their habit of setting up currents of water which are continually filtered through the gill filaments serves to remove the bacteria and other microorganisms along with quantities of floating organic particles which, if left in the water, would lead to stagnation. They constitute, therefore, one of the great purifying agents of our lakes, ponds, and streams.

The United States Bureau of the Census reported the value of the mollusk fisheries of the United States for 1908 as follows:

Oysters	$15,713,000
Hard clams	1,317,000
Long clams	553,000
Scallops	317,000
Fresh-water mussel shells	392,000
Slugs and pearls	300,000
Sea mussels	11,600
Oyster and other shells	20,000
Squid	43,000
Cockles, winkles, conchs	35,000
Total	18,701,600

ANATOMY AND PHYSIOLOGY OF THE SEA MUSSEL.

THE SHELL.

DESCRIPTION.

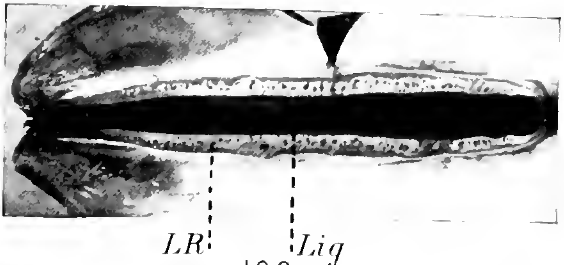
The sea mussel has a general form which may be described as triangular ovate. Anteriorly, in the hinge region, the shell presents its greatest breadth; posteriorly, it becomes narrower and flattened. The posterior edge of the shell is nearly semicircular in outline; in the dorsal region it forms almost a straight line up to the beginning of the hinge, where it bends obliquely downward at an angle of about 45° to the umbo, which is located at the tip of the shell. From the sharp point of the umbo the ventral edge of the shell extends backward in an almost straight line. In specimens of mussels growing on wharf piles in protected situations the ventral edge sometimes presents a slightly convex outline, while, on the other hand, mussels growing on the rocks or mud where they are subjected to swift currents and exposure often show a decidedly concave under surface.

The size of the adult mussel varies from 2 to 4 inches in length, from 1 to 2 inches in height, and from ¾ to 2 inches in breadth. Occasionally specimens 4½ inches long are found. The proportions of length to height and breadth vary with the age of the mussel. Individuals less than a year old show a length, breadth, and height which are to each other as 2.75 : 1.5 : 1; while in older ones they are to each other about as 2.25 : 1.15 : 1, indicating that in adults growth in breadth is proportionately more rapid than in length.

The color of the shell varies from violet or blue-black to a pale blue. When dried it takes on a brownish hue. This change of appearance is due to the hornlike covering of the shell, the periostracum, which is itself brown. The characteristic violet color of the shell comes from the thick prismatic layer which lies immediately below the thin periostracum and which contains a deep blue pigment. The general hue of the shell is therefore due to a combination of the brownish, transparent periostracum and the underlying layer of deep blue calcareous matter. This results in a variety of color variations according to the thickness and density of the periostracum and the amount and distribtion of the pigment in the prismatic layer of the shell. The arrangement of the pigment is in bands which run from the umbo in a radiating manner to the posterior end of the shell. Most commonly the stripes lie so closely together that it gives the shell surface a uniform dark blue color. Sometimes, however, the bands of color are few in number or entirely absent. In the latter case the mussel is colored a uniform brown or yellow-brown by the periostracum, while in the former case it is marked with alternate blue and brown bands which radiate from the umbo to the posterior edge of the valve.

The inner surface of the shell is divided sharply into two regions, an inner, glossy white or pinkish-white mother-of-pearl layer and an outer deep blue border about three-sixteenths of an inch wide. The line of demarcation between these two layers is sharp and may be either straight or serrated in outline. The blue layer is absent in the hinge region.

Six impressions which mark the attachment of muscles are conspicuous on the inner white surface: (1) The largest and most prominent is more or less circular in form and located posteriorly near the dorsal border. It marks the point of attachment of the posterior adductor muscle (fig. 104, *PAD*, opp. p. 132). (2) Running anteriorly from the dorsal edge of this impression is another, linear in form (fig. 104, *PRet*), which marks the point of attachment of the posterior retractor muscles of the foot and byssus. (3) A third, somewhat triangular impression lying just posterior to the impression of the posterior adductor muscle marks the insertion of the muscles of the anal membrane (fig. 104, *An*). (4) At the anterior end of the shell on the ventral border is an impression where the anterior adductor muscle is attached (fig. 104, *AAd*). (5) Just above it on the dorsal edge is another which marks the point of insertion of the anterior retractor muscles of the foot and byssus (fig. 104, *ARet*). (6) A long, narrow, linear impression extending along the lower edge of the shell from the impression of the anterior adductor muscle to that of the posterior adductor muscle and just inside the border of the nacreous layer forms the line of attachment for the pallial muscles (fig. 104, *Pal*).



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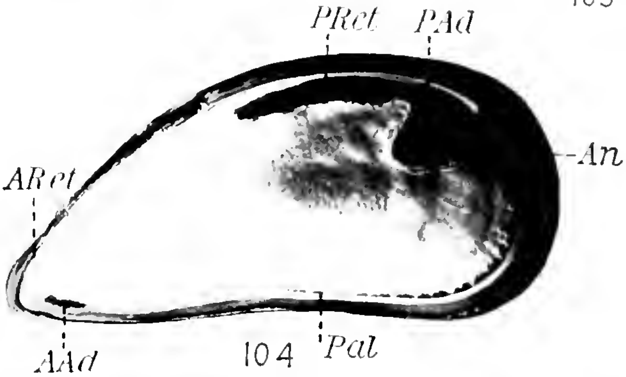

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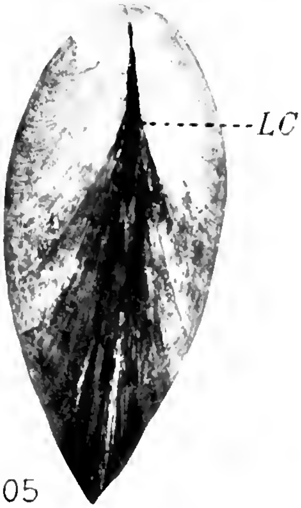

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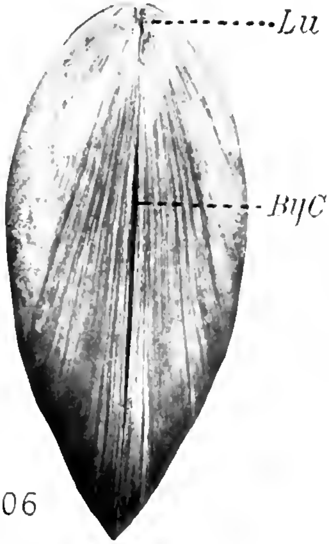

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FIG. 102.—Interior view of hinge ligament. *Lig*, ligament; *LR*, ligament ridge.

FIG. 103.—Interior view of anterior end of a valve showing four hinge teeth, *T*.

FIG. 104.—Inner surface of a valve showing muscle impressions. *AAd*, anterior adductor muscle; *An*, anal muscle; *ARet*, anterior retractor muscle; *PAd*, posterior adductor muscle; *Pal* pallial muscle; *PRet*, posterior retractor muscle.

FIG. 105.—Dorsal surface of a shell from which periostracum and ligament have been removed. *LC*, ligament cleft.

FIG. 106.—Ventral surface of a shell from which periostracum has been removed. *ByC*, byssus cleft; L*u*, lunula.

The two valves are attached at their anterior dorsal edges by means of a hinge plate over which the periostracum extends from one valve to the other. Teeth are present at the anterior end of the hinge in numbers varying from one to six, the most common number being three or four. The teeth of one valve are so arranged that they fit into the depressions between the teeth on the opposite side. In size they are small, rarely over a millimeter in length, and in form they are conical pointed knobs or wedge-shaped lamellæ (fig. 103, *T*).

The ligament (fig. 102, *Lig*), a straight, brownish colored, elastic rod, lies between the two valves just beneath the hinge band and helps to unite the shell edges. In cross section it presents the form of an ellipse with its long diameter lying in a horizontal position. It is bounded laterally by parallel ridges, the ligament ridges (fig. 102, *LR*), which have a very characteristic structure. They are chalky white in color and perforated with numerous pores. Each ridge terminates in a fine point both anteriorly and posteriorly. The median surfaces are concave to fit snugly against the ligament when the shell is normally open; consequently when the valves are closed by contraction of the adductor muscles the ligament is compressed and its elasticity tends to counteract the action of the muscles (fig. 107). As a result, when the adductor muscles relax the ligament forces the shell open again. This explains why the shells of dead mussels are always open.

The umbo is at the anterior end of the shell and forms a sharp beak, off the ventral side of which may be found, often hidden by the periostracum, a special structure called the lunula (fig. 106, *Lu*, opp. p. 132), which bears a definite relation to the hinge teeth. It consists of a series of semicircular furrows and ridges which run out peripherally from the teeth and terminate at the umbo. Each furrow corresponds to a tooth; and each ridge, to a depression between the teeth. The lunula is conspicuous only in individuals where the teeth are comparatively large in size and number.

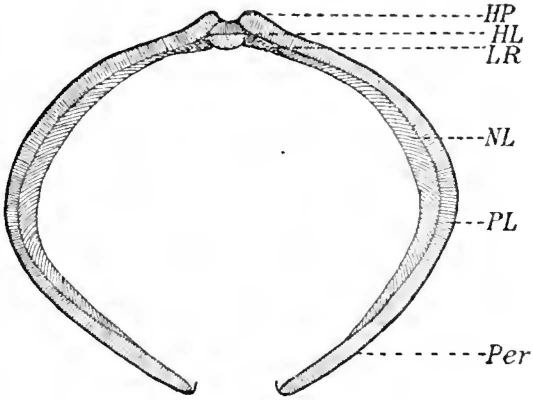

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FIG. 107.—Cross section of a shell in hinge region in diagrammatic form to show relation of ligament to hinge plate and valves. *HL*, hinge ligament; *HP*, hinge plate; *LR*, ligament ridge; *NL*, nacreous layer; *Per*, periostracum; *PL*, prismatic layer.

When the valves of a normal shell are shut they form a complete closure. If, however, they are first treated with a solution of potassium hydroxide, which removes all the periostracum, it will be found when they are closed that there are two places where the edges fail to come in contact. On the ventral side in the middle of the shell there is a fissure through which the byssus may project, the byssus cleft (fig. 106, *ByC*). In the normal shell this cleft is hidden by a fold of the periostracum which incloses the marginal blood sinus. The structure is such as to act as a cushion which presses against the byssus when the shell is closed. Corresponding to the byssus cleft on the dorsal side in the hinge region is another opening between the valves, the ligament cleft (fig. 105, *LC*, opp. p. 132). In the complete shell this depression is covered externally by the periostracum and internally by the underlying ligament.

HISTOLOGY.

If the shell of the sea mussel is broken or cut in cross section, three distinct layers, sharply defined from each other, are visible to the naked eye: An outer, thin, cuticular layer, the periostracum; a middle violet-colored portion, the prismatic shell; and an inner glossy white or pink substance, which often reflects iridescent colors, the mother-of-pearl, or nacreous, layer. Under high magnification each of these parts shows a characteristic structure.

The periostracum generally covers the whole outer surface of the shell and extends over the free edge for a short distance over the inner surface where it terminates in a fold of the mantle border. It is a smooth, glossy cuticula, thinnest in the region of the umbo, where it is often completely worn off as a result of exposure at low tide and the action of strong waves and currents. The hinge of the shell is formed from the periostracum which extends over from one valve to the other. In cross section the periostracum presents three layers (fig. 111, *Per*, p. 136). The outer and inner portions consist of a clear, transparent, brownish substance which does not readily stain with any of the ordinary dyes. The middle portion is colorless and has an affinity for plasma stains. In the region of the mantle edge from which it is an outgrowth the layer consists of a single layer of cells, but as the outer surface of the shell is approached the cells disappear, leaving a series of cavities to mark the middle zone. The periostracum may, therefore, be divided into three distinct areas: An outer, middle or hollow, and an inner layer. The periostracum is attached to the layer of the shell lying immediately below it by means of trabeculæ which are embedded in the calcareous substance.

The blue portion of the shell or middle layer is composed of fine needlelike filaments of calcareous matter closely united into a single structure by an organic matrix of conchiolin (fig. 108, p. 135). When a valve is broken in cross section and examined with a hand lens this layer presents a series of alternate ridges and grooves with glistening surfaces which extend across the shell. With higher magnification it is possible to see that the prisms are long and almost straight and so arranged as to form an angle of about 45° with the outer shell surface (fig. 111, *PL*, p. 136). The pigment, which is more abundant on the peripheral surface of the layer, is deep blue or violet in color and is distributed in the form of parallel bands which run across the prisms at an angle of about 30° (fig. 112, *PB*, p. 136). Around the ventral and posterior borders of the shell there is no inner nacreous layer present, consequently the prismatic shell lies in direct contact with the outer fold of the mantle edge.

The nacreous or mother-of-pearl layer covers the inner surface of the shell out to the mantle line as a boundary. It is thickest in the anterior and middle regions and thinnest at the border. This is the only layer which continues to grow in thickness throughout the life of the mollusk. The nacreous and prismatic layers lie in direct contact with each other without any intervening substance to connect them. The structure of the nacre consists of a series of thin lamellæ with irregular edges placed one on the other with their surfaces lying horizontal to the surface of the shell. When seen in cross section of the shell under high magnification they appear as fine irregular parallel lines (fig. 111, *NL*, p. 136). If a portion of the nacreous layer is dried for some time or is treated with sodium hydroxide it becomes fragile and has a tendency to break up into flakes whose surfaces mark the line of cleavage between the separate lamellæ.

Microscopic examination of the flat surface of one of these flakes near its edge will show distinctly the leaflike layers with their irregular edges (fig. 109). The transverse plane of cleavage always follows the zigzag edges. A surface view of a single lamella under very high magnification reveals a fine network with meshes of a polygonal form (fig. 110).

The ligament when examined in cross section with an ordinary hand lens presents three distinct layers; the outer portion is marked by the dark brown periostracum, the middle part is composed of a yellow-brown homogeneous substance, while the inner layer is of the same color but marked with numerous horizontal dark brown lines. Under higher magnification four distinct and separate layers are visible.

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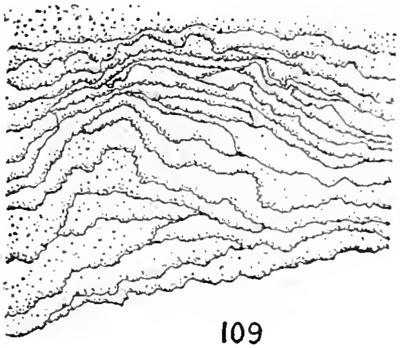

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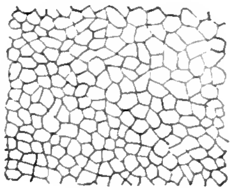

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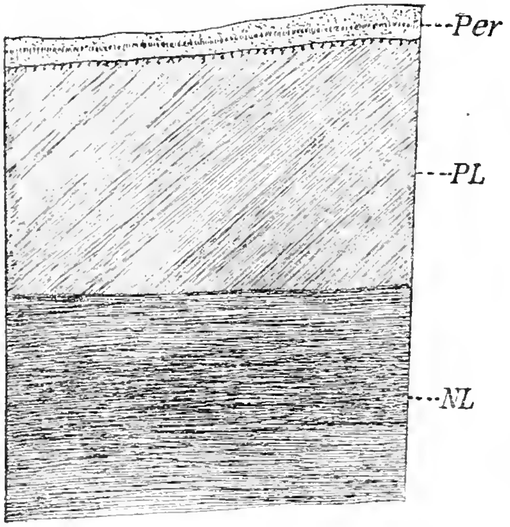
FIG. 108.—Transverse section through prismatic layer of shell, showing needlelike prisms, which are held together by an organic matrix of conchiolin. × 854.

FIG. 109.—Fragment of nacreous layer showing overlapping lamellæ. × 500.

FIG. 110.—Surface view of nacreous layer very highly magnified.

The outermost layer consists of the periostracum (fig. 113, *Per*, p. 136), which is really not a part of the ligament proper, although it is fused so closely with it as to form a unit body. What appears to be the middle layer under low magnification is divisible into two sharply separated parts when examined with stronger lenses. The outer portion of this layer presents a homogeneous structure similar to a film of gelatin, with a yellowish color often tinged with blue or green (fig. 113, *HyL*). The inner part of the middle layer is of a darker shade and strongly granular in appearance, due to an abundance of irregular masses of lime crystals, many of which are aggregated into starlike bodies. A few of these crystals may be seen scattered in the homogeneous layer close to its border next the granular layer (fig. 113, *GL*). The inner layer is distinguished from the others by its cross-striped appearance (fig. 113, *IL*). It is marked by numerous fine vertical lines across which there run at right angles many dark brown bands of varying width. Crystals of lime salts are present in small numbers scattered throughout the substance of this layer. The crystals may be readily removed by treating the sections



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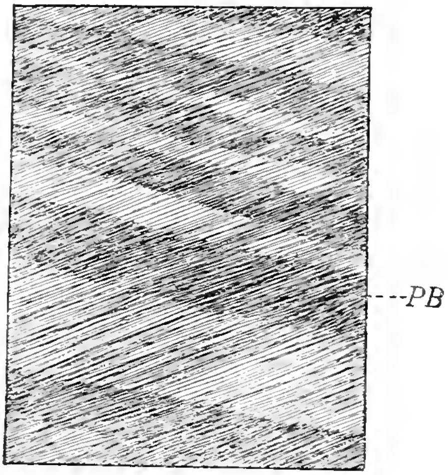

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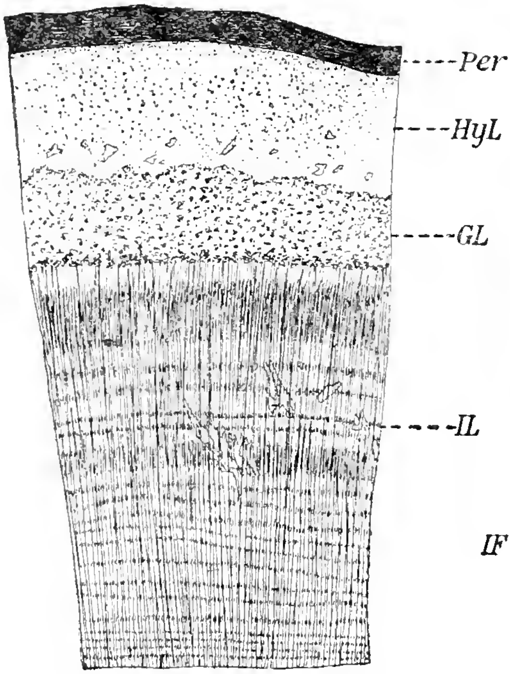

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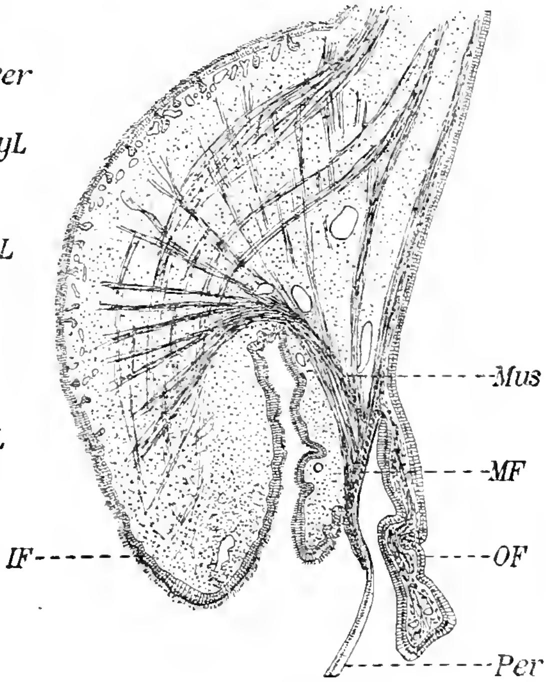

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FIG. 111.—Cross section of piece of shell. × 50 approximately.

FIG. 112.—Section through prismatic layer. × 45.

FIG. 113.—Cross section through ligament. × 26.

FIG. 114.—Cross section through edge of mantle. × 35. Fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red.

ABBREVIATIONS.—*GL*, granular layer; *HyL*, hyaline layer; *IF*, inner fold; *IL*, inner layer containing a few groups of calcium crystals; *MF*, middle fold, showing origin of periostracum (*Per*) from its outer edge; *Mus*, muscle fibers; *NL*, nacreous layer; *OF*, outer fold; *PB*, pigmented bands; *Per*, periostracum; *PL*, prismatic layer.

with weak nitric or hydrochloric acid. The staining reactions of the decalcified sections of the ligament are characteristic; the middle layer has a tendency to take up the plasma stains, while the inner layer takes up the basic dyes.

FORMATION.

The periostracum is an outgrowth from a specialized portion of the mantle edge. If a cross section of the mantle is examined under low magnification it will be seen that the edge of the mantle is divided into three distinct folds which run parallel with its edge. They may be designated by their position as the outer, middle, and inner folds. From the outer surface of the middle fold the periostracum arises as a thin cuticula which is secreted by a layer of epithelial cells having characteristic, long, elliptical nuclei and fibrils which lie at an oblique angle with the surface of the periostracum. Numerous muscle fibers from the mantle terminate among these cells (fig. 114, *Mus*, p. 136). The youngest portion of the periostracum, which lies in contact with the secreting cells, is a thin, transparent, homogeneous structure, but as it extends out beyond the limits of the mantle edge it grows progressively thicker and becomes differentiated into the three layers which have already been described. The periostracum grows over the edge of the outer fold, beyond which it becomes attached to the outer surface of the prismatic layer of the shell.

The prismatic or blue layer of the shell is secreted by the low columnar epithelial cells which cover the outer surface of the outer fold of the mantle edge. As fast as the material is built up along the edge of the shell its outer surface comes in contact with the outgrowing periostracum, to which it becomes attached.

The epithelium of the outer mantle surface is composed of small cubical cells and gland cells which secrete the mother-of-pearl (fig. 114, p. 136). The process is continuous, so that as the animal grows older this layer continues to grow thicker, giving the shell the unusually firm and heavy character which is often noted in old mussels. Exposure to the rough action of waves and currents stimulates the cells to more rapid secretion.

The ligament arises from a layer of tall columnar epithelial cells which lies immediately below it.

ATTACHMENT TO THE BODY.

The whole outer surface of the fleshy part of the body is more or less intimately connected with the inner surface of the shell. The epithelium of the mantle forms a rather weak attachment, while the muscles adhere most tenaciously at their points of union with the shell.

The epithelial cells of the outer surface of the mantle lie in direct contact with the inner surface of the shell and are attached to it by the secretion of a soft, gummy substance from which the shell is being formed constantly. The attachment may be likened to that of a label pasted on a bottle.

In case of the muscle attachments, a very different type of adhesion is found. Here the epithelial cells of a highly specialized nature serve as anchoring organs. They are so intimately attached to the bundles of muscle fibers at their proximal ends that it is difficult to distinguish them from the contractile tissue without applying staining methods. Ordinarily muscle fibers stain more deeply than do the supporting epithelial cells. Distally the epithelial cells are embedded in the surface of the shell, making an attachment so strong that it is impossible to separate the mass from the shell without applying acid to dissolve away the calcareous substance in which they are firmly fixed.

CHEMICAL COMPOSITION.

The shell of the mussel consists of an organic base infiltrated with mineral salts, as has been shown above in the description of its histological structure.

The organic matrix is an albuminoid substance called conchiolin, the composition of which, according to Wetzel (1900), is carbon 52.3 per cent, hydrogen 7.6 per cent, nitrogen 16.4 per cent, and sulphur 0.65 per cent. It is readily obtained by mascerating the shells in hydrochloric acid and boiling the residue in sodium hydroxide in which the conchiolin remains undissolved. Treated with hot mineral acids it goes into solution. Wetzel (1900) found that the substance gives Millon's reaction, and from the decomposition products formed in boiling sulphuric acid he obtained glycocoll, leucin, and an abundance of tyrosine. He assigns this compound to a place between casein and egg albumin.

The inorganic constituents of the shell consist chiefly of calcium carbonate with which are present small quantities of sulphates, oxides, or carbonates of magnesium, iron, manganese, and silica. The following analysis by Mr. Adrian Thomas will serve to show the various elements and compounds:

Composition of the mussel shell.

	Per cent.
Calcium oxide	51.21
Magnesium oxide	.27
Iron and manganese oxides	.32
Silica	.11
Carbonates	37.33
Sulphates	1.02
Organic matter	8.05
Water	.58
Phosphates, chlorides, sulphides	Trace.

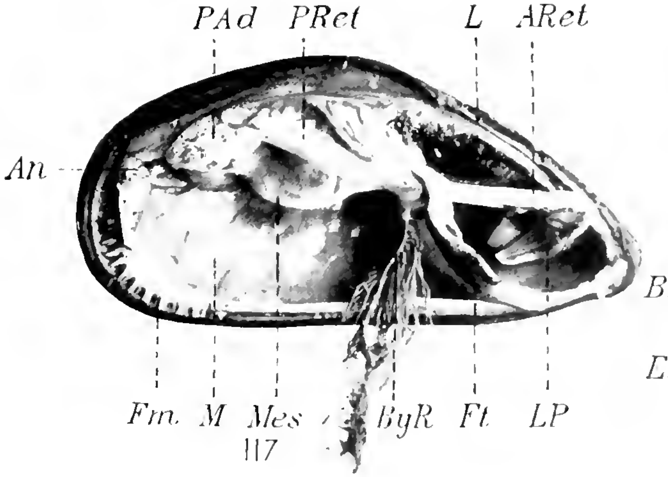
Traces of sodium and potassium which probably came from unremoved sea water were also detected.

THE MANTLE.

The mantle is a fold of integument which almost completely envelops the body. It is composed of the two lobes which lie symmetrically placed on the right and left sides of the body. They arise dorsally as an outgrowth of the body wall, cover the entire inner surface of the shell, and terminate in a free ventral border which is firmly attached to the edge of the shell by means of the pallial muscles. The free mantle edges unite anteriorly near the posterior edge of the anterior adductor muscle. At the posterior end of the shell they are joined together by a triangular-shaped band of deeply pigmented integument, the branchial membrane (fig. 115, *BrM*, opp. p. 138).

The exhalent syphonal opening (fig. 115, *Exs*, and fig. 116, *Exs*) lies just dorsal to the branchial membrane and is surrounded by a tough ring of heavily pigmented tissue. The mantle edges separate to pass on either side of this opening and converge forward to the apex of the shell, where they unite and terminate. Between the syphonal opening and their point of termination they are joined together by a continuation of the branchial membrane. The space between the mantle lobes lying just below the exhalent corresponds to the inhalent syphon of many lamellibranchs.

The structure of the mantle lobes in young animals is quite simple. In cross section they are thin and membranelike, consisting of an outer layer of simple epithelial cells, an



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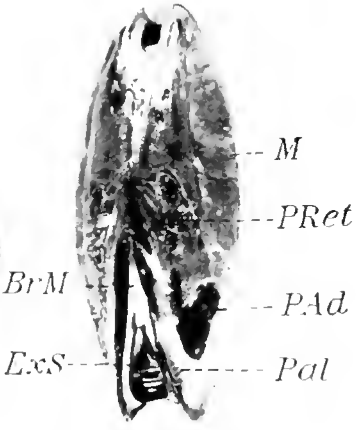

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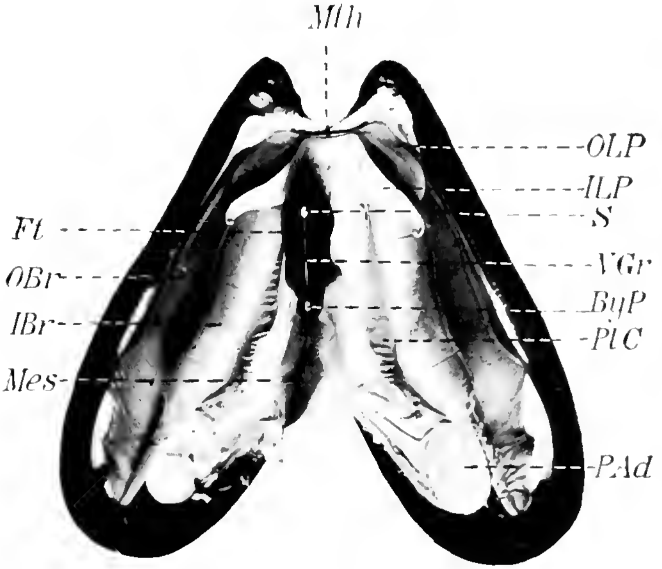

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Fig. 115.—Dorsal view of an adult mussel with valves open normally.

Fig. 116.—Dorso-lateral view of an adult mussel from which shell has been removed.

Fig. 117.—Median view of a mussel with right valve, right mantle lobe, and gills removed.

Fig. 118.—Ventral interior view of a mussel with anterior and posterior muscles cut and valves laid open.

Abbreviations.—*An*, anal muscle; *ARet*, anterior retractor muscle; lower *BrM* in fig. 115, main portion of branchial membrane, upper *BrM* in fig. 115 and *BrM* in fig. 116, extension of branchial membrane; *ByR*, byssus root bearing threads; *ByP*, byssus pit; *ExS* and *Exs*, exhalent syphon; *Fm*, fimbriæ of mantle; *Ft*, foot; *IBr*, inner branchial fold; *ILP*, inner labial palp; *InS*, inhalent syphon; *L*, liver; *LP*, labial palp; *M*, mantle; *Mes*, mesosoma; *Mth*, mouth; *OBr*, outer branchial lamella; *OLP*, outer labial palp; *PAd*, posterior adductor muscle; *Pal*, pallial muscles; *PlC*, plicate canals; *PRet*, posterior retractor muscle; *S*, sucker; *VGr*, ventral groove.

inner layer of ciliated epithelium, and a middle layer of supporting tissue, gland cells, nerves, and blood vessels. In adult animals this condition is profoundly modified by the development of the genital organs. Preliminary to the growth of the reproductive products the middle tissue layer of the mantle increases greatly in bulk, genital canals proliferate out through it up to the border of the pallial muscles, the blood supply is greatly increased, and fatty tissue is deposited. During the change the mantle increases in size from a thin membrane to a thick fleshy organ. The ratio in mantle thickness before and after the production of genital products may be as much as 1: 100.

The free edges of the mantle are different in structure from the rest of the organ. They are firmer and tougher and constitute the region of rigid attachment to the shell. Their edges, which are attached to the ventral and posterior borders of the shell, are divided into three parallel folds that run longitudinally. The inner fold (fig. 114, *IF*, p. 136) is much thicker than the others; anteriorly the edge is smooth, but toward the posterior region it becomes thicker and is fringed with tentacular processes of fimbræ (fig. 117, *Fm*, opp. p. 138). This region of the mantle edge is dark brown in color, due to the numerous pigment granules which fill the outer portion of the ciliated epithelial cells (fig. 165, *PgG*, p. 178). The interior of the fold is rich in muscle fibers which give to it considerable contractile quality. When the mussel is resting undisturbed in the water with its shell open, the inner fold of the mantle in the posterior region may extend some distance beyond the edge of the shell. A sudden change in light intensity by casting sunlight or a shadow over it or by applying some slight mechanical stimulus will cause it to be withdrawn and the shell closed.

The middle fold is narrower than the outer one but, like it, is richly supplied with muscle fibers (fig. 114, *Mus*). Its inner surface and free edge are lined with pigmented ciliated epithelium, while the outer surface is composed of fibers and simple epithelial cells which secrete the periostracum (fig. 114, *MF*).

The outer fold is the narrowest of the three. The upper part of its inner surface is covered with tall columnar epithelium, while the rest of its surface is bounded with epithelium of the low columnar type. The interior of the fold is richly supplied with muscle fibers. Ordinarily this fold is not visible because of the periostracum, which grows out from the outer surface of the middle fold across to the outer surface of the shell, where it is firmly attached (fig. 114, *OF*). The inner fold is therefore completely shut off from the exterior.

The space which is inclosed between the mantle lobes constitutes the pallial or mantle cavity. In it lie the foot, byssus, gills, mesosoma, and the visceral mass.

DIGESTIVE SYSTEM.

ANATOMY.

The alimentary tract of *Mytilus edulis* presents the characteristic specialized type of digestive organs found in the Lamellibranchia, consisting of an anterior mouth, œsophagus, stomach, a long complicated intestine, and a posterior anus together with two pairs of accessory mouth structures, the labial palps, which serve to convey food into the mouth, and a large digestive gland, the liver.

The mouth is situated between the anterior retractor muscles of the byssus just posterior to the anterior adductor muscle (fig. 118, *Mth*, opp. p. 138). When seen from in front or from below it appears as a transverse slit with distinct upper and lower lips from the corners of which two pairs of triangular gill-like folds extend backward. These are the labial palps.

The labial palps arise as a prolongation of the lips on both sides of the mouth, forming a two-paired organ which is so situated that the upper pair lie externally to the lower pair when they are in normal position. They are therefore distinguished as outer and inner labial palps (fig. 118, *OLP* and *ILP*). The angle which is formed between the palps at their point of origin on each side marks the anterior termination of the gills and the position of the pigmented eye spots. In form the palps are long, smooth, triangular bands marked on the median side with transverse ridges which extend from the middle to the ventral edge of each palp. A single longitudinal ridge runs from the corner of the mouth to the tip of each palp and forms the line of demarcation between the smooth and ridged side (fig. 119). The inner palps are much broader at the base than are the outer ones and are continuous with the lower lip on their ridged side, while the smooth side is attached to the surface of the liver. The outer palps are continuous with the upper lips on their ridged side and attached to the inner wall of the mantle with the opposite side.

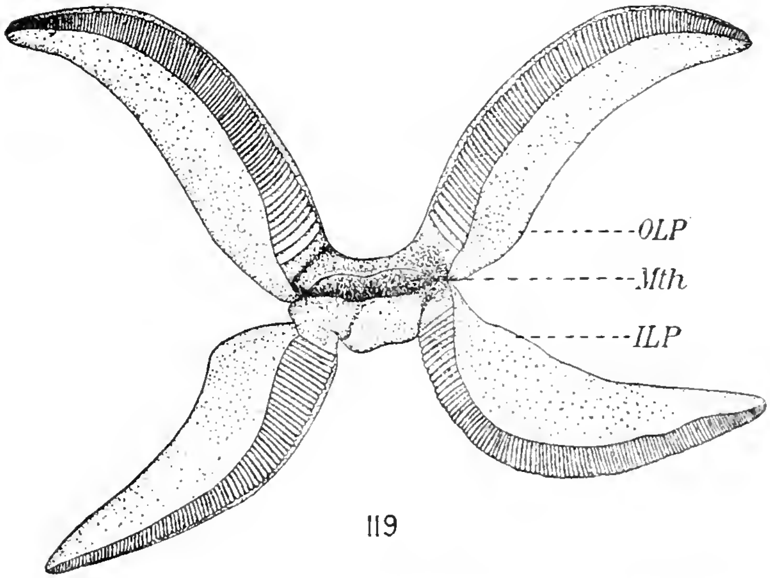
The œsophagus arises directly at the mouth opening and continues backward and upward, bending off slightly to the right of the median plane to enter the anterior end of the stomach.

The stomach is a small sac of irregular form, usually more or less elliptical, with small pockets sometimes present in the dorsal, lateral, or ventral walls. It is situated dorsally just below the middle region of the hinge ligament and lies chiefly on the right side of the body, completely surrounded by liver tissue (fig. 120, *St*). The ventral stomach diverticulum described by Sabatier (1877) was not found to be regularly present.

Numerous large canals open into the stomach from the liver. In *Mytilus galloprovincialis* List (1902) generally found 13 in all, 6 emptying in on the right ventral side, 4 on the left ventral side, 1 on the left wall, and 2 on the left dorsal wall. Sabatier states for *Mytilus edulis* that a number of gland canals empty into the stomach, without giving the number. Purdie (1887) says that in *Mytilus latus* the vessels empty into the under half of the stomach. In the author's observations there could be found no definite number nor regular arrangement to the liver canals. In number they varied from 8 to 14. A majority of these might open on either the right or left side or on the floor of the stomach.

The direct intestine arises from the posterior end of the stomach and passes backward almost on the mid line except in its posterior third, where it bends slightly to the left side and terminates in a blind sac or cœcum of the crystalline style on the dorsal surface of the posterior adductor muscle (fig. 120, *DI* and *Coe*, p. 141). When the animal is well nourished the direct intestine is almost filled with a transparent, gelatinous rod which extends its whole length from the stomach to the cœcum.

The recurrent intestine arises from the median side of the direct intestine at the point where it crosses the mid-dorsal region of the posterior adductor muscle. It runs transversely for a short distance to the right side of the animal and then turns directly forward to run parallel with the direct intestine as far as the posterior end of the stomach; at this point it bends gradually to the left, passing over the direct intestine and then downward and forward over the left side of the stomach almost to its anterior end, where the intestine suddenly makes a posterior loop. This bend marks the beginning of the terminal intestine.



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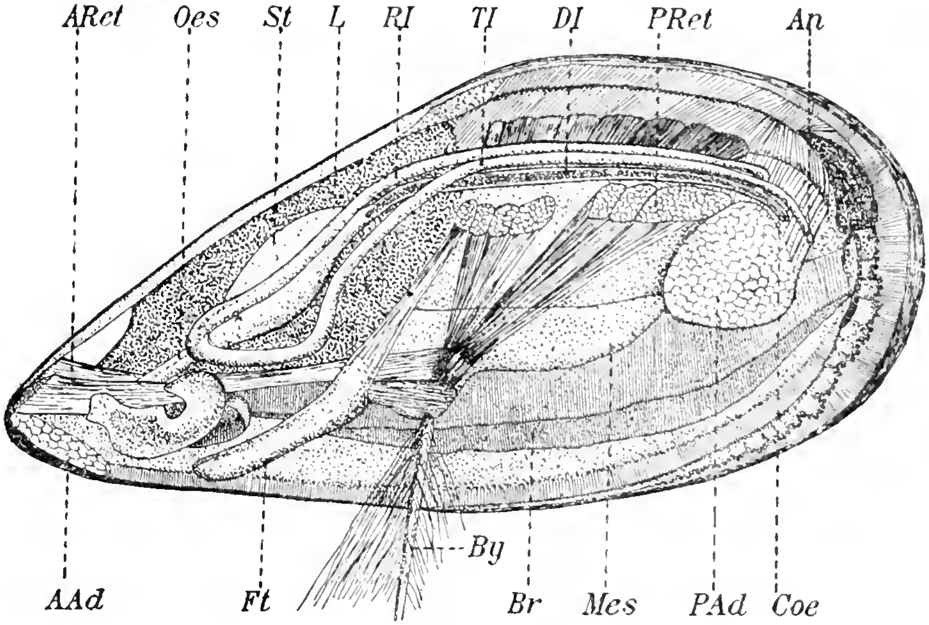

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FIG. 119.—Anterior view of mouth showing relation of lips to labial palps. *ILP*, inner labial palp; *Mth*, mouth; *OLP*, outer labial palp.

FIG. 120.—Digestive organs dissected out and shown in side view. *AAd*, anterior adductor muscle, *An*, anus; *ARet*, anterior retractor muscles; *Br*, gills; *By*, byssus; *Coe*, coecum of the crystalline style; *DI*, direct intestine containing the crystalline style; *Ft*, foot; *L*, liver, *Mes*, mesosoma; *Oes*, œsophagus; *PAd*, posterior adductor muscle; *PRet*, posterior retractor muscle; *RI*, recurrent intestine; *St*, stomach; *TI*, terminal intestine.

The terminal intestine, or rectum, as it is sometimes called, runs backward a short distance from its point of origin, parallel and almost in contact with the left anterior retractor muscle of the byssus, then it turns obliquely upward to the anterior end of the pericardial chamber. At this point it turns backward and passes directly through the ventricle of the heart, continuing on in the mid line over the posterior adductor muscle and terminating in an anus surrounded by dark-brown pigmented epithelium, situated on the posterior surface of the muscle (fig. 120, *TI*, p. 141).

In a mussel 80 mm. long, the mouth opening has a width of 7 mm., the œsophagus a length of 12 mm., the stomach 13 mm., the direct intestine 32 mm., the recurrent intestine 48 mm., and the terminal intestine 52 mm.

HISTOLOGY.

List (1902) has carefully worked out the microscopic structure of the labial palps of *Mytilus galloprovincialis*, and since it is practically the same as that found in those of *Mytilus edulis* his description is followed. The entire upper surface is uniformly covered with a thick layer of cilia. On the under surface cilia are also present, but they are distributed in small scattered clusters which are difficult to demonstrate (figs. 121 and 122, opp. p. 142).

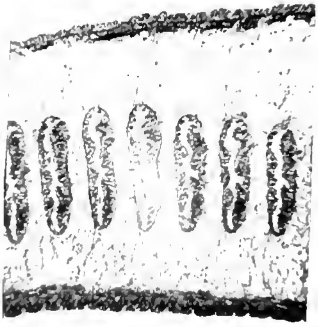
The epithelial cells of the ridges are distinguished from those of the other parts of the palp by their height. They are very small, cylindrical cells with a definitely streaked cuticular border on which the cilia rest, and contain long, oval-shaped nuclei in which are small chromatin granules. The cuticula is also characteristic of the epithelial cells lining the smooth surface. At the base of the epithelial cells there are sometimes present small, round cells which are perhaps ganglionic in nature. There are also some small cells with peripherally running protoplasmic processes, the nuclei of which lie close to the basal membrane. Whether or not special sense cells are present List was unable to determine.

In the epithelium of both the upper and lower surfaces single-celled glands of the beaker type are present and are filled either with eosinophile granules or so-called mucin—a slimy substance which stains strongly with mucin carmine, hæmalum, methyl green, etc. Both kinds of cells are especially abundant at the ends of the ridges.

Nerve fibers run over the surface of the palps in large numbers, and from these, side branches arise to supply each ridge with a fiber (fig. 160, *BuN*, p. 173).

The musculature of the palps is well developed, as would naturally be expected for an organ which can perform such complicated movements. Large bundles of longitudinal muscles lie just below the epithelium of the dorsal and ventral surfaces. They extend from the base of the palps to the tip and are especially well developed on the under side. Directly under the epithelium there are a few fine circular muscle fibers. There are also fibers, somewhat better developed than these, which run through and across the organ. Three sets of muscles are present on the rigid side of the palps. They consist of (1) fine, circularly running fibers which lie just below the epithelium (2) bundles of fibers which run from one ridge to the next, thus joining all of them together, and (3) fibers which run from the base of the epithelial cells of the ridges to the epithelium of the under side.

The epithelium of the lips is continuous with the ridged epithelium of the palps but differs from it by having taller ciliated cells. Below the epithelium of the lips



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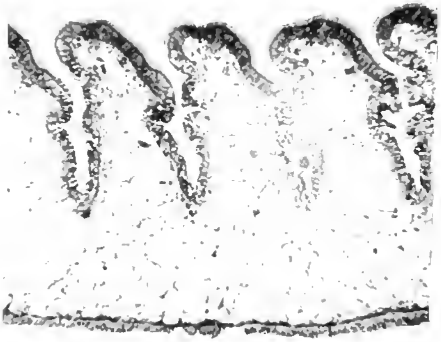

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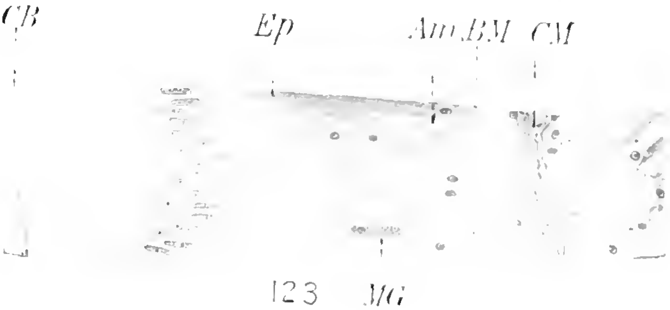

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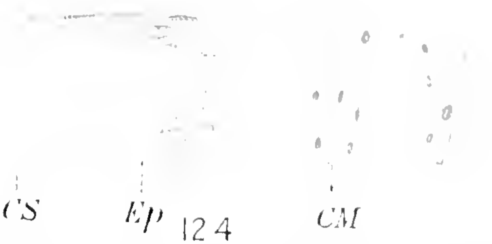

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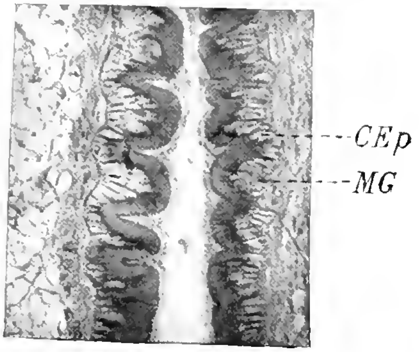
Fig. 121.—Photomicrograph of a longitudinal section through the smooth side of a labial palp. × 30. Fixed in Flemming fluid and stained with Delafield hæmatoxylin. The centrally located ciliated canals are continuous with furrows shown in fig. 122.

Fig. 122.—Photomicrograph of a longitudinal section through the ridged side of a labial palp. × 30. Preparation same as fig. 121.

Fig. 123.—Section through the stomach epithelium. *Am*, amoebocyte; *BM*, basal membrane, *CB*, cuticular border; *CM*, circular muscles; *Ep*, stomach epithelium, *MG*, mucous gland. (After List, 1902.)

Fig. 124.—Section through the stomach epithelium in the posterior region. *CM*, circular muscles; *CS*, crystalline style substance; *Ep*, stomach epithelium. (After List, 1902.)



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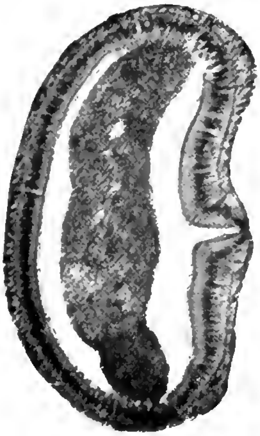

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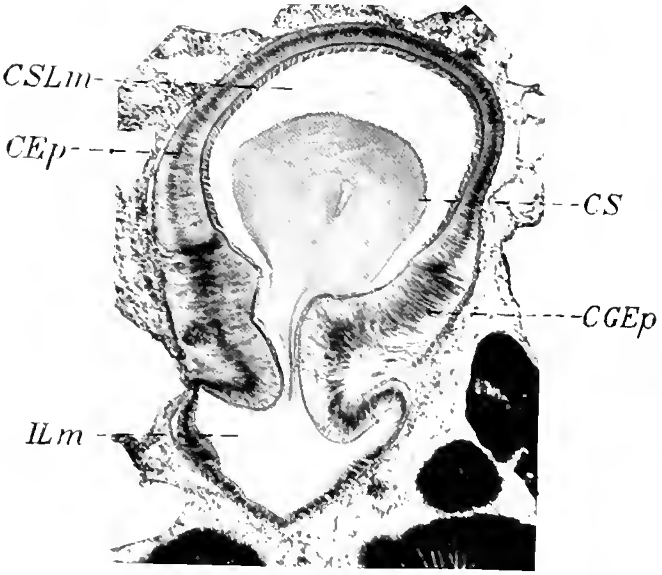

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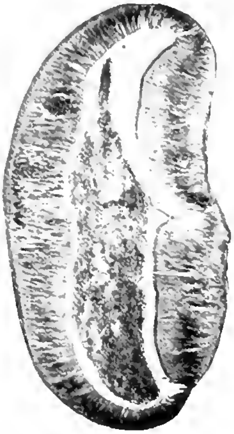

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PHOTOMICROGRAPHS. × 50.

Fig. 125.—Longitudinal section through œsophagus. Fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red. *CEp*, ciliated epithelium; *MG*, mucous glands.

Fig. 126.—Cross section through recurrent intestine. Preparation same as fig. 125. The lumen is filled with diatoms and detritus.

Fig. 127.—Cross section through terminal intestine. Preparation same as fig. 125.

Fig. 128.—Cross section through direct intestine. *CEp*, ciliated epithelium; *CGEp*, ciliated and glandular epithelium; *CS*, crystalline style; *CSLm*, crystalline style lumen; *ILm*, intestinal lumen

there is a thick layer of gland cells whose contents stain deeply with Delafield's hæmatoxylin. A second type of gland cell lies peripherally to these just below the epithelium or, in some cases, in the epithelium itself, as single cells filled with round granules which stain deeply with Bordeaux red or eosin.

The epithelium of the œsophagus is a continuation of that of the lips, but in the transition the surface changes from a smooth to a convoluted condition. The epithelium is of the columnar ciliated type similar to that on the lips except that in the basal region the gland cells increase greatly in number as the stomach is approached (fig. 125, *MG*, opp. p. 143). They are the type of gland cell which stains with hæmatoxylin. There are also small cells of irregular form containing yellow granules which lie scattered throughout the basal region of the epithelium in varying numbers. List (1902) thinks they are probably amœbocytes which were caught while wandering through the epithelium of the œsophagus where they were loading themselves with food material to be carried to assimilation organs in the manner suggested by the researches of Carazzi (1893) on the oyster.

The epithelium rests on a distinct basal membrane, below which there is a thin layer of circular and longitudinal muscle fibers. According to Sabatier (1877) the circular fibers form an inner layer in relation to the longitudinal muscles, but in the author's preparations the two sets of fibers seem to be intermingled.

The stomach has its inner surface thrown into numerous folds and prominences of various sorts in different individuals. Sometimes it gives rise to one or more pockets from the dorsal, lateral, or ventral walls.

The epithelium of the stomach is similar to that of the œsophagus except that it is higher and almost without any mucous gland cells (fig. 123, opp. p. 142). The cells are all ciliated, but the cilia are proportionately shorter. In many places, chiefly on the dorsal wall, they may be entirely covered with a homogeneous substance very similar to the crystalline style (fig. 124, *CS*, opp. p. 142). The basal membrane on which the cells rest varies in thickness in different places, being more strongly developed where the greatest folds appear and showing scattered nuclei lying within its substance.

Circular muscles lie immediately below the basal membrane, and, according to Sabatier (1877), external to these there is a layer of longitudinal fibers. This layer, however, the author could not demonstrate to his own satisfaction.

The direct intestine or tubular stomach, in the terminology of Sabatier (1877), arises from the posterior end of the stomach as a canal which at first is round in cross section, becoming oval in the middle region, the large end usually placed ventrally (fig. 128, opp. p. 143). Sometimes it is found in a dorsal position. Often the lateral walls of the canal project inward so as to divide the direct intestine into a dorsal and a ventral canal. In each case the larger lumen contains the crystalline style, the smaller one performing the usual functions of an intestine. The epithelium of the two regions is very different, that which lines the walls of the lumen occupied by the crystalline style being composed of low columnar cells covered with relatively heavy cilia, while that of the intestinal portion is lined with a columnar ciliated epithelium whose cells are much higher. The lateral walls form thick folds of very high cells which also carry a heavy coat of cilia. The wall lying opposite to the crystalline style cavity is lined with a relatively low columnar ciliated epithelium between the cells of which lie numerous gland cells of the beaker type.

The recurrent intestine is either round or elliptical in cross section at its posterior end. As it runs forward one side becomes flattened and develops a high columnar, ciliated epithelium which is parted in the middle by a longitudinal furrow (fig. 126, opp. p. 143). The walls which are continuous on either side with this thickened portion are composed of comparatively low epithelial cells, but as they pass around to the opposite side of the intestinal wall they become progressively higher, although they do not reach the height of those on the flat side. Between the epithelial cells there are scattered a few tall mucous cells. The epithelium is bounded externally with a basal membrane which is thickest on the side where the epithelial cells are highest. External to it there is a thin layer of circularly running fibers.

The terminal intestine is a continuation of the recurrent intestine and preserves the same semicircular outline of the latter with the very tall epithelium lining the flat side. The furrow, however, which divides this thickened portion into right and left halves is much deeper than that in the recurrent intestine, and the ciliated cells gradually become much lower (fig. 127, opp. p. 143). Mucous cells are distributed in considerable numbers between the epithelial cells. The basal membrane on which the ciliated cells rest is well developed and covered externally with a thin layer of circular muscle fibers.

The crystalline style as observed by Haseloff (1888) and List (1902) is composed of a somewhat firm, elastic substance of gelatinous consistency. In the fresh state it is perfectly clear and transparent. In cross section it shows a series of concentric layers, the central portion presenting a homogeneous structure, while that near the periphery is granular in appearance. According to List (1902) the crystalline style is formed from secretions produced by the high epithelial cells, in the side walls of the direct intestine. The secretion consists of granules which are molded into the surface of the crystalline style.

The liver occupies the anterior part of the visceral mass and completely surrounds the stomach and those portions of the intestine which lie anterior to the heart. The larger portion of the liver occupies the right side of the body. The organ is single and composed of numerous lobules which in turn are made up of elongated glandular acini. The discharging canals unite successively with the main canals which empty into the stomach by large openings that often cause irregularities in the walls. The number of main canals appears to vary between 8 and 15.

List (1902) says in regard to their structure that the main canals to the stomach are unevenly ciliated throughout, the epithelium being composed of two distinctly different elements of which each circles one-half of the canal when seen in cross section. On one side the columnar cells are lower and broader than those of the opposite side and contain numerous granules lying in their distal ends; the nuclei are large, each one containing a conspicuous necleolus. Cilia are absent. The epithelium lining the opposite side of the canal is composed of high columnar cells which bear long cilia arising from distinct basal bodies; the nuclei are small and contain numerous chromatin granules with or sometimes without a nucleolus. Externally the canal is surrounded by a well-developed layer of circular muscles (fig. 129).

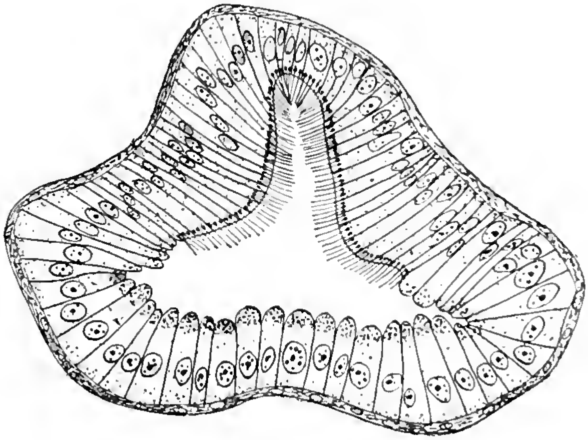
The epithelium of the secondary liver canals is continuous with that of the main canals and differs from it in having a lining of broad, low columnar cells that contain large nuclei with a conspicuous nucleolus (fig. 130). The protoplasmic portion is further characterized by the presence of numerous large granules which in the fresh tissue are yellowish or brown in color. The particular hue of the granules seems to depend upon the food of the animal according to List (1902). If the mussel is starved the liver granules become lighter in color, if fed with algæ they become green, and if given india ink or carmine they become black or red, respectively.

The granules contain albumin particles, fat droplets, and glycogen.

PHYSIOLOGY.

Erman (1833) believed that the function of the palps was to sweep into the mouth particles of floating food carried forward in the currents set up by the action of the ciliated gills. It was also considered that they might have a respiratory function.

Thiele (1886) thought that the chief function of the palps was to transfer food collected by the gills to the mouth. He pointed out that their structure and position clearly indicated this. The outer pair extend from the upper lip of the mouth to the outer pair of gills, while the inner pair reach from the lower lip to the inner pair of gills where they can pick up the food particles collected by these organs. The rich innervation of the palps suggests that they may possibly function as taste organs. List (1902) questions this latter theory on the ground that observations show it to be only slightly probable, as all foreign bodies which have been transported to the palps are taken into the mouth if they do not exceed a certain size. The experiments of Lotsy (1893), however, indicate that certain shellfish have the power of discrimination in the selection of food, for when clouds of diatoms from a culture were introduced near the ventral opening of the syphon of a clam they were immediately ingested, but when hashes of fish or shrimp were given they were refused or if ingested were forcibly ejected an instant later. Oysters, in a similar manner, exhibited the power of discrimination between different kinds of food which were given to them. How the mollusks were able to distinguish between the different kinds of food Lotsy does not attempt to explain. Anatomically, however, it seems likely that this center of discrimination is located in the palps.



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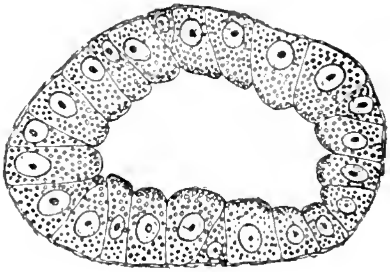

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FIG. 129.—Cross section of a primary liver canal to the stomach. Fixed in Flemming fluid and stained with Delafield hæmatoxylin. × 575.

FIG. 130.—Cross section of a secondary liver canal. Preparation same as fig. 129. × 575.

The composition and function of the crystalline style was studied by Haseloff (1888), who found that alcohol causes it to become opaque and thinner. Nitric acid makes it turn yellow, and dilute hydrochloric acid prevents it from decomposing. It dissolves in ordinary water, but more readily in salt water. In 1 per cent acetic acid it dissolves completely in from two to three minutes. Treated for some time with sulphuric acid it takes on a violet color. Picric acid will precipitate a solution of crystalline style. If the solution is first treated with acetic acid and then with potassium ferrocyanide, a white flocculent precipitate is formed. From these reactions Haseloff concluded that the crystalline style is composed of albuminous matter and is therefore a reserve food material. This view is given additional support by the fact that if mussels are starved the structure will disappear in a few days, after which, if plenty of food is again supplied, the structure reappears.

Many different functions have been ascribed to the crystalline style. Heide (1684) and Cailliaud (1850) thought it was related to the reproductive organs. Meckel (1829) took it for a tongue. Garner (1841) believed it had something to do with the swelling up of the foot. Milne-Edwards (1859) ascribed to it the function of stirring up the food during digestion. Vulpian (1869) found that it contained some crystals of calcium oxalate and concluded from this fact that it must be connected with the urinary function. Sabatier (1877) described it as functioning to grind up and press the food against the intestinal wall. Krukenberg (1880) considered it as a pestle which forced the digested food as closely as possible to the absorbing epithelium as it passed along. Hazay (1881) and Haseloff (1888) considered it as a reserve food material, while Barrois (1890) believed it served only in helping to transport the food becoming dissolved in the stomach and surrounding the food mass with a slippery coat. He evidently considered it a substance similar to mucin and chondrin and therefore without any food value.

The best researches on the origin and function of the crystalline style since that of Haseloff (1888) have been made by Mitra (1901), who employed chemical methods, and List (1902), whose plan was to feed india ink to the shellfish and observe its effects on the organ. List found that the strong bristlelike cilia of the cavity in which the crystalline style lies swept the india ink particles around the rod in continuous rotations which moved gradually forward. When it was completely covered with ink, he was able to observe that the anterior end was being gradually dissolved in the stomach while the posterior end was being formed of new crystalline style substance free from india ink. Furthermore, the coating of ink which remained on the rod was in turn covered with a layer of the crystalline style material. List therefore concluded that the crystalline style is secreted in the direct intestine from the tall epithelium of the side walls and that it gradually moves forward to the stomach by a rotating movement set up by ciliary action. In the stomach it dissolves and, as List assumes, probably serves as a food substance.

The function of the crystalline style has been most satisfactorily demonstrated by Mitra (1901), who worked with fresh-water mussels. His analyses gave the following as the chemical composition of crystalline style: Water, 88 per cent (approximately); globulin, 12 per cent; salts, 1 per cent. The composition is similar to that of the pancreatic secretion of dogs and suggests that the crystalline style may function as a digestive ferment. Further experiments gave strong support to this assumption, for it was found that two styles if added to 30 minims of starch solution would completely convert it into reducible sugar in about 3 hours, and if a solution of 7 styles in distilled water was added to 30 minims of the same starch solution it was transformed into a reducible sugar in about 20 minutes. Mitra concludes therefore that the crystalline style contains an amylolytic ferment. It acts upon raw starch and is able to convert glycogen slowly into sugar but appears to have no action on such protein matters as egg albumin, fibrin, or muscle fibers. He considers the protein matter (globulin) of the style and the ferment as identical substances and believes that the former in no way functions as a reserve food mass.

The conclusion to be drawn from the investigations recorded above is that the crystalline style originates from the tall columnar epithelium of the direct intestine and gradually moves forward with a spiral motion to the stomach, where it mixes with food and functions as a digestive ferment of starchy materials.

The experiments of List (1902) on the function of the liver show that the granular bodies in the liver cells take up nourishing materials (also carmine, india ink, iron, and litmus) in the form of very small particles until the granules are entirely filled; then the food materials emerge in the form of large particles which are removed by way of the main liver canals to the stomach and intestine. He demonstrated clearly that the characteristic color of the liver always depends upon the nature of the nourishment taken by the animal and concludes that the liver functions primarily as a storehouse of reserve food material.

CIRCULATORY SYSTEM.

HEART.

The heart lies in the mid-dorsal region just posterior to the upper extremity of the hinge where it is inclosed in a spacious pericardial cavity the walls of which are formed of a thin, transparent membrane that is continuous with the body wall (fig. 133, *PC*, p. 149). The floor of the pericardial cavity rests on the direct and recurrent intestines which run parallel to each other in this region. Laterally it is covered with a thin portion of the mantle that is usually free from any proliferations of the genital epithelium, while dorsally it is inclosed between the two bands of pallial muscles which are continuous with the mantle edge. In a mussel 8 cm. long the floor of the pericardial chamber is about 15 mm. long by 8 mm. wide, and the roof of the cavity which is shaped like an inverted V is about 5 mm. high. At the anterior extremity of its base the pericardial cavity opens into a wide duct that borders the anterior surface of the oblique vein and connects with the kidney. This wide duct was given the name *couloir* by Sabatier (1877) but may better be called the renipericardial canal (fig. 133, *RC*).

The heart is composed of a ventricle and two auricles. The ventricle is more or less elliptical in form and extends the whole length of the pericardial chamber. In a mussel 8 cm. long it has a length of 15 mm. and a breadth of 2 mm. when relaxed. When distended with blood the diameter becomes about 4 mm. The blood leaves the heart by a single aorta which leads off from it at the anterior extremity. The middle of the ventricle is traversed by the rectum which enters at the anterior end just above the aorta and passes out at the posterior extremity in the dorsal region, so that a blind sac is left in the posterior end of the ventricle.

The auricles are two large sacs which are symmetrically placed one on each side of the ventricle and connected with it by a short auriculo-ventricular canal (fig. 131, *AVC*, p. 149) in which are valves that permit the blood to flow toward the ventricle only. On the other hand, the auricles communicate with large afferent oblique veins on their respective sides. The afferent oblique veins enter the auricles in the ventral anterior region where they greatly enlarge and become continuous with the walls of the auricles (fig. 133, *AOV*, p. 149). The walls of the auricles are covered with a brown colored, spongy tissue which presents a rough, irregular surface. These are the *pericardial glands* (fig. 131, *PG*), which are described under the excretory system. The auricles lie almost free in the pericardial cavity. They are attached to the floor and lateral walls of the chamber at their posterior extremities by numerous small blood vessels which empty directly into the auricles. Anteriorly the auricles are held in place by the afferent oblique veins with which they are continuous.

ARTERIAL SYSTEM.

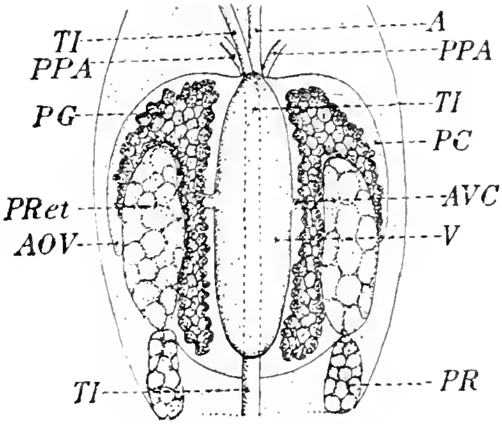
The blood leaves the heart by a single anterior aorta, from which it is distributed to the body through five channels which are as follows: (1) Three pairs of pallial arteries which supply the mantle and pallial muscles; (2) a pair of gastro-intestinal arteries which go to the stomach, intestines, posterior retractor muscles, posterior adductor muscle, lateral cavities, and mesosoma; (3) a single pericardial artery which carries blood to the walls of the pericardium, the direct and recurrent intestines, and the bordering genital glands; (4) three pairs of hepatic arteries which go to the liver; and (5) a pair of terminal arteries which furnish branches to the anterior parts of the body.

The aortic bulb marks the beginning of the aorta and gives rise to several of the most extensive arteries. It arises as a bulbous swelling from the anterior end of the ventricle immediately below and just anterior to the point where the rectum penetrates into the ventricle.

The *anterior aorta*, which is the largest of the arteries, arises from the anterior end of the bulb and runs forward on the dorsal surface of the body immediately below the hinge ligament (fig. 133, *A*, p. 149). When it reaches the point just below the anterior end of the hinge ligament it divides into two large right and left trunks that pass outward to the outer surface of the mantle and then bend sharply backward to supply numerous small vessels to the ventral anterior portion of the mantle. These are the *anterior pallial arteries* (fig. 133, *APA*). A very small artery continues forward and downward from the bifurcating point of the aorta to send out fine branches over the dorsal surface of the œsophagus.

A second pair of arteries of minor extent arise from the mid region of the anterior aorta and send branches to the anterior portion of the mantle folds. Because of their position the author has named them the *intermediate pallial arteries* (fig. 133, *IPA*). Sometimes two pairs of these intermediate pallial arteries are present.

The *posterior pallial arteries* are a pair of large vessels which arise from the ventrolateral surfaces of the aortic bulb. The trunks pass out to the surface where they fork into anterior and posterior vessels that in turn subdivide into numerous branches that supply the entire middle and posterior portions of the mantle and the posterior adductor muscle besides sending numerous small vessels into the liver (fig. 133, *PPA*). The main branches of the three pallial arteries give off many minor branches that continue to divide and subdivide into still smaller vessels which make a fine network throughout the whole mantle. The trunks that terminate at the periphery of the



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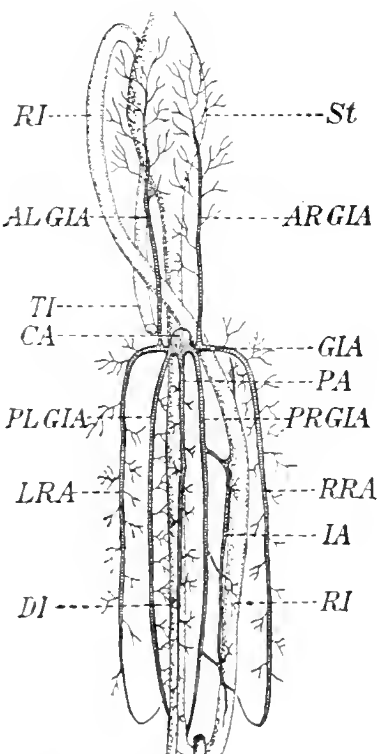

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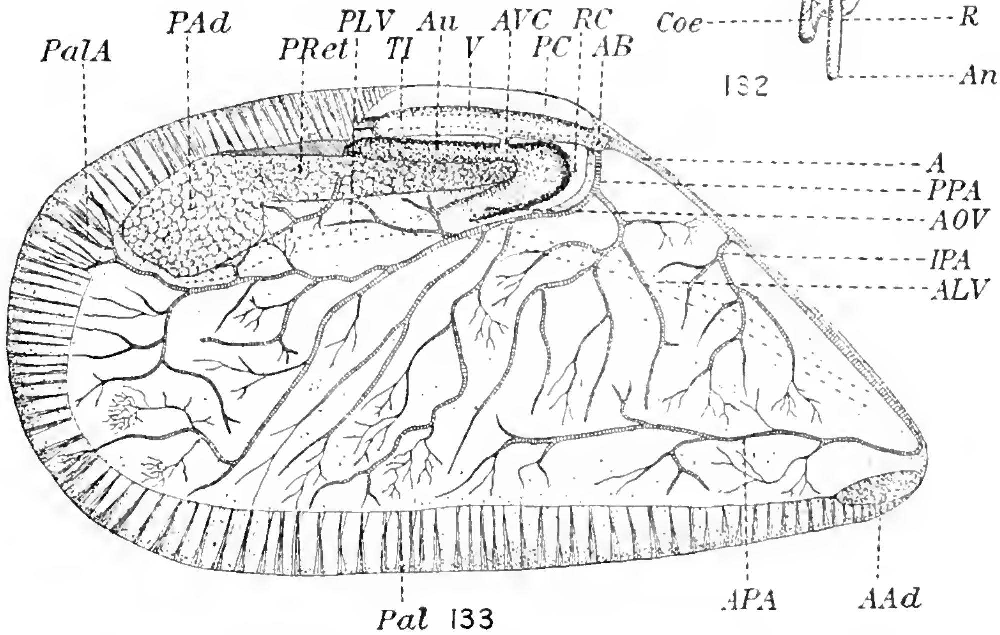

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FIG. 131.—Dorsal view of heart exposed in the pericardium.

FIG. 132.—Gastro-intestinal arteries seen from above. From dissection of a specimen which had been injected with carmine-gelatin mass.

FIG. 133.—Lateral view of mantle showing arteries injected with carmine-gelatin mass.

ABBREVIATIONS.—*A*, aorta (fig. 131), anterior aorta (fig. 133); *AAd*, anterior adductor muscle; *AB*, aortic bulb; *ALGIA*, anterior left gastro-intestinal artery; *ALV*, anterior longitudinal vein; *An*, anus; *AOV*, afferent oblique vein; *APA*, anterior pallial artery; *ARGIA*, anterior right gastro-intestinal artery; *Au*, auricle; *AVC*, auriculo-ventricular canal; *CA*, coeliac artery; *Coe*, coecum; *DI*, direct intestine; *GIA*, gastro-intestinal artery; *IA*, intestinal artery; *IPA*, intermediate pallial artery; *LRA*, left recurrent artery; *PA*, pericardial artery; *PAd*, posterior adductor muscle; *Pal*, pallial muscles; *PalA*, arterial network of pallial muscles; *PC*, pericardial cavity; *PG*, pericardial gland; *PLGIA*, posterior left gastro-intestinal artery; *PLV*, posterior longitudinal vein; *PPA*, posterior pallial artery; *PRet*, posterior retractor muscle; *PRGIA*, posterior right gastro-intestinal artery; *R*, rectum; *RC*, renipericardial canal, *RI*, recurrent intestine; *RRA*, right recurrent artery; *St*, stomach; *TI*, terminal intestine; *V*, ventricle.

mantle break up into a fine lacunar network that envelops the pallial muscles (fig. 133, *PalA*).

The *gastro-intestinal arteries* are a pair of large vessels leading off to the right and left, respectively, from a very short thick trunk, the *cœliac artery*, that arises from the ventral surface of the arterial bulb (fig. 132, *GIA*, p. 149). They immediately divide into two branches, one of which passes forward sending out many small vessels to the stomach, recurrent intestine, terminal intestine, and liver; the other of which runs posteriorly supplying blood to the direct intestine, recurrent intestine, and surrounding tissues. The *anterior gastro-intestinal arteries* are more or less symmetrical in their course, while the posterior ones are not. The left *posterior gastro-intestinal artery* lies to the left of the direct intestine to which it sends a rich supply of blood. The right *posterior gastro-intestinal artery* lies on the right side of the direct intestine deeply imbedded in the tissues. To expose this artery to view it is necessary to remove the rectum and overlying tissues and move the recurrent intestine slightly to the right. The right *gastro-intestinal artery* is slightly larger than its corresponding vessel on the left side and further differs from it by giving off a large trunk, the *intestinal artery* (fig. 132, *IA*) that runs posteriorly along the recurrent intestine, giving off small branches that spread over it. In its course backward from the point of origin of the *intestinal artery* the *right posterior intestinal artery* gives off two or three short trunks from its right side that pass directly to the recurrent intestine, where they divide into small vessels that spread out over the surface of the intestine. This artery also furnishes several vessels that carry blood to the right side of the direct intestine and to the rectum.

The *recurrent arteries* (fig. 132, *RRA* and *LRA*) are a pair of long trunks that arise from the lateral sides of the *anterior gastro-intestinal* arteries immediately after their point of origin. They pass outward and then turn abruptly backward, passing over the median side of the posterior retractor muscles to the anterior wall of the posterior adductor muscle, where they turn downward and forward and give out numerous branches to the walls of the lateral cavities and the mesosoma.

The *pericardial artery* (fig. 132, *PA*) is a single median vessel that arises from the ventral side of the *cœliac trunk* between the points of origin of the *gastro-intestinal arteries*. It runs posteriorly on the middle part of the floor of the pericardial chamber terminating in the region of the anus. In its course it gives off numerous small vessels which go to the base of the pericardial chamber, the direct intestine, the recurrent intestine, and adjacent tissues.

The *hepatic arteries* consist of several pairs of short vessels, usually three in number, which branch off from the aorta at right angles and penetrate directly into the liver, where they divide into many branches that form a rich network throughout the gland.

The *terminal arteries* arise from the anterior end of the aorta which forks at a position about midway between the point of origin of the *intermediate pallial arteries* and the anterior extremity of the body. The two resulting branches continue forward and downward to the anterior extremity of the body, where they turn back sharply on their respective sides to form the anterior pallial arteries which traverse the lower edge of the mantle for about one-half its length. In their course the *terminal arteries* also give rise to small vessels that go to the anterior part of the liver, the genital glands of the immediate region, the dorsal and lateral walls of the supra-œsophageal cavity, and to the anterior adductor and anterior retractor muscles.

The *anterior ventral artery* is a median trunk that arises from the *anterior aorta* ventral and slightly posterior to the point where the *terminal arteries* branch off. It runs forward in the middle of the floor of the supra-œsophageal cavity for about half its length and then turns sharply downward, crossing the œsophagus on its right side and continuing to the ventral body surface between the anterior retractor muscles. Here it turns backward and gives off in its course a large *pedal artery* to the foot besides a number of smaller vessels to the anterior and posterior retractor muscles and to the byssus organ.

The *tentacular arteries* are two anterior branches from the *anterior ventral artery*. The *dorsal tentacular* artery continues forward on the floor of the supra-œsophageal chamber from the angle where the *anterior ventral artery* turns downward and extends to the mid-dorsal region of the upper lip. There it forks into right and left branches that extend laterally to the dorsal palps on their respective sides. The vessels enter the basal region of the palps on their ribbed sides and pass transversely across to the smooth border, which they follow back to the distal extremity, giving off at right angles in their course numerous fine vessels which extend across the palp to its lower edge. The *ventral tentacular artery* branches off from the *anterior ventral* artery where it turns abruptly backward on the ventral side of the body. It runs forward slightly beneath the ventral surface between the anterior retractor muscles to the ventral surface of the lower lip, where it forks into right and left branches that go to the right and left inferior palps, respectively. The course of the vessels through the inferior palps is the same as that already described for the superior palps.

VENOUS SYSTEM.

The venous system collects the blood of the body into the 10 main groups of vessels through which it is conveyed to the heart. Briefly described, they are as follows: (1) A *marginal sinus* which extends around the border and receives the blood of the mantle, (2) a large number of *ascending pallial veins* on the inner face of the mantle which collect the blood of this organ, (3) a pair of *horizontal veins* which extend the length of the mantle just below the roots of the gills and receive the blood from the ascending pallial veins, (4) a pair of large *intermuscular veins* in the region of the muscles of the foot and byssus, (5) a pair of *mesosomal veins* which receive blood from the mesosoma, (6) *visceral veins* which conduct the blood from the liver, stomach, and intestines, etc., (7) *afferent branchial veins* and *efferent branchial veins* which carry blood to and from the gills, (8) a pair of *afferent longitudinal veins* which are closely associated with the kidney tissue and receive blood from the veins of the mesosoma and the branchial vessels from the horizontal veins by way of the plicate canals, and from the horizontal vein, visceral veins, intermuscular sinus, and branchial veins through the kidney, (9) a pair of *anastomosing veins* and the *transverse sinus* of the posterior adductor muscle which unite the horizontal veins with the longitudinal veins, and (10) a pair of *afferent oblique veins* which receive the blood from the longitudinal vein and conduct it to the heart.

The marginal sinus follows the free border of the mantle which is enveloped by the fold of periostracum that extends beyond the edge of the shell (figs. 134 and 135, *MS*,

p. 153). It receives blood from the area of the mantle lying close to the border through a network of fine vessels that empty into it throughout its course.

The *ascending pallial veins* are a series of vessels covering the internal face of the mantle extending upward, more or less parallel to each other, from the margin of the mantle to the horizontal vein that runs parallel and just below the line of attachment of the gills (fig. 134, *APV*). They result from the union of numerous fine capillary vessels that form a network all through the mantle and represent the principal channels by which the blood leaves the mantle.

The *horizontal veins* are paired vessels which follow a sinuous course the length of the mantle, parallel to and just below the roots of the gills (fig. 134, *HV*). Beginning anteriorly as a vessel of small diameter, each horizontal vein gradually increases in diameter as it runs backward. In the region of the posterior adductor muscle it reaches its maximum size and is quite conspicuous. Throughout its entire course it is connected with the ascending pallial veins which discharge their blood into it. Near the posterior end it receives the anastomosing vein and finally connects with the marginal sinus behind the posterior adductor muscle.

The *intermuscular sinus* is also a paired vessel. It arises between the palps at their point of attachment and extends back over the muscles of the foot and byssus in a series of cavities. One branch of the sinus lies between the anterior retractor muscles; a pair of vessels runs laterally to these muscles, extending back as far as the posterior adductor muscle; and still another pair goes between the posterior retractor muscles. In their course they receive veins from the liver, foot, kidney, and the mesosoma (fig. 135, *IMS*).

The *mesosomal veins* arise as three main trunks on each side of the mesosoma. A median vessel runs posteriorly close to the free border. Above it, two lateral vessels run backward and unite with it. The common trunk, thus formed, empties into a transverse sinus on the anterior ventral side of the posterior adductor muscle, which connects with the longitudinal vein and vessels of the kidney (fig. 135, *MV*).

The *visceral veins* include numerous small vessels which convey blood from the liver, stomach, intestines, etc., chiefly to the network of vessels within the kidney. The blood supply of the liver is particularly rich and involves a complicated mass of vessels which envelop the lobes. The blood from the dorsal and deeper parts of the liver is carried directly into the kidney, while that from the ventral portion and superficial area is conveyed to the kidney by way of the internal plicate canals (fig. 135, *IPlC*). A small amount of blood from the surface of the liver is carried off by small vessels that empty into the afferent vein of the gills.

The *branchial veins* on each side of the body consist of a single *afferent branchial vein* at the roots of the gills and a pair of *efferent branchial vessels* which border the free ends of the reflected filaments (fig. 134, *EBV*, and fig. 135, *ABV* and *EBV*). The afferent branchial vein is connected with vessels of the kidney from which blood is received and the efferent branchial veins open anteriorly into the anterior longitudinal vein near the base of the palps.

The *longitudinal veins* are paired vessels more or less enveloped by the kidney tissue. They extend from the base of the posterior adductor muscle to the anterior extremity of the gills. The position of the vessel on the right side of the body is indicated by a dotted outline in figure 133, *ALV* and *PLV*, page 149. Sabatier (1877), who named the

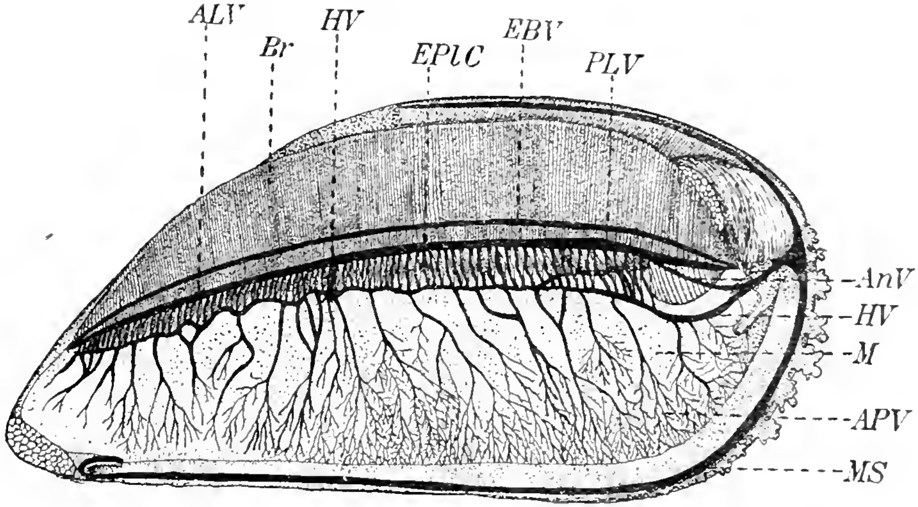

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FIG. 134.—Interior view of right mantle with veins injected with Berlin blue gelatin mass. Left mantle lobe with part of visceral organs has been removed and right branchial lamellæ reflected to expose external plicate canals and connecting veins. *ALV*, anterior longitudinal vein; *AnV*, anastomosing vein; *APV*, ascending pallial veins; *Br*, gills; *EBV*, efferent branchial vein; *EPlC*, external plicate canals; *HV*, horizontal vein; *M*, mantle; *MS*, marginal sinus; *PLV*, posterior longitudinal vein.

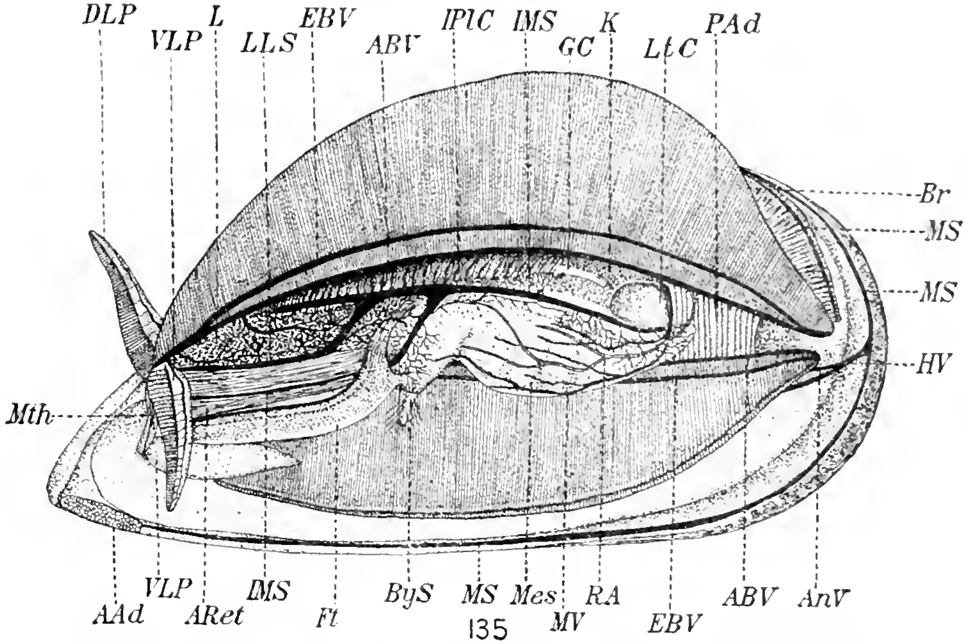

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FIG. 135.—Interior view of mantle cavity of an injected mussel with left branchial lamellæ reflected to expose foot and mesosoma. *AAd*, anterior adductor muscle; *ABV*, afferent branchial vein; *ARet*, anterior retractor muscles; *ByS*, byssus stalk, *DLP*, dorsal labial palp, *Ft*, foot; *GC*, genital canal, *IMS*, intermuscular sinus; *IPlC*, internal plicate canals; *K*, kidney; *L*, liver; *LLS*, left lateral sinus; *LtC*, lateral cavity; *Mes*, mesosoma, *Mth*, mouth; *MV*, mesosomal vein; *PAd*, posterior adductor muscle, *RA*, recurrent artery; *VLP*, ventral labial palp; other abbreviations same as in fig. 134.

vessel, divided it into two parts. The portion lying in front of the oblique vein was termed the *anterior longitudinal vein,* while that part which is behind and really continuous with the oblique vein was called the *posterior longitudinal vein.* The longitudinal vein is smallest at the anterior extremity and increases in diameter in its backward course. It is the central sinus that receives blood from all parts of the body and from which it is transferred directly to the heart.

The *anastomosing veins* are a pair of short trunks that establish connections between the horizontal vein, transverse sinus of the posterior adductor muscle, and the posterior longitudinal vein (fig. 134, *AnV,* p. 153). The vessel on each side arises from the horizontal vein near its junction with the marginal sinus, runs obliquely forward and upward to the ventral side of the posterior adductor muscle, where it connects with the transverse venous sinus and also with veins from the anal membrane, and from there continues forward to the kidney, where it terminates in the posterior longitudinal vein.

The *afferent oblique veins* of the heart are prominent oblique vessels on each side of the body which extend downward and backward from the pericardium to connect with the longitudinal vein (fig. 133, *AOV,* p. 149). They represent the final channel by which the blood reaches the heart. The oblique vein on each side is inclosed in the renipericardium canal, to which it is attached on the dorsal wall. The anterior and ventral surfaces are more or less covered with folds of kidney tissue similar to that of the pericardial glands which envelop the auricles and with which it is continuous. This portion of the oblique vein is free from any attachment and lies submerged in the fluid of the renipericardium canal.

BLOOD.

The blood, or hæmolymph, is a clear, transparent fluid except for a slight opalescent tinge. The corpuscles which are suspended in it are colorless, amœboid cells or lymphocytes. If a drop of the hæmolymph is placed under a cover glass on a microscopic slide and examined under a microscope, the lymphocytes exhibit considerable activity. The simplest form they assume is a sphere, but, being capable of pronounced and continuous amœboid movement, they take on all sorts of shapes from the sphere through the types with few pseudopodia to stellate forms with many slender, conical-shaped pseudopodia as shown in figure 136, *a, b, c.* During these movements the nuclei remain unchanged in form. When exposed to the air the amœbocytes collect together in tangled groups (fig. 136, *c*), after which the central mass runs together as a plasmodium. This phenomenon seems to be of great significance, for since the blood of lamellibranchs contains no fibrin and therefore is incapable of clotting, it is probable that this property of the corpuscles to form a plasmodium takes the place of the fibrin clot.

In size the corpuscles vary from 8 to 12 microns in diameter, with an average of about 10 microns. In histological preparations the nuclei are quite large and prominent; they contain one or two nucleoli and many chromatin granules (fig. 137). The cytoplasm appears as a fine reticulum or presents a uniform granular appearance. The number of corpuscles present in a given volume of hæmolymph is small when compared to the number of corpuscles present in the blood of vertebrates.

The fluid portion of the hæmolymph is an albuminous, salty liquid with an osmotic concentration equal to that of the sea water. When heated, a slight coagulation occurs. It is precipitated by picric acid, nitric acid, and mercuric chloride. It gives a decided biuret test, while the xanthoproteic acid is not pronounced. Glycogen is present in small quantities.

The volume of blood present in an animal varies with its size and condition. By cutting the posterior adductor muscle, after thoroughly draining a shellfish of the sea water held within the mantle cavity, it is possible by gently pressing the fleshy parts to extract most of the hæmolymph. The quantity obtained from well-nourished mussels about 3 inches long is between 5 and 6 cc.

PHYSIOLOGY.

The function of the circulatory system is to carry dissolved food materials and oxygen to the various tissues of the body and to remove the carbon dioxide and other waste products of metabolism. This is accomplished by the circulation of blood, or hæmolymph, through the system of arteries and veins which have been described. Circulation is maintained by regular pulsations of the heart, which in the adult beats at the rate of 25 to 30 times per minute when the body temperature is 20° C.

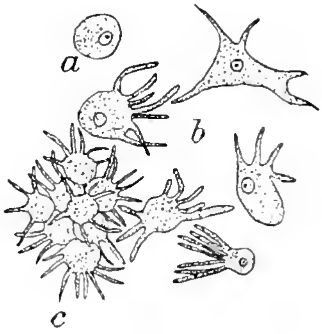

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Fig. 136.—Blood corpuscles drawn from life. ×500. *a*, contracted condition; *b*, showing pseudopodia formed during locomotion; *c*, tangled group of corpuscles.

Fig. 137.—Blood corpuscles drawn from histological section. ×500. Fixed in Gilson fluid and stained with Heidenhain iron hæmatoxylin.

The character of the heart beat is somewhat similar to that of the vertebrate. At first the auricles contract. This is followed immediately by a slight dilation of the posterior end of the ventricle, and then a wave of contraction moves forward rapidly over it. At the same time the ventricle contracts and discharges its blood into the aorta the auricles dilate with blood received from the oblique vein. This is followed by a period of rest, and then the process repeats itself.

The blood forced into the ventricle by contraction of the auricles is prevented from returning by the presence of auriculo-ventricular valves. In like manner blood pumped from the ventricle into the aorta is prevented from flowing back by valves present in both the anterior end of the ventricle and in the aortic bulb.

The blood flows from the aorta to the different organs of the body through a system of arteries which ultimately break up into a lacunar network of vessels that pervade all the tissues. The main arterial vessels lie on the outer surfaces of the mantle and run through the deeper parts of the body where the carbon dioxide accumulates in greatest abundance. Becoming laden with the waste products of metabolism, the blood accumulates in the veins and sinuses which, for the most part, lie on the inner walls of the mantle and superficial parts of the body where a continuous flow of water is maintained over them by the cilia of the gills. This allows a ready interchange of gases with the sea water, whereby oxygen is absorbed by the blood and carbon dioxide eliminated. This process is continued further in the gills and plicate canals, as will be described below.

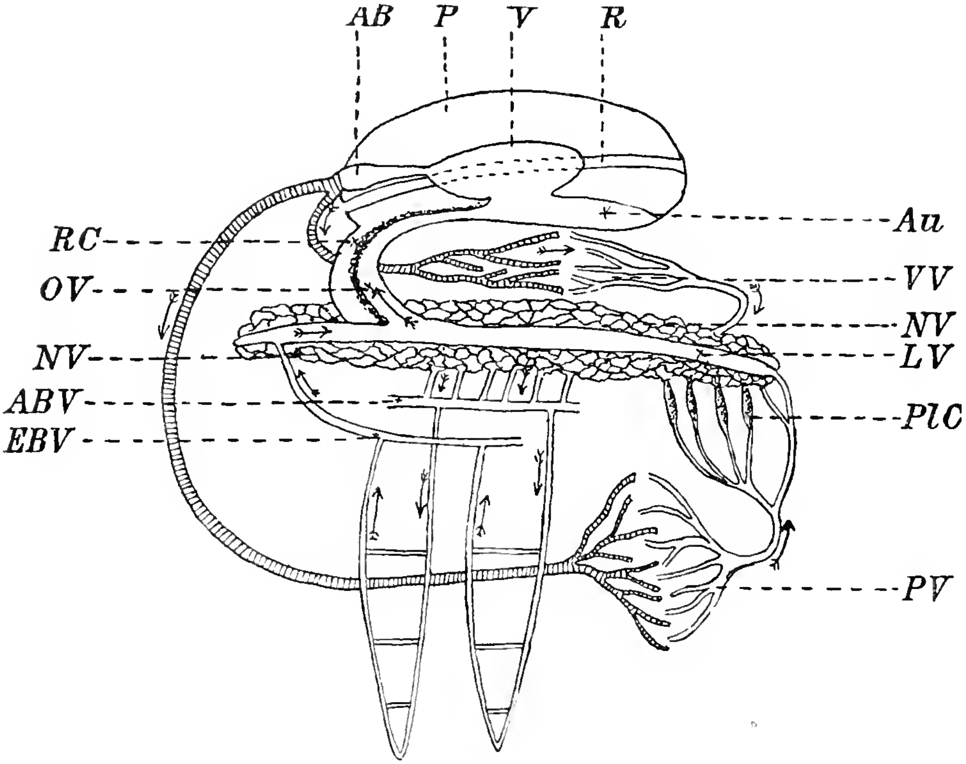

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FIG. 138.—Diagram of the circulatory system of *Mytilus edulis*. *Au*, auricle; *AB*, aortic bulb; *ABV*, afferent branchial vein; *EBV*, efferent branchial vein; *LV*, longitudinal vein; *NV*, nephridial veins; *OV*, oblique vein; *P*, pericardium; *PlC*, plicate canals; *PV*, pallial blood vessels; *R*, rectum; *RC*, renipericardial canal; *V*, ventricle; *VV*, visceral blood vessels.

The return of the blood to the heart may take place through several channels. Most of the blood from the visceral organs—stomach, intestines, liver, etc.—is discharged into the lacunar system of vessels in the kidney. The blood from the mantle may flow in small part into the posterior longitudinal vein and from thence be carried directly to the heart without penetrating the kidney tissue. Most of the blood from the mantle, however, passes into the kidney by way of the plicate canals, which have been mentioned before as a compact series of thin-walled ribbonlike organs extending the length of the mantle just below the roots of the gills (fig. 134, *EPlC*, and fig. 135, *IPlC*, p. 153). These canals contain a spongy reticulum of elastic fibers and externally are covered with long actively beating cilia which keep up a constant flow of water. Sabatier (1874) was the first to recognize these as respiratory organs and noted how important it was for them to take on this rôle when the mantle was distended with genital products. This view is in harmony with the fact that when the mantle is filled with reproductive elements the plicate canals are distended with blood and are most prominent. A small amount of blood from the mantle may flow into the kidney without passing through the plicate canals.

In the kidney certain impurities are removed from the blood, as has been stated in the account of the excretory system.

The return of the blood to the heart from the kidney may be by two channels, either directly by way of the longitudinal vein and the oblique vein, or by way of the branchial vessels, anterior longitudinal vein, and the oblique vein. By far the greater part of the blood takes the first-mentioned course. The branchial circulation of Mytilus is very weak compared with that of many other lamellibranchs. Sabatier (1874) assigned three reasons to account for this: (1) The small caliber of the branchial vessels, (2) the feeble course of the blood which comes to the gills after traveling an extensive capillary network, and (3) the existence of more easy paths of return which allow the blood to reach the heart without traversing the gills.

A diagram of the general course taken by the blood in Mytilus is shown in figure 138.

MUSCULAR SYSTEM.

The muscles of *Mytilus edulis* fall naturally into five groups: (1) The adductors which close the valves, (2) the muscles of the foot, (3) the retractor muscles of the foot and byssus, (4) the pallial muscles which attach the mantle to the border of the shell, and (5) the anal muscles.

The adductor muscles are two in number, consisting of a small anterior adductor and a large, much more strongly developed, posterior adductor. The ratio in volume between the two muscles varies from 1:8 to 1:10. The posterior adductor (fig. 117, *PAd*, opp. p. 138; fig. 141, *PAd*, opp. p. 158) serves as the powerful muscle to close the valves and is located in the posterior dorsal region of the body where it runs across from one valve to the other. Its ends are firmly embedded in the round impressions of the shell which have already been described. The muscle itself is more or less cylindrical in form and is composed of numerous bundles of fibers which run parallel with each other across the space between the valves. Owing to the convexity of the shell the fiber bundles of the lower portion are about twice as long as those on the dorsal surface.

The anterior adductor (fig. 141, *AAd*) lies at the anterior end of the ventral edge of the shell. It extends across from one valve to the other as a thin band of fibers which is traversed on its midventral surface by a narrow pigmented membrane that arises from the union of the inner folds of the right and left mantle edges. The muscle terminates on the anterior ventral surface just inside the edge of each valve in the impression shown in figure 104, *AAd* (opp. p. 132).

The muscles of the foot are of two types, an outer circular layer of fine fibrils and an inner longitudinal layer composed of large bundles of fibers (fig. 145, *CM* and *LM*, opp. p. 159). The longitudinal muscles make up the bulk of the foot and run its entire length. They occupy chiefly the dorsal and lateral portions; in the ventral region they are present as a single layer of small bundles. The circular layer surrounds the foot with a thin sheath of fibrils which lies just beneath the surface layer of pigmented, ciliated epithelium. Near the tip of the foot on the right and left sides the circular muscles give rise to numerous oblique muscles which run in various directions in such manner as to form a coarse network.

The purpose of this system of arrangement is obvious when the function of the foot is known. By contraction of the circular muscles the foot is thrust out as a long slender organ which may be directed in its course by the longitudinal and oblique muscles; contraction of the powerful longitudinal muscles with the synchronous relaxation of the circular muscles serves to draw the foot into a short, thick organ. The importance of these movements will be discussed later when the formation of the byssus and the movement of the mussel are described.

The anterior retractors of the byssus and foot (fig. 141, *ARet*, opp. p. 158) arise from the base of the byssus as a pair of cylindrical muscles which run forward on the ventral surface of the body (fig. 140, *ARet*, opp. p. 158) slightly diverging in the form of a letter V. They are inserted in elliptical impressions which lie on the dorsal anterior end of the shell parallel with the ligament. These impressions are about three times as long as they are broad, but are not symmetrical with each other, one usually being longer proportionately than the other. Although the name infers that these muscles are related to the foot, they really are not in the adult, for all the fibers terminate at the base of the byssus or are interwoven with the fibers of the posterior retractors of the byssus.

The posterior retractors of the foot and byssus may be described together since they are fused together in such close relation (fig. 140, *PRet*; fig. 141, *PRB*). Whereas the anterior retractors consist of a single cylindrical pair of muscles, those of the posterior retractors consist of several paired bundles which may vary in number from three to six or even more. They arise from the base of the foot and byssus as a single powerful muscle which divides up into separate bundles that spread out on either side in a fanlike manner and terminate in the impression of the valve which runs forward from that of the posterior adductor muscles parallel with the dorsal edge of the shell. The most posterior bundle runs directly over and in contact with the posterior adductor. The most anterior bundle arises from the base of the foot itself and properly constitutes the retractor of the foot (fig. 141, *PRB* and *PRF*).

The pallial muscles, or those of the mantle edge, are present on the ventral, posterior, and dorsal border of the mantle. They are composed of numerous small bundles of fibers which are separated a short distance from each other and run perpendicularly to the outer edge except in the region dorsal and anterior to the posterior adductor muscle where they slope backwards obliquely to the outer edge of the mantle (fig. 133, *Pal*, p. 149). The muscles are most strongly developed in the posterior region where the inner mantle fold is thicker and in the area about the anal syphon.

The anal muscles (fig. 117, *An*, opp. p. 138) are merely modified pallial muscles which arise from the wall of the anal syphon and are inserted in the shell impression which forms the triangular area on the posterior ventral edge of the impression made by the posterior adductor muscle.

With such a muscular system the sea mussel is wonderfully adapted for living in an environment where it is subjected to strong currents, the surge of the ocean, and other forces which exert great strains upon it. The pallial muscles firmly bind the edges of

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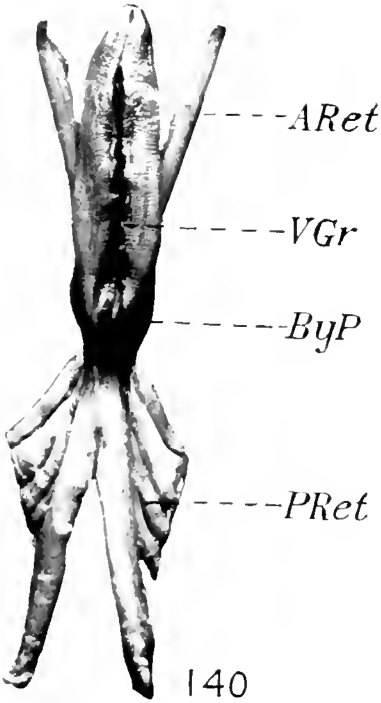

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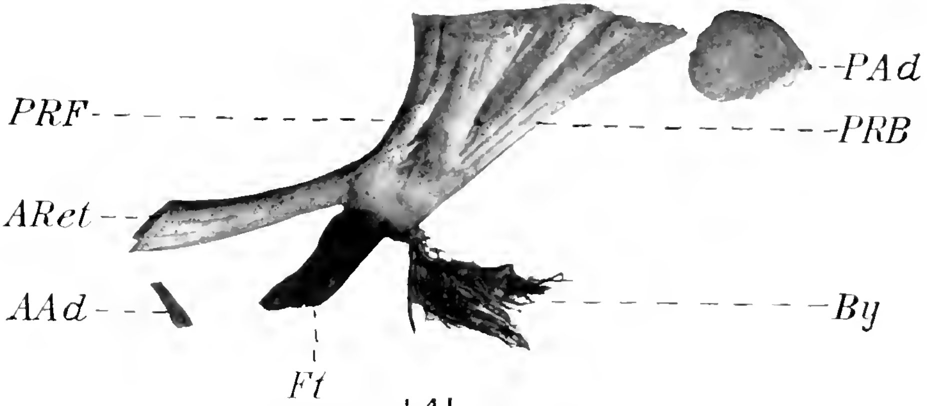

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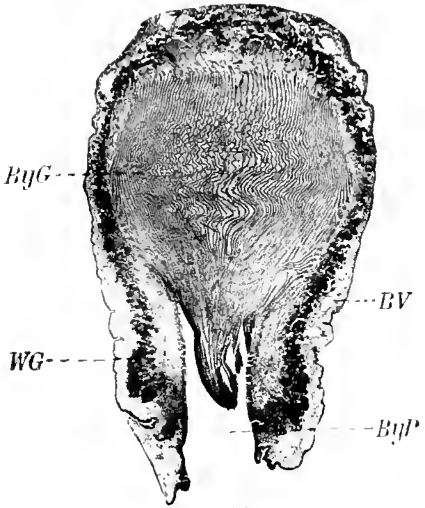
FIG. 139.—Photomicrograph of a byssus thread and end plate × 10.

FIG. 140.—Ventral view of foot and retractor muscle.

FIG. 141.—Side view of adductor and retractor muscles.

ABBREVIATIONS.—*AAd*, anterior adductor muscle; *ARet*, anterior retractor muscles; *By*, byssus; *ByP*, byssus pit; *ByT*, byssus thread; *EP*, end plate; *Ft*, foot; *PAd*, posterior adductor muscle, *PRB*, posterior retractor muscles of byssus; *PRet*, posterior retractor muscles; *PRF*, posterior retractor muscles of foot; *VGr*, ventral groove.



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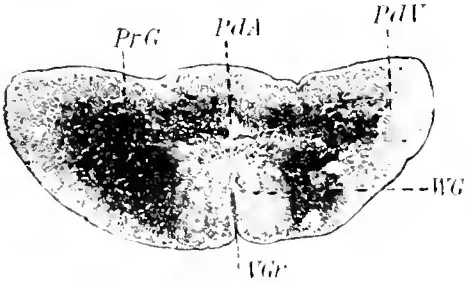

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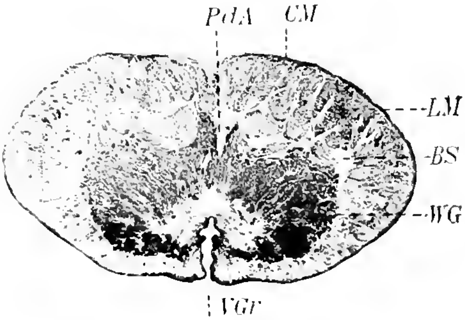

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FIG. 142.—Photomicrograph of main byssus gland in cross section. × 8. Fixed in Gilson fluid and stained with Delafield hæmatoxylin

FIG. 143.—Sagittal section through foot. × 6 approximately.

FIG. 144.—Cross section of foot taken just posterior to sucker.

FIG. 145.—Cross section of foot in the mid region. × 7 approximately.

ABBREVIATIONS.—*BS*, blood sinus; *BV*, blood vessels; *ByG*, glandular lamellae of byssus gland; *ByP*, byssus pit; *CM*, circular muscles; *LM*, longitudinal muscles; *PdA*, pedal artery; *PdV*, pedal vein; *PrG*, purple gland; *S*, sucker; *VGr*, ventral groove; *WG*, white gland.

the mantle to the shell, and the powerful retractors centered in the foot and byssus, which is the anchoring organ, are so firmly embedded in the calcareous walls of the shell that they can not be separated without tearing the muscles themselves. This enables the sea mussel to thrive in situations where no other shellfish can exist.

FOOT AND BYSSUS.

ANATOMY AND HISTOLOGY.

The foot is a muscular, glandular organ, tonguelike in form, with a deep longitudinal groove on the underside that terminates near the tip in a cuplike depression which serves as a sucker when the animal takes hold of a solid object. Posteriorly the groove becomes continuous with the byssus pit (fig. 118, *VGr* and *ByP*, opp. p. 138). When the foot is in a contracted state the groove forms an irregular line and its lips have crenated edges. As the foot becomes relaxed and extended, the groove and lips assume a straight form. The base of the groove is enlarged to make a closed canal leading from the byssus pit to tip of the foot when the lips are pressed together. This condition is readily seen in a cross section of the foot (fig. 145, *VGr*, opp. p. 159).

The entire surface of the foot is covered with a columnar, dark brown, pigmented, ciliated epithelium, the ciliated parts extending over the inner walls of the groove.

The portion of the foot which lies immediately below the epithelial covering is made up of numerous muscle bundles which have been described under the muscular system. Between the bundles numerous large blood spaces occur, as may be seen in a cross section of the organ (fig. 145, *BS*).

The central and ventral portions of the foot are filled with a mass of glandular tissue. Tullberg (1882) and Williamson (1907) have made quite thorough studies of the anatomy of the byssus glands and their results and terminology are used in the following description.

The byssus glands may be divided into two sets according to the region they occupy, (1) those of the foot and (2) those of the byssus pit which lies just behind the foot.

Two kinds of glands are distributed in the foot. The principal one is white in color and is therefore known as the white gland. It is of large size and occupies the middle region of the foot, inclosing the basal canal and extending more or less over the walls of the foot groove (fig. 145, *WG*). The white gland borders the groove for its whole extent and posteriorly continues backward to surround completely the byssus pit. The second type of the gland in the foot is known as the purple gland. It lies dorsal to the white gland and discharges its secretions into the cuplike depression at the end of the groove. It lies chiefly in the anterior region where it becomes much larger than the white gland. (See fig. 144, *PrG*, opp. p. 159.)

The glands of the byssus pit are also two in number. One set, as just described, represents a prolongation of the white gland which surrounds the opening of the byssus pit. Separated masses of glandular tissue of the same nature as the white gland occupy spaces between the muscle bundles and connective tissue of the walls of the byssus cavity (fig. 142, *WG*, opp. p. 159). The second set of glands is scattered through a series of thin lamellæ which are suspended from the dorsal wall of the byssus pit. They run parallel to the long axis of the body and hang down like the leaves of a book (fig. 142, *ByG*).

The origin of this very specialized type of molluscan foot which is found in Mytilus has been traced from the simple foot of Solenomya, which has a flat sole with a simple invagination but possesses neither groove nor byssus. Nucula and Leda have this same type of foot, but in addition there arises from the simple invagination a small lamella and a byssus is developed to a slight extent. The next step leads to the condition found in Mytilus where the invagination is differentiated into a cavity with a duct and the byssus with its glands is highly developed. Being no longer primarily an organ of locomotion, the foot has degenerated in size to a strap-shaped appendage without any sole. Its power of extension, however, is increased to serve the chief function of attaching the byssus. Parallel with this change from the primitive foot to the byssus-forming foot there is a modification of the pedal muscles which become attached to the byssus gland forming the retractors of the byssus.

The byssus is a bundle of tough threads secreted by the glands lying in the foot and byssus pit with which the animal anchors itself to convenient objects. It consists of a great number of very thin sheets or septa of byssal matter lying between the lamellæ which hang down into the byssus cavity. As the byssus septa grow downward they are molded together in the form of the cavity and pass outward through the external opening in the form of a solid rod, the so-called byssus root (fig. 117, *ByR*, opp. p. 138). Externally the root becomes a region of origin for numerous byssal threads which terminate in specialized endings, composed of a cementlike material capable of attaching them to solid objects with great firmness.

The byssus material is light to dark brown in color and appears to be made of numerous layers, one above the other, but when crushed or torn it breaks up readily into fine fibrils. Tullberg (1882) pointed out that the surface layer of the thread stained with carmine while the central portion did not and concluded therefore that it was a different substance. Williamson (1907), however, believes that the thread is homogeneous in character and that the reaction is due to the action of sea water in its surface. Tullberg (1882) further believed that the stem was enveloped with a rind, but Williamson (1907) pointed out that this was true only where the base of the threads enveloped it. The covering was nothing more than the numerous threads which were looped about it, for no rind was present where they were absent.

The attachment plates, or what Williamson calls the "buttons," are at the distal ends of the threads and serve as the direct medium of attachment for the byssus. They are gray in color and when stained with Bordeaux red or hæmatoxylin they show a typical alveolar structure with a byssal thread spreading out and terminating in the center. (See fig. 139, opp. p. 158.)

PHYSIOLOGY.

The foot serves as an organ of locomotion, and in conjunction with the glands of the byssus cavity it functions in producing the byssus and attaching the threads to favorable positions.

As a locomotor organ it is very effective in performing its functions, although considered degenerate anatomically. The author's attention was directed to the unusual locomotor powers of young mussels when he placed an incrusted mass of material covered with mussels of all sizes from 1 to 50 mm. in length in a glass battery jar under a tap of running sea water. Twenty-four hours later the very young mussels, which measured from 1 to 4 mm. in length, were found attached in a mass about the upper edge of the jar. These same mussels, with other young ones of larger size, were placed in a glass dish containing sea water and kept under observation. In less than a minute most of them thrust out the foot and began to creep about. The foot was extended for a distance beyond its base nearly equal to the length of the animal itself. The tip of the foot was then attached by means of its sucker, and then by contracting its longitudinal muscles the body was drawn almost up to the point of attachment. Mussels 1½ mm. long extended the foot for a distance of 2 mm., those 5 mm. in length extended it 4 mm., while mussels 10 mm. in length thrust it out for a distance of 8 mm. before contracting it.

The young shellfish were able to creep up the perpendicular walls of the glass dish almost as well as they could over the bottom, but their powers for moving under difficult conditions did not reach their limit here. A number of individuals, having reached the surface of the water, continued on by creeping out on the underside of the superficial film similar to the habit of the pond snail. Some of them succeeded in traveling across the dish without falling, while others lost their hold and sank slowly to the bottom with their feet fully extended and moving about as if in search of an object on which to anchor themselves. The slow rate at which they sank suggested that they were possibly being supported by ciliary action on the foot.

Ascending a perpendicular wall and creeping on the superficial film of the water is accomplished by using the entire ventral groove as a sucker. By distending and contracting the foot and alternately attaching the posterior and anterior ends progression is accomplished. Sometimes the young shellfish would allow themselves to slide down the wall of the glass dish on the bottom of the foot, catching hold every few millimeters in the descent and then relaxing their hold again.

The rate of locomotion was determined by allowing the mollusk to creep over measured distances which varied from 1 to 10 cm. in extent. Specimens 4 to 5 mm. in length were used, and these covered the distance at rates varying from 1½ to 2½ cm. per minute. The usual and average rate was 2 cm. per minute.

Before describing the functions involved in the formation of the byssus it will be well to state briefly the views which have been held in regard to its origin and nature. Von Nathusius-Königsborn (1877), Reichel (1888), and others took the view that the byssus grew from the animal's body, as does the cuticula of arthropods, and in like manner was shed from time to time. On the other hand, Müller (1837), Tullberg (1882), Jobert (1882), and Williamson (1907) have disproved the contentions of these writers by clearly demonstrating that the byssus arises as a glandular product. A few observations of the byssus-forming habit of the mussel are sufficient to convince one that this substance is a product of glandular secretion and not of cuticular growth.

The byssus stem, which represents the fused secretions from the cells of the epithelial walls of the glandular cells lying in the surrounding tissue, is molded into its characteristic form first by the cavity and then by the neck leading to the opening from which it passes out. Growth is continuous, but its rate probably depends upon the amount of strains the byssus has to bear, vigorous stimuli causing a more rapid secretion of material. Such growth is capable of producing a stem of cumbersome length, but the shellfish is able to avoid this by casting it off and starting a new one.

The threads are formed in the basal canal of the foot. When the mussel is in the act of producing a new thread the foot is extended and the depression near its tip placed in contact with the object to which the thread is to be attached. According to Williamson (1907), the secretions pour out from the white gland so that they surround the stem and fill up the groove, the flow probably being caused by internal pressure attained by distending with fluid the lacunæ which exist between the muscles and about the glands. In the depression at the end of the foot ducts from the purple gland pour out a cementlike secretion which forms the attachment plate for the thread. The secretions are thick when first discharged and of fibrous character. As soon as they are in place the lips of the groove open and allow the sea water to enter, which hardens them. This results in the formation of a thread which at the proximal end loops the byssus stem and at the distal end is cemented to some solid object by means of the attachment plate. In color the new threads are a glistening white, but in a few hours' time they become yellowish, then brownish, and when old may be of a very dark-brown shade.

The rate at which the threads may be formed was determined with some specimens about 1 inch long and which were probably less than 1 year old. It is advantageous to use young mussels for these observations, because after being transferred to a dish of sea water they become active far more quickly than do older shellfish and the production of byssal threads begins within a few minutes after they have crept about.

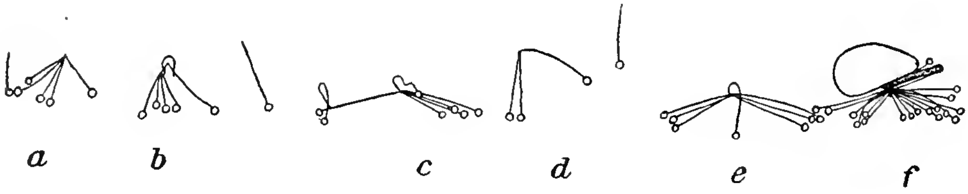

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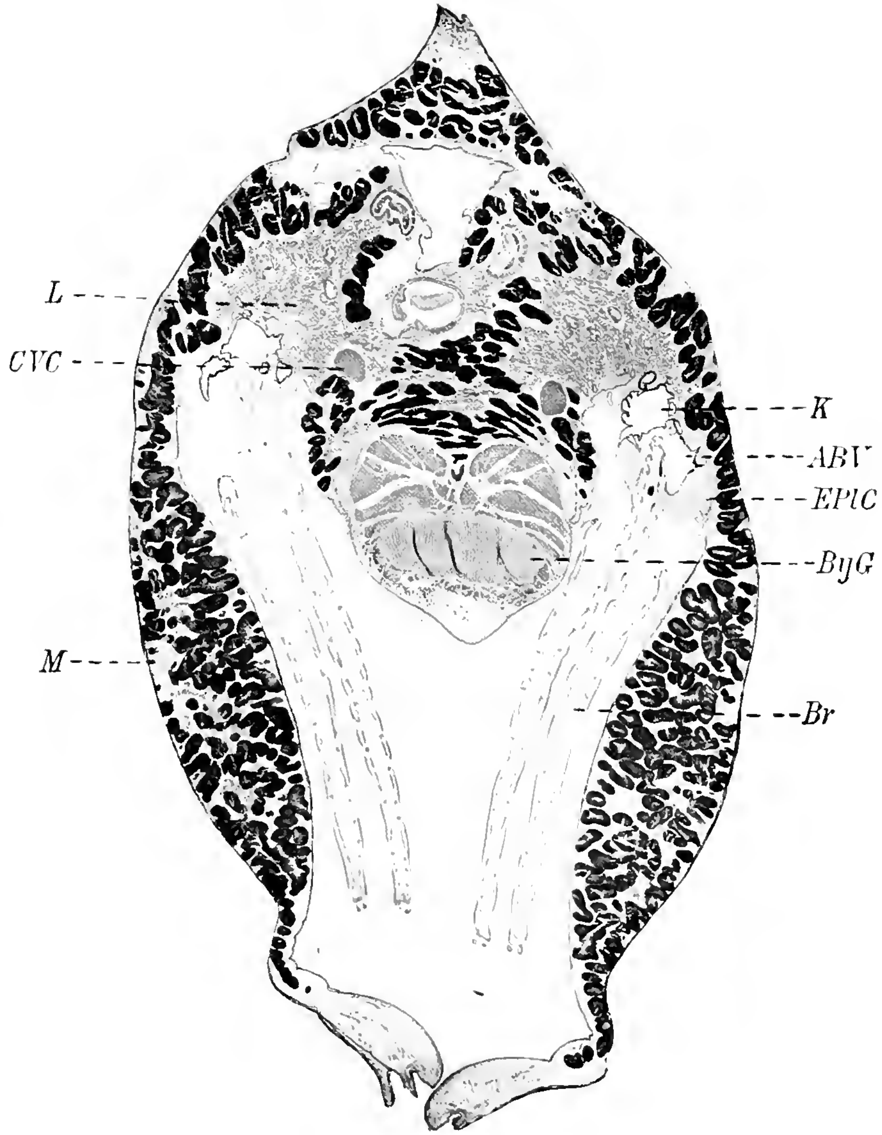
Fig. 146.—Tracing of a path of byssus threads left behind by a mussel 1 inch long during a period of three days.

In December, when the sea water was at a temperature of 45° F., two mussels, each 1 inch long, were placed in a 2-gallon battery jar containing sea water to a depth of 6 inches. In less than five minutes the shellfish began to creep about. When they came in contact with the side of the jar they promptly started to ascend the perpendicular wall and continued upward until they reached the surface of the water. There they stopped and began to attach themselves by means of byssal threads. The foot was extended and the cuplike depression at the end of the groove was pressed against the glass. The cavity of the depression appeared to become filled with a white cushion-like substance which flattened against the glass. With a strong hand lens the author tried to see what was taking place at this point of contact but could detect nothing. When, however, the foot was removed at the end of eight minutes a thread was found attached in this position by the usual attachment plate. The process was immediately repeated, this time the thread being formed and attached in three minutes. Then a third one was formed during the following five minutes. Four hours later this same mussel was found attached by 18 threads.

In another jar 14 young mussels were placed and left for a period of 3½ hours, when 4 of them were found attached to the side of the jar near the surface of the water with 10, 13, 15, and 16 threads, respectively.



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Photomicrograph of a cross section taken through mid-body region of a 1-year-old mussel. Fixed in Gilson fluid and stained with Delafield hæmatoxylin × 14.4. *ABV*, afferent branchial vein; *Br*, gills; *ByG*, byssus gland; *CVC*, cerebro-visceral commissure; *EPlC*, external plicate canals; *K*, kidney; *L*, liver; *M*, mantle filled with genital follicles.

Hescheler, in Lang (1896), states that most of the byssus-forming mussels are able to cast off the byssus and again replace it with a new one and many forms are able by alternately fastening threads forward and breaking off the old threads behind to move up a smooth, perpendicular glass wall. The sea mussel not only uses this method of movement on perpendicular glass surfaces but on horizontal surfaces covered with mud, as Williamson (1907) has described. Figure 146 represents a trail of byssus threads left by a mussel which was under the author's observation in the laboratory. It was in a glass dish half filled with sea water. The animal at first crept up the vertical side of the dish to the surface of the water, where it attached itself at *a*, then it started to move around the wall of the dish in the direction indicated by the letters *b*, *c*, *d*, etc., keeping just below the surface of the water. The distance of 7½ inches was covered in three days, at the end of which period the mollusk attached itself permanently with 18 threads and remained there until it died 10 days later, probably from starvation.

CHEMISTRY OF BYSSUS.

The composition of byssus is similar to that of the organic matter which is present in the shell. It is popularly spoken of as a horny or chitinous material, but in the opinion of Krukenberg (1886) it is closely allied to conchiolin, which forms the organic basis of the shell. According to Abderhalden (1908), it yields on hydrolysis glycocoll, tryosin, and proline in large amounts, besides alanine and aspartic acid. Treated with nitric acid the threads are stained yellow, which is a typical protein reaction. These results clearly indicate that byssus belongs in the albuminoid group and not in the class of chitin.

In regard to solubility, Winterstein (1910) states that the byssus threads are insoluble in boiling water, alcohol, ether, ammonia, dilute acids, or alkalis, but are slightly soluble in hot concentrated acetic acid or in concentrated mineral acids. The solution in acetic acid is precipitated by tannin or by mercuric chloride. According to Scharling (1842) and Schlossberger (1856), byssus is slightly soluble in potassium hydroxide. Byssus is classified by Hammarsten (1914) as a skeletin compound in the group of albuminoids.

RESPIRATORY SYSTEM.

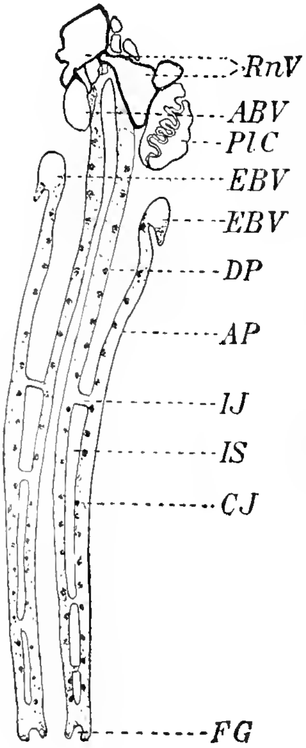
ANATOMY.

The organs of respiration in the Mollusca are usually the gills, but in the mussel, as in other lamellibranchs, the primary function of these organs seems to be the collection of food. The respiratory function is carried on only in part by the branchial apparatus. Aside from the gills, respiration takes place through the plaited membranes which extend across from the base of the gills to the mantle. To these folds Sabatier (1874) gave the name *Organes godronnes*. Respiratory exchange also takes place through the surface of the body, especially on the inner wall of the mantle.

The gills are suspended from the ventral side of the visceral mass on either side of the body (fig. 147, *Br*, opp. p. 163) and extend from the corners of the mouth to the branchial membrane (fig. 120, *Br*, p. 141). The posterior portion which extends from the ventral surface of the posterior adductor muscle to the branchial membrane is not attached to the body, but is supported by the large afferent branchial blood vessel which runs forward on its dorsal edge (fig. 135, *ABV*, p. 153). The right and left gills are most widely separated from each other in the middle of the body and from this point converge toward each other both anteriorly and posteriorly.

Our first knowledge of the finer structure of the gills of Mytilus is due to the careful work of Lacaze-Duthiers (1856), who studied both their constitution and development. The nomenclature which he introduced will be used in the description which follows. When observed in cross section the gills appear in the form of a narrow W suspended by the upper angle with the outer lamellæ terminating with a free edge in the mantle cavity (fig. 147, *Br*, opp. p. 163). This gives a branchial apparatus on each side of the body composed of two folds, each of which is made up of two lamellæ. The outer plates on each side are known as the right or left outer gill plates, and in like manner the inner plates are designated as the right or left inner gill plates (fig. 148). The separate lamellæ of each plate are known as the *descending portions*, which arise from the point of attachment of the gills and pass to the ventral edge, and the *ascending portions*, which arise from the ventral border and extend upward terminating with a free edge. The space inclosed between the ascending and descending lamellæ is known as the *interlamellar space* (fig. 148, *IS*).

In side view the gills are seen to be composed of numerous parallel filaments which lie one next to the other, with a slight interfilamentar space between them. They are cross-marked with fine, light-colored striations which form parallel lines running from the anterior to the posterior end of the gills.



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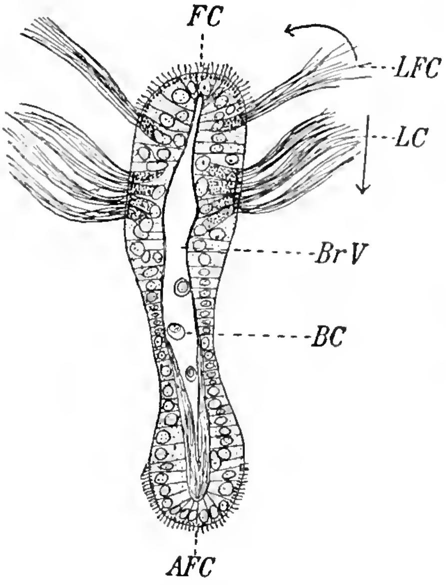
Transverse section of a gill. *ABV*, afferent branchial vein; *AP*, ascending portion of gill lamella; *CJ*, ciliary junction; *DP*, descending portion of gill lamella; *EBV*, efferent branchial vein; *FG*, food groove; *IJ*, interlamellar junction; *IS*, interlamellar space; *PlC*, plicate canal; *RnV*, renal veins lined with kidney tissue.

HISTOLOGY.

The filaments which make up the gills are composed of specialized groups of ciliated epithelial cells which surround a central canal or branchial blood vessel (fig. 149). In this cross section of a gill filament four types of cilia may be clearly distinguished: (1) Frontal cilia, which are relatively short (*FC*); (2) latero-frontal cilia, which are very long (*LFC*); (3) lateral cilia, also very long (*LC*); and (4) ab-frontal cilia, which are the least developed of all (*AFC*). Each group has a special function to perform, as will be explained later. Gland cells are also present in the latero-frontal region, according to Kellogg (1892). The author's own preparations do not show them unless the ciliated cells which bear the latero-frontal and lateral groups of cilia also function as gland cells. Their protoplasmic content is filled with fine granules which stain deeply with acid fuchsin when no other parts of the tissue take this dye. They have the appearance of gland cells, but at the same time seem to be nothing more than highly specialized ciliated cells.

Connections between the filaments are established by means of tufts of cilia which project from their anterior and posterior surfaces close to their interlamellar edge. These *ciliated junctions* occur at short intervals over the entire length of both the ascending and descending limbs, varying in number from 15 to 30, according to the age of the specimen (figs. 148, *CJ*, p. 164; figs. 150, and 151, *CJ*).

The ascending and descending fibers of each gill are attached by cross partitions of tissue which have the form of bars. These structures were given the name *interlamellar junctions* by Peck (1877). (See fig. 148, *IJ*.) They are usually three or four in number, separated by some distance and not grouped as Peck figures them. According to this author they are composed of longitudinal elastic or muscular fibers surrounded by a layer of epithelium which gives them great powers of extensibility and contractibility. He speaks of them as "bellowslike processes." They are traversed by a canal which allows cross communication between the vessels of the ascending and descending limbs. The walls of the latter canals, according to Peck (1877), are lined with chitin, while those of the interlamellar junctions are not. Kellogg (1892) makes a similar statement but in addition says an endothelial lining is present. What these authors refer to as chitin is probably not that substance but conchiolin or some related compound.



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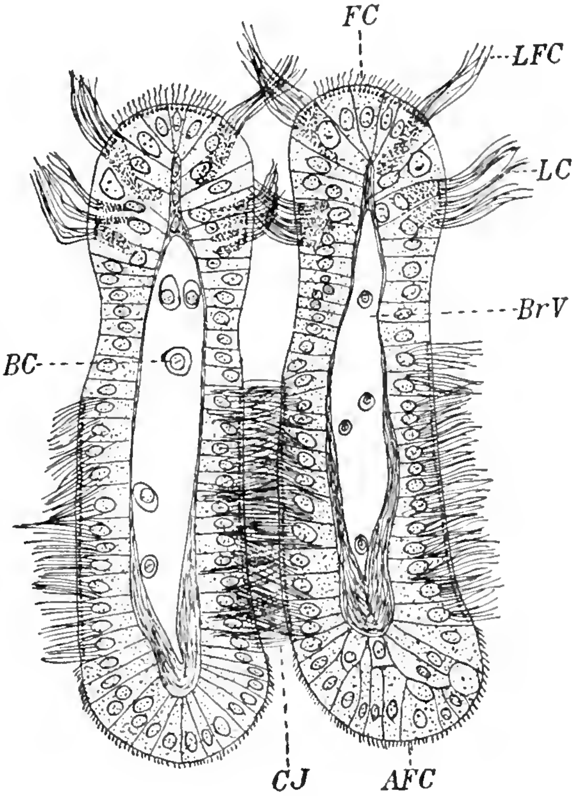

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FIG. 149.—Transverse section of gill filament taken through the area between ciliary junctions. × 500.

FIG. 150.—Transverse section of two gill filaments taken through a ciliary junction. × 500.

ABBREVIATIONS.—*AFC*, abfrontal cilia, *BC*, blood corpuscle; *BrV*, branchial vein; *CJ*, ciliary junction, *FC*, frontal cilia; *LFC*, latero-frontal cilia which lash in direction indicated by arrow; *LC*, lateral cilia which lash in direction indicated by arrow.

The free ends of the filaments which form the ascending lamellæ are hook-shaped, with their anterior and posterior ends firmly attached to each other. This free edge is traversed for its whole length by the efferent branchial blood vessel (fig. 148, *EBV*), which increases in size toward the anterior end of the body.

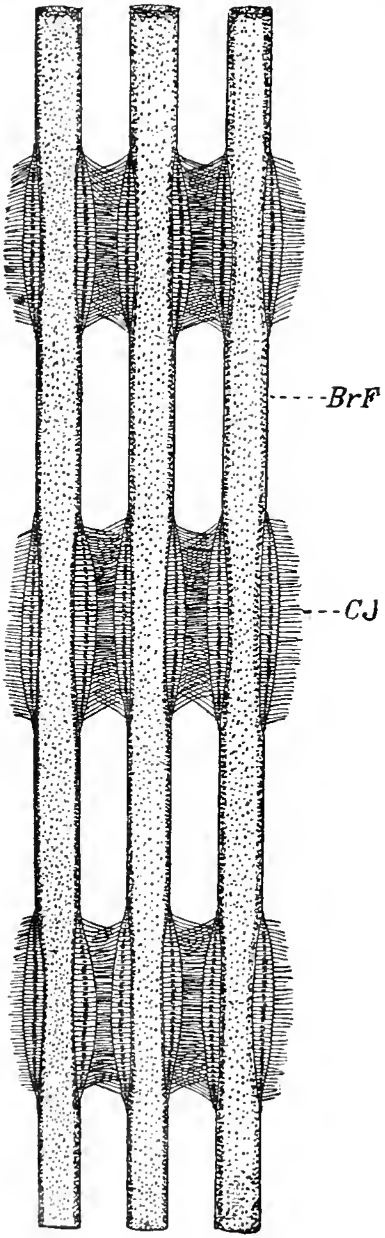

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FIG. 151.—Lateral view of a portion of a lamella showing three gill filaments. × 130. *BrF*, branchial filaments; *CJ*, ciliary junction.

The *plicate canals* or *Organes godronnes* of Sabatier (1874) are membranous structures which extend from the mantle to the base of the gills across the tip of the angle formed at the junction of these two organs. They are so arranged as to form a series of parallel lamellæ running forward slightly oblique to the line of attachment of the gills (fig. 134, *EPlC*, and fig. 135, *IPlC*, p. 153). Externally they appear as smooth triangular plates covered with a fine ciliated epithelium (fig. 118, *PlC*, opp. p. 138).

They are composed of two thin membranes of fibrillar connective tissue united to each other by strands of the same kind of tissue, which form a regular spongy reticulum in the cavity. The space between them is a blood channel which connects the veins of the mantle with the blood vessels of the kidney and with the longitudinal vein.

PHYSIOLOGY.

Primarily the gills of Mytilus function as food-collecting and filtering organs; secondarily they serve as organs of respiration. By means of the powerful cilia which cover the gills, strong currents of water are swept in by way of the inhalent syphon. The strength of the current flowing out of the exhalent syphon is frequently so strong as to make the water appear to be boiling over a mussel which is lying 2 or 3 inches below the surface. The floating food materials, consisting of diatoms, protozoans, and minute organic particles, are thus swept in by these food currents where they are filtered out and transported to the mouth. The currents of water, in addition to bringing in a constant supply of food, also carry the necessary oxygen for the respiratory exchange which takes place through the gills, plicate canals, and the mantle wall.

The action of the different sets of cilia in performing this function has been ably studied by Orton (1912). He found that the lateral cilia which lash across the length of the filaments are the chief cause of the inhalent current and that the frontal cilia which lash toward the free edge of the gill collect the food particles and sweep them toward the food groove on the ventral edge (fig. 152). On the interlamellar or ab-frontal surface the cilia sweep upward or in just the opposite direction of the frontal cilia. They serve to help in producing the main current and in keeping the inner surfaces of the gills clean.

The long latero-frontal cilia are undoubtedly the straining mechanism. They project out from the sides of the filaments, forming a sieve, and lash relatively slowly across the middle of the frontal face of the filament (fig. 152; fig. 149, p. 165). Orton (1912) summarizes his results as follows:

> Thus Nucula and Mytilus have four kinds of cilia, the lateral cilia producing the main current, the frontal for collecting and transporting the food, the fronto-lateral which assists in food collecting and the ab-frontal or inner cilia which help in producing the main current, in collecting food, and in cleaning the filaments.

The gland cells which Kellogg (1892) says are present in the latero-frontal region of the filaments probably serve to secrete a mucus which cements the food particles together in morsels of convenient size. These are swept by the frontal cilia into the food groove, in which they are carried forward by the cilia lining its walls to the labial palps, which transfer them into the mouth.

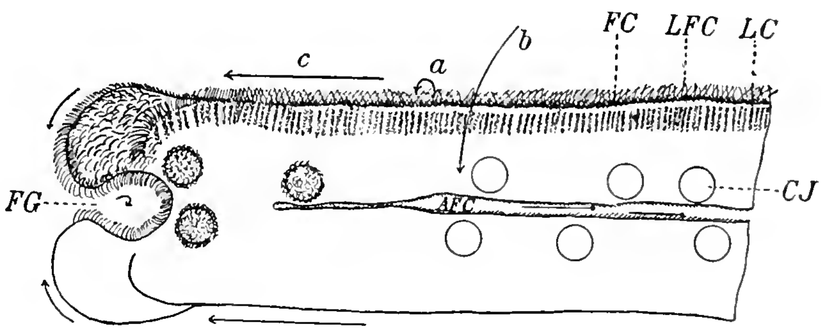

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FIG. 152.—Longitudinal interfilamentary view of a living filament of the left outer lamella of the gill. × 84 approximately *a*, *b*, *c*, arrows indicating roughly the directions in which the latero-frontal, lateral, and frontal cilia, respectively, lash. *CJ*, ciliary junction; *FC*, frontal cilia, *FG*, food groove; *LC*, lateral cilia; *LFC*, latero-frontal cilia.

As an organ of respiration the gills perform their function incompletely. This was recognized by Sabatier (1874), who found that circulation took place within the filaments in a very imperfect manner. The defective circulation, according to this author, is due (1) to the small caliber of the branchial vessels, (2) to the weak current of the blood which flows to the gills after having traversed the kidney or other capillary network, and (3) to the existence of other and larger channels which allow the blood to return to the heart without traversing the gills.

The mantle serves as an organ of respiration when it is not distended with genital products. During the period of reproductive quiescence it is a thin-walled organ, with the blood vessels separated from the outside medium by a very thin layer of tissue. During reproductive activity, however, the walls of the mantle become thick and the blood vessels are covered with heavy layers of tissue in which metabolic activity is accelerated by the formation of reproductive elements causing the production of large quantities of carbon dioxide. The respiratory function is greatly increased in the plicate canals at this time. They become enlarged and well filled with blood which flows through them from the mantle to the kidney and longitudinal vein. Being composed of thin convoluted membranes and covered externally with cilia which keep up a constant circulation of water, these organs are able to bring the blood into intimate relation with a rich supply of oxygen. They might well be termed the accessory gills.

EXCRETORY SYSTEM.

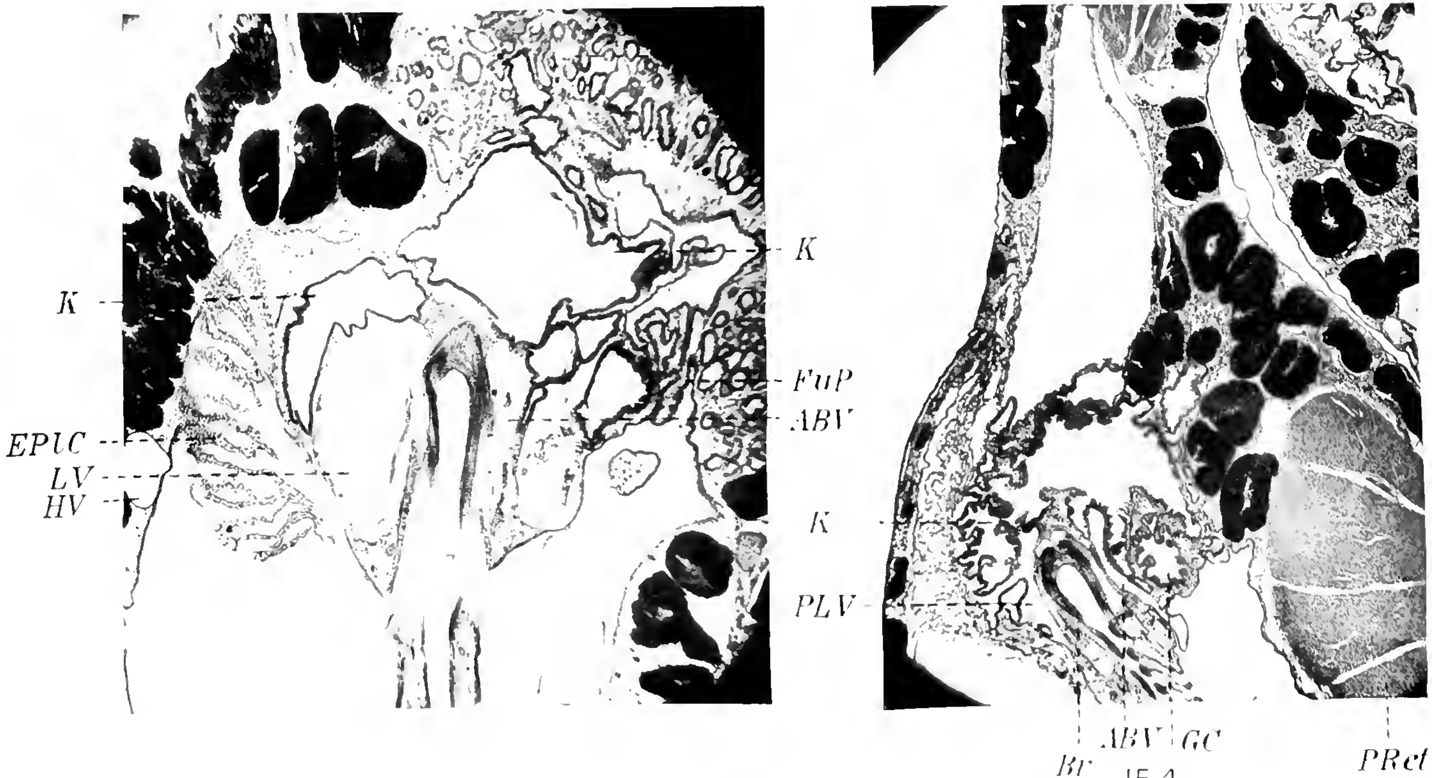
ANATOMY.

In the sea mussel the excretory system consists of two sets of organs, the kidney, or so-called organ of Bojanus, and a pair of pericardial glands which invest the outer walls of the auricles. If the posterior adductor muscle of the shellfish be cut and the valves laid open so that the gills lie flat on the mantle wall as is shown in figure 118 (opp. p. 138), the kidney may be seen as a dark brown band of tissue along the ventral body wall at the base of the gills, extending from the posterior border of the labial palps to the posterior adductor muscle (fig. 135, *K*, p. 153). Sabatier (1874) divided the kidney into two parts, (1) that which is independent of the blood vessels and (2) that which covers the walls of the great veins. The former type lies anteriorly on the lateral walls of the liver, where it is thrown into conical folds which extend across to the main canal of the kidney like the teeth of a comb. These folds are designated by Sabatier as the "fusiform pillars of the kidney" (fig. 153, *FuP*, opp. p. 168).

The second type of kidney tissue, or that dependent on the blood vessels, consists of plates of tissue which cover the walls of the great veins. This portion of the organ forms a long sac with numerous diverticula which cover the walls of the large longitudinal vein or line its cavity. As the central cavity of the kidney extends backward it increases both in size and in number of diverticula, as may be seen in figures 153, 154 (opp. p. 168), and 157 (opp. p. 169), which are cross sections taken at the anterior, middle and posterior regions of the body, respectively. The kidney discharges exteriorly through a small excretory pore located on a slight elevation at the base of the genital papilla on its posterior side (fig. 158, *EO*, opp. p. 169). It was first discovered by Lacaze-Duthiers (1854).

The pericardial glands, so named by Grobben (1888), but previously described by Sabatier (1877), are an extensive part of the kidney tissue which invests the outer walls of the auricles. The enveloping tissue consists of numerous small folds of various sizes which are dark brown in color similar to that of the kidney proper. Posteriorly the glands are attached to the wall of the pericardial cavity; while anteriorly each gland extends downward into the afferent oblique vein and becomes intimately attached to its walls.

The pericardial cavity, just anterior to the oblique vein, is in open communication with the collector canal of the kidney by what Sabatier (1874) termed a "couloir placé," which consists of a spongy partition of kidney tissue through which are many fine openings that allow passage of the contents of the pericardial chamber into the kidney canal but render difficult any return backward (fig. 138, *RC*, p. 156).



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Photomicrographs of transverse sections through the kidney in the middle region of the body (fig. 153) and in the posterior region of the body (fig. 154). *ABV*, afferent branchial vein; *Br*, gill; *EPlC*, external plicate canals; *FuP*, fusiform pillars of Sabatier; *GC*, genital canal; *HV*, horizontal vein; *K*, kidney; *LV*, longitudinal vein; *PLV*, posterior longitudinal vein; *PRet*, posterior retractor muscle.

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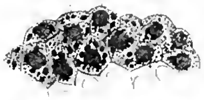

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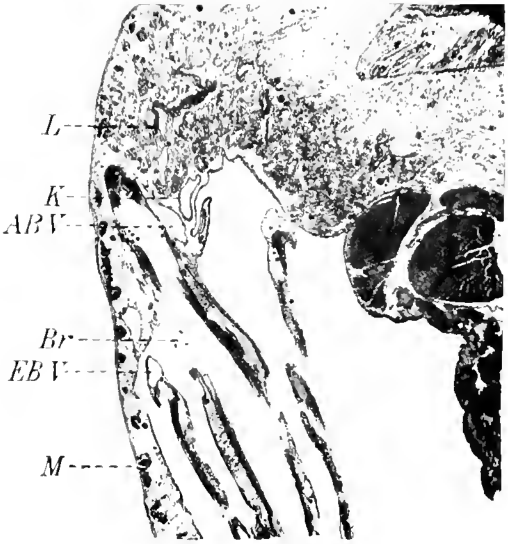

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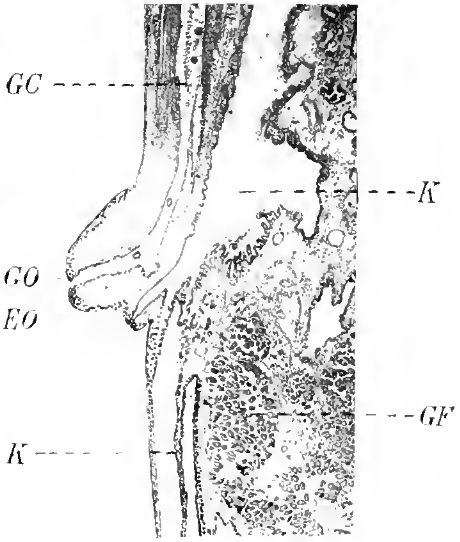

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FIG. 155.—Transverse section through the pericardial glands. × 350 approximately. *CS*, blood corpuscle; *Ep*, epithelium of the pericardial gland; *Ms*, muscle fibers (After Grobben, 1888.)

FIG. 156.—Pericardial gland epithelium drawn from life. × 490. (After Grobben, 1888.)

FIG. 157.—Photomicrograph of a transverse section taken through the anterior region of the kidney. *ABV*, afferent branchial vein, *Br*, gill, *EBV*, efferent branchial vein, *K*, kidney; *L*, liver; *M*, mantle

FIG. 158.—Photomicrograph of a longitudinal section through the genital papilla. × 12. *EO*, excretory opening; *GC*, genital canal; *GF*, genital follicle filled with ova; *GO*, genital opening; *K*, kidney

HISTOLOGY.

The cells which make up the kidney tissue are of two types, as described by Sabatier (1874). One class is found in what he termed the free or independent part, as is best seen in the pillars of the kidney and the membrane which separates the kidney canal from the pericardial cavity. These form a pavement epithelium of nearly cubical cells, with the free edge presenting a convex surface. A large, round nucleus lies in the center or near the base of the cell. The cytoplasm is clear and transparent and often contains either few or numerous small greenish granules. In size these cells vary from 8 to 10 microns in diameter.

The second type of cell is found in that portion of the kidney which lines the wall of the veins. They form a columnar epithelium in which the cells may vary from 5 to 24 microns in height with a diameter of from 4 to 6 microns. The nucleus lies near the base of the cell. Between the nucleus and the distal end of the cells the transparent protoplasm is filled with numerous fine granules in which are often seen one or two large roundish bodies which are apparently nuclear concretions of a crystalline nature. The free edges of the cells present a decided convex surface.

The structure of the pericardial glands has been most thoroughly worked out by Grobben (1888). He pointed out that the glands consist of numerous small flaps or folds of different sizes which are dark brown in color and that they completely surround the auricles. The cells are of different shapes and sizes, some being low and broad, while others are tall, narrow, and cylindrical in form (fig. 155, opp. p. 169). The cells in most cases are more or less separated from each other, and where connection does exist between them it is in the basal region only. Exception to this rule occurs in the case of the very tall cylindrical cells, which are often so thickly crowded together that their entire side walls are in direct contact with those of the neighboring cells. Spaces, however, are often observed between them. The outer ends of the cells are convex and bear on the apex a single vibrating flagellum (fig. 156, opp. p. 169). The flagella are visible on the living cells, but when prepared histologically they disappear.

The cells contain nuclear concretions of various sizes and forms near their peripheral ends. In color these particles are brownish-green to black and highly refractive. It is to their presence that the dark shade of the gland is due. Sections through the glands show that the concretions are larger and more abundant in the cells lying in the deeper invaginations.

Grobben also occasionally observed pale, spherical bodies lying close to the refractive concretions and, in the deeper invaginated parts, vacuoles were found present in the cells (fig. 155). Whether or not the vacuoles exist in living cells the author was unable to determine.

In the lumen of the invaginated folds epithelial cells richly laden with concretions are often seen cut off from the epithelium (fig. 155). They contain their concretions molded either into a single large sphere almost the size of the cell body or as several large concretions which make up the greater part of the cell contents. These leave the pericardial cavity whole or in a disintegrated form by way of the opening to the kidney.

PHYSIOLOGY.

The function of the lamellibranchiate kidney and of the pericardial glands has been studied by Kowalevsky (1889), Letellier (1891), and Cuénot (1899). Their method in all cases was to inject acid and basic dye substances and to observe their reactions in the organ where they were eliminated. Indigo carmine, for example, is discharged through the kidney and usually shows an acid reaction according to Cuénot; Kowalevsky and Letellier, on the other hand, state that it is usually neutral. Ammonium carminate is eliminated through the pericardial glands where, all the authors agree, the reaction is very acid. The strong reaction in this case was established by Letellier to be due to the fact that the pericardial glands secrete hippuric acid in the free state. He concludes that among certain lamellibranchs the urinary function is accomplished by means of two separate organs, (1) the kidney which lies below the heart serving to eliminate excess of water, urea, various nitrogenous bodies, phosphates, and possibly uric acid and (2) the pericardial gland which covers the auricles serving to extract the acid contained in the blood. This acid in at least two mollusks, Pecten and Cardium, was found to be hippuric acid. Kowalevsky assumes that the kidney, or organ of Bojanus, is analogous to the Malpighian corpuscles of vertebrates, which are neutral or basic in reaction, and that the pericardial glands are analogous to the convoluted tubules, which are acid.

NERVOUS SYSTEM.

The central nervous system consists of three pairs of ganglia, symmetrically placed and connected by nerve commissures. The arrangement is strictly bilateral, one ganglion of each pair giving off nerves to its own particular side of the body. In *Mytilus edulis* the form of the nervous system is but slightly modified from the typical type found in the Lamellibranchia.

The *cerebral ganglia* are triangular bodies which lie with their apices pointing backward on the ventral side of the œsophagus just under the posterior edge of the lower lip (fig. 159, *CG*, p. 171). They are laterally placed so that in an adult mussel they are separated by a distance of 4 to 6 mm. In some specimens they are very conspicuous to the naked eye, owing to the presence of an orange-red pigment, while in others they are difficult to find, because the bright pigment is absent and their color is like that of the tissue in which they lie. The cerebral ganglia are united by the *cerebral commissure* which runs dorsally over the œsophagus (fig. 159, *CC*). Each ganglion gives rise to a large anterior trunk, the anterior pallial nerve, and a posterior trunk which contains the combined cerebrovisceral and cerebropedal nerves. Besides these there are two fine fibers, one of which supplies the labial palps and the other the eye.

The *anterior pallial nerve* (fig. 159, *APN*) arises from the outer anterior corner of the cerebral ganglion, runs forward and slightly outward over the anterior adductor muscle, to which it supplies a few fine fibers, and then turning backward it traverses the inner fold of the mantle edge, giving off along its course numerous side branches that form a network of fibers in the border of the mantle. A short distance posterior to the anterior adductor muscle the nerve trunk gives off a large branch (*BAPN*) that runs forward to the ventral side of the anterior adductor muscle.

The *cerebropedal* and *cerebrovisceral connectives* leave the posterior angle of the cerebral ganglion in a common trunk that passes backward and outward across the ventral side of the anterior retractor muscle. When it reaches the lateral side of the muscle the trunk divides into its two separate components. The cerebropedal connective continues backward and around the anterior retractor muscle to its dorsal wall and terminates in the pedal ganglion (fig. 159, *CPC*). The cerebrovisceral connective at the point of bifurcation with the cerebropedal connective turns upward and continues in a posterior direction across the lateral surfaces of the posterior retractor muscles to its point of termination in the visceral ganglion (fig. 159, *CVC*). Along its course several delicate nerve branches are given off which go to the liver, intestines, genital glands, and kidney. Of these the last branch forward, the *anterior renal nerve* (fig. 163, *ARN*, p. 175) is the most prominent. The *otocyst nerve* is a very fine fiber that arises from the cerebropedal connective at its junction with the cerebrovisceral connective and continues a short distance backward to the otocyst (fig. 163, *OtN*).

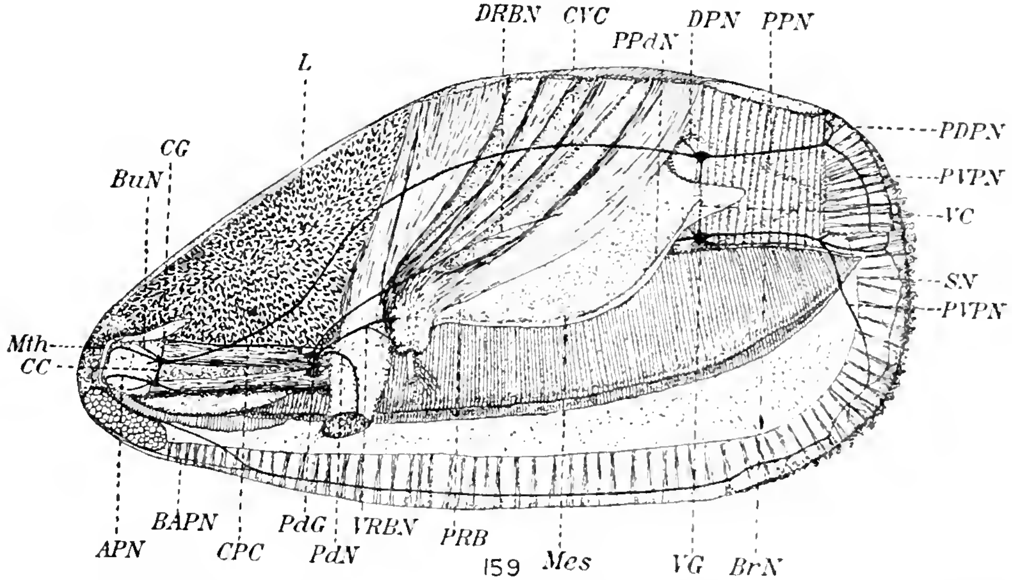


FIG. 159.—Ventro-lateral view of the nervous system in a transparent total preparation of a mussel 10.5 mm. long, separated from the shell, mantle and gills removed from one side, and a portion of foot cut off. Fixed in strong Flemming fluid, exposed in 70 per cent alcohol to strong sunlight, dehydrated in alcohol and cleared in benzol and wintergreen oil. × 15. *APN*, anterior pallial nerve; *BAPN*, branch of anterior pallial nerve; *BrN*, branchial nerve, *BuN*, buccal nerve; *CC*, cerebral commissure; *CG*, cerebral ganglion; *CPC*, cerebropedal commissure; *CVC*, cerebrovisceral commissure; *DPN*, dorsal pallial nerve; *DRBN*, dorsal retractor byssus nerve; *L*, liver; *Mes*, mesosoma; *Mth*, mouth; *PdG*, pedal ganglion, *PdN*, pedal nerve; *PDPN*, posterior dorsal pallial nerve; *PPdN*, posterior pedal nerve; *PPN*, posterior pallial nerve; *PRB*, posterior retractor muscle of byssus; *PVPN*, posterior ventral pallial nerve; *SN*, syphonal nerve; *VC*, visceral commissure; *VG*, visceral ganglion; *VRBN*, ventral retractor byssus nerve.

The *buccal nerve* is a relatively fine fiber which arises from the anterior end of the cerebral ganglion and runs forward to supply the labial palps (fig. 159, *BuN*). Branches of the nerve enter the palps and run along the smooth edge as a loose bundle of fibrils from which single fibers run out laterally across the palp and penetrate the transverse ridges (fig. 160, *BuN*, p. 173).

The *optic nerve* arises from the cerebral ganglion just posterior to the buccal nerve as a very fine fiber and runs in an anterio-latero-dorsal course to the eye at the base of the first inner branchial filament (fig. 163, *OpN*, p. 175).

A few very fine nerves that are distributed about the mouth region are also given off from the median sides of the cerebral ganglion and from the cerebral commissure.

The *pedal ganglion* lies on the dorsal side of the anterior retractor muscles just in front of the posterior retractor muscles of the foot (fig. 159, *PdG*). The ganglia are more or less pear shaped with the apex pointing forward and uniting with the cerebropedal connective. In most specimens there is a heavy deposit of pigment which gives the ganglia a deep orange-red color. Unlike the other ganglionic centers, the pedal glanglia are fused together into a single mass, but the dual structure is shown by the distinct furrow which runs around the body and separates the stems which project forward to connect with the cerebropedal nerves. Three nerves arise from each ganglion.

The *pedal nerve* emerges from the ventral side of the pedal ganglion, passes backward over the anterior retractor muscle, penetrates the posterior retractor muscle of the foot, and then continues downward into the foot (fig. 159, *PdN*).

The *ventral retractor byssus nerve* arises from the posterior side of the ganglion and subdivides into several branches that supply the byssus organ and the anterior and posterior retractor muscles in that region (fig. 159, *VRBN*).

The *dorsal retractor byssus nerve* arises from the dorsal surface of the pedal ganglion and runs obliquely backward and upward, subdividing in its course into several branches that go to the posterior retractor muscles above the region supplied by the ventral retractor byssus nerve (fig. 159, *DRBN*).

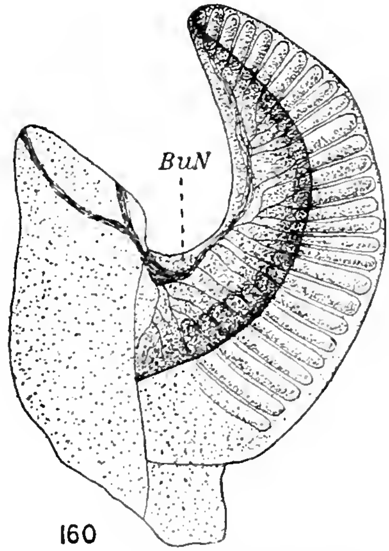
The *visceral ganglia* are situated on the anterior ventral surface of the posterior adductor muscle just under the epithelium. They lie just inside the line where the gills are suspended (fig. 159, *VG*), which places them some distance apart. A large *visceral commissure* (*VC*) connects them. Each visceral ganglion receives the cerebrovisceral connective at the anterior surface, while laterally and from behind several important nerves are given off.

The *posterior pallial nerve* arises from the posterior side of the visceral ganglion and runs backward and slightly outward across the ventral surface of the posterior adductor muscle (fig. 159, *PPN*). At the posterior ventral surface of the muscle it divides into two branches, one of which penetrates the mantle edge and runs dorsally (*PDPN*), whereas the other runs obliquely downward and backward some distance across the mantle before it enters the mantle edge (*PVPN*).

The *posterior dorsal pallial nerve* is the branch that arises from the posterior pallial nerve just behind the posterior adductor muscle, penetrates the mantle edge, and continues dorsally and anteriorly, giving off in its course many fine fibers to the surrounding tissues. It terminates in the mid-dorsal region in the trunk of the dorsal pallial nerve (fig. 162, *PDPN*).

The *posterior ventral pallial nerve* is the ventral branch of the posterior pallial nerve (figs. 159 and 162, *PVPN*). It runs downward and slightly backward until it penetrates the inner fold of the mantle edge, where it begins to give off numerous fine side branches that form a network of fibers throughout the inner and middle folds. In its course forward it becomes continuous with the anterior pallial nerve, forming what is commonly called the *pallial nerve* (fig. 162, *PN*).

The *syphonal nerve* arises from the posterior ventral pallial nerve, passes backward directly into the mantle edge, and then runs downward to unite again with the posterior ventral pallial nerve where the latter enters the mantle edge (fig. 162, *SN*). The syphonal nerves take their course through the region where the inner folds of the mantle edge are fused to form the anal syphon. The distribution of the side branches and



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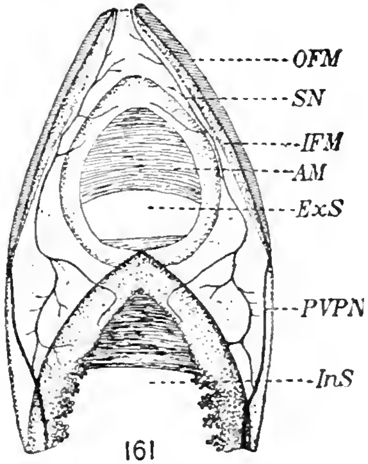

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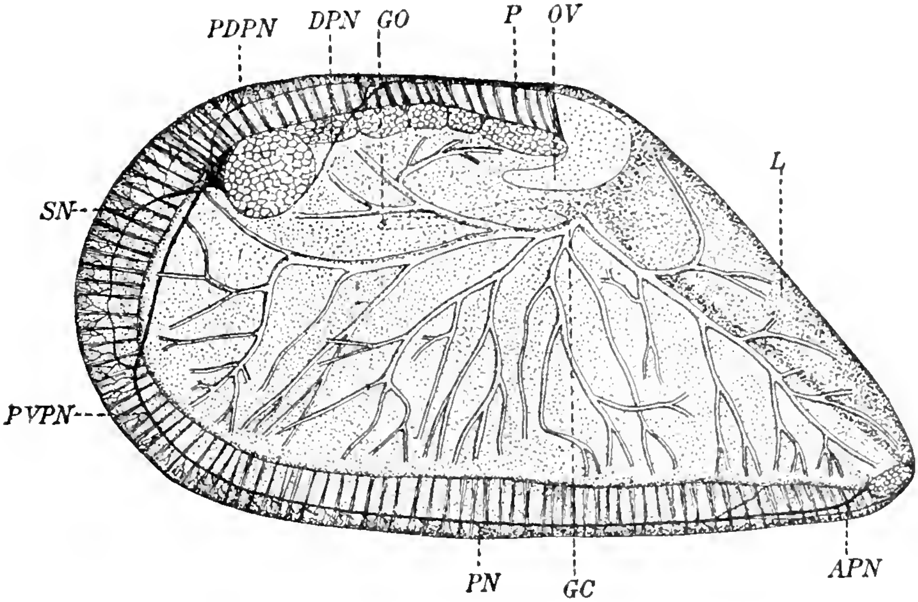

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FIG. 160.—View of labial palp in transparent preparation. Fixed in strong Flemming fluid, exposed in 70 per cent alcohol to strong sunlight, dehydrated, and cleared in benzol and oil of wintergreen. *BuN*, buccal nerve and its branches which run between the ridges.

FIG. 161.—Posterior view of the area surrounding the syphonal region showing the innervation of the anal syphon. Preparation same as fig. 160. *AM*, anal membrance; *ExS*, exhalent syphon; *IFM* inner fold of the mantle; *InS*, inhalent syphon, *OFM*, outer fold of the mantle; *PVPN*, posterior ventral pallial nerve; *SN*, syphonal nerve.

FIG. 162.—Lateral view of mussel with shell removed showing distribution of genital canals and pallial nerves. *APN*, anterior pallial nerve; *DPN*, dorsal pallial nerve; *GC*, genital canal; *GO*, position of the genital opening on the ventral wall inside the mantle, *L*, liver; *OV*, oblique vein, *P* pericardium; *PDPN*, posterior dorsal pallial nerve; *PN*, pallial nerve; rest as in fig. 161.

relation of the syphonal nerve to the posterior ventral pallial nerve is shown in figure 161. A short branch springs from the upper end of the syphonal nerve and connects above with the posterior dorsal pallial nerve in such a way as to form a triangle in the mantle edge immediately behind the posterior adductor muscle (fig. 162).

The *dorsal pallial nerve* arises as a fine fiber from the anterior outer side of the visceral ganglion and runs forward and upward between the posterior retractor muscles into the mantle, where it divides into an anterior and a posterior branch. The branch which takes the anterior course sends out small nerves into the mantle edge, while the posterior one makes connection with the posterior dorsal pallial nerve (figs. 159 and 162, *DPN*).

The *posterior renal nerve* goes out from the visceral ganglion in close connection with the dorsal pallial nerve and supplies the kidney (fig. 163, *PRN*).

The *branchial nerve* arises from the outer posterior side of the visceral ganglion and runs obliquely downward and backward to the base of the gills, which it follows to the posterior extremity. Throughout its course, but more so at its beginning, it gives off a great number of very fine fibrils that run in a mass anteriorly along the axis of the gills (fig. 159, *BrN*, p. 171; fig. 163, *BrN*).

The *posterior adductor nerve* is a small branch given off from the median side of the visceral ganglion. It supplies the posterior adductor muscle and the pallial sense organs in that region (fig. 163, *PAN*). Closely associated with the nerve endings in the posterior adductor muscle Galeazzi (1888) found great numbers of ganglion cells of both the unipolar and bipolar type. They form in the muscle a very fine reticulum, so that a nerve fiber is able by its ramifications to innervate many muscle fibers. This considerable number of ganglion cells between the bundles of muscles led Galeazzi to conclude that an automatic nerve center was present in the muscle itself which explained the great power of the adductor muscle in bivalves.

The *posterior pedal nerve* is an unpaired fiber which springs from the middle of the visceral commissure on its ventral surface. It runs posteriorly a short distance, and then, turning sharply downward and forward, it passes under the commissure and runs forward on the ventral wall of the body to the foot (fig. 159, *PPdN*, p. 171; fig. 163, *PPdN*).

The relation of the various nerve centers and their communications is diagrammatically represented in figure 163.

SENSE ORGANS.

ANATOMY.

The sense organs of the sea mussel fall naturally into five groups: (1) sensory cells in the epidermal layer, (2) a pair of osphradia, (3) a pair of abdominal sense organs, (4) a pair of otocysts, (5) a pair of eyes and extensive areas of light receptive epithelium.

The sensory cells of the epidermal layer are present in scattered groups or as single elements in the wall of the mantle cavity. The groups of cells which are sometimes referred to as the *pallial sense organs* (fig. 164, p. 178) are particularly abundant on the ventral epithelium of the posterior adductor muscle. The single sense cells, first described by Flemming (1870) as *pinselzellen* (fig. 167, p. 178), are scattered all over the inner walls of the mantle.

The *osphradia* are pigmented organs of dark brown color which lie ventral and lateral to the visceral ganglia (fig. 169, *Os*, p. 178). They extend as far as the inner side of the gill supports, each one covering an area about equal to that of the visceral ganglion.

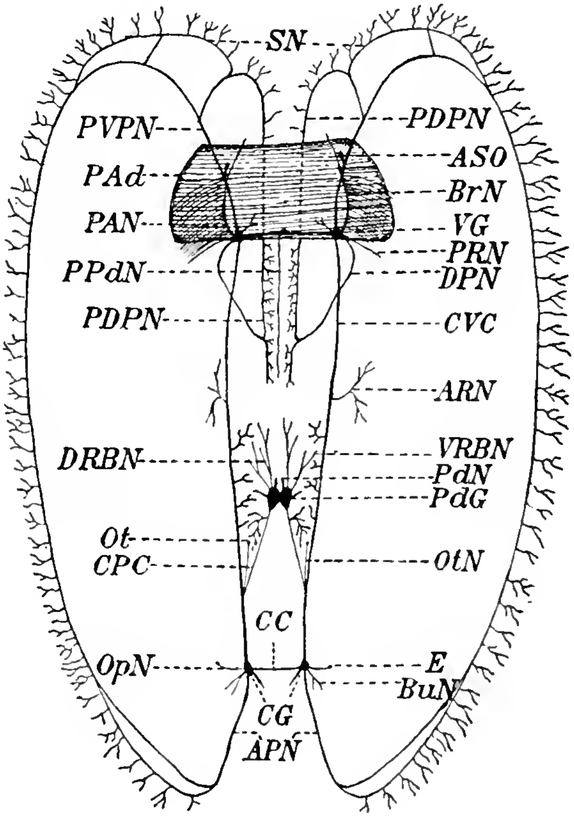

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FIG. 163.—Diagrammatic representation of the nervous system of *Mytilus edulis*.

APN, anterior pallial nerve.
ARN, anterior renal nerve.
ASO, abdominal sense organ.
BrN, branchial nerve.
BuN, buccal nerve.
CC, cerebral commissure.
CG, cerebral ganglia.
CPC, cerebropedal commissure.
CVC, cerebrovisceral commissure.
DPN, dorsal pallial nerve.
DRBN, dorsal retractor byssus nerve.
E, eye.
OpN, optic nerve.
Ot, otocyst.
OtN, otocyst nerve.
PAd, posterior adductor muscle.
PAN, posterior adductor nerve.
PdG, pedal ganglion.
PdN, pedal nerve.
PDPN, posterior dorsal pallial nerve.
PPdN, posterior pedal nerve.
PRN, posterior renal nerve.
PVPN, posterior ventral pallial nerve.
SN, syphonal nerve.
VG, visceral ganglion.
VRBN, ventral retractor byssus nerve.

The *abdominal sense organs*, first described by Thiele (1889) in Arca, were found by List (1902) to be present in some form or other in all species of the Mytilidæ. In *Mytilus edulis* they lie on the ventral posterior side of the posterior adductor muscle just outside of the gill supports. A microscopic cross section of a mussel taken through the posterior adductor muscle just behind the visceral ganglion will show the relative position of the osphradia and abdominal sense organs (fig. 169). The osphradia are always found on the inner side of the gill supports, while the abdominal sense organs are on the outer side. List (1902) finds these organs best developed in *Modiolaria marmorata* and *Modiolus barbaratus*, well formed in *Lithophagus lithophagus*, and less developed in *Mytilus galloprovincialis*.

Otocysts were first observed in Mytilus by von Ihering (1876), the position, size, and innervation of which he described briefly. List (1902) found the otocyst present in all the Mytilidæ of the Mediterranean region as a paired, symmetrical organ, which he states is always a pear-shaped pustule lying directly under the body epithelium between the two connectives which bind the cerebral ganglion with the pedal ganglion, on the one hand, and with the visceral ganglion, on the other. In *Mytilus edulis* the organ occupies this same position in the angle formed by the union of the cerebrovisceral and cerebropedal connectives. It lies approximately over the point where the œsophagus joins the stomach. In gross structure the otocyst is an oval body, which in mussels about 5 cm. long has a length of from 150 to 200 and a breadth of from 125 to 135 microns. The smaller end points anteriorly and gives off a canal having a diameter of 25 to 30 microns, which runs forward just beneath the epithelium for a distance of 700 to 1,000 microns, where it opens to the exterior in a funnel-shaped invagination. In very thin specimens a fine white nerve can be traced forward from the oval part of the body as far as the junction of the cerebropedal and cerebrovisceral connectives.

In favorable material it is possible to isolate the otocyst sufficiently from its surrounding tissues so that it can be observed in a living condition under the mircoscope. To do this it is necessary to select animals whose sex glands are spent or undeveloped and which have been starved for several days. The animals should then be narcotized with a saturated solution of chloretone in sea water or with cocaine to bring about complete relaxation of the muscles. Then it is possible with small, sharp scissors or with a clean scalpel to cut around the area occupied by the otocyst, strip it off with the epithelium, and spread it out in a drop of water on a microscopic slide where it may easily be examined under the microscope. Under these conditions the otocyst appears as an oval body with a long, slender handle. It is a hollow structure, the walls of the oval part of the body being several times thicker than the wall of the canal and forming a clear, thick outer zone which stands in sharp contrast with the dark inner zone, in which vibrating cilia may be seen distinctly (fig. 173, p. 180). The walls of the canal are comparatively thin, and within its lumen the effects of active ciliary movement are visible, the effective stroke of the cilia being inward.

The visual organs of the sea mussel are of two types, consisting of a pair of well-developed direction eyes and of pigmented epithelial cells of the mantle edge capable of responding to changes in light intensity. Lovén (1848) first pointed out that Mytilus possessed an eye in the larval stage. Lacaze-Duthiers in his studies failed to note the fact at all, but Wilson (1887) observed that an eye was present in larvæ that had reached the four branchial filament stage. After such authors as Balfour, Fischer, and Lang had stated that the eyes were lost before the adult condition was reached, Pelseneer (1899) announced that the eyes persisted in the adult mussel. List (1902) found that in all the Mytilidæ studied by him, the larval eye was retained throughout life and that in all the species it occupied the same position. It is always found at the base of the first anterior inner gill filament on its lateral side (fig. 168, *E*). Ordinarily it is hidden from view between the pair of labial palps. It is most easily made accessible for observation by laying the two gills apart and following up the inner gill support to its anterior end, where a little dark spot which represents the eye may be easily observed, especially if use is made of an ordinary hand lens. It is an invaginated cup, oval in form and consisting of epithelial cells filled with coarse granules of a dark-brown pigment (fig. 166).

In the larval mussel the eye occupies this same position at the base of the inner first anterior gill filament. In young specimens that have been fixed in toto the pair of eyes stand out distinctly under the microscope as large, pigmented oval spots.

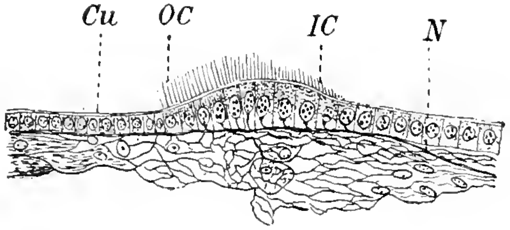
In addition to this pair of complex direction eyes, the sea mussel has a wide area of its body, extending the whole length of the free mantle edge and over the entire surface of the anal membrane and the foot, covered with brown densely pigmented epithelial cells, which are capable of being stimulated by light. Sometimes spots of the pigmented epithelium are present on the lips, although their presence in this position is unusual.

HISTOLOGY.

The *pallial sense organs*, which are most commonly found on the ventral epithelium of the posterior adductor muscle, consist of small groups of cells that are so related as to form little sense hills (fig. 164, p. 178). The surrounding epithelium consists of cubical cells covered with a relatively thick cuticula and bearing no cilia. The outer cells of the pallial sense organs are slightly taller than the epithelial cells, and as one passes from the periphery to the center of the sense body the cells become taller, the central cells being about twice as high as those of the surrounding epithelium. They are furthermore characterized by being ciliated, the cilia of one side of the elevation being much longer than those of the opposite side. The longest cilia are about as long as the tallest cells. The nuclei are large and contain several large chromatin granules, and each nucleus gives off from its base a nerve fiber. These fibers pass down into the connective tissue below, where they unite into a trunk that apparently runs to the visceral ganglion.

The *pinselzellen* of Flemming (1870), which are scattered over the epidermal layer of the mantle cavity, differ but little in form and size from the epithelial cells which surround them. Sometimes they are narrower or their outer ends flare outward. They are tall, columnar cells with a height about three times their breadth. They contain large oval or elliptical nuclei in which are several chromatin granules. Their most characteristic feature is the group of long cilia which extends from the outer end of the nucleus to a distance beyond the surface cuticula equal to the total length of the cell. (See fig. 167, p. 178.) These cilia stain deeply with iron hematoxylin. Dakin (1909) in his studies on Pecten found these same epidermal sense cells and states that each one is connected with a nerve fiber. The author has failed to demonstrate any nerve connection in Mytilus.

The *osphradium* is conspicuous because of its large columnar cells and nuclei which stand out in sharp contrast to the small cubical epithelial cells that surround it. The organ extends on either side of the body from a point ventral to the visceral ganglion to the inner side of the gill support and is one layer of cells thick. (See fig. 172, p. 180.) Numerous fine nerve fibers arise from the basal portion of the organ and run into the



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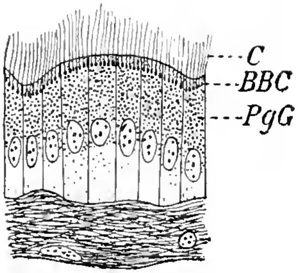

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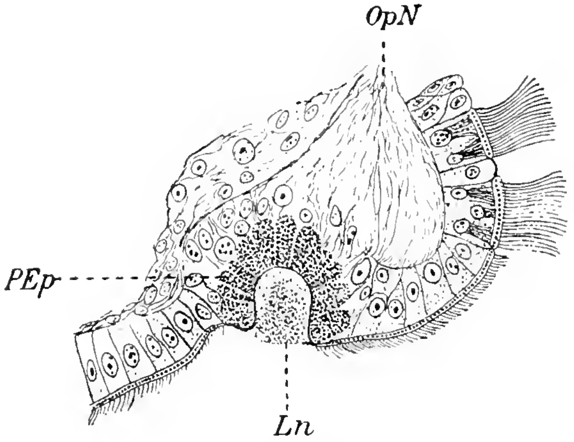

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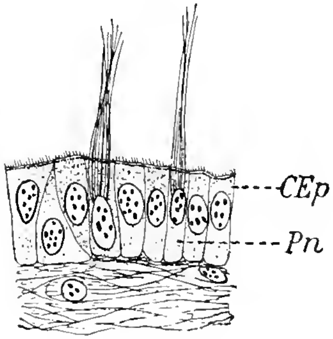

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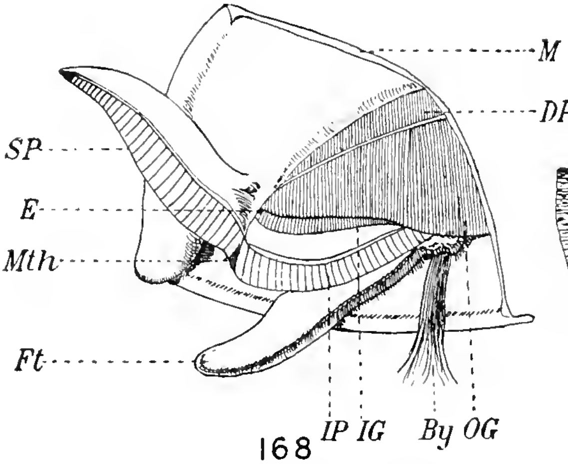

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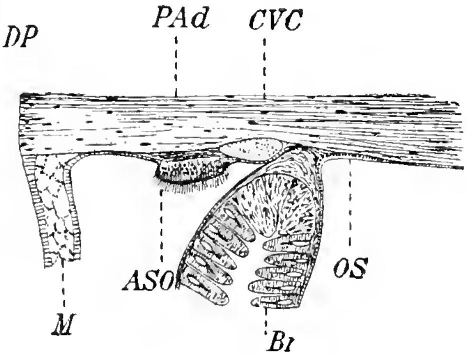

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Fig. 164.—Cross section through a pallial sense organ. × 575. Fixed in Gilson fluid and stained with Delafield hæmatoxylin. *Cu*, cuticula; *IC*, inner cilia; *N*, nerve supplying the sense organ; *OC*, outer cilia.

Fig. 165.—Cross section of anal epithelium. × 1,000. Preparation same as fig. 164. *BBC*, basal bodies of cilia; *C*, cilia *PgG*, pigment granules.

Fig. 166.—Transverse section through eye of young mussel 15 mm. long. × 500. Fixed in Flemming fluid and stained with Heidenhain iron hæmatoxylin and congo red. *Ln*, so-called lens; *OpN*, optic nerve; *PEp*, pigmented epithelium of eye cup.

Fig. 167.—Cross section through body epithelium containing two pinselzellen of Flemming. × 1,000. Preparation same as fig. 166. *CEp*, ciliated epithelium, *Pn*, pinselzellen of Flemming.

Fig. 168.—Lateral view of anterior end of gills with superior palp reflected to show position of eye at base of first filament of inner gill lamella. *By*, byssus, *DP*, descending portion of outer gill lamella; *E*, eye; *Ft*, foot; *IG*, inner gill lamella; *IP*, inferior palp, *M*, mantle, *Mth*, position of mouth, *OG*, outer gill lamella; *SP*, superior palp. (After Pelseneer, 1899.)

Fig. 169.—Cross section passing through posterior adductor muscle to show positions of abdominal sense organ and osphradium in relation to roots of gill. × 50. Preparation same as fig. 166. *ASO*, abdominal sense organ; *Br*, gill, *CVC*, cerebrovisceral commissure; *M*, mantle; *OS*, osphradium; *PAd*, posterior adductor muscle.

visceral ganglion. The cells are devoid of cilia, which differentiates the osphradium from all the other sense organs

The structure of the *abdominal sense organ* is similar to that of the pallial sense organ, but it is larger and more complex. It forms a sense hill from three to four times as high as the contiguous epithelium, from which it arises with a steep slope. The transition from the body epithelium to the sense epithelium is sudden, without any cells of an intermediate character intervening. A characteristic feature of the organ is that it is several cells thick. The distal ends of the cells show distinct striations and are covered with a thick cuticula. The innervation of the abdominal sense organ comes from a side branch of the principal posterior pallial nerve. The nerve enters at the base of the sense organ and sends out numerous branches which spread throughout its structure, some of which connect with or surround the nuclei, while others, passing the length of the cells, penetrate the cuticula and project out some distance as tactile hairs. (See fig. 171, p. 180.)

The *otocyst*, when examined under the microscope, is found to lie just under the body epithelium between the cerebropedal and cerebrovisceral connectives. The main body of the otocyst, which is oval in form, is made up of several layers of cells, which inclose a cavity containing numerous small irregularly-shaped particles varying from 1 to 4 microns in diameter and which, on account of their insolubility in acid, are probably silicious in character. The anterior and posterior walls are thicker than the others, and the nuclei of their cells are longer. The cavity is lined with a layer of epithelium, each cell of which bears a long tuft of cilia. (See fig. 173.)

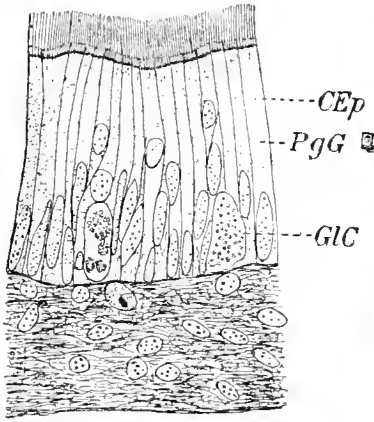
The *otocyst canal* is made up of a single layer of more or less cubical cells containing small spherical nuclei. These cells bear very fine cilia that, in the beginning of the canal at least, slope inward, preventing the passage outward of any of the contents of the otocyst. The anterior end of the canal opens to the exterior in the bottom of a funnel-shaped pit formed by an invagination of the body epithelium. The cells which form this pit are arranged in concentric layers. The whole otocyst is inclosed in a homogenous, structureless substance which is thickest about the oval-shaped portion.

The *otocyst nerve*, carrying an abundance of fibers, arises from the cerebropedal connective just posterior to its junction with the cerebrovisceral connective and passes backward just under the otocyst canal into the main body of the sense organ.

Microscopic examination of the eyes of *Mytilus edulis* reveals the fact that they are formed from an invagination of the ciliated body epithelium. This gives a cuplike depression whose walls are formed from the transformed epithelial cells of the body. These cells have lost their cilia and are filled, especially toward the periphery, with rather coarse granules of brown pigment (fig. 166, p. 178). The transition from optic epithelium to body epithelium is abrupt, but the two groups of cells are covered with a continuous layer of cuticula. Mucus or some other crystalline secretion fills the optic cup and is thought by some to constitute a lens.

A very delicate nerve arises from the cerebral ganglion and passes directly back to the eye, where it breaks up into numerous fibrillæ that spread over and enter the optic epithelium.

The *pigmented epithelium*, covering the mantle edge and other parts of the body, is composed in most part of columnar ciliated, epithelial cells which are partially filled with fine, brown granules. These granules lie for the most part in the region distal to the nuclei (fig. 165, p. 178).



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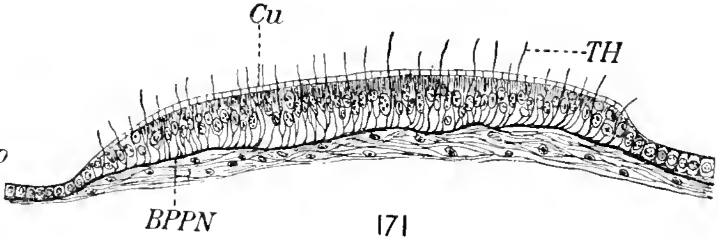

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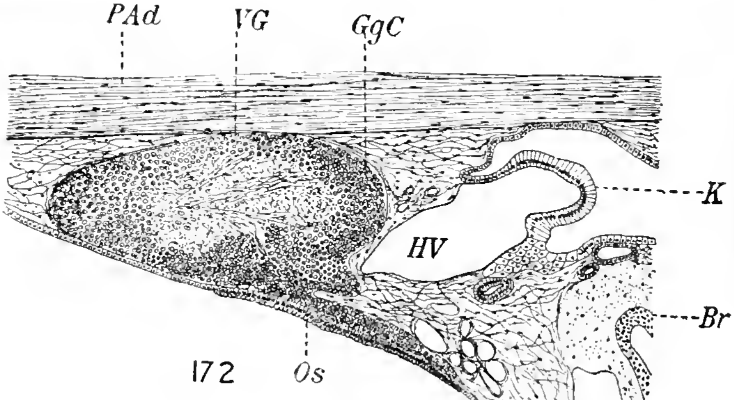

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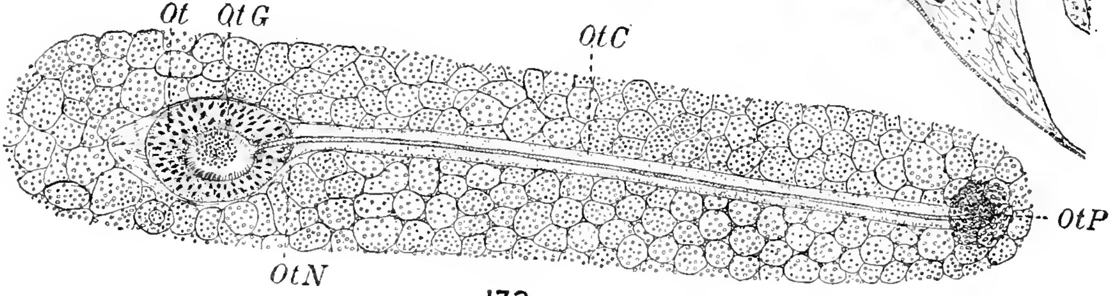

173

FIG. 170.—Cross section of a pigment spot on the lips. × 750. Fixed in Gilson fluid and stained with Delafield hæmatoxylin. *CEp*, ciliated epithelium; *GlC*, gland cell; *PgG*, pigment granules.

FIG. 171.—Cross section through an abdominal sense organ. × 375. Preparation same as fig. 170. *BPPN*, branch of posterior pallial nerve; *Cu*, cuticula; *TH*, tactile hair.

FIG. 172.—Cross section passing through visceral ganglion and osphradium. × 100. Fixed in Flemming fluid and stained with hæmalum and congo red. *Br*, gill, *GgC*, ganglion cells; *HV*, horizontal vein; *K*, kidney; *Os*, osphradium; *PAd*, posterior adductor muscle; *VG*, visceral ganlion.

FIG. 173.—Lateral view of otocyst drawn from a living preparation. × 100. *Ot*, main body of otocyst; *OtC*, otocyst canal; *OtG*, otolith granules; *OtN*, otocyst nerve; *OtP*, otocyst pit containing the external opening.

Round, pigmented spots found on the lips of some mussels are similar in character to the pigmented cells of the mantle edge, except that the cells are taller and more irregular in form. In size the cells vary from 38 to 40 microns in length by from 2 to 3 microns in width. The pigment granules are finer than those of the cells on the mantle edge, are more abundant, and extend into the basal regions of the cells. At the distal ends of the cells the granular group tapers out to a point (fig. 170, p. 180). Each cell bears many cilia that arise from a layer of basal bodies which stain deeply with hæmatoxylin. The cilia are about 7 microns in length. The nuclei which lie at the proximal ends of the cells are long and narrow and filled with fine chromatin granules. The portion of the cells distal to the nuclei is filled with finely granulated, yellowish-brown pigment. Large gland cells more or less oval or elliptical in outline occur at frequent intervals, between the proximal ends of the pigmented cells (fig. 170, *GlC*, p. 180).

PHYSIOLOGY.

The functions of the various sense organs just described in Mytilus remain undetermined up to the present time. Literature on the subject is of a speculative nature, but a brief review of it may be worth while.

In regard to the *sensory cells* scattered throughout the epidermal layer, Dakin (1909) says they seem to be stimulated by very slight movements in the water. He also ventures the assumption that in addition to being tactile organs they may be olfactory in function.

Concerning the function of the *osphradium* there is no experimental evidence. Because of its similarity to the osphradium of gastropods such authors as Lankester (1883) and Pelseneer (1888) have assumed that it is olfactory in function.

The *abdominal sense organ*, according to Dakin (1909), functions to test the quality of the incoming water either as an olfactory or as a gustatory organ; but since this sense is usually ascribed to the osphradium, it is difficult to understand why these two organs should be placed side by side. Since the histological structure is so remarkably like that of the lateral line organs described by Eisig (1887) in the Capitellidae, Thiele (1889 and 1890) assumes that they are homologous with the lateral line not only of the chætopods but of fishes, and therefore probably function to perceive wave movement or vibrations in the water. He considers furthermore that they may be olfactory in function.

No literature on the function of the *otocyst* in Mytilus has been found, but it may be assumed that, as in other invertebrates, it serves as an organ of orientation.

Neither has the author been able to find any references to the physiology of the eyes or pigmented epithelium of the mussel. A single series of experiments performed September 6, 1912, furnishes all the data the author has. Some mussels, whose mantle edges were expanded from between the open valves, were lying in a trough of running water in the laboratory, so situated that a number of them were subjected to the direct light of the sun while the others were shaded. When the hand was held so as to cast a shadow on the mantle fringe a rather quick response followed. The mantle edge contracted decidedly and sometimes was completely withdrawn, followed by closing of the valves. A similar response was obtained from the mussels lying in an expanded condition in the shade when direct sunlight was reflected with a small mirror onto the mantle edge. Response came, however, only when there was a decided change in the intensity of the light one way or the other. This would indicate, therefore, that the pigmented epithelium of the mantle edge is a light receptor, but at best is a very crude sense organ.

REPRODUCTIVE SYSTEM.

ANATOMY.

The reproductive system consists of numerous ducts which branch throughout nearly the entire body, giving off in turn smaller branches which terminate in pockets or follicles. The greater part of the system occupies the mantle lobes, which are filled almost exclusively with reproductive tissue just prior to spawning. It also fills the mesosoma, penetrates through the tissues just below the pericardial chamber, lines the walls of the lateral cavities, and spreads over the outer surface of the liver. Practically every part of the body with the exception of the gills, muscles, and foot is covered or occupied by the genital organs. This is well shown by a cross section taken through the middle of the body of a mussel 1 year old which was about to spawn for the first time. (See fig. 147, opp. p. 163.)

The main genital ducts lie near the outer surface of the mantle lobes and converge to a point of common union which lies just below the pericardium. In general there are five principal canals which meet at this point: (1) A main branch which supplies the anterior region of the mantle and the surface of the liver, (2) and (3) two lateral branches which supply the mid region of the mantle, (4) a posterior branch which connects with the hinder parts of the mantle, and (5) a dorsal branch which supplies the area between the posterior adductor muscle and afferent oblique vein and the dorsal body wall (fig. 162, *GC*, p. 173).

From the point of union of these several ducts, the main genital canal thus formed on each side of the body penetrates the mantle to its inner surface, where it turns backward and runs on the ventral body wall just inside and parallel with the attached edge of the inner gills to the genital papilla on which it opens to the exterior. The genital papilla lies a short distance in front of the posterior adductor muscle in the angle formed at the base of the mesosoma with the inner gill. A median branch from the common genital canal connects with the mesosoma on each side of the body.

HISTOLOGY.

If the mantle of a mussel which has almost finished spawning is treated with Gilson's fluid or some other suitable fixing solution and then stained with borax-carmine, dehydrated, and cleared, preferably in oil of wintergreen, the minor canals and the follicles connected with them can be seen easily under the microscope when examined with low-power lenses.

In male animals, the follicles are small outgrowths from the sides of the canals. They are of almost uniform size, very numerous, and situated about the same distance apart (fig. 174).

In the female the arrangement of the canals is the same as in the opposite sex, but the follicles are larger, much less numerous, and more variable in size.[2] In some cases they appear to be lateral outgrowths of the genital canals, while in others they form the blind ends of the ducts (fig. 175).

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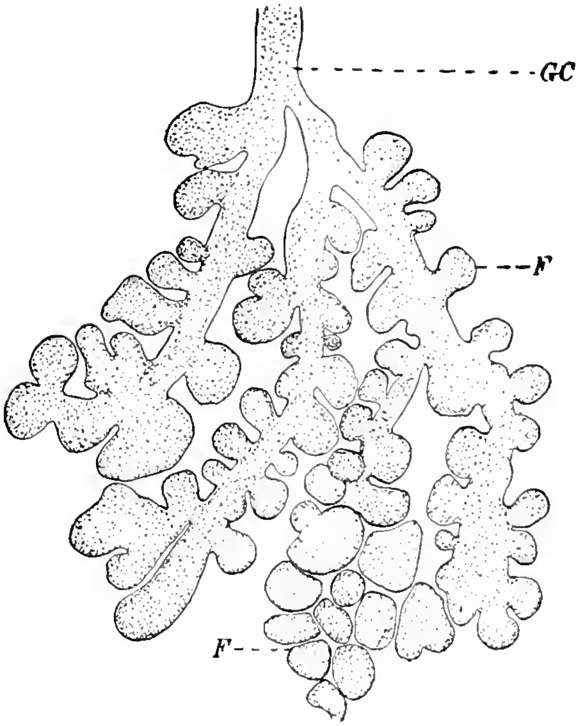
[2] The relative sizes of the follicles shown in figures 174 and 175, according to the magnifications given in the legends, do not correspond with the description in the text and suggest that a mistake was made in the figures given for the magnification of either figure 174 or 175, or both.

In both sexes the follicles are lined with germinal epithelium, the minor genital ducts are bordered with germinal epithelium on one side and ciliated epithelium on the other (fig. 177, p. 184), and the main canals have their walls thrown into longitudinal ridges which are covered entirely with columnar ciliated epithelium. They are surrounded by a thin layer of fine muscle fibers which increase in number toward the genital orifice. The opening on the papilla has two distinct lips which may completely close it when they are brought together by muscular action (fig. 162, *GO*, p. 173).



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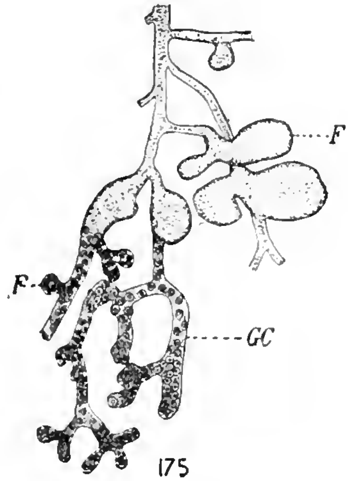

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FIG. 174.—Terminal branches of a minor genital canal in a male mussel showing follicles which are lined internally with germinal epithelium and filled with genital products. × 25.[2] Drawing made from a total preparation which was fixed in Gilson fluid, stained with borax-carmine, dehydrated in alcohol and cleared in oil of wintergreen. *F*, follicles; *GC*, a minor genital canal.

FIG. 175.—Branching genital canals and follicles in a female mussel. × 23.8[2] Preparation same as fig. 174. *F*, follicles, smaller ones with transparent walls showing ova contained within; *GC*, minor genital canals also filled with ova.

The ova and spermatozoa arise from the germinal epithelium lining the follicles and minor genital canals. Before the germ cells begin to grow the epithelium is membranous in character and composed of very small cells. As the ova develop, their area of attachment increases greatly in thickness (fig. 177, *GE*, p. 184). Their nuclei are very prominent, containing large, conspicuous nucleoli, and are surrounded by a thin layer of

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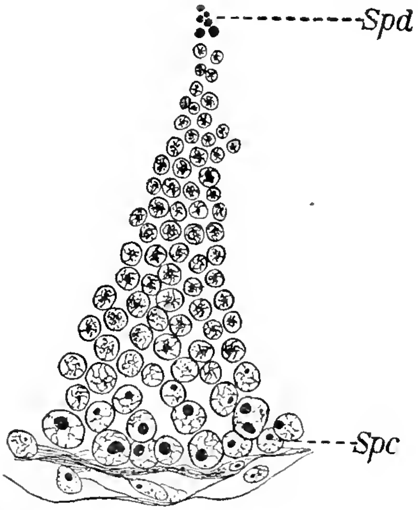
[2] The relative sizes of the follicles shown in figures 174 and 175, according to the magnifications given in the legends, do not correspond with the description in the text and suggest that a mistake was made in the figures given for the magnification of either figure 174 or 175, or both.



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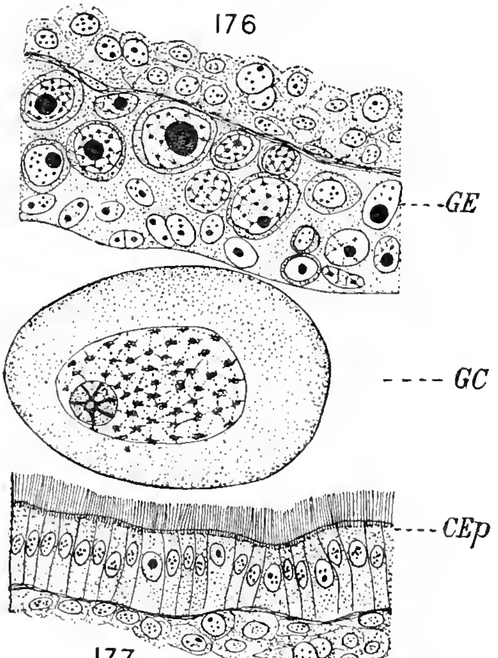

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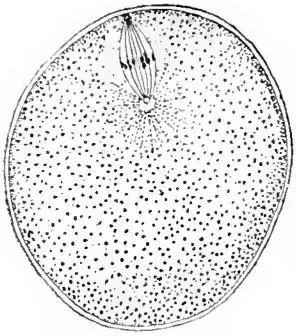

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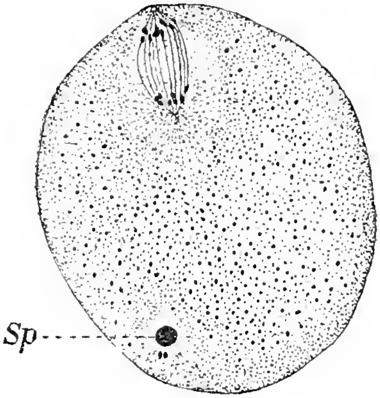

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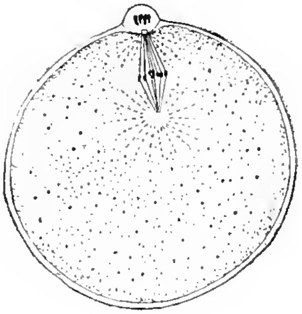

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Fig. 176.—Sector from a male follicle prepared on April 1. × 900. Fixed in Flemming fluid and stained with Heidenhain iron hæmatoxylin. *Spc*, sperm mother cells or spermatocytes on wall of follicle; *Spd*, spermatids in center of follicle.

Fig. 177.—Longitudinal section through a minor genital canal of a female mussel. × 765. Preparation same as fig. 176. *CEp*, ciliated epithelium which lines one side of canal only; *GC*, genital canal, containing a ripe ovum; *GE*, germinal epithelium containing developing ova.

Fig. 178.—Longitudinal section through a freshly laid egg that has not been fertilized. The spindle of the first polar body is formed and does not pass beyond this stage normally unless the egg is fertilized. Fixed in Bouin fluid and stained with Heidenhain iron hæmatoxylin and congo red.

Fig. 179.—Longitudinal section through an egg showing the condition which follows immediately after impregnation. × 900. Head of spermatozoon, *Sp*, enlarges greatly as it migrates toward center of cell. At same time spindle of first polar body passes into anaphase stage and process of maturation continues rapidly from this time on until completed. Preparation same as fig. 176.

Fig. 180.—Longitudinal section through an egg showing spindle of second polar body which is formed immediately after first polar body is extruded. Preparation same as fig. 178.

cytoplasm. As fast as the ripe ova are formed they burst out into the follicles and canals which they come to fill so tightly that they are compressed into a characteristic, polygonal form. A cross section of either the mantle or mesosoma at the height of the breeding season will show how completely these organs are filled and distended with eggs (fig. 215, opp. p. 226).

The sperm follicles just previous to the reproductive period, when seen in cross section, are irregularly circular in outline, from 300 to 800 microns in diameter. They are almost completely filled with sperm mother cells and spermatozoa, the latter occupying the central portion. The peripheral region of the follicle is occupied with large sperm mother cells, which consist of nuclei surrounded with only a film of cytoplasm and containing one or two large nucleoli. Passing toward the center of the cavity, the nuclei become smaller and the contained chromatin is in the form of threads, which indicates that the cells are in the active process of division. In no preparations, however, was a single mitotic figure observed. In the center of the follicle spermatids and spermatozoa were present which were very small compared with the mother cells and which stained uniformly deep blue or black with iron hematoxylin (fig. 176, p. 184). Later in the season when the ripe products are ready to be liberated, the follicles present a different appearance. They are densely filled with spermatozoa, which appear as minute, round dots arranged in bands or lamellæ which converge toward the center, or they may be so arranged as to make a coarse network (fig. 220, opp. p. 227).

The number of follicles which are contained in the mantle of a mussel depends upon the age and size of the animal. In small specimens just approaching maturity a single follicle will fill the space between the outer and inner walls of the mantle, while in large specimens, 3 or more inches long, the same space may accommodate a series of 6 to 8 follicles (fig. 220).

PHYSIOLOGY.

When the genital products are first formed, they are mature to all appearances, morphologically, but physiologically they are immature, for when such eggs and spermatozoa are mixed together fertilization fails to take place. The spermatozoa have tails but make no movement, and the eggs, though containing a well-developed germinative vesicle, fail to form the spindle of the first polar body when they come in contact with the sea water as is normal for mature ova. Both elements are perfectly inert. Before reaching functional activity they must undergo a period of rest which apparently lasts for several weeks. As they reach the stage of functional activity they begin to crowd out into the main canals and are swept onward by strokes of the powerful cilia which line one side of the canals (fig. 177, *CEp*). They are forced up close to the genital opening, which is closed by two lips of tissue and furthermore sealed by a plug of granules and minute pigmented cells which are reddish brown in color.

The expulsion of the reproductive elements begins suddenly and takes place rapidly. The first sign is when the plug of pigmented granules is discharged. This is followed, in the male, by a continuous stream of milt which renders the water milky for a distance of several feet from the spawning individual. The discharge may continue for half an hour, with little or no interruption. In the female the process is similar, except that the eggs usually are expelled while sticking together in the form of rods, which may be from 3 to 5 mm. in length. They represent the form into which they were molded together while in the oviduct. The eggs flow out in a continuous stream and in quiet water settle to the bottom in a pink or reddish mass. The ova, which are clustered together in the shape of rods, soon fall apart and assume the normal spherical or oval form. The process sometimes continues until nearly all the genital products are removed; sometimes the process is incomplete and occurs periodically from two to three days apart; and sometimes the animals fail to expel any of the elements. In the latter case the eggs and spermatozoa degenerate and are absorbed by the tissues of the body.

The normal stimulus which starts up the act of spawning still remains an unsolved problem. Ripe specimens were transferred from cold to warm water and vice versa, from water of high density to that of low density and back again; they were exposed to the air from one to three hours and then submerged, subjected to swift currents and then still water, but in no case was there positive evidence that it influenced the act of spawning. Rough handling, such as shaking them up and down in a bucket of water or stirring them about vigorously with the hand, caused spawning to take place within a few minutes to an hour later, but this can not be called a normal stimulus. It is a common belief that the presence of spermatozoa in the water stimulates the female to the act of spawning, but the author could not verify this statement. Often the females spawned before the males began to liberate sperm, and isolated individuals in filtered sea water were observed to deposit eggs in great quantities on several different occasions. On the other hand, sometimes the trough in which quantities of ripe mussels were kept would be milky with sperm and not a female would show a sign of laying an egg. The following day, when very few or no spermatozoa were present, a dozen or more females might spawn. The nature of the spawning stimulus, therefore, remains doubtful.

EMBRYOLOGY.

GERM CELLS.

The early history leading up to the formation of the germ cells could not be worked out from any of the author's slides, although histological preparations were made from material collected every two weeks during the year. Dividing cells were rarely observed, but it was clearly evident that the sexual elements arise from the epithelial lining of a vast number of canals that proliferate throughout the whole body. The germ cells begin to form early in the winter and reach maturity by early spring or late summer, according to the temperature of the water and, possibly also, the amount of available food. On our Atlantic coast the spawning season begins in April and continues on through the summer well into September. At the Woods Hole (Mass.) Biological Station, the author has secured spawning individuals every week throughout the season from June 20 to September 15.

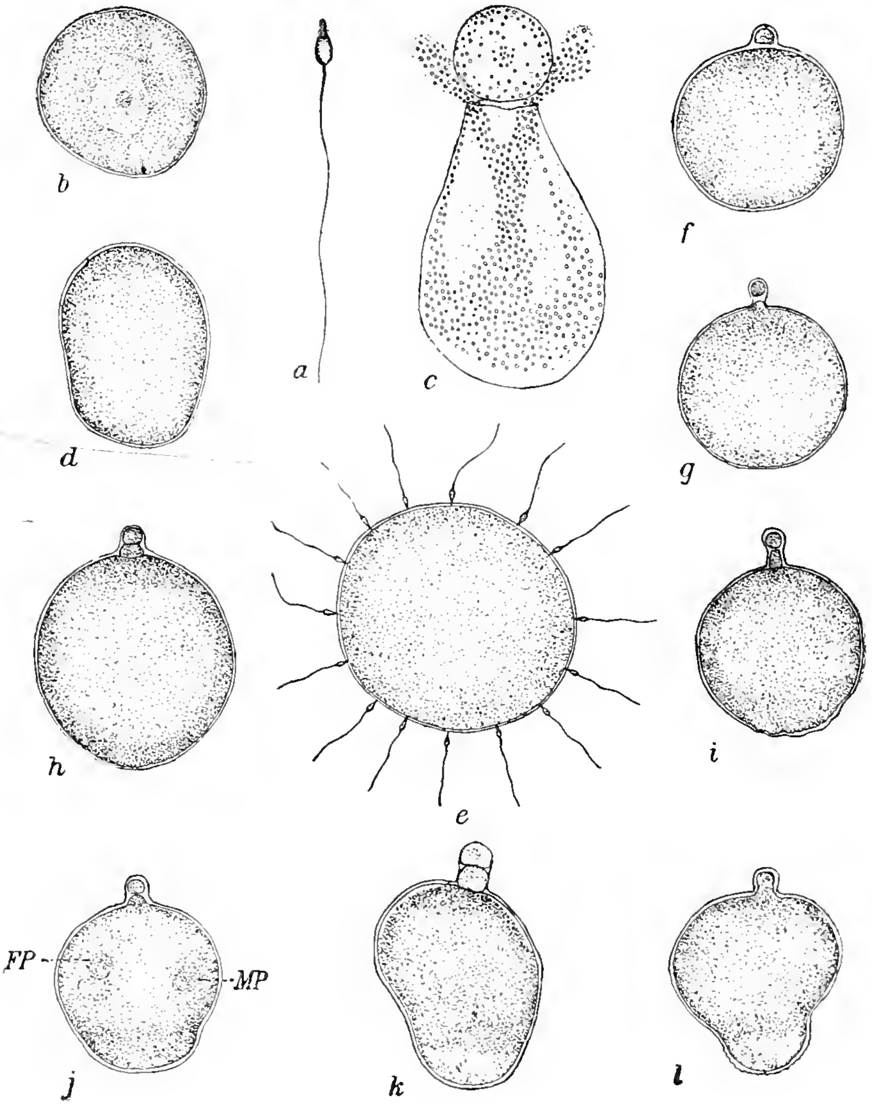
The number of germ cells liberated is something enormous, but that is to be expected when we consider that practically the whole body functions as a genital gland. In figure 147 (opp. p. 163) the genital follicles filled with their products are shown to occupy almost the entire portion of the mantle, the floor of the pericardial region, the wedge-shaped mesosoma, and the outer walls of the liver. A male mussel discharges a stream of milt that in a few minutes' time will render milky all the water in a trough 10 feet long, 1½ feet wide, and 3 inches deep. Figures can not be used to express the countless numbers of fertilizing elements that swarm in the water under these conditions.

The number of eggs spawned by a female mussel at a given time can be determined fairly accurately by determining the size of the egg and the volume liberated. The eggs average about 0.07 mm. in diameter, and the volume liberated at single intervals is from 2 to 4 cc. If the eggs were placed side by side in a line it would require 142 to make a centimeter, and 142 such lines, or 20,164, to cover a square centimeter with eggs one layer thick. A cubic centimeter would contain 142 layers, or 2,863,288 eggs, if placed one directly upon another. As a matter of fact, however, this does not occur, for the eggs settle in the depressions formed between those of the layer beneath, which results in adding some 500,000 more to the total number. But owing to the various errors that occur in making the measurements, such as the presence of foreign matter and the buoying property of the water, which prevents the eggs from coming into actual contact with each other, it probably more closely approximates the truth to assume that there are 2,863,288 eggs to the cubic centimeter. This would mean, therefore, that a mussel during a single act of spawning liberates from 5,000,000 to 12,000,000 eggs. By comparing the volumes of water displaced by the mantle and mesosoma of large mussels 3½ to 3¾ inches long, before and after spawning had occurred, the author found the difference to be a little less than 10 cc., which would indicate that large specimens are capable of producing as high as 25,000,000 eggs.

The spermatozoa are pin-shaped bodies when observed under the low power of the microscope. Under high magnification the head appears as an oval body, with the small end terminating anteriorly in a conical protuberance. At the base of the conical structure are two small, doubly refractive bodies that stain deeply with janus green in the living element. A long slender vibrating tail projects from the opposite end of the head (fig. 181*a*, p. 188). In size the head measures 5 microns long and has a width of 2.5 microns. The tail has a length of 35 microns.

The egg, before leaving the follicle, is more or less spherical in form, with a diameter of 0.07 mm. With transmitted light its color is a pale brownish-yellow. A distinct vitelline membrane no less than 1 micron in thickness envelops the egg, while the center is occupied by a large germinative vesicle containing a conspicuous nucleolus (fig. 181*b*, p. 188). The portion of the egg outside the germinative vesicle is filled with fine yolk granules that render the egg more or less opaque, especially after the germinative vesicle breaks down, which occurs at the time of spawning (fig. 181*d*).

No microphile is visible in the ovarian egg, but if the egg is slightly crushed under a cover glass, it becomes balloon-shaped and an opening appears at the tapering end. Yolk granules flow out from this point of exit, constantly vibrating with the Brownian movement. If pressure continues to be applied to the cover glass the nucleus will also slip out through the opening (fig. 181*c*). The ripe egg, just before it is expelled from the main oviduct, or immediately after it comes in contact with the sea water, undergoes considerable change internally. While externally it retains a form that varies between a long oval and an imperfect sphere, internally the germinative vesicle breaks down and forms the spindle of the first polar body (fig. 178, p. 184). This explains why no nucleus is visible in the freshly laid egg, as noted by Wilson (1887) and Williamson (1907), rather than the presence of abundant deutoplasmic granules to which they attributed the fact. Unless fertilized within three or four hours after extrusion, the eggs die without passing beyond the stage of the first polar spindle



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a. Spermatozoon. Note oval head bearing conical protuberance (at base of which are two doubly refractive bodies) and long, slender tail. × 1,185.

b. Ovarian egg removed from mantle. Imperfect sphere with an external membrane. Germinative vescicle with large nucleolus visible. × 375.

c. Ovarian egg slightly crushed under cover glass showing escaping nucleus and yolk granules. × 375.

d. Ripe egg immediately after being shed. No definite form. Germinative vescicle has disappeared. × 375.

e. Egg a few minutes after fertilization. Perfectly spherical. Spermatozoa acting against it cause it to roll about. × 450.

f. Egg 20 minutes after fertilization, showing protrusion of first polar body. × 375.

g. Egg 10 minutes later, showing appearance of second polar body just below first. × 375.

h. Another egg showing a stage 5 minutes later. The two polar bodies are distinctly separated from egg proper which has now become elongated. Cytoplasmic border at vegetative pole is beginning to take on an irregular outline and to withdraw from cell wall. × 375.

i. Egg 2 minutes later, showing increased activity at nutritive pole. Wavy outline of cytoplasm is more pronounced. Cell membrane opposite to it is wrinkled and beginning to draw away from egg. × 375.

j. Egg 10 minutes later, showing continued protuberance of nutritive pole, contents of which become more transparent than rest of egg. Male pronucleus, *MP*, clear spot near nutritive pole; female ptonucleus, *FP*, similar body near formative pole. × 375.

k. Egg 10 minutes later. Unsymmetrical pear form. Pronuclei have fused and disappeared. × 375.

l. Egg 2 minutes later. Pear form more symmetrical. Nutritive pole contains finer granules, and is therefore more transparent. × 375.

MATURATION AND FERTILIZATION.

That fertilization of the mussel egg takes place in the water has been observed by McIntosh (1885) and Wilson (1887), while Scott (1901), who studied mussels kept in tanks, believes that impregnation of the eggs occurs in the branchial chamber of the mother. According to his observations, "the embryos flow from the female in a slow distinct stream." Of the hundreds of spawning mussels which have been under the author's observation, not one to his knowledge has discharged fertilized eggs into the water. The eggs are discharged in short rodlike masses, which have been described in the chapter dealing with the reproductive system. If the water is quiet they settle to the bottom and the eggs fall apart, forming a brick-red to pinkish mass, according to the amount of pigment present, which is variable. If the locality is subject to the influence of currents or wave action, the eggs flow away and are more or less widely scattered over the bottom. Spermatozoa are generally liberated into the water at the same time that eggs are being shed, and with their long, rapidly vibrating tails, they are able to locomote with surprising rapidity. They are attracted to the eggs, about which they cluster in large numbers, with their conical pointed heads pressing against the vitelline membrane and the tails beating so that the egg keeps twisting around with a spiral motion (fig. 181*e*). Normal freshly laid eggs permit but one spermatozoon to enter, whereas stale or anesthetized eggs allow many to penetrate the cell wall.

As soon as the spermatozoon enters the egg, rapid changes begin to occur in both bodies. The spermatozoon loses its tail and the head begins to increase greatly in size as it moves toward the center of the egg, leaving a clear path behind it (fig. 179, *Sp*, p. 184). The spindle of the first polar body, which has remained stationary at the end of the prophase period since the egg was first deposited, now becomes active again. The chromosomes in the equatorial region divide and migrate toward their respective poles (fig. 179), and at the same time the egg, which hitherto has had no definite form, becomes a regular sphere. When the eggs assume the spherical form it is a pretty sure sign that impregnation has occurred.

The first polar body appears in from 18 to 20 minutes after the eggs and spermatozoa are mixed together, provided the sperms are in an active state (fig. 181*f*, p. 188). Wilson (1887) states that the polar cells appear four hours after mixing ova and sperm, which indicates that his material was abnormal or that the water was very cold. For several years the author has been repeating the experiment with the uniform result that in sea water at about 68° F. the first polar cell appears within 20 minutes after the eggs are discharged and mixed with spermatozoa.

Ten minutes after the appearance of the polar cell a second polar cell is extruded behind the first (fig. 181, *g* and *h*, p. 188), after which the egg remains quiescent, to all external appearances, for a period of about 20 minutes.

At the end of this period the vitelline membrane on the side of the egg opposite to the polar bodies becomes wrinkled, and the margin of the cytoplasm adjacent to it takes on an irregular and wavy outline (fig. 181, *h* and *i*, p. 188). This end of the egg, which represents the vegetative or nutritive pole, now begins to protrude itself in such a way as to give the egg a pear shape, the stalk of the pear including the nutritive pole and the broad end the formative pole. At the same time, two clear spots are usually visible in the granular cytoplasm, which represent the male and female pronuclei (fig. 181*j*, p. 188).

The pronuclei move toward each other, fuse, and disappear during the following 10 to 15 minutes.

CLEAVAGE AND FORMATION OF GERM LAYERS.

The pear shape of the cell becomes more pronounced, and one side of the broad end increases more rapidly in size than does the opposite side (fig. 181 *k*, p. 188). At the same time the cytoplasm becomes less dense at the vegetative pole, which permits more light to pass through and therefore makes this region appear brighter and less granular than the rest of the egg.

One or two minutes later the opposite side of the egg bulges rapidly, making the pear shape more symmetrical, as is shown in figure 181*l* (p. 188). The sides continue to protude outward, a depression appears at the formative pole, and a constriction begins to form about the proximal end of the nutritive pole (fig. 182*a*). Then two planes of constriction appear as shown in figure 182*b* and, to all external appearances, a body of three nearly equal cells results. This, however, is really not the case, for during the next 10 minutes radical changes occur in the egg. One of the apparent cells fuses with the one that corresponds to the nutritive pole, as shown in figure 182, *c* to *e*, resulting ultimately in two cells of very unequal size. The large one is known as the macromere, and the small one as the micromere. The nuclei are visible as clear round spots in the center of the two cells. During the next 10 minutes two more micromeres result. The first one of these is given off from the macromere, and almost at the same time the second one results from the division of the original micromere, as shown in figure 182, *f* and *g*.

From this point on, cell multiplication through the division of the micromeres and the giving off of new micromeres from the macromere is very rapid. The stages represented in figure 182, *h* to *j*, are passed through in about half an hour. The result is a macromere almost covered with a cap of micromeres and a small segmentation cavity inclosed by the group of cells. The relation of the cells to the segmentation cavity at this stage is best seen in an optical section represented in figure 182*k*.

As cell division proceeds, the ectodermal cells become smaller and ultimately completely envelop the macromere, which finally divides into two equal cells (fig. 182*l*). These two cells are apparently the forerunners of the mesoderm.

Figure 183*a* (p. 193) shows a later stage where the embryonic cells have become more uniform in size. The first polar body has, in the meantime, divided so that three polar cells are visible at this stage. Very fine cilia develop on the exposed surface of the cells at this time, and by their vibrations cause the embryo to move slowly about. The period of development from fertilization to the free swimming embryo requires normally 4½ to 5 hours.

Internal changes are difficult to follow in the living material from this stage on. Up to the end of the twenty-fourth hour the principal changes observed are the rapid multiplication of cells, the extraordinary growth of cilia over the outer surface of the body, and the development of a long flexible flagellum, which is composed of several filaments. This flagellum is situated on the anterior end of the body and is held forward like an antenna as the trochophore propels itself rapidly through the water by means of the cilia (fig. 183*c*, p. 193).

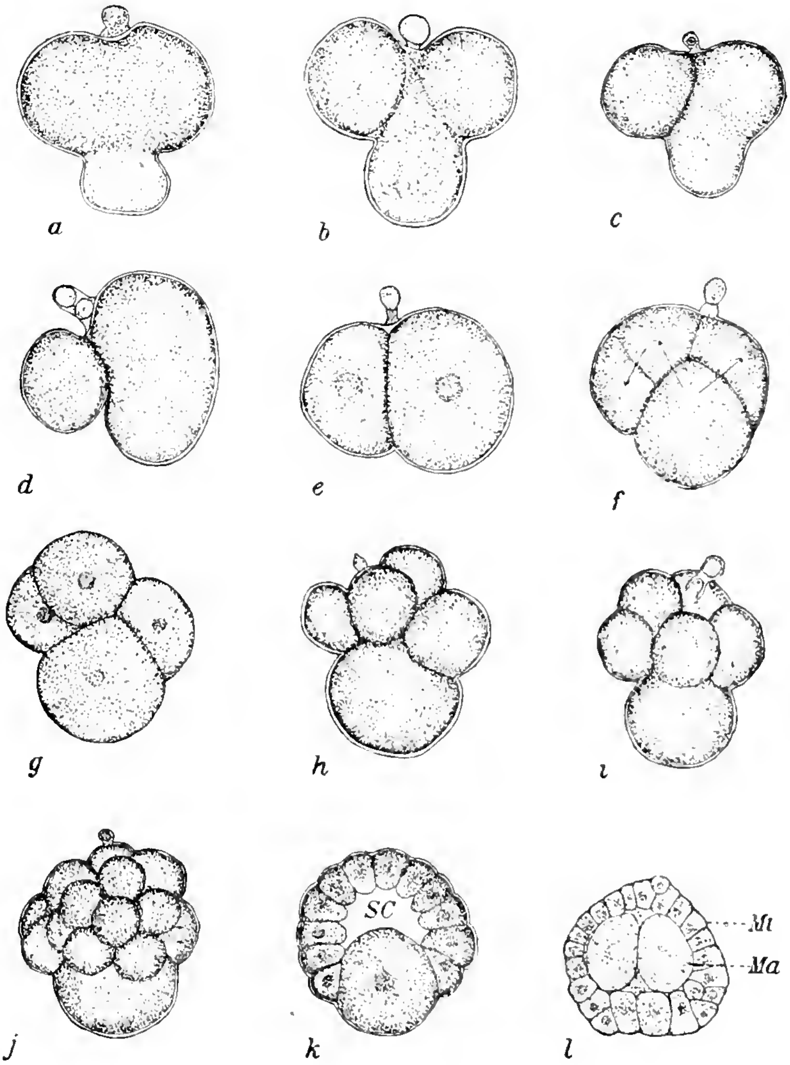

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FIG. 182.—Egg at various stages. × 375.

a. Egg at stage 4 minutes later than 181*l*. Three nearly equidistant furrows have formed, separating formative pole into two masses and setting nutritive pole off as single mass.

b. Two minutes later. Nutritive pole has enlarged to form macromere. Left mass at formative pole is about to be cut off as first micromere.

c. One minute later, showing fusion taking place between macromere and yolk mass to right of formative pole. First micromere is now completely separated by a furrow.

d. Two minutes later, showing continuation of same process.

e. Ten minutes later with macromere and micromere in resting stage. Their nuclei are visible as clear spots in centers of the cells.

f. Ten minutes later. Macromere has given off a second micromere, and first micromere has divided into two as indicated by arrows.

g. Three minutes later.

h. Twelve minutes later.

i. Two minutes later.

j. Fifteen minutes later, showing cap of micromeres gradually growing down over macromere.

k. Optical view of a little later stage, showing segmentation cavity, *SC*.

l. Few minutes later. Macromere now completely surrounded by micromeres, *Mi*, and has divided into two equal cells, *Ma*, that are apparently forerunners of the mesoderm.

Figure 183*b* (p. 193) shows an embryo of this same stage that was placed in a dilute solution of glycerine and water. The solution was not strong enough to destroy the organism through osmotic action, but served to stupefy and render it more transparent. The invagination process of gastrulation was occurring as represented, and mesodermal cells were scattered throughout the segmentation cavity. A typical invagination gastrula is formed in the mussel, therefore, as in the oyster, after first starting as an epibolic gastrula.

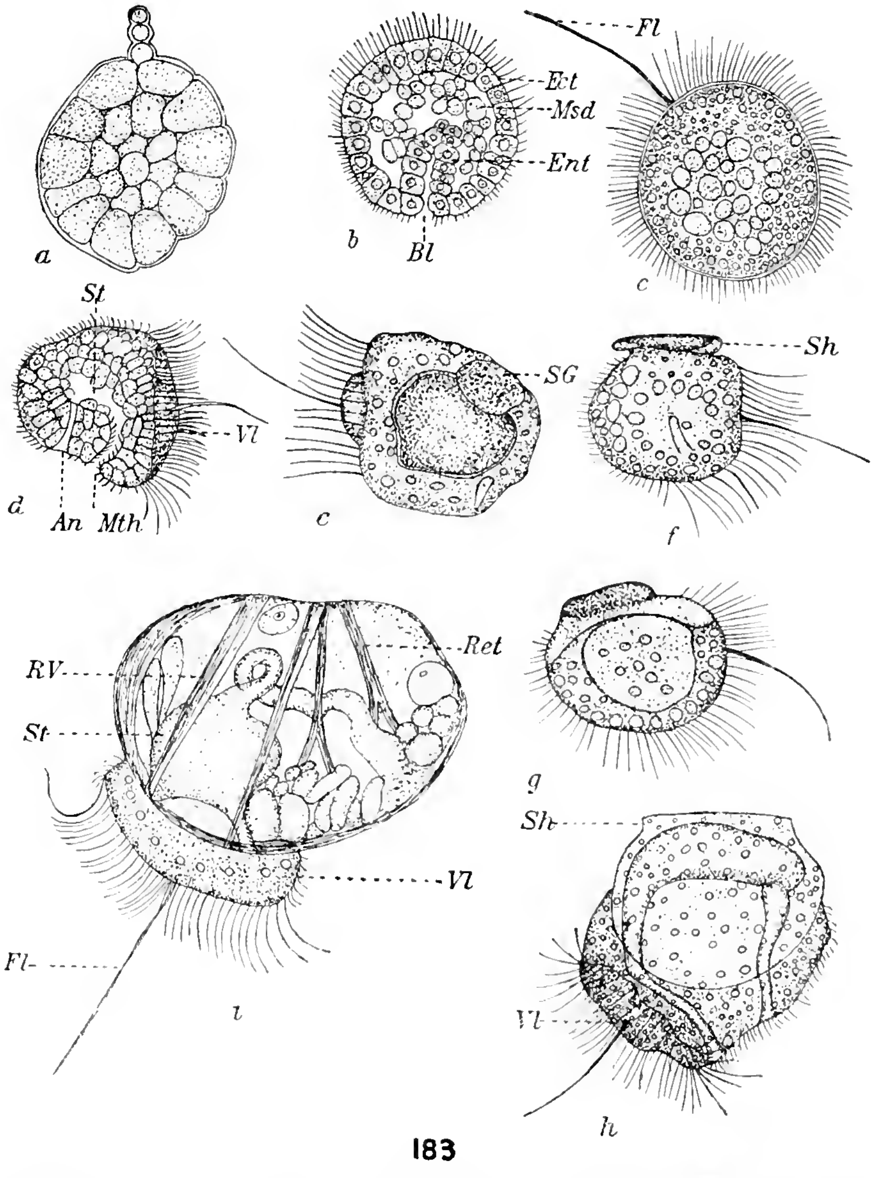
Observations on the living eggs during cleavage and formation of the germ layers would lead to the conclusions that the ectoderm arises from the cleavage of the first micromeres formed, the entoderm from an invagination of the micromeres that come to lie in the region of the vegetative pole, and the mesoderm from the macromere that is ultimately surrounded by the micromeral cells.

DEVELOPMENT OF THE TROCHOPHORE LARVA.

When the developing Mytilus larva has reached the age of about 20 hours, it begins to enter on a stage very characteristic of the free-swimming larvæ of the Lamellibranchia and which so closely resembles the trochophore larva of the Annelida that it has been designated by the same name. The cilia, already weakly developed over the entire surface of the larva, become very prominent. The body gradually elongates and at the anterior pole, just in front of the mouth, a zone of very large cilia is formed which encircles the apical plate. The similarity to the annelidan trochophore is still further emphasized by the flexible flagellum that protrudes from the center of the apical plate, as shown in figure of embryo 42 hours old (fig. 183*d*). At this stage the larvæ become very active swimmers. The flagellum is carried forward and appears to serve as a tactile organ, while the body cilia beat with the effective stroke backward in such a way as to drive the larva forward with a spiral, clockwise motion.

The fate of the blastopore could not be determined. It apparently disappears in the region later occupied by the proctadeum. At about the fortieth hour of development the digestive tract appears in well-defined form (fig. 183*d*). The stomadeum arises as an invagination of the ectoderm just behind the apical plate and is lined with well-developed cilia which beat with the effective stroke inward. It connects with the anterior end of the stomach. The stomach, when it first appears, has an oval form and is lined with large cells. At the same time the stomadeum is formed the proctadeum arises a short distance behind the mouth and connects with the posterior region of the stomach.

The shell gland is observed, immediately following the formation of the digestive tract, as a thickened portion of the ectoderm in the posterior dorsal region (fig. 183*e*, *SG*). The cells are glandular in character and continue to grow anteriorly until they cover the mid-dorsal line. Two or three hours later the beginning of the embryonic shell is visible as a thin integument over the dorsal surface of the gland (fig. 183*f*, *Sh*). When first secreted it is unpaired, but as growth continues over the sides of the larva a median dorsal dividing line is formed which separates the shell into right and left valves (fig. 183h, *Sh*). This line of division corresponds to the hinge line of the adult shell. During the next few hours the growth of the shell is the most conspicuous change observed in the larva. At the age of 69 hours the valves are almost large enough to inclose the fleshy parts completely (fig. 183*i*).



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a. Optical section of embryo 4 hours old. First polar body has divided making a total of three polar cells which still adhere to embryo. Macromeres shown inclosed within the blastula (*Ma* in fig. 182*l*) have multiplied into smaller cells which more or less fill the segmentation cavity. Cilia, too fine to be shown in the drawing, are developed and embryo begins to rotate slowly.

b. Optical section of embryo 20 hours old, showing formation of gastrula and origin of germ layers. Epibolic process of gastrulation shown in fig. 182, *h* and *l*, now becomes typical embolic process which results in formation of entoderm, *Ent*, and a blastophore, *Bl*. *Ect* is ectoderm; the mesoderm cells, *Msd*, which are scattered throughout the segmentation cavity, are derived from the macromeres originally inclosed by epibolic process. Cilia are well developed and trochophore larva swims about actively.

c. Trochophore larva 24 hours old, showing flagellum, *Fl*.

d. Trochopore larva 42 hours old, showing formation of digestive tract and apical plate. *An*, anus or proctadeum, *Mth*, mouth or stomadeum; *St*, stomach; *Vl*, apical plate, anlarge of velum.

e. Trochophore larva 45 hours old, showing shell gland, *SG*.

f. Trochophore larva 48 hours old, showing first formation of shell.

g. Another larva 48 hours old, showing further growth of shell.

h. Trochophore larva 69 hours old, showing straight hinge shell, *Sh*; anlage of velum, *Vl*; and digestive tract.

i. Trochophore larva 5 days old with well-developed velum, *Vl*, and retractor muscle fibres, *RV*; *Fl*, flagellum; *St*, stomach. Actual size of lavra 91.4 by 68.5 microns.

Jackson (1888) observed that in the oyster this first formed shell was strikingly different from that which immediately succeeds it and which is retained throughout the rest of its life. It is different in form, composition, and histological structure and covers different organic soft parts. He considered it to be the homologue of the protoconch of cephalous mollusks and the periconch of Dentalium and has named it therefore the *prodissoconch* (early double shell). For the adult double shell, which is believed to be homologous with the adult single shell of cephalous mollusks, he has suggested the name *dissoconch* (double shell). The age at which the dissoconch begins to form could not be determined by the author, for it was impossible to keep larvæ growing normally in the laboratory for more than five days. Specimens showing the developing dissoconchs had to be collected from the open sea, where it was impossible to estimate their age with any degree of accuracy.

The velum becomes the organ of locomotion when the prodissoconch incloses the body. It is formed from the apical plate with its encircling zone of cilia and the surrounding tissue. It keeps its location in the anterior region, where it grows relatively very large. Retractor muscle fibers, which have their origin in the dorsal region of the valves, are inserted into the velum and provide for the contraction and withdrawal of the organ into the cavity between the valves (fig. 183*i*, *RV*, p. 193). When fully protruded, the velum projects laterally, considerably beyond the margins of the shell, especially when the valves are nearly closed. Its large, vibrating cilia make it a powerful locomotor organ, by means of which the larva is able to swim with great rapidity in any direction or to creep on solid surfaces under the water. The velum is also highly sensitive and may be withdrawn with a sudden jerk the instant it is touched by a foreign object.

TRANSITION TO THE ADULT.

The metamorphosis of the larva into the adult is characterized by the degeneration of the velum, which is the most prominent organ of the trochophore stage, a marked advance in the number and complexity of the internal organs, and a decided change in the external form of the animal. In describing this transition the development of the organs will be considered separately as nearly as possible in the order in which they appear.

MANTLE.

The mantle has its origin in the shell gland which first grows to cover the whole dorsal surface of the trochophore larva. This is indicated by the extent of the prodissoconch shell shown in figure 183, *e* to *g* (p. 193). Lateral folds of the shell gland are then formed, which grow downward as the right and left mantle lobes. These develop so rapidly that before the end of the trochophore stage is reached they come to envelop the entire body except when the velum is extended. The result is a decided change in the shape of the animal from a cylindrical to a laterally compressed form (fig. 183, *e* to *i*, p, 193).

SHELL.

The origin and development of the embryonic cuticular shell, or prodissoconch, have been described above. Later the calcareous, prismatic shell, or dissoconch, which is characteristic of the adult mussel, develops. It begins as a limy glandular secretion from the mantle that is deposited in two centers symmetrically placed on the right and left sides of the body, where they may be seen lateral to the stomach and inside the prodissoconch at the stage when the larva has attained a length of 0.274 mm. (fig. 184, *Dis*, p. 197). The dissoconch continues to grow rapidly in size by further deposition of calcareous matter. By the time the young mussel has reached a length of 0.512 mm. the prismatic shell can be seen extending far beyond the limits of the prodissoconch (fig. 187, *Dis*, p. 198). At this stage the form of the developing mussel is undergoing a radical change from the more or less circular, straight hinge-line embryonic shell to the triangular ovate form of the adult (figs. 187 and 188, p. 198). This is accomplished by growth taking place most rapidly in the ventral and posterior directions. The prodissoconch persists as the covering, periostracum, of the umbones and is shown in its final position in the 0.72 mm. stage (fig. 188, *Pds*).

ALIMENTARY ORGANS.

In the trochophore larva it has been shown that the œsophagus is large and leads from the posterior border of the velum to the stomach. The intestine is short and straight, leading directly from the posterior end of the stomach to the anus, which, at this stage, is located à short distance behind the oral opening. During the transition from the larva to the adult the intestine increases in length, which results, first, in a bending to the left with the formation of a loop. The portion anterior to the loop grows directly backward to form the direct intestine, while the loop continues to lengthen in the anterior direction on the left side of the stomach until it reaches the œsophagus. This results in the formation of the recurrent and the terminal portions of the intestine (fig. 188, *RI* and *TI*, p. 198).

When the larva is about 0.27 mm. long the liver appears as a pair of diverticula composed of large, loosely aggregated endodermal cells from the anterior lateral walls of the stomach. In a short time they become tinged with a brownish pigment, which is characteristic of the gland and makes it stand out distinctly from the other tissues, (fig. 184, *L*, p. 197). By the time the embryo has attained a length of 0.72 mm. the liver tissue has grown to envelop the stomach completely (fig. 188, *St*).

The labial palps, to all appearances in total preparations, are developed the same way in Mytilus as Meisenheimer (1901) observed them in *Dreissensia polymorpha*. They arise from the cerebral pit, after the fundaments of the cerebral ganglia have been laid down, by a flattening of the tissue into two lateral bands of ciliated epithelium above and at the sides of the mouth (fig. 187, *LP*, p. 198). From these, the superior and inferior palps are developed by growth from the upper and lower edges, respectively.

MUSCLES.

As the end of the larval period approaches the various systems of muscles, characteristic of the adult, develop in rapid succession. According to Wilson (1887) the pallial muscles appear first as a band of considerable width running round the entire margin of the valves before the embryo is 0.134 mm. long, or about 12 days old. Then the anterior adductor muscle is formed from a group of large mesoblast cells which appear in the anterior region (fig. 184, *AAd*, p. 197). This is followed immediately by the development of the posterior adductor muscle from a similar group of mesoblast cells in the posterior dorsal region (fig. 184, *PAd*). At this stage the anterior adductor is much larger than the posterior adductor muscle, but as development proceeds it becomes narrower and finally much smaller than the posterior adductor muscle.

The foot, which is a muscular glandular organ, appears next as a hollow outgrowth of ectodermal cells into which there grows a large mass of mesodermal tissue from immediately behind the velum (fig. 185, *Ft*, p. 197). At this stage of development specimens are 0.36 mm. long and show three or four gill papillæ. In its early appearance the foot is wedge-shaped, but as growth continues it becomes long, slender, and highly contractile, and is covered with fine cilia (figs. 187 and 188, *Ft*, p. 198). During this development a deep invagination occurs on the posterior ventral side of the foot, which results in the formation of the byssus gland (fig. 188, *ByT*).

As soon as the foot begins to take on form the posterior retractor muscle of the foot and byssus can be seen running from the base of the foot back over the posterior adductor muscle to the shell where it is inserted (figs. 185 and 186, *PRet*). At this stage the young mussel has attained a length of 0.385 mm.

The anterior retractor muscle of the foot and byssus is the last one developed. The smallest specimen in which it was observed was 0.512 mm. long (fig. 187, *ARet*).

GILLS.

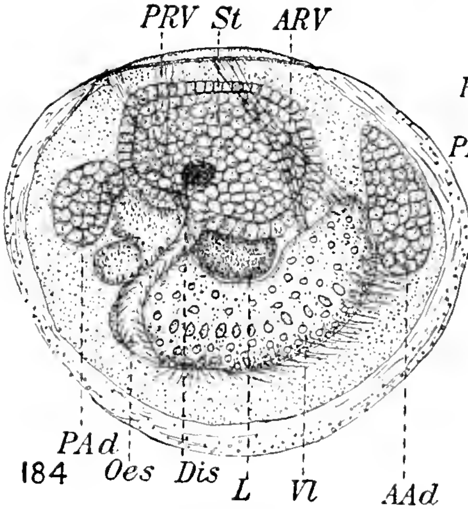
The development of the gills was worked out first by Lacaze-Duthiers (1856) and more recently by Rice (1908). According to these investigators a papilla arises on each side of the body between the mantle and median visceral mass when the larva is about 0.3 mm. long, or approximately at the stage shown in figure 184. New papillæ arise behind these in succession and grow downward to form the branchial filaments (figs. 185–188, *BrF*). The free ends of the filaments are thickened, and as they increase in number the anterior and posterior faces of the succeeding swollen tips fuse together making a continuous membrane of the sheet of filaments. As the filaments continue to grow they are reflected inward to form the ascending lamellar leaf. At the same time interfilamentar junctions are developed by the interlocking of some specially long cilia which hold the adjacent filaments together firmly. Immediately following this stage, in fact before the ascending lamella is well formed, there arises, just outside and parallel with the first series, a similar row of papillæ which grow downward to form the filaments of the descending lamella of the outer gill. As growth continues they bend outward and are reflected upward to produce the ascending lamella of the outer gill. The outer branchial filaments begin to appear when the mussel is about 1.4 mm. long and possesses 20 of the inner gill filaments. In specimens that had reached a length of 1.6 mm. Rice (1908) found 25 filaments in the inner gill and 15 in the outer one.

KIDNEY.

The first sign of the kidney is a mass of small mesodermal cells immediately in front of the posterior adductor muscle in specimens 0.36 mm. long (fig. 185, *K*, p. 197). The anterior end of the mass grows forward, finally forming a pair of longitudinal canals which lie on either side of the body at the roots of the gills (fig. 188, *K*).

NERVOUS SYSTEM.

The ganglionic centers arise independently from thickenings of the ectoderm and become connected later by commissural fibers which grow out from them. Wilson



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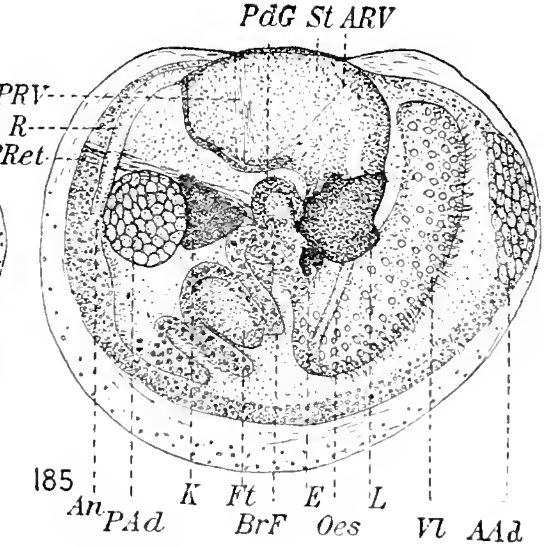

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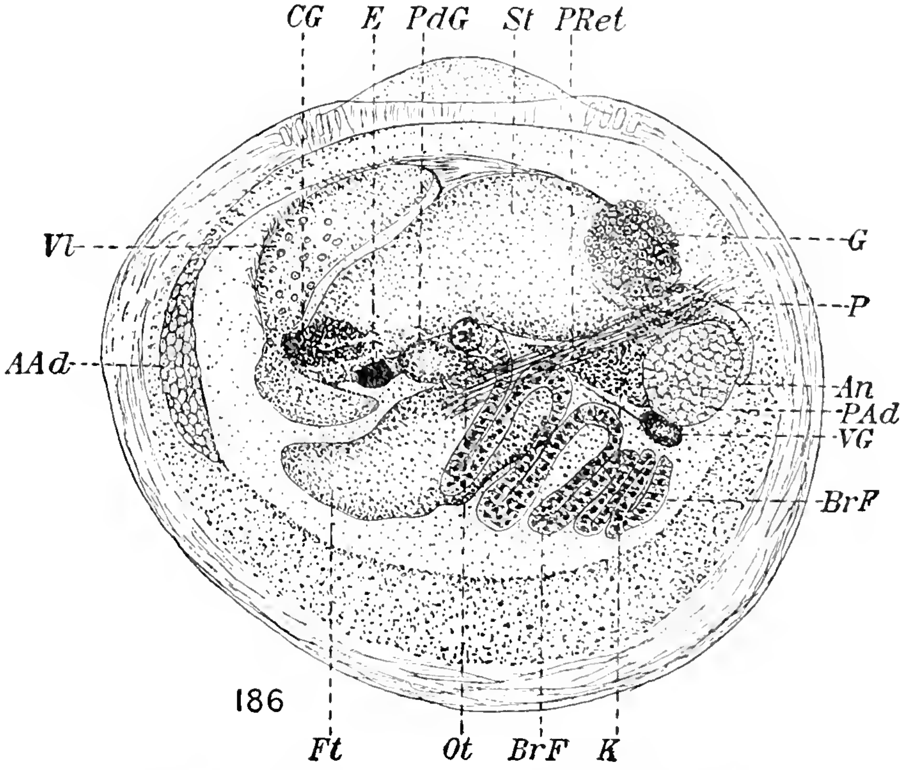

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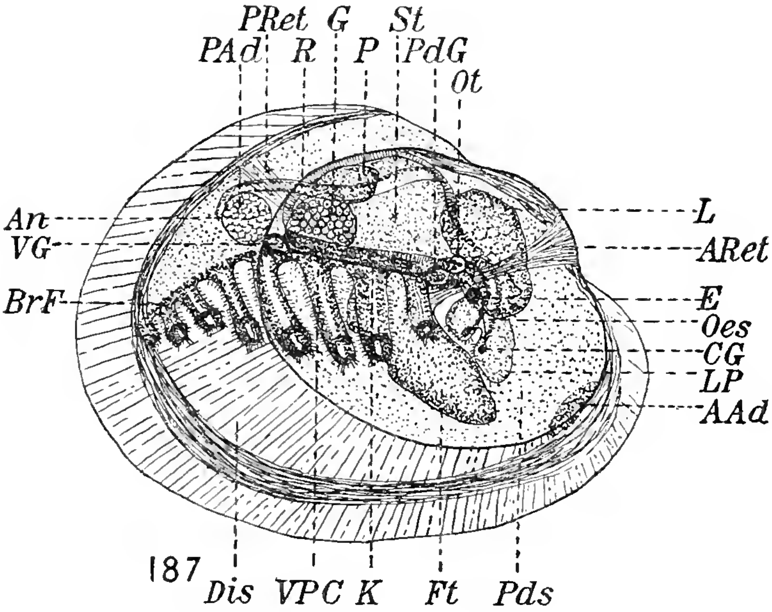
FIG. 184.—Transparent preparation of a larva, 0.274 by 0.260 mm., with well-developed anterior adductor muscle, *AAd*, and posterior adductor muscle, *PAd*. Liver, *L*, and prismatic cell or dissoconch, *Dis*, just appearing. *ARV*, anterior retractor muscle of velum; *Oes*, œsophagus; *PRV*, posterior retractor muscle of velum; *St*, stomach; *Vl*, velum.

FIG. 185.—Transparent preparation of a larva, 0.360 by 0.260 mm., showing first appearance of foot, *Ft;* four branchial filaments, *BrF;* eye, *E;* pedal ganglion, *PdG;* posterior retractor muscle of foot and byssus, *PRet;* and kidney, *K*. *An*, anus; *R*, rectum; other abbreviations same as in fig 184.

FIG. 186.—Transparent preparation of a larva, 0.385 by 0.329 mm., showing first appearance of cerebral ganglion, *CG;* visceral ganglion, *VG;* otocyst, *Ot;* pericardium, *P;* and genital gland, *G*. The velum is degenerating, the anterior adductor muscle is reduced in relative size, and the foot has undergone considerable growth. Other abbreviations same as in figs. 184 and 185.



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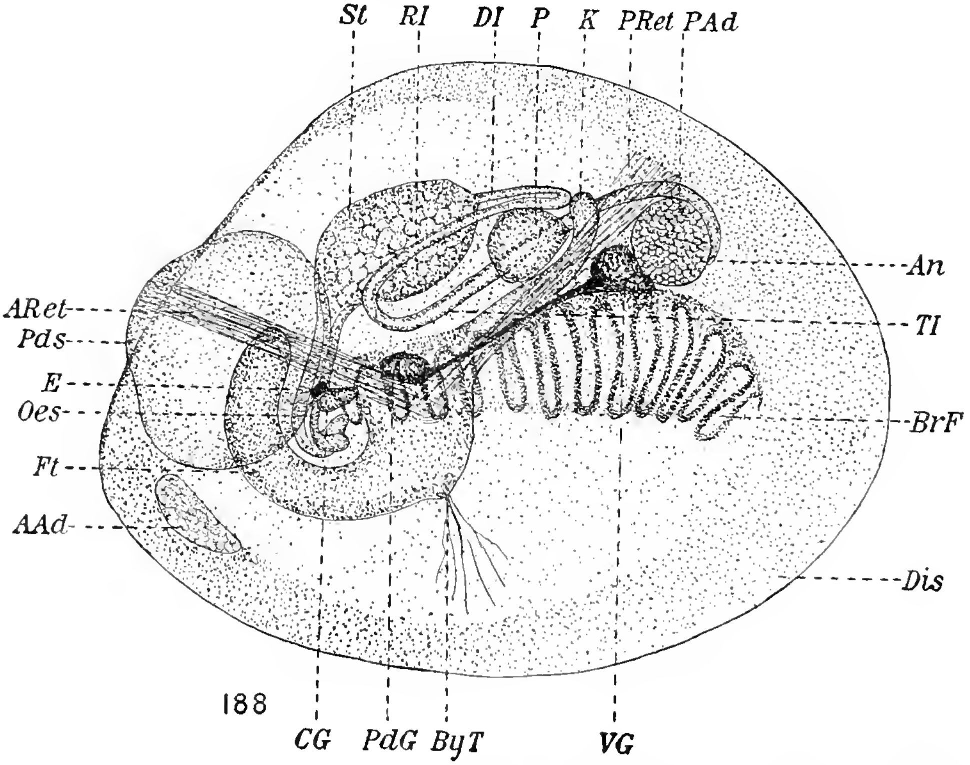

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FIG. 187.—Transparent preparation of a young mussel showing relation of prodissoconch, *Pds*, or larval shell, to dissoconch, *Dis*, or adult shell. Anterior retractor muscle, *ARet*, beginning of the labial palps, *LP*, and commissural nerve, *VPC*, appear at this stage. The velum has degenerated and disappeared. Other abbreviations same as in figs. 185 and 186.

FIG. 188.—Transparent preparation of a young mussel, 0.72 mm. long, showing the prodissoconch, *Pds*, which is destined to cover the umbo; the well-developed liver which has come to envelop the stomach, *St*, completely; the looping of the intestine to form the direct intestine, *DI*, the recurrent intestine, *RI*, and the terminal intestine, ***TI***. Byssus threads, *ByT*, extending from byssal gland, are present for the first time, and the kidney, *K*, pericardium, *P*, and gills, *BrF*, show considerable advance in development over the previous stage figured. Other abbreviations same as in figs. 185, 186, and 187.

(1887) observed that the cerebral ganglion is the first to be formed in the trochophore larva at the base of the velum in the cerebral pit. Next in order the pedal ganglion is formed. It is readily distinguished as a large group of cells situated at the base of the anterior edge of the developing foot in specimens 0.36 mm. long (fig. 185, *PdG*, p. 197). The visceral ganglion appears later on the anterior ventral edge of the posterior adductor muscle, where it is readily seen in mussels 0.385 mm. long (fig. 186, *VG*, p. 197). At the same time a commissural nerve can be seen growing forward from the visceral ganglion. In specimens 0.512 mm. long commissures are completely established between the visceral and pedal ganglia and between the cerebral and pedal ganglia (fig. 187, p. 198). The direct connection between the visceral and pedal ganglia is soon lost, however, for the commissural nerve grows forward to terminate in the mid region of the cerebropedal commissure which is the adult condition (fig. 163, p. 175).

SENSE ORGANS.

A pair of direction eyes appears at the time the first gill papillæ are formed. The position they occupy corresponds to what will be the base of the first anterior inner gill filament. They are formed from a cuplike invagination of ectodermal cells which later become filled with a mass of dark brown granules that make the eyes appear as conspicuous dark round spots in specimens rendered transparent (figs. 185 and 186, *E*, p. 197).

Shortly after the eyes are developed a pair of otocysts arise as ectodermal invaginations just dorsal to the eyes. The invagination proceeds backward to a position where the capsules with their contained otoliths lie dorsal to the pedal ganglion (fig. 186, *Ot*). As growth of the animal continues the pedal ganglion shifts backward, leaving the otocyst inclosed in the angle formed by the union of the cerebropedal and cerebrovisceral commissures (fig. 163, *Ot*, p. 175).

The osphradium and the abdominal and pallial sense organs are clearly modifications of the body epithelium, but at just what period the transition takes place was not determined.

PERICARDIUM.

The pericardium is first seen when the young mussel reaches a length of 0.385 mm. It arises from a mass of mesodermal cells around the terminal intestine just dorsal to the posterior adductor muscle (fig. 186, *P*, p. 197). As the intestine lengthens, the pericardium migrates forward to the mid-dorsal region of the body (figs. 187 and 188, *P*, p. 198). Pulsations of the heart were noted by Wilson (1887) as first visible in embryos 0.65 mm. long, possessing 10 or 11 gill papillæ.

GENITAL ORGANS.

The genital organs begin to form after the animal has almost completed its metamorphosis. According to the author's assumption, based on the observations of Ziegler (1885) on *Cyclas cornea*, the paired mass of mesodermal cells, which appears just dorsal and anterior to the posterior adductor muscle, in close relation to the pericardium when the embryo is 0.385 mm. long, is the forerunner of the reproductive system (fig. 186, *G*, p. 197). This position corresponds to the external opening of the genital system in the adult. At this stage the further course of development from the cell group was lost. In the next stage of the author's series, which was 0.72 mm. long, no trace of the cell groups could be seen in total preparations rendered transparent, which led to the conclusion that in the interval between the 0.512 mm. and the 0.72 mm. stages a sudden change in the activity of these cells occurs which results in a rapid proliferation to form the series of reproductive canals that ramify throughout the body tissue. This latter condition was observed in sections of specimens 1 mm. long.

The age at which the various organs appear during the later metamorphosis can be stated only approximately, since it was impossible to carry normally developing embryos beyond the first week. All the stages represented beyond figure 183*i* (p. 193) were drawn from specimens [3] collected in Casco Bay near Harpswell, Me., during the month of August, which offers no clue as to age, since the reproductive process is more or less continuous throughout the summer. Matthews (1913), however, was able to rear mussel larvæ in the laboratory by feeding them on cultures of Nitzachia, and she succeeded in keeping them alive for months. Metamorphosis in these artificially reared mussels appears to have taken place more rapidly in proportion to increase in size than in normally grown specimens. The artificially reared larvæ, for example, measured 0.31 by 0.24 mm. when at the five-gill filament stage, whereas normal larvæ of the same stage measure 0.385 by 0.320 mm. On the basis of Matthews's observations it is probable that the stage represented in figure 184 (p. 197) is approximately 6 weeks old; that in figure 186 (p. 197), 2 months old; while that in figure 188 (p. 198) is not more than 10 weeks old.

GROWTH.

The rate of growth which takes place in the mussel after it reaches the attachment stage depends upon several factors, the chief one of which is abundance of food. If food is scarce, growth is retarded regardless of all other conditions. On the other hand, if diatoms, Protozoa, and spores of algæ are abundant in the water which flows over the beds and at the same time mud, sand, and filamentous algæ are absent, growth will take place rapidly. These conditions are further influenced by the rate and volume of the currents flowing over the beds and by the length of time the mussels are exposed to the air during each tide. Large volumes of water moving slowly supply food most advantageously to the mollusk, and where the beds are not exposed the food is continuously brought to the shellfish without interruption. For this reason the largest and best mussels are found in beds where the water covers them to a depth of from 6 to 15 feet.

Salinity of the water is thought by some observers to influence the rate of growth. Brandt (1897) noted that in Kielwight the mussel grows to a length of 4½ inches, while in the Gulf of Bothnia, where the salinity of the water is less, the mussel only attains a size of about 1 inch. In the Kaiser Wilhelm Canal, where the salinity of the water decreases from east to west, he found that the ripe mussels in the fresher parts were only about half the size of those growing in the saltier regions.

Under ideal conditions the mussel will increase about an inch in length annually for the first two or three years, and then the rate of growth gradually diminishes. Mussels, however, do not frequently find such situations, so that the average rate of growth as actually found on the natural beds is much less. Ordinarily the time required for the shellfish to attain a length of 3 inches is five to seven years. ?

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[3] The author is indebted to Dr. Edward L. Rice, of Ohio Wesleyan University, for these specimens.

Williamson (1907) made observations on the growth of some mussels which he kept in the laboratory for one to two years. He divided them into three sets, according to size, and designated them as A, B, and C. Lot A consisted of individuals 0.3 inch long, lot B of specimens 1 inch in length, and those of lot C measured about 1.5 inches in extent. Individuals of the A group, on the average, doubled their length during the first year, but owing to the artificial conditions they assumed a peculiar form, which was described roughly as barrel-shaped. At the end of the second year the increase in size was very slight. The greatest growth observed during the entire period was three-eighths inch; the least, one-eighth inch. Lot B gained from one-sixteenth to five-sixteenths inch the first year; at the end of the second year the total gain in length was from one-eighth to three-eighths inch. Lot C did least well of the three. During the two years five out of the seven specimens died. Of the remaining two, one showed an increase of one-eighth inch in length, while the other exhibited no growth at all.

The above experiments were performed under such artificial conditions that the results appear to be of little value. In order to find out the actual rate of growth under normal conditions, the author selected five groups of mussels which were located in different environments and situated where they were least likely to be disturbed. Five specimens were selected from each group and measured for three successive summers. During this period two of the experimental groups disappeared. The three remaining ones, however, represent a variety of situations and show some interesting results.

Table 1 shows the record of specimens kept on Pine Island, Woods Hole, Mass. They were firmly attached by byssal threads to a rocky bottom which was kept perfectly free from mud by a very swift tidal current that swept over it. The shellfish were so situated that they were exposed at low tide for a period of from two to three hours daily.

TABLE 1.—RATE OF GROWTH OF MUSSELS ON PINE ISLAND, WOODS HOLE, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Length.	Height.	Length.	Height.	Length.	Height.
1	47.2	27.2	49	27.5	51	28	1.9	0.4
2	38	20.5	44	22	46	23	4	1.2
3	56	31	63	32.5	65	33	4.5	1
4	50.5	25	54	26	56.3	26.1	2.9	.5
5	48	24	50.3	24.5	52.8	24.8	2.4	.4
Total average growth per year							3.1	.7

Table 2 represents the growth of mussels which were attached to one of the piles of the Government wharf at Woods Hole, Mass. They occupied a position slightly below the level of low-tide mark and were exposed only at very low tides. A moderately strong current of water which was rich in food materials flowed over them. Slack water prevailed for about three hours each day. In this situation it will be observed the mussels grew more than twice as fast as those on Pine Island.

TABLE 2.—RATE OF GROWTH OF MUSSELS ON WHARF PILE, WOODS HOLE, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Length.	Height.	Length.	Height.	Length.	Height.
1	63	36	69.5	36.8	72.9	37.5	4.9	0.7
2	50	30.8	61.7	34.5	66.6	35.4	8.3	2.3
3	67	34.7	77.5	39	84.1	40.6	8.5	2.9
4	64.5	36.1	67.6	37.5	72.2	39.3	3.8	1.6
5	52	28	65.5	31	73	33.8	10.5	2.9
Total average growth per year							7.2	2.1

Table 3 indicates the rate of growth of mussels on a mud bottom at the mouth of Menemsha Pond, Marthas Vineyard, Mass. A rather strong tidal current of water, rich in food matter, swept back and forth over them with but a few minutes of slack water prevailing at each turn of the tide. They were exposed only when the tides were extremely low. Algæ and eelgrass grew about them to considerable extent, but they were at no time covered with the vegetation. In this situation growth took place at about three times the rate of that in the Pine Island mussels.

TABLE 3.—RATE OF GROWTH OF MUSSELS IN MENEMSHA POND, MARTHAS VINEYARD, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Lengtb.	Height.	Length.	Height.	Length.	Height.
1	71.5	35	80	40	89.5	41	9	3
2	72.5	34.8	81.5	39.7	89.7	41.1	8.6	3.1
3	78	35	83	36.1	90	38	6	1.5
4	67.2	32.5	76.3	37	82.4	39.2	7.6	3.3
5	61.3	31	71	34.8	79	36.7	8.9	2.9
Total average growth per year							8.6	2.7

Comparison of these results with those of Williamson (1907) show that they are almost identical. The least amount of growth observed, 4 mm. or one-seventh inch, compares favorably with Williamson's one-eighth inch minimum increase, while the 10.5 mm., or nearly seven-sixteenths inch, compares well with his three-eighths inch maximum growth.

These results, however, should not be taken to mean that the rate of growth of the sea mussel is from one-fourth to one-half inch per annum, for specimens are often found which show an annual growth of 1 inch or more. It is not uncommon to find mussels 3 inches long on beds which are from three to four years old. Orton (1914) reports that the Plymouth (England) mussels attain a length of from 1⅖ to 2 inches the first year and when 18 months old average 2 inches long. In France, where they are cultivated on wooden frames, the mussels attain a length of from 1¾ to 2 inches in from 12 to 15 months. At Woods Hole, Mass., ropes on fish traps put out in April and taken in the last of August were found covered with young mussels, many of which were nearly three-fourths of an inch long and which could not have been more than 4 months old (fig. 189). Less rapid growth has been found to occur in the older shellfish. Wright (1917), after careful examination, has shown for the mussels of Cardigan Bay that the

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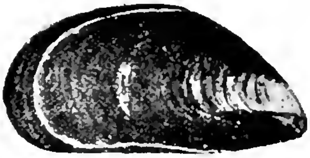

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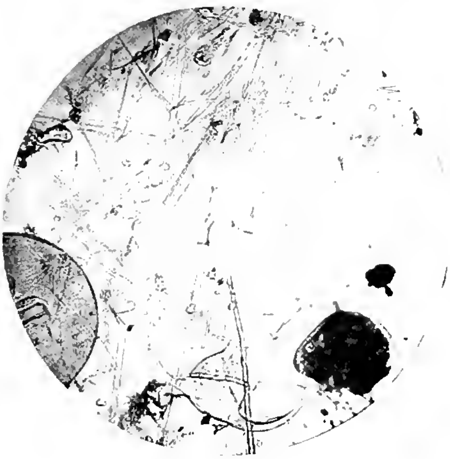
FIG. 189.—Growth stages of young mussels which collected on the rope of a fish trap put out in Buzzards Bay near Woods Hole, Mass., in April and taken up the last week in August. The largest individuals were nearly three-fourths of an inch long and could not have been more than 4 months old.

FIGS. 190 and 191.—Side views of young mussels showing amount of growth, indicated by area outside the light colored growth line, which took place in transplanted specimens at Morecambe, England, during a period of seven months.. (After Bjerkan, 1911.)

FIGS. 192 and 193.—Lateral and dorsal views of an old mussel showing growth, indicated by the new shell area, that was stimulated by transplanting after it had remained almost stationary in size for years. (After Bjerkan, 1911.)



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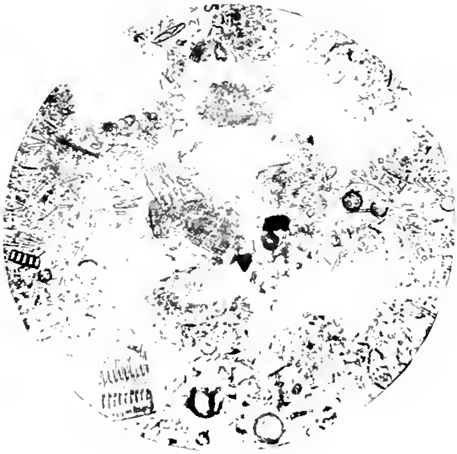

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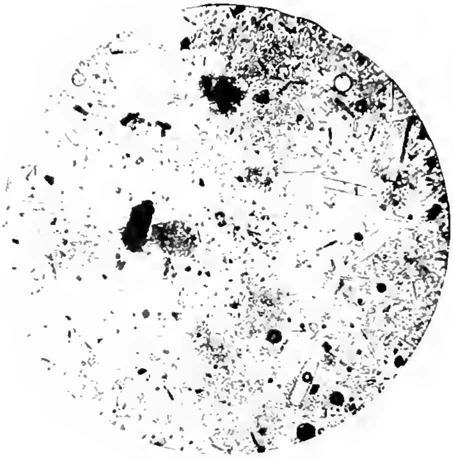

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Fig. 194.—Photomicrograph of a bit of tow material collected over a mussel bed near Woods Hole, Mass.

Fig. 195.—Photomicrograph of a bit of material from the stomach contents of a mussel. Plankton organisms and detritus are present in about equal amounts.

Fig. 196.—Photograph of the fresh fecal discharges of a mussel which was cast out in ribbonlike form. Slightly enlarged.

Fig. 197.—Photomicrograph of the feces of a mussel after the ribbonlike discharges have disintegrated. Note the finely divided state of the material compared with that of the stomach contents.

average increase in length made by 2-inch specimens, between March 30 and November 15 of the same year, is nine-sixteenths of an inch.

It appears, therefore, that in both Europe and America the growth rate of mussels under favorable conditions amounts to 1 inch annually for the first two years, after which the rate decreases gradually in the third year and rapidly thereafter. However, as will be described later, the transplanting of old individuals which for a long time have exhibited no growth to a new environment will cause rapid growth to start again (figs. 192 and 193).

FOOD OF THE SEA MUSSEL AND ITS SIGNIFICANCE.

In a former paper (Field, 1911) the author stated that the food of the mussel consisted of microscopic plants and animals and gave a list of 29 species of diatoms and 9 species of Protozoa which were found in the stomachs of mussels taken in the vicinity of Woods Hole, Mass., In the light of more recent research, which is discussed later in this section, his attention was turned to the fact that the food organisms mentioned do not form more than one-half of the bulk of material actually ingested and that the remaining matter, which was considered not worth reporting, may be of prime importance in the nutrition of the mussel. Other observers also have noted the same conditions in the stomachs of different species of shellfish, and likewise also have disregarded the mud-like contents as of no food value. Lotsy (1893), who examined the stomach contents of oysters, reported that he found in addition to the diatoms "a quantity of decaying organic matter at least equal in amount." Quahogs, soft clams, and ribbed mussels living in the same vicinity as the oysters had the same proportion of things in their stomachs. He asserted, however, that the decaying organic matter went through the alimentary tract unchanged. Moore (1913), discussing the food of the oyster, states:

> It appears that finely divided organic débris, or detritus, which constitutes the major part of the material ingested, plays a more important rôle in the oyster diet than has been conceded.

In the stomach of the mussel this detritus is present in relatively the same proportion as has been reported for the oyster. Figure 194 is a photomicrograph of a sample of plankton tow taken over a mussel bed on Pine Island near Woods Hole, Mass., August, 1915. Figure 195 is a photomicrograph of the stomach contents of a mussel on this bed. A comparison of the two pictures shows that the mussel feeds exclusively on fine particles of detritus and the smaller plankton organisms. The larger organisms and those with long spinous processes, as well as the coarser particles of decaying organic matter, are excluded almost entirely from its diet. The feces are discharged in flat ribbonlike segments of varying lengths, which are shown somewhat enlarged in figure 196. After lying on the bottom a few hours they fall apart into the separate fine particles of which they are composed. These are shown in the photomicrograph, figure 197. It reveals the diatom shells empty and, in most cases, finely broken and the detritus ground to a fine powder.

In an attempt to determine the daily quantity of material ingested by the mussel, measurements were made of the volume of feces cast off each day by a group of 3-inch mussels which were thoroughly washed and placed in a trough having a clean, white bottom. Sea water to a depth of 4 inches was kept flowing over the shellfish, but the current was not permitted to become swift enough to carry away the excrement. Each day for three days the discharged feces were carefully picked up with a pipette and placed in a graduate with a few drops of formalin to prevent decomposition. When the material had settled completely the quantity was read off. The observed result was that 75 mussels discharged a daily average of 3,065 c. mm. of digested matter, or 40.8 c. mm. for each individual. This means that the volume of solid food actually consumed by a 3-inch mussel is not less than 40.8 c. mm. per day and probably is considerably more. This brief series of observations is too limited to form the basis of any conclusions as to the amount, kind, and quantity of food utilized by the mussel, but it suggests a means for solving the problem. What is required is that the observations of this sort be made to cover a long period and be supplemented with chemical analyses of stomach contents and feces to show the quantity of carbon and nitrogen absorbed in a given time.

Whether or not the phytoplankton and detritus constitute the entire food of the mussel we do not know at present, but that there must be an enormous supply of food materials available in the sea is demonstrated in a most striking way to one who witnesses the appearance and rapid growth of a bed of sea mussels on vast areas of the sea bottom, sometimes hundreds of acres in extent. In three years time this shellfish may attain a length of 3 inches and cover the ground to the amount of more than a bushel to the square yard. This phenomenal growth indicates that the mussel must be fed from some great and constant source of food supply for, according to the well-known physical laws, neither matter nor energy can be created or destroyed. The source of the enormous amount of matter and energy represented in a 3-year-old mussel bed presents a most interesting problem upon which much light has been thrown but which, as stated above, has not been completely solved. To appreciate the principles it is necessary to compare the conditions of life as they are found on land and in the sea.

On the land the most conspicuous form of life is vegetation. Almost everywhere the land presents a vast expanse of verdure consisting of green plants of all sizes from the minute algæ to the giant trees. They represent a particularly important organization in that, as distinguished from animals, they have the power of uniting solar energy, water, the common salts of the earth, and gases of the air into the food principles which supply not only the needs of the plants themselves but provide also for the existence of all forms of animal life. The animals are, for the most part, herbivorous. Carnivora are necessarily few in number, for if it were not so they would soon destroy the Herbivora and thus bring about their own extinction. Green plants, therefore, furnish the ultimate source of food supply for terrestrial organisms.

In the ocean, life conditions are found to be quite different, although, as we shall see, the relations are the same in principle as for those on land. Vegetation, however, is as inconspicuous in the sea as it is conspicuous on the land. A fringe of seaweed may be found along the coast and some rather extensive masses of algæ, such as the Sargasso sea, may be found floating in the middle of the ocean; but taken as a whole the ocean is barren of visible vegetation. Under these conditions there can be very few or no animals that correspond to the terrestrial Herbivora. A few fishes may browse on the seaweeds which fringe the shore or float in the water, but they are not numerous. Most of the marine animals commonly seen are carnivorous and voracious beasts of prey. The larger species devour the smaller ones, and these in turn feed upon those smaller than themselves. Furthermore, animal life swarms in the sea in incredible multitudes. The naturalists of the *Challenger* expedition reported that the waters of the equatorial Pacific contained great banks of pelagic animals through which the vessel sailed. Chiercha wrote that the equatorial calms of the Atlantic are rich beyond all measure in animal life and that the water often looks and feels like coagulated jelly. The *Challenger* expedition reported having encountered banks of copepods a mile thick and on one occasion to have steamed for two days through a dense cloud formed of a single species, one found distributed from the Arctic regions to the Equator. Brooks (1893) states that he cruised for more than two weeks, from Cape Hatteras to the Bahama Islands, surrounded continually, night and day, by a vast army of dark-brown jelly fishes, *Linerges mercutia*, whose dark-brown color made them very conspicuous in the clear water. They were so abundant that nearly every bucketful of water dipped up contained some of them, and at noon, when the sun was overhead, they could be seen through a well in the middle of the vessel drifting by at all depths down to 50 or 60 feet, which was as far as sufficient light would penetrate to make them visible. The area explored covered more than 50,000 square miles, in which they were everywhere in equal abundance. Of the fishes Prof. Brooks says: "Herring swarm like locusts and a herring bank is almost a solid wall." Goode tells of a school of mackerel which was estimated to contain a million barrels and of another which was a windrow of fish half a mile wide and at least 20 miles long. In the bays and estuaries beds of sea mussels are often found covering hundreds of acres of bottom and containing 4,000 to 6,000 bushels to the acre.

How this vast multitude of animals can be supported in a region destitute of visible vegetation has been a problem of investigation since the microscope came into use, and it is interesting to note that the first contribution on the subject was written October 16, 1699, by the old pioneer, Antony van Leeuwenhoek, who ground lenses and made the microscopes with which he opened up a new field of investigation. After observing many of the minute organisms which were discovered in fresh water by means of his microscope, he came to the following conclusion:

> If it be then asked, to what end such exceedingly minute animalcules were created, no answer can readily be given which seems more agreeable to the truth than that, in like manner as we see constantly the bigger kinds of fish feed on the smaller; as, for example, the codfish preys on the haddock and other smaller kinds of fish; the haddock again on the whiting; these on still smaller fishes, and among the rest on shrimps; and shrimps on still more minute fishes; and that this gradually prevails among all the kinds of fish; so that, in a word, the smaller are created to be food for the larger. Again, if we consider the nature of our sea, abounding with fish, yet having nothing at the bottom of it save barren sand stored with various shellfish, yet destitute of every green herb; and if we, moreover, lay it down for a truth that no fish can be supported on water alone, there will not remain a doubt that the smaller fishes are destined by nature to be subsistence for the larger.

It is evident from Leeuwenhoek's illustrations that his use of the expression "smaller fishes" refers to what we now recognize, in general, as plankton, which includes both animal and vegetable organisms, particularly of the groups Protozoa and Protophyta.

Peck (1896), in his splendid paper on The Sources of Marine Food, gives us an excellent example of the food relations described by Leeuwenhoek. Reporting on the stomach contents of the squeteague, he says:

> On the morning of July 23 there was taken a large specimen whose stomach contained an adult herring. In the stomach of the herring were found two young scup (besides many small crustacea), and

in the stomach of one of these scup were found copepods, while in the alimentary tract of these last one could identify one or two of the diatoms and an infusorian test among the mass of triturated material which formed its food. This is an instance of the universal rule of this kind of food: The squeteague captures the butterfish or squid, which in turn have fed on young fish, which in their turn have fed upon the more minute crustacea, which finally utilize a microscopic food supply.

These microscopic organisms constitute an unfailing, ultimate food supply and, without it, the larger animals of the ocean, whose chief business is to devour each other, would soon exterminate themselves. It consists of single-celled plants and animals, chief among which are the diatoms and radiolarians. According to Peck these two groups alone may be regarded as the great primary food supply for the larger marine animals. The diatoms, in particular, may be said to constitute the pastures of the sea.

How these minute organisms can support such a large and extensive fauna may be readily understood when their habits are known. In the first place they exist in the ocean in countless myriads. Brandt (1902) describes a haul made in Kiel Bay with a net having a mouth area of 0.1 square meter which was lowered down to a depth of 20 meters and then hauled up. It was found to contain 3,173,000,000 diatoms, 500,000 peridinians, and 15,000 copepods. He estimated that this represented not more than one-third the total number of organisms in the column of water, owing to the escape of the smaller and more abundant species through the pores of the net and the fact that all the water entering the net did not pass out through the pores of the silk. According to his calculation the number of diatoms per liter would be about 6,000,000. Kiel Bay is particularly rich in plankton organisms, so these observations may be taken to represent a maximum value. For a minimum value we may take the observations of Lohman (1903), who examined the water of the Mediterranean Sea off Syracuse, which is poor in plankton. He found that 1 cubic meter of the water contained 2,082,740 Protophyta, 325,510 Protozoa, 17,415 Metazoa, 785,000,000 bacteria. Moore (1907) made careful measurements of the number of diatoms in the waters of Matagorda Bay, Tex., and found from 13,250 to 70,500 to the liter. The west Baltic was found by Hensen to contain about 457,000 diatoms per liter at the time of maximum abundance, and according to Johnstone (1908) the number of diatoms that inhabit the North Sea or the Baltic beneath every square meter of surface is between one and four millions. It is evident, therefore, that they represent the most abundant organisms in the sea, numbering anywhere from thousands to millions per liter of water. They occur in all parts of the world and are more abundant in the temperate than in the tropical seas. They appear in maximum numbers in the spring and fall of the year.

In structure a diatom is a minute, single-celled plant surrounded by a cell wall of cellulose and inclosed in a flinty case which is often most elaborately sculptured. Pelagic forms have thinner shells, and the characteristic ornamentations are less prominent. Some possess organs for suspension, such as buoying vesicles, enlarged flattened surfaces, projecting hairs, lamelliform outgrowths, or secretion of mucilaginous filaments. The outside case is always made up of two valves, one of which fits over the other like the cover of a pill box. The interior of the cell is filled with cytoplasm containing a nucleus usually located in the center. Colored bodies, called chromatophores, are present in the cytoplasmic contents, often as two large plates which lie parallel and extend nearly the whole length of the cell, or as numerous, small, oval bodies like those common in the higher plants. They contain chlorophyl, but the green color is disguised by the presence of a golden-brown pigment called diatomin. In addition to these structures, one or more conspicuous oil droplets are often visible within the cell.

The function of the chromatophores is a subject that deals with one of the most fundamental principles of marine food supply, for it is through these bodies that the plant is able, in the presence of sunlight, to convert inorganic materials into organic compounds which may be utilized as food.

The chemical elements required for the nourishment of the plant are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, calcium, silicon, iron, and chlorine. If all of these elements were present in the ocean in unlimited quantities there would be no limit to the quantity of plankton organisms that might be produced. The limited presence of a single one of these elements, however, is sufficient to limit plankton production. According to von Leibig's "Law of the Minimum," a plant requires a certain number of foodstuffs if it is to continue to live and grow, and each of these food substances must be present in a certain proportion. If one of them is absent the plant will die; and if it is present in minimal proportion the growth will also be minimal. This will be the case, no matter how abundant the other foodstuffs may be. With the exception of nitrogen, silicon, and phosphorus compounds, the foodstuffs necessary for the support of plants are exceedingly abundant in the sea. The quantity of marine plants, therefore, fluctuates in relation to the proportions of these rarer but indispensable foodstuffs. The water of the warmer seas is lower in its nitrogen content than that of the colder seas, and in accord with these conditions we find a much richer plankton population in the latter region. Brandt (1898) showed that the lakes which Apstein (1896) found richest in plankton also contained the greatest amount of inorganic nitrogen. In the Bay of Kiel, where silicic acid was proportionately the least abundant of the required foodstuffs, Raben (1905) found that the increase and decrease in the number of diatoms ran parallel with the amounts of silicic acid present.

The myriads of diatoms scattered throughout the sea represent so many chemical laboratories in which the solar energy is utilized to combine the air, water, and salts of the sea into the three food principles—proteins, fats, and carbohydrates—upon which all animals are dependent. This is one reason why they have been considered as important for the support of the animals of the sea as the grasses, vegetables, and fruits are for the terrestrial fauna.

Diatoms are peculiar in that many of them possess the power of movement. They may glide slowly over a solid substratum or over moist surfaces which serve as a fulcrum for movement. The direction of motion is usually along a more or less curved path and may be reversed. How the locomotor energy is developed was explained by Siebold in 1849, who demonstrated a streaming movement of external protoplasm which undergoes a periodic reversal of direction. This was shown by the fact that particles of sand or indigo adhering to the upper valve of a fixed diatom are moved alternately backward and forward from one pole to the other. It has more recently been shown by O. Müller that the protoplasm exudes through the polar furrow on each of the valves, streams along the crevice of the raphe to its termination at the median nodule, where each stream returns to the interior, and travels back internally. The result of the movement of these extracellular masses of protoplasm is to create friction against the surrounding media and cause a forward movement of the organism in the opposite direction. The extracellular layer of protoplasm is extremely thin, and if it moves at a rate of 3 mm. per minute it will produce a velocity of movement of about 1 mm. per minute.

Light has a slight effect on the response of diatoms. In general the chlorophyllous forms appear to be positively phototropic, while the colorless ones are negative. The orienting action, however, is feeble, and the oscillating forms follow irregular paths toward or away from the light. In the presence of light of moderate intensity negative forms creep into the mud.

The minimum temperature which diatoms can withstand varies considerably with the species. Some have been reported to withstand −200° C., but, in general, actively vegetating forms are killed by freezing at −8 to −10° C. In southern Newfoundland, where the Labrador current mingles with the warm water of the Gulf stream, a great mortality of a certain species, *Cosinodiscus radiatus*, has been taking place, for in this region enormous quantities of the dead shells are found covering the bottom.

Reproduction is by means of simple cell division or by the formation of what is called an auxospore. In the first case the nucleus and protoplasm divide into two parts, the valves separate, and a new valve develops within each of the old. The valves, once formed, are fixed in size which determines that each successive generation will become smaller. This constant decrease in size is compensated for by the formation of the auxospore. In doing this the diatom leaves its shell, swells up to the maximum size, and secretes a continuous membrane about itself. Within this there is first formed a single valve, like one of the original ones, and soon after a second one fitting into it. Sometimes the naked protoplast of two cells may escape and fuse together as one, in true sexual union. From the cell thus produced a diatom is either formed at once or after a preliminary division of the protoplast. The rate at which this process takes place varies with the conditions, but, on the whole, we know it must be exceedingly rapid in order to keep almost every part of the sea in the constant condition of a living broth. Being bathed in a uniform medium containing dissolved nourishment and subject to the full benefit of the sunlight without being exposed to extreme changes of temperature, growth and reproduction become so rapid that they pass beyond our powers of conception. As the late Prof. Brooks has written:

> Their vegetative power is wonderful past all expression. Among land plants, corn, which yields seed a hundredfold in a single season, is the emblem of fertility, but it can be shown that a single marine plant, very much smaller than a grain of mustard seed, would fill the whole ocean solid in less than a week if all its descendants were to live. This stupendous fact is almost incredible, but it is capable of rigorous demonstration, and it must be clearly grasped before we can understand the life of the ocean.

This wonderful productive power, together with their chemical composition, show that they occupy an exceedingly important place in the economy of nature. Brandt (1898) analyzed several samples of plankton. One, consisting chiefly of Chaetoceros, gave the following composition: Albumin, 10 to 11.5 per cent; fat, 2.5 per cent; carbohydrate, 21.5 per cent; and ash, 64.5 to 66.0 per cent (50 to 58.5 per cent SiO_2). Another sample, consisting of *Ceratium tripos*, had a very different composition, as follows: Albumin, 13 per cent; fat, 1.3 to 1.5 per cent; carbohydrate, 80.5 to 80.7 per cent; and ash, 5.0. As Brandt points out, these results compare very favorably with those of analyses of land crops.

PERCENTAGE COMPOSITION OF THE DRY SUBSTANCE OF LAND CROPS.

	Protein.	Fat.	Carbohydrate.	Ash.
Ordinary meadow hay	8.7	1.7	83.6	5.8
Good meadow hay	13.6	3.2	75.0	8.2
Rye (grain)	12.8	2.3	82.3	2.1
Peas	26.4	2.2	68.2	3.1
Potatoes	8.4	.8	87.2	3.6

Because of their silicious skeletons, the diatoms show a small proportion of protein with a high percentage of ash. Samples, however, containing many such Protozoa as Ceratium will have a composition similar to rye or good meadow hay. It is on this evidence that many persons have concluded that diatoms and, to some extent, such Protozoa as the peridineans, represent the ultimate source of marine food supply. As Moore (1910) has remarked, it is this invisible vegetation of our bays and estuaries which, useless to man in its original state, is annually converted into oyster flesh worth $18,000,000. In fact there is good evidence for believing that the total value of our entire fisheries products is derived, in large measure, from this source. So great is the economic value of this group of plants that it has been made a subject of important investigation by the Governments of many nations, including England, France, Germany, Denmark, and the United States.

The most recent advances in methods for determining quantitatively the available amount of these food organisms in the water, such as are utilized by the oyster, have been made by Moore (1910), who devised a bottle which has a capacity of a little more than a liter and can be filled in such a way as to "inclose a vertical column of the stratum lying between 2 inches and 12 inches above the bottom, and as the currents do not flow over the beds in horizontal strata, but roll over and over, the specimen is regarded as a fair sample of that in which the oysters are bathed." A liter of this sample is concentrated in 10 cc. of water by filtration through sand or precipitation in an Erlenmeyer flask after the addition of a little formalin. The filtrate is then agitated and a measured quantity transferred to a Rafter cell, where the organisms are listed and counted by species and a calculation made of the total number of each per liter. Careful measurements of the length, breadth, and thickness of each species are made based on Van Heurch's "c. d. m." (0.01 millimeter) as a unit of measurement, the unit of volume being the cube of this, "cu. c. d. m." (0.000,001 cubic millimeter). By this means a fairly accurate measurement of the actual bulk of the organisms present in a given volume of water can be made.

Using this method in connection with careful measurements of the stomach contents of oysters and the amount of water they are able to filter, Moore (1913) was forced to the surprising conclusion that "the volume of living food is insufficient to account for the actual growth of the oyster, making no allowance for the requirements of the other vital activities." Such investigators as Pütter, Petersen, Blegvad, and Jensen are of the same opinion and claim to have found other equally important sources of food supply for the marine fauna. Pütter (1907 and 1908) maintains that the sea is an immense reservoir of foodstuffs in the form of dissolved organic carbon and nitrogen compounds on which many marine animals actually feed as saprozoic creatures. His investigations on the metabolism of several marine animals showed that it would be impossible for the plankton organisms that could be consumed to provide the required amount of carbon or nitrogen. He found surprisingly large amounts of organic matter dissolved in the sea water. His results have been checked up by Raben (1915), who found an average of 12.25 mg. of organic combined carbon per liter in the Bay of Kiel, while in water from the Baltic it amounted to 3 mg. per liter. Compared with the amount of organic substance present in the form of living organisms, these results are very high. The total amount of the organic combined carbon in the plankton at Laboe in Kiel Bay was found by Lohman (1908) to vary between 12.7 and 189.8 mg. per 1,000 l. of sea water. As an estimate of the maximum amount of organic matter in the form of plankton that may be found in the ocean, we may refer to the phenomenal haul made in the Bay of Kiel referred to by Brandt (1898), which contained 0.19 mg. of protein, 0.05 mg. of fat, 0.43 mg. of carbohydrate, or a total of 0.67 mg. per liter. Raben (1905), who analyzed water from the same vicinity, found the mean value of organic combined carbon in dissolved form to be 12,250 mg. per 1,000 l., or about 60 times as much as that ordinarily present in the form of plankton organisms and nearly 20 times as much as that present in the plankton when at its maximum. Pütter's view is that the plankton organisms are only of secondary importance in the nutrition of marine animals, just as insects are to insectivorous plants which depend primarily on the photosynthesis of starch to supply their needs. The facts presented by Pütter present some ground for his hypothesis, but the actual utilization of these dissolved organic compounds as food by marine animals remains undemonstrated.

Another great source of marine food supply has been suggested by Petersen (1890), who expressed the idea that the abundance of fish on the Danish coasts was due chiefly to Zostera, which is better known to fishermen as eelgrass. Petersen and Jensen (1911) tried to show that, in all probability, the plants of the eelgrass belt and not the plankton organisms should be regarded as the main sources of the organic matter of the sea bottom in Danish waters. Their reasoning is based on the fact that the quantity of carbon in a series of bottom samples is directly proportional to the amount of Zostera vegetation and not to the quantity of plankton present.

The study was continued in greater detail and published by Jensen in 1914. He showed that the eelgrass plays an important part in the production of organic matter in the sea. In all the Danish waters he found fragments of eelgrass deposited in greater or less quantities, for the most part in very fine particles as detritus. In this detritus he found comparatively few diatom shells. Much of the detritus particles were too small to be identified by the microscope as of eelgrass or plankton origin. By chemical means, however, Jensen was able to determine the source of the organic matter in the sea bottom. He found that the eelgrass cells contain a considerable quantity of starchlike substances known to the chemists as pentosans, whereas those of diatoms are composed mainly of silica and those of peridineans of fairly pure cellulose. By comparing analyses of various bottom samples of organic matter with those of eelgrass and diatoms the following conclusions were reached:

(1) In the more sheltered waters the organic matter of the sea bottom is to a preeminent degree formed by eelgrass. (2) In the more open waters, at least half of the organic matter is probably formed by eelgrass. (3) In the deepest waters the organic matter is probably formed chiefly by the plankton organisms.

Calculations on the production of phytoplankton and eelgrass per square meter of surface have been attempted, but what has been done so far approaches a mere approximation only. In regard to the phytoplankton, Hensen (1887) figured that 1 square meter of surface produces annually 15 to 18 grams of dry organic matter exclusive of the phytoplankton consumed by the surface fauna. The total annual production of phytoplankton he estimated to be 150 grams per 1 square meter. Jensen, by very careful calculations, estimated that in the Danish waters about 100 grams of organic matter per square meter are produced each year by the phytoplankton. For eelgrass the percentage of dry organic matter produced annually per square meter he found to be 1,920, 1,120, and 344 grams in good, moderate, and bad localities, respectively. Eelgrass beds cover about one-seventh of the area studied (between the Skaw at the most northern tip of Denmark and the Baltic Sea), which means that the annual production of eelgrass per square meter of the water as a whole is 120 grams of organic matter. Comparing the production of eelgrass and plankton on a basis of Jensen's calculations we see that eelgrass produces 120 grams of organic matter per square meter, while the plankton produces 100 grams.

Now the question arises, How much of the organic matter from each source is deposited on the sea bottom? Undoubtedly much of the matter of the plankton dissolves following the death of the organisms due to the action of bacteria. Admitting that a portion of the eelgrass material is similarly lost, it is evident that the plankton organisms, with their relatively far greater surface, are in a much higher degree liable to destruction than the eelgrass. Furthermore, a large part of the plankton is devoured by the plankton fauna, which would lead one to believe that but a limited portion of plankton production is deposited on the sea bottom. These calculations are supported by the results of chemical analyses of the organic matter in the sea bottom. Jensen has done this and states his conclusions as follows:

> In the more sheltered waters the organic matter of the sea bottom is derived almost exclusively from the Zostera (eelgrass); in the more open waters it is possible that the plankton organisms may play a not altogether important part as a source of the organic matter of the bottom.

The transformation of nitrogen during the decomposition of eelgrass and its relation to the nitrogen content of the organic matter in the sea bottom was also investigated by Jensen. He found that the green eelgrass is as rich in nitrogen as peas or beans, which contain about 3 per cent. As the eelgrass decomposes the percentage of nitrogen decreases until it is as low as 0.88 per cent, then as decomposition continues it rises again up to 1.39 per cent. Analyses of the organic matter in the sea bottom indicate that the average amount of nitrogen present is 4 per cent. Thus it is evident that the organic substances of the sea bottom contain a greater proportion of nitrogen than the eelgrass.

Why the organic matter in the sea bottom is so much richer in nitrogen than the eelgrass, from which it is formed chiefly, is readily explained by Jensen. As has been shown the amount of nitrogen in the green eelgrass is greater than that in the early stages of decomposition. Later the amount of nitrogen increases, becoming much greater than in the green eelgrass. The diminution in nitrogen during the first stages may be due to the fact that a portion of the nitrogenous protoplasm is dissolved in the sea water as the cells die. The increase in proportion of nitrogen in the final stages of decomposition may be due to two causes—(1) either by the destruction of nonnitrogenous substances in the sea bottom to a greater extent than is the case with the nitrogenous matter or (2) by the fixation of inorganic or free nitrogen by bacteria.

It has been established beyond all doubt that nonnitrogenous substances of the sea floor are to a very considerable extent destroyed by bacteria, at least one step in the process being the fermentation of the pentoses. Another is the formation of methane from the fermentation of cellulose. On the other hand, it is probable that the nitrogenous substances are acted upon to a lesser degree, due to the fact that they are comparatively easily transformed into humic compounds, which are less easily destroyed.

It is also possible that the excremental action of the fauna contributes to render the bottom richer in nitrogen. The nitrogenous portion of the bottom is indigestible, while the nonnitrogenous matter contains considerable quantities of digestible pentosans. Hence, when fed upon in the form of detritus by such organisms as mussels and oysters, the nonnitrogenous matter would be removed and the nitrogenous portion returned to the bottom. This was well illustrated by comparing the composition of oyster excrement, which consisted of almost pure detritus, with bottom samples taken at the same place where the oysters were found. The nitrogen of the bottom samples amounted to 0.187 per cent, while that of the excrements was 0.71 per cent.

That nitrogenous matter of the bottom can also be increased by the fixation of inorganic nitrogen through the action of bacteria is likewise probable. The nitrogen may be taken from the ammonia or nitrates dissolved in the water or from the free nitrogen, which is also present in solution. Bacteria such as Azotobacter and Clostridium, which perform this function, are of common occurrence on the bottom, and a considerable amount of nitrogen fixation has been shown to take place where the vegetation is abundant.

In addition to the above sources of nitrogen, it should be mentioned that the fauna itself, by dying and forming detritus, also serves to increase the amount of nitrogen in the sea floor.

A determination of the total quantity of detritus and plankton in sea water was also attempted. Ten-liter samples of sea water from various localities were carefully filtered and the total quantity of detritus and plankton measured. It was first weighed and dried at 100° C. and then weighed again. Samples were also subjected to microscopical examination to determine the amounts of detritus and plankton organisms present. The results were that nearly all the samples showed a greater proportion of detritus than plankton. The weight of the dry matter in the residue varied between 9.6 and 72.3 mg. per 10 l. of sea water. No relation could be shown to exist between the weather conditions and the amount of detritus in the water. The conclusion to be drawn from these results is that sea water is rich in the quantity of detritus it contains.

The next question which arises is, What value does this organic matter of the sea bottom possess as a source of nourishment for the benthos or bottom fauna?

Having assumed that the organic matter of the sea bottom forms a source of nourishment for the majority of the fauna living in and near the bottom, Jensen considered it advisable to investigate the question as to how far suitable nourishment for such fauna can be shown to exist among the substances of which the sea floor is composed. Since eelgrass contributes most of the organic matter of the bottom, it was natural to examine quite closely the chemical composition of this weed. It was found to compare favorably with the composition of the common fodder grasses. Proteinw as found present to the amount of 7.5 per cent and pentosan to the amount of 8 to 9 per cent. No fat determination was made. When eelgrass is treated with pancreatin, from 23 to 26 per cent of the nitrogen is digested. Since the eelgrass contains 7.5 per cent proteins, of which about one-fourth is digestible by pancreatin, the amount of digestible proteins contained may be put at 1.08 per cent. Decomposed eelgrass contains less nitrogen and is less digestible. For example, black eelgrass (dead) was found to contain 1.39 per cent nitrogen, of which but 6.6 per cent was digestible. These figures should, however, in all probability mainly be taken as minimal.

Experiments on the digestible nitrogenous compounds in the sea bottom brought out the fact that there is only a very small amount of proteins in the bottom which is digestible with pancreatin. In fact, the amount is so small as to be very nearly within the limits of possible error. The analyses for the top layer, however, give such positive results that it is justifiable to conclude that the uppermost layer of the bottom really does contain a certain amount of proteins digestible by pancreatin. In the upper layer from 44 to 68 mg. of digestible proteins per 100 square cm. are found, which means that the amount of digestible proteins per square meter is approximately 5 g.

On the other hand, digestible nonnitrogenous compounds in the sea bottom consist of a fairly considerable amount of material in the form of pentosans, amounting to from 0.3 to 1.0 per cent. This is an important fact, for there is reason to suppose that the bottom fauna is able to digest pentosan. It has been well established that herbivorous animals utilize pentosan as a food, and Biederman and Moritz (1899) showed that gastropods were able to digest pentosan. It is probable, therefore, that bivalves also can digest pentosan and that the considerable amount of pentosan present in the sea bottom besides other possible substances (hemicellulose generally) plays an important part as nonnitrogenous nourishment for a great portion of the bottom fauna.

In support of Jensen's observations, Blegvad (1914) has made an interesting study of the food of the commonest and most widely distributed bottom-inhabiting animals in the various communities of the Danish waters. His report is based on the analysis of stomach contents. Three main sources of nourishment for the bottom fauna of the sea were determined: (1) Plants—fresh growing plants of the benthos formation, chiefly eelgrass which in the Danish waters produces about 8,232,000 kilograms annually. In course of time, this decays and falls to pieces, forming (2) detritus. This includes dead or dying organisms or portions of them, whether vegetable or animal in origin, as are found in suspension (or solution in the sea water) or deposited upon the bottom. Most of this detritus is of eelgrass origin. (3) Animal or carneous food, or the third source, includes all living animals found in the sea, together with their carrion, save where these are to be reckoned as forming part of the detritus as just defined.

The plankton, heretofore considered as of greatest significance, he does not list as an important source of food. Whereas previous observers have emphasized the great importance of plankton, Blegvad emphasizes the importance of detritus. He furthermore questions Pütter's (1908) theory to the effect that the carbon compounds present in solution in the sea water are of very extensive importance as food for certain animals of the bottom fauna. At least it must for the present be regarded as unproved. It is possible, however, that some organisms may live on dissolved organic matter, and so for the sake of convenience Blegvad classifies dissolved organic matter under detritus.

The commonest animal forms in Danish waters are classified into three groups according to their mode of feeding: (1) Herbivores, which include certain gastropods, two echinoderms and some Crustacea. (2) Pure detritus eaters, which comprise all the Lamellibranchia, Holothurians, Sipunculidæ, Cumacea, Diptera larvæ and Ascidiæ, two gastropods, Balanoglossus, Amphioxus, ostracods, Bryozoa, Porifera, and Foraminifera. The great mass of material in the alimentary tracts of these animals is detritus and when analyzed chemically it corresponds to that on the ocean floor. Plankton organisms are only incidentally present. These observations led Blegvad to make the extreme statement: "The living phytoplankton is thus of no importance at all as a food for the bottom fauna." (3) Purely carnivorous animals, including a few Polychæta, some gastropods, some Crustacea, some echinoderms, coelenterates, nemerteans, planarians, and pantopods, constitute the last group. Quite a large number of animals are both carnivores and detritus feeders.

The Danish investigations tend to show the vast importance of detritus as a food for the fauna on the sea bottom. To use Blegvad's words:

> Detritus forms the principal food of nearly all the invertebrate animals of the sea bottom, next in order of importance being plant food from fresh benthos plants. The value of the live phytoplankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton copepods.

This view is given some support by the recent researches of Mitchell (1917), who presents evidence that oysters can utilize fragments of seaweed (*Ulva lactuca*) as food.

That detritus is formed so abundantly in the shallower waters of the ocean and constitutes such an important source of food supply for most of the bottom-inhabiting animals is of great significance in its bearing on the coming science of sea farming. If the investigators of the Danish biological station are right in their conclusions concerning the importance of detritus as food for the benthos fauna, then we shall have to revise our methods of determining the available oyster, mussel, or clam food supply in the waters of a given locality. It also means that the available fields for the cultivation of oysters or other shellfish may be more fertile than we have ever dreamed in the past. The knowledge of the rôle played by detritus in its relation to the benthos fauna helps us to understand better the phenomenal growth which often takes place in many mollusks. For example, many mussel beds are known to yield on an average 2,000 bushels per acre annually, and experiments have shown that 1 bushel of seed clams planted in a barren flat will yield 10 bushels of marketable clams one year later. This serves to show what splendid opportunities for increased food production lie within our reach. Between the plankton organisms and the detritus there is an inexhaustible ultimate food supply which can be quickly and readily converted into a form available for human consumption. A partial solution of the serious problem of increasing the food production of the Nation lies in the appropriation of this vast resource for conversion into mussels, clams, and oysters. Mussels planted in protected situations, where the water currents will bring them an abundance of these materials, will produce flesh food at a rate far in excess of any resource on which we have depended in the past. Cultivating the ocean promises to yield the fisherman far greater returns, with less expense of time and energy, than the farmer is able to derive from the land. Each new discovery in marine biology is making it more clear that for the comfort and economy of the Nation we ought to be doing more in the scientific development of our fisheries.

ENEMIES AND PARASITES.

The sea mussel, as are all the smaller marine species of animals, is preyed upon by a host of enemies. The destructive forces with which it has to compete are so numerous it seems almost incredible that the species can maintain itself so successfully. From the moment the egg is laid to the end of its life, dangers of various sorts threaten it constantly from every side. Inanimate as well as animate forces unite in working toward the destruction of this mollusk. The animate forces which act against the life and welfare of the mussel may be divided into the active enemies, which include the predacious animals, and the passive, which comprise a number of sedentary organisms that intercept the food supply or cause depositions of silt which interfere with the digestive processes or smother the mollusk.

The following account does not by any means include all the enemies of the sea mussel. It serves merely to show some of the tremendous forces with which the species has to contend in order to maintain itself.

INANIMATE DESTRUCTIVE FORCES.

A slight change of current may cause a deposition of sand over the beds which may be acres in extent and smother the mussels out of existence. Some years ago such a wholesale extinction by this agency took place in Menemsha Pond, Marthas Vineyard, Mass. The bed, a photograph of which was published in a previous paper of the author (Field, 1911), was in perfect condition in August, 1911, but when visited in July, 1912, nothing but a barren flat of white sand was visible at low tide. Investigation revealed the presence of the decaying shellfish about 4 inches below the surface. Exposure at low tide to the frost of winter proves fatal to enormous numbers. The young larval mussels succumb to sudden falls of temperature and are often swept up on the shore by winds, waves, and tidal currents to perish by the millions.

ACTIVE ENEMIES.

STARFISH.

The starfish *Asterias forbesii* and *A. vulgaris*, are the arch enemies of the sea mussel. The former species ranges from Massachusetts Bay southward to the Gulf of Mexico and is abundant south of Cape Cod. *A. vulgaris* ranges from North Carolina to Labrador, but is abundant only north of Cape Cod. The starfish feed upon almost any kind of mollusk, but the sea mussel constitutes their favorite food. The method of feeding is to seize the shellfish in such a position that the mouth of the starfish comes to lie opposite the opening of the shell (fig. 203, opp. p. 216). Then by attaching its numerous tube feet to the opposite valves it sets up a constant pull, which in the case of a large starfish has been shown by Schiemenz (1896) to equal more than 2½ pounds. The starfish can rest by shifting its work from one set of muscles to another, while the mussel, relying only on its single set of adductors, becomes exhausted and succumbs to the weaker but tireless pull of the enemy. When the valves open, the starfish turns its stomach inside out and envelops it about the soft parts of the prey and digests them outside its own body. This accomplished the starfish withdraws its stomach and moves on in search of another victim. Young starfish, especially, have voracious appetites; specimens less than a quarter of an inch in diameter were observed stripping the young mussels, little less than their own size, from wharf piles. Every starfish picked up was found in the act of eating a Mytilus. The larger starfish move back and forth across the mussel beds in regular armies, up and down the wharf piles and rocks where the mollusks grow, feeding on them at a rate which it is difficult to estimate.

The mussel, which heretofore has not been of sufficient commercial value to be cultivated, has escaped the attention of the fisherman who would be the most capable of estimating the depredations of its enemies. For the oyster, however, whose every enemy is watched by the jealous cultivator, we have been able to learn more of the devastating habits of the starfish. In Connecticut waters alone it was estimated in 1888 that this echinoderm destroyed $631,500 worth of oysters after not less than 42,000 bushels of the starfish had been removed from the beds. If mussels are a more favorite food of the starfish, what must be the destruction wrought on the unprotected beds of this shellfish? The answer must be up in the hundreds of thousands of bushels. Mead (1903) states that some mussel beds which had recently disappeared were probably destroyed by starfish. Lebour (1907) states that a whole bed of mussels at the mouth of the river Tyne, England, completely disappeared owing to the ravages of this animal.

DRILLS.

The oyster drill, *Urosalpinx cinerea*, is a small snail commonly found on mussel and oyster beds where it plays havoc with these bivalves, doing damage which undoubtedly amounts to thousands of dollars yearly. So great has been its injury to the oyster beds that the United States Bureau of Fisheries has recently started a special investigation to determine the possibility of protecting the oyster beds from its depredations. T. E. B. Pope, who has been carrying on these investigations for the Bureau, finds that the drills are abundant on the oyster beds where the salinity is above 1.010, and that a single female is capable of producing about 100 young each season. Its method of attack is like that of the winkles, Lunatia and Neverita. With a powerful radula it is capable of drilling holes through shells of almost any thickness, but it prefers to prey upon thin-shelled forms, such as mussels and young oysters. The time required to perforate shells was found by Mr. Pope to be for oysters about 1½ inches long, two days; 2½ inches long, 4 days; 3½ inches long, 6 days; 4 inches and over, 7 days. The perforation is made at no particular point on the shell, but is generally somewhere near the middle of the valve. When completed the proboscis is thrust through the opening to the soft parts on which the snail feeds. One drill was seen to kill five young oysters in succession without taking any rest between its attacks. The author's experiments with drills kept with mussels in a trough of running sea water demonstrated that the time required for the snail to perforate the shell of a mussel less than an inch long was about 18 hours, while for large ones the time varied from 24 to 36 hours. Figure 201 (opp. p. 216) shows a drill and a shell which was perforated by it.

The dog-whelk, *Purpura lapillus*, is another species of drill similar in appearance to Urosalpinx, but somewhat larger and more powerful. Its favorite food is the sea mussel, which it attacks even more voraciously than does the oyster drill. It does not cover such a wide area as the latter species, being confined to the rocky shallow waters; consequently it is limited to doing much less harm than the oyster drill, which ranges over

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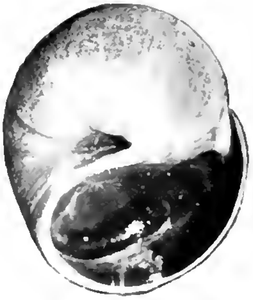

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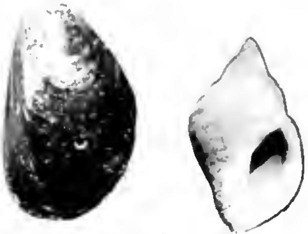

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Fig. 198.—The winkle, *Neverita duplicata.*

Fig. 199.—Valve of a sea mussel which has been perforated by one of the winkles, *Neverita duplicata* or *Lunatia heros.*

Fig. 200.—The winkle, *Lunatia heros.*

Fig. 201.—The oyster drill, *Urosalpinx cinerea*, and a mussel shell it had perforated.

Fig. 202.—The dog whelk, *Purpura lapillus*, and a mussel shell it had perforated.

Fig. 203.—The starfish, *Asterias forbesii*, attacking a mussel

Fig. 204.—The conch, *Busycon carica.*

Fig. 205.—The conch, *Busycon canaliculata*, feeding on a mussel.

both rocky and sandy bottoms. The dog-whelk drills a hole from one and one-half times to twice the diameter of that made by Urosalpinx and makes it in any part of the shell, even through the umbo (fig. 202, opp. p. 216). The time required to make the perforation varies from one to two days, according to the age of the mussel. On the rocky shore off Sandwich, Mass., near the opening of the Cape Cod Canal, the author found the Purpuras in great abundance on the scattered mussel beds, where the perforated shells of the latter mollusk could be picked up by the handful. It was amazing to see the destructive work that was being carried on by hundreds of these snails which could be seen adhering to mussels here and there busily engaged at their deadly work. They preferred the young shellfish which were about half an inch long. In one case two snails were found clinging to the opposite sides of a young mussel. Further examination revealed that both animals had perforated the shell at the same time and were competing for the maximum share of the prize within. They eat the softer parts of the body first, leaving the edges of the mantle and adductor muscles to the last.

The snails, *Lunatia heros* and *Neverita duplicata*, sometimes called winkles, are common all along our eastern coast as far south as Cape Hatteras and constitute an important enemy of the mussel. The two species are much alike in habit and appearance and may be easily confused. They are most readily distinguished by the thick, dark lobe, which nearly covers the wide umbilicus, which is characteristic of the space ventral to the opening of the shell of *Neverita duplicata* (fig. 198), but absent from that of *Lunatia heros* (fig. 200). The latter species seems to frequent deeper waters than does the former. They attack mussels and other mollusks with their rasping tongues, which bear chitinlike teeth, and bore holes 3 to 6 mm. in diameter through the side of the shell (fig. 199). The proboscis is then inserted through the opening and the contents devoured. Quantities of mussel shells perforated by these predacious mollusks have been dredged up by the steamer *Fish Hawk* in Vineyard Sound, which demonstrate their destructive powers.

The best measure of the devastation worked by *Neverita duplicata* on shellfish was made by Mead and Barnes (1903). Their experiment was to invert an ordinary orange box, which has two compartments, over a clam bed and sink it into the soil after clearing away the surface débris. A single Neverita was placed in each compartment. A fortnight later the contents of the box was examined. In one compartment neither snail nor any perforated shells were found, while in the other the single Neverita was found 5 inches below the surface of the ground with the perforated shells of eight clams as witnesses of its voracity. This would indicate that the normal appetite of these snails is satisfied with a clam or mussel once every two or three days. Snails which the author kept in captivity with mussels during July and August refused to eat at any time during that period.

OTHER GASTROPODS.

The conchs or winkles, *Busycon carica* (fig. 204, opp. p. 216) and *B. canaliculata*, are supposed to be greater enemies of mussels, oysters, and clams than they really are. Ingersoll (1887) states that these snails seize oysters with the concave under surface of the foot and by muscular action crush the shell into fragments, then feed upon the flesh thus exposed. He gave the estimate of one planter who believed that one winkle was able to destroy a bushel of oysters in a single hour. Colton (1908), who carried on a long series of experiments on the feeding habits of these creatures, came to a very different conclusion. He found that they spend about 65 per cent of the time buried in the sand. They may eat two oysters a day on two successive days, but this is invariably followed by a long period of several days to months during which the animal remains buried in the sand. The method of attack is to crawl on top of an oyster, mussel, or clam and wait for the victim to open its valves; then, rotating its shell on the axis of the columella to the proper position, to thrust its own shell between the valves of the prey, introduce its proboscis, and with its radula tear out the flesh of the victim.

These observations are in harmony with those of the author who, during the summer of 1917, kept an individual of each of the two species of Busycon in an aquarium with several mussels. During a period of six weeks five mussels only were eaten, three of them being consumed during the night. The method of attack, as observed, was somewhat different from that described by Colton (1908), but the principle was the same. On one occasion the author saw one of the conchs creep up to a mussel which was lying on its side with the valves open. Moving very slowly it thrust the edge of its foot between the valves and then inserted the edge of its shell in such a manner as to pry the valves open so that the proboscis could be inserted. After feeding on its victim for a few minutes the snail turned the mussel over onto its back and forced the prolonged portion of its shell between the two valves, in which position it held the bivalve until every particle of the flesh was eaten (fig. 205).

Ilyanassa obsoleta is a gastropod often found on the mussel beds, especially where they are located on protected muddy flats. The author has never seen anything to indicate that it is an enemy of the mussel, but the observations of Belding (1910) suggest that it belongs to the class of predatory mollusks. He observed that these snails are active enemies of the scallop, forcing themselves in between the open valves of the unwary shellfish to form a wedge while other members of their species creep in and feed on the victim. If this is true for the scallop, it undoubtedly holds for the mussel also.

FISHES.

Fishes of various species depend upon the mussels for their food supply. Killifish, cunners, scup, and tautog greedily strip them from wharf piles, seaweed, and from the beds. The squeteague, flounders, and cod also eat them in great quantities. Vidal (1871) states that young eels are very destructive enemies. He says they dart in between the open valves into the mantle cavity, where they gnaw the muscles free from the shell, so that the valves can not remain closed, and then devour all the soft parts of the shellfish. The fact that mussels constitute the best bait known next to squid indicates how they rank as a food for fish.

BIRDS.

Birds, such as herring gulls, night herons, crows, and ducks, find this mollusk a desirable morsel. At Menemsha Pond, Marthas Vineyard, Mass., the author has seen herring gulls, *Larus argentatus*, apparently eating mussels. They would seize the shellfish, which were about 2½ inches in length, in their bills and shake them to break their byssal threads which bind them together. When frightened the gulls would seize a string of the mussels and fly off with them, but they never succeeded in carrying their burden more than a hundred yards without dropping it. The gulls would then return and make other attempts to carry them off. Laughing gulls, *Larus atricilla*, which were also present on the beds, were never seen to pick up mussels, but it may be that they were feeding on the very young ones, which at the time of the observations were from 5 to 8 mm. in length. The author was not able to kill any of the birds to examine their crops for shellfish, but judging from their behavior it is reasonable to assume that they were feeding upon mussels. Black ducks, *Anas obscura*, were several times seen on the Menemsha mussel beds feeding over places where the young shellfish were particularly abundant. L. L. Dyche (*in* Field, 1910a, p. 165), at the New York meeting of the American Fisheries Society in 1910, said:

> The eider ducks eat the small ones, about an inch in length, and you will find the ducks oftentimes full of these mussels clear to the throat; I do not believe I would be exaggerating if I should say there was a pint in each.

MAMMALS.

Mammals of various sorts depend upon the mussels as a source of food. The common gray rat, *Mus decumanus*, and the muskrat, *Fiber zibethicus*, often eat them. Ingersoll (1887) states that seals, especially young ones, feed largely upon the Arctic mussel, but that the mammal which preys most extensively upon them is the walrus. According to Mr. Dyche:

> They constitute the sole food of the walrus. The walrus crushes and spits out the shell and swallows the mussel. I have killed from 24 to 30 walruses and have found in the stomach on occasions a ball containing two quarts of pieces of shell and other material from sea mussels. Seals eat squid and small fish, but the only thing that the walrus feeds on in the north is the sea mussel.

PASSIVE ENEMIES.

The passive enemies include a large number of plant and animal forms which do not attack the mussel directly but by their habits intercept the currents, causing deposition of silt, which interferes with the nutrition of the mollusk; or they may so envelop the shellfish as to cut off their food supply and even suffocate them; or they may come into direct competition for the food substances in the water.

EELGRASS.

Eelgrass, *Zostera marina*, is one of the most destructive weeds which grows in profusion on the sheltered beds. It not only intercepts the currents which bear the food supply of the mollusk but causes very often such a heavy deposition of silt that the mussels are smothered or even completely buried beneath it. Their decomposing bodies then form the richest kind of fertilizer on which the eelgrass thrives.

ALGÆ.

Algæ of various species are oftentimes present in great abundance on the beds or on the mussels which encrust wharf piles, buoys, etc. The most common species found associated with the mussels are *Fucus vesiculosus*, *Laminaria saccharina*, *Chorda filum*, *Champia parula*, *Enteromorpha erecta*, *Rhabdomia tenera*, and *Ulva lactuca*.

INVERTEBRATES.

Invertebrates in great variety and abundance swarm over and in the mussel beds. The ascidians, Molgula, Cynthia, and Amorecium; numerous Bryozoa; sea anemones, *Metridium marginatum* and *Sagartia luciæ;* hydroids, Eudendrium and Tubularia; and sponges grow on the mussels themselves, especially where they are attached to wharf piles (fig. 99, opp. p. 127; fig. 206, opp. p. 220). On the beds other species find it advantageous to take up a similar position on the mussels. In some localities, as at Sandwich, Mass., barnacles, *Balanus* sp?, cover the beds so completely as to hide the shellfish. Lamp shells, *Anomia glabra*, and boat shells, *Crepidula fornicata*, also have the habit of attaching themselves to the mussels and competing with them for their food supply. The same is true of the little sea anemone, *Sagartia luciæ*, which is very abundant on the Menemsha mussel beds. Worms of various sorts, Nereis, Lepidonotus, and others, burrow beneath and between the mollusks, and on their shells *Hydroides dianthus* often secretes its limy tubes.

The ribbed mussel, *Modiolus demissus* (*Modiola plicatula*), common clam, *Mya arenaria*, hard-shell clam, *Venus mercenaria*, oyster, *Ostrea virginiana*, and the scallop, *Pecten irradians*, are often associated with the mussel, and the periwinkle, *Littorina littorea*, is nearly always present on the exposed beds in great numbers, especially if eelgrass or algæ is present in abundance. Crabs, Carcinus, Cancer, Libinia, and Panopeus, hermit crabs, *Eupagurus longicarpus*, and the king crab, *Limulus polyphemus*, run about over the beds in the shallow, protected estuaries, while in the mantle cavity of the mussel a little crab, *Pinnotheres maculatum*, finds its abode. Some authorities say the relation between the two species is symbiotic, while others claim it is parasitic, the crab occupying this position to collect the food particles swept in by the ciliary currents of the mollusk.

PARASITES.

Polydora ciliata.

Parasites in the mussel are apparently few in number, only one having been described previously by Lebour (1907), who found a boring annelid, *Polydora ciliata*, which burrows through the shell, making a hole about the size of a pin. It causes pearly excrescences to grow over the internal surface of the shell which prevents muscular development and oftentimes almost destroys the posterior adductor muscle. It furthermore often interferes with the production of the genital products wherever the calcareous ridges press against the mantle. This results in giving the shellfish an unsightly appearance, which renders it unfit for market.

Haplosporidium mytilovum, n. sp.

A new species of sporozoan parasite was recently discovered while the author was studying the maturation of the Mytilus egg. This protozoan occurs in the egg, and its presence there gives rise to a phenomenon suggesting the formation of a chromatin vesicle which for a long time the author took to be a normal process in the development of the egg. The peculiar condition was observed by several prominent zoologists who offered different explanations for its presence. It was finally identified for the author through the kindness of Dr. Gary N. Calkins, of Columbia University, as a probably new species of the genus Haplosporidium. In its vegetative state it is amœboid in

FIG. 2[illegible].—A group of living mussels whose shells are encrusted with Bryozoa, barnacles, sea anemones, and serpulids

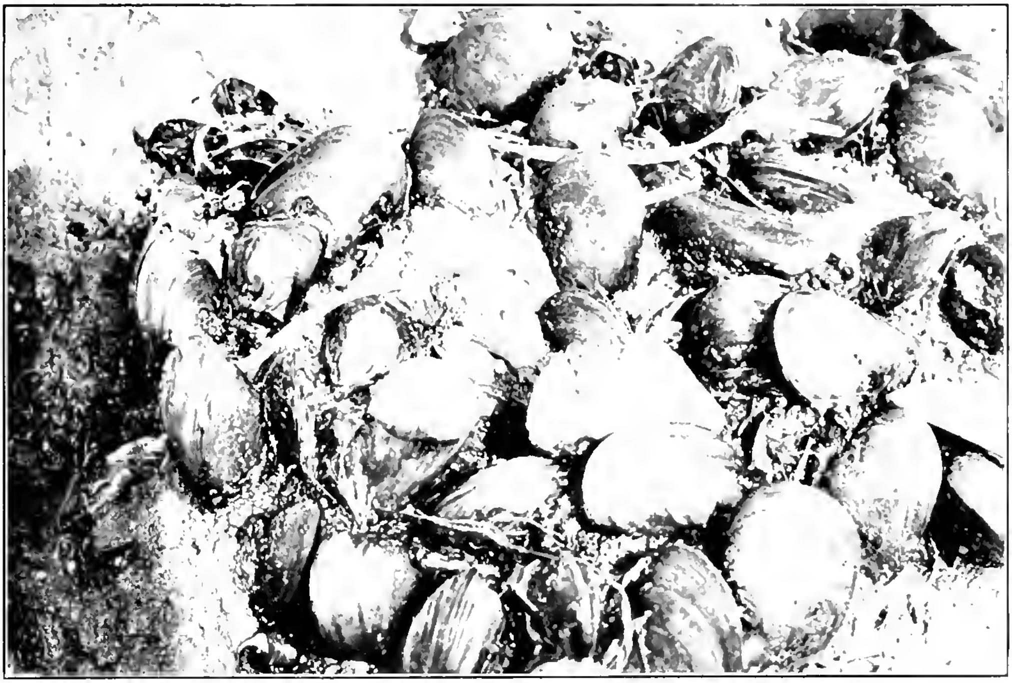
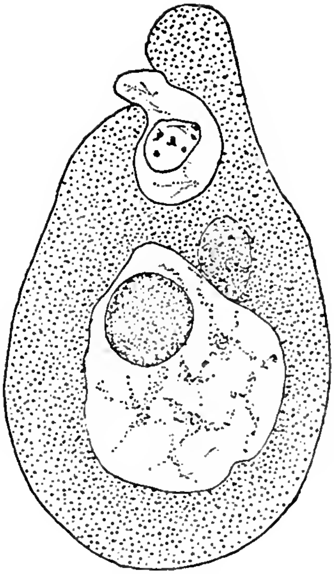


FIG. 2[illegible].—Vertical view of mussels on a natural bed, showing the characteristic position they assume with the anterior end buried in the sand and the posterior or syphon end projecting well above the level of the bottom.



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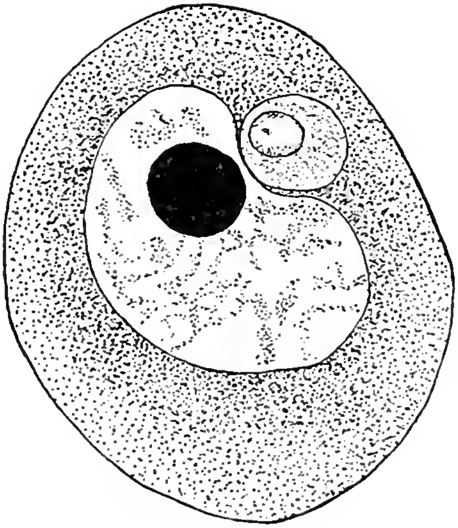

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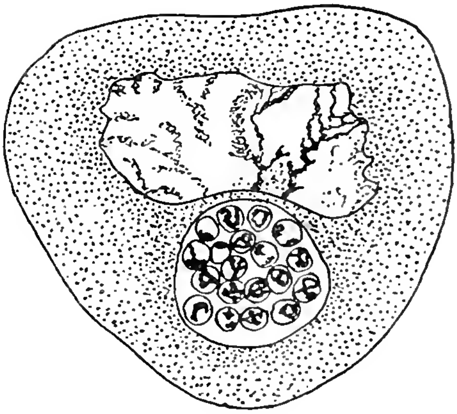

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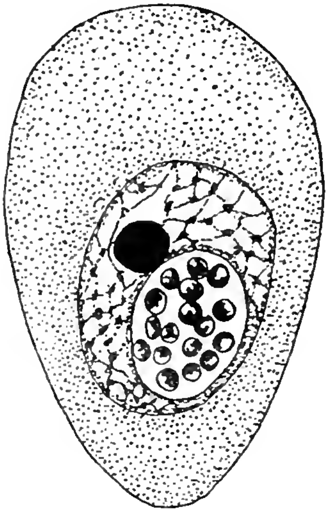

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FIG. 208.—A sporozoan parasite, *Haplosporidium mytilovum*, new species, in its vegetative stage, shown penetrating the wall of a mussel egg.

FIG. 209.—*Haplosporidium mytilovum* encysted in the cytoplasm of a mussel egg where it is undergoing a period of growth.

FIG. 210.—A later stage than fig. 209, showing multiplication of nuclei within the cyst. The cyst is in the cytoplasm just below the egg nucleus.

FIG. 211.—A group of spores of *Haplosporidium mytilovum* encysted within the nucleus of a mussel egg.

All figures are fixed in Gilson fluid and stained with Heidenhain: iron hæmatoxylin. × 1500.

character and creeps about in the follicles and genital canals of the female mussel. It is able to penetrate the egg membrane (fig. 208) and sometimes even penetrates into the very nucleus (fig. 211). Inside the egg it begins to grow in volume and the nucleus divides into two, then four, etc., until a large number of nuclei are formed. The resulting plasmodial mass forms a cyst (fig. 209), and the contained nuclei become simple, uninucleate spores without undergoing any internal differentiation (figs. 210, 211). This characteristic clearly places this protozoan in the genus Haplosporidium, which was founded by Caullery and Mesnil (1899) under the name of Aplosporidium. Lühe (1900), however, pointed out that the term was a misnomer, being evidently derived from ἁπλους, meaning simple, and not from ἀπλους, which means unseaworthy, and therefore should be Haplosporidium.

Since this particular species parasitizes the egg of Mytilus, the author has given to it the name *Haplosporidium mytilovum*. The parasites appear to be most abundant late in the breeding season, and mussels which have retained their eggs until late in the fall are most heavily infected. It may be, however, that infection by the parasite prevents complete spawning, although the author has found quantities of the infected eggs which were laid in the troughs where mussels were kept. Thousands of eggs in a single individual may contain one or more cysts of the parasite. Whether its presence does any more injury than to destroy the eggs has not been learned. It is the intention of the writer to investigate the organism further and publish a more complete description of its life history and habits.

USES AND COMMERCIAL VALUE.

Sea mussels are used in a variety of ways in different countries. In France they constitute one of the principal marine food products, the value of the fishery being approximately one-eighth that of the oyster fishery. The demand for mussels in France exceeds what the nation is able to produce, although the most refined methods of myticulture are practiced in that country. Hundreds of thousands of bushels of the shellfish are imported annually from Holland and Belgium. They are also considered a cheap and healthful food in Spain and Portugal. They are eaten to some extent in Great Britain, Germany, and Norway, and are now beginning to be appreciated as a wholesome food in this country.

They rank next in importance as a bait in the fisheries, especially in Europe, where they are considered the best hook bait known. The quantity used in Great Britain for this purpose amounts to more than 100,000 tons annually. In America they are not rated so highly as a bait, but are given preference when squid can not be obtained. Mackerel fishermen often crush mussels and throw them overboard to attract the fish to their boats.

As a fertilizer they constitute another useful and important product. Where the beds are exposed to the deposition of silt the mussels are gradually smothered to death, while new generations are constantly becoming attached to the layers above. The result after a number of years is a thick layer of blue, ill-smelling matter called mussel mud, which is rich in lime, sulphur, and nitrogen. It is considered one of the best fertilizers known, especially for carrots and onions. A writer from Essex County, Mass. (*in* Ingersoll, 1884, p. 621), stated that for 30 years he had seen it applied to lands where onions had been grown with a yield varying from 300 to 600 bushels per acre. The material is usually gathered during the winter, allowed to freeze, and is then distributed in amounts which vary from 4 to 8 cords per acre.

The shells are used by oyster planters for cultch on which to catch oyster spat. Artists use them as receptacles for gold and silver paint. When polished they may be used for ornamental purposes. In this form they have been mounted on marble for paper weights. Buttons, pretty needle books, scent bottle holders, earrings, crosses, pins, and pin cushions have also been made from them. Since the shell is composed of a large proportion of albuminous matter, the suggestion is offered here that the cracked shells would probably make a valuable food for poultry. Experiments to determine their food value from this standpoint ought to be undertaken.

Mussels also yield pearls which are sometimes of value, but usually they are small, of irregular form, and of poor color, selling in England for from 50 cents to $1 an ounce. When formed near the border of the shell they are blue-black in color, but when produced near the middle of the inner shell surface they may take on the beautiful character of the nacreous tissue.

The value of the mussel fishery in the United States for 1908 is reported by the United States Bureau of Census on the contained meat basis. The statistics were furnished by six States and are given in Table 4.

TABLE 4.—QUANTITY AND VALUE OF SEA MUSSELS MARKETED IN THE UNITED STATES IN 1908.

	Quantity in pounds.	Value.		Quantity in pounds.	Value.
New York	8,175,000	$8,200	Rhode Island	3,500	$100
California	68,000	1,600	Massachusetts	1,100	100
New Jersey	287,000	1,400			
Connecticut	7,200	200	Total	8,541,800	11,600

The statistics given in Table 4 are for the year 1908, since which time there has been considerable increase in the consumption of mussels. The present quantity used probably exceeds several times the amount indicated in the above table, for a single firm in New York during the year 1912 reports having handled 50,000 bushels, valued at $17,500.

In Europe the mussel fisheries are much better developed and of far greater importance than in this country. The statistics of the European fisheries were difficult to secure with any degree of completeness, and what is here presented is to be regarded as only a partial record. It is sufficient, however, to show the great wealth which lies in this fishery.

TABLE 5.—QUANTITY AND VALUE OF MUSSELS MARKETED IN EUROPE.

Country.	Year	Quantity in pounds.	Value.	Country.	Year.	Quantity in pounds.	Value.
France	1909	90,044,010	$559,276	Germany	(?)	370,100	$2,375
Belgium	1906	56,129,356	255,133	England	1911	[1] 3,519,860	15,125
Netherlands	1910	3,737,481	23,300				
Ireland	1908	(?)	15,510	Total			882,994
Portugal	1909	(?)	12,275				

[1] Returns from Grantees of Mussel Fishery Orders.

Lankester, in his article on the Mollusca, published in the Encyclopedia Britannica, states that in 1873 the mussels exported from Antwerp alone to Paris to be used as a human food were valued at $1,400,000. If this production still continues, the total yearly value of the mussel fishery for Belgium and France alone equals nearly $2,000,000.

Owing to the food shortage in Europe caused by the war, the boiling and salting of mussels in Holland for German consumption has developed into a large and valuable industry. According to the Seafood Journal for February 12, 1917:

> Up to a month or two ago these humble shellfish which abound in the shallow waters of the Scheldt delta were retailed for local consumption and constituted a cheap popular food. They have now suddenly disappeared from the market, and instead of being eaten are salted down in great quantities and bought up for Germany. Some of the workmen's families that have taken up the new occupation are earning about $6 a day, for them a princely wage.

Consul Frank W. Mahin, of Amsterdam, also states in Commerce Reports No. 61, Washington, D. C., Thursday, March 14, 1918, page 963, that—

> Mussels abound in the vicinity of Texel, an island at the mouth of the Zuider Zee. They have been eaten more or less, but now it is probable they will become very popular. Samples of smoked mussels have been received from Texel, which are pronounced "uitstekend" (substantially, "delicious"). Smoked and salted, the mussel is said to resemble smoked meat (similar to American dried beef), but tenderer and fatter.

These facts serve to show how important and valuable the mussel fishery is to Europe and suggest the possibilities of developing an equally great food-producing industry in this country from the abundance of natural mussel resources at our disposal and the vast unutilized areas along our shores that are especially adapted for the cultivation of this particular shellfish.

CHEMICAL COMPOSITION AND NUTRITIVE VALUE.

Chemical analyses made by Atwater (1892), Atwater and Bryant (1906), and Alsberg, whose account is published in Field (1911), show that the sea mussel not only contains the same kinds of nutrients as other shellfish but contains them in greater abundance. These nutrients are: (1) Protein, which forms the nitrogenous basis of blood, muscle, connective tissue, etc., and supplies energy to the body; (2) carbohydrates; (3) fats, which may be stored up as fat or consumed for fuel; and (4) mineral matters or ash, which are used chiefly in the formation of bone. The energy-yielding power of a nutritive substance is measured in terms of its fuel value, which refers to the number of calories of heat equivalent to the energy that the body is supposed to obtain from 1 pound of the thoroughly digested food. A calorie as here used equals approximately the amount of heat required to raise the temperature of 1 pound of water 4° F. According to the factors of Rubner, the fuel value of each pound of protein or carbohydrate is equivalent to 1,860 calories of energy, while that of fat is equal to 4,220.

Table 6 shows the comparative composition and fuel value of the mussel and several shellfish most commonly found on the market. Of the five species the mussel ranks first, second, and third, respectively, in the yield of carbohydrate, fat, and protein, while in the total production of nutrients it surpasses all the others. Its superiority over the oyster in this respect amounts to 365 per cent, and over the round and long clams to 220 per cent and 11 per cent, respectively. The lobster most nearly approaches the mussel in fuel value, but even this occupies a lower rank. The general excellence of the mussel is due chiefly to the fact that there is little waste in the animal as a whole. It is in the same class with the long clam, where the amount of edible material supplied exceeds 50 per cent. The oyster, on the other hand, is at its greatest disadvantage in this respect, for its heavy shell makes the percentage of refuse amount to more than 81 per cent.

TABLE 6.—COMPARATIVE COMPOSITION AND FUEL VALUE OF CERTAIN SHELLFISH.[1]

Species.	Refuse.	Water.	Protein. N×6.25.	Fat.	Carbohydrate.	Ash.	Total nutrients.	Calories of fuel value per pound.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	
Sea mussels	46.7	44.9	4.6	0.6	2.2	1.0	8.4	.50
Lobsters	61.7	30.7	5.9	.7	.2	.8	7.6	141
Long clams	41.9	49.9	5.0	.6	1.1	1.5	8.2	136
Round clams	67.5	28.0	2.1	.1	1.4	.9	4.5	68
Oysters	81.4	16.1	1.2	.2	.7	.4	2.5	41

[1] Data from Langworthy (1905).

The relative value of food substances from the standpoint of economy can not be determined from their chemical composition alone. It is necessary to know the actual cost of the food principles supplied and the proportion which the body is able to metabolize.

In regard to the palatability of the sea mussel little need be said aside from the fact that the flesh is tender and of fine quality and the flavor is superior to clams and equal to that of the oyster. This statement is based on the testimony of a hundred or more persons who reported on the comparative merits of these shellfish.

Metabolism experiments made by Dr. D. D. Van Slyke, assisted by Dr. W. M. Clark and Dr. C. B. Bennett, and reported in Field (1911) demonstrated that the rate of digestion and proportion of nutrients supplied to the body approximate very nearly those of steamed beef, which is considered very digestible. It is unfortunate that we have no similar data for the clam, oyster, and lobster flesh.

The above evidence, however, is sufficient for drawing the conclusion that the sea mussel is not only as palatable as the oyster, but is now the cheapest and most nutritious shellfish which can be placed on the market.

SEASONAL CHANGES IN STRUCTURE AND FOOD VALUE.

Mussels, like oysters, undergo a series of structural and physiological changes during the year which render them prime for market during one season and of very poor quality in another. These changes are caused primarily by the reproductive activities of the animal and secondarily by the rhythmic changes in the amount of food organisms present in the water.

It has been shown that by far the greater part of the mussel's body is devoted to the production of genital products. Just before the spawning season the mantle and mesosoma are greatly distended with reproductive tissue. It also covers the pericardium and often envelops completely the outer walls of the liver. When in this state the shellfish are of maximum nutritive value, most palatable, and most attractive in appearance.

In Narragansett Bay and Long Island Sound mussels usually reach this condition in the late winter or early spring, while in the more open waters of the ocean, such as along the south shore of Long Island, they do not attain it until June or July.

Following the maximum development of genital tissue there is a shedding of the reproductive elements that leaves the body in a shrunken condition and with a comparatively large and conspicuous dark-green liver. Such shellfish are unattractive in appearance and undesirable for use as food. This change takes place in the mussels of Narragansett Bay and Long Island Sound during the months of June and July, or sometimes as late as August, according to the depth of the water in which the beds lie. Those in shallow water subject to the higher temperatures, direct rays of the sunlight, and wave action are the first to spawn, while those in very deep water are the last to begin the process, or they may even retain the genital products throughout the season and absorb them as reserve food. Such mussels are nearly always in good condition.

Mussels on the south shore of Long Island put on flesh and mature their reproductive elements in the late spring and early summer, coming into prime just as the Narragansett Bay and Long Island Sound mussels go out of season. They continue in marketable condition until the latter part of September.

From Narragansett Bay and Long Island Sound, on one hand, and the south shore of Long Island, on the other, there may be obtained a continuous supply of marketable mussels from March to October. This fact is of much significance, for since the mussel season supplements that of the oyster it offers an opportunity to oystermen to keep their expensive equipment busy the year round in case a mussel industry is established.

The series of structural changes which occur during the year are illustrated in the photomicrographs of cross sections taken through the mantles of mussels from Woods Hole, Mass., during the months of December, January, April, June, and August (figs. 212 to 220). The figures are all represented on a uniform scale of 30 diameters magnification, so that the relative thickness and condition of the mantle at the different seasons may be compared at a glance.

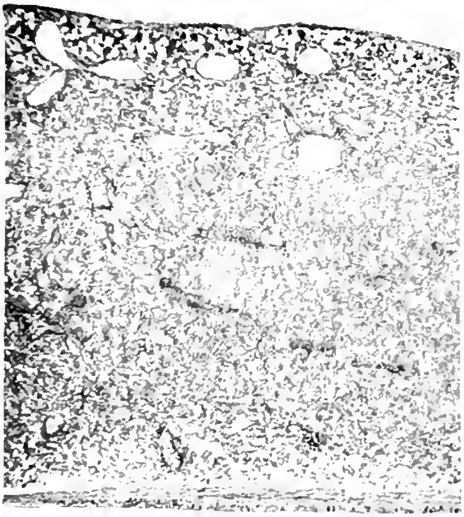
On December 1 the mantle of a female mussel was found to be composed of a rather uniform reticular tissue, with blood vessels running just below the outer surface and small genital canals and follicles extending to a slight extent throughout the middle and inner side (fig. 212). On the same date the mantle of a male mussel was found to be thinner, but the follicles were much more completely formed and were filled with developing spermatozoa (fig. 213).

Six weeks later the mantle of a female mussel was found to be thinner than that of the specimen examined December 1, but the genital canals and follicles were more numerous and better developed (fig. 216). On the other hand, the mantle of a male mussel taken on the same date was thicker than that of the male specimen examined on December 1, and the tissue was firmer and less vacuolated (fig. 217).

During the next three months considerable increase in growth was found to have taken place in the tissue as well as the formation of large numbers of genital cells in both the female (fig. 219) and the male (fig. 220).

The maximum development was found in the middle of June when the female mantle in particular was distended with the reproductive products (fig. 214).

Shortly following this condition, spawning takes place and practically all of the genital elements are shed, which results in a decided shrinkage of the mantle and other



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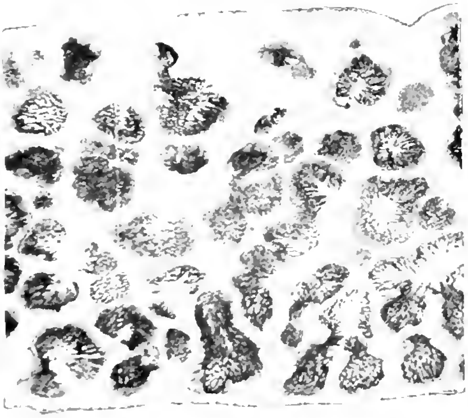

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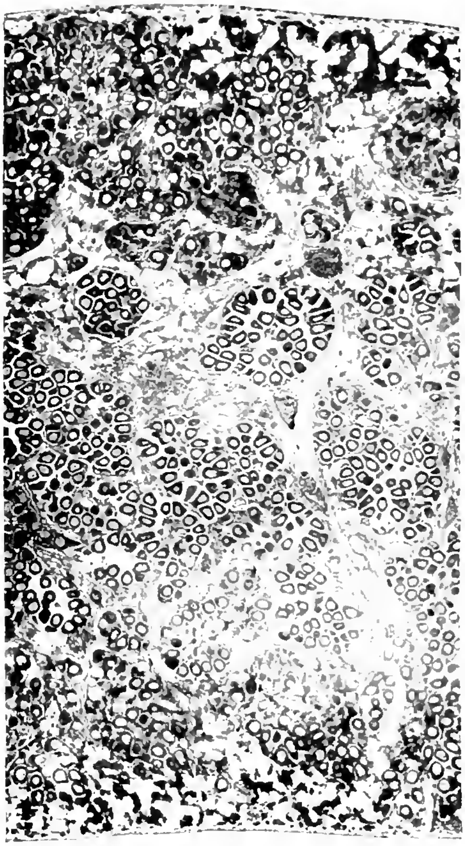

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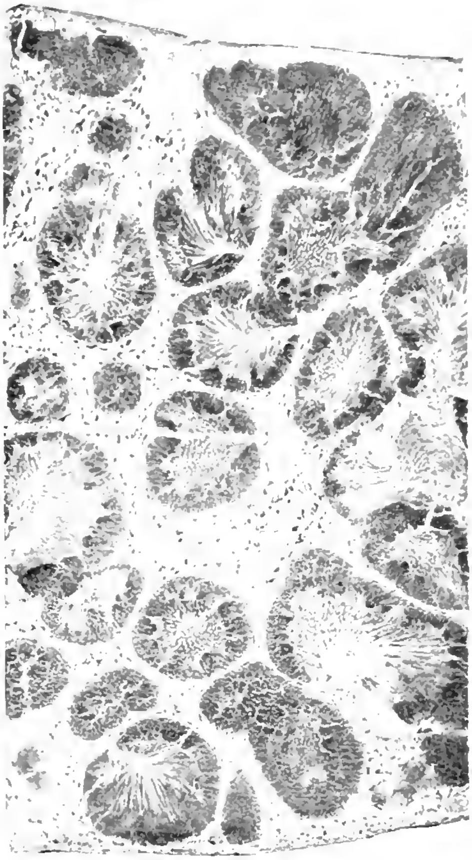

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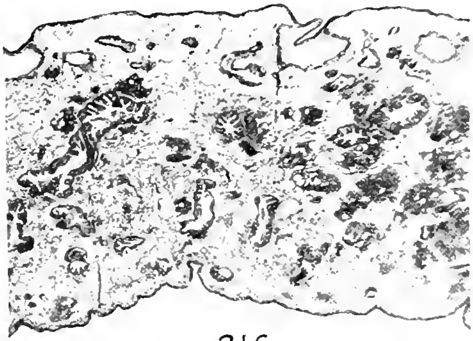
Cross sections through the mantles of mussels collected at Woods Hole, Mass. All figures are photomicrographs of material fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red. 30.

FIG. 212.—From a female mussel collected on December 1.

FIG. 213.—From a male mussel collected on December 1.

FIG. 214.—From a female mussel collected on June 16.

FIG. 215.—From a male mussel collected on June 16.



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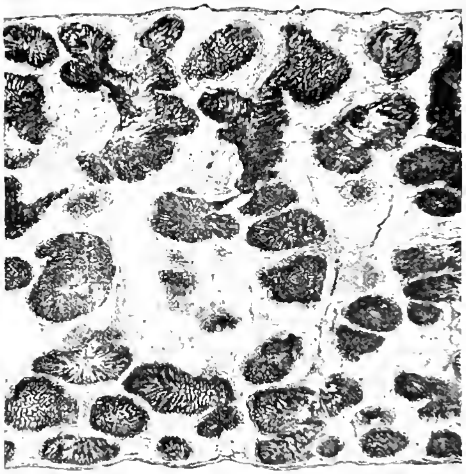

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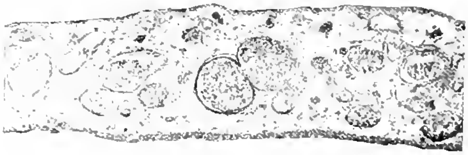

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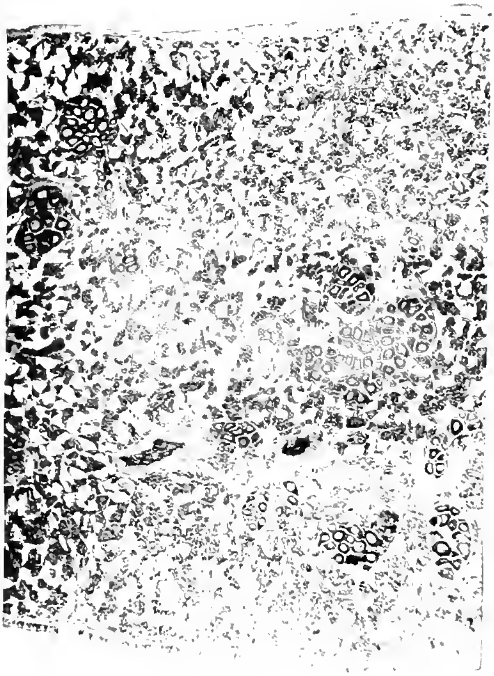

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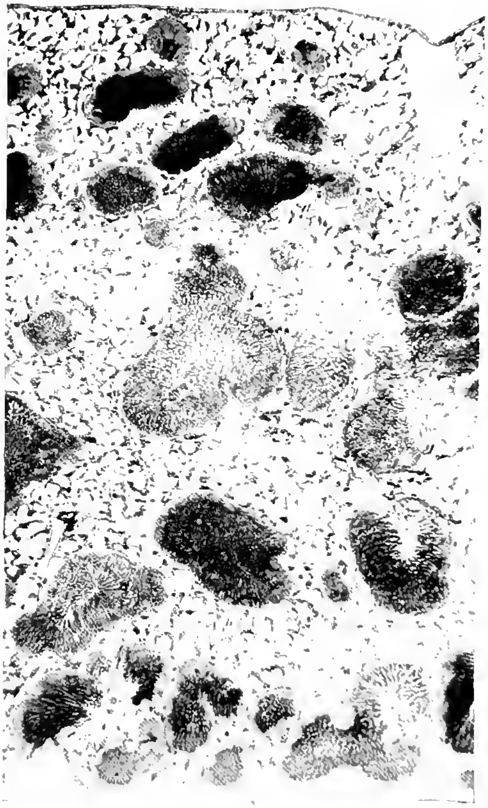

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Cross sections through the mantles of mussels collected at Woods Hole, Mass. All figures are photomicrographs of material fixed in Gilson fluid and stained with Delafield haematoxylin and congo red. × 30.

FIG. 216.—From a female mussel collected on January 12.

FIG. 217.—From a male mussel collected on January 12.

FIG. 218.—From a female mussel collected on July 10 after spawning had taken place.

FIG. 219.—From a female mussel collected on April 27.

FIG. 220.—From a male mussel collected on April 27.

parts of the body pervaded with genital tissue (fig. 218). An idea of the relative food values of a mussel before and after spawning is shown in a most striking manner by comparing figures 214 and 218.

WHEN MUSSELS ARE UNFIT FOR FOOD.

While advocating the use of mussels for food, the author has often encountered persons who protest against so using them on the ground that they are a dangerous product which can never be eaten with safety. But having eaten them for years himself and knowing many other persons who have been doing the same thing without ever experiencing disagreeable symptoms, the author is convinced that the idea of their possessing any poisonous qualities is false. However, to say that they are never poisonous would be as wrong as to say that oysters, clams, or lobsters are never toxic. When infected with disease-producing germs, ptomaines, or other injurious substances any of these shellfish are a menace to human life if ingested; and the record of suffering and fatalities which appears in the medical journals and daily papers serves to show how important it is to select these foods with care. A study of mussels as a human food shows that they are a most wholesome shellfish and that they are no more dangerous to eat than are oysters, clams, or lobsters, provided the same care is used in selecting them.

The purpose of this section is to show the causes and symptoms of poisoning which have resulted from eating unwholesome mussels, with the hope that similar occurrences may be averted in the future. The subject may be considered under two heads—diseases resulting from eating mussels taken from polluted waters, and diseases resulting from ingesting poisonous substances secreted in the body of the mussel itself

MUSSELS AND TYPHOID FEVER.

Buchan (1910) collected some very important data on the relation of mussels from polluted waters to typhoid fever. The results of his paper are based on evidence collected at Birmingham, England, between June 1, 1904, and June 1, 1909, during which period there were 855 cases of typhoid fever, of which 124, or 14.5 per cent, were attributed as due most probably to mussels and 32 to other shellfish.

Investigations demonstrated that several of the sources from which mussels were supplied to Birmingham were polluted with sewage. Bacteriological examinations of mussels taken from the Birmingham market showed that the number of microorganisms to a single mussel varied from 2,000,000 to 1,000,000,000. The most common number was between 10,000,000 and 100,000,000 per mussel, which is considered high. Where the number reaches 1,000,000,000 it undoubtedly indicates gross pollution. In 5 samples the *Bacillus coli communis* was actually isolated, while evidence of its presence was found in 26 other cases. Since the *Bacillus coli communis* is so closely associated with the *Bacillus typhosus* it is reasonable to infer that the presence of this germ in mussels means the possible and probable pollution by the typhoid bacillus. Sewage pollution was also indicated by the presence in large numbers of the *Bacillus enteritides sporogenes* and of numerous *streptococci*. The investigations of Johnstone (1912) further show that there is abundant epidemiological evidence that enteric fever has been transmitted by mussels.

The above evidence proves that mussels may be carriers of typhoid fever in the same way as oysters or clams if taken from waters polluted with sewage. The problem of protection in each case is the same. Either the sewage must be purified before it is allowed to flow into waters where the shellfish are propagated or the law should forbid the marketing of shellfish taken from polluted waters. Some writers have advocated transplanting oysters and mussels from regions of sewage contamination to clean waters for a period sufficient to allow them to be freed from any pathogenic germs. The practicability of this method, however, is doubtful, for as Klein (1905) has demonstrated, cockles infected with typhoid organisms and thereafter kept in clean sea water frequently changed allowed the bacilli to multiply, and bacilli in mussels similarly treated were still plentiful after seven days. Johnstone (1909) found that mussels taken from polluted beds and placed in sea water half a mile from the nearest discharging sewer were able to rid themselves of 93 per cent of intestinal bacteria in four days, but that a further period of eight days did little if anything to effect a further reduction.

Wright (1917) describes a type of purification tank that is being erected under the supervision of the Lancashire and Western Sea Fisheries Committee in order to remove as much risk as possible from the consumption of polluted mussels in Great Britain.[4]

> They are solidly built concrete structures, in several compartments, on the wooden grids of the floor of which the mussels are placed, in layers not exceeding three deep. They are designed to fill over the top at about high water of neap tides, when the mussels will rest under a depth of about 2 feet of clean sea water. As the fecal matter is ejected, it falls through the gratings on to the cemented floor beneath, which slopes away to outlet pipes of large diameter. The water is allowed to escape when the tide is low, and carries, as it flows out, the excretory products. Exhaustive tests (bacteriological and others) are carried out before the site of the tank is decided upon, in order to insure the purity of the water gaining access to it. The shellfish remain in the structure for the space of 48 hours, and they are then put into bags bearing the lead seal of the committee, to show that they have undergone treatment.

PTOMAINES.

Another source of danger in utilizing sea mussels for food is from the ptomaines and other poisons which often occur in shellfish. The cause of prejudice which has grown up against this mollusk is due to the fact that fresh mussels which exhibited no signs of decomposition have on several occasions fatally poisoned groups of persons who ate them at a particular time. Aurel Krause (1885), in Flinkit-Indianer, Jena, reports that in 1799 a company of soldiers stopping at Peril Way, near Sitka, Alaska, ate of these mollusks and that in less than two hours 100 men died in great pain. This incident is doubtless the same one referred to by Dall (1870) and Petroff (1884). The place and date in the two accounts are the same, but according to Dr. Dall the victims were Aleut hunters from Unalaska and Kodiak instead of soldiers. It was this calamity which gave the place its name of Peril (in Russian Pogibshi) Strait. In this case the poisoning was supposed to have been caused by ptomaines generated in the liquor of the mussels which had been exposed to the sun for a long period. The Aleuts of that region informed Dr. Dall that mussels which were not exposed at low tide were always safe to eat.

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[4] A method of purification which has been used for three years at Conway, in Wales, and proved to be commercially successful is briefly summarized in the Fisheries Service Bulletin No. 61, June 1, 1920, p. 3. "This method consists essentially in placing the shellfish on wooden grids in vats of 40,000 gallons capacity, cleansing them with water from a hose, and allowing them to stand in sterilized sea water for 24 hours, then cleansing with the hose again, followed by immersion in sterilized sea water for another period of 24 hours, after which water containing 3 parts per 1,000,000 of available chlorine is run over the shellfish and allowed to stand 1 hour. The shellfish are shipped in sterilized sealed bags."

PECULIAR POISONS.

A class of poisons different in some respects from that of the ptomaines has appeared in the sea mussel at various times in certain restricted localities. In some cases large groups of people have been suddenly stricken with severe illness after eating this shellfish and death has often quickly followed. The most prominent case of this sort occurred at Wilhelmshaven, Germany, October 17, 1885, when 19 persons were taken severely ill after eating *Mytilus edulis*. Four of the people died. Consternation followed this event and numerous investigators began to study the nature and effects of the poison. The result has been an extensive and most valuable literature, knowledge of which should protect us from again falling into the fatal error of eating poisonous mussels of this type.

Netter and Ribadeau-Dumas (1907b) published a table showing the fatal cases of poisoning which have been known to result from the ingestion of such mussels. In modified form it is as follows:

Author.	Locality.	Month.	Year.	Number of sick.	Number of deaths.
Vancouver (1798)	North America	(?)	1793	3	1
Combe (1828)	Leith	June	1827	30	2
Crumpe (1872)	Tralee	(?)	(?)	3	3
Crumpe (1872)	Tralee	(?)	1872	1	(?)
Virchow (1885)	Wilhelmshaven	Oct. 17	1885	19	4
Schmidtmann (1888)	Wilhelmshaven	September	1887	3	1
Permewan (1888)	Liverpool	August	1888	3	1
Cameron (1890)	Dublin	June 30	1890	7	5
Hill (1899)	Richard Surrey	Jan. 8	1895	1	1
Thesen (1902)	Christiania	May	1901	5	2
Rolfe (1904)	Avonmouth	June	1904	2	1
Netter and Ribadeau-Dumas (1907)	Calais	May 23	1907	13	2
Boinet, Ed. (1911)	Paris	(?)	1911 (?)	2	2
Total				92	25

The symptoms which follow the ingestion of poisonous mussels may be one or more of three distinct types.

(1) The erythematic form is the lightest in which the toxine takes effect. The symptoms are similar to those which appear in many persons after eating strawberries, pineapple, or fish, when red spots appear on the body. This is also frequently accompanied by a swelling of the face and abdomen and sometimes with a sense of suffocation.

(2) The choleratic form is more severe in its effects. A few hours after ingesting poisonous mussels diarrhea and vomiting appear, which last for from 24 to 36 hours. The symptoms are similar to those of the dry-weather cholera, which appears periodically at Trieste, Austria, and with which cases of mussel poisoning have been confused.

(3) The paralytic form is the worst, being rapid in its action and often fatal. It was this form of poisoning which occurred at Wilhelmshaven. On that occasion the physician Schmidtmann (1888) made a study of the subject from the clinical and etiological standpoint, while Virchow (1885) investigated it from the standpoint of pathology.

The symptoms as described by Schmidtmann (1888), Permewan (1888), Cameron (1890), and others, indicate that there are three stages to the paralytic form of poisoning.

The first signs are a prickling or burning sensation in the hands or feet, a constriction of the pharynx, mouth, and lips, and a sensation in the teeth similar to that produced by acid substances. The lips become numb, and this condition gradually passes down over the arms. A consciousness of lightness and that objects have no weight comes over the patients; they believe that they can fly.

The second stage is marked by a feeling of restlessness and fear. No rise of bodily temperature takes place, but the pulse rate is quickened to a frequency of 80 to 90 per minute. The pupils of the eyes are dilated and reactionless, there is a feeling of giddiness, and the patients speak in a weak voice and with difficulty. They hold themselves in an upright position with great pain. The secretion of urine is suspended or passed with pain and great effort.

The third stage follows with vomiting and cramps and sometimes, but rarely, with diarrhea. The pulse grows feeble, and the limbs become cold. The condition of restlessness increases with a feeling of suffocation. Through it all the senses remain intact. Finally the body becomes cold, the patient sinks into a state of unconsciousness, and death follows in a quiet sleep. Cameron (1890) states that some of his patients appeared to have died from asphyxiation, their faces being intensely livid. In some cases the symptoms do not begin to show themselves until 12 hours after eating the poisonous shellfish, while in others death has resulted within 2 hours after the meal.

Rolfe (1904), who had two patients afflicted with the paralytic type of poisoning under his observation, noticed that hot strong coffee had a marked beneficial effect upon the pulse and general condition. He reports that the patient which gave least promise of getting well drank coffee and survived, while the other took no coffee and died.

The autopsies made by Virchow (1885) established the facts that as a general rule there is an accentuated rigor mortis in the bodies of persons who die from this form of poisoning; the cardiac and arterial blood is dark in color and viscous in consistency except where the arteries are more exposed to the action of oxygen, in which places it is clear red. The most pronounced alterations appeared in the omentum and the large intestine, which with the stomach were strongly hyperemic. The mucosa of the small intestine was likewise strongly injected with blood and covered with mucous swellings. The spleen was swollen, and the liver presented a congested condition.

The characters of the mussels which cause this type of poisoning are different from those of the normal shellfish. Schmidtmann (1888) observed a nauseating odor to the broth prepared from them. The mussels had a yellow color and the shells were unusually thin and fragile. while the liver was darker than the ordinary and very brittle.

SOURCES OF POISON.

Wolff (1886), Schmidtmann (1888), Lustig (1888), Thesen (1902), and Netter et Ribadeau-Dumas (1907) determined that the poison was confined entirely to the liver, but how it gets into the organ is still a theoretical matter. Wolff (1886) believed that the poison was secreted as the result of a disease and stored up in the liver. The change in volume, color, and consistence of the liver and of variation in toxicity supports this view. Schmidtmann (1888) established the fact, however, that the toxic mussels are found only in certain special restricted localities, where the water is in a stagnant condition, and that if removed to open, freely circulating water of the sea they lose their poisonous qualities in less than four months. And, on the other hand, if harmless mussels are transferred to the stagnant waters of the inner harbor of Wilhelmshaven they develop toxic properties in from two to three weeks. This would suggest that there was some injurious compound present in the water which was taken up by the mussel and stored in the liver.

To test this, Thesen (1902) placed some mussels in weak solutions of strychnine, curare, and the poison of mussels. He was confident that at the end of a certain time these poisons were taken up by the liver. Schmidtmann's (1888) evidence supports this view. He observed that harmless mussels placed in the suspected Wilhelmshaven basin became more toxic the longer they remained there. After 24 hours they developed sufficient poison to kill a rabbit in 1½ hours, after 48 hours in 12 minutes, after 72 hours in 4½ minutes, and after 96 hours in from 2 to 4 minutes. Mussels which were capable of killing rabbits in a few minutes, after being placed in the open water of the sea for a period of 8 hours, were unable to cause the death of rabbits in less than 1½ hours. But all efforts to isolate the mussel poison in a preformed condition from the stagnant water met with negative results.

Lindner (1888) assumed that the poison was produced by certain Protozoa which he found present in considerable numbers in the toxic mussels. Popular opinion has attributed the production of the poison to various sources. Some think it is due to the absorption of copper salts which come from the metal sheaths of ships; others believe that it comes from the eggs of starfish which are consumed by the mollusk. This view is evidently without foundation, for there is apparently no authentic record of starfish eggs being poisonous or ever being found in the mussel. It has also been assumed without reason that the poison comes from the little crab, *Pinnotheres maculatum,* which lives in the mantle cavity. It has also been accredited to the byssus.

The most plausible explanation of the origin of the poison is contributed by Lustig (1888), who studied the subject from the bacteriological standpoint. He obtained some mussels from Genoa and Trieste which exhibited all the physical characters of the poisonous variety. A sample of them which was fed to a cat and a rabbit produced vomiting which was followed by death in less than 24 hours, accompanied with the characteristic anatomical features of enteritis. From the livers of these mussels he obtained, by Koch's method, cultures of two microorganisms, one of which proved to be pathogenic. The latter organism is a straight, slender bacillus varying from 0.8 to 1.0 micron in length. It stains with gentian violet, fuchsin, methyl violet, and Grams method. In old cultures the bacilli unite into a spiral form. They liquefy gelatin. Twenty-four hours after infection they produce rather large colonies, having a funnel form with a dense whitish mass at the center similar to that of the bacillus of Finkler and Prior.

Test-tube inoculations show a bubble of gas on the surface of the gelatin at the end of 12 hours, and at the end of 24 hours the gelatin at this point is liquefied into the funnel form. The depression continues to deepen by liquefaction, until at the end of 8 hours more all the gelatin is dissolved into a cloudy, grayish liquid, on the surface of which there is a delicate green ring. The cultures give off a nauseating odor. The bacillus grows readily on agar-agar at a temperature of 16 to 20° C. and on potatoes at ordinary room temperature. The potato culture takes the form of a yellow film. It also develops well in sterilized milk or bouillon.

To show the relation of this organism to the Mytilus poison, Lustig performed a series of feeding experiments and of injections on rabbits and guinea pigs. From some 24-hour gelatin cultures he transferred by means of a sterilized platinum needle about 4 to 6 drops to small cubes of sterilized potato which were preserved in sterilized glass receptacles. The infected portions of potato were fed to rabbits and guinea pigs in doses of three cubes to each individual. The animals were then isolated and allowed nothing more to eat. All the rabbits, eight in number, died within 12 hours. Of these, two died in two hours after having suffered from severe diarrhea. Of the guinea pigs, four in number, two survived and two died.

An autopsy demonstrated the same conditions which have been described for persons who have succumbed to the effects of mussel poisoning, and microscopic examination of the cardiac blood and of the intestinal contents revealed the presence of the bacillus in question.

After these results of natural infection he injected from 15 to 20 drops of 24-hour cultures into the skin of rats and rabbits, but both cutaneous and subcutaneous injections proved to be without effect. However, if injected into the peritoneum in small quantities it produced death in rabbits and guinea pigs in from 8 to 24 hours. The clinical and pathological phenomena presented by these animals were the same as of those naturally infected. An injection of these bacteria into the blood vessels of the ears of four rabbits produced no harmful results. Cultures from the alimentary tracts of animals which died as a result of these infections if taken within 24 hours after death are just as capable of infecting other animals when ingested as are the original cultures from the mussel liver. As the cultures grow older they become less virulent in their effects and after a few hours cause nothing more serious than diarrhea when injected into the peritoneum.

Lustig admits that the above evidence is not complete enough to definitely prove this organism to be the cause of the poison which is sometimes found in the mussel liver. It is very suggestive, however, and calls for further research when the opportunity presents itself again. Other investigators, Netter et Ribadeau-Dumas (1907), who secured some of these poisonous mussels at Calais, France, were unable to isolate a specific germ.

CHEMISTRY OF MUSSEL POISON.

The chemical nature of the poison classes it with the ptomaines according to Schmidtmann (1888), while Virchow (1885) is inclined to group it with the alkaloids. Our first knowledge of its chemical properties was furnished by Salkowski (1885), who extracted the poison by means of alcohol. He found that alcoholic solutions of non-poisonous mussels were almost colorless, while those from the diseased livers of poisonous mussels were golden yellow in color and if treated with warm concentrated nitric acid gave a grass-green color. He furthermore found that the activity of the poison is not affected by heat up to 110° C. but that it is destroyed by warm sodium carbonate.

Mytilotoxin is a poisonous compound which Brieger (1886, 1888, 1889) succeeded in isolating from the livers of toxic mussels. Its formula according to his determinations is $C_6 H_{15} NO_2$. This compound, Brieger claims, is the specific curare-like active toxin of the sea mussel.

The method of extracting the mytilotoxin is as follows: Several hundred of the pathologic mussels are heated in water with some hydrochloric acid, and the mixture is then filtered. The poisonous compound is in the filtrate as hydrochloric mytilotoxin. This filtrate is evaporated to dryness, and the residue is dissolved in alchool. The alcoholic solution is neutralized with sodium carbonate, then acidified with nitric acid, and gradually precipitated with phosphomolybdic acid. The first precipitate which comes down contains albumin bodies and color substances, while that which is precipitated later contains the mytilotoxin. This latter precipitate is dissolved in a solution of lead acetate, slightly warmed and filtered. The filtrate is treated with hydrogen sulphide to remove the lead and then evaporated after adding some hydrochloric acid. The residue is dissolved in alcohol and reprecipitated with platinic chloride. The filtrate then contains the mytilotoxin which may be precipitated by means of gold chloride after first removing the platinum with hydrogen sulphide.

The mytilotoxin forms a double gold salt which crystallizes into minute cubes having the composition $C_6H_{16}NO_2AuCl_4$. They have a melting point of 182° C. With the ordinary alkaloid reagents mytilotoxin gives oily precipitates only. It was further found that when the hydrochloric mytilotoxin is distilled with potassium hydroxide trimethyl amine $N(CH_3)_3$ is produced. Brieger therefore says that mytilotoxin is a quaternary base and its power to paralyze the motor apparatus is no longer surprising since it has been demonstrated by Glause and Luchsinger (1884) that all trimethylammonium bases produce muscarin effects.

If the hydrochloric acid extract of poisonous mussels is boiled with some sodium hydroxide a nauseous odor is liberated. Brieger recommends therefore that this method be used as a test for mussels which may be under suspicion.

In addition to the mytilotoxin Brieger found several other substances of a basic nature, some of which are poisons. Among these is the nonpoisonous betain—oxyneurin, trimethylglycin, $(CH_3)_3.\ NOH.\ CH_2.\ CO_2H$. The mytilotoxin may arise from the betain by introducing the radical CH_3, which may be represented by the following formula: $(CH_3)_3.\ NOH.\ CH(_3).\ CO_2H$. This relationship, however, is not at all clear.

In support of the above observations, Cameron (1890), in attempting to extract an alkaloid from some poisonous mussels which came under his observation, clearly proved the presence of a leucomaine which was obtained in crystals visible under the microscope. These crystals corresponded to those described by Brieger and were considered as identical with them.

On the other hand, Thesen (1902), who investigated a large number of poisonous mussels from the haven of Christiania, was unable by the Brieger method to identify the poison with that of Brieger's mytilotoxin. Griffiths (1890), who studied a case of mussel poisoning at Dublin, Ireland, states that the effects were undoubtedly due to the action of alkaloids (ptomaines) which were developed by the action of microbes in the muscles of the shellfish. The poisonous compounds formed, he says, are all members of the pyridine and hydropiridine organic bases. We are therefore still uninformed as to the exact nature of the mussel poison, and further research on this subject should be encouraged.

Jourdain (1891) believes that mytilotoxin is always present in Mytilus and that other ptomaines are always present in other shellfish, such as the oyster, which often causes poisoning of a serious nature. The quantities of these toxines present, however, is rarely ever sufficient to be injurious.

Mytilocongestine is a toxic substance which has been extracted from the bodies of *Mytilus edulis* by Richet (1907, 1907a). It is analagous to the congestine which he obtained from the bodies of Actinians, and was therefore given the name of mytilocongestine. It is prepared by grinding up frozen mussels with sand and water; the product is filtered as quickly as possible and precipitated with three times its volume of alcohol. The precipitate is dissolved in water, filtered, and reprecipitated with alcohol. This precipitate is collected on the filter and washed with alcohol and then allowed to dry. A white powder is obtained which browns a little in the air and which almost completely dissolves in water. When precipitated again the substance is obtained in pure form, but naturally the quantity is very small, scarcely more than 5 g. from 24 kg. of mussels.

When injected intravenously into dogs it produces diarrhea, bloody stools, rectal pain, vomiting, prostration, and decrease of arterial pressure. Autopsy reveals an intense hemorrhage of the mucous digestive lining, including the stomach and rectum. The poison produces the phenomenon of anaphylaxis; that is, the animal can withstand a comparatively heavy dose at the first injection, but a short time after that it becomes extremely sensitive and dies when injected a second time with a small fraction of the original amount. The difference in sensitiveness to the mytilocongestine between normal and anaphylactic dogs was found to be about 1:25, while in an extreme case it was 1:100.

CONCLUSION.

What has been stated above furnishes no evidence to support the assumption that the sea mussel is a dangerous food, but it sounds a warning that it is just as capable as the oyster or any other shellfish of transmitting typhoid fever if it is taken for consumption from waters polluted with sewage containing the germs of this disease; and that if taken from water so stagnant that it makes the fishes and eels which inhabit it lose almost all their vitality, as was the case at Wilhelmshaven, then it is apt to contain a poison which is rapid and severe in its effects. It should be borne in mind, however, that mussels possessing this poisonous quality are very rarely met with, and to the knowledge of the author have never been discovered on either the Atlantic or Pacific coasts of the United States.

Finally, let it be noted that all sea mussels which have been found unwholesome or dangerous to human health have come from waters polluted with sewage, from stagnant basins, or were exposed to the heat of the sun for such a long period that ptomaines were able to develop in the liquid held within the shell. On the other hand, mussels from pure water subject to the ebb and flow of the tides have always been found wholesome and delicious articles of food. If selected and marketed with due regard for the facts already mentioned, it is probable that their use in this country will never be accompanied by the disasters which have occurred in certain localities of Europe.

CULTIVATION OF MUSSELS.

In the past few years there has been considerable talk of the sea farms of the future. It has been predicted that the fisherman will grow his oysters, clams, lobsters, etc., under artificial cultivation in a manner similar to that employed by the farmer in raising his crops. The idea, however, is not new, for centuries ago, in the year 1235, a shipwrecked sailor was rescued at the point of Escale, about a mile and a half from Esnandes, France, where, in order to earn a livelihood he devised a system of myticulture that has yielded wonderful results. The method proved so successful that it has been continued to the present day in this locality, where it gives support to 3,000 or more inhabitants of the villages Esnandes, Marsilly, and Charron. If one should visit this locality in the Bay of Aiguillon he would find hundreds of men and women busily engaged day and night, whenever the tide permits, attending to their mussel farms. The spectacle of the army of mussel culturists going to and from their work is said by Coste (1883) to be most curious and grotesque, impossible to portray. With their peculiar types of foot canoes, which will be described later, they glide back and forth over the slippery surface of the mud like a flock of birds driven by the tide, in and out of the mazes formed by the 6,000 palisades which cover the marsh. They speak of the various operations of the industry in agricultural terms, such as sowing, planting, transplanting, weeding, pruning, and harvesting.

Patrick Walton, the founder of the method of mussel cultivation now practiced in France, was a native of Ireland and a sailor by trade. In the fall of 1235 his ship was driven by a northeast gale onto the rocks at the point of Escale near the port of Esnandes. Of the three sailors aboard the ship, Walton was the only one saved, and that was due only to the timely help offered by the fishermen who lived on the coast. Having lost practically everything that he possessed, and being without means for returning home, there was nothing to do but look for a means of subsistence in that place. Previous to his arrival the French fishermen had made poor success at earning a livelihood from the sea, but Walton with his great ingenuity was able to devise a means which not only gave him bountiful support but has proved a lasting legacy to all the inhabitants of that coast.

With the mind of an investigator Walton, seeing the great lake of mud before him, examined it to see if it could be turned to any profit. The problem of getting over the mud through which it was impossible to walk was solved by the invention of his "acon," or foot boat. This device is made of a plank about 10 feet long by 2½ feet wide bent up in front to form the prow. The sides and stern are each composed of straight boards about 1½ feet wide. The boat is further reinforced by a shelf in the stern and a narrow thwart close to the bow. A board may extend across the middle to serve for a seat or it may be replaced by a wooden stool. A paddle and short pole complete the equipment. When the boatman wishes to travel over the mud flats he faces the prow of the boat, puts his left knee on the bottom, and thrusting his right leg, incased in a long sea boot, over the side of the boat, pushes it along (fig. 221, 4*B*, opp. p. 236). By this means he is able to glide over the mud at a very rapid rate. Coste (1883) says the speed attained with one of these boats is equal to that of a trotting horse. With this foot boat the inventor was able to explore every part of the marsh. He could propel it over the mud by means of his foot, through shallow water by means of the short pole, and when deeper water was reached he could use the paddle.

The first thing which attracted Walton's attention was that a large number of land and sea birds were in the habit of skimming over the water in the evening. He promptly determined to catch them as an object of trade. In order to do so he invented a second device, the "alluret," a large net 1,000 to 1,200 feet long and 10 feet wide suspended in a vertical position on stakes driven into the mud for a distance of 3 or 4 feet. Birds flying into its meshes became entangled and were held securely. After his nets had been up a short time Walton discovered that young mussels were attached to the stakes in great numbers. He observed that they grew more rapidly than those on the mud and furthermore were better flavored. With this new discovery he began putting down more stakes in various places and watched for the result. These also, in turn, became covered with growing colonies of mussels. Continuing his observations, he soon concluded that the young of native mussels could be collected and profitably raised under artificial conditions. The result of his investigations was the establishment of the bouchot system of mussel culture for which France has become famous.

The bouchot system as finally perfected by Walton consists of rows of stakes arranged in the form of a V, with its apex pointing toward the sea or the direction from which the strong waves and tide come. This arrangement is to protect the structure from the destructive action of the wind, waves, and ice. The stakes are trunks of trees 6 to 12 inches in diameter and from 10 to 15 feet in length. They are placed from 2 to 3 feet apart and driven into the mud for about half their length. Then branches of osier or chestnut are twisted back and forth between the posts in horizontal rows about 20 inches apart from the top to within a foot of the bottom. If placed closer together than this they are apt to accumulate mud and cause deposition of silt. Walton left an opening from 3 to 4 feet wide at the apex of the two wings where traps were placed to catch the fish which went out with the tide, thus making the structure serve a double purpose.

The length of the wings depends on the size of the area covered by the tide, which is about one-fourth of the distance between the extreme limits of high and low tides. At the present time in the Bay of Aiguillon they are about 250 yards in length but are no longer arranged in the historic V form. According to Herdman (1894) they are now arranged at right angles to the shore in parallel rows about 30 yards apart, as is shown in figure 221, 4.

The bouchots are arranged in three series, according to the particular function each is to perform. One set consists of large solitary stakes placed about 1 foot apart out in deep water where they are uncovered only by the lowest tides. These serve for the collection of spat and are known as the bouchots d'aval, or low crawls (fig. 221, 2).

The second series of bouchots is placed halfway between tide marks and serves for the growth and fattening of the mussels. Several rows of crawls, each with a separate name, may enter into this series. The general term applied to this group is the bouchots batards, or false crawls (fig. 221, 3).

The third series of bouchots is in the upper limits between tide marks where they are exposed several hours each day during low water. These crawls are known as the bouchots d'amont and serve to inure the mussels to exposure and consequently make them keep longer and fresher than those from the lower rows (fig. 153, 4).

The method of working the bouchots is to collect seed mussels and transfer them successively from the lower to the higher bouchots at the proper times. The spat is liberated in the Bay of Aiguillon during February and March and is caught on the low crawls which are situated in an ideal position for the preservation and growth of the young shellfish, since they are rarely exposed to the air. When such an event does occur it is for a short time only. When the set of spat first appears the young mollusks are smaller than a grain of flaxseed and are called *naissan*. The young mussels grow rapidly so that by July they reach the size of an ordinary bean. In this condition they are termed *renouvelain*. They are then ready for transplanting.

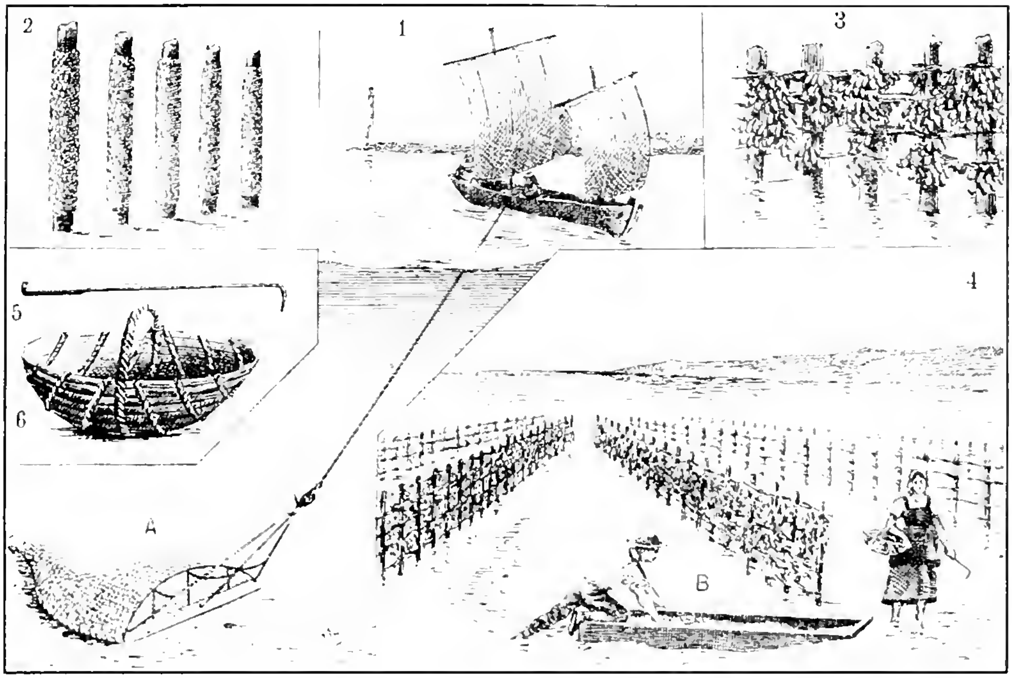

Fig. 221.—Cultivating mussels in France. 1, Method of collecting mussels by means of a dredge (A); 2, bouchot d'aval; 3, bouchot batard covered with mussels; 4, view of a series of bouchots d'amont showing mussels under cultivation and mussel fisherman operating his acon, *B*, which is used for transporting mussels over the mud flats; 5, iron hook used in collecting seed mussels; 6, basket for receiving mussels. (After Nouveau Larousse Illustré Dictionnaire Universel Encyclopédique, Paris.)

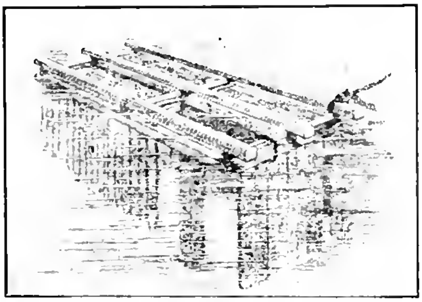

Fig. 222.—A raft collector for catching spat and rearing mussels. (After Fraiche, 1883.)

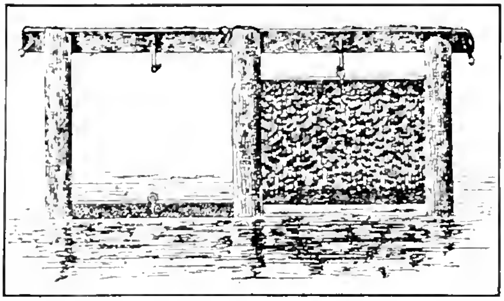

Fig. [illegible].—A claie or movable wooden frame used for growing mussels in the Lamotte canal near Marseilles. (After La Grande Encyclopédie, Paris.)

The seed mussels are collected by means of a hook set in a handle like the one shown in figure 221, 5. A characteristic type of basket (fig. 221, 6) is used to receive them and is filled with the young shellfish to the limit of its capacity. When the baskets are filled they are transported by means of the "acon" to the bouchots batards, where parcels of the young mussels are tied to the wickerwork of the frames by means of old netting. The shellfish immediately begin to attach themselves to the wooded structures by means of their byssal threads, so that by the time the netting has rotted or washed away, they are firmly united to the crawls.

The rate of growth in this position is very rapid, and in a few months they become so crowded as to almost hide the frames. It then becomes necessary to transplant them again, this time to the next series of crawls lying nearer the shore. The mussels are attached by the same method used in the first transference, but are not fastened so securely, since they are able at this stage to attach themselves to the bouchots much more quickly. After one year's treatment on the crawls the mussels reach a length of 1¾ to 2 inches, which is marketable size.

The net returns from an investment in a series of bouchots has been published by Fraiche (1863) and Coste (1883), showing that it is approximately 11½ per cent. To quote from Coste, the production and value of cultivated mussels in the Bay of Aiguillon is as follows:

> A bouchot well stocked, furnishes generally, according to the length of its wings, from 400 to 500 loads of mussels; that is to say, about 1 load per meter. The load is 150 kilograms, and sells for 5 francs. One bouchot, therefore, produces a crop weighing from 60,000 to 75,000 kilograms, and valued at 2,000 to 2,500 francs; from which it follows that the crop of all the bouchots united would weigh about 30,000 000 to 37,000,000 kilograms, which at the figures already given would be worth about 1,000,000 to 1,200,000 francs. These figures and the abundant crops from which they result give an idea of the food supplies and of the great benefits that may be derived from a similar industry, if, instead of being confined to only one portion of the Bay of Aiguillon, it should be extended to the whole of it, and carried from the locality where it originated to all the coasts and salt water lakes where it could be successfully carried on. In the meantime the prosperity which it secured to the three communes of which it has become the patrimony will remain as an end worthy of effort; for, thanks to the precious invention of Walton, wealth has succeeded to poverty, and since the industry has been developed here no healthy man is poor. Those whose infirmities condemn them to idleness are cared for in most generous and delicate manner by the others.

Other methods of mussel cultivation have been suggested and are being used in France. Fraiche (1863) states that this shellfish can be raised in claires or artificial reservoirs the same as oysters, especially in places where the abundance of mud and silt renders oyster culture impossible. The settling basins of the oyster claires in particular can be utilized for this purpose, if proper care is taken to exclude the mussel spat from the inner reservoirs during the season of reproduction.

A modification of the bouchot method of myticulture is employed in a part of the Lamotte Canal near Marseille. This canal is one of the branches which puts the sea in connection with Berre Lake and is traversed back and forth continually with the tidal waters, which contain great quantities of diatoms and Infusoria, making it an especially rich place for the cultivation of mussels. Because of the slight rise and fall of the tide in this stream, it is impossible to use here the bouchot system of culture. In place of it, claies, or movable wooden frames, are placed vertically between grooved stakes on which they can rise and fall by means of a floating axis. The grooved stakes are mounted with a crosstree bearing a ring on the underside. The frame is surmounted with a hook so that it can be raised from the water and hung on the ring of the crosstree above (fig. 223, opp. p. 236). With this device the mussel culturist can at any time gather, replenish, wash, or do any necessary work at his convenience, and when through, return the frame to the water.

The capacity of one of these claies is about 10,000 mussels, weighing from 660 to 880 pounds. The young mussels are collected on the shores of Berre Lake and placed on the claies by the same method employed in fixing seed mussels to bouchots. When of sufficient size they are marketed without any further transplanting.

Still another means for collecting spat and rearing mussels is by means of the raft collector (fig. 222, opp. p. 236) recommended by Fraiche (1863). It consists of a raft from which hang planks or frames in a vertical position. It is anchored in a region where mussels are spawning and when covered with spat is towed to a breeding basin where the rearing can take place without any further care than to see that no mud accumulates on the frames. The chief objection to this contrivance is that the planks or frames decay rapidly, often causing an entire loss of the harvest. This difficulty can not be remedied, as some have thought, by replacing the wood with metal, because spawn will not set on it.

Myticulture is also practiced in Italy, especially in the vicinity of Taranto, where mussels are raised to supply the southern markets of the peninsula as far north as Rome. Here the shellfish are cultivated on ropes made from rushes or "alfa" suspended in the water from stakes, which are placed from 20 to 30 feet apart, depending on the depth of the water. The ropes are hung over the mussel beds close to the shellfish in order to catch the free-swimming young. Six months after a set of spat has occurred the ropes are taken up and all the shellfish on them which have attained the size of an almond are removed. The smaller ones are left to grow until the following season, when they will have attained sufficient size for food purposes. The larger mussels selected are interlaced, either singly or in bunches, into ropes which are then suspended vertically in the water from a main rope extending between two stakes planted out in deep water. Parks are also utilized in the culture of mussels by this means, some of them extending 2,600 to 2,925 feet into the sea. Bouchon-Brandely (1883) states that the yearly yield of such a park is 40,000 to 50,000 pounds, worth from $880 to $1,100.

In Germany the Bay of Kiel contains extensive areas where mussels are raised by artificial means. The method employed there is to drive stakes into the bottom and leave them there for a period of three to five years, during which time they become covered with mussels of marketable size. They are then taken up, stripped of the shellfish, and replaced by others. About 1,000 stakes are planted annually in this locality, from which the yield of mussels amounts to about 800 tons.

The systems of myticulture which have been described above are especially adapted for regions where the bottom is composed of mud too soft to support a bed of mussels and where there is considerable rise and fall of tide over large areas. Where the bottom is hard or covered with only a thin layer of mud and where silt is not being deposited too rapidly, a much more economical method of cultivation is merely to transplant the mussels from crowded situations to more extensive areas where food is abundant. It is in this manner that mussels are grown for market in England and for that reason it is often spoken of as the British method to distinguish it from the bouchot system or French method. The practice is to collect young mussels from salt water and sow them on artificial beds in favorable localities. The best regions for planting are rich estuarine flats where there is plenty of sand and gravel covered with mud rich in diatoms, Infusoria, and spores of algæ. Care is taken to avoid planting the beds where they will be uncovered at low tide or subject to the ill effects of floods, gales, shifting sands, or frost. Furthermore, the individuals should not be placed so near together that one must lie on another. In this crowded condition the food supply is cut off from a large number of the shellfish and death or arrested development results, destroying the good effects of transplanting.

Harding (1883) and others believe that the spat will not mature in anything but pure sea water, but that for fattening the full-grown mussel brackish water of the density 1.014 is the most suitable. It is very doubtful, however, if brackish water is advantageous in perfecting the development of the mussel. The finest mussels ever seen by the author were cultivated in the water of the open ocean where there was no dilution with fresh water. In Menemsha Pond, Marthas Vineyard, Mass., where the mussels are fat and of unusually large size, the specific gravity of the water varies from 1.021 to 1.023. In this particular locality the author has found many individuals which exhibited an annual growth of an inch in length for the first three years of their existence. In Oyster Bay and Long Island Sound first-class mussels of excellent quality are grown in water where the density varies from 1.017 to 1.018. In these localities there is some dilution of the sea water, but not to the extent recommended by Harding.

The advantages of the bed system of cultivation are now being recognized in other countries. Bjerkan (1910) is recommending this method in Norway and figures samples of transplanted shellfish to show the splendid results obtained. Figures 192 and 193 (opp. p. 202) are views of an old mussel which had shown little or no signs of growth for years, but when transplanted added on the new portion of the shell, which is conspicuously shown in the photograph. Figure 191 (opp. p. 202) represents the exceptional growth which took place in a young mussel during a period of seven months after being transplanted at Morecambe, England.

Some of the progressive fishermen in this country have also recently put the transplanting method into practice with great success in certain regions of Long Island Sound. In one case a fisherman was paid by an oysterman to remove great quantities of mussels which were growing on and about his oyster beds. The fisherman carefully planted them at the mouth of Oyster Bay and three years later dredged them up by the hundreds of barrels, which he marketed in New York City at $1.25 per barrel. After paying all his expenses he found that he had left a net profit of $0.75 per barrel. For two months he was able to ship 100 barrels a day, which will indicate the income he was able to derive from the business. It is needless to say that this man is still cultivating mussels.

For harvesting the mussels a rake or dredge is used. In England the rake is recommended as the better instrument to employ for the reason that it does not crush the shells nor stir up sand over the bed. In size it has a breadth of about 18 inches, with teeth 1 inch apart. It has a handle 20 to 25 feet long and a wire net bag attached behind it for holding the catch. The mussels are sorted by means of a riddle, which is a sieve having a 1-inch iron mesh. After the mussels have been separated by hand they are sifted in the riddle. The large ones are taken for the market and the small ones replanted.

The yield from a crop of mussels properly cared for is something enormous and difficult to comprehend. In agriculture, corn is considered one of the most prolific and valuable of farm products, producing on the maximum 246 bushels to the acre. If marketed at $0.75 per bushel, the farmer realizes $184.50. However, when compared with a crop of mussels this yield appears small. Harding (1883) estimates for the English beds that the average yearly production is 108 tons per acre, worth at least $262. George A. Carman reports that the artificially planted mussel beds in the vicinity of New York produce from 4,000 to 6,000 bushels per acre, which at the market price of $0.40 per bushel amounts to from $1,600 to $2,400. Allowing three years for the growth of these beds, it leaves an annual average income of from $500 to $800 per acre. Furthermore, the time and labor required to plant and care for an acre of mussels is almost nothing compared with that expended by the agriculturist in raising his grain.

To the question, "which is the better method to use for cultivating mussels in the United States, the bouchot system or the bed system?" it is safe to answer that the latter is the only reasonable and practical one to attempt. There are probably few, if any, places on our coast where the bouchot could be utilized, and even if there were such places the cost of building materials and of labor are so high compared with the value of the shellfish that the method would prove unprofitable. On the other hand, we have thousands of acres along our shores that are adapted for mussel beds, with plenty of seed with which to plant them. The experiment of transplanting, as described above, has been tried, and it has proved not only successful but exceedingly profitable. Cultivation by means of the bed system is therefore the one to be recommended for use in this country.

DURATION OF MUSSEL BEDS.

One of the important facts brought out from the study of mussel beds is that, in general, they are short lived. Vast areas of bottom suddenly become covered with countless numbers of the shellfish, and three or four years later little or no trace of the bed can be found. George A. Carman, of Canarsie, N. Y., reported one bed in Jamaica Bay from which he took fine healthy mussels on one occasion and, on returning for a second load about 10 days later, found that practically all of the mussels were dead. A number of the Long Island oystermen stated that in their experience the average life of a mussel bed was three to four years.

In the course of the reconnaissance conducted during the summer of 1917 more than 3,000 acres of mussel grounds which had been reported on the best of authority were found to contain nothing but dead shells or no traces of mussels ever having been present. These reports included two beds on the north side of Long Sand Shoal, aggregating about 600 acres in extent, one in Fishers Island Sound between Latimer Reef and Eel Grass Ground of 500 acres, one at the mouth of Fort Pond Bay of 1,000 acres, one in Orient Harbor of 50 acres, and one off Sandy Hook of considerably more than 1,000 acres. In the case of the Sandy Hook bed, which bordered the south side of the Main Channel and Gedney Channel from a point 1 mile east of bell bouy 5 on the Main Channel to light buoy (Occ. W) 5 on Gedney Channel, a distance of nearly 2 miles, George A. Carman had reported finding a dense growth of 2¾-inch mussels in the fall of 1916 which he thought would be ready for the 1917 market. With his services as a guide, a series of dredgings was made the entire length of the bed, with the result that not a single large mussel was taken. A heavy set of young mussels from three-eighths to three-fourths of an inch long, however, was found to cover the entire territory. The explanation for the complete disappearance of the old bed was that during the heavy storms of the winter the tidal currents and wave action had been strong enough to strip the shellfish from the bottom and carry them to distant points.

Other causes which account for the damage or destruction of beds are freshets, shifting sand and ice, freezing of mussels exposed at low tide, depredations of starfish, drills, and other enemies, and suffocation from the mussels' own excrement. It is well known that mussel beds collect great quantities of mud, but few persons have realized that this mud, in large part, represents the excrement discharged by the mussels themselves. To determine roughly the quantity of waste matter which is thrown off by mussels daily, twenty-five 3-inch mussels were placed in a clean trough of slowly running sea water where the body discharges could be collected with a pipette from time to time. During a period of 72 hours the excrement given off measured 3,065 c. mm. Its composition, as revealed by the microscope, was diatom shells and detritus. This means that where mussels of this size lie no thicker than 500 to the square yard they discharge not less than 20 cc. of feces daily, and if this rate is maintained throughout the year the result would be an annual deposit of 7,000 cc., or about 1 peck, of the muddy matter per square yard. Viallanes (1892), making similar observations, states that in proportion to the numbers covering the same area of ground the mussel will deposit 3 times as much material as a Portuguese oyster and 18 times as much as a French oyster. Knowledge of this fact makes it easy to understand how a mussel bed, in a few years time, can build up a thick layer of mud and be destroyed by its own waste products.

Under natural conditions a uniform supply of mussels can not be depended upon, for, as past history has shown, there are years when they are exceedingly abundant and others when they are very scarce. The problem of maintaining a large and constant supply can be easily solved, however, by transplanting the young shellfish from exposed natural beds to favorable grounds in protected bays and estuaries as is now being practiced in Cold Spring Harbor. Minimum waste will occur where cultivated beds are completely cleaned up when ready for market and promptly planted again with seed mussels. The mortality rate will be low on beds that are permitted to stand not more than three years. Hard bottom is the most convenient ground on which to grow and handle a crop of mussels, but the shellfish will thrive equally well on mud bottoms which are unfit for oyster culture. The chief objection to raising mussels on mud is that it increases the cost of gathering and preparing them for market.

EFFORTS TO DEVELOP A MUSSEL INDUSTRY IN THE UNITED STATES.

Recognizing the importance of the extensive sea-mussel beds on the north Atlantic coast as a valuable source of food supply and the fact that as a nation we are failing to utilize them through ignorance or unreasonable prejudice, the Bureau of Fisheries undertook a limited publicity campaign in the spring of 1914 to acquaint the people of Boston and vicinity with the food qualities of this little-known shellfish. A 5-page pamphlet for public distribution was issued March 24, 1914, under the title "Sea

Mussels: What They Are and How to Cook Them," U. S. Bureau of Fisheries Economic Circular No. 12. It bears the photograph of a sea mussel on the first page, states briefly the magnitude of the sea mussel industry in Europe, points out the close relationship of mussels to clams and oysters, and shows that as a food they are delicious, nutritious, wholesome, and cheap when properly collected, handled, and prepared. The account concludes with a list of 18 recipes furnished by the French chef of a prominent Boston hotel. Some placards, 14 by 20 inches in size, were printed in heavy type with the words:

SEA MUSSELS

A CHEAP AND NUTRITIOUS FOOD

Recommended by

U. S. BUREAU OF FISHERIES

These were loaned to reputable fish dealers to put in their store windows, with the understanding that they should market mussels collected from waters knows to be free from pollution. In some cases this card of indorsement, with a hundred of the economic circulars, was all that was necessary to start a fish dealer in the mussel business. This was especially true in localities populated with English or French people, who possessed knowledge of their importance as a food in Europe.

Another method employed to get the shellfish before a large class of persons was to serve them on the tables of many first-class hotels, restaurants, and clubs. Boston offered the best opportunity for starting such a campaign, for in one of her leading hotels there was a French chef, Charles Doucot, whose enthusiasm for the mussel knew no bounds when he learned that the species could be procured on the New England coast. He had served them formerly in his father's Paris restaurant and was eager to be the pioneer in getting them introduced into the Boston hotels and eating houses. The Bureau arranged to furnish mussels without charge to every first-class hotel, club, and restaurant in Boston on the condition that they be given a prominent place on the menu card and the patrons urged to order them. The success of the plan surpassed expectations, largely due to the energetic support given the movement by Mr. Doucot, who was then president of the Boston Chefs' Club. In this influential position he persuaded the chefs of practically every first-class hotel, club, and restaurant in Boston to put sea mussels on their bills of fare. The newspapers appreciated the importance of the propaganda and with the active support of Mr. Doucot devoted considerable space from day to day to the campaign and the merits of the mussel as a food.

To bring the food value of the mussel to the attention of another large class of people who do not commonly eat at hotels and restaurants, the Bureau placed a barrel of the shellfish in each of the Boston police stations for free distribution to members of the force. As was expected, the chief topic of conversation on the following day, as the men went over their beats, was concerning the qualities of the "new sea food." The plan proved very successful in bringing the food to the attention of the general public for a short time.

In Lowell, Mass., the Bureau developed a market for mussels quickly by cooperating with the Y. M. C. A. in its educational lecture course. An agent of the Bureau arranged for a dinner in the association building at which mussels were made the conspicuous feature. The dinner, which was well attended, was followed by an illustrated lecture on the biology and economic importance of the sea mussel. The event was well advertised beforehand, and briefs were furnished to the newspapers of the city. The fish dealers were prepared with a fresh supply of mussels, a sufficient quantity of economic circulars containing the recipes for cooking them, and the placards bearing the recommendation of the Bureau of Fisheries. Persons who purchased mussels were presented with a circular. As a consequence the whole city was eating or talking about mussels on the day following this active campaign. Similar dinners, followed by a lecture, were given in one of the large Worcester churches and the Brockton (Mass.) Y. M. C. A.

The general result has been to create what promises to be a permanent and growing demand for this shellfish. In Boston a year after the campaign many dealers who never handled them before were selling mussels and were getting higher prices than had prevailed previously. In Worcester several of the markets experienced a growing mussel business, and the conditions were apparently the same in Lowell. Brockton seems to be the only place where the people could not be persuaded to eat them. A Providence dealer reported a considerable increase in his mussel sales, which he attributed to the publicity given the campaign by the newspapers. Pushcart venders in Boston have been selling them, and doubtless many other parties not known to the Bureau have taken up the business. The demand on the Narragansett Bay beds, which were hundreds of acres in extent, was so heavy during the campaign that the Bureau was lead to believe it unwise to continue the publicity work further until new sources of supply were found available.

In the summer of 1917 the writer was directed by the Bureau to make a reconnaissance of the mussel beds on a limited portion of the north Atlantic coast, with the object of locating positively beds which were sufficiently large and productive to support a commercial fishery and to collect data concerning their areas, depth of water over the beds, abundance, size, and quality of the shellfish, and also to consult with local fishermen to ascertain if they would engage in the fishery for mussels provided there should be a market for them. The territory examined included Plymouth Harbor, Mass.; Narragansett Bay, R. I.; and the north and south shores of Long Island, N. Y. Approximately 3,715 acres of mussel beds were located and charted. Of this area it was estimated that about 1,000 acres of the shellfish, containing not less than 2,000,000 bushels, were ready for the immediate market and that 1,500 acres would yield 1,000,000 bushels of seed mussels less than 1 inch long. The rest of the area was occupied by old beds which were depleted or mixed with such a great quantity of dead shells and trash as to make working them unprofitable commercially. The survey was necessarily incomplete owing to the brief time allotted for it, but was sufficient to show that for the time there was an abundant supply of mussels available immediately for the market besides vast quantities of seed mussels which could be transplanted to favorable situations and made ready for future needs.

In the year 1914, while the Bureau of Fisheries was engaged in placing the merits of the fresh sea mussel as a food before the public in Boston and vicinity, an oyster company in Providence was conducting some important experiments on the preservation of mussels by pickling and canning. Splendid samples in the form of canned mussels, pickled mussels, deviled mussels, or Muscello, and mussel cocktail were produced. The materials used were of excellent quality and they were put up in a most attractive manner. Except for minor defects, such as using wrong proportions of vinegar and spices in their preparation, which could be readily corrected, the products were of superior quality and promised to find a good market if properly advertised. But unfortunately the president of the packing company grew pessimistic about the possibilities of the business and stopped the packing of mussels without making any serious attempt to put them on the market.

The method employed in handling the shellfish for canning purposes as worked out by this company is recorded here because of its historic importance in marking the first step toward developing a mussel-canning industry in the United States.

For collecting mussels the same equipment is employed as in the oyster fishery, since the shellfish grow under essentially the same conditions as oysters, on the bottom and in water of varying depths from between tide marks to 100 feet. In Narragansett Bay most of the beds lie in from 10 to 60 feet of water. The principal difference in character between mussel and oyster beds that has to be taken into consideration in harvesting methods is that in the former the shellfish lie together much more thickly, are firmly attached to each other by byssus threads in the form of a carpet, and often accumulate much mud, while in the latter the shellfish are loosely distributed over a clean, hard bottom.

The type of oyster boat shown in figure 224 furnishes the most efficient means of collecting mussels. It is propelled by a gasoline or kerosene engine and carries two 5 to 7 bushel oyster dredges that are operated by power and manipulated from the pilot house. They are situated on the forward deck, one on each side of the boat. To operate the dredges successfully on a mussel bed requires both skill and experience, for if not enough warp is let out the dredge will slip over the surface of the shellfish, which are woven together, without picking them up, while, on the other hand, if too much warp is let out the dredge will plunge deep into the mud and fill with it to greater extent than with mussels. This involves a waste of time, labor, and energy to separate the mussels from the mud, which is accomplished by alternately raising the filled dredge from the water and dropping it back again. Two men are stationed on the deck to receive and empty the dredges as fast as they come up. Properly manipulated on a good bed of mussels, a boat equipped with two 7-bushel dredges can take on a load at the rate of 150 bushels per hour.

The mussels thus collected and brought to port are bound together in tangled masses and mixed with dead shells, mud, and much débris. A device for tearing the individuals apart and separating them from the foreign matter was devised from a standard coal screen over which there was made to play jets of water, as shown in figure 225. Mussels dumped into one end of the revolving screen are tumbled about, torn apart, and freed from débris by the running water.

After this preliminary treatment the shellfish are shoveled upon a shelf where they are rapidly culled by hand (fig. 228) and then given a final washing in a cylindrical screen which revolves, partially submerged, in a tank of water (fig. 226). After this cleansing they are placed in wire baskets, such as shown to the right in figure 226, and transferred to a steam chest or process kettle (fig. 227) which holds about 15 of the bushel baskets. When filled, the lid of the kettle is clamped in place, and this completes the preparation for cooking.

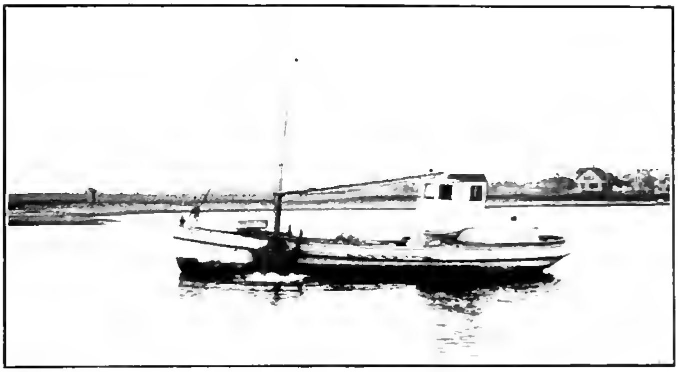

FIG. 224.—Oyster boat dredging up mussels in Narragansett Bay.

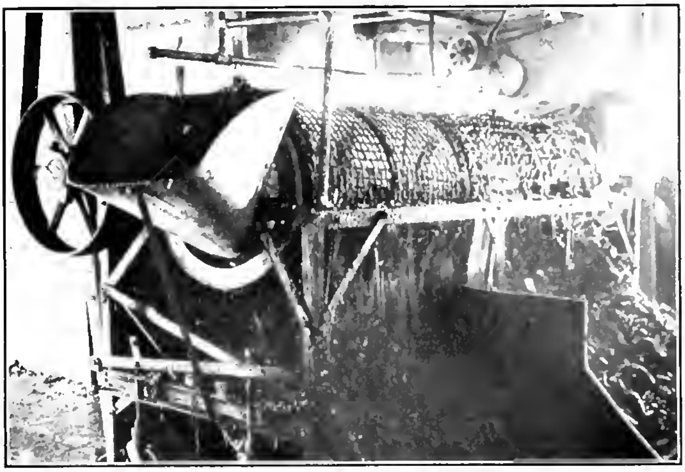

FIG. 225.—Modified coal screen used for cleaning and separating mussels.

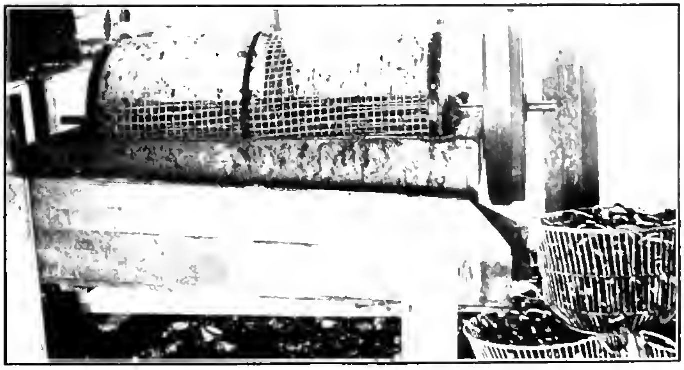

FIG. 226.—Revolving screen cylinder in tank of water used for final cleansing of mussels. Wire baskets for holding mussels are shown at right.

FIG. 227.—Steaming mussels in a process kettle.

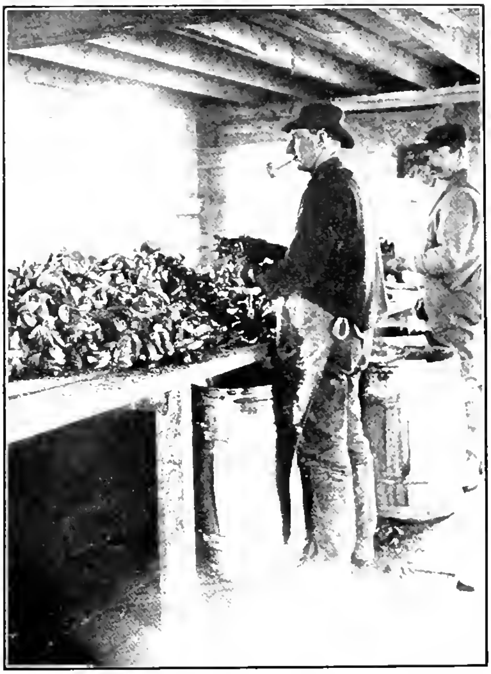

FIG. 228.—Culling mussels by hand.

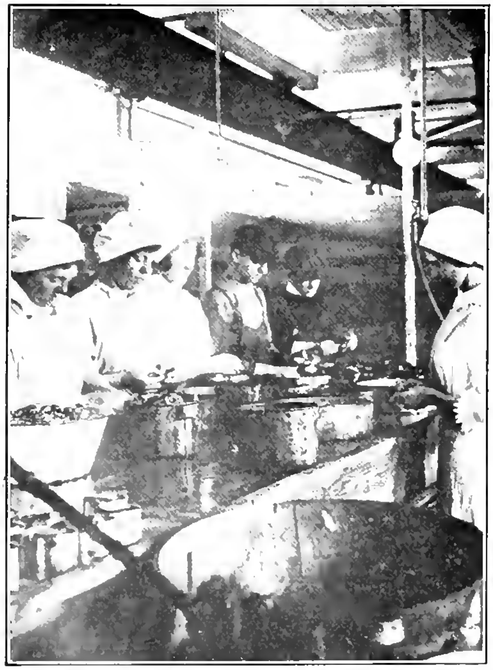

FIG. 229.—Girls shucking steamed mussels which are to be canned or pickled.

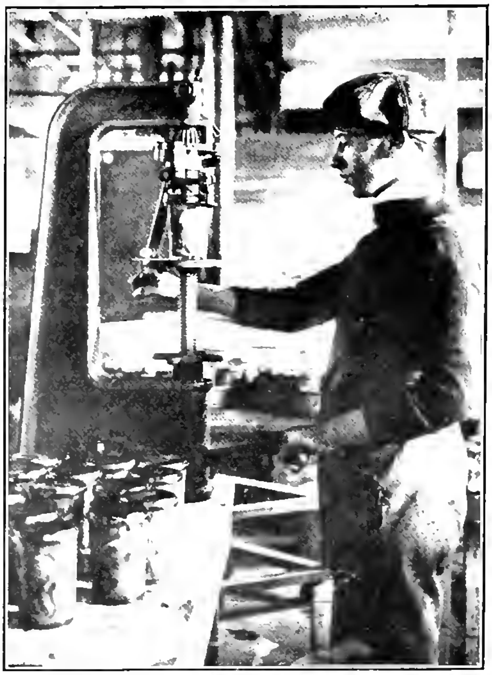

FIG. 230.—Sealing glass jars which have been packed with picked mussels.

The mussels are cooked with steam, which is turned gradually into the bottom of the kettle by an operator who watches the thermometer closely to see that the temperature does not rise above 100° C. or 212° F. Turning live steam directly against the shellfish or cooking them at a temperature higher than the boiling point of water hydrolyzes protein compounds in the shell and flesh, transforming them into products possessing a disagreeable odor and flavor. Some investigators, however, claim to have steamed out mussels under pressure at temperatures much higher than 212° F. without injuring the delicacy of flavor. They assert, moreover, that cooking at high temperatures is absolutely essential to the successful handling and preservation of the shellfish. The process is complete when the shells open and the flesh becomes readily detached. The proper length of time during which the shellfish must be steamed to obtain the desired results varies with the temperature employed and the quantity of material introduced at a given time.

When cooked to the proper degree, the baskets of mussels are removed from the process kettle and allowed to cool until they can be handled with comfort with the bare hands. Then they are taken to a shucking room, where girls and boys dexterously take out the meats and remove the byssus. The waste matter is dropped into barrels under the table and the meats collected in metal measures (fig. 229).

The mussel meats, after being measured, are packed in glass jars or tin cans with enough of the body liquor, which collects in the bottom of the process kettle, to nearly fill the receptacles. The filled jars or cans are next transferred to a machine which crimps on the covers air-tight without the use of solder (fig. 230). They are then packed in a crate and processed in the steam chest for about half an hour at a temperature varying between 240 and 280° F. Except for labeling, this completes the process of canning.

Mussels, after being steamed and shucked, can be pickled by placing them in a solution of 1 part strong vinegar and 2 parts water. White wine vinegar is best to use as a preservative. The flavor can be improved to suit the taste by the addition of a little spice, vegetables, such as carrots and onions, or slices of lemon. The pickled form can be canned and, if processed, will keep for a long time without deteriorating. Care must be exercised not to get too much spice in the mixture, for the strength continues to increase with age, especially where peppers are employed. Submerged in pickling liquor in wooden tubs of 5 to 10 gallons' capacity, mussels will keep well for weeks and are conveniently handled in this form for the immediate trade.

At the beginning of 1918 several prominent firms took active steps to put large quantities of mussels on the market in fresh or preserved form. With extensive advertising and a well-organized propaganda in its favor, there is every reason to believe that the result will be the establishment of a new and valuable fishery that will rank second only to that of the oyster, and at the same time add millions of pounds of flesh food to our annual food supply.

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS.

1. The sea mussel *Mytilus edulis* Linnæus is a bivalved mollusk closely related to clams and oysters and is one of the most abundant shellfish on our north Atlantic and north Pacific coasts.

2. The anatomy and physiology of the different systems of organs have been described.

3. The sexes are separate and mature their products at the end of the first year. Single females may spawn from 5,000,000 to 12,000,000 eggs annually. A ciliated larva is formed 4½ hours after fertilization, and when 10 weeks old possesses nearly all the organs of the adult. Under favorable conditions growth amounts to about 1 inch per year for the first three years. After that the rate is much reduced. A mussel bed represents one of the greatest organizations in nature for making flesh food by a short and rapid process.

4. The food of the mussel is practically unlimited, consisting of plankton organisms (chiefly the smaller diatoms and Protozoa) and detritus. It is possible that some of the dissolved organic carbon and nitrogen compounds are absorbed directly from the medium in which the shellfish are bathed.

5. Destructive agencies operating against the mussel are storms, shifting sands, extensive growths of eelgrass and other seaweeds which smother them, and a host of predacious enemies, including starfishes, conchs, winkles, oyster drills, dog-whelks, numerous fishes, gulls, ducks, rats, muskrats, seals, and walruses. A parasite, *Haplosporidium mytilovum*, which is described as a new species, destroys enormous numbers of mussel eggs.

6. In European countries mussels are prized as a food and hundreds of millions of pounds are consumed annually. In France the value of the fishery is second only to that of the oyster. Although exceedingly abundant in many places along our shores, very limited quantities have been eaten in this country up to the present time. Some use has been made of them for bait and fertilizer.

7. In chemical composition and nutritive value the mussel ranks equal to or superior to any other shellfish. The flesh is tender, palatable, and easily digested. The cost of production and marketing is less than for any other shellfish.

8. Marketable mussels are generally in season when oysters are out of season. Narragansett Bay and Long Island Sound mussels are usually in prime condition from March to June, while those on the south shore of Long Island are best from June to September.

9 Fresh mussels only, taken from pure water subject to the ebb and flow of tides and free from sewage contamination, should be eaten.

10. Mussels are cultivated extensively in France, Italy, Germany, and England, where they yield large returns. At the time of preparing this report cultivation by the bed system was being practiced successfully on a small scale in Cold Spring Harbor, L. I., and in the vicinity of New York with an annual yield of 2,000 to 3,000 bushels per acre. Thousands of acres of unutilized bottom on our north Atlantic coast are adapted to the culture of mussels.

11. Natural mussel beds, under normal conditions, last from two to four years. Unless utilized commercially before the end of this period they are destroyed by natural enemies or by physical forces.

12. That the mussel beds on our north Atlantic and north Pacific coasts, if utilized, are capable of yielding millions of pounds of wholesome, palatable flesh food annually is established beyond question. The time has come when we can no longer afford to waste this great natural resource by failure to utilize it.

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A NEW BACTERIAL DISEASE OF FRESH-WATER FISHES.

By H. S. DAVIS, *Fish-Pathologist, U. S. Bureau of Fisheries.*

Contribution from the U. S. Fisheries Biological Station, Fairport, Iowa.

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INTRODUCTION.

While working on the protozoan parasites of fishes at the U. S. Fisheries biological station, Fairport, Iowa, during the summer of 1917 a number of fish which had been recently placed in aquaria were found to be dying from the effects of a bacterial infection. Later in the season the disease was quite prevalent among fishes confined in aquaria, but owing to the pressure of other work no particular attention was paid to it at that time.

Early the following summer (1918) the disease again made its appearance, this time in one of the ponds. In the course of a series of feeding experiments being carried on at the Fairport station a large number of fingerling buffalofish were held in a pond in which had been placed a considerable quantity of horse manure. These fish grew rapidly for some time and appeared to be in a healthy, vigorous condition. However, early in July they began to die in large numbers, and a careful examination showed that the dying fish were infected with the same species of bacteria found the previous summer on fish in aquaria. A little later in the season the disease appeared among fishes that had recently been transferred to troughs for feeding experiments and caused considerable mortality.

On account of its evident importance it was decided to undertake an extended investigation of the disease to determine, if possible, a practicable method of control. This investigation was begun during the latter part of the summer of 1918 and continued during the summer of 1919. During the summer of 1919 the writer was assisted by Miss Miriam Mackenzie.

DESCRIPTION OF THE DISEASE.

The disease is easily recognizable, being distinguished by well-defined characteristics. Ordinarily the first indication of the disease is the appearance of one or more characteristic dirty-white or yellowish areas on some part of the body. The infected areas are usually quite conspicuous and increase rapidly in size. In some cases a large proportion of the body may eventually become infected. With the increase in the size of the lesions the fish become greatly weakened and usually die from 24 to 72 hours after the lesions first become visible.

The lesions may occur on any part of the body, but in the majority of cases first appear on the fins, especially the caudals, and from there spread to adjoining portions of the body (figs. 231–237). In late stages of the disease the lesions may cover from one-half to two-thirds of the body, while the fins become badly frayed, the caudal sometimes becoming worn to a mere stub (figs. 233 and 234). There is considerable variation in the site of the initial infection. As will be shown later the disease is usually the result of injuries and first makes its appearance in the injured region. There is also considerable variation dependent on the species of fish infected. In the crappies, for instance, the disease is usually confined to the fins and gills (figs. 231, 232, and 243) and only rarely does the infection spread to the body. Possibly this may be due to the fact that these fishes are especially susceptible to the disease and die before there is time for the bacteria to become widely spread over the surface of the body.

Lesions on the gills first appear as small, white patches (figs. 243 and 244). These spread rapidly, and the fish usually dies within a few hours (fig. 245).

On bullheads (*Ameiurus melas* and *A. nebulosus*) the lesions have a somewhat different appearance from those on scaled fishes. They usually first appear as numerous small, circular areas with sharp, distinct outlines (fig. 238).

The centers of the lesions are dark blue overlaid by a whitish veil or cloudiness. Surrounding this is a well-defined zone about 5 mm. wide characterized by a distinctly reddish tinge due to hyperemia. This region, like the central portion of the lesion, is overlaid by a slight cloudiness. Later the lesions often become confluent and cover the greater portion of the body (figs. 239–241). For some reason, in fingerling bullheads the disease more commonly starts on the caudal fin, as in other fishes, and the infected area gradually advances toward the anterior end, the entire posterior end of the body becoming a dirty white (fig. 242).

In many respects the lesions resemble those produced by Saprolegnia and, in fact, have usually been confused with them. A careful examination will, however, readily enable one to distinguish between the two, since the bacterial lesions do not present the fuzzy appearance so characteristic of those infected with fungus. Of course they can easily be distinguished by a microscopical examination, but this is usually not necessary.

In some instances a bacterial infection may be followed by an infection with Saprolegnia, but in such cases the fungus is of secondary importance. During the summer very little fungus has been observed at Fairport and infection with Saprolegnia appears to be dependent on the temperature of the water. When the temperature is high (above 75° F.) the bacteria develop rapidly and the fish die so quickly that the fungus does not have time to develop to any appreciable extent. However, the bacteria are much more susceptible to any decrease in temperature than is the Saprolegnia, the result being that at temperatures below 75° F. the bacteria develop much more slowly and the fungus growth may become evident before the fish succumbs.

This is notably the case early in the fall. With the advent of cooler weather a considerable number of the diseased fish may show characteristic fungus growths in connection with the bacterial lesions. But even in these cases there can be little doubt that the lesions were primarily due to bacteria and that the Saprolegnia was a secondary invader.

Occasionally fish may die from the disease without showing any lesions on the body or fins. In such cases the gills are always badly infected, a large part of them being entirely destroyed. In late stages of gill infection the fish often show characteristic signs of suffocation, such as swimming at the surface and gasping for breath. In the majority of cases, fish with infected gills will also show lesions on the surface of the body or fins, but here again there is considerable variation in different species.

OCCURRENCE OF THE DISEASE.

It seems probable that most species of fishes are liable to attack by this disease, although some species are much more susceptible than others. While it has been necessary to confine our observations to a comparatively small number of species the disease has been observed on the following fishes: The buffalofishes (*Ictiobus bubalus* and *I. cyprinella*), the sunfishes (*Lepomis incisor* and *L. humilis*), the carp (*Cyprinus carpio*), the black basses (*Micropterus salmoides* and *M. dolomieu*), the crappies (*Pomoxis sparoides* and *P. annularis*), the warmouth (*Chænobryttus gulosus*), the yellow perch (*Perca flavescens*), the white bass (*Roccus chrysops*), the brook trout (*Salvelinus fontinalis*), the minnow (*Pimephales notatus*), the channel catfish (*Ictalurus punctatus*), and the bullheads (*Ameiurus nebulosus* and *A. melas*). From the above list it will be readily seen that the disease is widespread, and there is little reason to doubt that under favorable conditions it may occur on nearly all species of fresh-water fishes.

In one instance several tadpoles which were confined in a tank with a number of infected buffalofish developed well-defined lesions on the tail. The tadpoles were just beginning to metamorphose, which may have made them more susceptible to infection. Attempts to inoculate adult frogs with the disease have proved unsuccessful.

So far it has not been possible to obtain any data regarding the geographical distribution of the disease. However, while on a visit to the St. Lawrence River at Ogdensburg, N. Y., during the first week in July, 1919, the writer found the bacteria in lesions on the smallmouth black bass and the common perch. In this case the fish did not appear to be seriously injured by the bacteria which were evidently growing very slowly.

CAUSE OF THE DISEASE.

The disease is produced by an apparently undescribed species of bacteria for which I propose the name *Bacillus columnaris*. It has not yet been possible to grow the organism in pure culture, but its appearance is so characteristic that it is always easily recognizable if present in any numbers. It is a long, slender, flexible, rod-shaped organism, 5 to 12μ long and 0.5μ wide (figs. 246 and 247). The bacteria are very transparent and unless present in considerable numbers are difficult to distinguish on this account. They usually appear perfectly homogeneous, but rarely may exhibit a slightly granular structure. The bacteria are motile and probably possess flagella, although owing to lack of facilities this has not been determined with certainty. They can often be seen to move in a straight line for a considerable distance, the movement being accompanied by a sinuous bending of the rod which may temporarily assume an S-shape. One of the characteristic movements is to turn one end slowly in a circle, the other end remaining stationary and forming a pivot on which the entire rod revolves. This movement is very noticeable along the edge of scales or bits of infected tissue when placed on a slide. Large numbers of bacteria can usually be seen in such places with one end attached while the free end moves back and forth in the manner described above.

Another characteristic is the formation of small chains of bacteria from one object to another while on the slide. The chains are formed by the bacteria arranging themselves in rows joined end to end, the ends slightly overlapping. Usually these chains consist of two or three rows of bacteria arranged parallel to each other, but occasionally there may be but a single row. Bacteria can be seen continually moving back and forth along these living chains in a very characteristic manner.

However, the most characteristic movement and the one which usually serves to make the species easily recognizable is well shown when a little material scraped from a lesion is placed on a slide in a drop of water. Possibly owing to the pressure of the cover glass the bacteria soon collect in immense numbers on the edge of bits of infected tissue, scales, etc. Here they form short columnlike masses, each column being separated a short distance from its neighbor (figs. 248 and 249). The columns usually taper slightly toward the free end, which is ordinarily rounded but in rare cases may be pointed. In some cases the ends of the columns may be distinctly enlarged. In favorable cases a whole series of these columns may form along the edge of a scale. These columnar masses of bacteria are very characteristic, and it is apparently in this way that they free themselves from the gelatinous matrix in which they are embedded while growing on the fish. Along the sides and rounded ends of the columns can be seen bacteria with one end attached while the free end waves back and forth in the manner already described. Bacteria continually break loose from the columns while others swarm out to take their place. Occasionally short chains may be formed extending out from the ends of the columns, the bacteria at the ends continually becoming free but often managing to work their way back along the chain after a time. When free, the bacteria at first exhibit a peculiar vibratory movement somewhat different from the Brownian movement and which, when once seen, is easily recognized. After being free a short time they usually collect on the underside of the cover glass and become perfectly motionless.

These characteristic swarming movements of the bacteria are no doubt continually taking place on the fish, at least in late stages of the disease, for it has been found that badly diseased fish are continually shedding bacteria in enormous numbers.

Owing to the fact that a variety of stains was not available the staining reactions of the bacteria were not studied in detail. They stain readily with fuchsin and Giemsa's stain, the stained preparations appearing perfectly homogeneous.

No evidence of sporulation has been observed, and that they do not form spores is also indicated by the fact that the bacteria are easily killed by chemicals and drying.

All attempts to grow the bacteria on artificial media have so far proved unsuccessful. During the summer of 1918 the writer made several attempts to isolate the bacteria, and these experiments were continued by Miss Mackenzie during the summer of 1919. On account of the limited facilities at our disposal it was only possible to try a few of the simpler media. Standard beef-broth agar and fish agar were tried, and although bacteria appeared in the plates in large numbers no trace of *columnaris* could be found. Several lots of media with a less acid reaction than the standard were tried, including one with the same reaction as the river water, but the results were all negative. Attempts to grow the bacteria on fish serum were equally unsuccessful. Possibly with facilities for employing a wider range of media it may be possible to isolate the bacteria. However, the failure to isolate the bacteria did not prove so serious a handicap in the study of the disease as would ordinarily be the case. The bacteria can easily be procured in large numbers from the lesions of infected fish, and their appearance is so characteristic that they can be readily recognized.

While, of course, the failure to isolate the bacteria in pure culture has rendered it impossible to demonstrate the cause of the disease beyond question, the evidence is so conclusive as to leave little room for doubt. The bacteria can always be found in abundance in the lesions, and the disease can easily be produced in healthy fish by scraping off a few scales and applying a few bacteria from a diseased fish. In advanced stages of the disease there are usually large numbers of bacteria present in addition to *columnaris*, but it has been found that in small lesions *columnaris* is invariably enormously more abundant than any other organism, and in some cases when the lesions first become visible there is a nearly pure culture of this species present.

Strong evidence for the causal relationship of *columnaris* to the disease can be seen in infected bullheads. The reader will recall that the lesions on these fish are characterized by an outer reddish zone about 5 mm. wide, while the center of the lesion has a quite different appearance. When very small the entire lesion presents the same appearance as the peripheral zone in later stages. As the lesions increase in size the characteristic blue center appears and enlarges with the growth of the lesion. It is obvious that the red zone is found only where the skin has been recently infected and that the darker color is due to destructive changes produced by the bacteria. If a little material is scraped from the darker central portion of the lesion it will be found that considerable numbers of bacteria are present in addition to *columnaris*. On the other hand, if material from the red zone is examined it will be found that nearly all the bacteria present are *columnaris*. Other species are so few as to be scarcely noticeable. Of course the same thing is true of lesions on other species of fishes, but owing to the absence of scales it is more striking in the case of the bullheads than elsewhere. The great abundance of *columnaris* around the advancing edge of the lesions is so noticeable that it soon became a matter of routine in our work to always procure the bacteria from this region. The smears from which the photomicrographs (figs. 246 and 247) were taken were made from such material.

PATHOGENESIS.

As previously stated the bacteria grow only on the surface of the body or on the gills. No case has been observed where they had penetrated any distance into the tissues. When growing on the body they destroy the integument, the muscles sometimes being exposed in late stages of the disease. For obvious reasons the development of the lesions can be more easily studied in the case of scaleless fish, such as the common bullhead. Figure 250 is a cross section through a lesion which is just beginning to develop. The outer layer of the epidermis has begun to disintegrate, but the inner layer is not yet noticeably affected. Figure 251 shows a little later stage. The epidermis is now entirely destroyed in one place at the right in the figure. On either side the epidermis is rapidly disintegrating. A somewhat later stage is shown in figure 252. The outer layer of the corium which has been exposed by the destruction of the epidermis is now beginning to show signs of disintegration. In late stages of the disease the corium may be entirely destroyed in the center of the lesion, as shown in figure 253.

As previously described, the lesion grows rapidly outward in all directions from the center of infection. Figures 254 to 257 are from photomicrographs of sections through the margins of lesions and show the disintegration of the epidermis caused by the outward growth of the bacteria. Usually there is a noticeable hyperemia just underneath the epidermis in this region. This is well shown in figures 255 to 257. The capillaries in the outer portion of the corium become gorged with blood; eventually their walls disintegrate and the blood fills the interstices of the corium and crowds between the corium and the epidermis. Occasionally the blood corpuscles may even penetrate a short distance into the epidermis (fig. 255). This is the cause of the reddish zone which is often quite distinct around the margin. Later as the epidermis is destroyed the corpuscles also disintegrate. It is scarcely necessary to add that the hyperemic zone advances outward as the lesion enlarges. Usually the hyperemia is noticeable only underneath that portion of the epidermis which is undergoing disintegration, but occasionally may occur before the overlying epidermis shows any change. No case has been observed where the muscles showed any appreciable pathologic changes. Possibly this may be due to the fact that the fish usually die by the time the lesions have developed to the stage shown in figure 253.

While the above account is based on a study of the lesions in bullheads the same conditions are found in other fishes with some slight modifications due to the presence of scales. In these fishes the scales become loosened and slough off as the integument disintegrates.

In all cases there is a thick, matted layer of bacteria covering the lesion. This layer is not shown in the figures since it invariably drops off during the treatment to which the tissues are subjected in preparation for sectioning. Although the bacteria occur in enormous numbers in this superficial layer only a few scattered individuals can be found among the disintegrating cells of the epidermis and corium.

When growing on the gills the bacteria produce much the same effects as on the integument. The epithelium and blood vessels are entirely destroyed until only the skeletal parts are left. As would be expected gill infections are much more quickly fatal than infections on the surface of the body.

METHODS OF INFECTION.

Since the bacteria grow only on the surface of the body and gills it is evident that infection can easily take place by their being carried in the water from one fish to another. As previously pointed out the bacteria are continually being set free from infected fish, especially in late stages of the disease. Where fish are crowded closely together, as in aquaria, the bacteria can thus readily pass from one individual to another. They are also easily rubbed off onto the nets or hands when diseased fish are handled and then can readily be transferred to healthy fish. We have several times infected healthy fish by simply holding them in our hands after having previously handled diseased fish. There is also a possibility that the disease may be transmitted by predacious insects, but no experiments have as yet been carried out along this line.

Undoubtedly the most important factors in the spread of the disease under ordinary conditions are those which render the fish more susceptible to infection. All the evidence at hand indicates that the bacteria rarely or never attack healthy, uninjured fish under ordinary circumstances. If, however, a fish is injured or its vitality lowered in any way it is liable to contract the disease. Most outbreaks of the disease which have come under the writer's notice have occurred among fish which had been recently handled. As is well known it is almost impossible to handle fish without some slight injury to the fins or body, and even a very slight injury is all that is necessary to enable the bacteria to gain a foothold, and once started they are able to spread rapidly over the body. During warm weather, when the temperature of the water at Fairport averages about 75 to 80° F., an outbreak of the disease is almost certain to occur within 48 to 72 hours after the fish are handled. Well-defined lesions may sometimes appear in 24 hours, but the fish usually do not begin to die until after 48 hours. The greatest mortality usually occurs on the third and fourth days, after which there is a gradual decrease until the disease finally disappears. If the fish are again handled, however, there is almost certain to be another outbreak.

In a large percentage of cases the disease first makes its appearance on the fins, especially the caudal. This is, of course, readily explained since no other part of the body is so liable to be injured by the struggles of the fish when taken in a net. Of course, any slight abrasion on the surface of the body, such as the removal of a few scales or even a slight injury to the epithelium, is equally liable to infection. It has been found very easy to infect fish artificially by simply scraping away a few scales with a scalpel and applying a small amount of material scraped from a diseased fish. Usually a characteristic lesion will develop around the site of infection in 24 to 48 hours.

There is also evidence that in some cases lowered vitality unaccompanied by mechanical injuries may result in the fish becoming infected. This is probably the explanation of the epidemic which appeared in one of the ponds at Fairport in which young buffalofish were being held for a feeding experiment. These fish had not been handled for some weeks previous to the outbreak of the epidemic. Just before the disease appeared the water had become noticeably foul and this, no doubt, so lowered the vitality of the fish as to make them susceptible to infection. The writer has also been informed by fishermen that they had seen fish with the same disease in isolated ponds and sloughs along the Mississippi River late in summer. At this time the water in these ponds becomes very warm and stagnant, conditions which would favor the development of the bacteria while tending to lower the vitality of the fish.

Another important factor influencing the spread of the disease is the temperature of the water. As already pointed out *columnaris* is very susceptible to temperature changes and grows rapidly only at a comparatively high temperature. The disease is distinctly a warm-weather disease, and so far as our observations go is not ordinarily of great importance when the temperature of the water is low. This was very noticeable at Fairport during September, 1919. With the advent of cooler weather there was a considerable decrease in the temperature of the water in the aquaria in which the experimental fish were kept. After the first week in September the average temperature of the water decreased from about 75 to 80° to about 70° F. and there was a notable decrease in the severity of the disease. The percentage of infected fish decreased, the disease developed more slowly, and a considerable percentage of the infected fish recovered.

The writer does not, however, wish to give the impression that there is no danger of an outbreak of the disease when the water temperature falls below 70° F. There is some evidence that an epidemic may occur at a comparatively low temperature, but it is probable that under such conditions the disease is much less severe and more easily controlled. That the bacteria may develop at lower temperatures is shown by an experiment with brook trout. A number of fingerlings were shipped to Fairport from the hatchery at Manchester, Iowa, and placed in a trough supplied with running water from a well. The temperature of the water averaged about 62° F. On September 13 two badly diseased fish, one buffalofish and one bluegill, were placed in the trough among the trout. At a temperature of about 75° F. both fish would in all probability have died in less than 24 hours. However, after being placed in the trough with the trout the bluegill lived 48 hours and the buffalofish about 72 hours. One of the trout was found dying with the disease on September 17. Unfortunately, owing to the writer's departure from Fairport, it was impossible to continue the experiment longer.

During the first week in July, 1919, the writer found a slight infection on a yellow perch and one on a smallmouth black bass from the St. Lawrence River at Ogdensburg, N. Y. In each case the infection was in wounds on the side of the body. These fish were in a tank with a large number of other fishes, and during the three days they were under observation none of the other fish contracted the disease. Furthermore, the lesions on the infected fish did not increase noticeably in size during this time and the fish showed no ill effects from the disease. Since the temperature of the water averaged about 65° F. it is probable that the failure of the disease to develop rapidly and spread to the other fishes in the tank was largely due to this fact. Many of the other fishes confined in the tank had been more or less injured when captured, so there would seem to have been every opportunity for the disease to spread. However, in this case it was impossible to determine definitely whether the failure of the disease to develop was due to the low temperature or to the fact that the bacteria may have belonged to a much less virulent strain than that at Fairport. It has not yet been possible to carry out any detailed experiments to determine the effect of temperature on the virulence and growth of the bacteria, but it is hoped to do so in the near future.

There is also evidence that, in general, fish are more likely to contract the disease from fish of the same species than from one of another species. This means, of course, that physiological strains of bacteria may be developed on different species of fish. As is well known such physiological strains are common among many species of bacteria. The strongest evidence of the occurrence of physiologically distinct strains in *Bacillus columnaris* was obtained in the course of some experiments with the black bullhead (*Ameiurus melas*). This species is ordinarily not very susceptible to the disease, and during the summer of 1919 a number of these fish were kept in the same tank with infected buffalofish and bluegill without any of them contracting the disease. After several weeks one of the bullhead was artificially inoculated with bacteria obtained from a diseased buffalofish. Inoculation was made as usual by scraping away the epidermis from a small area on one side of the body and rubbing the bacteria into the wound. The bullhead developed a characteristic lesion, and within 3 or 4 days practically every bullhead in the tank became infected. The epidemic among the bullhead was not confined to this tank but soon spread to bullhead in adjoining tanks. This can be easily explained. On account of their apparent immunity to the disease no precautions were taken to prevent the bacteria getting from one tank to another, and they could easily have been transferred on the hands or nets. The epidemic developed with remarkable rapidity, and within a few days nearly all the bullhead which had been held in the tanks from one to several weeks without showing any signs of the disease were dead or dying. Only by the use of control measures to be described later was the epidemic checked and a few fish saved. It was noticeable that although the infected bullhead were in several instances kept in the same tanks with buffalofish and bluegill the disease did not spread among them nearly so rapidly as among bullhead, although ordinarily both buffalofish and bluegill are more susceptible to the disease.

It has also been observed in making artificial inoculations that while it is usually not difficult to infect a fish with bacteria from another species a larger percentage of positive results is often obtained when the bacteria are taken from a fish of the same species. Further investigations along this line are greatly to be desired.

As intimated above, while most species of fresh-water fishes are liable to be attacked by the disease some species are much more susceptible than others. It is, of course, by no means easy to determine accurately the relative susceptibility of different species, but there can be no question that there is a great deal of variation in this respect. It is possible to divide the fishes which have been most studied into two classes. The first includes those species which are very susceptible and are almost certain to contract the disease in large numbers if handled during warm weather. In this class we would include the buffalofishes (*Ictiobus bubalus* and *cyprinella*), the crappies (*Pomoxis annularis* and *sparoides*), and possibly the bluegill (*Lepomis incisor*). The second class includes those fishes which are ordinarily only moderately susceptible and do not usually contract the disease in such numbers, even in warm weather. Furthermore, a considerable percentage of the diseased fish may recover if kept under favorable conditions. In this class we would include the largemouth black bass (*Micropterus salmoides*), the channel catfish (*Ictalurus punctatus*), the bullheads (*Ameiurus nebulosus* and *melas*), the sunfish (*Lepomis humilis*), the carp (*Cyprinus carpio*), the warmouth (*Chænobryttus gulosus*), and the white bass (*Roccus chrysops*). Of course it is not to be understood that all of the species in each class are equally susceptible, for that is certainly not the case, but in the present state of our knowledge it does not seem advisable to attempt a more detailed analysis of their relative susceptibility to the disease.

It is also noticeable that the young of any species are, in general, more susceptible than are the adults. This is especially true in the case of the carp, the young of which are quite susceptible, while the adults are nearly immune.

At first it was assumed that the bacteria must be widely distributed in the water, since this would most readily explain the appearance of the disease when the fish are handled, but we have no proof that this is the case, and there is some evidence that the bacteria do not live for any length of time off the fish. If this is true, we are forced to assume that they are able to live in small numbers on perfectly healthy fish without injuring them, but are capable of increasing enormously whenever proper conditions arise. Such a state of affairs is not unknown as in the case of streptococci and pneumococci in man.

TREATMENT AND CONTROL OF THE DISEASE.

On account of the great economic importance of the disease special efforts have been made to develop effective methods of control. Early in the investigation it became evident that reliance must be placed chiefly on methods for preventing the spread of the disease rather than to attempt to cure fish already infected. This is due to the fact that the bacteria, although living exclusively on the exterior of the fish, form a thick, matlike growth which protects the bacteria underneath from the effects of chemicals. Furthermore, the bacteria soon make their way underneath the scales which form an additional protection. To kill bacteria in such protected situations requires a comparatively strong solution.

A number of chemicals have been tried in the effort to find an effective control for the disease, but only potassium permanganate and copper sulphate have been found to be of any value. In all our experiments with chemicals we have first determined the maximum concentration of the chemical which the fish can stand without serious injury. Different species differ greatly in this respect, and unfortunately the fishes which are least resistant to chemicals are often very susceptible to the disease. It was soon found that the buffalofishes are among the most susceptible species, both to chemicals and to the disease, and it is believed that any treatment which will succeed with these fish will be equally successful with most of our common fishes. Having ascertained the strength of the solution which the more susceptible fishes could stand without injury, we then attempted to determine the minimum concentration which will kill the bacteria when fully exposed to the chemical. Since the bacteria can not be grown on culture media it is obviously impossible to determine with certainty when they are killed. It was found, however, that fairly accurate results could be obtained by placing the bacteria on a slide and then treating them with solutions of various strengths. The cessation of all movement by the bacteria was taken as evidence that they were seriously injured if not killed. While, of course, there are serious objections to this method it was found in practice to work out remarkably well.

Of course the time element is important in the use of any chemical. Treatment with a very weak solution may be as effective as a much stronger solution if the time is sufficiently increased. Temperature may also be an important factor, but we have only meager data as to its effects. With few exceptions our experiments have been carried on with river water at a temperature of 75 to 80° F.

During the summer of 1918 an extensive series of experiments with potassium permanganate was undertaken. It was found to greatly weaken or kill the bacteria in solutions so dilute that most species of fish could be kept in them for some time without serious injury. In order to kill the bacteria it is necessary to treat the fish with a 1 to 50,000 solution for 10 to 15 minutes. Weaker solutions have little effect. Buffalofishes can undergo this treatment without serious injury, while the black bass and sunfishes can stand a much stronger solution. A 1 to 20,000 solution was used on black bass for the same length of time with good results. However, very few fishes can stand a 1 to 20,000 solution, and weaker solutions do not seem to penetrate far into the bacterial mat covering the lesions. Furthermore, potassium permanganate is expensive and dissolves slowly in water. For these reasons the potassium-permanganate treatment was later abandoned in favor of copper sulphate.

A number of experiments with copper sulphate were made during the summer of 1918, and it was found that a 1 to 30,000 solution is more effective than a 1 to 50,000 solution of potassium permanganate and not so injurious to the fish. A solution of this strength will not, however, kill bacteria which are well protected, such as those beneath the scales. Our experiments showed that normal fingerling buffalofish are not appreciably injured when placed in a 1 to 30,000 solution for 30 minutes, but diseased or weakened fish are not so resistant. Buffalofish over 1 year old are not injured by treatment with a 1 to 25,000 solution for 30 minutes, and black bass and bullheads can stand a 1 to 20,000 solution for the same length of time without injury. As a result of these experiments the following treatment was recommended and used with much success: The fish previous to the appearance of any lesions are placed in a 1 to 30,000 solution of copper sulphate for 20 minutes and are then removed at once to running water. If properly handled they rarely suffer any permanent injury. Wooden vessels are preferable, and if it is necessary to use galvanized vessels they should be painted to prevent chemical action between the copper sulphate and the metal sides of the vessel. A thin coating of melted paraffin over the inside of a galvanized tank serves the purpose admirably. During the treatment some of the less resistant species of fishes may swim around at the surface and show more or less signs of distress, but this does not necessarily indicate any serious injury.

It should be distinctly borne in mind that the treatment to be effective must be given within a few hours after the fish have been handled and before any signs of infection appear. If the fish are to be confined in aquaria, two or three successive treatments at 12 to 24 hour intervals are advisable. When this treatment is properly used it is believed it will effectually prevent any serious outbreak of the disease. It must be repeated, however, every time the fish are handled or subjected to injury in any way.

In an experimental test of this treatment 30 fingerling buffalofish were seined from one pond. They were handled quite roughly, and 14 controls were placed in a small aquarium without being treated. The remaining 16 fish were treated with a 1 to 30,000 solution of copper sulphate for 20 minutes and then placed in a small aquarium like that in which the controls were held. Throughout the experiment both aquaria were supplied with running water, and the conditions in each were as nearly identical as it was possible to make them. Two of the treated fish died within 12 hours, probably as a result of mechanical injuries. At the end of 24 hours the fish were again treated with a 1 to 30,000 solution for 20 minutes. Twenty-four hours later two of the treated fish were found dead, but a careful examination failed to disclose any signs of *Bacillus columnaris*. Since the remaining fish showed no signs of infection no treatment was given at this time, but 6 hours later one fish showed a well-defined lesion at the base of the tail. This fish was at once removed and the rest given the same treatment as before. Since no further signs of infection appeared in this lot in three days the experiment was discontinued.

Among the controls 3 fish showed well-defined lesions after 24 hours, and at the end of 48 hours 11 out of the 14 were dead, while 2 of the remaining 3 had well-developed lesions on the tail and died a few hours later. The remaining control died the next day with a large lesion on the side of the head. In short, there was a loss of 31¼ per cent among the treated fish and 100 per cent among the controls. Four of the five fish which died among the treated lot were in all probability killed by the direct effects of the copper sulphate. A large number of experiments have shown that fish when weakened in any way, as by handling or being kept in water deficient in oxygen, are much more susceptible to the injurious effects of the treatment than perfectly normal fish and are often killed by solutions which will not appreciably injure fish in good condition. It is this fact which has made it impossible to devise a treatment which will be successful under all conditions. Of course it is evident that the fish which are so weakened as to be injured by the treatment are the very ones which are most liable to contract the disease if not treated.

It has not been practicable to conduct many experiments so completely under control as this one, but we have in a number of instances successfully checked by this treatment an outbreak of the disease among fish which were being kept in aquaria for other purposes. Another test of the treatment under somewhat different conditions is of considerable interest: On July 20, 1919, in connection with a series of feeding experiments which were being carried on at the Fairport station, a number of 3-year-old buffalofish were seined from the pond in which they had been confined for some time and distributed among four different ponds. This necessitated handling the fish rather roughly and transferring them some distance in a galvanized tank. To make matters worse it was a very hot day and under ordinary circumstances there would undoubtedly have been considerable loss, especially since many of the fish were badly rubbed during the transfer. Before being liberated in the ponds all the fish were treated for 20 minutes with a 1 to 30,000 solution of copper sulphate. Of the 551 fish treated only 4 died as a result of the transfer, and none of these showed any evidence of the disease. It is unfortunate that in this case it was not practicable to keep any controls for comparison with the treated fish.

While the treatment described above has been very successful it has the great disadvantage of requiring considerable time, and this is a serious objection where many fish are to be treated. During the summer of 1919 extensive experiments were carried on with a view to shortening the treatment. As a result a rapid treatment has been devised which is believed to be even more effective than the longer treatment previously in use. Briefly, the new method consists in treating the fish with a 1 to 1,000 solution of copper sulphate for one to two minutes. This treatment is so great an improvement on the earlier treatment with a 1 to 30,000 solution that in our later experiments we entirely discarded the latter.

When the fish are in good condition they can be placed in the 1 to 1,000 solution for two minutes without injury, but if they have been previously weakened in any way they should not be exposed to the solution for more than one minute. Such hardy fishes as the black bass, sunfishes, and bullheads can be safely left in the solution for three minutes if in good condition. In some cases it is advisable to repeat the treatment after 12 to 24 hours.

A number of experiments with the rapid treatment were carried out during the latter part of the summer of 1919, but it will suffice to describe a few representative experiments.

Experiment No. 1.—September 6 a number of buffalofish and crappie were seined from a wire inclosure in the river (see fig. 258) where they had been held since September 2. The fish were in good condition and were divided into two lots before being placed in aquaria well supplied with running water. Except for the copper-sulphate treatment both lots were kept under as nearly identical conditions as possible. Sixteen crappie and eight buffalofish were treated with a 1 to 1,000 solution of copper sulphate for two minutes (water temperature 71° F.) before being placed in the aquarium. The controls, 10 crappie and 8 buffalofish, were placed directly in an aquarium without treatment. September 8 among the controls there were two crappie dying with the disease, while most of the remaining fish showed considerable infection on the fins and sides of the body. Among the treated fish, one buffalofish and two crappie were slightly infected. At this time there was a very striking difference in appearance in the two lots of fish. The untreated fish were nearly all in bad shape, with well-developed lesions and considerable mucous on various parts of the body. On the other hand, the treated fish appeared bright and clean, and those infected showed only slightly developed lesions. September 9 two more crappie and one buffalofish were found dead among the controls. There were no new infections among the treated fish and one infected crappie was improving. September 10 there were one dead buffalofish and one dead crappie among the controls. The treated lot were in good condition, and those infected, with the exception of one crappie which died, were recovering. Since there were no new infections and the slightly infected fish in both lots were recovering, the experiment was discontinued on September 11. The treated lot at this time was noticeably in better condition than the controls.

SUMMARY OF EXPERIMENT NO. 1.

Species.	Treated fish.			Controls.		
	Number.	Loss from disease.		Number.	Loss from disease.	
		Number.	*Per cent.*		*Number.*	*Per cent.*
Crappie	16	1	....	10	5	.. ..
Buffalofish	8	0	....	8	2	... .
Total	24	1	4.16	18	7	38.88

Experiment No. 2.—September 13 a number of buffalofish and crappie were removed from the same inclosure and treated as in the preceding experiment. Since the details of the experiment do not differ in principle from the preceding, it will be sufficient to summarize the results:

SUMMARY OF EXPERIMENT NO. 2.

Species.	Treated fish.			Controls.		
	Number.	Loss from disease.		Number.	Loss from disease.	
		Number.	*Per cent.*		*Number.*	*Per cent.*
Crappie	3	0	....	3	2	....
Buffalofish	12	0	....	10	5	.. .
Total	15	0	0	13	7	53.84

These two experiments indicate what the copper-sulphate treatment can accomplish when used under favorable conditions. If the fish have been greatly weakened before being given the treatment, however, the results are far from encouraging.

As pointed out, fish which have been seriously weakened by previous treatment are often killed by the copper sulphate, and it is doubtful if any treatment can be devised which can be safely used while the fish are in this condition. This is especially true if the fish just previous to being treated have been confined for some time in a small vessel where the oxygen supply is deficient. Several experiments were carried out with fish seined from small ponds which had been isolated from the river when the waters receded after the spring floods. These fish were transported in galvanized washtubs, often for a distance of 2 or 3 miles, and held in the tubs an hour or two before reaching the station. A large number of fish were carried in each tub, and although attempts were made to keep the water aerated they were partially asphyxiated when reaching the station. All our experiments in treating such fish were unsuccessful, the great majority being killed by the copper sulphate. Possibly the fish could be successfully treated if first held in running water for several hours. The two following experiments are typical of results with these exhausted fish.

Experiment No. 3.—The fish were brought to the station at 5 p. m., September 10, in a greatly weakened condition. Part were treated with 1 to 1,000 copper sulphate for two minutes and then placed in an aquarium well supplied with running water. The remainder were placed in a similar aquarium without being treated. Most of the fish in the treated lot died within 24 hours. In the following summary all fish which died during the first 48 hours are tabulated as having died from the effects of the copper-sulphate treatment or injuries sustained on their way to the laboratory. These fish showed no well-developed bacterial lesions, and our previous experiments had shown that fish rarely die from the effects of bacteria until more than 48 hours have elapsed.

SUMMARY OF EXPERIMENT NO. 3.

Species.	Treated fish.					Controls.				
	Number.	Loss from treatment and injuries.		Loss from disease.		Number.	Loss from injuries.		Loss from disease.	
		Number.	*Per cent.*	*Number.*	*Per cent.*		*Number.*	*Per cent.*	*Number.*	*Per cent.*
Crappie	16	11	....	0	....	21	1	....	1	....
Buffalofish	20	9	....	0	....	15	0	....	5	....
Bluegill	3	1	..	0	....	7	1	....	1	....
Total	39	21	53.84	0	0	43	2	4.65	7	16.27

This case is remarkable for the small number of infected fish among the controls. Possibly this can be explained by the fact that although the fish had been much weakened from lack of oxygen they had evidently been handled carefully and showed only slight mechanical injuries.

Experiment No. 4.—September 11 a number of buffalofish and bluegill were brought to the laboratory from the same pond as in the preceding experiment and were treated in the same way.

Summary of Experiment No. 4.

Species.	Treated fish.					Controls.				
	Number.	Loss from treatment and injuries.		Loss from disease.		Number.	Loss from injuries.		Loss from disease.	
		Number.	*Per cent.*	*Number.*	*Per cent.*		*Number.*	*Per cent.*	*Number.*	*Per cent.*
Buffalofish	15	10		0		16	0		11	
Bluegill	9	2		0		10	1		3	
Total	24	12	50	0	0	26	1	3.85	14	53.84

As in the case of the more dilute solutions, the 1 to 1,000 solution of copper sulphate to be effective must be used before the appearance of any lesions. When the bacteria have become abundant enough to produce visible lesions many of them are too well protected to be reached by the solution during the short time the fish are exposed to it. However, while this treatment is not recommended as a cure, it has been shown experimentally that fish may be cured by its use, provided the gills are not infected.

Experiment No. 5.—At 5 p. m., September 9, seven badly diseased fish, two crappie and five buffalofish, were treated with a 1 to 1,000 solution for two minutes. These fishes were so badly diseased that they would undoubtedly have died within a few hours if not treated. They were so weak from the disease that three buffalofish turned on their backs during the treatment, but two recovered later. The next morning, September 10, another buffalofish was found dying and the other fish showed no improvement. The remaining fishes, two crappie and three buffalofish, were again treated with a 1 to 1,000 solution for two minutes at 11 a. m. One buffalofish died shortly after treatment. At 11.30 a. m., September 11, the fish were again given a 1 to 1,000 treatment for two minutes. No further treatments were given, and one buffalofish and one crappie died on the 13th. The remaining fishes, one buffalofish and one crappie, showed great improvement, and on the 16th, when the experiment was discontinued, had entirely recovered. No doubt the relatively low temperature of the water, which averaged about 70° F. during this experiment, was an important factor in aiding their recovery.

Of course a longer treatment with the copper sulphate would be more destructive to the bacteria but would not be advisable on account of the bad effects on the fish. All our experiments indicate that too strong a solution or too long a treatment with a weaker solution is worse than no treatment at all. While the fish may not be noticeably injured at the time, they may be so weakened as to easily succumb to a later infection. This is well illustrated by one of our experiments in which five bluegill were treated with a 1 to 1,000 solution of copper sulphate for six minutes. These fish showed no ill effects from the treatment at the time, but two days later all had become infected and died within 24 hours. In another series of experiments to determine the effects of various chemicals six normal buffalofish were treated with a 1 to 1,000 solution of formalin for eight minutes. The fish appeared in good condition after the treatment, but during the next three days all developed a fatal case of the disease.

In most cases it will probably not be worth while to attempt to cure fish with well-developed lesions, but in case it should be thought advisable the most effective treatment consists in local applications of a 1 per cent solution of copper sulphate. We have cured a number of badly diseased fish in this way, and the treatment is successful in a large percentage of cases, provided the gills are not affected. The solution can best be applied by gently swabbing the lesion with a small piece of cotton which has been previously dipped in the solution. Two or three applications at intervals of 6 to 12 hours should be sufficient. After each local application of the copper sulphate the fish should be placed in a 1 to 1,000 solution for one minute.

Since, in most cases, the disease is primarily due to injuries or weakened vitality the old adage, "An ounce of prevention is worth a pound of cure," is peculiarly applicable in this case. Above everthing else, anyone handling fish should exercise the greatest care to prevent injuring the fish in any way. Even the slightest injury, such as the rubbing off of a few scales or even a small portion of the mucous covering, may lead to infection. When taken in a net or seine the delicate caudal fin is very easily injured by the struggles of the captured fish and every effort should be made to reduce the injury to a minimum. A large percentage of infections among fish taken in this way first appear on the caudal fin, and undoubtedly injury to the fins is one of the most common causes of infection.

Great care should be taken to prevent the spread of the disease through the use of infected nets or vessels. This can be easily prevented, since the bacteria are entirely destroyed by thorough drying for several hours in direct sunlight.

Finally, in the case of fish confined in aquaria it is essential that all infected individuals be removed at once. As in the case of any contagious disease all contact of healthy with diseased individuals should be guarded against. It has been shown that bacteria are continually leaving diseased fish and thus may readily get on any healthy fish in the same aquarium.

It should be said in passing that this treatment is also very effective for ectoparasitic Protozoa. Experiments on fish infected with Costia, Chilodon, and Cyclochæta have shown that these parasites are entirely destroyed by a single treatment with copper sulphate. In the case of fish infected with Ichthyophthirius the treatment is not so successful, since the encysted stages are not affected. The exposed parasites are, however, entirely destroyed.

A number of other chemicals have been tried, but none of them has given encouraging results. Lysol and creolin were found to stop all movements of the bacteria in four to five minutes when diluted 1 to 5,000. The use of such strong solutions is, however, not practicable, since buffalofish and bullheads placed in a 1 to 5,000 solution for 1 minute died within 24 hours. Formalin was also found to be of no value for the same reason.

Since sodium chloride is used a great deal by fish-culturists for fungus a number of infected fish were treated with solutions of various strengths. It was soon found that the bacteria are not appreciably affected by solutions which seriously injure the fish, and it is not believed that this treatment is of any value against the disease. In fact our experiments indicate that it may actually aggravate the disease by weakening the fish.

ECONOMIC IMPORTANCE OF THE DISEASE.

At the present time it is impossible to make any general statements regarding the importance of this disease. So far, with the exception of two slightly infected fish at Ogdensburg, N. Y., the disease has been recognized only at Fairport. Here it has caused a very considerable mortality each summer for several years. This mortality for the most part has occurred in fishes which were being transferred from one pond to another, or to aquaria for experimental purposes. It was not until the past summer (1919) that the disease was shown to occur on fish in the Mississippi River as well as in the ponds. However, fish-culturists are well aware that is is impossible to handle many species of fish during warm weather with any degree of success. Undoubtedly part of this mortality among fish which have been handled is due to the direct effects of the treatment to which they have been subjected, but there is no question in the writer's mind that a much larger part is directly due to this disease and only indirectly to the handling which has simply rendered the fish more susceptible to infection. We are convinced that a great part of the mortality usually ascribed to fungus is in reality caused by *Bacillus columnaris*. In fact the writer is inclined to doubt if fungus is ever an important cause of fish mortality. In all probability *Bacillus columnaris* is widely distributed over the country and during warm weather, at least, is the most important agent in the destruction of fish which have been injured in any way.

Anglers are often advised to remove small fish from the hook and return them to the water. In the light of our experience with the disease at Fairport it is doubtful if many fish which have been handled in this way actually survive. Since the disease would not make its appearance until two or three days later, it is obvious that only through carefully conducted experiments can their chance of survival be ascertained. An incident which occurred at Fairport during the summer of 1918 is very suggestive in this connection. A number of largemouth black bass were needed for some experimental work in mussel propagation. They were taken from one of the ponds on a hook and line and placed in a large tank supplied with running water. Within two or three days nearly every fish had become infected with *Bacillus columnaris*. As previously mentioned, this species of fish is not very susceptible to the disease, and, furthermore, the fish in this case were several years old. As the reader will recall the older fish are much less susceptible than the young.

During the last few years the Bureau of Fisheries has been rescuing large numbers of young fishes from the small pools and ponds in which they are imprisoned when the spring floods recede. These pools and ponds are widely scattered over the flood plain of the Mississippi, often only a few hundred yards from the river. In some instances they may be 2 or 3 miles from the main channel. As the waters recede these ponds continually grow smaller and may eventually become entirely dry. They are often crowded with fish and the shallow waters exposed to the hot sun of July and August become heated to a relatively high temperature. These conditions combined with a limited supply of oxygen often result in the death of large numbers of fish. The conditions are such as to render the fish susceptible to infection by *Bacillus columnaris*, and fishermen have told the writer of having seen large numbers of diseased fish in such ponds.

In transferring the fish to the river they must first be seined from the ponds, a process which necessitates considerable rough handling, and then carried in galvanized washtubs (often under a broiling sun) to the river. It is obvious that such treatment is likely to result in infection by *Bacillus columnaris*. That the fish when liberated in the river quickly swim away and are seen no more proves nothing. The disease would not be evident for two or three days in any case.

In order to determine the prevalence of the disease among rescued fishes a long series of experiments will be required, but owing to the limited time at the writer's disposal only a few preliminary experiments have as yet been carried out. In these experiments a special effort was made to duplicate so far as possible the average conditions found in rescue work. The fish were seined from small, isolated ponds, one of which is shown in figure 259, and then carried in washtubs to the river, where they were placed on a launch to be carried to the station. These fish were in the tubs from one-half to one hour, which the writer was assured by the fishermen is somewhat less than the average time they are held in tubs in ordinary rescue work. On reaching the station the fish were at once placed in an inclosure surrounded by fine-meshed poultry wire. This inclosure (fig. 258) was constructed in shallow water along the river shore and was sufficiently large to obviate any danger of the fish being crowded. A small stream carrying the overflow from the fishponds flowed into the inclosure, so there was a good supply of running water at all times. The cross partition shown in the figure was added later for some special experiments which are not considered in this paper. It is believed that the fish held in this inclosure were in fully as favorable an environment as they would have been if liberated in the river.

Experiment No. 6.—September 2, 1919, 42 buffalofish, 41 crappie, and 8 bluegill were seined from the pond shown in figure 259. This pond was believed to be typical of those from which fish are taken in rescue work. It was about 400 feet long by 100 feet wide and quite shallow, being not over 3 or 4 feet in depth at the deepest part. The bottom, as in most ponds of this kind, was composed of fine, soft mud. The temperature of the water at the time the fish were removed was 83° F. All the fish appeared in good condition when placed in the inclosure. The next day (Sept. 3) six crappie were found dead. Since no bacteria could be found on these fish they are believed to have died from injuries due to handling. September 4 one badly diseased buffalofish was removed, and the next day there were two dead buffalofish, both with well-developed lesions. The inclosure was seined on September 6 and all the fish removed. Only four dead fish were found, three buffalofish and one crappie. However, many of the living fish were badly diseased and in all probability would have died in a short time, but it was not thought best to leave them in the inclosure longer, since there was great danger of the disease spreading from the infected to the healthy fish. It is not believed that any of the fish which are classed as infected at this time had contracted the disease in this way, since all were in advanced stages of the disease. The diseased fishes included 19 buffalofish and 10 crappie. They were removed to aquaria well supplied with running water, but all died within 24 hours. It is believed justifiable to assume that all the fish classed as diseased became infected as a result of the treatment to which they had been subjected and would have eventually died if set free in the river.

SUMMARY OF EXPERIMENT NO. 6.

Species.	Number of fish.	Fish lost from injuries.		Fish lost from disease.		Total loss of fish.	
		Number.	*Per cent.*	*Number.*	*Per cent.*	*Number.*	*Per cent.*
Buffalofish	42	0	0	25	59.52	25	59.52
Crappie	41	6	14.63	11	26.83	17	41.46
Bluegill	8	0	0	0	0	0	0

Experiment No. 7.—September 6, 1919, 36 buffalofish and 3 crappie were seined from the same pond as in the preceding experiment and placed in the inclosure. The next day eight buffalofish were found dead, evidently from the effects of injuries due to handling. All the fish were removed from the inclosure on September 9. There were 17 dead buffalofish, 8 living badly diseased buffalofish, and 3 badly diseased crappie. The remaining fish were in good condition.

SUMMARY OF EXPERIMENT NO. 7.

Species.	Number of fish.	Fish lost from injuries.		Fish lost from disease.		Total loss of fish.	
		Number.	*Per cent.*	*Number.*	*Per cent.*	*Number.*	*Per cent.*
Buffalofish	36	8	22.22	25	69.44	33	91.67
Crappie	3	0	0	3	100	3	100

Experiment No. 8.—Since there was a possibility in the above experiments that the fish might have injured themselves on the poultry wire in trying to escape from the inclosure a fine-meshed seine was attached to stakes so as to form another inclosure by the side of the one constructed of poultry netting. September 10, 21 buffalofish and 12 crappie were placed in this inclosure. These fish were taken from a different pond from that used in the preceding experiments, but conditions were much the same, except that the pond was somewhat farther from the station.

SUMMARY OF EXPERIMENT NO. 8.

Species.	Number of fish.	Fish lost from injuries.		Fish lost from disease.		Total loss of fish.	
		Number.	*Per cent.*	*Number.*	*Per cent.*	*Number.*	*Per cent.*
Buffalofish	21	0	0	12	57.14	12	57.14
Crappie	12	8	66.67	2	16.67	10	83.33

While the above experiments are only preliminary and too much weight should not be placed on the results, it is evident that the conditions are especially favorable for the development of this disease among rescued fish and that in all probability it causes a very considerable mortality during warm weather. Much of the rescue work is carried on in the fall and early winter, and with the low temperatures then prevailing there is no doubt much less danger of infection by bacteria, but on this point we have no data at present.

It is obvious that great care should be exercised to injure the fish as little as possible and that, whenever practicable, rescue operations should not be undertaken until cool weather. If the fish have not been greatly weakened by unfavorable conditions, especially lack of oxygen, treatment with 1 to 1,000 copper sulphate just before they are liberated in the river would doubtless cause a marked decrease in the loss from disease. Some experiments were attempted along this line in September, 1919, but owing to an accident the results were of no value.

EXPLANATION OF FIGURES.

All figures, with the exception of figure 249, are from photographs by the author. Abbreviations used are as follows: bl, blood; cor, corium; ep, epidermis; and mus, muscles.

FIGS. 231 and 232.—Crappie, *Pomoxis sparoides*, with dorsal, caudal, and anal fins infected. Note lesions just starting in three places on anal fin of fish in figure 232.

FIG. 233.—Bluegill, *Lepomis incisor*, with dorsal, caudal, and anal fins infected.

FIGS. 234 and 235.—Fingerling buffalofish, *Ictiobus bubalus*, with caudal fins badly infected.

FIG. 236.—Largemouth black bass, *Micropterus salmoides*, showing infection on dorsal, anal, and caudal fins.

FIG. 237.—White bass, *Roccus chrysops*, with infection developing on dorsal, anal, and caudal fins.

FIG. 238.—Bullhead, *Ameiurus melas*, with a number of small lesions on dorsal surface of body.

FIGS. 239 and 241.—Bullheads, *Ameiurus melas*, in late stages of the disease.

FIG. 240.—Bullhead, *Ameiurus melas*, with nearly entire side of body covered with lesions.

FIG. 242.—Small bullhead, *Ameiurus melas*, with posterior end of the body infected and another lesion just back of pectoral fin.

FIG. 243.—Head of crappie, *Pomoxis sparoides*, with operculum removed to show small lesion on gill.

FIG. 244.—Head of buffalofish, *Ictiobus bubalus*, with operculum removed to show a somewhat larger lesion on gill than in figure 243.

FIG. 245.—Head of buffalofish, *Ictiobus cyprinella*, with operculum removed to show gills in late stages of the disease.

FIGS. 246 and 247.—*Bacillus columnaris*. From a dried smear stained with carbolfuchsin. × 800.

FIG. 248.—Small portion of scale of bluegill to show formation of columns by bacteria along the edge. Photomicrograph from preparation mounted in glycerin jelly and stained with eosin. Columns are more slender and pointed than normal, due to shrinkage by the preserving fluid.

FIG. 249.—Showing formation of columns by bacteria along edge of a bit of infected tissue after being removed to slide. Somewhat diagrammatic. ×340.

FIGS. 250 to 257 are from cross sections through lesions in integument of bullhead, *Ameiurus melas*.

FIG. 250.—Lesion just beginning to develop. × 70.

FIG. 251.—A little later stage in development of lesion. The epidermis is entirely destroyed at one place to the right in the figure. × 70.

FIG. 252.—A somewhat later stage than figure 251. The corium is beginning to disintegrate where the overlying epidermis has been destroyed. × 70.

FIG. 253.—Cross-section through lesion in late stage of disease. The corium is entirely destroyed at center of lesion. Less highly magnified than preceding figures.

FIG. 254.—Showing disintegration of epidermis in early stage of development of lesion. × 108.

FIGS. 255 to 257.—Sections through margin of well-developed lesions, the epidermis at the right has been entirely destroyed. Note the blood corpuscles (*bl*) in the outer layer of the corium and between the corium and the epidermis. In figure 255 the blood has broken through into the epidermis for a short distance. × 108.

FIG. 258.—Inclosure constructed of poultry netting in which fish were held in experiments 6, 7, and 8.

FIG. 259.—Small pond from which fish were taken in experiments 6 and 7.

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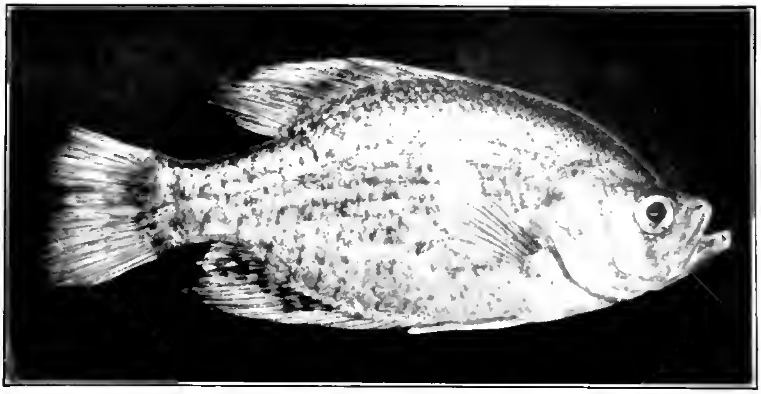

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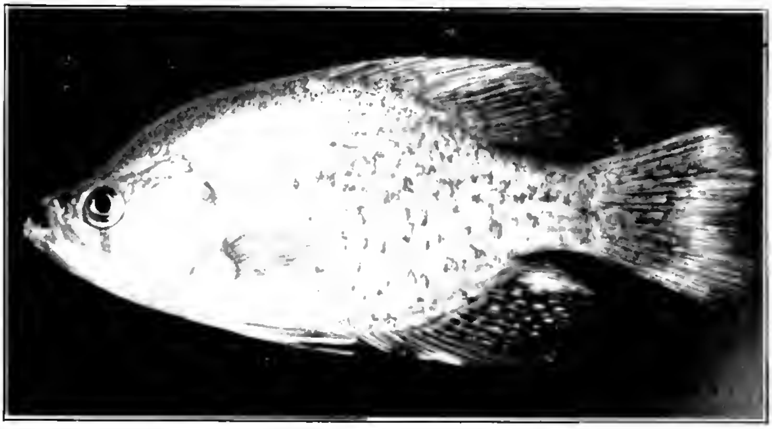

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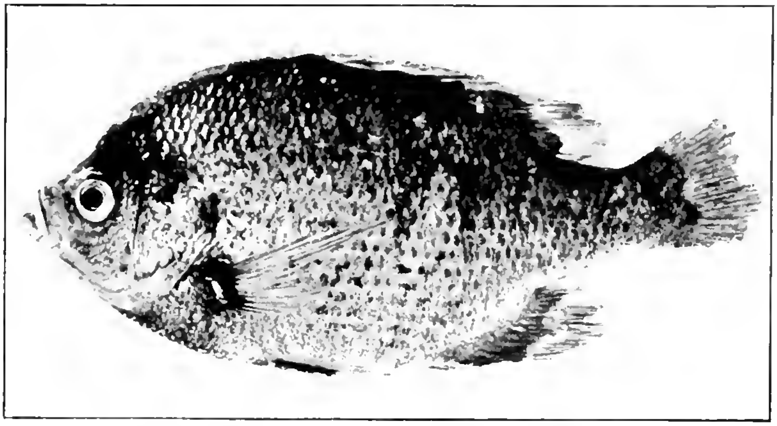

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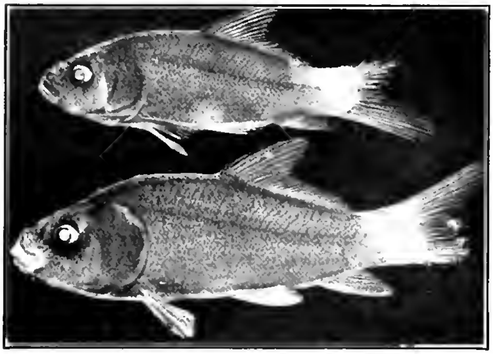

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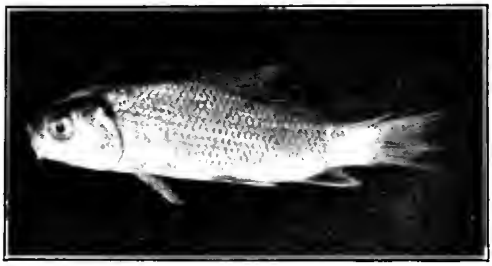

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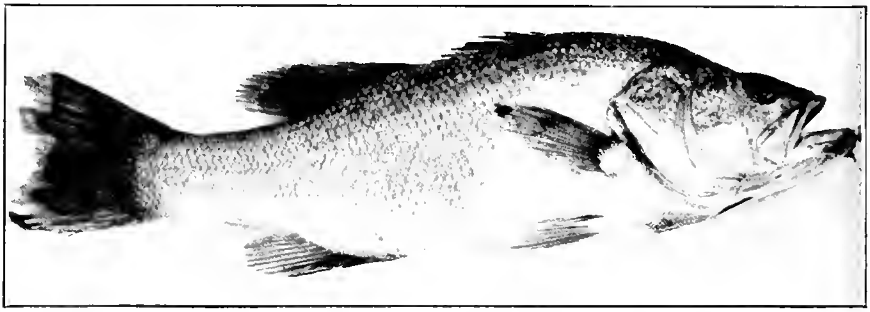

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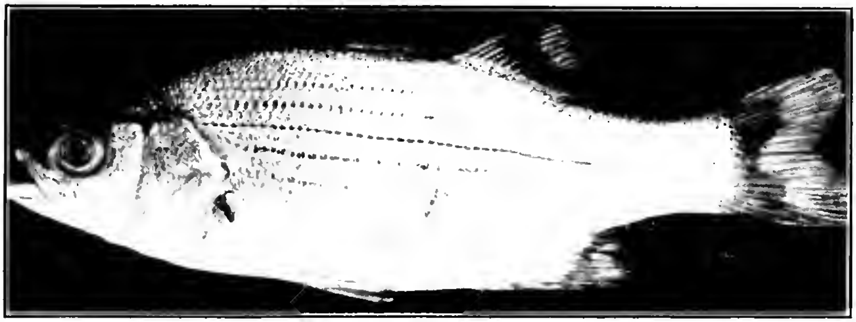

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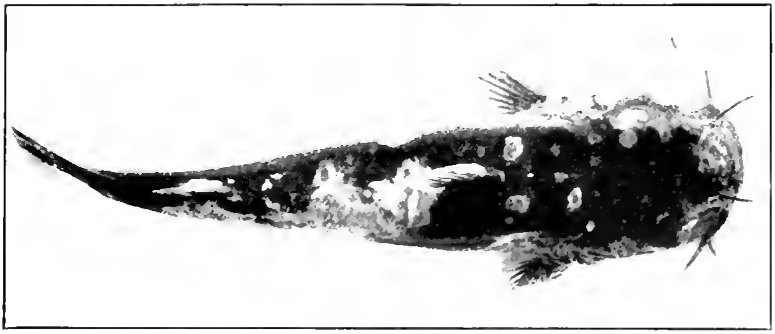

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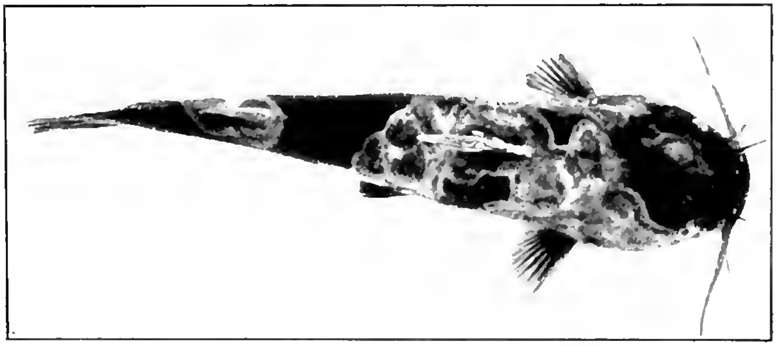

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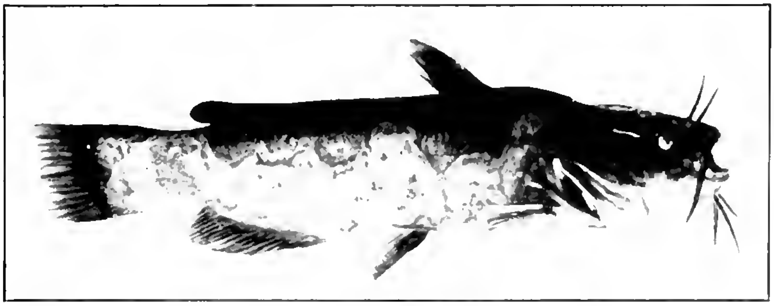

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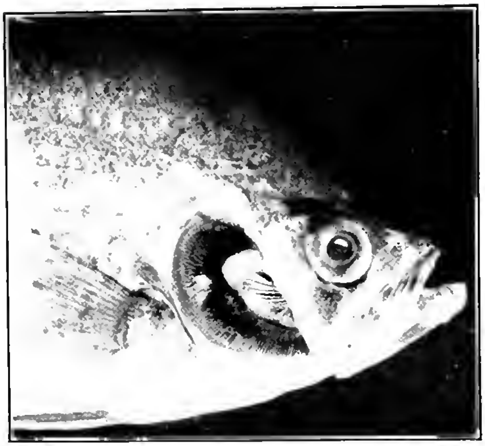

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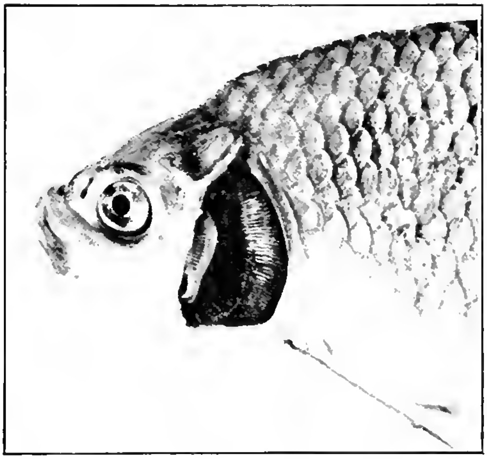

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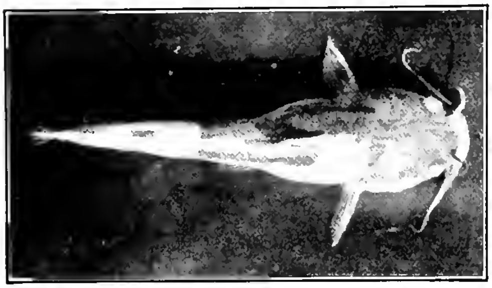

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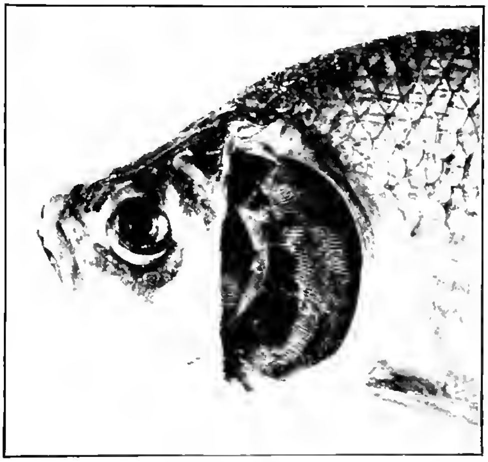

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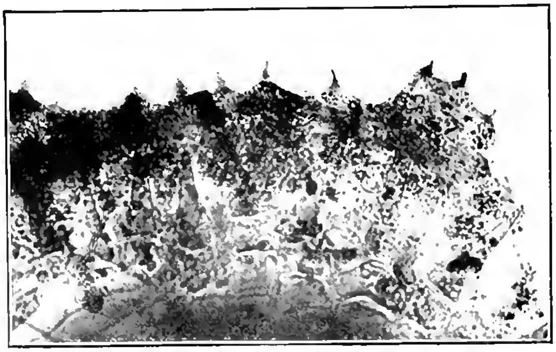

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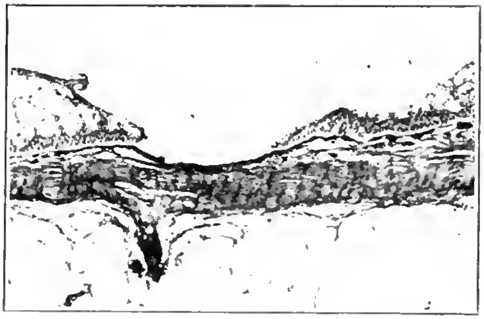

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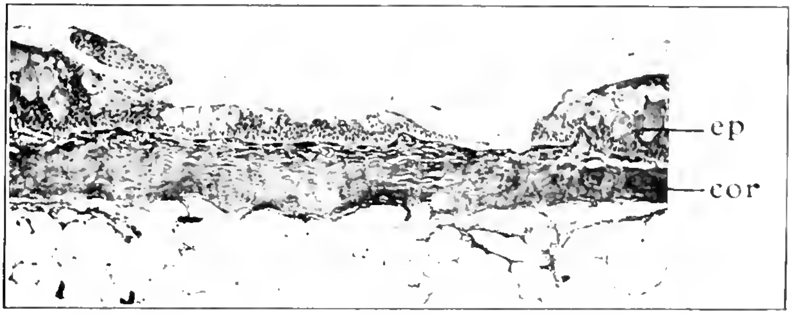

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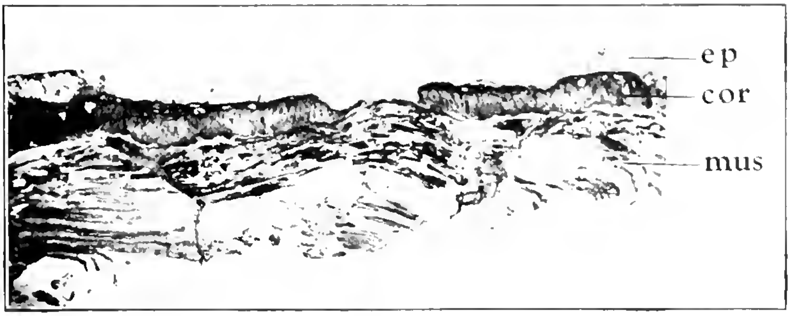

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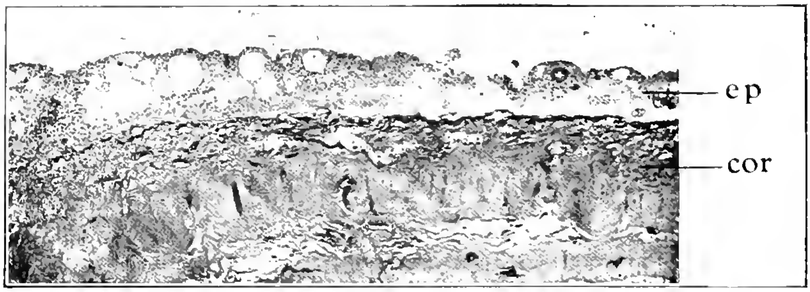

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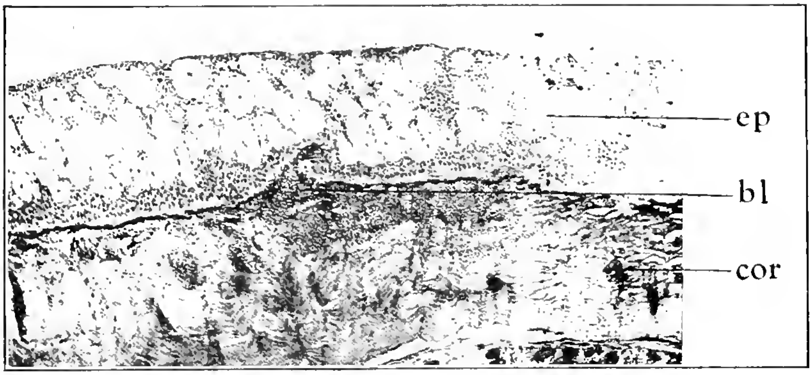

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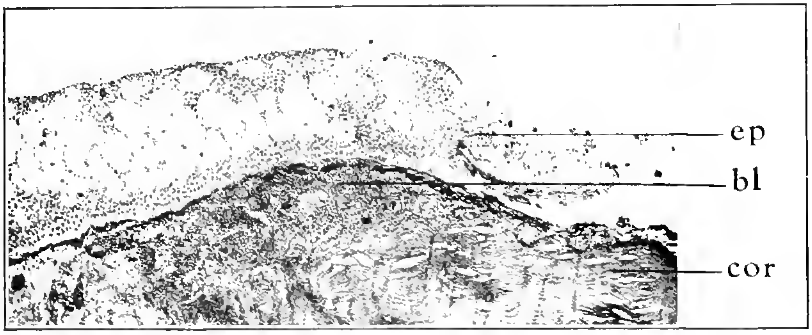

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THE SPINY LOBSTER, Panulirus argus, OF SOUTHERN FLORIDA: ITS NATURAL HISTORY AND UTILIZATION.

⁂

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Contribution from the U. S. Fisheries Biological Station, Key West, Fla.

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INTRODUCTION.

CLASSIFICATION AND DISTRIBUTION.

The spiny lobsters belong to the family Palinuridæ, which is represented by six genera and numerous species distributed throughout the tropical and subtropical seas. The genus Panulirus, of which the spiny lobster, or crawfish, found around the Florida Keys is a species, is represented by species of economic importance on both the Atlantic and Pacific coasts of America, in the Hawaiian Islands, and in Japan.

The northern limit of *Panulirus argus*, apparently, is Beaufort, N. C., where a few small specimens are caught occasionally by the fishermen seining for shrimps; but the spiny lobster does not often reach a large size there, and it is of little, if any, economic importance in that region.[1] This genus probably does not extend farther south than Rio de Janeiro, Brazil.[2]

Panulirus argus is very abundant on the Florida Reef from Miami to the Dry Tortugas, a distance of over 200 miles. The best fishing grounds are known to be along the southern shores of the reefs and keys. Spiny lobsters are found in less abundance on the northern shores of the keys, and an occasional individual is seen as far north as Cedar Key.

COMMON NAMES.

The spiny lobster is known about Key West as crawfish and langouste, a name borrowed from the French. Other names are rough, thorny, or rock lobster, and sea crawfish. The most common name among the fishermen and dealers is crawfish.

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[1] Hay, W. P., and C. A. Shore: The Decapod Crustaceans of Beaufort, N. C., and the Surrounding Region, p. 398. Bulletin U. S. Bureau of Fisheries, Vol. XXXV, 1915-16, p. 369-475, Pls. XXV-XXXIX, 20 text figs., Washington, 1918.

[2] Gruvel, A.: Contribution à l'Étude générale systématitique et économique des Palinuridæ. Annales de l'Institut océanographique, Monaco, Tome III, Fasc. IV, p. 5-54, VI Pls., 22 text figs. Paris, 1911.

Part 1.—THE SPINY LOBSTER FISHERY OF SOUTHERN FLORIDA.

THE SPINY LOBSTER FISHERY AT KEY WEST, FLA.

IMPORTANCE OF THE FISHERY.

The importance of the spiny lobster can not be questioned. Besides being of value as food for human consumption, it is the favorite food of many fishes and other marine animals. Were it not used for fish-baiting purposes the catch of fish by hook and line and small traps would be greatly curtailed. According to the United States Bureau of the Census, Fisheries of the United States, 1908, the catch for the State of Florida was 53,000 pounds, having a value of $3,600. The total value of all fishery products for the State at that time was $3,289,000. The spiny lobster industry, therefore, constituted a very small part of the total value. It has been estimated that the present annual catch is 300,000 pounds, valued at $25,000. It is impossible to determine the number of spiny lobsters used for bait, but it is said that fully one-half of all caught are used for this purpose. It can be seen that the lobster industry, although still small, has been developing.

In the local fishing with hook and line, or with traps, or pots, the fishermen depend almost entirely on spiny lobster meat for bait. The tail of this animal consists of solid meat, and it is said to be equal in quality to that of the northern lobster. The spiny lobsters utilized in the fishing industry are caught by the fishermen on the way to the fishing grounds. Spiny lobsters which die before the fishermen can market them are also utilized in this manner. It is said that four or five dozen, with a market value of $1 per dozen, when used for bait usually net the fishermen $40 to $50 worth of fish.

The industry is of greater importance at Key West than elsewhere in southern Florida, though the markets at Miami, Fla., are handling more and more spiny lobsters each year.. The demand is sometimes greater than the supply. During the migratory periods, when spiny lobsters are plentiful and easily taken, it is more profitable to catch them than fish. Consequently, a large majority of the fishermen engage in the industry at this time. Only about one dozen boats are engaged in the industry throughout the year, and two men per boat usually constitute the crew.

FISHING GROUNDS.

LOCAL DISTRIBUTION.

The spiny lobsters are found throughout the Florida Reef but are most numerous along the southern shore, where the bottom is rocky and ledges are prominent. The local fishing grounds are about 25 miles in length, extending from Boca Grande Key on the west to Sugar Loaf Keys on the east. The principal and most important fishing grounds are between these extremities off the following Keys: Boca Grande, Mann, Ballast, Mule (Little Mullet Key),[3] Woman, Man of War, Barracouta, Joe Ingams, Mullet (Big Mullet),[3] and King Fish Shoals (Crawfish Bar).[3] The older fishing grounds are off

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[3] Local names in parentheses.

the southern coast of Key West and to the eastward off the following: Cow Key, Boca Chica, Geiger's Key, Saddle Bunch Keys, and Sugar Loaf Keys. A few fishermen with power boats sometimes go 6 miles beyond Boca Grande Key to the Marquesas Keys on the west and 26 miles beyond Sugar Loaf Keys to Bahia Honda, on the east. Big Pine Key, which lies between Sugar Loaf Key and Bahia Honda is known to be an excellent fishing ground. Some spiny lobsters are obtained from East Harbor Keys, Middle Keys, and Cayo Agua, about 5 miles northeast of Key West. A few are obtained to the south on the shoals off the Eastern Dry Rocks. When the local supply is limited and the weather is favorable, a few fishermen go to the Dry Tortugas. Since the "Tortugas" are about 65 miles to the westward, it is seldom, and only under the most favorable weather conditions, that fishermen with power boats undertake this trip. Not more than a few thousand spiny lobsters are brought from there annually. Nearly all of these are of large size, much larger, indeed, than any others brought to the local markets.

SEASON OF THE FISHERY.

Spiny lobsters are caught throughout the year, but the best season is from February to July, during which time about 60 per cent of the total annual catch is taken. A majority are caught while feeding in water that varies from 1 to 10 feet in depth. In order to catch them in deeper waters, it is necessary to use traps or pots. In February the spiny lobsters begin to return to the shallower waters, probably for the purpose of spawning. During this period they are very active and can be seen at all times during the day but are more numerous during the early evening and throughout the night. During the day most of them are concealed in hiding places, under rocks, sponges, corals, and other places that protect them.

During the last part of February and the greater part of March it is a common sight to see them in groups by the hundreds, in shallow water in the most favorable places. Because of their great abundance at this time they net the fishermen better returns than any of the other fisheries. The fishermen avail themselves of this opportunity, and it is not unusual for two men, having spent a day and a night "crawfishing," to return with a thousand or more spiny lobsters. This season of the fishery is a short one, and by the early part of April or May many of the fishermen have returned to their vocation, the hook-and-line fishery. The female spiny lobsters, now carrying eggs, have migrated to the deeper waters, but they come to the shallower waters to a limited degree during the night for the purpose of feeding, while the males seem to be regularly present on the flats in normal numbers.

APPARATUS AND METHODS IN GENERAL USE.

The methods of capture employed in the industry have changed materially during the last decade. The greater part of the catch formerly was made with cast nets, gill nets, and haul seines. Since the shellfish were then more abundant and less in demand, very satisfactory catches were made with the cast net, which was particularly effective for taking spiny lobsters that had collected in groups, as during the mating season. These nets were of woven twine, 12 to 16 feet in diameter, with sufficient leads to prevent the spiny lobster from making its escape under the net after it had been thrown over the animal. This method of capture is not now in general use, and few fishermen are able

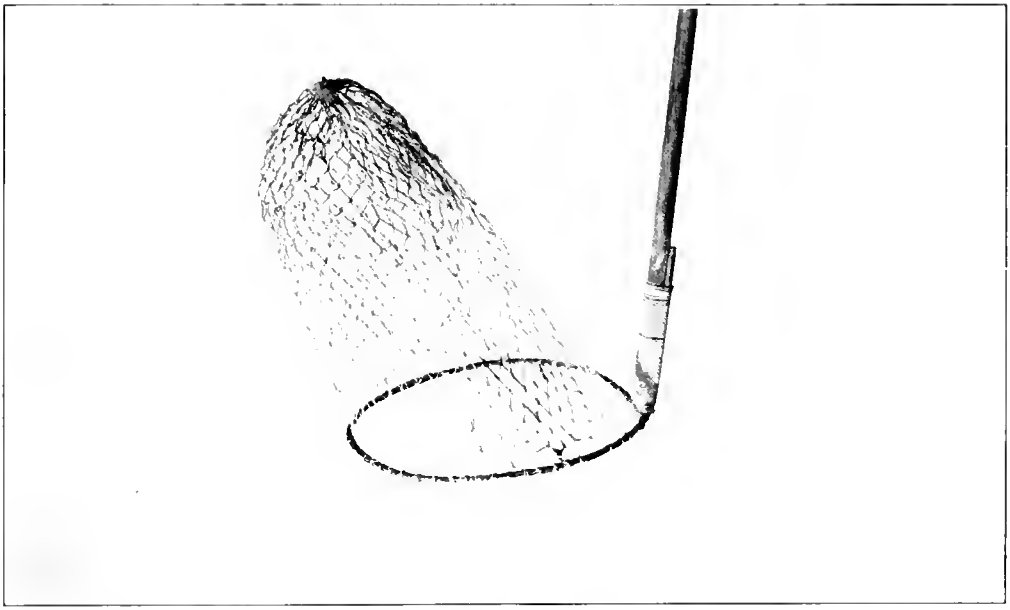

FIG. 260.—The bully net.

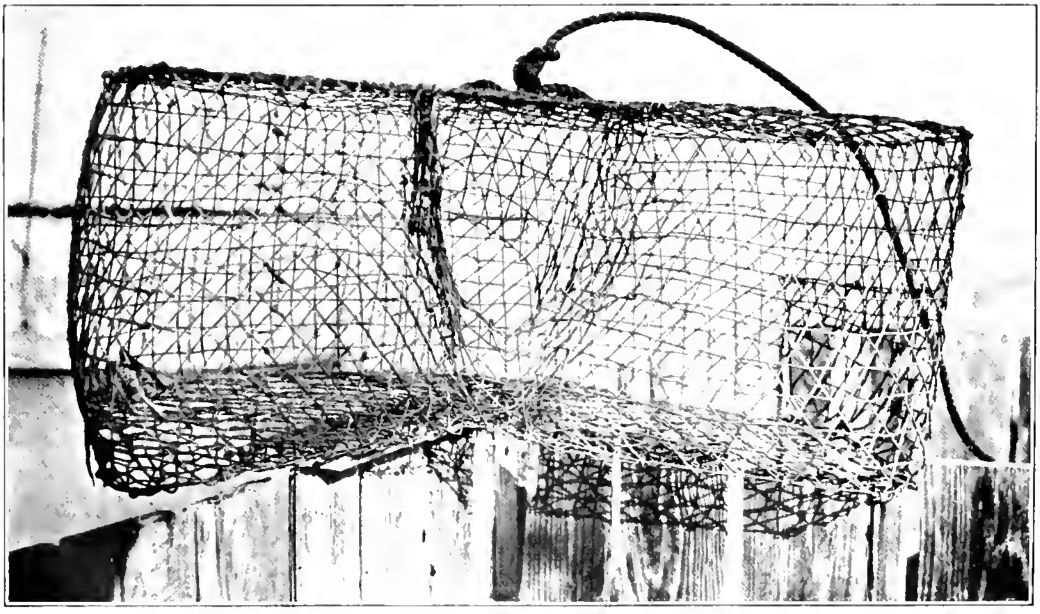

FIG. 261.—Spiny lobster trap.

to handle such a net skillfully. Gill nets and seines were hauled for the purpose of catching spiny lobsters which, while engaged in feeding, were scattered over the flats. Gill nets are no longer being used in this fishery, although a few spiny lobsters are often taken accidentally, when nets are operated in the other fisheries.

The apparatus used today is distinctly different, as the following list and estimates of the percentage of the catch made by each shows:

	Per cent.		Per cent.
Bully	50	Hoop nets	5
Fish traps	20	Seines	5
Grains	15	Hooks, and all other means	5

THE BULLY.

The "bully" (Fig. 260) is used by the fishermen in general throughout the Florida Reef. It is the best-known device employed in catching the spiny lobsters while they are moving about in the waters where they can be seen. The bully is a small hoop net 15 to 18 inches in diameter, 2 feet or more in depth, and with mesh of 1¼-inch bar measure. The hoop is set at right angles to a pole or handle 8 or 12 feet in length.

In using the bully the bag of the net is pulled through the hoop and allowed to hang over one side of it. This allows the net to open upwards when placed over the lobster. The hoop of the net surrounds the lobster, but the bag of the net has been lowered in such a manner that when the lobster tries to escape from the imminent danger by swimming backward it lands in the net. The fisherman then raises the net, causing the bag of the net with the imprisoned animal to hang over the side of the hoop. The lobster is released by pulling the center of the net upward, allowing the animal to fall through the hoop.

In some cases, when using the bully, the fishermen work singly in a small boat which is ballasted in the stern. The fisherman stands in the bow, using the handle of the bully to propel the boat. In this way, upon seeing a spiny lobster, the boat can suddenly be brought to a standstill, the bully inverted, and the spiny lobster captured. A good fisherman seldom misses, unless the depth of the water causes the bully to be deflected from its course, or the bottom is rough so that the hoop does not fit snugly on the bottom, which is often the case when working on a rocky ledge. Occasionally two men work together, one sculling the boat according to directions of the fisherman in the bow.

FISH TRAPS.

The fish traps or pots (Fig. 261) are of galvanized wire construction. They are usually made by the fishermen. The woven wire meshes are about 1½ inches square. These traps vary in size, but on the average are 3 feet wide, 2 feet long, and 20 inches high. The side containing the opening to admit the spiny lobster is the longest, being about 3 feet in length. The two parallel sides of the trap at right angles to the former are each about 1 foot long. The trap is closed behind by two sides which meet at an angle directed outward. The floor and top of the trap are parallel to each other. The shape of the trap is roughly cardiform, the entrance lying in the concave side. The longest side is bent inward at the center, forming a conical funnel-shaped passageway which is inclined slightly upward. The lower side of the entrance to the passageway is placed about 2 inches above the bottom of the trap. This entrance is somewhat irregular in form, being about 6 inches in diameter at the smaller end which is closed, except for an elliptical opening, about 4 or 5 inches in the passageway through which the lobster falls about 6 inches to the floor of the trap. A wire door, hinged above, is provided in one side to take the catch from the trap.

These traps are used for catching spiny lobsters in deep water. The bottom is usually weighted, so that the trap when lowered will reach the bottom of the water in the desired upright position. This also tends to prevent strong tides from tumbling the pots about. The trap is always set with the pointed end, which the fishermen call the "front," directed against the flow of the tide. A few fishermen fasten buoys to their traps, but most of them know the fishing grounds so well that they are able to locate the traps without the use of attached floats. The traps are raised once or twice a day but usually only once during the morning. A fisherman who depends on this method usually has 15 or more traps. The same traps when baited with spiny lobster meat are used in catching fish.

THE GRAINS.

The "grains" (Fig. 262) is a two-tined spear on a long handle. Every fishing boat includes a "pair of grains" or "grain hook" in its equipment for spearing spiny lobsters and large fish in general. Spiny lobsters speared with this apparatus are usually killed, so the grains are used chiefly in catching them for fish-baiting purposes, though a few caught in this manner are sold where immediate consumption is possible. The spiny lobster hides under rocky ledges, and usually the antennæ are visible. It can be induced to leave its hiding place by scraping and jabbing on the rocks, giving the fisherman an opportunity for spearing it.

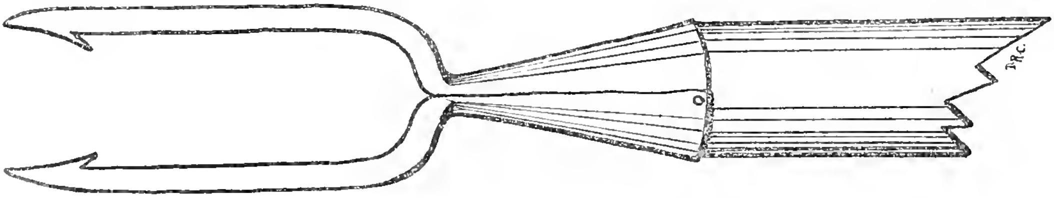

FIG. 262.—The grains.

HOOP NETS.

The hoop net, or lift net, consists of a metal hoop varying in diameter from 3 to 6 feet, to which fish net is woven in such a manner as to allow it to sag in the center. The net is raised and lowered by means of a single rope, one end of which is tied at the middle and intersection of two short loose ropes, the ends of which are tied to the hoop. At night the nets are lowered to the bottom and inspected frequently by carefully raising the net to the surface. This means of capture is seldom used except by those having no boats. It is employed chiefly around wharves and piling where spiny lobsters are known to be hiding.

SEINES.

Seines are used but little, because the spiny lobsters are not plentiful enough to warrant using them often. They are the same as the beach seines used in capturing fish. The nets are hauled over the shallow flats, keeping the lead line on the bottom. They are then dragged up on shore, and the spiny lobsters and fish are easily taken. Once out of water the legs of the spiny lobster are not strong enough to enable the animal to walk to any appreciable extent. It is said that the spiny lobsters are caught in seines more frequently off the coast of Cuba than off the coast of Florida.

HOOKS AND ALL OTHER MEANS.

On the southern coast of Florida, in the vicinity of Miami, a common way of catching these lobsters is by "hooking" them. A large fishhook is tied to the end of a pole, and in order to catch the lobster it is necessary to get the hook under it and then give the pole a sudden jerk. Since the shell of the animal is hard, this device is not very successful. A few spiny lobsters are caught by diving for them. It is common to observe fishermen reaching under rocky ledges trying to catch any that may be hidden there.

BOATS AND EQUIPMENT.

The boats (Fig. 263, opp. p. 289) used in the spiny-lobster fishery are identical with those used in the hook-and-line fishery. Cypress and yellow pine are the principal woods used in their construction. All of them are of the sail type, and a few of them have gasoline engines installed. The latter are the more profitable, since there is no delay in waiting for favorable winds. A prolonged delay in getting the crawfish to market often results in the loss of many.

All boats are equipped with wells, located in the middle of the boat. The sides of the well are made of double thickness matched cypress, and the bottom is perforated with many 1-inch holes. The depth of water in the well varies according to the load carried, but it is never less than 1 foot. Spiny lobsters when placed in the well are brought to the market alive. They are also held in these wells at the markets until the fisherman is ready to sell his catch. The wells may be of any convenient size. Those of the smaller boats are usually able to carry a few hundred spiny lobsters, while the wells of the larger boats may hold as many as 1,000.

A boat crew usually consists of two to four men. The sleeping quarters are in the bow of the boat. In the cockpit, immediately back of the well, food, water, oil, lamps, cooking utensils, and other paraphernalia are kept. The cooking is also done in the cockpit. It is necessary to have considerable food on board the sail-type boats, since storms often break without much warning, and it is often safer to anchor on the shoals than to attempt to reach port. It is not practical to fish during stormy weather, and often these fishermen remain anchored for more than a week without catching any spiny lobsters. The power boats have the advantage in being able to make daily trips when the weather is most favorable.

Upon arriving at the fishing grounds the boat is anchored. One or more small boats or skiffs can be seen riding at anchor, having been left by these same fishermen before departing for the market on their previous trip. These skiffs are from 10 to 15 feet in length and are not supplied with wells. Some of the fishermen always tow their skiffs, as there are certain risks involved in leaving them at the fishing grounds. If the men begin their operations during the day, it is often necessary to hold a water glass on the surface of the ripple water, thus enabling the observer to see the bottom. The water glass is merely a glass-bottomed wooden bucket. This is held in one hand and the bully in the other. At night a lamp similar to a street lamp is fastened to the bow of the boat, thus enabling the fisherman to examine the flats.

METHODS OF FISHING.

The men work singly or in pairs from the small skiffs. There is no advantage in working two-men crews except when it is necessary to use the water glass. One man can not manipulate the boat and the water glass and bully. More spiny lobsters can be caught in a few hours during the night than in a whole day. Most of the fishermen plan to arrive on the fishing grounds late in the afternoon, when the spiny lobsters begin to move about. After fishing four or five hours the men rest awhile and again fish a few hours before sunrise. If they fail to catch enough from the flats, they may attempt to get more during the day from the deeper water by means of the water glass. However, most of them prefer to spend another night on the grounds in an attempt to catch the desired number.

The shellfish that are caught are tossed into the skiff. They can be safely kept there several hours, providing there is no bilge water in the boat, as bilge water tends to kill the animals. From the skiff they are transferred to the well of the larger boat. If more are caught than the well will hold, they are put into wet sacks and are kept well watered until they are delivered at the market.

When there is a dew, it is necessary to keep the spiny lobsters covered as soon as they are taken from the water. Some fishermen carry a tub or barrel partly filled with water in which the catch is placed. The same precautions have to be taken in the summer when the sun is very warm; but most of the time the spiny lobsters can be carried in the bottom of the boats without any attention.

The fisherman who depends on spiny lobster pots usually spends a few hours in the morning taking the catch from the traps. Some fish are usually found in the traps, and these may be used in rebaiting. The average catch for a given night from pots is never as good as that of the fisherman who has spent the night using the bully. However, the pots have the advantage of operating regardless of weather conditions. During the summer months, when the spiny lobsters are in deep waters and are scarce, the pot fisherman is almost certain of a steady supply. Spiny lobsters at this time command higher prices, and the men using the bully are able to get but few. On the other hand, the pot fishermen lose many traps, and they require constant mending due to the corrosive action of the sea water on the wire.

VALUE OF APPARATUS.

There is no general uniformity of design in the apparatus used in this industry. Most of the apparatus is made by the fisherman according to his individual ideas. The fishing boats, depending on size, age, and equipment, range in value from $200 to $700 each. Some of these boats have been in service daily for almost 50 years and are still seaworthy. The smaller boats or skiffs range in value from $20 to $40, according to the material used in their construction. Below is a list of some of the apparatus with an estimate of the value of each:

Fish traps or pots	$6.00–$10.00	Grains	$1.00–$1.50
Boat lamps	3.00– 5.00	Water glass	.75– 1.25
Bully	1.25– 1.50	Hoop nets	1.50– 3.00

FIG. 263.—Fishing vessels and market for spiny lobsters, Key West, Fla.

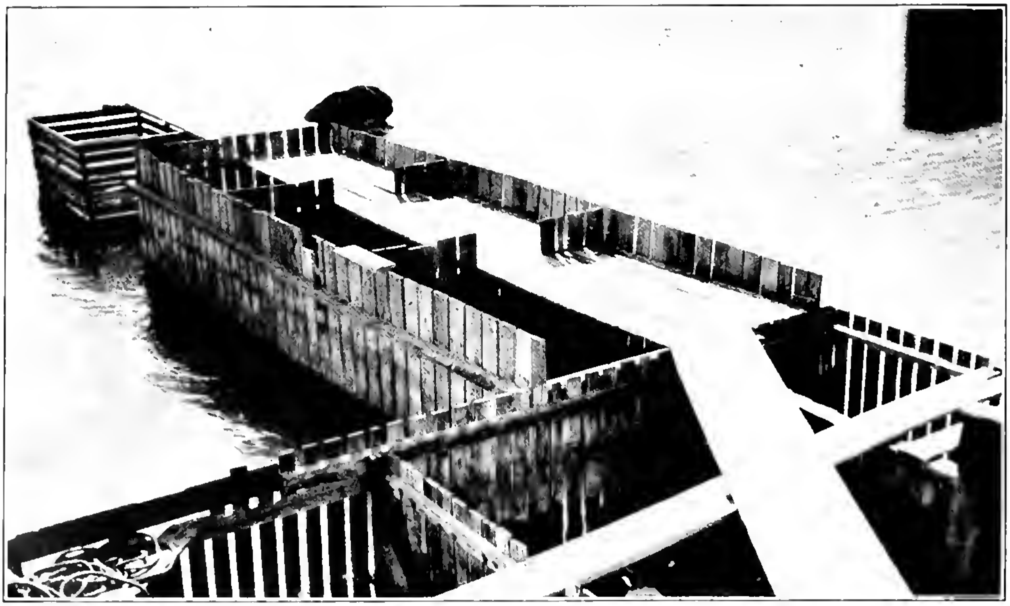

FIG. 264.—Experimental pens for spiny lobsters, Fisheries Biological Station, Key West, Fla.

MARKETING THE CATCH.

The spiny lobsters are taken to the local markets alive, having been kept in the wells where there was a free circulation of water. It sometimes happens when lobsters are plentiful that the well will not hold the entire catch. This surplus is put into bags which are carried on deck. It is necessary to keep the animals cool and wet by frequently pouring water over them.

At the market (Fig. 263) the catch is sorted, counted, and transferred to floating cars or inclosures where it is kept until ready for shipment. Spiny lobsters which have died and those in a dying condition are sold as bait to the hook-and-line fishermen. The market value varies from $0.75 to $2 per dozen according to season and demand and size. The average price obtained by the fishermen is $1 per dozen. The dealers sell by the pound. The average spiny lobster weighs about 1½ pounds or 6 dozen weigh 100 pounds.

During cool weather spiny lobsters shipped to points in southern Florida are simply placed in wet sacks, and under such conditions they will live four or five hours. If properly packed, they will live from two to three days. During the winter and spring months many spiny lobsters are shipped as far north as Philadelphia, New York, and Boston. They are packed in barrels containing alternate layers of ice and shellfish. The method of packing is the same as that employed in preparing fish for shipment, except that a layer of sponge clippings or seaweed separates the shellfish from the ice.[4] The average barrel will hold 10 to 12 dozen spiny lobsters.

Spiny lobsters caught by means of the grains are seldom sold at the market but are disposed of readily at the local hotels and restaurants. This product does not command as high a price as the live shellfish. When caught, the tails are twisted from the back and the latter thrown overboard. In order to dispose of this produce, it must be sold a few hours after capture. When spiny lobsters are plentiful and bring a low price, some of the fishermen salt and dry the meat for their own consumption.

ABUSES IN THE FISHERY.

Since there is always a ready sale for the spiny lobster, it is constantly being sought by the fishermen, both for its food value and value as bait in fishing. The fishermen generally believe that the supply is decreasing to some extent, since each year finds them going farther and farther for their prey. However, the old fishing grounds are known to yield very large catches after intervals of neglect, and it is doubtful whether these grounds have been actually depleted. From observations and data obtained it is known that spiny lobsters have not reached sexual maturity until they have attained a total body length of 8 to 9 inches, and a great many that are sold have not had an opportunity for spawning. The smaller spiny lobsters have a very delicate flavor, and those too small for market are consumed either by the fishermen and their families or are used for bait in fishing.

Formerly, the egg-bearing spiny lobsters sold as well as the others, but within the last few years the fishermen have been unable to sell the berried females. In this stage and until after the eggs have hatched they are said to be unwholesome.

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[4] The method of packing spiny lobsters in barrels with ice is not a good one, for heavy losses frequently are sustained in long-distance shipments.

Those methods of capture which tend to injure and kill the spiny lobsters are prohibited by law. Egg-bearing spiny lobsters are protected, but this protection can not be successful as long as spears, grains, hooks, and other injurious devices are used illegally in capture. Many of the spiny lobsters struck with these implements are injured, although not taken, and are left in the water to die sooner or later from their injuries. The pots in use catch all spiny lobsters regardless of size, but it could be required that the mesh be of sufficient size to permit the escape of the smaller animals.

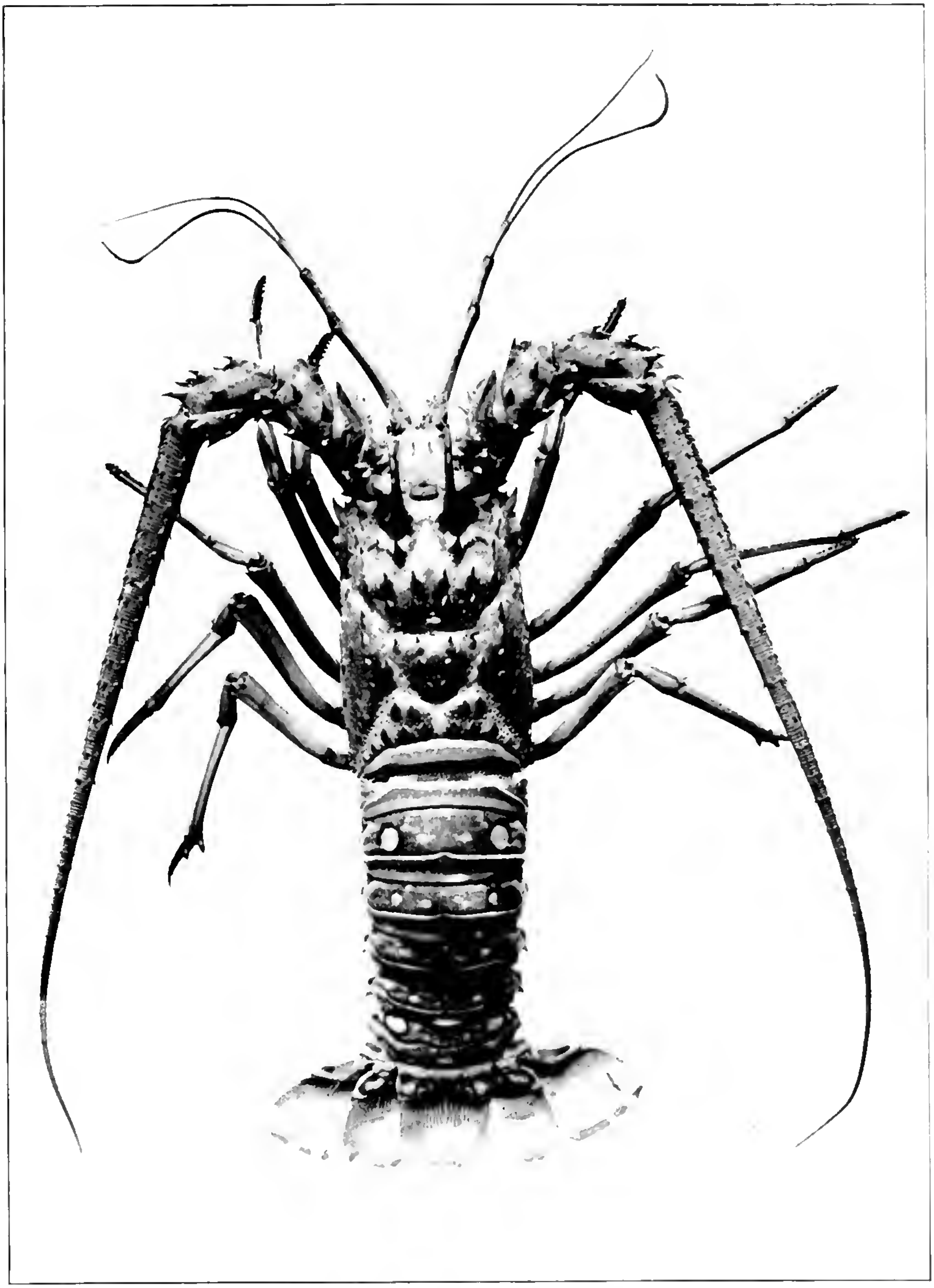

FIG. 265.—Spiny lobster, *Panulirus argus.* Dorsal view of young adult female.

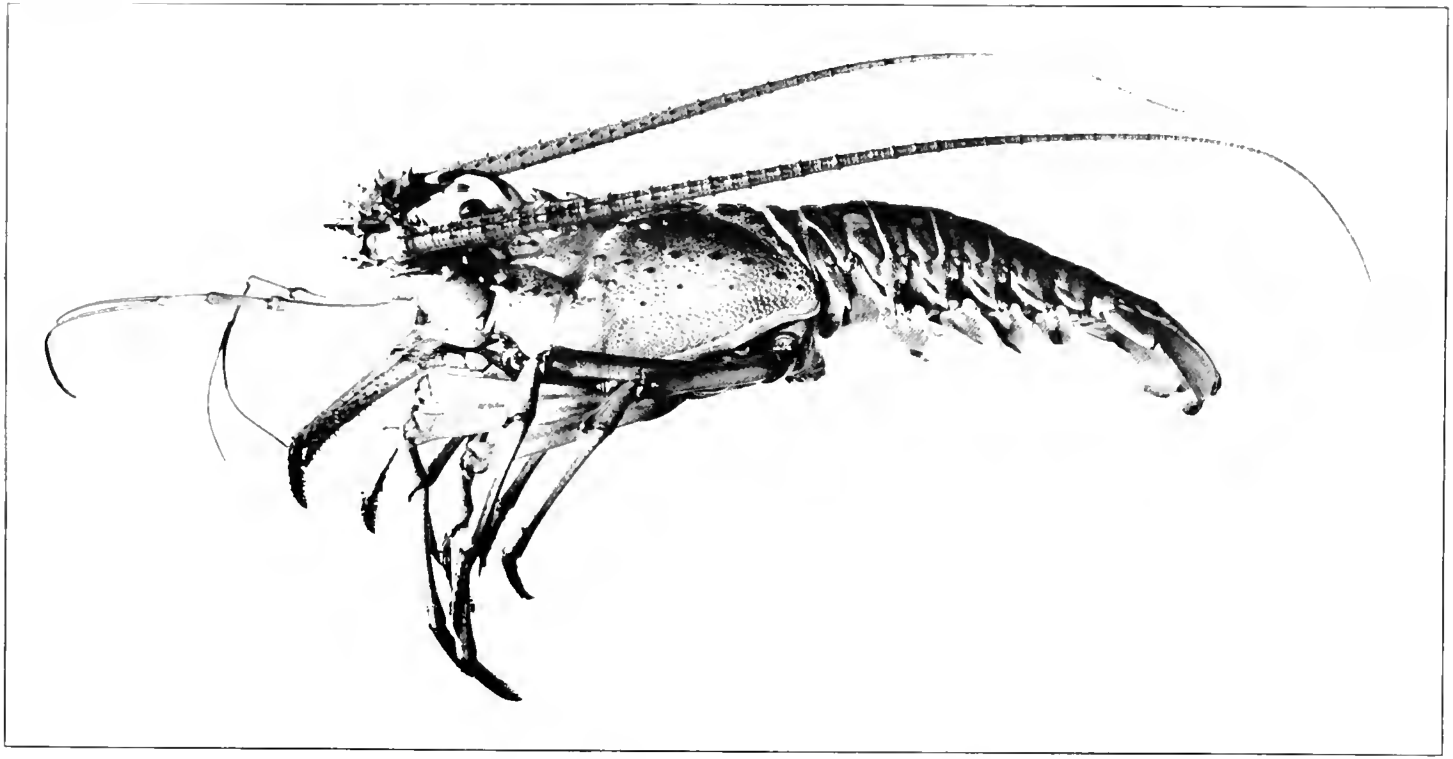

FIG. 266.—Spiny lobster, *Panulirus argus*. Lateral view of adult male.

Part 2.—LIFE HISTORY OF THE SPINY LOBSTER.

DESCRIPTION.

EXTERNAL CHARACTERISTICS.

The spiny lobster, *Panulirus argus* Latreille (Figs. 265 and 266), is compared frequently with the northern lobster, *Homarus americanus*, but even a cursory examination shows that there are many differences between the two crustaceans. The carapace of the spiny lobster, as the name implies, is studded with many sharp, forward-pointing spines which are arranged in more or less regular longitudinal series. The largest spine projects forward and curves above the eyes. The base of each spine is continuous with a low, flattened ridge which passes forward and downward below the eye. The base of the first segment of the antenna is modified into a padlike structure which engages this ridge and produces a strident sound when the antenna is moved.

The spiny lobster does not possess chelate appendages or large claws, like those of the northern lobster, the legs all ending in sharp dactyls which bear tufts of setæ. The three basal segments of the antennæ are very heavy and spinous, and the flagellæ are somewhat longer than the body in perfect specimens. The flagellæ are heavy and stiff, although they taper out to fine ends, and they are encircled with small spines at irregular intervals for almost the entire length. The inner edges of the flagellæ are fringed with short setæ which are probably sensory receptors. The antennules, or inner antennæ, are long and biramose, and the inner branch of each is fringed with cilia.

The pleon, or tail, is smooth and without spines or setæ, and each segment is crossed by a furrow which is more or less continuous, being broken in many small individuals. The furrow across the sixth segment of many adults is broken, but it is continuous in many others. The lower angle of each segment is produced into a strong tooth which is directed backward and deeply notched on the posterior margin.

The first segment of the tail does not bear appendages, but on the next four segments there are paddlelike swimmerets, or pleopods. The inner limb, or endopodite, of these appendages is not developed in the male, but in the female both exopodite and endopodite are developed, and the last three endopodites are developed into biramose structures for carrying the eggs. The tail fan is composed of five parts, the middle one being the telson, or seventh segment of the pleon, and the outer parts, which are the appendages of the sixth segment, known as the uropods, each being composed of exopodite and endopodite. The telson is covered by longitudinal series of small spines directed backward, and the distal parts of the tail fan are roughened by minute spines scattered over the surface.

COLORATION.

The sexes can not be distinguished by their color, although there is well-defined sexual dimorphism, as will be shown presently (p. 293). The coloration varies from very light shades to very dark shades, but the light and dark areas cover the same regions in all individuals, thus forming a definite color scheme. The tail is spotted with yellowish ocelli, and the posterior margin of each segment is edged with yellow or orange. The lower angles of the segments are marked with dark bluish or greenish tints and sometimes additional colors. The pleopods are usually orange, about half the area being covered by a black blotch. The legs are striped longitudinally with blue. The ventral surfaces of the body are cream colored or light yellow, and the thoracic sternum is marked with irregular, radiating stripes. The tail fan is crossed by bands of orange, yellow, and black and is fringed with white.

The coloration of the young differs from that of the adults in some respects. The colors of the carapace in very small individuals are arranged in transverse bands, usually three, the middle one being dark. The antennæ are frequently ringed with alternate light and dark bands, and the legs are ringed with blue.

Panulirus argus, like other species of the same genus, varies considerably in color. Coloration, apparently, is correlated with habitat, two groups of coloration being distinguished, one consisting of lightly colored individuals and the other of darkly colored individuals. The range in color of the former group is from light gray and tan to shades of green and light brown, while the second group varies from shades of red to deep browns and blues.

Large catches have been observed in the market, and it was noted, when it was possible to learn where they had been caught, that the lightly colored spiny lobsters came from places where the bottom was known to be lightly colored, and the darker individuals came from places where the bottom is covered by growths of sea fans and sponges. Such growths have been raised occasionally with the traps when it was noted that the color is similar to that of the spiny lobsters taken. Large numbers of spiny lobsters which have been caught in a given area have been found to vary only in slight degree in this respect.

Depth of water does not influence the color except indirectly, since the growths of sea fans and sponges are sometimes heavier in deep water and lightly colored bottoms are more generally found in shallow water. A migration, therefore, from one kind of habitat to another is indicated when spiny lobsters of different colors are caught in the same trap.

DIFFERENCES BETWEEN YOUNG AND ADULTS.

The young of both sexes possess antennæ which are longer in proportion to the body than they are in the adults. The spines on the carapace are better developed in the young, and very small individuals have on the carapace numerous setæ which gradually disappear with age. Specimens measuring 2 inches in length of carapace do not possess these setæ. The spines on the carapace of very large spiny lobsters are replaced frequently with tubercles, only those on the anterior parts of the carapace remaining acute.

Adolescent males, while often nearly as large as the adults, differ from them in the development of the second pair of legs and the size and shape of the second dactyl. The dactyl of the adult male is rather slender and curved and provided with a brush of long setæ which is not as well developed in the young or adolescent males. The second dactyl of adolescents is stouter and less curved and the setæ are shorter than those of the dactyl of the adult.

Adolescent females differ from the adults in the development of the fifth claw. The dactyl of the young is more curved and more acute than the dactyl of the adult, and the number and arrangement of the setæ on the dactyl of the young also differ. The cheloid part of the fifth claw is shorter in proportion to the dactyl in the young than it is in the adults.

Small individuals of both sexes are found in shallow water at all times and can be caught by means of traps set there. Large numbers of them are often taken by the fishermen for bait, and they are brought to market during stormy weather when fishing is restricted to sheltered places. The adults are more commonly taken in deeper water, but they are taken in large numbers in shallow water during migrations.

MORPHOLOGICAL DIFFERENCES IN SEX.

Adult spiny lobsters exhibit well-defined sexual dimorphism. The young of both sexes can be distinguished readily, although the differences are not as well marked as they are in the adults. The sexes can be distinguished by the fifth dactyl of the female, the second pair of legs of the male, the pleopods, the difference in the shape of the carapace, and the development of the thoracic sternum.

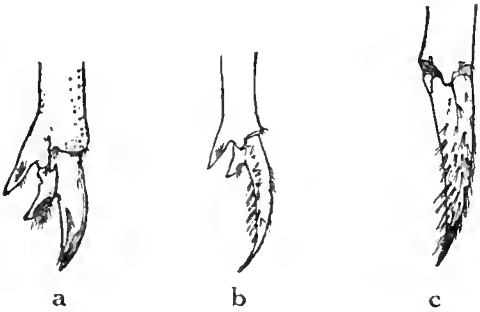

Fig. 267.—Fith dactyl of spiny lobster, *Panulirus argus*. × 1.5 approximately. *a*, fifth dactyl of mature female; *b*, fifth dactyl of immature female; *c*, fifth dactyl of mature male.

FIFTH CLAW OF THE FEMALE.

The fifth claw of the female (Fig. 267) furnishes the most ready means of distinguishing the sexes. The most striking difference between the dactyl of the male and that of the female is the development of a small chela on the fifth dactyl of the latter. This chela is composed of spurlike extensions of the propodus and dactyl, both parts being concave on their inner surfaces and provided with tufts of soft setæ, those on the dactyl being longer.

The fifth dactyl of the female is shorter in proportion to the length of the propodus than the fifth dactyl of the male, and the number and arrangement of the setæ differ to a marked degree, since the dactyl of the female is almost naked.

Spawn-bearing females have been observed using the fifth dactyls to manipulate the eggs, and in one instance a female was observed to use the fifth dactyl to scrape off the surface of the seminal vesicle just before the eggs were laid.

SECOND PAIR OF LEGS OF THE MALE.

The second pair of legs of the adult male (Fig. 268) is extraordinarily developed, being so long that these legs are rarely used in walking and are usually extended forward. The dactyl is long and curved and provided with a brush of long setæ which probably aids in clinging to the shell of the female during copulation. (See Copulation, p. 305.)

The second dactyl increases in length with age, becoming more curved, until, in very old individuals, it is almost falcate. The setæ also increase in length with age, and the brush is more conspicuous in older individuals than in the young. The tufts of setæ which are found on the propodus of the young and adolescent males disappear gradually with successive molts, until their places in large individuals are marked by small pits.

PLEOPODS.

The pleopods of the male differ from those of the female (Fig. 269) in having only the outer limb, or exopodite, developed. Both exopodite and endopodite are developed in the female. The exopodites of the female are somewhat longer and broader than those of the male. The first endopodite is similar in shape to the exopodite, but the remaining three endopodites are bifurcate, and in adult females they are fringed with long setæ upon which the eggs are carried. These bifurcate endopodites are not colored, being composed of white, flexible chitinous material. The edges are reinforced with scutes from the undersides of which the long setæ project in tufts. Some of these setæ are plumose and shorter than the others which are nonplumose.

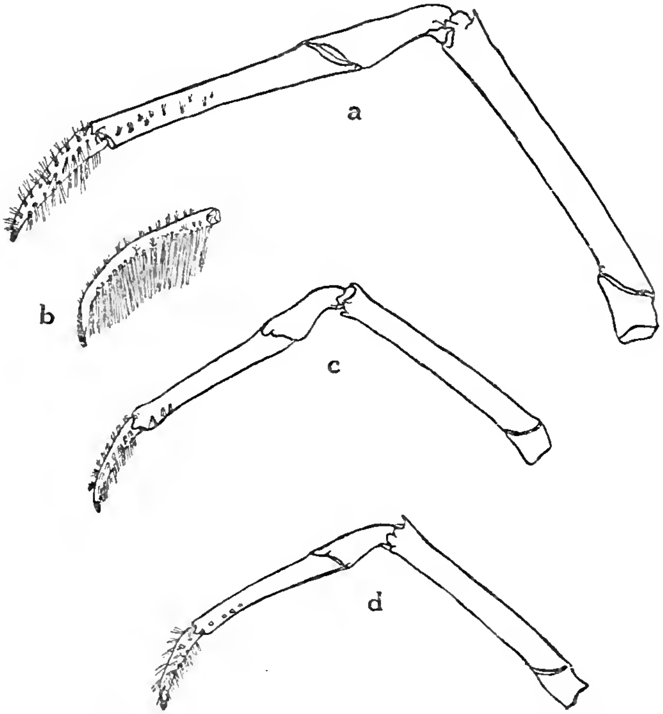

Fig. 268.—Development of second pair of legs of spiny lobster, *Panulirus argus*. Natural size. *a*, second leg of mature male; *b*, second dactyl of old male; *c*, second leg of young male; *d*, second leg of adult female.

The exopodites appear to the naked eye to be finely ribbed. These ribs appear under the microscope as dense, granular masses, along which at intervals are groups of minute setæ. All of these groups of setæ do not appear to be the same, some being composed of two or three comparatively long setæ and one seta which is short. The longer setæ are segmented and plumose, while the shorter seta is segmented and nonplumose. Nerve fibers extend through these setæ, which indicates that they may be sense organs, but whether they receive tactile or chemical stimuli is not apparent. The bases of these setæ are flask shaped, the distal portion of the segment being greatly enlarged.

Other groups of setæ are composed of three or four short setæ, none of which are plumose. They may represent the remains of longer setæ which have been broken off, although their ends are rounded.

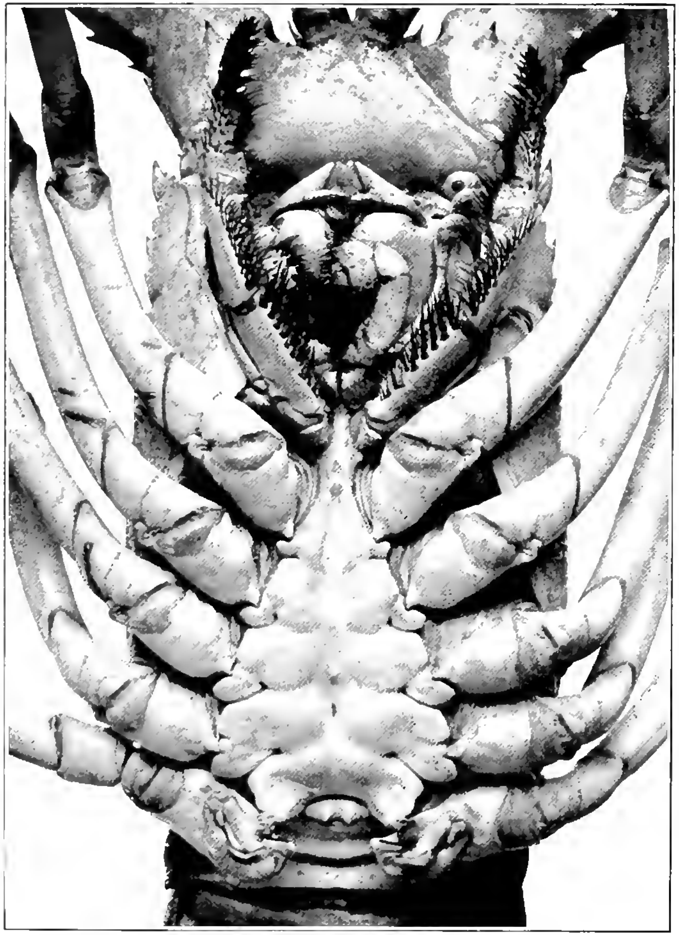

FIG. 270.—Sternum of adult male spiny lobster, *Panulirus argus.*

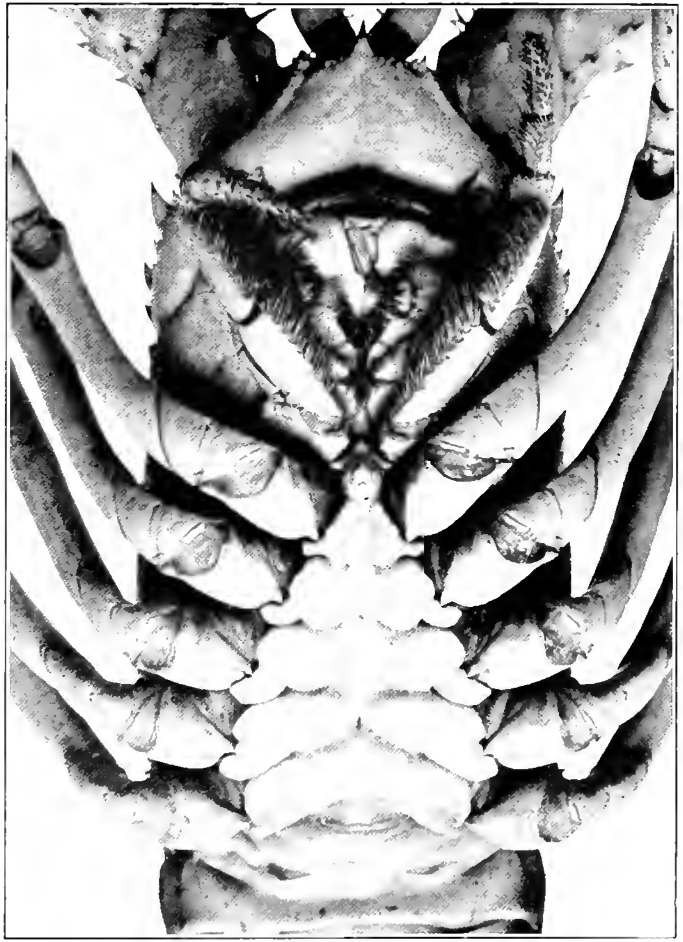

FIG. 271. Sternum of adult female spiny lobster, *Panulirus argus*

The margins of the exopodites are finely scalloped and fringed with short, plumose setæ which are provided with nerve fibers, indicating that they are probably sense receptors.

CARAPACE.

The carapace of adult males is of different shape from that of adult females. The branchial lobes are highly developed and give this region an oval appearance in contrast to the more cylindrical appearance of the carapace of the female.

The abdominal somites of the male are progressively narrower posteriorly causing the tail to taper and the uropods to appear proportionately wider than they do in the female, which, however, is merely an optical illusion, since there is no actual difference in width in individuals of the same size.

THORACIC STERNUM.

The posterior margin of the sternum of the male (Fig. 270) is narrower than the posterior margin of the female, the last thoracic segment being constricted posteriorly between the greatly developed coxopodites which extend inward, and is raised into small ridges which extend from the articulations with the fifth pair of legs toward the center. A small, bilobed part of the sternum lies between the bases of these ridges and extends posteriorly. The sternum of the male is longer than the sternum of the female.

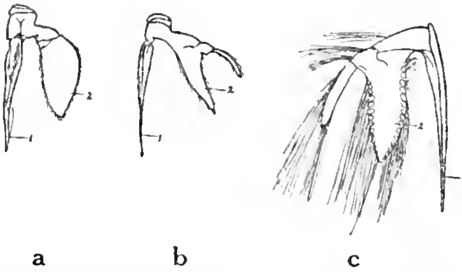

FIG. 269.—Pleopods of female, spiny lobster, *Panulirus argus.* × 0.75 approximately. *a*, first pleopod of adult female; *b*, second pleopod of young female; *c*, second pleopod of mature female; 1, exopodite; 2, endopodite.

The sternum is furrowed by a median groove which extends from between the first pair of legs to between the fourth pair. A narrow pit lies at the termination of this groove, and in the male there are three small tubercles anterior to and in line with the pit. The first of these tubercles is conical and acute and lies somewhat posterior to the bases of the first pair of legs. The second and third tubercles are rounded and but little elevated and lie between the bases of the second and third pairs of legs, respectively. These tubercles seem to form a locking device with those on the sternum of the female.

The median groove in the sternum of the female (Fig. 271) contains two small tubercles, both of which are conical and lie between the bases of the second and third pairs of legs. The seminal vesicle when present covers the sternum of the female from the third to the fifth pair of legs. The surface of the sternum when the vesicle is removed is striated, these small grooves or striæ probably serving to hold the material of the vesicle more firmly in place.

The posterior margin of the sternum of the female forms a rather broad arch. Small ridges extend from the articulations of the fifth pair of legs toward the center. It is seen when a male and female of the same size are placed with their ventral surfaces together that the grooves in the sterna form a mold which is nearly filled by the seminal vesicle. The extensions of the coxopodites of the fifth pair of legs of the male upon which the external genital organs are located press against the posterior margin of the sternum of the female, and the little brushes which are located on the anterior sides of the external sexual organs of the male are in such a position that the backward flow and escape of the seminal fluid would be prevented. It seems, therefore, that the seminal vesicle is formed between the sterna and that its shape is determined by the depressions.

HABITS AND MOVEMENTS.

HABITS.

The spiny lobster is nocturnal in its habits and remains hidden during the day under shelving rocks, large sponges, or other growths offering protection. Spiny lobsters may be detected in such places by the protruding antennæ or forepart of the body. Feeding evidently occurs at night while they are crawling about, and most of those taken by the fishermen are caught at this time.

Spiny lobsters are observed frequently crawling about in trains, the antennæ of one in contact with the body of the one in front. These trains probably constitute the so-called schools reported at times. Several small individuals are seen usually under the same sponge or rock, and numbers of them often crowd together in a small space. They seem to be gregarious, it being well known among the fishermen that where one spiny lobster is seen there may be several more close at hand.

The spiny lobster in captivity tends to avoid the light, and the character of its natural habitat is indicated by its habits. The best fishing grounds are found where plenty of cover is available, such places being rocky bottoms, coral heads and reefs, places where sponges are growing, or where artificial shelter has been provided accidentally. There is no evidence that the spiny lobster burrows into muddy banks or inhabits muddy bottoms. None was taken with traps set repeatedly in such places, while better success was attained with traps set on rocky bottoms or where sea fans were plentiful.

MOVEMENTS.

It is generally believed that the spiny lobster is rather sluggish in its movements. The usual method of locomotion is crawling slowly but nimbly about on the tips of the claws, but movements can be made to either side or backward with considerable rapidity. The most powerful movements are accomplished by flexures of the pleon or tail, but no great distance is covered in this way between rests. Short distances are covered rapidly sometimes by swimming on the side, or even on the back. Swimming is used principally in escaping from enemies and is not often employed in going from place to place while feeding. There is no reason to believe, however, that the range is restricted to a small area. Considerable distances could be covered by crawling, and it does not seem probable that the spiny lobster actually returns to the same shelter except by accident.

HABITS IN CAPTIVITY.

Spiny lobsters upon being impounded crawl about the inclosure and seek a sheltered place away from the direct rays of the sun. The antennæ are carried above the ground while the spiny lobster is crawling about, and if there is sufficient room they are spread out on either side. They are thrust forward or switched up and down when an enemy approaches. The tail is flexed under the body usually while the animal crawls slowly about, but at times it is straightened out and the pleopods aid in buoying up the body while more rapid movements are accomplished.

The tail is flexed under the body while the spiny lobster is at rest and the antennæ are spread outward. One or more legs sometimes move back and forth or from the body outward with slow rhythmic movements. The flagellæ of the antennules are drawn frequently through the setæ of the third maxillipeds, probably for the purpose of cleansing the cilia of sediment or growths of red algæ and diatoms which sometimes burden the cilia.

FOOD.

The natural food of the spiny lobster consists of worms, small mollusks, and probably smaller crustaceans. The lobsters are often scavengers, for it has been observed that they eat a great variety of food, such as bits of fish, and fish offal, meat, bits of crushed blue crab, pieces of clams, conchs, and garbage. The fishermen bait their traps with beef ribs or fish, but it has been found that bait is nonessential, since larger catches have been made at times when no bait was used than when the traps were baited.

Bits of seaweed have been found in the stomachs of a few spiny lobsters, but it is supposed that this material was ingested with small crustaceans or other small animals and does not form a part of the regular diet, since it was scarcely acted upon by the strong digestive fluids.

Spiny lobsters in captivity have been fed successfully on fish—either fresh, dried, or salted—clams, conchs, or any kind of meat scraps. Plenty of food should be provided and some regularity in feeding should be observed. The lobsters are not cannibalistic naturally, but when food is scarce they will not hesitate to eat the smaller individuals or those that have recently molted. Cannibalism has been observed more particularly among the larger males, and they should be kept separated from the spawning females and smaller individuals.

ENEMIES.

The spiny lobster at all stages of its existence is the prey of numerous enemies. The greatest losses no doubt occur during the larval development, when great numbers of them are probably eaten by pelagic animals. The black grouper, the mutton fish, and the jew fish are known to devour adult spiny lobsters, since the remains are found frequently in the stomachs of these fish. The stomach of a jew fish weighing about 350 pounds was found to contain 16 spiny lobsters of marketable size.

MODES OF PROTECTION.

The stiff heavy antennæ are used to ward off the attacks of enemies. They are raised upward or backward according to the direction of the attack or thrust directly forward and held rigidly, thus preventing large fishes or other animals from reaching the body. The flagellæ are rather brittle and break off when an attempt is made to draw the spiny lobster along by them. The loss of the flagellæ is the most common mutilation observed.

The heavy armature and sharp forward-pointing spines of the carapace form an effective means of defense, making it almost impossible for a person to escape injury while handling live spiny lobsters for examination. The legs separate readily from the body, especially in large individuals, and escape from capture is often effected in this way.

SENSE ORGANS.

Simple experiments showed that receptors for the sense of smell are located on the flagellæ of the antennæ. No specialized organs have been found, unless the setæ are the receptors, and it is not possible to locate any definite region where the sense of smell is most acute. Pieces of fish suspended in the water near the antennæ will attract the spiny lobster, and the flagellæ are moved so that they come into contact with the fish even though the food may be hidden by seaweeds. Experiment showed that in still water the reaction takes place to a piece of fish suspended a meter away from the antennæ, but the scent of food under natural conditions is probably carried much farther by currents.

Different sense organs are located on the legs. Pieces of fish dropped on the legs cause a definite response The legs are moved, causing the piece of fish to be brought under the body. This takes place even though the spiny lobster is eating other food. The response is different when inorganic materials, such as stones, are dropped in place of food. There seem to be similar receptors at the bases of the antennules and about the mouth parts. These two chemical senses differ from each other only in sensitivity. Particles of food must be dissolved in the water before they can stimulate either kind of receptor, but since one set of receptors receives stimuli from a distance it is more closely allied to the olfactory sense organs of air-breathing animals, while the other set of receptors receives the stimuli of particles of food directly in contact with it and is similar to the sense organs of taste in other animals.

Vision does not seem to be acute, for objects thrust near a spiny lobster do not always cause movement, and in diffused light the lobsters are more readily caught with a dip net than in bright sunlight. The antennæ are raised when a shadow passes over the spiny lobster, which will turn in different directions as the shadow moves. Vision, therefore, appears to be limited to distinguishing the quality of light rather than the qualities of definite images as in higher animals. It has been observed that food is not located by vision, since pieces of fish suspended in a current below the spiny lobster will not attract it although the distance is very short.

It is often thought that animals capable of producing sound are able to hear. If this is the case, the spiny lobster should respond to various noises, but experiments do not show that the auditory sense is present. The strident sound produced seems to be made only when an enemy has driven the spiny lobster into close quarters and hearing may not accompany it. This noise may be a means of defense.

HABITAT AND MIGRATIONS.

No direct observations have been made to determine the depth and distance from shore at which spiny lobsters may be found, but the following has been inferred from observations of catches brought into the market.

Traps are often set in deep water by the fishermen while they are fishing for large fish along the reefs 5 miles off Key West. Spiny lobsters are caught frequently on the outside of these reefs in 70 feet of water, and several fishermen claim to have taken a few with hook and line from somewhat deeper water. It is not probable that spiny lobsters in deep water inhabit different kinds of places from those found in shallow water; that is, they are restricted to rocky places or places where the growths of sponges and other forms offer protection. It is known from a limited local knowledge of the bottom near these reefs and also from the charts that the character of the bottom outside these reefs is less rocky and apparently does not afford good protection for spiny lobsters. The inference, therefore, is that the limit of distribution is bounded by these reefs, or it may extend a short distance beyond to detached coral reefs farther out.

Fishing operations are thus practically limited to shallow water and to an area not over 7 miles in width, including all places where all sorts of gear could be used. The region actually covered by the regular fishermen is not more than half this width and is confined to shallow banks not far from shore. The remaining strip is now, in reality, a natural reservation where protection is enforced by the limitations of the fishermen. This reservation, however, may be destroyed easily when the demand for spiny lobsters will make it profitable to invest in more elaborate gear, and it may be necessary then to establish definite reservations protected by law. The situation now prevents the concentration of large numbers of fishermen on a limited area, and extermination of the spiny lobster is not imminent. The dangers of overfishing, however, are obvious, and the present laws should be enforced.

The causes for migrations are numerous and rather obscure, but the three which seem to be the most important are molting, mating, and changes in temperature which probably affect both molting and mating. Local movements of relatively small numbers of spiny lobsters take place, which are probably caused by varying conditions of the water and food supply. A migration, as here considered, is a movement of a large number of spiny lobsters over a wide area, the movement being marked by more or less definite conditions.

The approach of the maximum molting season is marked by an increasing number of spiny lobsters in shallow water which differ in color from those usually found there, and many of which are about to molt. This condition does not exist merely locally but is found to be general over an extensive area. Catches of spiny lobsters brought into the market at Key West from widely separated places, such as Sugar Loaf Key and Marquesas Keys, show that the spiny lobsters about to molt migrate into shallow water at both places within the same month. Fewer spiny lobsters are taken at the height of the molting season than at other times, probably because the animal is less active at this time, and few spiny lobsters with soft shells are taken by the fishermen. This has led to the belief that, although the old shell is cast in shallow water, the spiny lobster soon retires to greater depths. Spiny lobsters with soft shells have been caught in quite shallow water near Key West, and it may be that there is no extensive movement of newly molted ones into deeper water unless the changes in temperature of the shallow water become unfavorable to the animal in its delicate condition.

The maximum breeding season varies somewhat in time from year to year and in different places. The number of spiny lobsters is known to increase in certain places during this time and also during the spawning season. Migrations of large numbers of spiny lobsters must then occur, for large catches of spawn-bearing females are made in certain places and not in others, and after the spawning season is over the catches of females decrease in places where they were formerly plentiful.

The following table (1) is a summary of the catches of spiny lobsters taken by means of a group of three traps set in about the same location from March to August, 1919, inclusive, the purpose of which is to demonstrate the decrease in the number of large females in shallow water during the maximum spawning season (March, April, and May) and the increase in the number of large females in shallow water after the hatching season is over and the molting period of the females has begun (June, July, and August).

TABLE 1.—SUMMARY OF CATCHES OF SPINY LOBSTER TAKEN IN THREE TRAPS, MARCH TO AUGUST, 1919.

Month.	Males.	Females.	Ratio of females to males.	Month.	Males.	Females.	Ratio of females to males.
March	30	14	0.45	June	65	32	0.49
April	38	10	.26	July	39	53	1.35
May	28	5	.17	August	42	73	1.73

The numbers of individuals involved in these data are small, but the catches brought into the markets at Key West were observed and the relative numbers of females to males were approximately the same as given in the table.

It is not evident that there are migrations parallel to the coast. Traps set offshore at various depths always take spiny lobsters regardless of the directions of the openings. Places known to be depleted from overfishing are not repopulated in a short time, which it seems reasonable to suppose would be the case if migrations occurred parallel to the coast. Migrations occur from deep to shallow water and back again to deep water.

Large numbers of spiny lobsters come into shallow water at times, apparently for the purpose of feeding. These constitute a type not usually found in such places, and they can be distinguished by their size and color, since they are larger and darker than those usually found in shallow water. The causes for this migration are obscure, but the changes in the temperature of the water probably are a determining factor.

INFLUENCE OF CHANGES IN TEMPERATURE.

Changes in temperature of the shallow water about Key West are often great and occur abruptly. The direction of the wind and condition of the weather account for these changes, and their influence upon the sizes of the catches of spiny lobsters is marked.

It is well known among the fishermen that the spiny lobsters are more abundant in shallow water after gales than during long continued calm spells. Closer observation has shown that when the wind blows from the sea more of them are taken in traps set off a lee shore, or the shore upon which the wind is blowing, than in traps set in the shelter of small islands or banks. It has also been observed that the catches are smaller when the wind blows from the shore.

The fluctuations in the abundance of spiny lobsters in shallow water at various times can be explained as follows. Sea winds cause the water to move shoreward, and as this water is generally cooler than that over the shallow banks it causes a temporary fall in the temperature of the shallow water. Conditions in shallow water then approach the conditions found in deeper water and spiny lobsters come into shallow water while feeding. Continued offshore winds tend to drive the water from the shallow banks, and thus prevent the cooling of the shallow water offshore. The spiny lobsters do not come into shallow water, because the temperature is excessive. The temperature of the shallow water rises rapidly during calm weather, and few spiny lobsters are caught.

INFLUENCE OF TIDES.

The influence of tides is not noticeable except where there are definite currents, such as occur between the keys and reefs. Traps set in such places have shown repeatedly that more spiny lobsters are taken when the tide is flowing out during the night and early morning, or when the moon is in perigee, than when the tide rises during the night and early morning, or when the moon is in apogee. It is thus possible to predict the relative sizes of catches in a given place with considerable accuracy. This is the reason, no doubt, for the belief among the fishermen that the moon influences the movements and abundance of spiny lobsters.

Traps set on the sides of a channel usually take more spiny lobsters than traps set in the middle, which indicates that the lobsters avoid strong currents.

MOLTING AND REGENERATION.

No sharply defined season during which spiny lobsters molt could be determined, since individuals of all sizes showing signs of molting can be found throughout the year. From observation of a small number held in captivity the young are known to molt more frequently than the adults, and it is supposed that females molt more regularly than the males because they carry spawn. The males, however, attain a larger size than the females, which probably indicates that their rate of growth is more rapid and perhaps that they molt more frequently than the females. The time of the molting season apparently varies somewhat from year to year, the variation being due probably to the temperature of the water and to the abundance of food, both of which seem to affect the rate of growth.

Numerous males of medium size which were caught during February, 1919, had recently molted or were in the process of molting. Larger males and females of small and medium size molt during April, May, and June. Females which have carried spawn molted in the summer from June to September or after the eggs had hatched. Several large females caught in 1918 were observed to molt as late as October, but several large males molted in the pounds as late as December. Several large females were observed to molt three or four days after the eggs had hatched.

PREPARATIONS FOR MOLTING.

Spiny lobsters preparing to molt can be distinguished from the others by the dull appearance of the shell, which is usually covered with fine silt and growths of seaweeds and stalked diatoms. It has been observed among spiny lobsters in captivity that such individuals seek sheltered places and remain inactive unless disturbed. Very little, if any, food is taken by them. The second pair of legs is used to rub the eyes and anterior parts of the carapace, and the fifth pair of legs frequently is used to rub the posterior parts of the body.

Hairlike lines appear about 80 hours before the shell is cast, one extending along the branchial region of the carapace and another downward between the first and second pairs of legs. These lines mark the places where the carapace will break and are apparent only when molting is about to occur, although their places are marked after molting by the regular arrangement of the tubercles. The lime salts of the shell are gradually dissolved away along these lines until the shell is broken, and molting usually occurs three or four hours afterward.

A period of activity immediately precedes molting, during which the spiny lobster crawls about with intermittent intervals of rest. During this time the anterior legs are used more frequently to rub the eyes and surface of the carapace and mouth parts. The fourth and fifth pairs of legs are brought over the other legs and held there momentarily at irregular intervals, and sometimes in a pushing position, while the other legs are placed forward as though pulling. Crawling ceases when the carapace becomes disarticulated at the pleon.

CASTING OF THE SHELL.

The spiny lobster while molting remains in an upright position, with the three anterior pairs of legs extended forward and the fourth and fifth pairs of legs extended somewhat backward, the dactyls apparently gripping the ground. This position was observed in at least seven instances while molting took place (Fig. 272).

FIG. 272.—Newly molted shell of spiny lobster, *Panulirus argus*, showing position at instant of molting. × 0.5 approximately.

The posterior rim of the carapace begins to rise as soon as it is separated from the pleon and crawling has stopped. No violent movements are made at this time, and the old carapace slowly rises as the cephalothorax is withdrawn from the old shell. The cephalothorax is elevated until the eyes and bases of the antennæ are on a level with the posterior rim of the old carapace, which is at an angle of about 75° with the ground. The critical time has now arrived, and the antennæ are moved upward, downward, and to both sides as the flagellæ are withdrawn. The cephalothorax and legs are freed by a lunge backward, and the shell is cast from the tail by a few movements.

THE NEWLY MOLTED SPINY LOBSTER.

The appearance of the newly molted spiny lobster is much the same as the old shell in details, but the colors are fresher and brighter, and the appendages which were lost before molting have been regenerated. The new shell is soft to the touch, and all of the spines can be bent.

The spiny lobster remains near the cast-off shell for a short time unless disturbed and then seeks shelter. The belief among the fishermen that the newly molted spiny lobster eats part of the old shell has been verified by observation, but also spiny lobsters which have hard shells have been observed eating such material when other food was scarce.

HARDENING OF THE NEW SHELL.

The time required for hardening of the new shell varies considerably with individuals. The shell does not harden appreciably for 24 hours after molting, but by the end of the second or third day the mandibles, legs, claws, spines, and branchial regions of the carapace have hardened sufficiently to have rigidity, and in four or five days the shell has a papery firmness. The shell can not be dented easily after 14 days. One spiny lobster was impounded without other sources of lime than the cast-off shell, and it was observed that the new shell hardened after 18 days to the extent that it could not be easily dented.

AUTOTOMY.

Autotomy has been observed to take place among spiny lobsters lying in the bottom of a boat, the third pair of maxillipeds and first pair of legs being lost more frequently than the other appendages. Autotomy, or reflex amputation, occurs along definite lines where the tissues are probably prepared to check bleeding. This provision of nature undoubtedly saves the life of the spiny lobster, for it has been observed that when a leg is broken off at any other place than that where autotomy occurs bleeding is usually unchecked, and such an injury often proves fatal. The plane of fracture when autotomy occurs is between the coxa and basis, and if a leg is broken off at any other place the remaining part is cast off at this plane. The legs of very large males often drop off while the body is temporarily suspended, and it has been observed that autotomy occurs when a spiny lobster comes into contact with certain objects, such as a sun-heated plank or tin bucket. The flagellæ of the antennæ break off at their bases when an attempt is made to pick up the spiny lobster by the antennæ.

REGENERATION.

The completeness of regeneration of lost appendages depends upon how long before the next molt they were broken off. It has been observed that legs lost six months or more before molting are regenerated to about two-thirds their normal length, but if a leg is lost a month or less before molting regeneration is very incomplete and the appendage is represented by a small papilla. One female was observed which had lost the dactyl of the fifth leg two months before molting. This segment was replaced at the next molt by a budlike papilla.

It has been observed that the flagellum of a broken antenna is regenerated sometimes before the next molt by the outgrowth from the stump of a small, soft flagellum. This form of regeneration of the antenna has been observed infrequently. Regenerated appendages are always smaller than the originals and are usually malformed, but they gradually approach perfection of size and shape in succeeding molts. Broken places in the shell, if they have not proved fatal, are poorly mended after molting, and holes which were punched in the uropods of large individuals under observation remained open after the shell was cast. Such holes, however, were observed to close in a few young individuals.

RATE OF GROWTH AND SIZE.

The rate of growth depends upon the frequency of molting, and consequently varies with age, abundance of food, and temperature of the water. The young increase in length more rapidly than the adults because they molt more frequently. The actual increase at each molt was found, however, to be small. This increase was not noticeable immediately after molting, but when measurements were made three or four days later it was observed that the percentage of increase in the length of the carapace of females averaged 3.32 and of males 2.75. The ratio of the increase in length of the young at each molt is about the same as that of the adult. The actual increase in length of the adult at each molt is, of course, greater than that of the young, because the percentage of increment at each molt is based upon the length of a larger individual. For example, the actual increase at molting in the case of a male spiny lobster 2 inches long would be 0.055 inch, while that of one 5 inches in length would be 0.1275 inch.

The most rapid increase in weight at each molt occurs in the young, the percentage of increase in weight at each successive molt becoming smaller. Table 2 shows the general relationship between the length and weight of spiny lobsters of various sizes.

Persistent fishing apparently has reduced the size of spiny lobsters near Key West, but very large individuals are found around the Dry Tortugas and parts of Florida Reefs unfrequented by the fishermen. Measurements of a few of the largest spiny lobsters brought into the Key West market indicate that the maximum size of those caught near Key West is 14 inches total length, excluding the antennæ, with a weight of about 5 pounds. Several very large males brought from the Dry Tortugas measured 18 inches in total length, excluding the antennæ, and weighed from 6 to 8 pounds. No females of this size have been observed, the largest measured being not over 13 inches in total length.

The weight increases rapidly with increase in length, but individuals vary greatly in weight because of the loss of appendages and differences in the proportions of the body. The pleon of the female is wider than the pleon of the male, and females weigh more than males of the same length.

Table 2 is compiled from the measurements and weights of over 150 individuals. It is a comparison of the lengths and weights of the sizes of spiny lobsters usually brought into the market at Key West.

TABLE 2.—COMPARISON OF LENGTHS AND WEIGHTS OF SIZES OF SPINY LOBSTERS BROUGHT TO KEY WEST (FLA.) MARKET.

Length carapace (inches).	Average total length (inches).	Average weight.		Length carapace (inches).	Average total length (inches).	Average weight.	
		Pounds.	Grams.			Pounds.	Grams.
2.0-2.4	5.5	0.26	120	4.0-4.4	10.50	1.85	840
2.5-2.9	6.875	.54	245	4.5-4.9	11.50	2.51	1,140
3.0-3.4	8.25	.87	395	4.9-5.0	12.50	3.42	1,550
3.5-3.9	9.375	1.29	588				

GENITAL OPENINGS AND COPULATION.

GENITAL OPENINGS OF THE MALE.

The external sexual organs of the male (Fig. 270, opp. p. 295) are located on the greatly enlarged coxopodites of the fifth pair of legs. The coxopodites extend inward, the inner ends nearly meeting on a median line, and curve anteriorly and outward, the anterior part being compressed into a sharp ridge which is flatly concave on the anterior side. The ventral surfaces of the coxopodites are concave, forming a cup in which the external sexual organs of the male lie. These organs are somewhat pear-shaped and appear in life as suckerlike pads. Each of these pads is provided with a small brush of short setæ which project from the anterior side next to the sharp ridges and which are set obliquely to the axis of the coxopodite. The external openings are curved slits protected by thin lips of chitinous material, which are usually kept tightly closed in life.

GENITAL OPENINGS OF THE FEMALE.

The external openings of the oviducts (Fig. 271, opp. p. 295) are located on the coxæ of the third pair of legs at the articulation of the coxopodites with the sternum. These openings are roughly ovoid in outline, measuring 3.5 mm. on the major axis and 2.0 mm. on the minor axis. The oviducts do not open directly downward, since the anterior margin is somewhat higher than the posterior margin. The opening of the oviduct is protected by a flap of thin chitin which narrows the opening itself to a small pore.

COPULATION.

The manner in which copulation is effected has been deduced from observations of spiny lobsters in captivity. The male crawls nimbly about, approaching females approximately his own size. The legs are used to fence in the female, and an attempt is then made to turn her over. Sometimes the female is met head on and forced upward and backward, the second pair of legs being used to hold the female. The female successfully repulsed the male each time during these observations, and coitus did not actually take place, but there seems little doubt that the female is turned over upon its back during copulation.

One female was observed carrying a seminal vesicle while the shell was still quite soft, showing that copulation evidently had taken place soon after molting. This spiny lobster died, and it was not learned how long the seminal vesicle is carried before spawning takes place. Later observations indicated that the sperm is probably carried over winter.

Observations during two seasons (1918, 1919) were made upon large numbers of spiny lobsters brought into the Key West market during August, September, and October. It was noted that over half of the females which evidently had recently molted were bearing fresh seminal vesicles, which seems to support the belief that mating takes place soon after the female molts. The mating season, judging from these observations, occurs from August to November.

THE SEMINAL VESICLE.

The seminal vesicle is deposited on the sternum of the female between the last three pairs of legs and is composed of a dark gray or black material which has the consistency of whalebone. Males taken in July and August contain a dark gray, waxy material in a coiled tube under the carapace. This seems to be the material of which the seminal vesicle is composed.

The interior of the seminal vesicle is porous and has much the appearance of a piece of coarse, dry bread, which suggests that the material contained in the testes and vas deferens of the male during the mating season is composed of two different substances. One substance, which hardens soon after being deposited upon the sternum of the female, forms the bulk and body of the vesicle, while the other substance remains liquid. This liquid does not harden, since it can be expressed when the surface of the vesicle is scraped away. These two substances, however, form a homogeneous waxy fluid before the vesicle is deposited, and they are probably separated from each other by the process of hardening of the waxy material around the liquid, the pores being formed in a way analogous to the air bubbles in thick glue, or molten glass. A large part of the old vesicle is picked off by the females with the fifth dactyls soon after the eggs hatch. In three instances it was observed that molting took place from three to five days after the eggs had hatched. The end of the spawning season and the beginning of the molting season of the female are indicated by the condition of the seminal vesicle.

SPAWNING.

AGE OF FEMALE AT SEXUAL MATURITY.

The age at which the female reaches sexual maturity is not definitely known, but, judging by the development of the secondary sexual characteristics, the female reaches sexual maturity at a smaller size than the male. The smallest females observed carrying spawn measured 3 inches on the carapace, or about 9 inches in total length, exclusive of the antennæ. The size of spawn-bearing females varies considerably, the variation probably indicating differences in age.

THE SPAWNING ACT.

One spiny lobster was observed closely while spawning was taking place. The position of the female was that which is normally assumed while at rest and not upon its back. The abdomen was flexed, and the uropods formed a pocket with the exopodites of the pleopods. The fifth legs moved rapidly from the seminal vesicle to the pleopods during short intervals and then remained at rest. The vesicle was scraped frequently with the fifth and sometimes with the fourth pair of dactyls. The exopodites of the pleopods beat slowly and rhythmically at times, the movement being from side to side. The pleopods remained inactive and extended while the vesicle was being scraped, and they moved rapidly while the fifth pair of legs moved backward to them.

DEPOSITION OF EGGS.

The eggs were not seen as they left the oviduct and passed to the pleopods, nor was the method by which they are attached to the setæ observed. The eggs are fastened to the setæ in bunches of different sizes, which indicates that they were laid either in bunches or issued from the oviducts in a steady stream and were driven backward against the pleopods by the beating of the exopodites. Examination under the microscope shows each egg to be stalked, and the stalks of a bunch of eggs are tangled together to form a common stem whose distal end is flattened where it comes into contact with the seta, to which it is fastened. All of the eggs were laid from four to six hours after spawning commenced.

DEVELOPMENT OF THE EGG.

The earliest stage in the development of the egg which was seen was that of eight cells. Subsequent stages were observed to the blastula, but the exact time between consecutive stages is not known, because the eggs died quickly in water under the microscope. Eggs of 16 cells were found in the same lot with eggs of 8 cells, and the inference is that they do not all develop at an equal rate. Some were found which segmented abnormally, the yolk remaining in a solid mass at one pole, while it was segmented at the other pole. The 8-cell stage was not found on the pleopods after 12 hours, and the 16-cell stage was not found after 24 hours. The morula was observed 30 hours after the eggs were known to have been laid and the blastula after 48 hours. These later stages may have been reached at an earlier period in other eggs than those observed. The yolk material of the eggs is dense and opaque, and further study of the embryo was impossible without resorting to sectioning. The eyes of the embryo can be seen after seven days, and examination under the microscope shows that at least five pairs of appendages are developed. Much yolk is present at this time and but little detail can be seen. It is known from observation of three females carrying spawn that the eggs were all hatched in 18 days from the time they were laid. The time probably varies as it does in the development of other eggs, but the maximum time evidently does not exceed three weeks.

Recently laid eggs are of a bright orange-red color, but as the embryo develops the color changes to clear, light brown, and just before hatching the eggs are almost colorless. This change in color is due to the absorption of the yolk material. It is not difficult, therefore, to judge the approximate age of the eggs by their color and general appearance.

SIZE AND NUMBER OF EGGS.

The eggs are quite uniform in size and shape. Eggs which have been recently laid are slightly oval or spheroidal in shape, the major axis measuring 0.5 mm. and the minor axis 0.45 mm., but they become more spherical as the embryo develops. The eggs increase slightly in size and the diameter is about 0.55 mm. just before the larva hatches.

Several estimates of the number of eggs carried by the female have been made. The number for a female measuring 3½ inches, length of carapace, is about 500,000. A larger individual, measuring 4 inches, length of carapace, carried about 700,000 eggs, which seems to be about the maximum number. The eggs measure about 7,500 to the cubic centimeter.

Practically all of the eggs hatched on females observed, only a small number of dead eggs remaining. The dead eggs were opaque and dull in appearance, and it is possible that they were never fertilized. It is known that mud covering the eggs will cause their death. It therefore is important that the fifth dactyls of the female remain intact, for it has been shown that these appendages are utilized in keeping the eggs free of sediment,

CHARACTER OF OVARIAN EGGS.

The ovaries are greatly distended just before spawning and appear as a bright red, bilobed organ extending from the head beyond the cephalothorax, the posterior end lying between the muscles of the first segment of the abdomen. The ovary has a mealy appearance when the eggs are fully developed, and it is very fragile. The eggs under the microscope appear to be without a shell or other protecting covering, and they soon coagulate in water, becoming white and opaque. The eggs are not round, but of various shapes, due to being packed closely together in the ovary. Their greatest diameter, however, is not more than 0.5 mm. The yolk material is very dense and granular, and the nucleus of the cell is rather difficult to find.

HABITS OF THE FEMALE DURING SPAWN BEARING.

Spawn-bearing females in captivity seek sheltered places in the pens and are less active than those not bearing spawn. It was observed that females bearing eggs about to hatch were less active than those whose eggs were newly laid, and this was of considerable aid in selecting individuals with ripe eggs for experiments in hatching.

The female while carrying spawn normally assumes a resting position; that is, it rests on the bottom on the tips of the dactyls with the tail somewhat extended and the uropods curved downward. The exopodites of the pleopods beat slowly and rhythmically, evidently for the purpose of keeping the water about the eggs in circulation. There are two movements of the pleopods which alternate at frequent but irregular intervals. One movement is backward and forward at the rate of 55 or 60 times per minute. The tail is slightly raised and the pleopods extended before the other movement, which is more rapid, the pleopods beating obliquely 65 to 70 times per minute, begins. The fifth legs are used frequently to manipulate the eggs and no doubt clean away any sediment or débris that might settle on them.

Small fishes sometimes attack spawn-bearing females, but they are often repulsed with the antennæ. There is little tendency for the female to move, and usually but little food is taken when the eggs are about to hatch.

TIME OF SPAWNING.

There is no sharply defined spawning season, since spiny lobsters bearing spawn have been found throughout all the year except during the winter. The maximum number spawn in the spring and early summer, the first being females of large size. Small females measuring 2¾ to 3 inches, length of carapace, have been observed bearing eggs late in the fall, but no spiny lobsters have been seen with spawn in November, December, or January. It is known that spawn-bearing females are brought to market later in the season from places west of Key West than from banks near Key West, and that the earliest spiny lobsters observed with spawn come from places considerably east of Key West.

The time between successive spawning periods of individuals is not known, but it is certain that spawning does not occur more than once a year. Females kept in pounds did not spawn the second year of captivity, and but one out of over a hundred was observed bearing a new seminal vesicle after molting during the second season.

EXPERIMENTS IN HATCHING.

Preliminary experiments were made by the junior author in 1917, which showed that the eggs would hatch while attached to females placed in floating boxes. The young, however, could not be reared in such apparatus and died within a day or two after hatching.

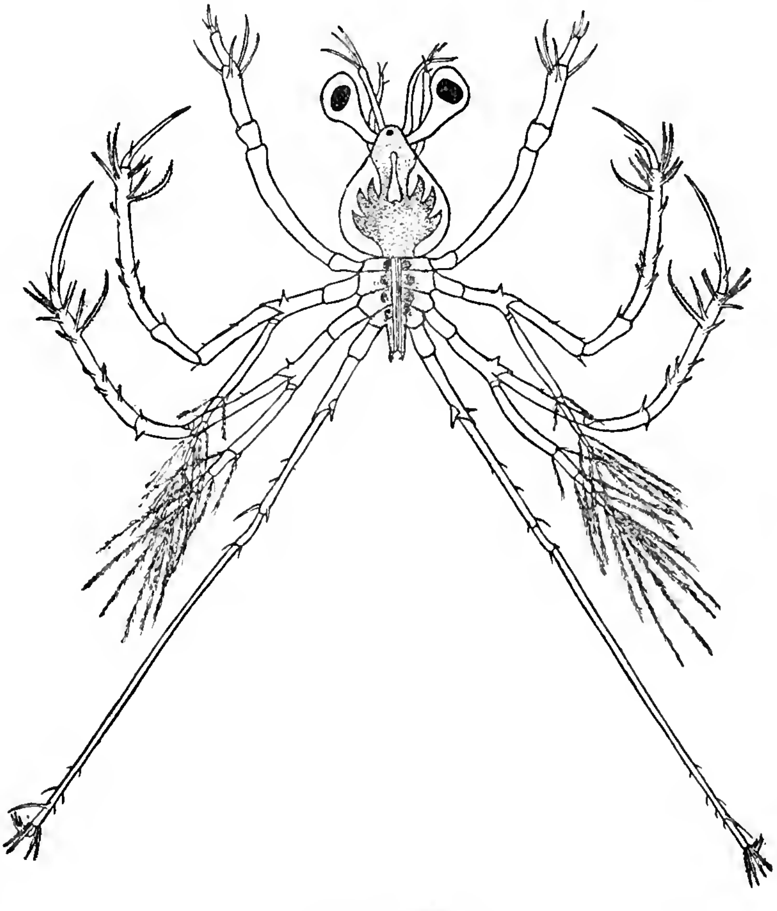

FIG. 273.—Newly hatched larva of spiny lobster, *Panulirus argus*, hatched at Key West (Fla.) Biological Station, June, 1918. × 33⅓, approximately

Another attempt was made to hatch the larvæ in 1918. The eggs were stripped from a number of females and placed in MacDonald hatching jars, which were supplied with running salt water. This method proved to be more convenient than floating boxes for observation, but as a practical method it can not be recommended, since a very small per cent of the eggs hatched normally. It was found that the eggs hatch much better when left on the pleopods of the female. Newly laid eggs were observed to be slightly heavier than water, but as the embryo develops the specific gravity of the eggs decreases, and when the eye of the embryo is visible the eggs are more buoyant. The newly laid eggs did not hatch in the jars, since they could not be prevented from adhering to each other in masses, and they soon died.

The effects of changes in temperature of the water on hatching were observed. The highest temperature at which the larvæ were observed to hatch normally was 78° F. The temperature of the water fluctuated considerably during the day, the range being from 76 to 98° F. The changes often occurred abruptly and marked the death of many larvæ. Many of the eggs did not hatch at 98° F., and the larvæ which did emerge at the higher temperatures usually died before becoming entirely free of the egg membrane.

It was observed that the temperature of the water fluctuated less during the night, especially when the tide was rising, and it remained not far from 76° F. It was inferred from this that the temperature offshore was not far from 76° F. It, therefore, does not seem probable that hatching takes place in shallow water where the temperature conditions apparently either inhibit the hatching of the eggs or cause the larvæ to emerge in a weakened condition. It is known that the phyllasomes of closely related species have been taken in 75 fathoms of water far offshore.

The embryo about to hatch is much compressed within the egg membrane, and it is colorless and transparent except for the black eyes and bright yellowish red dot of unabsorbed yolk, which are opaque. It was found necessary to reduce the flow of water in the jars at this stage, because the embryos are buoyant and hatch as they float upward. The larva emerges much doubled up, like a fleck of cotton waste, but quickly straightens out into the normal position and at once begins to move about actively.

The first-stage larva (Fig. 273) is a phyllasome which is a modification of the mysis or schizopod larva of other Macrura, such as the northern lobster, but the subsequent development is by no means the same. The short embryonic development predicts a long larval development which may render artificial propagation a very difficult problem.

No cannibalistic tendencies were noted among the larvæ, but plenty of space should be provided, to prevent their appendages which are long and provided with numerous spines and setæ, from becoming closely entangled with those of other larvæ. This danger is especially great unless the light is diffused, since the larvæ are decidedly heliotropic. They become massed together and must be separated by means of some stirring device. Silt suspended in the water becomes lodged on the setæ and spines of the larvæ and weights them down to their death. Feeding was attempted, but the results were negative. The food of the larvæ is probably other plankton, and any method that can be devised to increase the growth of these organisms will greatly aid the solution of a difficult problem.

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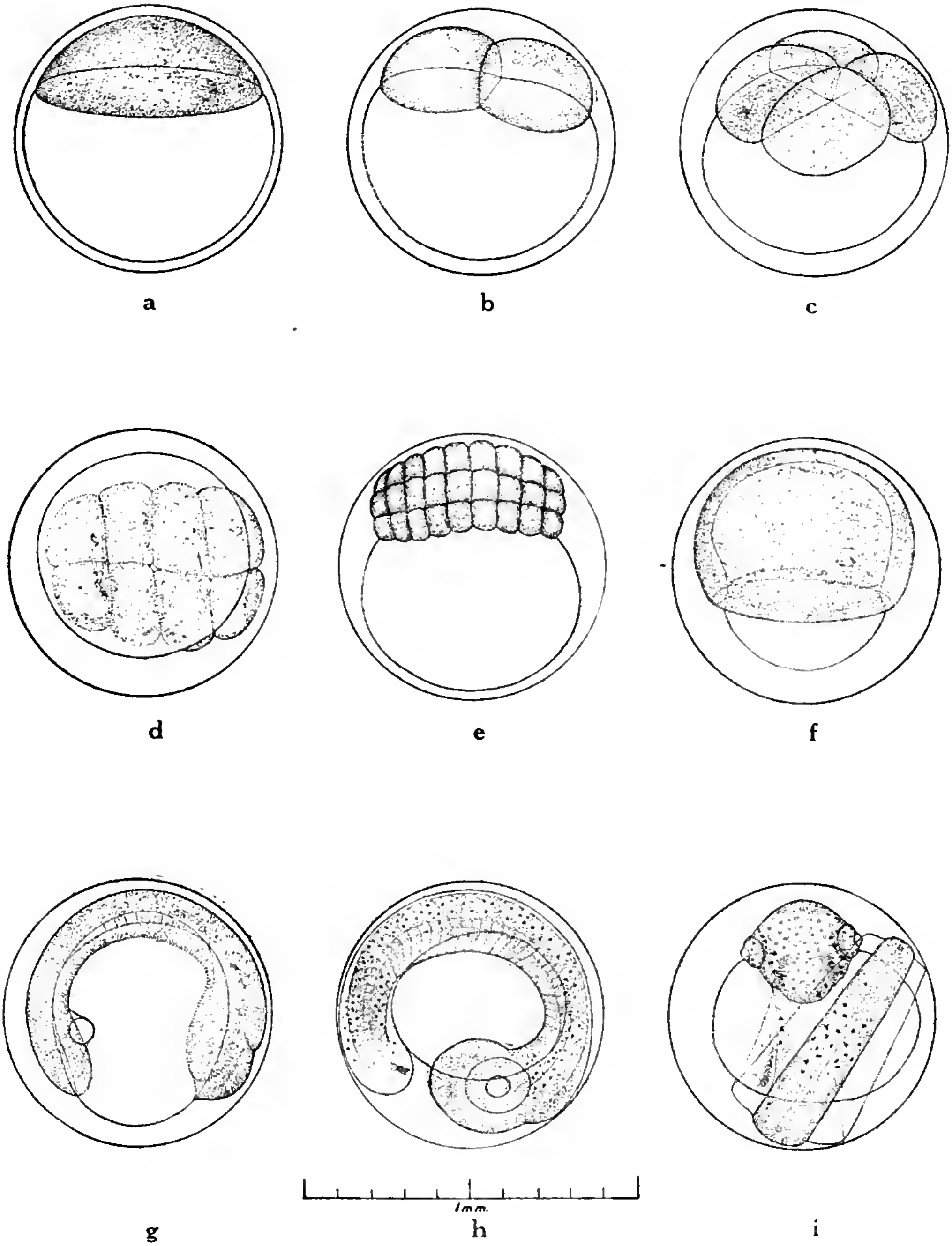

Fig. 274.—Egg of winter flounder, *Pseudopleuronectes americanus*.

a, Unfertilized egg.
b, Egg with blastoderm of two cells.
c, Egg with blastoderm of four cells.
d, Egg with blastoderm of eight cells.
e, Egg with blastoderm of many cells.
f, Embryo in early stage of differentiation.
g, Embryo further differentiated. Note small sphere similar to an oil globule.
h, Embryo in an advanced stage of differentiation.
i, Egg about to hatch.

SOME EMBRYONIC AND LARVAL STAGES OF THE WINTER FLOUNDER.

By C. M. BREDER, Jr.
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The height of the spawning season of the winter flounder, *Pseudopleuronectes americanus* (Walb.), in the vicinity of Woods Hole, Mass., is reached at what is usually the coldest time of the year, most frequently during February. The material on which this paper is based was acquired during the period extending from January 28 to February 23, 1921, the spawn being gathered from Bowen's pond, Poket, and Waquoit. These are small arms of the sea superficially quite lacustrine in appearance and of rather low salinity, due to a considerable influx of fresh water. The fish were taken in small fyke nets set at a depth of about 8 feet through breaks in the ice. The temperatures and salinities of these spawning grounds during the period of observation, which probably give a fair indication of the average variation, were as follows:

Locality.	Temperature ° F.	Specific gravity at 60° F.
Bowen's pond	33-37	1.011-1.020
Poket	32-37	1.010-1.011
Waquoit	35	1.016-1.022

Possibly the temperatures dropped a little lower at times when no records were taken.

On February 23 the entire catch of one fyke net (85 specimens) was examined in detail and 24 per cent was found to be ripe, 37 per cent spent, 33 per cent partly spent, and 6 per cent immature. These data would seem to indicate that the season was well under way and about to wane, which was substantiated by statements of the men and subsequent observations. A few examples of the younger fish were always found along with the mature fish, apparently following them to the spawning grounds, although sexually immature and unable to partake of the activity.

These fish had fed sparingly if at all. Seven were completely empty, and of the remainder very few contained more than mere traces of a yellowish white paste destined only to become offal. The volumetric percentages of the various items of the stomach contents were as follows: Gastropods (*Haminca solitaria*-?), 1+ per cent; amphipods (sand fleas), 8− per cent; prawns (small), trace; mud, 11− per cent; yellowish white paste, 80 per cent. The yellowish paste might well have been the remains of food taken before migration to the spawning grounds, as the peristalsis of fishes in winter is usually extremely slow.

In the latitude of New York this species is angled for in the fall and sometimes as late as the middle of December. From then on it usually ceases to take the hook until it is next taken in late February, the anglers' belief being that the flounders lie dormant in the mud during the coldest weather. Along the New England coast the fall season closes earlier and the fishes do not reappear to the anglers much before the middle of March or later. Correlating this with the preceding study of the stomach contents it is evident that these fish feed little, if at all, during the period of sexual activity.

The spawning act in the confinement of the hatchery tanks was invariably performed at night, most frequently between the hours of 10 p. m. and 3.30 a. m. The details of this are fully described in Copeia for January 22, 1922.[1]

Embryology.—The eggs of *Pseudopleuronectes americanus* are minute, adhesive, and demersal. They have a modal diameter of 0.81 mm. and vary from 0.71 to 0.86 mm. Due to their adhesive nature, they are frequently more or less distorted, in some cases being quite ovoid; but it is doubtful if the deformed eggs produce normal larvæ. Laid along a ruler, as fish-culturists measure, the eggs run 31 to the linear inch. The blastodisk (fig. 274*a*) is large and of a pale amber color, while the yolk is colorless. The surface of the yolk is finely tuberculate, and the egg membrane resembles fine grain leather in texture. The spermatozoons average about 0.030 to 0.035 mm. in total length.

At a temperature of 69° F. the first cleavage took place at about 2¼ hours after fertilization (fig. 274*b*). Eggs when isolated from their companions showed flat marks on the membrane where others had been adhering, some presenting the appearance of fairly regular polyhedrons. Such pressure marks on the membrane appear not to affect the development in any way and, being purely mechanical, are not shown in the sketches, as eggs isolated from the start are perfectly spherical. The further cleavages followed after the typical manner of teleostian eggs. By the time 24 hours had passed the blastoderm was broken up into a high number of cells (fig. 274 *c* to *e*). By the end of the third day differentiation had begun and the eggs appeared as shown in figure 274*f*. At six days the differentiation had reached the stage shown in figure 274*g*, primitive segmentation having commenced and the cephalic region having become more recognizable as such. It might be noted that in many of the eggs a small sphere similar to the oil globules in pelagic ova was observed, and in a few several such globules were present in a small cluster. Such a structure is indicated in figure 274*g*. Eggs beyond this stage failed to show this peculiarity. The embryo was a pale amber of the same tint as the unfertilized blastodisk, and the "oil globule" was colorless. Figure 274*h* shows the appearance at nine days. The embryo was well differentiated, and chrome yellow chromatophores were sprinkled over the body, as indicated by black dots. These were punctulate and difficult to see by transmitted light, but they stood out prominently on a dark field. Figure 274*i* gives the appearance at 15 days. The chromatophores presented a similar appearance at this stage, but there was a noticeable concentration of them as a vertical band in the caudal region. The heart could be seen beating in slow rhythm, but no other motion was noted. The cephalic region appeared

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[1] Breder, C. M., jr.: Description of the Spawning Habits of *Pseudopleuronectes americanus* in Captivity. Copeia, January 22, 1922, No. 102, pp. 3-4. New York.

to be finely tuberculate. At 15 days hatching had commenced, although comparatively little activity on the part of the embryo had been observed at any time while in the egg.

Larval development.—On hatching the larva appeared as in figure 275*a*. In some individuals the eyes were entirely unpigmented, while in others chrome yellow pigment similar to that present on other parts of the body was present in the iris, a type of ocular pigmentation developed by all the larvæ within a few days. Later the pupil became generally tinged with greenish, and by the time the larva reached the stage shown in figure 275 *b* and *c*, 19 days, the pupil had become black and the iris presented a metallic greenish iridescence. The eyes were directed slightly forward and downward, the mouth was large and functional, and the yolk was absorbed at this stage. The entire animal was perfectly symmetrical as yet. The pigment had become a little darker, approaching a light orange. None of the larvæ survived for more than 22 days.

Preserved material which had been collected at Boothbay Harbor, Me., by Supt. E. E. Hahn near the end of the same season was also examined, and it was found that the development had been quite similar to that of the material studied at Woods Hole. Mr. Hahn succeeded in holding some larvæ until the twenty-seventh day after hatching. The chief advancement beyond that condition shown in figure 275 *b* and *c* was one of size. These examples, which were preserved in formalin, averaged about 5 mm. in length, while those found to be living at the end of 22 days at Woods Hole averaged about 4.5 mm., which is a trifle over that of the example illustrated by figure 275 *b* and *c*. The larvæ were held in Chester jars, the mouths of which were covered with a double thickness of cheesecloth. It was difficult to find a screening which would hold the fishes in and at the same time allow smaller food organisms to pass through and permit a sufficient change of water. The cloth employed was far from satisfactory, but fine bolting cloth was found to be entirely unsuitable, as it clogged too readily with diatoms and fine débris. A similar difficulty was reported from the Boothbay Harbor station.

In 1885, under the name of *Pleuronectes americanus* Walb., from material studied at Newport, R. I., during July and August, Agassiz and Whitman[2] described and illustrated the development of what they believed to be this species. It is now apparent, however, that these splendidly rendered illustrations and carefully written descriptions refer to some species of a very different habit. Aside from the fact that the illustrations do not agree with those accompanying the present paper, which have been based on material definitely known to be *P. americanus*, it is evident, since their material was pelagic and was taken in midsummer, that their work was a study of the development of another fish. It is doubtful, indeed, if the material was of a Pleuronectid nature at all, principally owing to the long gut shown in their plates, which is highly unusual for members of this group. In a previous paper Prof. Agassiz[3] illustrates more advanced stages of some flounder which he also identified as this species, but it is thought that his sketches represent some other form, although the insufficiency of data presented therewith precludes any very conclusive statement at present.

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[2] Agassiz, Alexander, and C. O. Whitman: Studies from the Newport Marine Laboratory. XVI. The Development of Osseous Fishes. I. The Pelagic Stages of Young Fishes. Memoirs of the Museum of Comparative Zoology at Harvard College, Vol. XIV, No. 1, Part I, 56 p., XIX pls. Cambridge, 1885.

[3] Agassiz, Alexander: Development of the Flounders. Proceedings, American Academy of Arts and Sciences, Vol. XIV; p. 1–25, pls. Boston, 1879.

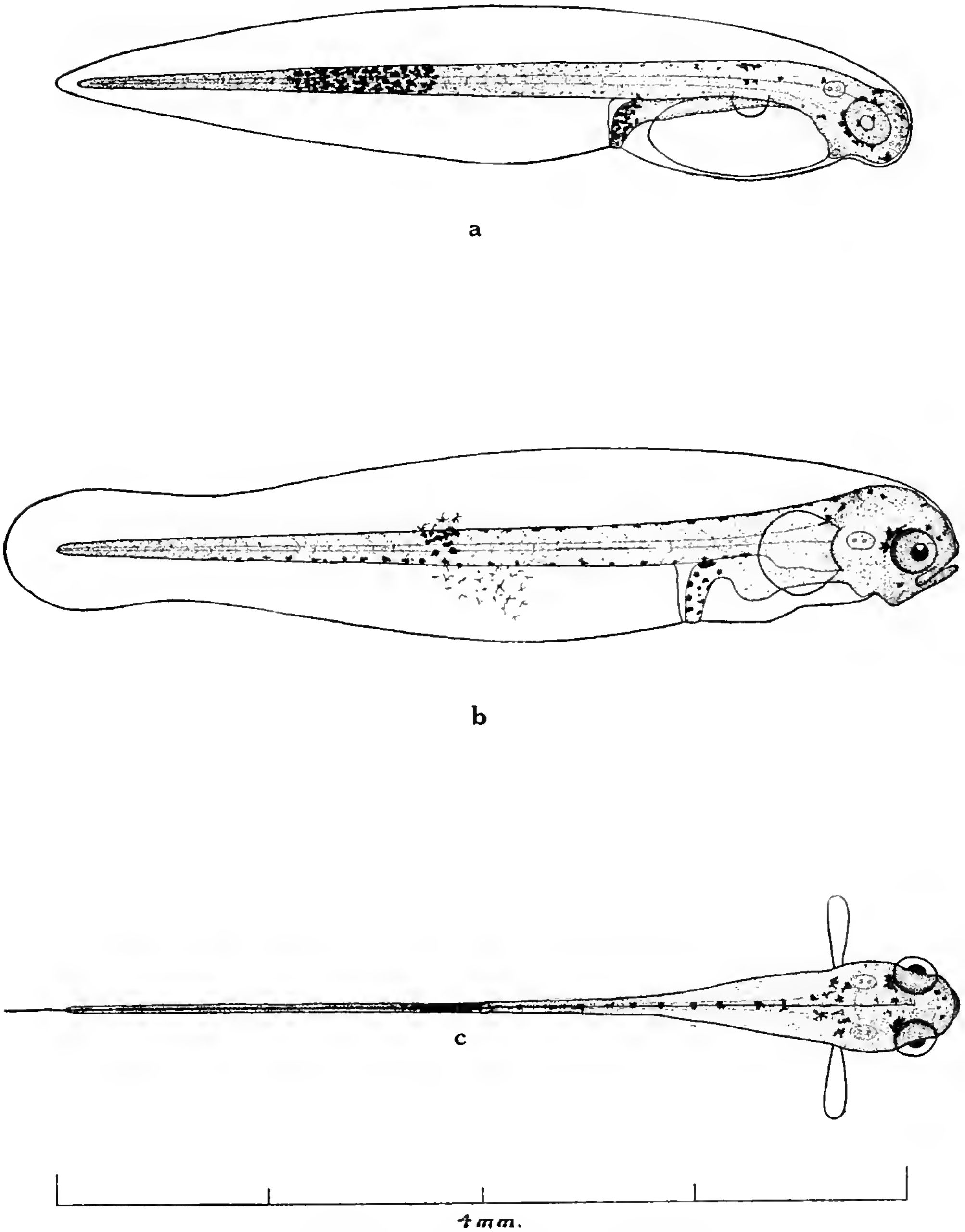

FIG. 275.—Larva of winter flounder, *Pseudopleuronectes americanus*.
a, Newly hatched larva.
b, Larva 19 days old—lateral view.
c, Larva 19 days old—dorsal view.

THE SALMON OF THE YUKON RIVER.

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By Charles H. Gilbert,

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INTRODUCTION.

The summer of 1920 was spent by the writer, in company with Henry O'Malley, at that time field assistant of the United States Bureau of Fisheries, in investigating the runs of salmon to the Yukon River. The primary object of the expedition was to ascertain the advisability of permitting the operation of one or more salmon canneries on the Yukon, in view of the possibility that they might so curtail the salmon supply that it would fail to provide natives, and white inhabitants as well, with the stores of fish that they find essential under the rigorous conditions of the far northern climate. It was to be determined whether there existed an excess above the needs of the inhabitants that could safely be used for commercial purposes for export beyond the boundaries of Alaska.

This phase of the situation has been dealt with in a report to the Commissioner of Fisheries and was published in 1921.[1] Some of the details that are given in that report concerning the movements of the salmon during their run and the rate of travel that they maintain in their ascent of the river are herein repeated, but the body of the present paper is concerned with the growth-history of the Yukon salmon and the ages at which they have reached maturity. The Yukon River is near the northern limit of range for the Pacific salmon. The effect of the arctic cold on growth and age of maturing is an interesting problem.

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[1] Investigation of the Salmon Fisheries of the Yukon River, by Charles H. Gilbert and Henry O'Malley. Bureau of Fisheries Document No. 909a, pp. 128–154. Washington, 1921.

Three of the five species of salmon that occur along the Pacific shores of North America enter the Yukon Basin in sufficient numbers to constitute distinct runs. These are the king or chinook salmon, the chum or dog salmon, and the coho or silver salmon. The names here given are those by which these species are known in other districts of Alaska and generally along the coast to the southward. Unfortunately, in the Yukon Basin, there is confusion in this regard. The coho or silver salmon is most frequently called *chinook*, while the various grades of the chum or dog salmon are known as "*silvers*," "*half-breeds*," and "*dogs*." The king salmon alone, of the three species that ascend the river in numbers, is called by the same name by which it is elsewhere designated.

The two remaining species of Pacific coast salmon, the humpback and the sockeye or red salmon, enter the river each year in small numbers and have no economic importance. To what extent the individuals of these species may be strays from other streams that have well-defined runs has not been determined.

The material on which the present paper is based was obtained from June 15 to July 31, 1920, at the cannery of the Carlisle Packing Co., located in the entrance to Kwiguk Channel, a branch of the Kwikluak or South Mouth of the Yukon.

THE KING SALMON (Oncorhynchus tschawytscha).

The king salmon is the most highly prized for human consumption of the three Yukon species. It is also valued for dog feed, especially in the upper course of the river, for by the time the salmon have fought their way upstream a thousand miles or more even the richest species contains no more oil than is needed to furnish satisfactory dog feed. As it enters the mouth of the river, the Yukon king is the richest salmon known to us. It there drips oil profusely when hung on the racks to dry and is, in fact, too rich for most successful canning. The canned product, if handled roughly, or if shipped to distant points, is in danger of breaking down to a substance of mushlike consistency. King salmon taken at some point higher up the river, where a portion of the oil would have been expended during the ascent, would in this respect furnish a better commercial product.

RATE OF TRAVEL.

The run begins at the mouth of the river in the latter part of May or early in June, almost as soon as the river is clear of ice after the spring break-up; and it lasts as a commercially valuable run for about three weeks. Tradition has it the king salmon appear at points as high as Tanana and the Ramparts at the same time as the first steamer that ascends the river from St. Michaels on the opening of navigation. This would indicate an unprecedentedly high rate of travel in a river with very swift current. Such incomplete data as we have concerning the ascent of salmon in other rivers indicate a rate not to exceed 10 to 20 miles per day. But in the Yukon Basin the distances to be traversed are great—some of the spawning beds being 2,000 to 3,000 miles from the sea—and the summer season is much shorter than in any other large salmon river. These two factors necessitate a high rate of speed in ascending the river, and the fact that this has been developed in the Yukon salmon is one more instance of close adaptation to the conditions of their environment on the part of a highly localized race. Rapid ascent of a river means expenditure of energy out of all proportion to the distance to be traversed. Unusual stores of potential energy in the form of oil are therefore required by the Yukon salmon. We have already referred to the unusually rich provision of oil in the case of the king salmon, and the same is true of the chum or dog salmon of the Yukon, which excels in richness and amount of oil the chum salmon from all other rivers in as great a degree as that which distinguishes the Yukon kings from other king salmon.

As regards the rate at which they ascend the river, we have more reliable and complete data for the Yukon than have been secured in any other stream. Records were obtained of their first appearance at a large number of localities. Some of these were ascertained by means of wireless messages sent during the early days of the run, before the dates of the first captures should be forgotten. Many others were obtained during our ascent of the river in early August, when all fishing camps were visited and records were inspected concerning the run of the summer. In a number of instances complete written records were available, which gave not only the date on which the first captures were made, but the numbers of fish taken on each day of the season. While we recognize that the capture of the first salmon of the season at different points along the river may vary within a few days in relation to the beginning of the run, we are convinced from an examination of our data that this source of error is not serious and that reliable conclusions concerning rate of travel can be drawn from the table (1) presented below. Whenever two or more records were obtained from different fishermen in the same locality the earliest has been selected.

It will be noted that the lowest rates of travel apparently occur in the lower course of the river. But the results are here obscured by the known fact that salmon, on entering the tidal area of a stream, move back and forth with the tides for an undetermined period, before seriously undertaking the ascent of the river. The influence of this factor, however, will not alone suffice to explain the constant increase in rate of travel as far up the river as Tanana, where it had reached an average for the entire river below this point of 62 miles per day over a period of 13 days.

Above Tanana, the rate again decreases, possibly due to the retarding influence of the Rampart Rapids together with the general increase in current found in the upper portion of the river, but the rate exhibits an unmistakable tendency again to augment as Dawson is approached. The first king salmon to reach Dawson in the middle of July, 1920, had been traveling against a consistently rapid current for 29 days, at the rate of 52 miles per day, and during this period, as always within the river, had taken no food.

TABLE 1.—DATES OF CAPTURE OF FIRST KING SALMON AT A SERIES OF LOCALITIES ALONG THE YUKON RIVER DURING SEASON OF 1920.

Locality	Date.	Approximate number of miles traveled.	Miles traveled per day.	Locality.	Date.	Approximate number of miles traveled.	Miles traveled per day.
South mouth of river	June 13			Whiskey Creek, above Louden	June 27	622	52
Run begins south mouth	June 15			Ruby	do	659	55
Pilot Station	June 20	107	21	Tanana	June 28	804	62
Marshall	do	144	29	Fish Creek, above Rampart Rapids	July 3	851	47
Russian Mission	June 21	204	34	Circle	July 11	1,227	47
Paimiut	June 22	259	37	Charlie Creek	July 12	1,317	49
Holy Cross	June 23	279	35	Eagle	July 13	1,402	50
Halls Rapids, above Anvic	June 24	346	38	De Wolf's fish camp	July 14	1,478	51
Camp 51 miles below Kaltag	June 27	440	37	Dawson	do	1,504	52
Kaltag	June 28	491	38				
Koyukuk	June 29	555	40				

The season of 1920 was notably late in Alaska; the break-up occurred in the Yukon fully a week later than usual, and the salmon were equally delayed in entering. As shown by the above table, the first king salmon taken in the delta was captured June 13.

The run culminated quickly within a week after that date, then maintained itself at a fair level for about three weeks, and was practically over by the close of the first week in July. Stragglers appeared during subsequent weeks in July and August but became less and less numerous.

GROWTH AND AGE AT MATURITY.

We have no knowledge concerning the feeding grounds of the Yukon salmon and must leave the question open to what extent, if at all, the young traverse the passes in the Aleutian Chain and attain their growth in the North Pacific. It is entirely possible that throughout their life in the ocean, they remain within the confines of the Bering Sea. None of them have been detected traversing the channels between the Aleutian Islands, nor have they been recognized elsewhere along lines of their migration routes in the sea.

Conditions in Bering Sea, it would seem, must be less favorable for rapid growth than in districts farther south. The northern part of the sea and a strip around the coasts, including Bristol Bay, are covered with ice floe during the winter and early spring months. The temperatures to which the salmon are then exposed must be near the freezing point. At the time they seek the river mouth in May or June the surface temperature in Bering Sea approaches 40° F. Under such adverse conditions growth during the winter season must be at or near a standstill and in the spring might well not be resumed before the beginning of the streamward migration. In that event the scales would exhibit no growth accomplished during the year in which the fish was captured. A salmon in its fifth year would indicate in its scale structure the completion of four full years' growth, and the margin of the scale would be formed by the winter check of the fourth year. In other districts to the southward the salmon of the spawning run have already responded to spring conditions and have begun a period of rapid growth before entering the streams. The scales have participated in this renewed growth, and the margins exhibit a larger or smaller band of widely spaced rings, which lie outside the winter check of the previous year. But in the case of the Yukon king salmon this is not present. The winter check of the previous year forms the margin, and usually no trace exists of any growth belonging to the current year. A very few cases form doubtful exceptions to this generalization, with the outer one to three rings more widely separated at least in a portion of their course. This feature is shown distinctly in the accompanying series of photographs of the scales of Yukon king salmon, ranging from those in their third to those in their seventh year (Figs. 276 to 285).

Another striking peculiarity of the Yukon king salmon is found in their early history as fry and fingerlings. We did not secure any of the young, although attempts were made to capture them with minnow seines on their downward migration, near the mouth of the river. But the central areas of the adult scales contain records of the early history and show conclusively in every instance that the young remained in fresh water for a full year's growth before descending to the sea. In the photographs that follow, the line "1" points to the outer margin of the stream growth, which presents a nucleus of finely crowded lines, beyond which are the widely spaced lines indicating rapid growth after reaching the sea.

This habit of the Yukon kings is in striking contrast to what is observed in streams farther south. In the Fraser River, the Columbia, the Klamath, the Sacramento, and all other streams thus far examined a considerable proportion of the adult salmon are developed from fry that passed to sea during their first year and completed only a small portion of their first year's growth in fresh water. This "sea type" develops at an earlier age than do those that tarry a year in fresh water, and it frequently constitutes half or more than half the entire run. The absence of the "sea type" in the Yukon may well be related to the severity of the fall and winter, the lateness of the spring, and the shortness of the summer season. It would seem that the hatching of the eggs, the absorption of the yolk, and the emergence of the fry from the gravels must be correspondingly retarded.

A third peculiarity of the Yukon king salmon consists in the retardation of the age at which they attain maturity. In the Columbia River, where, owing to the use of beach seines, wheels, and traps, the smaller salmon are captured in due proportion with those of larger size, the youngest chinooks of stream type that are captured in the spawning run are in their second year. These are all male fish, as are those of the next larger size, which are in their third year. Female chinooks of stream type do not mature in the Columbia until their fourth year, when they are not far inferior in numbers to males of equal age. The commercially valuable portion of the Columbia River run consists of 4 and 5 year fish. Comparatively few individuals reach their sixth year, and none has to my knowledge been reported in its seventh year. The condition in the Yukon is far different. No 2-year fish were secured, and but one 3-year fish, which was a male, 16 inches long, the scale of which is represented in Figure 276.

In spite of the fact that fishing was prosecuted exclusively by gill nets, which during the king salmon run were of large mesh ($8\frac{1}{2}$ or $8\frac{3}{4}$ inches), fish of diminutive size were frequently entangled in the web and captured. Special attention was paid to these, with the object of ascertaining the earliest age at which maturity would be attained in the Yukon race. In addition to the 16-inch individual in its third year, above noted, we examined 44 specimens ranging from 17 to 27 inches, all of them males, in their fourth year. From this it is apparent that no female king salmon mature on the Yukon until after their fourth year. They are therefore retarded at least one year in reaching maturity, as compared with king salmon in the more southern part of the range of the species. (See Figs. 277 and 278.)

Continuing the examination of larger sizes we encountered the first 5-year male at 25 inches, the males of this age ranging from 25 to 40 inches. In the fifth year, for the first time, we encountered female salmon, but these were very few in number. Among the 131 individuals in their fifth year that we have examined, selected wholly by size without reference to sex, there are 119 males and only 12 females. This indicates a still further retardation in age of maturing of females. Not only are there no 4-year mature females (so abundant in more temperate latitudes), but comparatively few females develop maturity even at the age of 5. The 12 of which we have record lie in size within the range of the 5-year males, the smallest being 30 and the largest 37 inches long. (See Figs. 279 and 280.)

The male 6-year fish are numerous, the 79 individuals represented in our series ranging widely from 29 to 48 inches. There is thus a wide overlap in size between the 5 and the 6 year fish, as is always the case, although, as will be noted, the 4 and the 5 year males show but little overlap. Among the 6-year fish, for the first time, females are really abundant, exceeding in number the males of equal age. Of the 185 6-year individuals, selected without reference to sex, 79 are males and 106 females. (See Figs. 281 to 283.)

Another evidence of retarded development is found in the class of 7-year fish. In streams thus far studied from the Sacramento to the Fraser it is very rare for a king salmon to attain the age of 7 years. Only two such specimens have been observed to my knowledge. In the Yukon, however, members of this class are not uncommon. Although not specially sought for, 42 are included in our series, 10 of these being males and 32 females. Here, again, the late development of females compared with males is made evident. (See Figs. 284 and 285.)

Table 2 gives the distribution by sex, age, and length of all the king salmon of our Yukon series of the run of 1920. For comparison similar data from a series taken from the run of 1919 by C. F. Townsend, fisheries inspector for the Bureau of Fisheries, are included in this table. It should be noted that the relative size of these various classes in our series does not represent their relative abundance in the run. While no selection was made by sex, frequent selection was made by size at critical points. Thus, special attention was paid to the smaller sizes, and these appear in our series in more than their normal proportions. The same is true of individuals approximating 30 inches in length. It was at this size that females first were found, and individuals of this length were specially selected for examination.

TABLE 2.—KING SALMON FROM MOUTH YUKON RIVER, 1920 AND 1919, DISTRIBUTED BY AGE AND BY LENGTH.

Length.	Number of specimens, 1920.							Number of specimens, 1919.						
	4 years—Males.[1]	5 years.		6 years.		7 years.		4 years—Males.[2]	5 years.		6 years.		7 years.	
		Males	Females.	Males.	Females	Males.	Females.		Males.	Females.	Males.	Females.	Males.	Females.
17 inches	1													
19 inches	2													
20 inches	4													
21 inches	3													
22 inches	3													
23 inches	6							1						
24 inches	10							5						
25 inches	8	4						5	2			1		
26 inches	3	2						11						
27 inches	4	8						10	1					
28 inches		7						6			1			
29 inches		20		1				2	2					
30 inches		18	1	1					1		1			
31 inches		12		1	1				3			1		
32 inches		11	3	4					1		1	2		
33 inches		5	3		8				1	1	2		1	1
34 inches		10	2	5	3				3		1			
35 inches		9		9	10		2		1	1	1	10		1
36 inches		4	2	3	10		2		1	1	1	4		1
37 inches		1	1	9	8		1			2	2	5		1
38 inches		4		7	14		4					5		1
39 inches		2		7	7	1	3				2	2		
40 inches		2		5	13	4	6				2	3		1
41 inches				3	13		2				2		2	1
42 inches				7	8	2	7					1	1	1
43 inches				6	7	1	2				2	1		
44 inches				4	2	1	2				1		2	
45 inches				3	1						1			
46 inches				1	1		1							
47 inches				2									1	
48 inches				1		1								
Total	44	119	12	79	106	10	32	40	16	5	20	35	7	8
Average length in inches	23.4	31.3	33.5	38.7	38.5	41.8	40.1	26.3	31	35.6	37.5	36	41.7	37.7

[1] One 3-year-old 16-inch male was discovered in 1920. No 4-year-old females were observed.

[2] No 4-year-old females were found.

The following table (3) gives the average sizes attained by the different year classes in the two years 1919 and 1920, the males and females being stated separately. In comparing these with similar averages obtained in other districts, we must bear in mind that our Yukon material shows no growth belonging to the season in which the fish were captured. Our 4-year individuals had completed three years of growth, but no more, and similarly with each of the other year groups. However, no strict comparison is possible between Yukon 4-year fish and the 3-year fish from other localities, for although the latter had produced a certain amount of new growth in their third year, they had not completed the growth of the third year when they ceased feeding and were captured. In like manner no exact correspondence can be expected between 5-year Yukon individuals and 4-year material from the Columbia or the Fraser. In comparing growth rates from these different localities, the most satisfactory basis will be found in completed lengths of the different year classes, computed from the scales. By length is meant the distance, measured over the curve of the body, from tip of snout to distal end of middle caudal rays.

TABLE 3.—AVERAGE LENGTHS FOR CERTAIN YEAR GROUPS OF YUKON KING SALMON, 1920 AND 1919.

Sex and year.	3-year group.		4-year group.		5-year group.		6-year group.		7-year group	
	Number.	Average length.	Number.	Average length.	Number.	Average length.	Number.	Average length.	Number.	Average length.
Males:		*Inches.*		*Inches.*		*Inches.*		*Inches.*		*Inches.*
1920	1	16	44	23.4	119	31.3	79	38.7	10	41.8
1919	0	....	40	26.3	16	31	20	37.5	7	41.7
Females:										
1920	0	....	0	.	12	33.5	100	38.5	32	40.1
1919	0	..	0	.	5	35.6	35	36	8	37.7

For comparison with other regions we have calculated the growth for each year of their lives of 77 fish belonging to the fourth, fifth, sixth, and seventh year classes and present the results in Table 4. We have followed Fraser's latest paper[2] in taking 1.5 inches (40 mm.) as the average length of the fry when the first scale ring was formed. Several differences are encountered in comparing our results with Fraser's. His material was largely taken in the Gulf of Georgia and included a mixture of fish that would mature during the then current season with others that would delay maturing for one or more years; also, doubtless, a mixture of races, bound for different river basins and unlike in certain of their characteristics. His measurements are throughout smaller than by our method, inasmuch as they do not include the length of the middle caudal rays.

Table 4, which follows, shows with regard to each year class that the growth during the year that precedes maturity is greater than during the corresponding year of classes that reach a greater age. Thus the third year's growth of fish that mature in their fourth year is greater than the third year's growth in fish that would not mature until their fifth, sixth, or seventh years. Furthermore, it is greater in 5 than in 6 year fish and greater in individuals that mature in their sixth than in those that mature in their seventh year. The third-year growths form a regularly ascending series from 7.3 inches in the oldest year class to 12.4 inches in the youngest, and the lengths of the fish at the end of their third year form a similar advancing series. According to this table we should find that the largest series of 3-year fish in the sea at any time is composed of those individuals that will earliest mature. The same is true of the growth of the fourth year

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[2] Further Studies on the Growth Rate in Pacific Salmon, by C. M. Fraser. Contributions to Canadian Biology, 1918–1920, pp. 7–27. Ottawa, 1921.

and of the fifth. Slow growth and smaller size mean deferred maturity in all years except the first and the second.

The failure of similar results to appear in Doctor Fraser's article, above referred to, may be due to the mixed nature of his material. His second, third, and fourth year classes are not composed of fish maturing in their second, third, or fourth years, but are accidental assemblages of fish that were in their second, third, and fourth years at the time they came into his hands. His second-year class doubtless contained individuals that would eventually mature variously in their second, third, fourth, and fifth years; and his third-year class, fish that would mature in their third, fourth, and fifth years. Under such conditions differential methods of growth of year classes could not be discovered, even if they should exist. In Doctor Fraser's 1915 material it was indicated that the 4-year fish that were preparing to spawn were larger than those of equal age that would remain in the sea for another year. That result was in harmony with our present findings but was not verified by him in the material of 1916.

TABLE 4.—CALCULATED GROWTH OF YUKON KING SALMON.

Year class.	Number of specimens.	Inches of growth at end of—						Inches of growth during—					
		First year.	Second year.	Third year.	Fourth year.	Fifth year.	Sixth year.	First year.	Second year.	Third year.	Fourth year.	Fifth year.	Sixth year.
Fourth	7	2.6	11.5	23.9	...	...	...	2.6	8.9	12.4	0	...	...
Fifth	33	2.7	12.6	22	33.7	...	...	2.7	9.9	9.4	11.7	0	...
Sixth	22	3	11.6	19.2	27.8	38	...	3	8.6	7.6	8.0	10.2	0
Seventh	15	2.5	11.7	19	27	34	40.7	2.5	9.2	7.3	8	7	0.7
Average		2.7	11.9	21	29.5	36	40.7	2.7	9.2	9.2	9.4	8.6	0.7

In the following table (5) is given the average weight for all specimens of a given length, the males and females being stated separately. The weights were taken with an ordinary spring-balance scales reading to pounds and half pounds. No high degree of accuracy can be claimed for this method, but the results present interesting terms of comparison with the king salmon races of other rivers. The number of records available for each length is insufficient for a wholly reliable average, a fact that will explain irregularities in progression in the table. It will be noted that females of equal length with males average slightly heavier than the latter. There was no noticeable elongation of the jaws in the males at the time this material was examined.

TABLE 5.—AVERAGE WEIGHTS BY UNITS OF LENGTH, YUKON KING SALMON, 1920.

Length.	Males.		Females.	
	Number of specimens.	Average weights.	Average weights.	Number of specimens.
		Pounds.	*Pounds.*	
16 inches	1	2		
17 inches	1	2		
20 inches	4	4		
21 inches	3	4.7		
22 inches	3	5		
23 inches	6	5.8		
24 inches	10	6.1		
25 inches	11	7.4		
26 inches	5	7.8		
27 inches	13	9.6		
28 inches	7	10.1		
29 inches	21	11.3		
30 inches	19	12.6	11	1
31 inches	13	14	14	1
32 inches	15	14.8	17	3
33 inches	5	16.4	17.1	11
34 inches	15	18.2	18.3	4
35 inches	18	20.3	20.4	12
36 inches	7	21.7	22	14
37 inches	9	22.4	23.9	11
38 inches	10	25.2	26.3	19
39 inches	10	26.8	28	13
40 inches	12	29.8	30.5	19
41 inches	4	34.3	32.9	15
42 inches	9	36.2	34.1	16
43 inches	7	35.9	38.3	9
44 inches	5	41.2	41.8	4
45 inches	3	43.7	42	1
46 inches	1	46	46.5	2
47 inches	2	49.5		
48 inches	1	48		

The nuclear area of the scales of Yukon king salmon is of extremely small size and contains correspondingly few rings. Undoubtedly this indicates comparatively very small size for the fingerlings at the time of their downward migration. Our table indicates an average size for migrating fingerlings of 2¾ inches. This is based on the assumption that the fry are 1½ inches long when the first scale ring is formed. If, as seems more probable, they are slightly longer than this, our computed lengths of migrating fingerlings would be correspondingly increased but could not much exceed 3 inches. The greatest length indicated on any scale examined by us is 4⅛ inches. The number of nuclear rings for each year class is as follows:

TABLE 6.—NUMBER OF NUCLEAR RINGS, YUKON KING SALMON, 1920.

Year class.	Individuals having nuclear rings to the number of—											Average number of rings
	5	6	7	8	9	10	11	12	13	14	15	
Fourth	1	1	6	18	7	9	1	......	......		......	8.5
Fifth	1	4	11	9	34	18	5	3	1		1	9.1
Sixth	1	10	26	30	29	29	7	11	1		......	9
Seventh	2	8	7	9	5	......	......	1	......		......	7.9

THE CHUM OR DOG SALMON (Oncorhynchus keta).

The chum or dog salmon of the Yukon does not differ from other races of chums that frequent streams in the more southern portion of its range either in external appearance or in any of the structural peculiarities that distinguish this species. As is the case elsewhere, individuals captured in the sea or those that enter streams well in advance of the spawning period are symmetrical silvery fish, easily mistaken at a glance for the sockeye salmon. The discoloration of the skin and the elongation of the jaws, which are later provided with greatly enlarged teeth, are of universal occurrence in this species (as, indeed, in all of the species of Pacific salmon) when sexual maturity is approached. In shorter streams that are colonized by chum salmon, the fish delay entrance until nearly ripe and when first seen have already lost their silvery livery. But in the Yukon, this species penetrates to spawning gravels in the far upper reaches of the river, and it populates as well practically all the tributaries in the middle and the lower course of the stream. We find, accordingly, among the chums entering the mouth of the river a mixture of colonies, some of which are bound for the headwaters, in reaching which they will spend six weeks or more, and others that have not far to go. It is undoubtedly for this reason that the entering fish vary so widely in different portions of the run in the extent of development of those striking characteristics that accompany maturity.

During the season of 1920 all the early chums were of bright silvery color and had abundant oil and a pinkish flesh that turned a deeper red on drying. But in a short time changes appeared, even at the mouth of the river. At first occasional individuals, usually males, appeared in a more advanced stage, with brightly colored bars on the sides of the body and with long hooked jaws. When these were first observed they stood out conspicuously from their fellows, which were still in the "silver" stage. By the last of June these seasonal changes had become obvious in the great mass of chums then running. It was the rule for the males to exhibit elongated jaws, provided with canine teeth, and to show the beginnings of the bright cross-bars that characterize the spawning males of this species. It might be thought that this development would continue unchecked until the end of the season, but, strangely, during the second week in July a fresh run of chums that was no further advanced than were the chums of early June made its appearance. These also were of bright silvery color and had symmetrical jaws and abundant oil. Although entering relatively late, it seems safe to assume that this run was far from its spawning period and had far to go. Along all the lower and middle portions of the river fishermen who prepare dried salmon for winter use distinguish between the silvery chums and the others. The "silvers" have flesh of brighter color, rich in oil, and of more substance when dried. The others are known as "dog salmon," with intermediate stages called "half-breeds," and are far inferior in value for human consumption or as dog feed.

The Yukon chums in their prime are doubtless of far higher quality than chums from any other river. The differences between them and other races of chums are of similar nature to those that distinguish the Fraser River sockeyes from the same species known as red salmon in the average Alaska streams and to those that distinguish the chinook salmon of the Columbia from the same species ("king salmon") in the shorter streams of the north. The differences in all these cases are not only of similar nature, they are due to the same cause. The fine quality of Yukon chums, Fraser sockeyes, and Columbia chinooks is due to the great length of stream which they must traverse, while fasting, on the way to their spawning grounds and to the large store of oil that they must lay up for use at this time. In no other respects are the chum salmon of the Yukon different from the same species found elsewhere. The Yukon king salmon, as we have previously noted, are characterized by the same excessive provision of oil. They also exhibit in the different portions of the run equally striking differences between bright individuals, relatively green as to eggs and milt, and the sexually advanced forms, with hooked jaws and discolored skin. It would be no less logical to recognize two or three kinds of king salmon than it is to distinguish, as is popularly done on the Yukon, two or three kinds of chums, according to the degree of their advancement toward spawning.

RATE OF TRAVEL.

The chum salmon is generally known as a species that spawns exclusively in the lower courses of streams, often scarcely above the reach of the tides and never far from salt water. It is a remarkable reversal of habit in the Yukon chums that colonies of them should penetrate more than 2,000 miles to the upper tributaries of that great river; and it testifies to the flexibility of organization in salmon that a species that is in general not adapted to long journeys while fasting, can, under spur of necessity, make such journeys without food and exhibit great speed and endurance. From records of the first appearance of chums at a large number of stations during the season of 1920, it was apparent that their rate of travel was not far below that of the powerful king salmon. They entered the river about a week later than the kings, at Tanana they were not more than 10 days behind the latter, and at Dawson they were some 14 days behind the kings. The lower 800 miles of the river, as far as Tanana, were traversed at the rate of 50 miles per day, and the next 700 miles, between Tanana and Dawson, were covered at the rate of 35 miles per day. The lower 1,500 miles were ascended at the rate of 42 miles per day.

YEAR CLASSES.

We have already noted that the king salmon of the Yukon are retarded in their development and mature on the average more than one year later than the king salmon from southern waters. A similar retardation is observed in chum salmon, which average distinctly older in the Yukon than in any other region of which we have record.

The earliest report on the ages attained by this species and on the relative proportions of the year classes was based on a small collection taken at Bellingham, Wash., early in August, 1910.[3] The number investigated was too small (58 in all) to give reliable averages, but the percentages indicated do not differ materially from those obtained in 1916 by Dr. C. M. Fraser from collections of adequate size taken at Nanaimo and Qualicum, in the Gulf of Georgia. In both cases the majority of the chums were found maturing at the age of 3 and 4 years, with very few individuals at 5 years and an occasional rare specimen in its second year. Table 7 gives the results derived from both sources and also, for comparison, includes a similar grouping of Yukon chums.

TABLE 7.—YEAR-CLASS DISTRIBUTION, SOUTHERN AND YUKON CHUM SALMON.

Origin of salmon.	2 years.	3 years.	4 years.	5 years.	Total.
Southern chums:	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Number.*
Bellingham	0	53.5	44.8	1.7	58
Qualicum	0	34.5	64.3	1.2	1,300
Nanaimo	0.1	46.6	52.4	.9	700
Average of southern chums	0.1	44.8	53.8	1.3	2,058
Yukon chums	0	3.3	68.1	28.6	448

The Yukon chums mature in their third, fourth, and fifth years, as is the case in more southern waters, but the number of 3-year-olds is diminished from nearly half to one-thirtieth of the total number, and the 5-year fish show a corresponding increase from 1 to nearly 30 per cent. The retardation in the maturing of the northern race is thus evident.

PROPORTIONS OF SEXES.

It has commonly been reported that dog-salmon males are greatly in excess of the females, but no thoroughly satisfactory investigation of this subject has been made. To accomplish this, an examination would have to be made of the ratio of males to females at frequent intervals throughout an entire run. It might well be expected that the proportions of the sexes would differ widely during consecutive portions of the run, with the result that any deficiency in the number of females observed at the beginning of the run would be compensated for by an excess of females later on. Such an occurrence has been repeatedly observed in certain sockeye colonies. Four-year male sockeyes entering Rivers Inlet, British Columbia, in 1917, varied from 100 per cent of the 4-year class in early July to 52 per cent on July 31; and the 5-year males varied from 59 per cent of the 5-year group on July 10 to 23 per cent on July 31. It is clear, therefore, that a series of observations on fish bound for one river only will be necessary to enable us to determine this point.

Doctor Fraser's results, from fish taken partly near the mouth of the Little Qualicum River and partly from the vicinity of Nanaimo, agree in showing from both districts an increased percentage of males in the older year classes. The percentages of males in the third, fourth, and fifth year classes in the Nanaimo lot, range 42.6, 62.1, and 100; in the Qualicum lot, 51, 63.8, and 86.4. If these represented the average percentages

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[3] Age at Maturity of the Pacific Coast Salmon of the Genus Oncorhynchus, by Charles H. Gilbert. Bulletin, U. S. Bureau of Fisheries, Vol. XXXII, 1912 (1914), p. 18. Washington, 1913.

during the entire season we should have a considerable preponderance of males over females on the spawning beds and we should also have indicated a relatively earlier maturing of females than of males. Both of these results would be unexpected. While no determination has been made of the ratio of the sexes in dog-salmon fry, analogy with other species of salmon would make it appear probable that males and females are in approximately equal numbers at the time of hatching. If this be true, a final excess of males in the spawning run could only be brought about by selective mortality directed against the females. It does not seem probable that this exists. As regards an earlier maturing of the females than of the males, producing a heavier percentage of females in the younger groups, we can only note that this would be the reverse of what occurs in king salmon, sockeyes, and cohos.

In the Bellingham material, previously referred to, we found 67 per cent males and 33 per cent females, the proportion of males and females being approximately the same in the third and the fourth year groups. In Doctor Fraser's material, the totals showed 59 per cent males and 41 per cent females.

The Yukon specimens, 448 in number, contained 57.6 per cent males and 42.4 per cent females. The 3-year fish had 53.3 per cent males; the 4-year fish, 53.8 per cent; and the 5-year fish 67 per cent.

SIZE AT MATURITY.

The length and weight frequencies are given in Tables 8 and 9, which follow. These indicate unmistakably that the northern race is retarded in its growth and reaches a smaller size in each year class than is attained in Puget Sound and the Gulf of Georgia by fish of equal age. To compare with the average lengths of Yukon chums, we repeat below those given by Doctor Fraser based on Qualicum and Nanaimo material. As measurements of the latter were taken only to the base of the middle caudal rays and our measurements include the length of the middle rays themselves, we have added 7½ per cent to Doctor Fraser's measurements to make them comparable.

TABLE 8.—YUKON CHUM SALMON, 1920, GROUPED BY AGE, SEX, AND LENGTH.

Length.	Number of individuals in—					
	Third year.		Fourth year.		Fifth year.	
	Males.	Females.	Males.	Females.	Males.	Females.
21 inches	......	1	......	......	......	......
22 inches		......	......	2	......	......
22.5 inches	......	3	......	4	......	......
23 inches	2	......	......	11		
23.5 inches	......	1	1	16	......	......
24 inches	2		3	31	1	[illegible]
24.5 inches	[illegible]	2	9	21	......	[illegible]
25 inches			19	14	1	[illegible]
25.5 inches			16	15	......	9
26 inches			24	12	3	4
26.5 inches			20	4	4	4
27 inches			25	......	10	5
27.5 inches			24	1	10	1
28 inches			7	......	16	1
28.5 inches			5	......	15	1
29 inches	......	......	2	......	9	......
29.5 inches	......	......	2	......	7	......
30 inches	......	......	1	......	3	......
30.5 inches				......	1	......
31 inches				......	4	......
31.5 inches					2	......
Total	8	7	164	141	86	42
Average length in inches	24	23	26.4	24.4	28.2	25.7
Gulf of Georgia, average length in inches (Fraser)	28	26.9	30.7	29.1	......	......

Table 9.—Yukon Chum Salmon, 1920, Grouped by Age, Sex, and Weight.

Weight.	Number of individuals in—					
	Third year.		Fourth year.		Fifth year.	
	Males.	Females.	Males.	Females.	Males.	Females.
4 pounds	......	1	......	1	......	......
5 pounds	1	2	......	17	......	......
6 pounds	3	3	7	51	......	3
7 pounds	3	1	28	52	3	17
8 pounds	1	......	52	18	8	13
9 pounds	......	......	47	2	20	6
10 pounds	......	......	22	......	18	3
11 pounds	......	......	6	......	14	......
12 pounds	......	......	1	......	13	......
13 pounds	......	......	1	......	5	......
14 pounds	......	......	......	......	4	......
17 pounds	......	......	......	......	1	......
Total	8	7	164	141	86	42
Average weight in pounds	6.5	5.6	8.3	6.5	10.5	7.7

The length-weight relationship, indicated in Table 10, is given without reference to age. The average weight of all males and, separately, of all females that have the same length is stated. According to this table, females average slightly lighter than males of equal length, those from 23 to 28 inches in length averaging 97 per cent of the corresponding males. The reverse of this might have seemed reasonable because of the slightly lengthened jaws in the males.

Table 10.—Average Weights, by Units of Length, Yukon Chums, 1920.

Length.	Males.		Females.	
	Specimens.	Average weight.	Average weight.	Specimens.
	Number.	*Pounds.*	*Pounds.*	*Number.*
21 inches	0	....	4	1
22 inches	0	....	5.1	9
23 inches	3	5.7	5.7	28
24 inches	19	6.7	6.4	73
25 inches	36	7.3	7.3	40
26 inches	56	8.2	7.9	24
27 inches	69	9.1	9	7
28 inches	43	10.3	9.5	2
29 inches	21	11.3	....	....
30 inches	5	12.6	....	....
31 inches	6	14.3	....	....

GROWTH AND SCALE READINGS.

In Figures 290 to 298 are presented photographs of a series of scales of Yukon chum salmon that include representatives of all the year classes found in our collection. All of these agree in belonging to the sea type—that is, the scales were wholly formed in the sea, the fry having passed out of the river at a very early age, before even the nuclear plate and the first scale ring had been formed.

The Yukon chums agree in this respect with their southern relatives. All leave their native streams as soon as the yolk is absorbed and they are free swimming. In more southern districts this seaward migration is easily accomplished. The eggs are laid in gravels not far removed from the tides, and the young, when free, easily drop down with the current to the shore line. The case is less simple with the Yukon fish, many of which have 2,000 miles or more to cover at a period when they average only 1½ inches long. No information is available concerning the dates on which this migration is effected. Observations farther south indicate a very early descent to the sea in the spring of the year. It is not known, however, to what extent hatching of the eggs and development of the young on the Yukon are retarded by the very low temperatures to which they are exposed. Growth during the seaward migration can not be considerable, for none of the material that we have examined indicates the formation of the scale nucleus while still in the stream.

Growth of this species in the sea seems to proceed with remarkable regularity, with the result that the scales are diagrammatic in their simplicity and seldom afford any difficulty in determination of age. In the case of the Yukon race, such uncertainty as may be experienced is concerned with the interpretation of the peripheral region of the scale and is based on the fact that the scale margins differ widely in condition among individuals captured on the same date. It is generally recognized that individuals of a given race will vary materially in the date on which they begin the rapid growth of the spring after the winter pause. Among the fish captured in May or early June in more southerly waters an occasional individual may indicate no growth of the current season, while others will vary in the number of peripheral wide rings by which the amount of spring growth may be computed. In the Yukon dog salmon, however, this variation at the time they leave their feeding grounds and enter on their spawning run is extreme. An occasional fish, as shown by Figure 296, had begun no new growth of the year, the margin of the scale being formed by the close-ringed check of the previous winter. Others, as represented in Figure 294, had barely inaugurated the new growth, which is indicated by two or three wide rings outside the winter check. There then follow fairly complete series with ever-increasing growth of the season, as shown in Figures 297; 290, 291, and 292, the last named having finished an average season's growth for the third year, with the exception of the winter check.

When it is recalled that these dog salmon enter the Yukon in company with the king salmon and that the king salmon have not in any case made unmistakable growth for the current season, the habit of the dog salmon in this regard seems most peculiar. In the early and middle parts of the run, to which alone we had access, none of the individuals examined had begun a winter check at the margin of the scales for the current year. Where a marginal winter check existed, it had been formed the previous winter and presented no real difficulty in determining age. If the latter part of the run should be found to contain a group of individuals in which a check was forming at the scale margin and also another group with scales like Figure 293, in which the marginal check belonged to the previous winter and no further growth had been registered, a real difficulty might arise in determining the age of such individuals. The two groups would show essentially similar scale structure, but one would be one year older than the other. It is not probable, however, that representatives of these two classes would be found together in any portion of the run. As the season advanced we should expect to find extremely few, if any, that had failed to produce some new growth of the year.

THE SOCKEYE SALMON (Oncorhynchus nerka).

A few scattering sockeyes (Alaska red salmon) enter the Yukon River during July and early August. In 1919 the Carlisle Packing Co. put up 22 cases of talls and 6 cases of flats of this species and handled a total of about 300 fish. The sockeyes appeared even less numerous in the following year, when only 5 cases, containing about 60 fish, were packed.

If a permanent colony of red salmon exists in the Yukon, it must ascend to the lakes near the source of the river, but we have no knowledge that such spawning grounds for this species exist. That individuals ascend the river for long distances is certain, for we learned of their occasional occurrence up the river from men who were acquainted with the different species of salmon, and we observed one, a male, decidedly pink in color, at Ruby on August 14, 1920, some 650 miles above the mouth of the river.

We examined 23 specimens in 1920 on July 5, 7, 8, 9, and 13. Thirteen of these were in their fifth year (see Figs. 299 and 300), having spent their first year (perhaps 15 months) in fresh water and having descended to the sea in their second year. The scales exhibit a vigorous fresh-water growth, followed by three complete year records at sea. A few of these scales, as in Figure 300, have a marginal check, which was formed during the preceding winter; but a majority have at the margin from one to four wide rings denoting new growth of the year.

In addition to the individuals in their fifth year, one year of which was spent in fresh water, we have eight that had remained in fresh water an additional year and were maturing in their sixth year. A scale of one of the latter class is represented in Figure 301, the division between first and second year's growth in fresh water being clearly indicated. Here, again, the growth of the new year is faintly but unmistakably shown along the anterior left-hand margin of the scale.

A third class of individuals is represented by Figure 302, these having descended to the sea soon after hatching and prior to the growth of the scale. The two salmon we examined belonging to the sea type, one a male 27½ inches long, the other a female 23½ inches long, had matured in their fourth year, one year earlier than any of those that had lingered in fresh water.

Whether the Yukon red salmon are strays from some colony to the southward or form an unflourishing local race can not be determined at present. There is no reason to believe that more than one race is represented in our meager material.

THE COHO SALMON (Oncorhynchus kisutch).

The coho or silver salmon develops a regular run in the Yukon River, appearing sparingly at the mouth of the river in the latter part of July, but the run does not show any real development until in August. The Carlisle Packing Co., in 1919, packed 7 cases of cohos on July 14 and 3 on August 2. From August 3 to 9, 59 cases were put up and in the following week 985 cases. The total pack to August 30 was 3,181 cases.

In 1920 this species was entering the mouth of the river in very limited numbers during the last week in July and does not appear in the cannery pack of that year, as canning operations were discontinued before the run had developed. During the early half of August, between the mouth of the river and Tanana, we found at all fishing camps that occasional individuals were being taken. But we were unable to learn of its occurrence in the main river above Tanana. It is well attested that the species enters the Tanana and spawns in one or more tributaries of the Kantishna. How generally it is distributed over the basin we were unable to ascertain.

When the coho enters the river it is a perfectly symmetrical fish, with brilliant silvery color, but in traversing the lower portion of the river it takes on a red livery, and the males assume at the same time the characteristic snub-nosed appearance of the breeding fish, the upper jaw becoming bluntly hooked over the lower in a manner characteristic of this species.

Scales of Yukon cohos are represented in Figures 286 to 289. As in all other coho colonies that we have examined, those from the Yukon are always in their second year of sea growth when captured.[4] Outside the narrow-ringed central area, which records the life in fresh water, we invariably find in this species a vigorous summer growth, succeeded by a well-marked winter check, and this in turn followed by an extensive marginal growth of widely-spaced rings, which measure the growth of the current season of capture.

In the southern part of its range, where the coho uniformly spends one season in fresh water before migrating seawards, the spawning run (aside from a few male grilse in their second year) consists exclusively of 3-year fish. As we proceed northward, however, we encounter individuals that have tarried two years in the streams and are maturing in their fourth year. These are more abundant in the Yukon than in any other stream we have examined. Our small collection of 31 individuals comprises 12 that have spent one year in a stream and are 3 years old (see Figs. 286 and 287) and 18 that remained two years in fresh water and are in their fourth year (Fig. 288). If the customary proportions are shown in this collection, some 60 per cent of the young spend two years in fresh water. One individual of our collection (Fig. 289) had apparently spent three years in the river and was maturing in its fifth year. The number of individuals at our disposal is too small in the various classes to give reliable averages. Six 3-year males average 23.8 inches in length (middle caudal rays included, as in all our measurements); four 3-year females, 24.6 inches. Eleven 4-year males (two years in fresh water) average 24.5 inches; six 4-year females, 25.3 inches. As males are consistently larger than females among Pacific salmon, we have additional reason for distrusting the adequacy of the above figures. The 5-year male (three years in stream) is 23 inches long.

THE HUMPBACK SALMON (Oncorhynchus gorbuscha).

Scattering humpbacks enter the river in July and August and are then so near their spawning time that they would be unable to ascend the stream for any considerable distance. We observed one ripe male at Andreafski on August 3 and were unable to learn of the occurrence of the species beyond that point.

The individuals observed were all small and without value, having often liquid milt and partly free eggs. Four specimens measured from 20 to 22 inches in length and weighed from 4 to 5 pounds. As in the case of all other humpbacks that have been examined for age, these were in their second year and had proceeded to sea as soon as free swimming, their scales registering none but sea growth. The small size was doubtless due in part to the fact that they were maturing so early in the season, thus greatly limiting the growth of the second year. The scales all indicated this history, for the area representing growth of the second year was narrow and contained a partial check at the margin.

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[4] We do not here include the few male grilse, which in more southern districts mature during the first year at sea.

⁂

FIG. 276.—Scale of king salmon taken from mouth Yukon River July 2, 1920. Male, 16 inches long, weight 2 pounds; in its third year.

FIG. 277.—Scale of king salmon taken from mouth Yukon River July 2, 1920. Male, 24 inches long, weight 6 pounds, in its fourth year.

FIG. 278.—Scale of king salmon taken from mouth Yukon River June 18, 1920. Male, 24½ inches long, weight 7 pounds; in its fourth year.

FIG. 279.—Scale of king salmon taken from mouth Yukon River June 18, 1920. Male, 31½ inches long, weight 14 pounds; in its fifth year.

FIG. 280.—Scale of king salmon taken from mouth Yukon River July 2, 1920. Male, 28 inches long, weight 9 pounds; in its fifth year.

FIG. 281.—Scale of king salmon taken from mouth Yukon River July 8, 1919. Male, 30½ inches long, in its sixth year.

FIG. 282.—Scale of king salmon taken from mouth Yukon River July 8, 1919. Female, 30 inches long, in its sixth year.

FIG. 283.—Scale of king salmon taken from mouth Yukon River July 8, 1919. Male, 28½ inches long; in its sixth year.

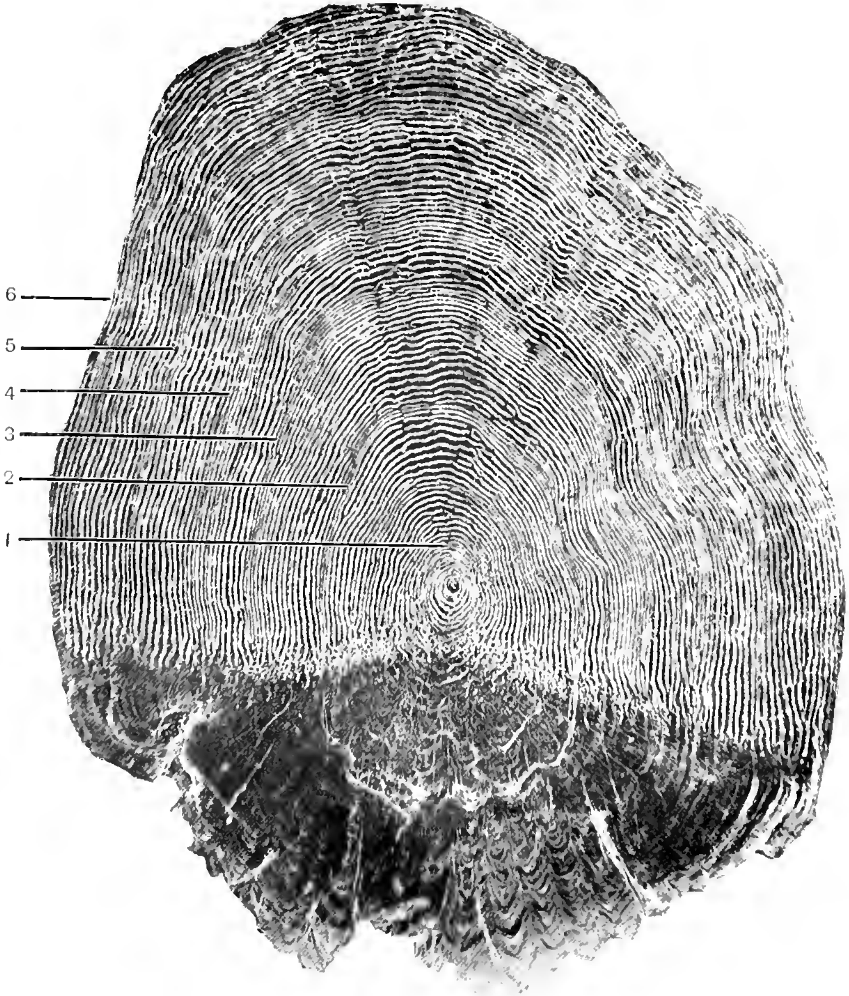

FIG. 284.—Scale of king salmon taken from mouth Yukon River June 25, 1919. Female, 37 inches long; in its seventh year.

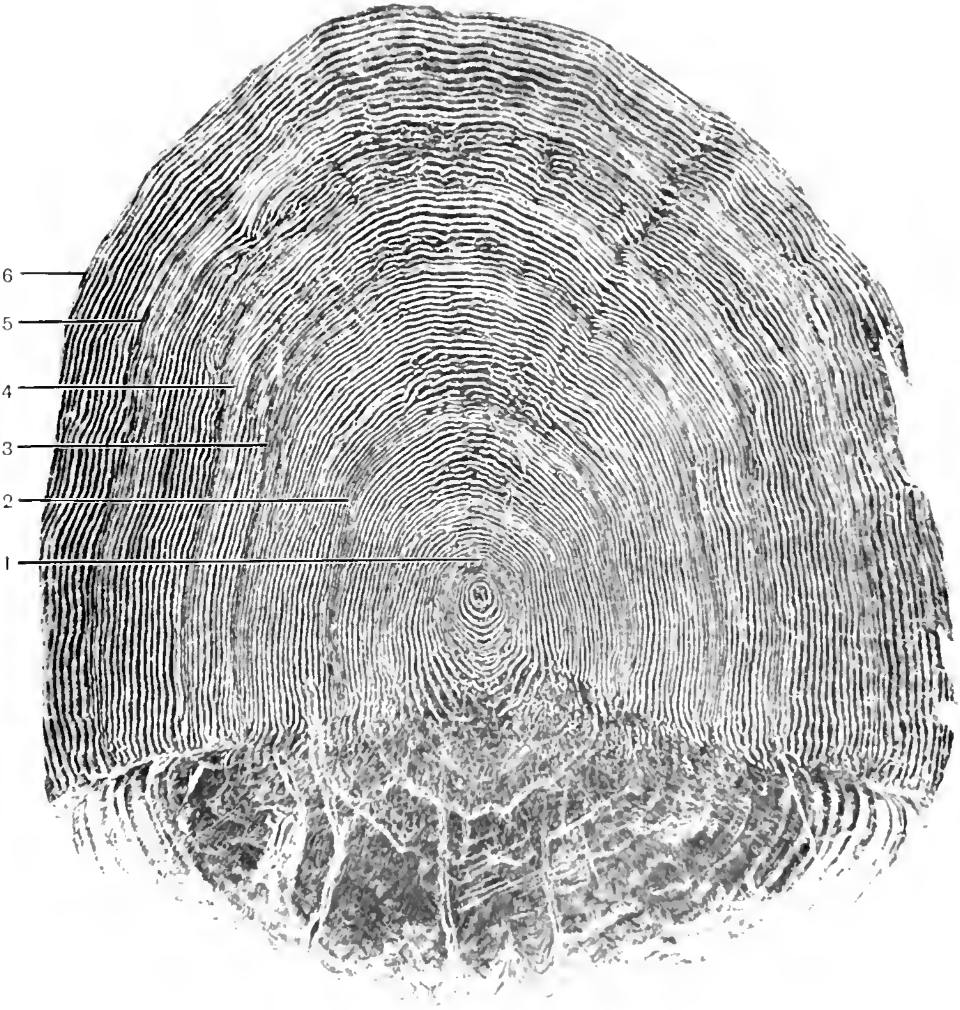

FIG. 285.—Scale of king salmon taken from mouth Yukon River July [illegible], 1917. Male, [illegible] inches long; in its seventh year.

FIG. 286.—Scale of coho salmon taken from mouth Yukon River August 1, 1920. Female, 25½ inches long, weight 9 pounds; in its third year.

FIG. 287.—Scale of coho salmon taken from mouth Yukon River July 31, 1920. Female, 24½ inches long, weight 7 pounds; in its third year.

FIG. 288.—Scale of coho salmon taken from mouth Yukon River July 30, 1920. Male, 23½ inches long, weight 6 pounds, in its fourth year, having spent the first two years in fresh water.

FIG. 289.—Scale of coho salmon taken from mouth Yukon River July 31, 1920. Male, 23 inches long, weight 6 pounds; apparently in its fifth year, having spent three years in stream as fingerling.

FIG. 200.—Scale of chum salmon taken from mouth Yukon River July 2, 1920. Female, 23½ inches long, weight 5 pounds; in its third year.

FIG. 291.—Scale of chum salmon taken from mouth Yukon River July 7, 1920. Female, 24½ inches long, weight 6 pounds, in its third year.

FIG. 292.—Scale of chum salmon taken from mouth Yukon River July 7, 1920. Male, 23 inches long, weight 6 pounds; in its third year.

FIG. 213.—Scale of chum salmon taken from mouth Yukon River July 31, 1920. Male, 27½ inches long, weight 9 pounds; in its fourth year.

FIG. 294.—Scale of chum salmon taken from mouth Yukon River July 7, 1920. Female, 23 inches long, weight 5 pounds; in its fourth year.

FIG. 245.—Scale of chum salmon taken from mouth Yukon River July 31, 1921. Male, 27½ inches long, weight 9 pounds, in its fourth year.

Fig. 296.—Scale of chum salmon taken from mouth Yukon River July 2, 1920. Female, 26 inches long, weight 7 pounds; in its fifth year.

FIG. 207.—Scale of chum salmon taken from mouth Yukon River July 7, [illegible] Female, 24½ inches long, weight 7 pounds; in its fifth year.

FIG. 298.—Scale of chum salmon taken from mouth Yukon River July 7, [illegible]. Male [illegible] inches long, weight 10 pounds; in its fifth year.

FIG. 299.—Scale of sockeye salmon taken from mouth Yukon River July 8, 1920. Male, 27 inches long, weight 9 pounds; in its fifth year.

FIG. 300.—Scale of sockeye salmon taken from mouth Yukon River July 8, 1920. Female, 23 inches long, weight 6 pounds; in its fifth year.

FIG. 301.—Scale of sockeye salmon taken from mouth Yukon River July 9, 1920. Male, 26½ inches long, weight 8 pounds; in its sixth year, having spent two years in lake after hatching.

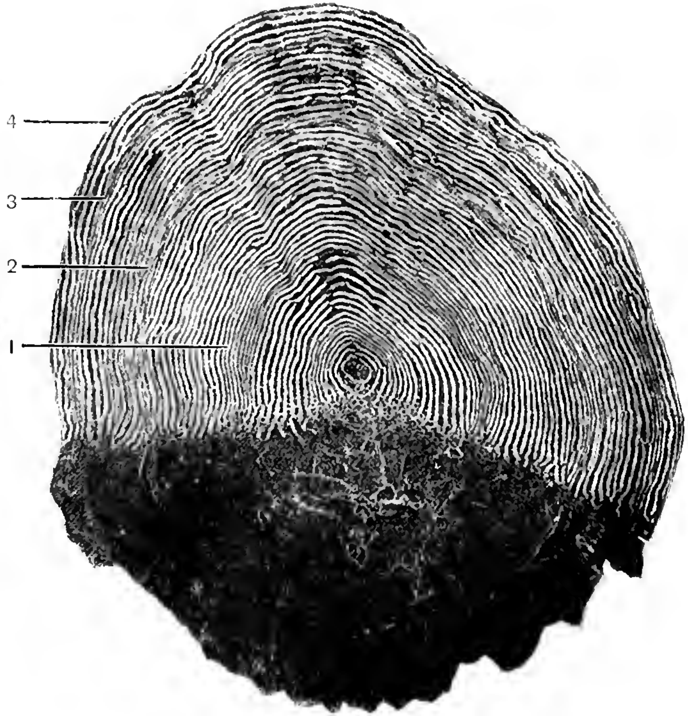

FIG. 302.—Scale of sockeye salmon taken from mouth Yukon River July 13, 1920. Male, 27½ inches long, in its fourth year, sea type.

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