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DIMENSIONS AND SHAPES OF LARVAE OF SOME MARINE BIVALVE MOLLUSKS

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ABSTRACT

Recent development of methods of rearing bivalve larvae under controlled conditions has made it possible to culture the following species: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria (=Venus) mercenaria, Mercenaria (=Venus) campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar (=Callocardia) morrhuana, Petricola pholadiformis, Ensis directus, Mactra (=Spisula) solidissima, Mya arenaria, Teredo navilis, Laevicardium mortoni.* These forms were grown past metamorphosis from eggs or recently released larvae of known parents. A series of photomicrographs and length-width measurements of larvae, from early straight-hinge stage to metamorphosis, is given for each species. In addition to these criteria, general shapes, prominence of the umbones and other morphological characters of the larval shells during growth are described. Problems and difficulties in identification, especially of closely related forms, are discussed, and suggestions for improved methods of identification are offered.

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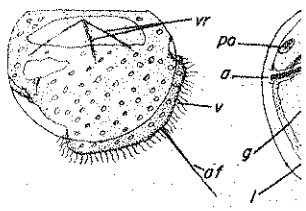
INTRODUCTION

A student of zooplankton of estuarine areas is usually impressed with the high percentage of larvae of bivalve mollusks, as compared to the numbers of larvae of other invertebrates. Extensive data illustrating this preponderance are given in the work of Thorson (1946) on reproduction and larval development of Danish marine bottom invertebrates. Thorson found that approximately 58% of the total number of larvae in water samples during the 3-year period of his studies were those of lamellibranchs. These larvae were normally dominant during the summer and winter maxima, far outnumbering the larvae of echinoderms, polychaetes, prosobranchs and other groups. Similar observations have been made in many other areas but, in spite of the common occurrence of bivalve larvae in estuarine waters, their taxonomic identity remains uncertain. It is often impossible to place a larva taken in plankton in a definite species, genus, or even family.

Because of the lack of knowledge of the larval stages, we cannot become familiar with the complete life histories of many pelecypods. Moreover, it is now generally recognized that identification of different bivalve larvae from natural waters ceases to be a matter of only academic curiosity. The complexity of modern society, its technological progress, and the reflection of this progress upon marine and especially estuarine environments, create many problems in which our ability to tell larvae apart may be important. This is especially true in studies of pollution of water basins with industrial wastes or improperly used pesticides. For example, if we can distinguish larvae of different species, we can learn, from examination of plankton samples taken from an area the degree of pollution of which is known, what larvae can exist under that condition. Moreover, plankton samples taken just before and after the use of pesticides in the vicinity of or over certain bodies of water permit us to determine accurately the species of larvae that disappeared after the treatment. Finally, by collecting water samples at definite intervals after the applications of pesticides, analyzing them for the presence of pollutants, and examining and counting the larvae of different species, we may ascertain the cumulative effects of the chemicals on the various organisms.

Similar opportunities would be open for the studies, under natural conditions, of the effects on larvae of changes in turbidity, drastic reductions in salinity and unusually severe physical disturbances of the water during storms and hurricanes. In the same manner we should be able to estimate the effects of biological phenomena, such as water blooms which, by producing heavy concentrations of external metabolites, may kill the larvae of some species without affecting those of the others. In Long Island Sound we have often observed well-defined periods when oyster larvae practically disappeared during dinoflagellate



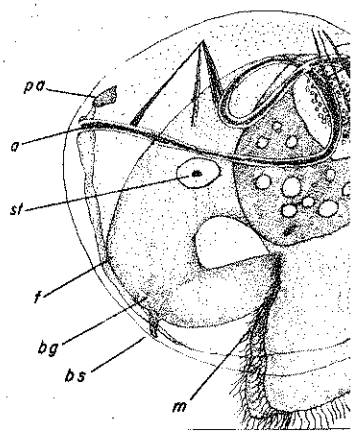


FIG. 1. Diagram of the promi
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i, digestive diverticulae; m, m
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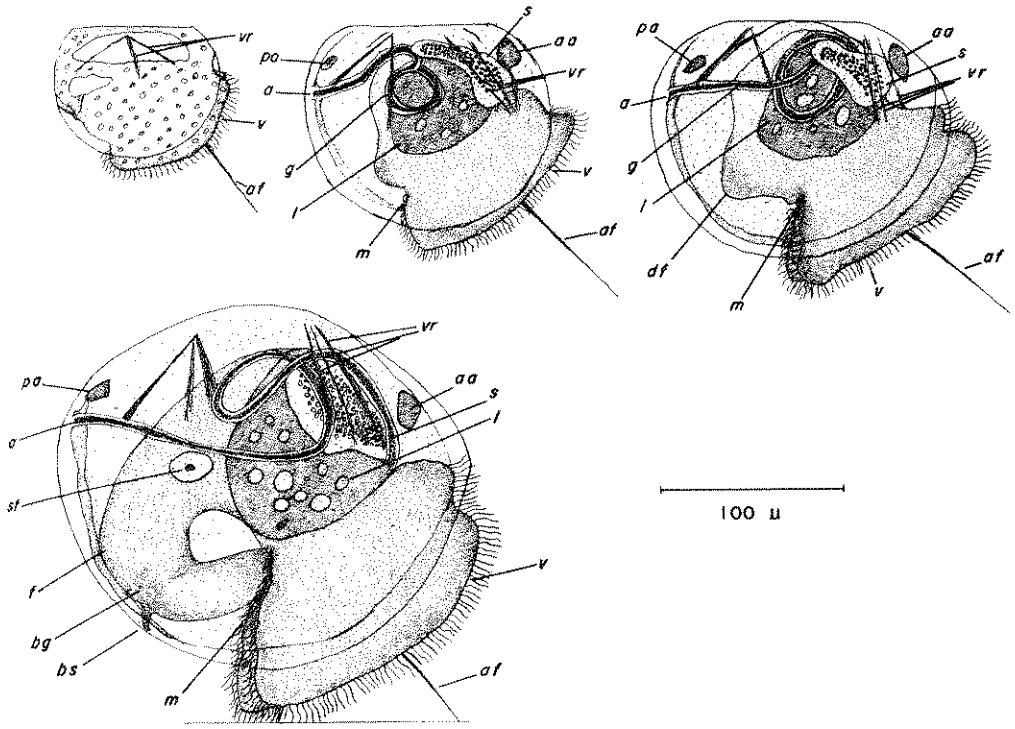

FIG. 1. Diagram of the prominent anatomical features of the larvae of the razor clam, *Ensis directus*, during different stages of development, from the first, shelled, straight-hinge stage to metamorphosis. a, anus; aa, anterior adductor muscle; af, apical flagellum; bg, byssus gland; bs, byssal spur used in laying down byssus threads; df, developing foot; f, foot; g, gut; l, digestive diverticulae; m, mouth; pa, posterior adductor muscle; s, stomach; st, statocyst; v, velum; vr, velum retractor muscles.

blooms, whereas larvae of some other bivalves remained apparently unaffected. In other situations larvae in the early stages of development were destroyed while the older larvae continued to live.

Studies of the type just outlined require, of course, the identification of the larvae in plankton samples; the present report is a contribution to the methodology of identification. In this report we give the sizes (length and width) of the 20 species of bivalve larvae reared at Milford Laboratory and the photomicrographs showing their shapes.

PROBLEMS IN THE IDENTIFICATION OF BIVALVE LARVAE

The difficulties in identification of larvae are due, in large measure, to a lack of knowledge of their shapes and dimensions from the time they attain the first shelled stage until they reach metamorphosis and change into juvenile mollusks (Fig. 1). Some authorities, as MacBride (1914), believed that the veliger larvae of bivalves are so similar in appearance and size that they cannot be distinguished at all and that the dif-

ferentiation of various species takes place only during their post-larval life. Regardless of the difficulties mentioned by MacBride, several workers have given descriptions of the larvae of one or more species. The best known contributors to this field include Stafford (1912), Kändler (1926), Wells (1927), Lebour (1938), Miyazaki (1935, 1936), Werner (1939), Jørgensen (1946), Sullivan (1948), Rees (1950), Quayle (1952), Yoshida (1953, 1964), Imai and his co-workers, whose contributions will be mentioned later in this article, and Loosanoff & Davis (1950, 1963).

Some of these contributions have added considerably to our limited ability to recognize bivalve larvae. Others, however, were of questionable value because they were based, fully or partially, on specimens whose identity could not be established definitely. In other words, the authors used the "indirect method" of identification, assuming, often with no basis whatsoever, that a specimen was the larva of a certain bivalve. The "indirect method" also consisted, sometimes, of following the development of unknown larvae, taken in plankton samples, through various stages of growth to metamorphosis and occasionally past it. Even this procedure is not entirely dependable, however, because juvenile mollusks of many species are almost identical and, therefore, can be easily mistaken for each other.

Examples of errors from the "indirect method" are not uncommon in the literature on recognition and identification of bivalve larvae. For example, Stafford (1912) stated that the larvae of the common clam of the Atlantic coast, *Mercenaria* (=*Venus*) *mercenaria*, reached a size of approximately 450 microns (μ) before undergoing metamorphosis. In our experience of approximately 20 years of growing larvae of this species successfully, as well as in the experiences of our colleagues engaged in similar studies (Carriker, 1961), free-swimming larvae more than 240 μ long were exceptional. As a rule, most of the larvae of this clam metamorphose before they reach 220 μ. Consequently, the larvae described by Stafford exceed the maximum length of our larvae by over 200 μ. Since our larvae were grown from the eggs of known parents, under controlled conditions, the sizes of our larvae as compared to those of Stafford, clearly show that he was not describing the larvae of *M. mercenaria* but those of some other bivalve.

Several investigators have suggested that the size of lamellibranch larvae at the time of metamorphosis cannot be used as a criterion for their recognition because it may vary greatly with environmental factors, especially temperature. For example, Nelson (1921) suggested that the maximum size of the larvae of the American oyster, *Crassostrea virginica*, grown in Canadian waters should be larger than those grown in southern areas because of the lower water temperature in the north. If this were true, as Carriker (1951) pointed out, one would find smaller larvae in Delaware Bay, New Jersey, and even smaller individuals in the waters of the Gulf of Mexico. Later, Sullivan (1948) expressed the opinion that the larvae of the soft clam, *Mya arenaria*, in Canadian waters are considerably smaller at Malpeque Bay than at St. Andrews, where the temperature of the water is several degrees lower. Still more recently, Tanaka (1954) came to the conclusion that the larvae of the Japanese oyster, *Crassostrea gigas*, metamorphosed at different sizes in different localities. Tanaka's conclusions, however, were diametrically opposed to those of Nelson (1921) and Sullivan (1948) because he believed he had found that prodissoconchs of *C. gigas* of the northern waters of Japan were smaller than those of the southern areas. Consequently, according to Tanaka, the size at metamorphosis increased with increasing temperature.

We do not share the point of view expressed by any of the above-mentioned authors because in our extensive studies of the larvae of different bivalves, grown from known parents and unde conditions, we found no ind such differences actually exis we have grown larvae of *C virginica* from parents broug merous points on the Atlant coasts, we have not disco nounced differences in the sizes. Normally, variation mum sizes of the larvae fro area were greater than tho larvae from different areas. vations are supported by Carr who, in studying the distributi larvae in New Jersey waters, the largest individuals in hi were within the metamorph range of our larvae origina Long Island Sound parents.

In our work with another species of the Atlantic coast, *ria mercenaria*, we again fai tect significant differences i metamorphosing larvae whos came from widely separated s the Atlantic coast. Finally, i of experiments on rearing la *mercenaria* at 5 different bu temperatures, ranging fro 30.0°C, we found no signif ferences with respect to th and maximum sizes at the setting (Loosanoff, 1959). C (1961) observations on the lar same species in New Jerse proved that their sizes at met sis agree closely with our fi larvae of Long Island Sound a sachusetts clams.

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from known parents and under controlled conditions, we found no indication that such differences actually exist. Although we have grown larvae of *Crassostrea virginica* from parents brought from numerous points on the Atlantic and Gulf coasts, we have not discovered pronounced differences in their setting sizes. Normally, variations in maximum sizes of the larvae from the same area were greater than those between larvae from different areas. Our observations are supported by Carriker (1951) who, in studying the distribution of oyster larvae in New Jersey waters, found that the largest individuals in his samples were within the metamorphosing size range of our larvae originating from Long Island Sound parents.

In our work with another common species of the Atlantic coast, *Mercenaria mercenaria*, we again failed to detect significant differences in sizes of metamorphosing larvae whose parents came from widely separated sections of the Atlantic coast. Finally, in a series of experiments on rearing larvae of *M. mercenaria* at 5 different but constant temperatures, ranging from 18.0°-30.0°C, we found no significant differences with respect to their mean and maximum sizes at the time of setting (Loosanoff, 1959). Carriker's (1961) observations on the larvae of the same species in New Jersey waters proved that their sizes at metamorphosis agree closely with our findings on larvae of Long Island Sound and Massachusetts clams.

Furthermore, Stickney's (personal communication) work at Boothbay Harbor, Maine, with larvae of *Mya arenaria*, the parents of which were collected from Maine to Maryland, indicated that the median size of the metamorphosing larvae was between 200 and 235 μ, about the same as we observed for larvae of the same species native to Long Island Sound. Stickney stated further that he never saw larvae of either Maine or Maryland clams that were smaller than 180 μ or larger than 250 μ at metamorphosis. Thus, his observations almost duplicate ours (Loosanoff & Davis, 1963).

The inadequacy of the "indirect method" is well illustrated again by Rees (1950), who stated that: "For example, the larva of *Mytilus edulis* has been described about 10 times. Yet Jørgensen (1946) undoubtedly described a mixture of *Mytilus edulis* and *Modiolus modiolus* under the former species, and Lebour (1938) identified larvae as '*Mytilus* or relative'." According to Rees (1950) "The apparent uncertainty in the identification of *Mytilus* larvae is due to ignorance of the extent of inter-specific differences; are the larvae of *Modiolus barbatus*, for example, so like those of *Mytilus edulis*, that there is uncertainty in the identification of *Mytilus edulis*?". Rees stated openly that: "The surest method of determining the species of larvae is by culturing."

Rees also admitted that he was not certain all the larvae he described were truly pelagic and that, since most of the larval forms discussed in his paper had been identified by indirect means, some identification might have been in error. As we will show, Rees was correct in anticipating these errors. We think that the uncertainty expressed by Rees would have disappeared if the larvae of different species had been grown under laboratory conditions. Had Jørgensen (1946) as well as Rees (1950) had available photomicrographs and measurements of the larvae of *Mytilus edulis* and *Modiolus modiolus*, which are offered in this article (Figs. 7, 10), those authors would not have expressed uncertainty about the similarity of larvae of the 2 forms.

It would be unfair to criticize earlier workers for using the "indirect method" because at the time of the studies the art of rearing bivalve larvae was only in its beginning and, as much of the new information in that field had not been published, few people were aware of the simplicity and efficiency of the "direct method" (Loosanoff & Davis, 1950; Loosanoff, 1954). Clearly enough, Sulli-

van (1948) selected the "indirect method" because: "Special apparatus must also be provided and special techniques developed for rearing larvae since there are no standard methods available."

A comparison of several morphological characters of bivalve larvae, after they become shelled veligers, should aid in their identification. Most students agree that these characters are principally those of the shell rather than of the soft parts. Dimensions of the larval shell (prodissoconch), its general shape, prominence of the umbones during the progressive stages of growth from early straight-hinge stage to metamorphosis, and ratios of length of hinge to maximum shell length or width have been recommended as means of identification. Position of the larval shell ligament and, especially, the details of the hinge structure, including its teeth, also have been suggested as aids in identification by several authors, of whom Werner (1939) and Rees (1950) may be mentioned.

In our studies of larvae of 20 species of bivalves, all grown to metamorphosis under laboratory conditions from eggs of known parents, we attempted to evaluate features of their soft parts and, especially, their shells. We were interested also, after the appearance of Rees' paper, in developing a comparatively simple but rapid method of identification by hinge characters. In the course of this work we attempted frequently to photograph hinge structures of larval shells but, unfortunately, often found it difficult to obtain clear-cut pictures that could be used as easy guides to identification (Fig. 2).

Moreover, from a practical point of view, considerable difficulties are involved in the use of hinge characters as a regular means of identification of larvae in plankton samples. Only freshly collected material can be used because, even if the larvae are preserved in a neutral formalin, the entire hinge structure may be altered by the preservative. Again, as our studies of some species have shown, the structure and general outline of the hinge changes with changes in size and shape of the larval shell. These observations indicate that to demonstrate the changes of the hinge structure of a larva of each species during the entire period of development, from straight-hinge to metamorphosis, an extensive series of photomicrographs of the hinge region would be required.

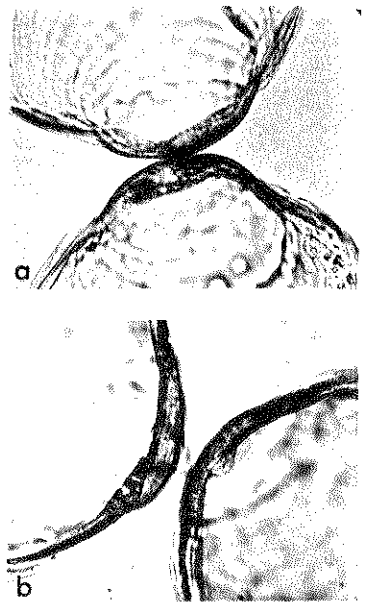

FIG. 2. Highly magnified photographs of internal surfaces of both valves of advanced veligers of (a) *Mercenaria mercenaria* (above) and (b) *Mytilus edulis* (below).

We also have found that if a relatively large number of larvae must be identified, it may be difficult to open and prepare them for microscopic examination within a reasonable time. A considerable dexterity is needed and, since the procedure is time-consuming, we doubt that this method will ever be used routinely by workers on plankton samples that contain the larvae of many species in different stages of development. If the procedure were relatively simple, we are certain that both Werner (1939) and Rees (1950), who so strongly recommended the use of the hinge apparatus as a means of identifying lamellibranch larvae, would have included photomicrographs of the hinges in their articles. Instead, both authors offered only schematic drawings of these structures. Moreover, although photographs of the hinge structure of larval bivalves have been published in several articles, Quayle (1952), working with *Venerupis pullastra*, is one of very few authors to give a good photomicrograph of the hinge area of the larval shell.

The existence of special structures, including teeth, in the hinges of larval bivalves is, nevertheless, undeniable. In many species these structures may be seen while the larvae are still in the straight-hinge stage. We are certain that, because of the considerable progress made during the last decade in culturing lamellibranch larvae in this country and Japan, the hinge structures of larval shells will soon be more comprehensively described, and good, readable photomicrographs of them obtained; as yet, however, they are not available. Finally, the lack of hinge structure in some species and the similarity between structures of others, make it possible that differences sufficient for the identification of closely related species may not be found.

A visual record of the outline of a larva during the period of its growth from straight-hinge stage until metamorphosis surely is one of the logical means of identification. Many bivalve larvae of the pelagic type, however, possess basically the same anatomical features and, because some of these features are not easily distinguishable in the early straight-hinge stages, this period is one when recognition of larvae presents a difficult problem.

The differences in shapes of molluscan larvae, nevertheless, are and will remain a criterion for identifying individuals of widely separated species. For instance, the general outlines of *Ostrea edulis*, *Crassostrea gigas* and *Mya arenaria* are so different that they are readily distinguishable (Figs. 19, 28, 55). Closely related forms, on the other hand, are hard to separate. For example, in some water basins we may find 2 or more species of the same genus whose larvae at all stages of development resemble each other so closely that it is virtually impossible to tell them apart. An example of this similarity is offered by 2 species of the genus *Crassostrea: C. virginica*, the eastern oyster (Fig. 25), and *C. gigas*, the oyster from Japan (Fig. 28), which have been introduced in several areas of our Pacific coast. Both species are found at present in Tomales Bay, California, although low water temperature prevents them from propagating every year. Nevertheless, spawnings occur occasionally and, when they do, the similarity of the larvae can make it virutally impossible to tell to which species they belong.

Similar problems may be encountered in waters where 2 species of the genus *Ostrea* are found. This situation is a definite possibility because we have introduced the European oyster, *O. edulis* (Fig. 19), in several areas of the Pacific coast (Loosanoff, 1951, 1955), where another species, *O. lurida* (Fig. 22), is native. Our recent observations on *O. edulis*, which were reared as spat at the Biological Laboratory in Milford, Connecticut, and then planted in Tomales Bay and Drake's Bay, California, have shown that these oysters bear the larvae in their gills as early as April. The dates of the end of spawning and swarming have not been determined but, on the basis of observations at Milford and the examination of a few oysters in California waters, we

may assume that some of the larvae will be discharged as late as the beginning of October. Larvae of *O. lurida* will probably be found in the same waters during the same time. Thus, during a period of several months, extending approximately from April until October, the larvae of the 2 species will be present in the same environment and, because of their similarity, will be extremely difficult to tell apart.

The recently developed technique of growing bivalve larvae from fertilized eggs to metamorphosis under controlled conditions has also provided us with a second aid for their identification: the dimensions of the larvae during different stages of their growth. The measurements reported in this paper are expressed in microns and refer to the length and width of the larval shells. The length measurement represents the longest distance along the anterior-posterior line of the shell, roughly parallel to the hinge. The width is the distance from the tip of the umbo to the ventral margin of the shell. Some authors prefer to call the latter measurement "depth" or "height". However, we will continue to call it "width" for several considerations, the principal being that numerous publications by members of the Milford Laboratory employ the words "length" and "width" to describe larval sizes (see Loosanoff & Davis, 1963). A change of our commonly used term "width" to a less familiar "depth" or "height" could create confusion. Moreover, measurements of post-larval and adult forms of many bivalves, such as *Mercenaria mercenaria* and other clams, are expressed in terms of "width" rather than "depth" or "height". Our terminology therefore seems to be most logical in the study of the entire life histories.

Workers who attempt to identify the larvae of different species may find the length-width data which we offer of value because they give, for each species, the possible range in width for the larvae of each length. Furthermore, our data indicate the frequency with which each width occurs at a given length. For example, the widths recorded for the larvae of *Arca transversa*, which measured 130 μ in length, ranged from 100-115 μ (Fig. 5). Of the 60 larvae of that length, however, only 12 individuals were 100 μ wide, 39 were 105 μ wide, 8 were 110 μ wide, and only 1 was as wide as 115 μ. Thus, a worker who encounters a larva 130 μ long and suspects that it is *A. transversa* can, by noting its width, refer immediately to our length-width curve to estimate the probability that the larva belongs to that species.

Larvae of some bivalves, such as *Ostrea edulis* and *O. lurida*, may, in the last stages of growth, measure as much as 200 μ in thickness if the measurement is taken near the hinge. Under the microscope, therefore, the larvae may appear as thick wedges tapering rapidly from the hinge to the sharp ventral side. This circumstance makes it difficult to obtain accurate measurements of the larval thickness and may also explain the considerable variations in the width measurements of larvae with the same length. For example, widths of larvae of *O. edulis* 230 μ long may vary from 185-220 μ, *i.e.* about 35 μ (Fig. 23). Conversely, the relative roundness of the larvae may influence the accuracy of the length measurements because the larvae 210 μ in width may vary from about 225-265 μ in length. The same difficulties are encountered in measuring the larvae of other species with thick umbones. These facts must be taken into consideration in forming conclusions based on shell measurements.

From the measurements now available it is also possible to offer length-width relationships of larvae of different sizes and to calculate the formula for the regression of width on length for each species. For example, the length-width data of *Crassostrea gigas* give a regression equation of W=1.104 L-8.94, while the same value for *Ostrea lurida* is W=0.897 L-4.1. The difference between the regression lines of these 2 genera is statistically significant. On the other hand, the median lines fitted by visual examination for the length-width data on

our graphs make it evident that regression lines for the larvae of *C. gigas* and *C. virginica* are so similar that they probably cannot be distinguished mathematically. The same is true of the larvae of *O. edulis* and *O. lurida*. We are continuing the mathematical analysis of the data and shall present the results of these studies in a separate article. Although these results may be of considerable theoretical interest, they probably would not help significantly in routine identification of the larvae in plankton samples.

The length and width measurements, although helpful in distinguishing the larvae of different genera, may be of little value in identifying larvae of closely related forms, such as *Crassostrea virginica* and *C. gigas* or the two species of the genus *Ostrea*, because measurements of the larvae of the 2 related species are almost identical.

The color of larvae has been suggested by some authors as one of the characters on which their identification could be based (Sullivan, 1948). We do not agree that it is a dependable criterion because we have noticed frequently that the color of laboratory-grown larvae, especially in the early stages of development, depends to a large extent on the color of the food they consume (Loosanoff & Davis, 1950). Since the color may be changed under laboratory conditions by feeding the larvae different foods, it may be assumed that in nature, where the quality and quantity of plankton, especially phytoplankton, undergo almost continuous change, the color of the larvae may be correspondingly affected. This view applies principally to younger stages, whereas the color of the older larvae with well-developed, heavy, thick shells may not be easily altered. The changes in color are due, of course, to the changes in color of the digestive tract.

Quayle (1952) was also of the opinion that the loss of color of veligers upon preservation makes color differences, even if sometimes displayed by living larvae, valueless to students of plankton. Certain other anatomical details, such as eye spots or the position of the digestive gland, likewise become fainter or disappear entirely soon after preservation. It is principally the outline of a prodissoconch, including degree of slope from umbone anteriorly and posteriorly, its size, and the hinge teeth when present, that will help most in identifying a larva. However, the hinge structure may also soon become useless by being partly dissolved by the preserving fluid if specimens are kept in formalin that is only slightly acid.

In this article we offer a series of photomicrographs of larvae of 20 species of bivalves in different stages of their growth and development. All the larvae were grown under contolled conditions from the eggs of known parents or released by them in swarming. Our photomicrographs show a succession of sizes and shapes of the larvae of each species, from early straight-hinge stage to the maximal or nearly maximal size.

Whole specimens were used for photography, although we realize that only the use of a single valve makes it possible to avoid the tilt of the umbo region, a condition which may change considerably the outline of a larval shell. Because most workers will deal with the entire animal, not with a single valve, they will see the larvae in positions similar to those given in our photographs. We prefer, therefore, to show photomicrographs of whole larvae with the 2 valves intact. We hope that the material offered will help workers engaged in studies of zooplankton in general and bivalve larvae in particular.

Since bivalve larvae have been described frequently, it would be superfluous to repeat the detailed descriptions. We offer, therefore, only a diagrammatic drawing showing the major features of a typical bivalve larva during several stages of its development (Fig. 1). Those interested in more detailed descriptions of larval structure should refer to the articles on their morphology offered by several authors, the most recent by Quayle (1952) and Ansell

(1962). The list of references in Ansell's paper should be helpful in pursuing the studies further.

We admit that we still do not have a fully dependable, simple method to identify easily the larvae of most species of bivalves. We have, nevertheless, several reliable means that, under certain conditions, may be extremely helpful. We offer especially the series of photomicrographs of the larvae showing their shapes and also give extensive data on their length and width. Use of these 2 criteria may resolve readily many problems of identification which appeared insoluble only a decade or so ago.

We believe also that, since the methods for culturing bivalve larvae are continuously being improved, better means for studies of their differences, applicable in field work, may become available. Chemical methods for the identification of larvae eventually may be used. Some of them may be based on differences in the enzyme complement of different species. In this method, a change of color when the larvae are placed in solutions of certain chemicals may indicate to which family, or perhaps even genus, they belong. It is also possible that microserological and micro-chromatographic methods can be applied.

The material for this article was collected over a period of approximately 15 years. At first we did not contemplate preparation of a paper describing the larvae of different species, and it was considerably later, only after we realized how much valuable material had accumulated, that we decided to summarize it in the present form. At the beginning of these studies our techniques were less refined than they are now. As a result, the quality of photographs of the larvae of different species varies. Those of the earlier period are somewhat inferior to those taken later. Several members of our staff took the pictures of the larvae used in this article, and during this long period different cameras, microscopes, and sources of illumination had to be used. Because of these circumstances the photographs of some species may appear lighter than others. The density of the photographs should not be considered a criterion for identification. For the same reasons the magnifications of the photomicrographs of all species of the larvae are not identical. Rather than give magnifications of the larvae, we offer the actual dimensions in microns.

Finally, some photographs, especially of the early larval stages, may have dark backgrounds. This defect is almost unavoidable because the young larvae are sometimes so transparent that to obtain sharp outlines the background of the photograph must appear dark. We hope, nevertheless, that these imperfections will be overlooked because a repetition of the studies needed to prepare more uniform photographs would require many years of persistent work.

Miner (1950) and Abbott (1954) provided most of the information on the geographical distribution of the different species. Sequence of the species in the manuscript is given also largely according to Abbott. The notable exception is *Laevicardium mortoni*, at the end of the list. This placement is not for reasons of classification but because we do not have a series of 4 photomicrographs of the groups of larvae of *Laevicardium* similar to those of the other 19 bivalves described in this article.

PREPARATION OF PERMANENT MOUNTS OF WHOLE LARVAE

Soon after we began rearing bivalve larvae it was decided to preserve them as whole mounts to provide a permanent record of their size and general outline. We thought that preparations of this type would be useful to students working on recognition of bivalve larvae in plankton collections and also for other studies of these organisms. After trying a variety of methods of preparing the slides we adopted the following technique, which gives satisfactory results, especially if the last 2 steps of passing the specimen through a mixture of alcohol and xylene are closely followed:

1. Kill and fix in 3.0% neutral formalin, using 40% commercial formalin as 100%, 30 minutes to 1 hour
2. Alcohol: 35%, 5 minutes
3. Alcohol: 50%, 5 minutes
4. Alcohol: 70%, 5 minutes
5. Alcohol: 80%, 15 minutes
6. Alcohol: 95%, 30 minutes
7. Alcohol: 100%, 15 minutes
8. Alcohol: 100%, 10 minutes
9. 3 parts of 100% alcohol + 1 part of xylene, 5 minutes
10. Equal parts of 100 % alcohol and xylene, 5 minutes
11. One part of 100% alcohol + 3 parts xylene, 5 minutes
12. Xylene, 5 minutes
13. Mount from xylene in synthetic resin mounting medium and place the cover glass on it.

It is sometimes advantageous to color the larvae artificially to bring out more clearly their outlines and internal structures in the final preparation. The living larvae are placed in a solution of 1 mg of Neutral Red in 1 liter of sea water for about 1-1/2 hours before killing and fixing them (Loosanoff & Davis, 1947). After the larvae acquire sufficiently dense color they are collected on a fine screen, washed and processed. If the Neurtral Red stored by the larvae in their bodies before fixation is partly lost during processing, it may be desirable to add to all alcohol solutions a few drops of Brilliant Vital Red (Evans) to restore the color.

During processing larval samples are carried from one solution to another in a small container made of the upper part of a small vial with a piece of number 20 silk bolting cloth or correspondingly fine plastic mesh securely tied around the lip. The fluid passes through the cloth, but the larvae are retained. This device, which one of us has used for more than 35 years, simplifies greatly the problem of preparing whole mounts of small organisms, including plankton.

Slides prepared in this way hav distributed to students of bivalve in several countries. Many sets of are still in use and in good con We believe that these slides, in c nation with the series of photor graphs and length-width measure of the larvae which we offer i article, will help significantly in tifying larvae.

DESCRIPTION OF DIFFERE SPECIES

1. *Arca transversa* Say

This species, known by the co names Transverse Ark Shell or Clam, ranges from New England Florida Keys, and in some area cluding Long Island Sound, is con tively numerous. It is a member Family Arcidae, several represent of which are found within the same of distribution as *Arca transversa*

The larvae of this species res in general, the rhomboidal shape adults; the umbo is directed slight ward. The resemblance betwe shapes of the larvae and the adu comes especially noticeable as th mer approach metamorphosis (F 4).

The smallest normal straight larva in our cultures was 70 μ lo 55 μ wide. The early straight-hin vae are usually somewhat larger ever, approximately 75 x 57 μ (F The difference between length and of the larvae is large. Among the gest straight-hinge individuals it approximately 20 μ, and at the of metamorphosis the length ma ceed the width by almost 70 μ (F Widths of larvae of the same lengt vary considerably. For example, 24 larvae all 255 μ long, widths from 175-200 μ.

Larvae of the early straight stage are considerably darker th larvae of corresponding stages o

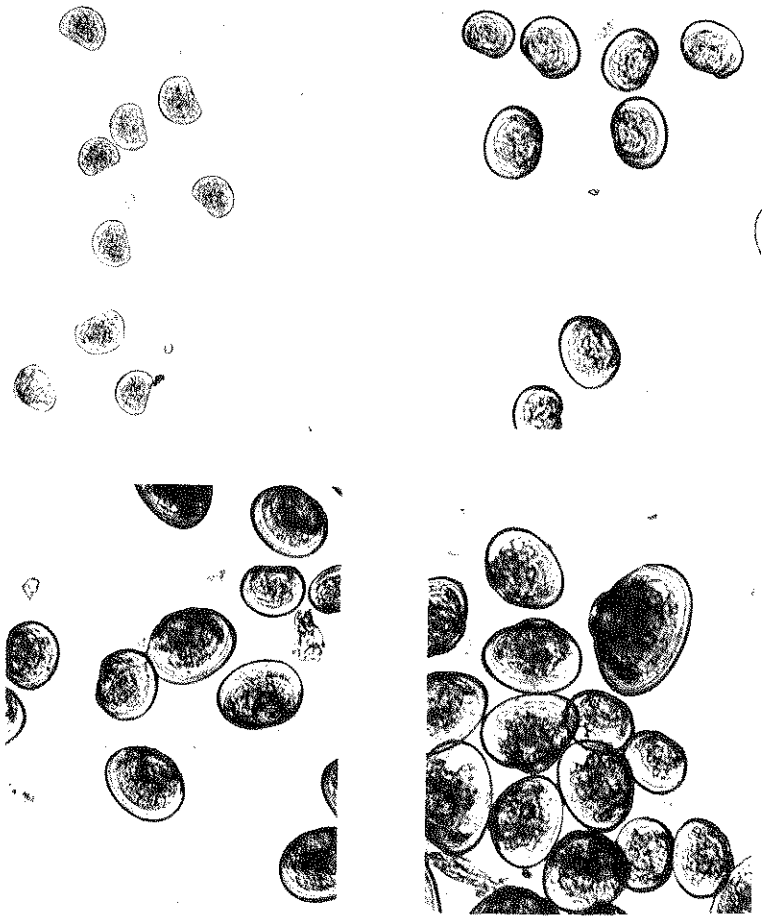

FIG. 3. Group photographs of different sizes of larvae of *Arca transversa*. Smallest individuals of the youngest group are approximately 70 μ long, and the largest of the oldest, approximately 230 μ.

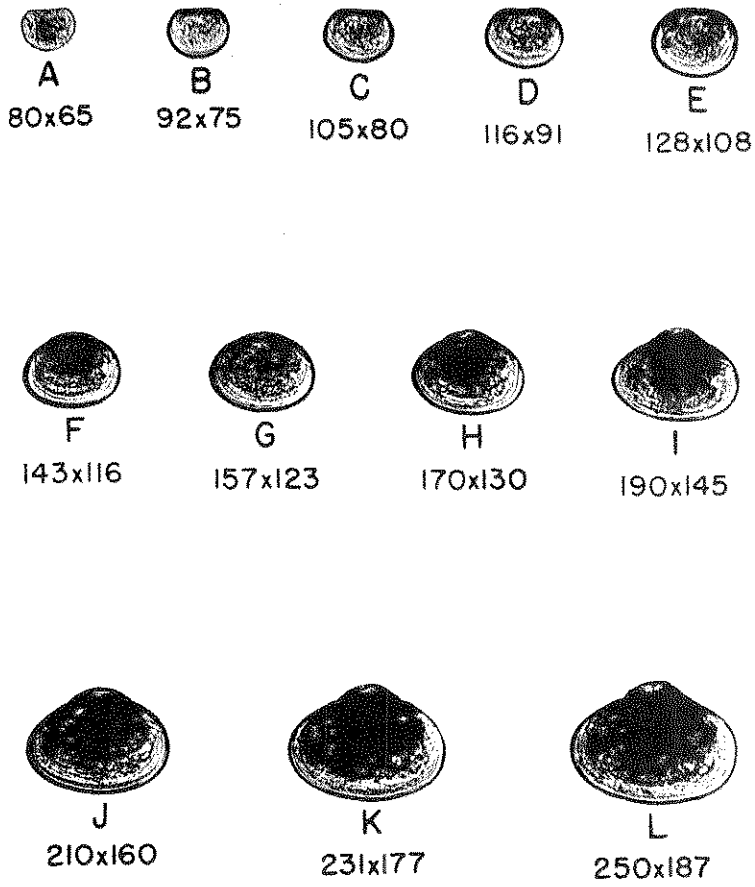

FIG. 4. Photographs of larvae of *Arca transversa* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

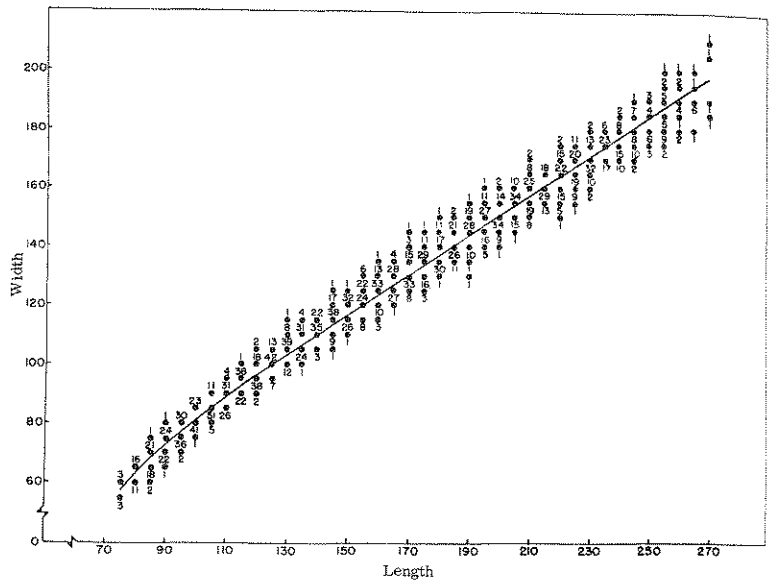

FIG. 5. Length-width relations of larvae of *Arca transversa* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

other species, and they become darker as their size increases. In living, laboratory-reared larvae, the pointed end of the shell normally displays a reddish-brown color when the individuals reach approximately 140 μ in length, while the opposite, or more rounded end remains brown. An "eye" spot usually appears at the length of about 225 μ and becomes more conspicuous as the larvae approach metamorphosis. In some individuals, however, especially those growing at a comparatively slow rate, the "eye" spot may be seen in larvae only about 205 μ long. An umbo begins to form when the larvae reach about 110 μ in length and is normally well-defined at the length of 130 μ (Fig. 4).

The majority of normal larvae begin to metamorphose at lengths ranging between 240 and 260 μ. However, as already reported for bivalve larvae in general (Loosanoff *et al.*, 1951; Loosanoff & Davis, 1963), considerable variations in setting sizes of *Arca transversa* are normal. For example, some larvae were only 215 μ long at metamorphosis, whereas others, possibly abnormal in some respects, were considerably larger than 260 μ. One individual of 310 μ was seen still swimming although it had already developed a large foot. Possibly it had already metamorphosed. Some individuals in the later stages of metamorphosis already possess a byssus with which they

can attach themselves to suitable surfaces.

The literature on *Arca transversa* contains no references describing its spawning or larval development. It appears certain, however, that this clam spawns during late spring because some individuals brought from Long Island Sound to the laboratory in the middle of May spawned within 2 or 3 hours after being placed in warm water (Loosanoff & Davis, 1963).

2. *Mytilus edulis* Linnaeus

The mussel family includes some of the most common and abundant species of bivalves. *Mytilus edulis* is probably one of the best-known representatives of the group. On our Atlantic coast it is found from the Arctic to North Carolina, and on the Pacific coast, from Alaska to California. These mussels are also numerous along the European shores, where they support important fisheries.

Because of their common occurrence, the larvae of *Mytilus edulis* have been described by a number of authors, including Borisjak (1909), Werner (1939), Jørgensen (1946), Sullivan (1948), Rees (1950) and Loosanoff & Davis (1963). The smallest straight-hinge larvae of the mussels grown in our cultures were approximately 94 x 64 μ, and the largest measured about 300 x 286 μ (Figs. 6, 7, 8).

Live mussel larvae display an "eye" spot, from 5-7 μ in diameter, near the center of their bodies. This spot appears when the larvae are approximately 215 μ long. Normally, all larvae about 230 μ or longer possess the "eye" spot. A well-developed foot may appear in larvae as small as 185 μ long, although normally the first signs of the foot are noticed when the larvae approach 210 μ. At the length of about 235 μ the majority of the larvae already possess this organ.

The smallest metamorphosed individual, found already attached by its byssus to old oyster shell placed on the bottom of our culture vessels, measured only about 215 x 200 μ. Fully metamorphosed mussels, also attached by a byssus but only 225 μ long, were not uncommon. In some cultures, however, larvae almost 300 μ in length were still swimming actively. Thus, the length at which mussel larvae metamorphosed in our cultures varied by nearly 90 μ.

Stafford (1912) reported that the largest swimming larvae of the mussel were 400 x 330 μ. It is doubtful that he actually measured the larvae of *Mytilus edulis* because his measurements are so different from ours made on larvae of known origin. Nelson (1928) also reported that the size of the larvae was much larger than ours. According to him the largest swimming larvae of *M. edulis* measured 376 x 344 μ. He stated that recognition of the larvae of this species is made easy because of their small width. Although this is true of most straight-hinge stages, the larger larvae become relatively wider (see Figs. 7, 8). Furthermore, Nelson's measurements contradict his contention as to the relatively small width of his larvae. Finally, photomicrographs of the larvae given by Nelson show at least one individual in which the length and width are almost identical.

Werner's (1939) measurements of length and width of the larvae of *Mytilus edulis* agree, in general, with ours, except that he gave the measurement of his smallest larvae as approximately 112 x 84 μ, which is considerably larger than the dimensions of our smallest larvae (Figs. 7, 8). Jørgensen (1946) commented on the remarkable peculiarities of the larvae of *M. edulis* because of the extensive variability of their shape and color of the shell. He also mentioned the large differences in sizes of larvae undergoing metamorphosis.

Sullivan (1948) reported that the larvae of *Mytilus edulis* ranged from about 155 x 120 μ to about 355 x 320 μ. Sullivan's data indicate, therefore, that her measurements of the smallest larvae were approximately 60 μ larger than ours, whereas her largest larvae measured about 50 μ more than the lar-

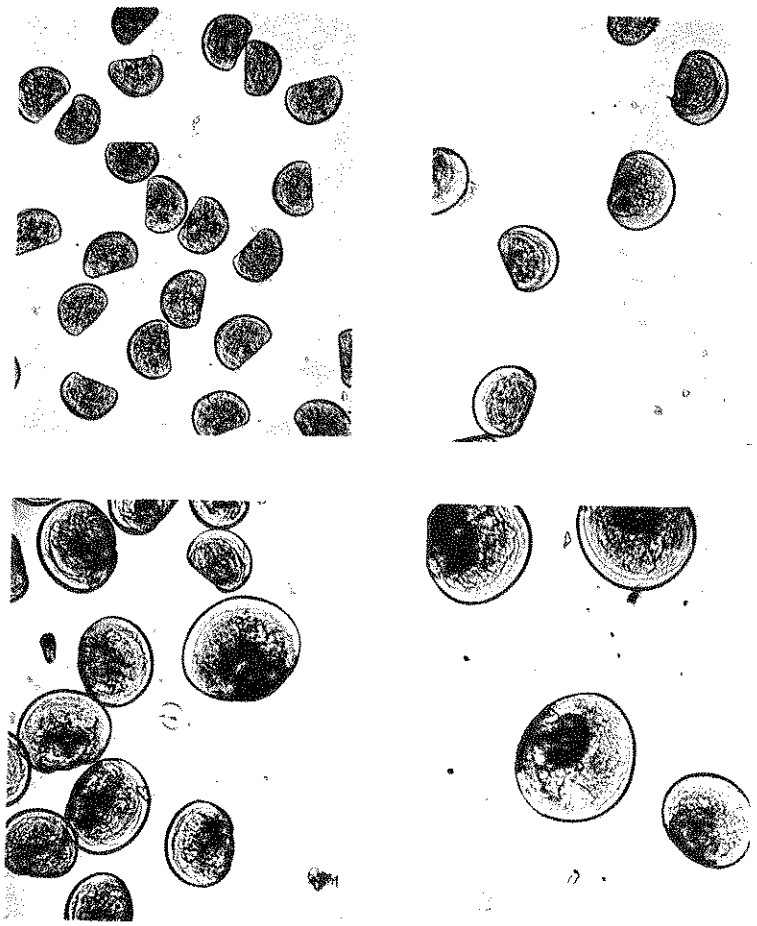

FIG. 6. Group photographs of different sizes of larvae of *Mytilus edulis*. Smallest individuals of the youngest group are approximately 90 μ long, and the largest of the oldest, approximately 225 μ.

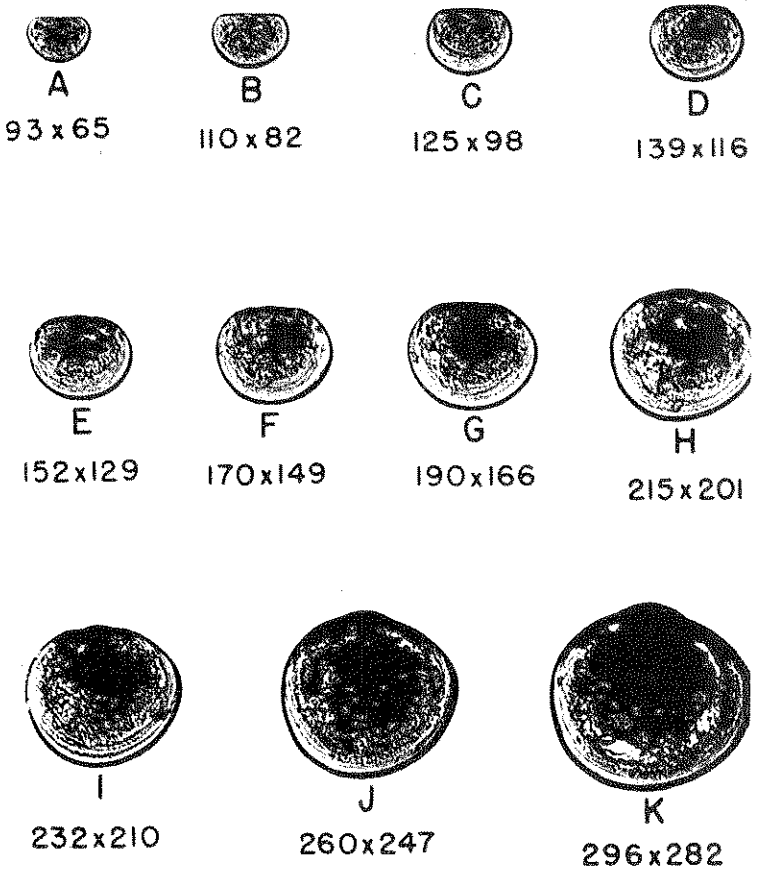

FIG. 7. Photographs of larvae of *Mytilus edulis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

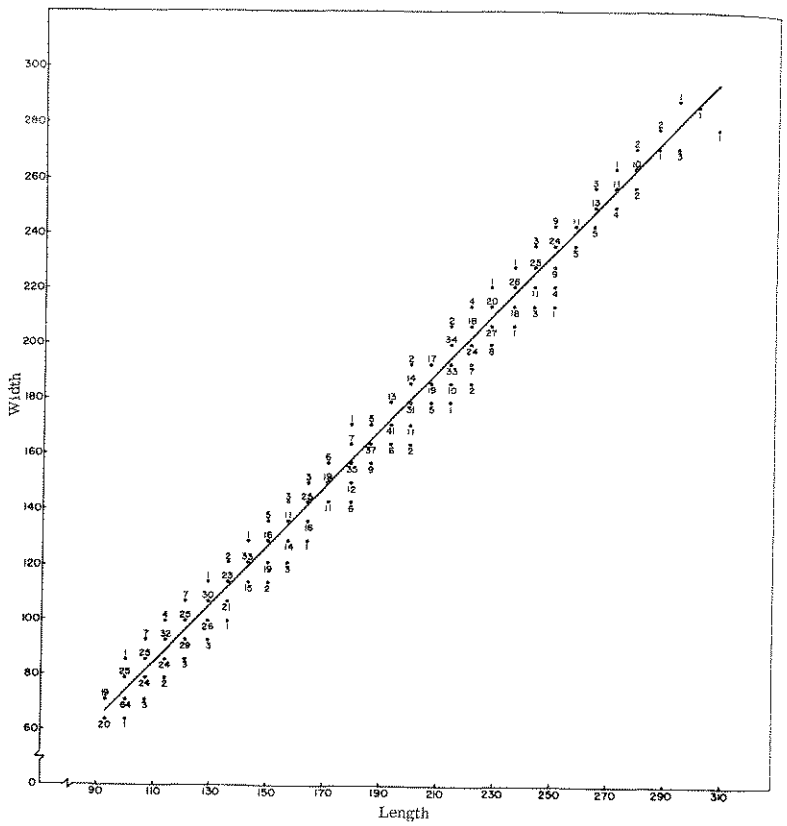

FIG. 8. Length-width relations of larvae of *Mytilus edulis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

gest larvae in our samples.

Rees (1950) stated that straight-hinge larvae of both *Mytilus* and *Modiolus* have similar shapes though in *Modiolus* the narrow end of the shell is less pointed than in *Mytilus*. In more advanced stages, however, the shape and general outline of the larvae of these 2 forms become increasingly different.

3. *Modiolus demissus* (Dillwyn)

Modiolus demissus, the common ribbed mussel of the Atlantic coast, is also called *Volsella demissus*, *V. plicatula*, *M. plicatula* and several other names. It ranges from Prince Edward Island to South Carolina and Georgia. In some areas it is extremely abundant, especially in tidal marshes, on mud flats and among the rocks a few feet above mean low-water mark.

At the early straight-hinge stage most of the larvae of *Modiolus demissus* measure from 110-115 μ in length and from 85-95 μ in width, although occasionally smaller individuals, only about 105 μ long, are found in cultures (Figs. 9, 10, 11). A few larvae develop a functional foot and a prominent "eye" spot at the length of about 200 μ, and some may metamorphose at only about 220 μ long. These larvae are exceptional, however, because the majority do not lose their vela until they are approximately 275 μ long. In some cultures a few individuals still possessing a functional velum were about 300 μ long. Thus, while we agree with Sullivan (1948) on the size of the smallest straight-hinge larvae of this species, our largest larvae, measuring approximately 305 x 260 μ, were considerably larger than the maximum size of 205 x 170 μ given by her.

Despite the common occurrence of *Modiolus demissus*, Sullivan's article was the only reference we found that described the larvae of this species. Partial descriptions of the larvae of *M. modiolus*, and other closely related forms, have been offered, however, by Werner (1939) and Jørgensen (1946). Jørgensen suggests a close resemblance between the veligers of *M. demissus* and *Mytilus edulis*. We find, however, that the larvae of these 2 presumably closely related species are different in their length-width ratios and also in their general appearance when they are near metamophosis (compare Figs. 7, 10). We may add also that the photomicrographs of the larvae of *Modiolus modiolus* given by Rees (1950) show that the shapes of larvae of this species appear to be rather different from those of larvae of *M. demissus* grown at our laboratory.

4. *Anomia simplex* D'Orbigny

This mollusk, commonly called the Silver or Jingle Shell, is abundant from Nova Scotia to the West Indies. It is extremely numerous during some summers in Long Island Sound where it sets, together with the new generation of oysters, on old shells and rocks, competing with the oyster set for space and food.

Larvae of *Anomia* have been described by a number of workers, including: Stafford (1912) and Sullivan (1948), who gave descriptions of *A. aculeata;* Miyazaki (1935), who described the larvae of the Japanese species, *A. lischkei;* Lebour (1938) and Jørgensen (1946), who offered descriptions of *A. squamula;* and Rees (1950), who referred briefly to 3 species of *Anomia*.

The smallest larvae in our cultures measured about 58 x 47 μ, although young straight-hinge larvae are normally somewhat larger (Figs. 12, 13, 14). During the early stages of development the length of the larvae is about 10 μ greater than the width. Later, when the length reaches approximately 135 μ, the width increases more rapidly than the length, and during the final stages the two dimensions are almost identical (Fig. 13).

Considerable difference is noticeable in the shape of the 2 shells of a larva even during the early straight-hinge stage. Normally, one shell is well rounded, while the other, which becomes the lower when the animal is attached, is nearly flat. This difference is noticeable at all stages of larval development. Moreover, the umbo of the right shell is not well developed. Jørgensen (1946) made the same observation on the shells of *Anomia squamula*.

During early development the shells of the larvae of *Anomia simplex* are almost transparent and nearly colorless. Even when the larvae approach metamorphosis their shells remain transparent. Because of the prominent umbo developed during advanced stages, the larvae of *A. simplex* may be mistaken for those of oysters of the genus *Crassostrea*, which also have a protruding umbo. This mistake can be avoided by remembering that

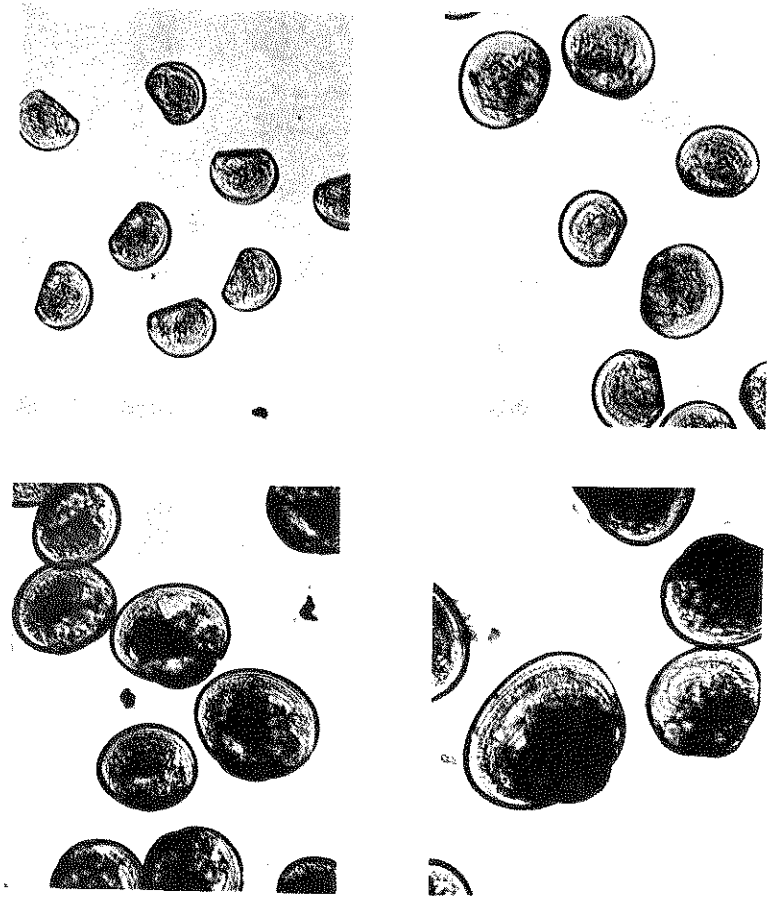

FIG. 9. Group photographs of different sizes of larvae of *Modiolus demissus*. Smallest individuals of the youngest group are approximately 105 μ long, and the largest of the oldest, approximately 290 μ.

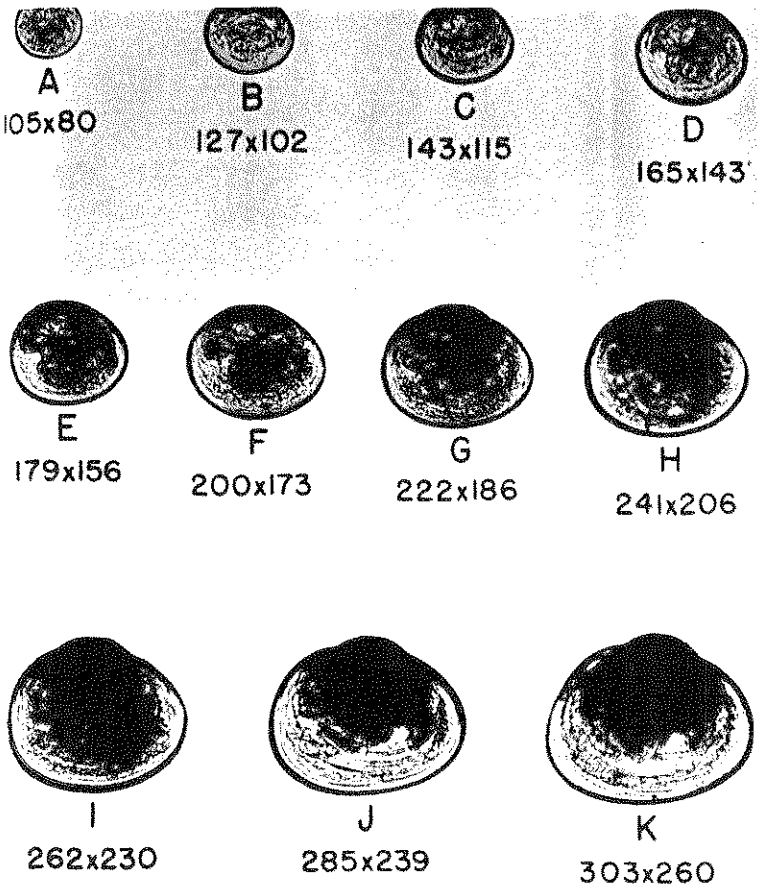

FIG. 10. Photographs of larvae of *Modiolus demissus* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

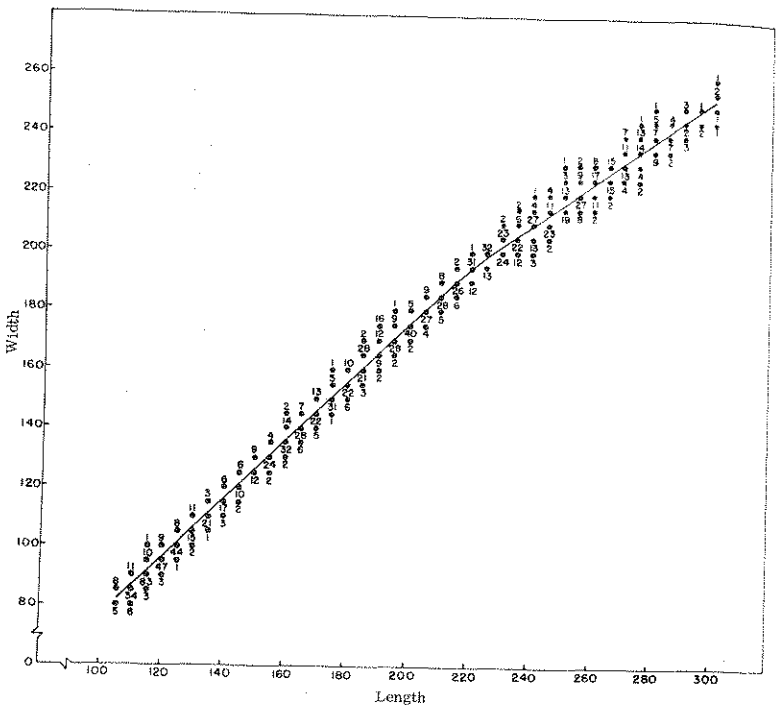

FIG. 11. Length-width relations of larvae of *Modiolus demissus* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

in *A. simplex* the digestive organs are located almost beneath the umbones, or much higher than in the larvae of *C. virginica* or *C. gigas*. Moreover, the umbo of *Anomia* points straight up from the hinge line, whereas the umbo of *Crassostrea* slants posteriorly.

The indentation known as the byssus notch, which, according to some authors, is a diagnostic feature of *Anomia* larvae, could not always be found in our specimens. Sometimes, however, this notch was seen in larvae only about 180 μ long. Even then, it was often only a thickening of the shell edge on the side opposite the foot (Figs. 12, 13).

An "eye" spot could not be found in all larvae, even those that were approaching metamorphosis. In other individuals, however, the "eye" was observed when they were relatively small, only about 135 μ long. Usually the "eye", composed of 4-6 united dark bodies, appeared in the larvae when they were approximately 160 μ long.

Metamorphosis of larvae of *Anomia*

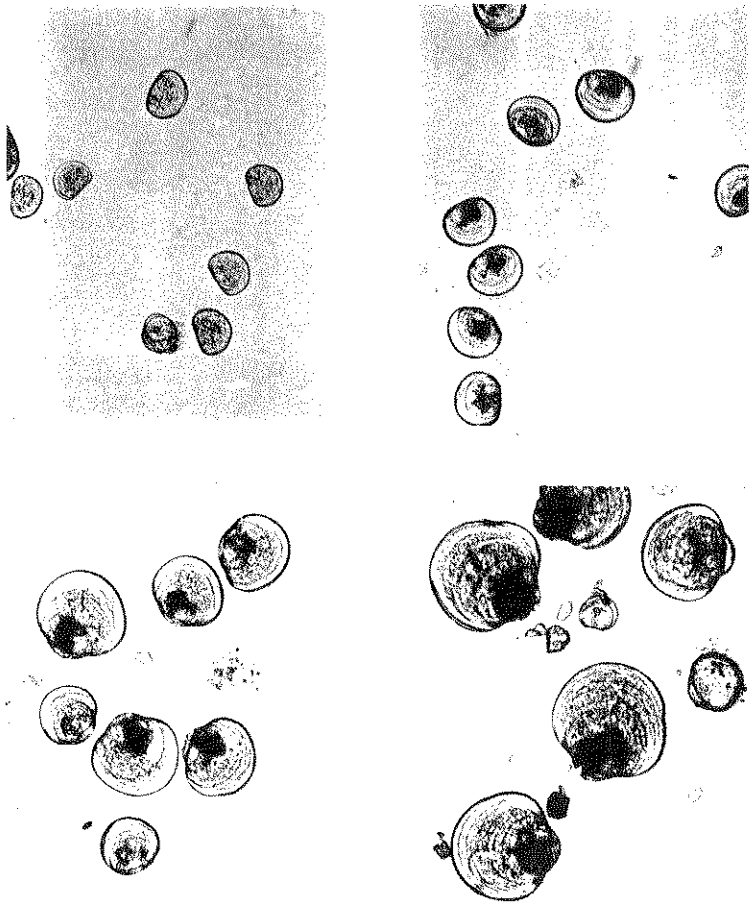

FIG. 12. Group photographs of different sizes of larvae of *Anomia simplex*. Smallest individuals of the youngest group are approximately 65 μ long, and the largest of the oldest, approximately 205 μ.

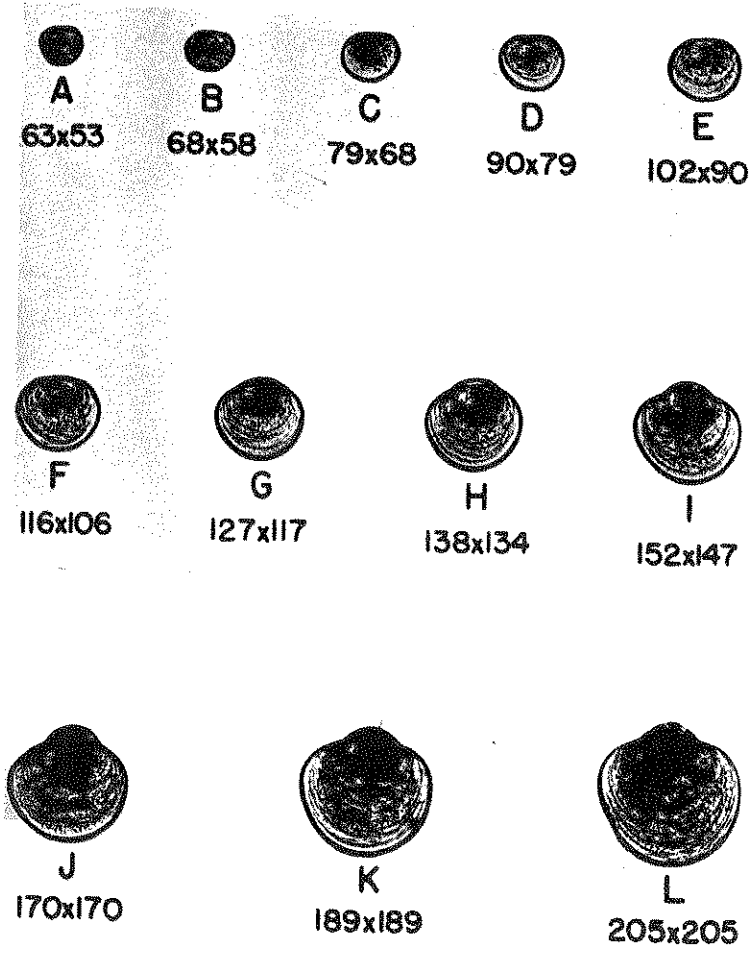

FIG. 13. Photographs of larvae of *Anomia simplex* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

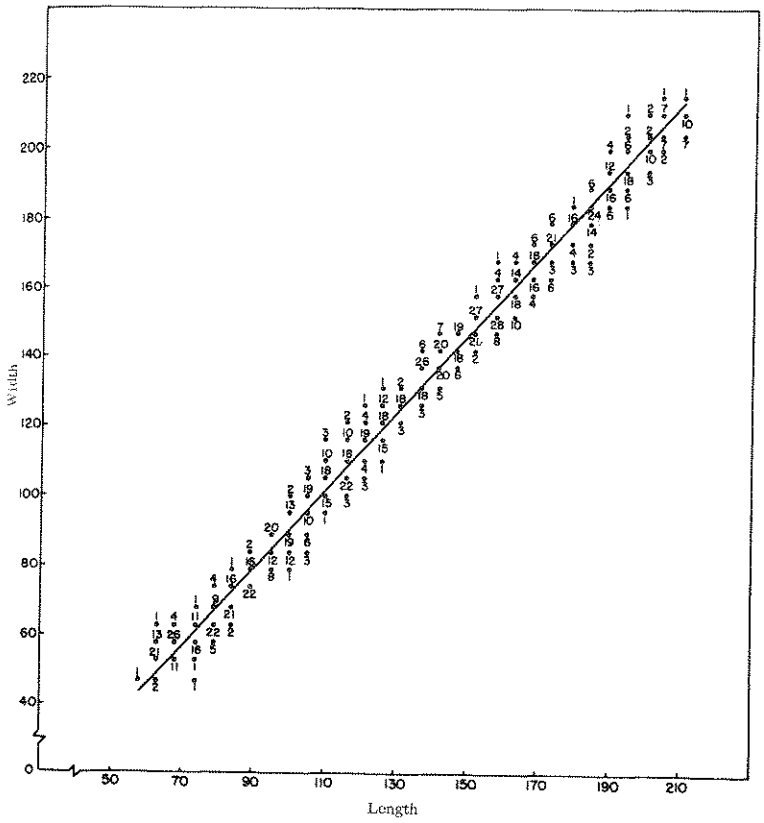

FIG. 14. Length-width relations of larvae of *Anomia simplex* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

simplex sometimes begins when the individuals are only slightly more than 180 μ long. Most metamorphosing larvae, however, measured between 195 and 210 μ; the largest swimming larvae were approximately 215 μ x 220 μ (Loosanoff & Davis, 1963).

Many larvae of *Anomia simplex* grown under laboratory conditions displayed an extremely interesting phenomenon called "partial metamorphosis" (Loosanoff, 1961). This condition is characterized by the disappearance of the velum but retention of a functional foot past the size at which metamorphosis and attachment normally occur. Even though some

of these individuals measured approximately 500 μ, they were apparently unable to attach to the substratum. These individuals had one pecularity in common, namely, the presence of a definite, narrow band on their shells. This band probably indicated the edge of the prodissoconch, or larval shell, and the beginning of the dissoconch, or post-larval shell. A similar abnormality may perhaps be observed in larvae of other species of the genus *Anomia* living under natural conditions, when some factors in their environment are unfavorable for metamorphosis.

5. *Aequipecten irradians* (Lamarck)

Aequipecten irradians, the common scallop of our Atlantic coast, sometimes identified as *Pecten irradians*, extends from Nova Scotia to the northern half of Florida and is also found along the coast of Texas. According to Clarke (1965) there are 3 distinct subspecies of this scallop; the type with which we worked, *A. i. irradians*, is found from Massachusetts to New Jersey.

Embryonic development of the scallop has been described by several students, including Costello *et al.* (1957), who offered a good review of the literature on this aspect of the scallop's life history. The more advanced stages, however, straight-hinge and later, have never been described in detail. Wells (1927), who grew the larvae of *Aequipecten irradians* to metamorphosis, gave only a brief description, but did include in his article a series of photomicrographs showing the different larval stages. His photographs were used later by several other authors.

The smallest normally developed straight-hinge larvae of *Aequipecten irradians* in our cultures measured 80 x 65 μ, and the largest, still unmetamorphosed, swimming individuals were approximately 200 μ long (Figs. 15, 16, 17). Some larvae metamorphosed when they were only about 175 μ long. In general, therefore, the average size of metamorphosing larvae of our scallops closely agrees with that given by Jørgensen (1946) for *Pecten striatus;* but our larvae were considerably smaller, by about 50 μ, than those of another European scallop, *P. opercularis*, which, according to Jørgensen, may be as long as 260 μ.

The larvae appear somewhat asymmetrical at all stages and this condition becomes more pronounced in the advanced stages of development (Fig. 16). A slight notch sometimes is visible at the base of the shells of larvae measuring 125 μ or more. The notch is located on the left, pointed end of the larval shell but generally is not pronounced and is difficult to photograph. This mark may be helpful, however, in identifying live or recently preserved larvae.

In general, scallop larvae are pale and are considerably lighter than most other forms with which we have worked (Loosanoff & Davis, 1963). The color darkens as the larvae grow older, although they still remain relatively transparent.

Most larvae measuring 170 μ or more have an "eye" spot. In larger larvae, however, this spot is difficult to find, possibly because the "eye" is not too well defined and because the shells become thicker. A small, inconspicuous "eye" was noticed in some larvae only 150 μ long.

6. *Ostrea edulis* Linnaeus

We introduced this European oyster in American waters because it propagates at a considerably lower temperature than our eastern oyster, *Crassostrea virginica*. *Ostrea edulis* can develop gonads and spawn in the waters of our northeastern states, such as Maine, and also along the Pacific coast where normally the water is too cold for the successful propagation of *C. virginica* (Loosanoff, 1951).

Since its introduction in the fall of 1949, *Ostrea edulis* has spawned naturally in the waters of New England and has become firmly established in Maine (Loosanoff, 1955, 1962). The set of *O. edulis* grown from selected parents

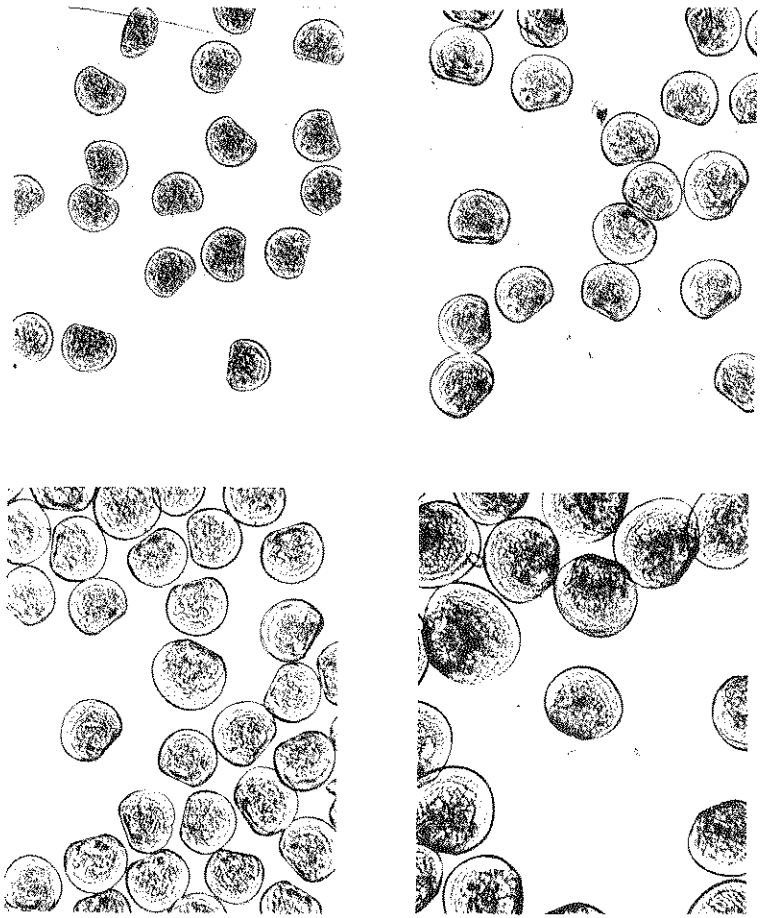

FIG. 15. Group photographs of different sizes of larvae of *Aequipecten irradians*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 180 μ.

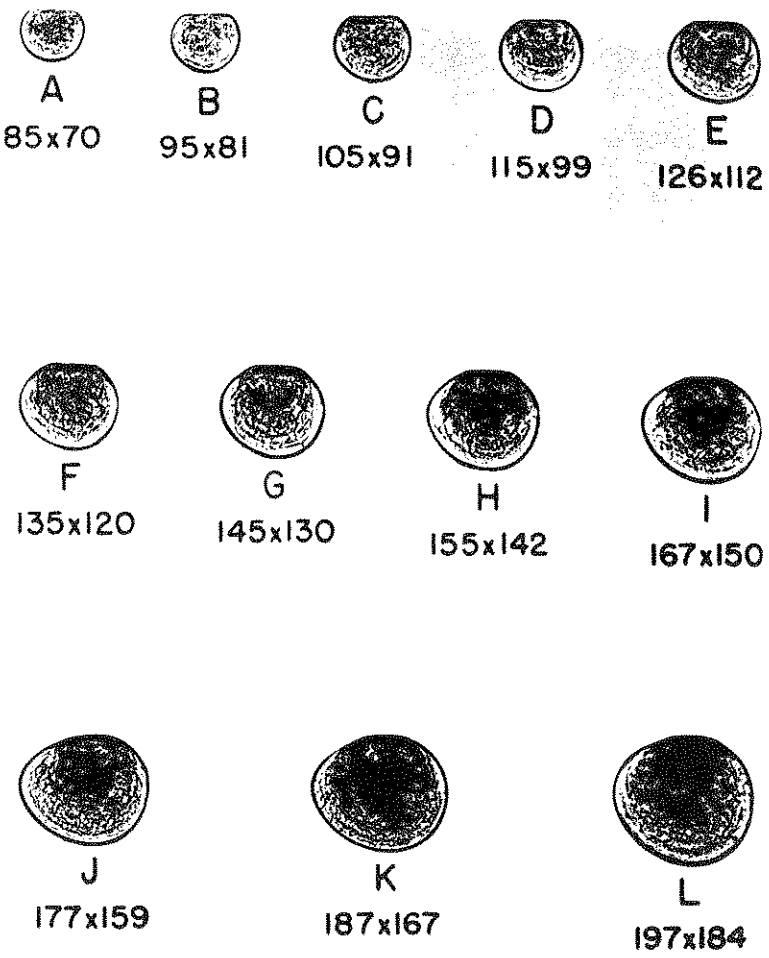

FIG. 16. Photographs of larvae of *Acquipecten irradians* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

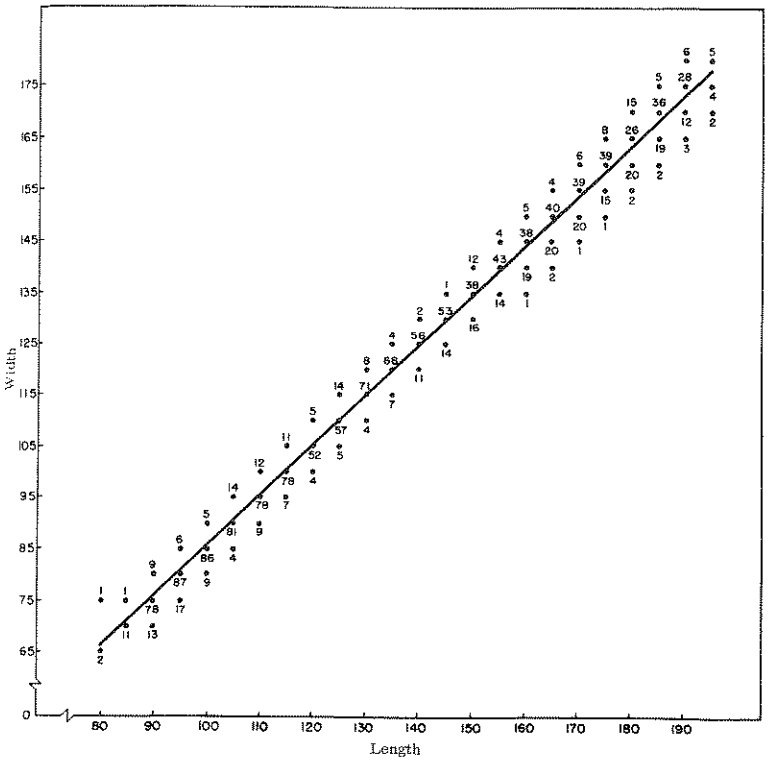

FIG. 17. Length-width relations of larvae of *Acquipecten irradians* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

at the Milford Laboratory was planted in several areas of our Pacific coast. Where it was protected and properly cared for the set grew well. The descendants of the European oysters grew unusually fast in California waters, reaching approximately 4-1/4 inches in about 2 years. They also developed gonads and released larvae in a normal manner. Larvae-bearing *O. edulis* were observed in Tomales Bay, California, in the middle of April.

Those interested in propagation of *Ostrea edulis* should consult reviews by a number of authors, including Orton (1937), Korringa (1941), Walne (1956), Yonge (1960) and Loosanoff & Davis (1963).

Ostrea edulis is a larviparous species which discharges its half-grown larvae into the surrounding water, 6-10 days after spawning, in a process known as

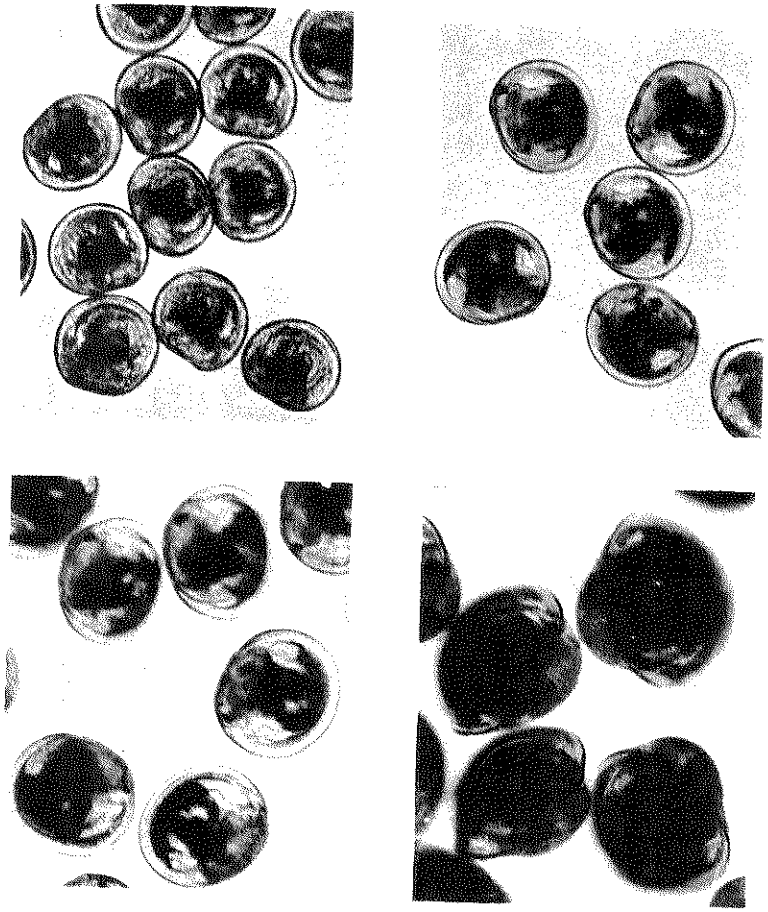

FIG. 18. Group photographs of different sizes of larvae of *Ostrea edulis*. Smallest individuals of the youngest group are approximately 175 μ long, and the largest of the oldest, approximately 300 μ.

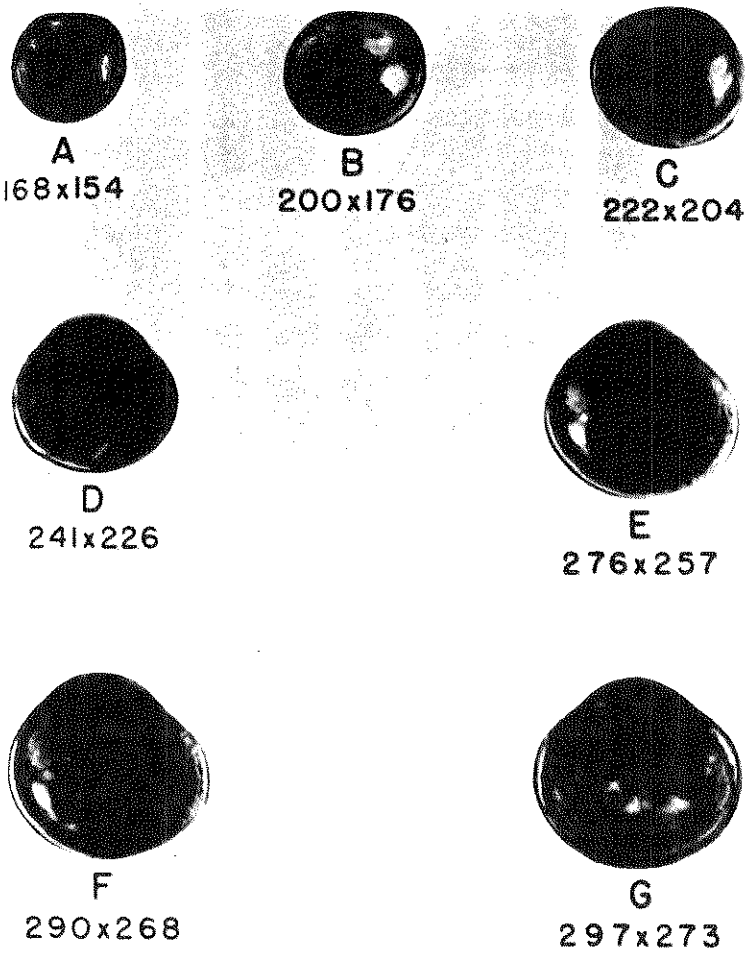

FIG. 19. Photographs of larvae of *Ostrea edulis* from the time they are released in swarming by the parents (A) until the time of metamorphosis (G). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

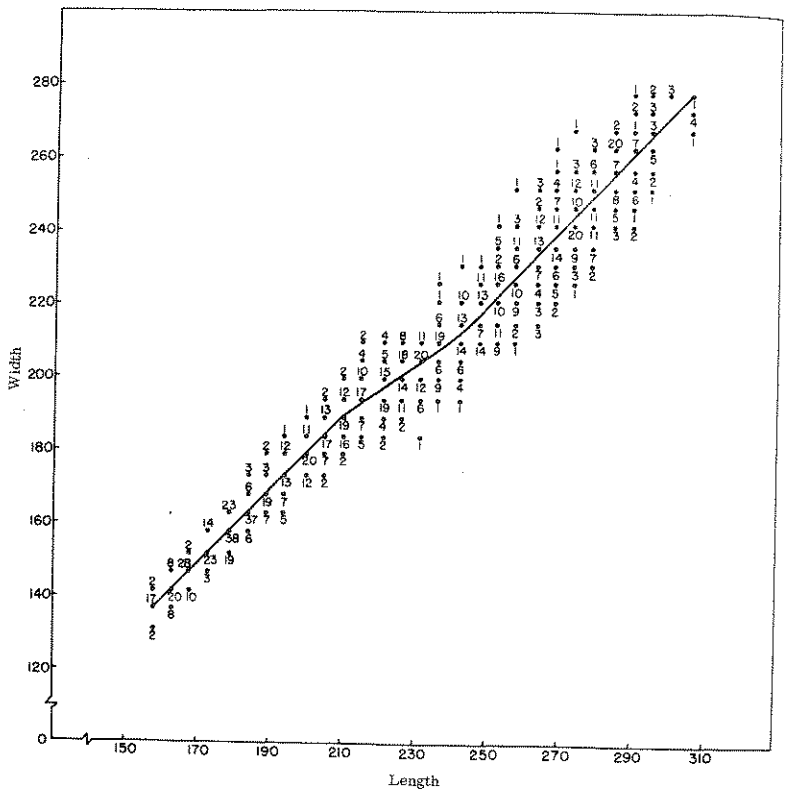

FIG. 20. Length-width relations of larvae of *Ostrea edulis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

swarming. Until then the fertilized eggs and, later, the larvae are retained in the mantle cavity of the mother oyster. The size of recently released larvae varies considerably even when they are released by the same female at the same swarming (Loosanoff & Davis, 1963). One female, for example, released larvae that ranged from 142 μ to 199 μ in length. The modal size of the larvae released by 6 separately kept females was about 184 μ. We consider, however, that larvae smaller than 160 μ in length are probably discharged prematurely. Larvae over 160 μ are, apparently, sufficiently developed to grow to metamorphosis without difficulty (Figs. 18, 19, 20).

Even recently released larvae of *Ostrea edulis* are considerably darker than those of most other species cultured at our laboratory, with the possible exception of the larvae of *O. lurida*, a close relative of the European oyster. As the size of the larvae increases, their shells become thicker and their color becomes darker, almost completely obscuring the internal organs. Soon after the larvae reach approximately 210 μ the umbo becomes more prominent, and at about 240 μ it is well defined (Fig. 19). Most of the larvae develop a prominently pigmented "eye" spot at 250 μ which, however, cannot be found easily in preserved specimens.

Setting occurred most commonly when the individuals were between 280 μ and 300 μ long. Cole (1936) came to the same conclusions. Nevertheless, we have never seen larvae as large as 350 μ observed by Cole in his cultures. Imai *et al.* (1953a) found that none of the larvae of *Ostrea edulis*, which they cultured under controlled conditions, reached 300 μ. In this respect we are in close agreement with our Japanese colleagues. Walne (1956) also reported that most of the larvae of *O. edulis*, which he reared, metamorphosed before reaching 300 μ.

As can be seen from the length-width relationship in Fig. 20, the median line displays a depression which begins at about 215 μ and persists until the length is approximately 255 μ. A somewhat similar depression is noticed in the median line of the related species, *Ostrea lurida* (Fig. 23).

7. *Ostrea lurida* Carpenter

Ostrea lurida, the native oyster of our Pacific coast, is found from Alaska to lower California. It is a common intertidal form which several decades ago was of considerable commercial importance. It is a close relative of *O. edulis*, the flat European oyster, but is much smaller.

Regardless of the difference in sizes of fully grown individuals of the 2 species, the average length of the normal larvae of *Ostrea lurida* at the time of swarming is about 185 μ, practically the same as that of the larvae of *O. edulis* (Loosanoff & Davis, 1963). Observations of other workers on the sizes of recently discharged larvae of *O. lurida* closely agree with ours (Hori, 1933; Hopkins, 1937; Imai *et al.*, 1954). Relatively small larvae measuring only 160 x 150 μ released in some swarmings at our laboratory (Figs. 21, 22, 23) were apparently immature because they were unable to withdraw the velum completely. Under favorable conditions some of these larvae may survive and finally reach metamorphosis.

Larvae become darker as they grow. Soon after they reach a length of about 205 μ the umbo region becomes more prominent, and larvae measuring 275 μ acquire a somewhat triangular outline (Fig. 22). The length becomes greater than the width as size increases, and at time of setting may exceed the latter by about 20 μ. A comparison of Figs. 19 and 22 shows that larvae of the same sizes of *Ostrea edulis* and *O. lurida* closely resemble each other.

The most common setting size of the larvae grown in our laboratory cultures was about 300 μ, which is not too different from the setting sizes of either the larvae of *Ostrea edulis* or, as we will show later, the larvae of the genus *Crassostrea*. Free-swimming larvae of *O. lurida* measuring more than 310 μ were uncommon and larvae somewhat larger, measuring 325 μ, were rare (Fig. 23). In this respect we agree with Imai *et al.* (1954) who reported that some of their largest larvae measured 328 μ.

As mentioned in the discussion of *Ostrea edulis*, the median line of the length-width relationships of the larvae of *O. lurida* shows a depression in its central portion (Fig. 23).

8. *Crassostrea virginica* (Gmelin)

The American, or eastern oyster, *Crassostrea virginica* (formerly *Ostrea virginica*), is the chief commercial

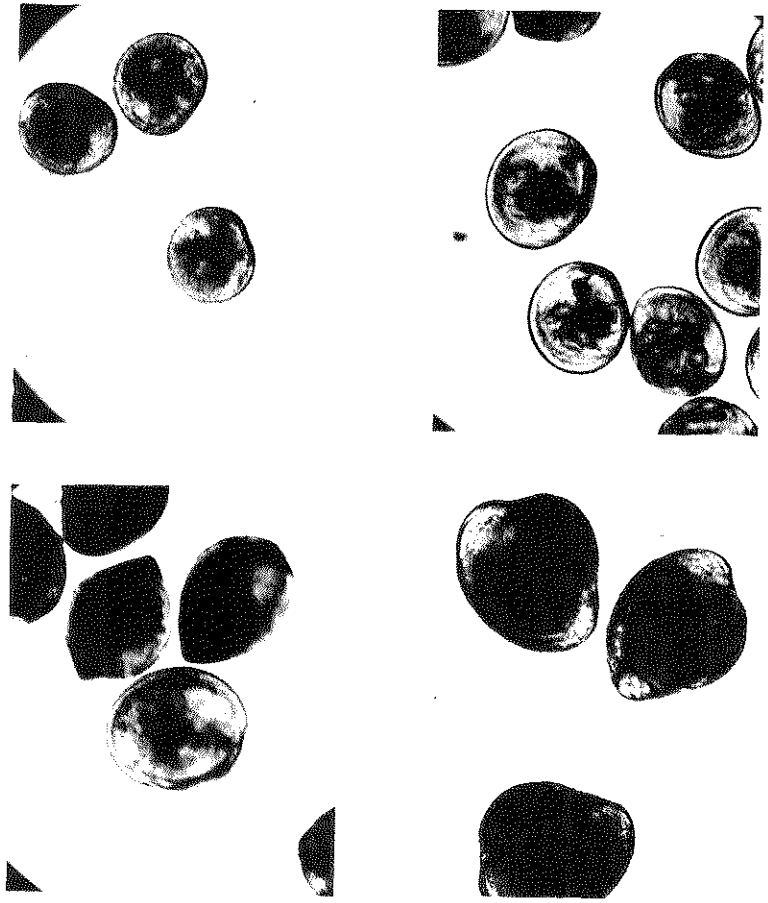

FIG. 21. Group photographs of different sizes of larvae of *Ostrea lurida*. Smallest individuals of the youngest group are approximately 165 μ long, and the largest of the oldest, approximately 295 μ.

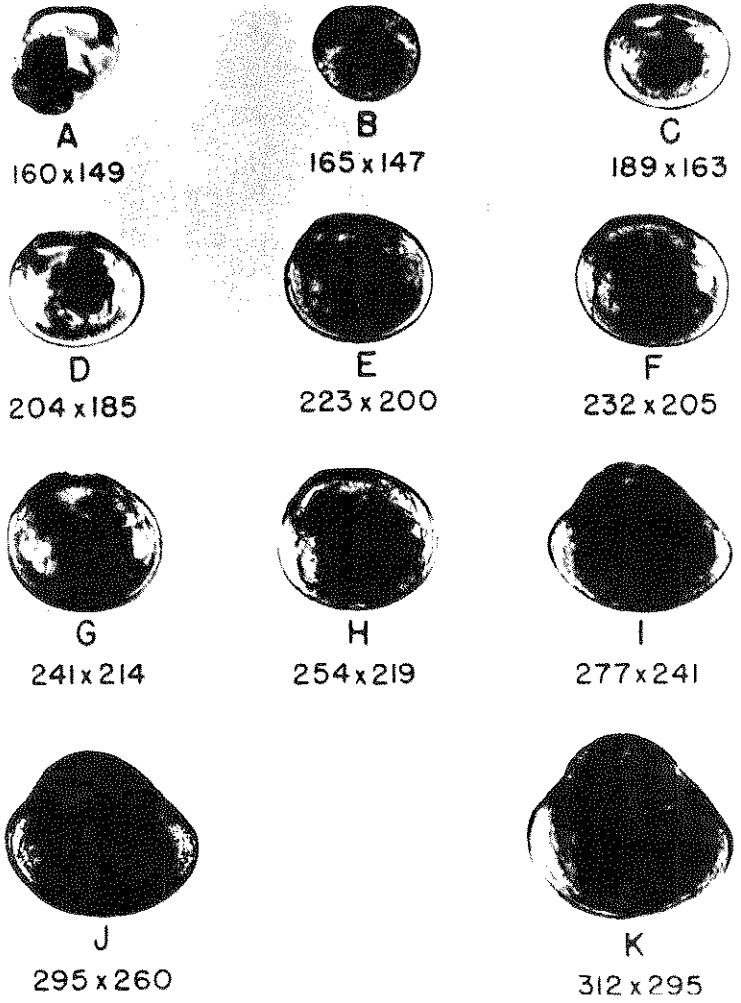

FIG. 22. Photographs of larvae of *Ostrea lurida* from the time they are released in swarming by the parents (A) until the time of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

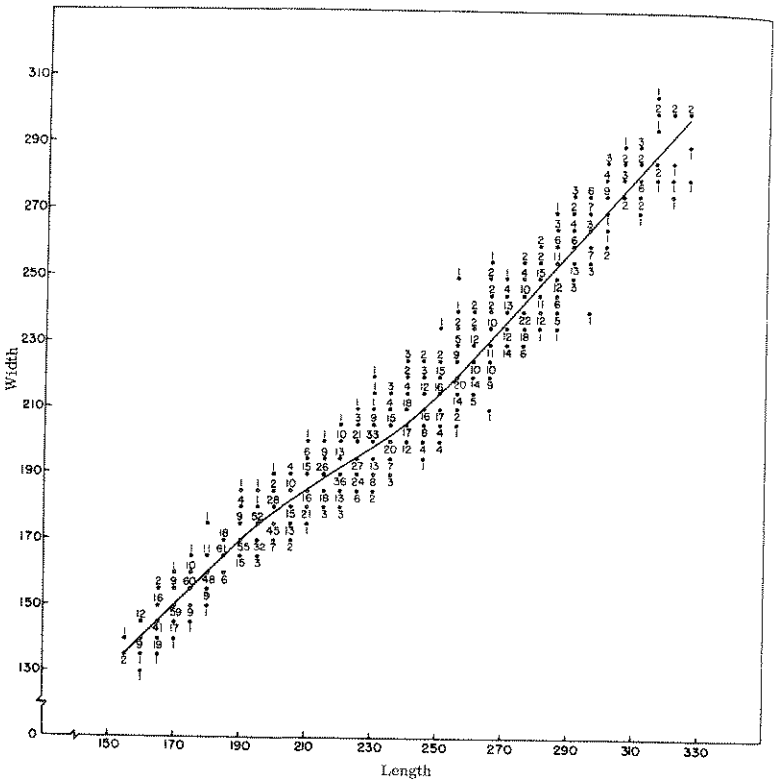

FIG. 23. Length-width relations of larvae of *Ostrea lurida* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

mollusk of our Atlantic and Gulf coasts. It is found in considerable numbers from Massachusetts south along the eastern coast of the United States and also along the Gulf of Mexico. Small groups of this oyster still live in the waters of Maine and New Hampshire. They are also cultivated in Canadian waters, mainly in the southern parts of the Gulf of St. Lawrence. Small quantities are regularly transplanted to several bays of our Pacific coast.

The larvae of *Crassostrea virginica* have been described by many investigators, including Brooks (1880), Stafford (1912), J. Nelson (1909), Churchill (1920), T. Nelson (1921), Wells (1927), Prytherch (1924), Sullivan (1948) and Carriker

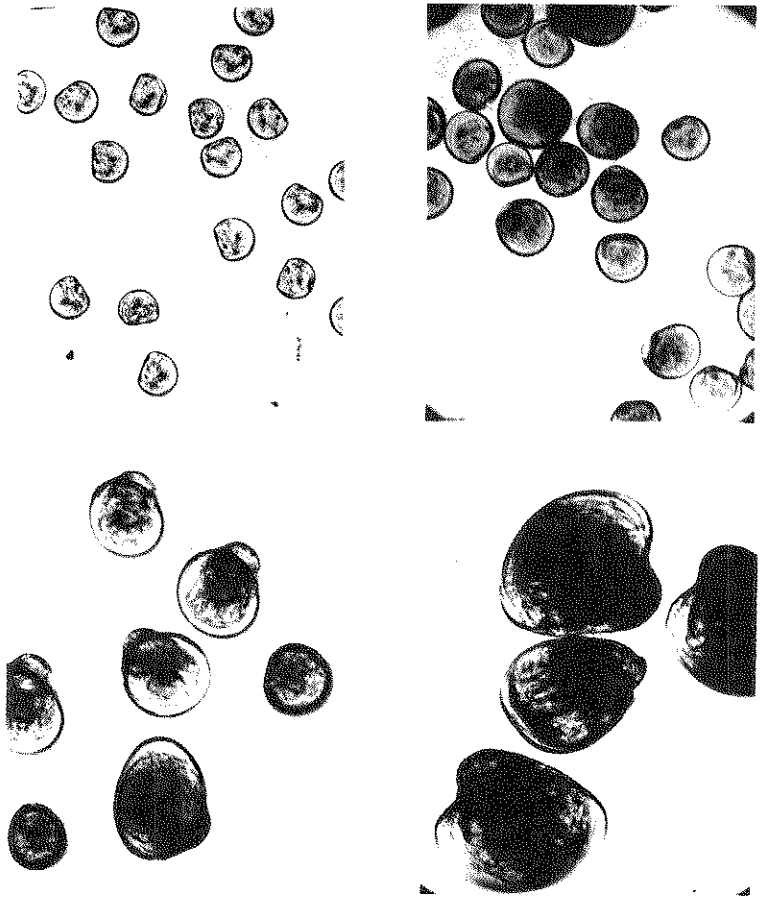

FIG. 24. Group photographs of different sizes of larvae of *Crassostrea virginica*. Smallest individuals of the youngest group are approximately 72 μ long, and the largest of the oldest, approximately 305 μ.

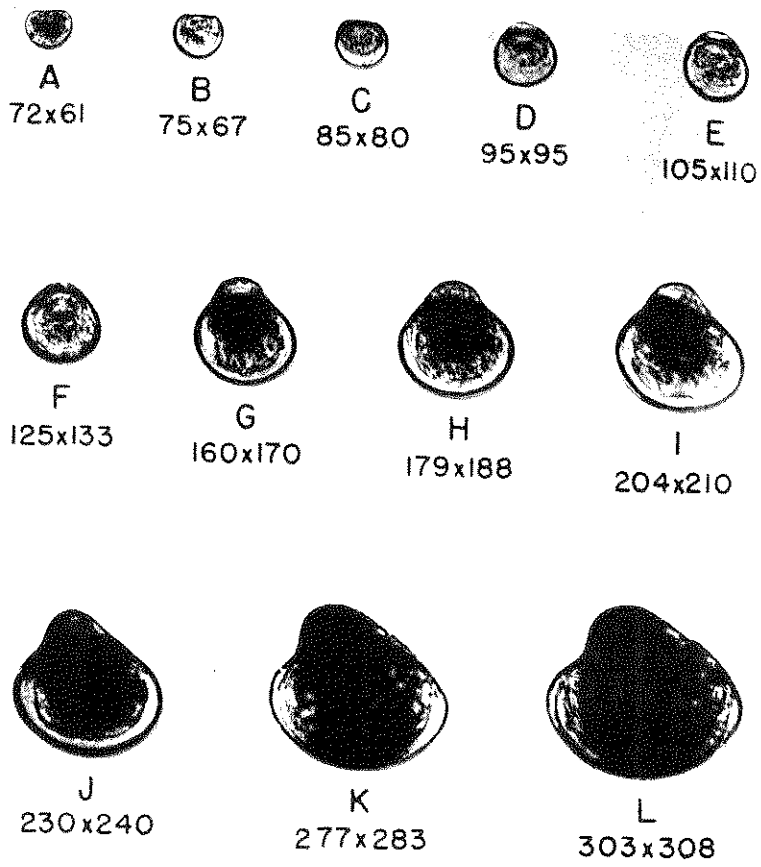

FIG. 25. Photographs of larvae of *Crassostrea virginica* in different stages of development from straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

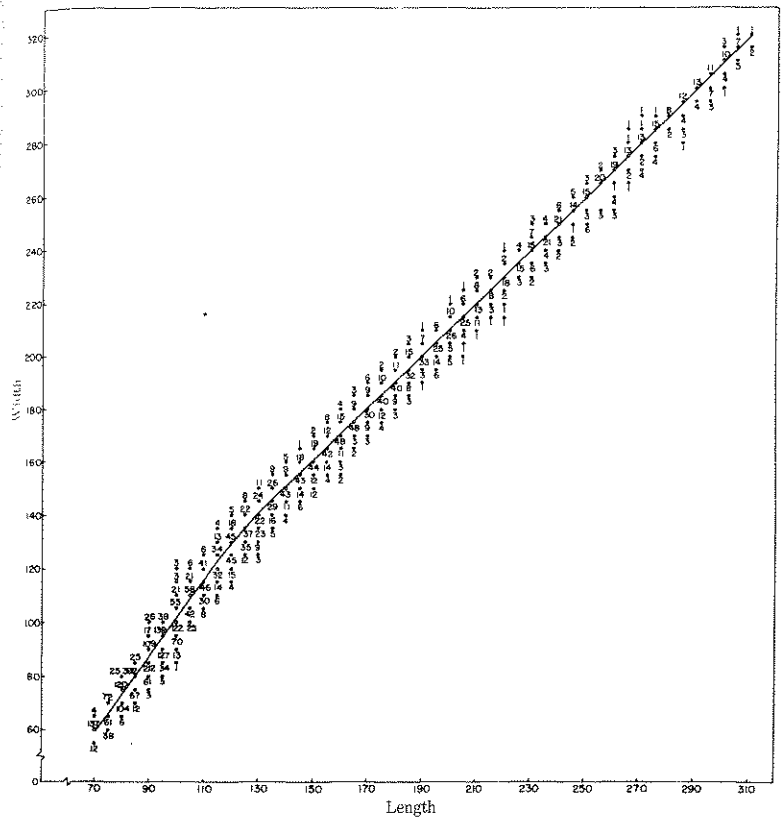

FIG. 26. Length-width relations of larvae of *Crassostrea virginica* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

(1951). Several of these authors offered drawings; J. Nelson (1909) was the first to publish photomicrographs. Later, Wells (1927) and, especially, Sullivan (1948) offered good series of photomicrographs of larvae of different sizes. The larvae shown in the photographs of other investigators, however, were mostly either in straight-hinge stage or near metamorphosis. Yonge (1960) included in his book a series of photomicrographs identical to those in our Fig. 25, which we sent him.

Considerable information on many aspects of the physiology, ecology and growth of the larvae of *Crassostrea*

virginica was given by Loosanoff & Davis (1963). Their observations show that the smallest normal straight-hinge larvae of *C. virginica*, grown under laboratory conditions, measure about 68 x 55 μ. Usually, however, these larvae are about 75 x 67 μ (Figs. 24, 25, 26). Until the larvae are about 85 μ, their length is normally 5-10 μ greater than their width. The length and width become almost identical, however, at approximately 100 μ. After that stage the increase in width is somewhat more rapid than in length.

The length-width relationship of oyster larvae is almost linear, with the exception of the part representing the length between 105 μ and 130 μ, where the line curves slightly (Fig. 26). It is shown later that *C. gigas*, another member of the genus *Crassostrea*, shows the same curvature in its length-width median line (Fig. 29).

In general, the color of both laboratory-grown and plankton-collected larvae changes with length from golden brown to deeper brown, to almost black when the larvae approach metamorphosis. An umbo begins to form when the larvae are between 85 and 90 μ long and becomes increasingly prominent as they grow larger. The umbo is one of the most pronounced characters of *Crassostrea virginica* larvae (Figs. 24, 25). The pronounced asymmetry of the umbones is an important feature of all larvae that are more than 115 μ long. The asymmetry is due to the much faster development of the left umbo, which eventually becomes so pronounced that it almost obscures the right umbo.

The majority of our laboratory-grown larvae began to metamorphose at lengths between 275 and 315 μ. Some larvae as long as 355 μ were still swimming actively. These observations are in agreement with those on sizes of larvae in plankton samples collected in Long Island Sound during the 30-year period of our observations on spawning and setting of oysters, and also with the measurements of Prytherch (1924), who has done much research on setting of oysters in the same area. The measurements given by Sullivan (1948) also resemble ours, whereas the measurements of Stafford (1912), who gave the maximum size of mature larvae as between 345 and 393 μ, are much greater. Moreover, we disagree with Stafford's measurements of the larvae of smaller sizes, especially within the length range from 105 to 210 μ. In this range Stafford's larvae measure, as a rule, much more in length than in width. This relation does not hold generally (Fig. 25).

9. *Crassostrea gigas* (Thunberg)

This oyster, formerly known as *Ostrea gigas*, is the most important commercial mollusk of Japanese waters. It was introduced to this country around the turn of the century and is now grown in the waters of Washington and California and to a limited extent in Oregon. It is also cultivated in British Columbia.

Because of the comparatively low water temperatures along our Pacific coast, *Crassostrea gigas* does not reproduce regularly there. As a result, the industry depends mainly upon seed oysters imported every spring from Japan. Nevertheless, these oysters spawn occasionally in some comparatively shallow, well-protected waters, and at times their larvae are abundant in plankton. Sets of commercial importance have occurred in certain areas.

The larvae of *Crassostrea gigas* have been studied extensively by many Japanese workers. These studies were reviewed by Cahn (1950) and Imai *et al.* (1950b). Our studies of larvae of *C. gigas* (Figs. 27, 28, 29) show that they are actually identical in size and appearance to the larvae of *C. virginica*. The length of the youngest well-formed straight-hinge larvae was approximately 70 μ, and the size at metamorphosis was near 300 μ. Regardless of the similarity of the 2 species, as far as size and shape of larvae were concerned, efforts to cross these 2 forms failed (Davis, 1950; Imai *et al.*, 1950b). Our observations on the sizes of *C. gigas* closely agree with those of our Japanese

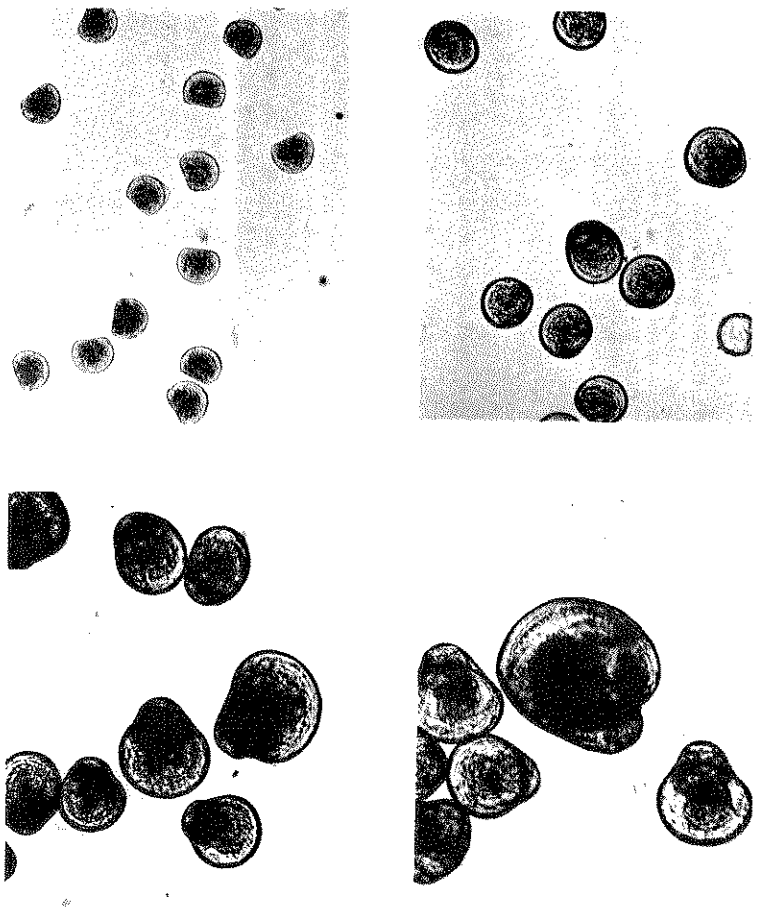

FIG. 27. Group photographs of different sizes of larvae of *Crassostrea gigas*. Smallest individuals of the youngest group are approximately 70 μ long, and the largest of the oldest, approximately 285 μ.

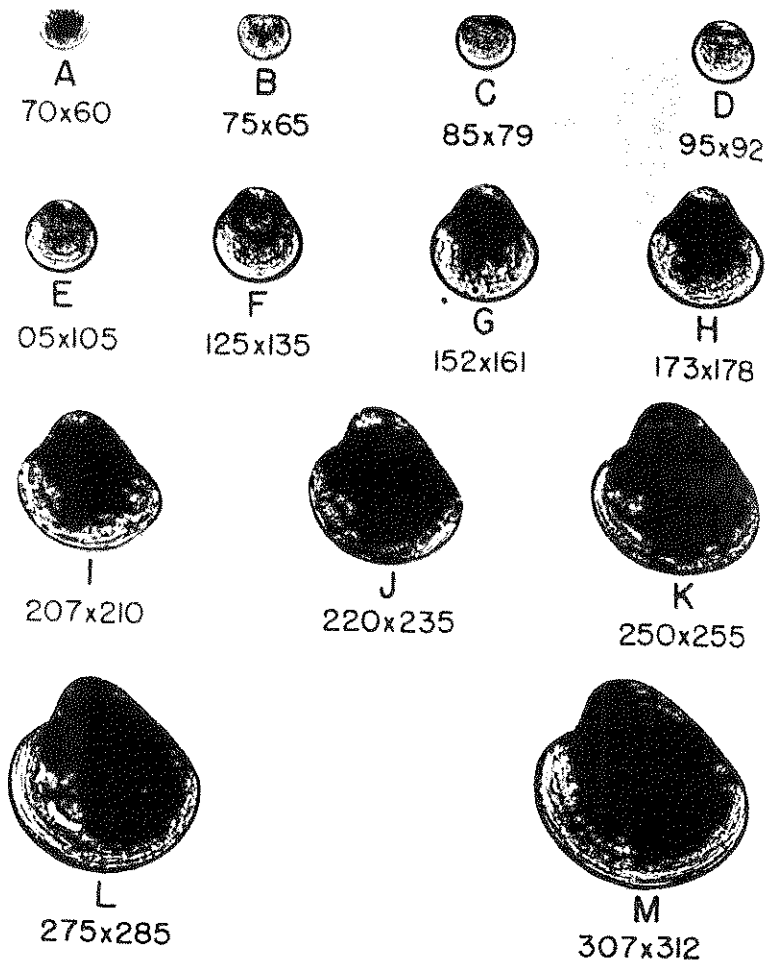

FIG. 28. Photographs of larvae of *Crassostrea gigas* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (M). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

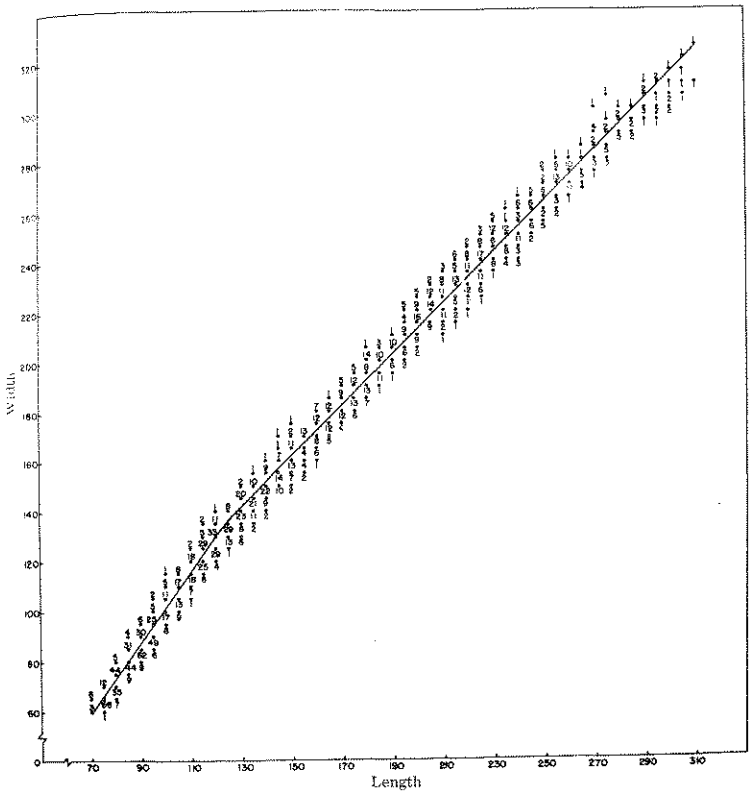

FIG. 29. Length-width relations of larvae of *Crassostrea gigas* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

colleagues, including Hori & Kusakabe (1926) and Imai et al. (1950b).

Tanaka (1954), from studies of *Crassostrea gigas* from widely separated oyster beds of Japan, concluded that the length of the prodissoconch of this oyster at the time of metamorphosis varied with locality. It was smaller in the northern areas and increased along the southern parts of the Japanese coast.

10. *Mercenaria* (=*Venus*) *mercenaria* (Linnaeus)

One of the most important commercial clams of our Atlantic coast, *Mercenaria mercenaria*, is known by many names, including Round clam, Hardshell clam and quahog. It is found from the

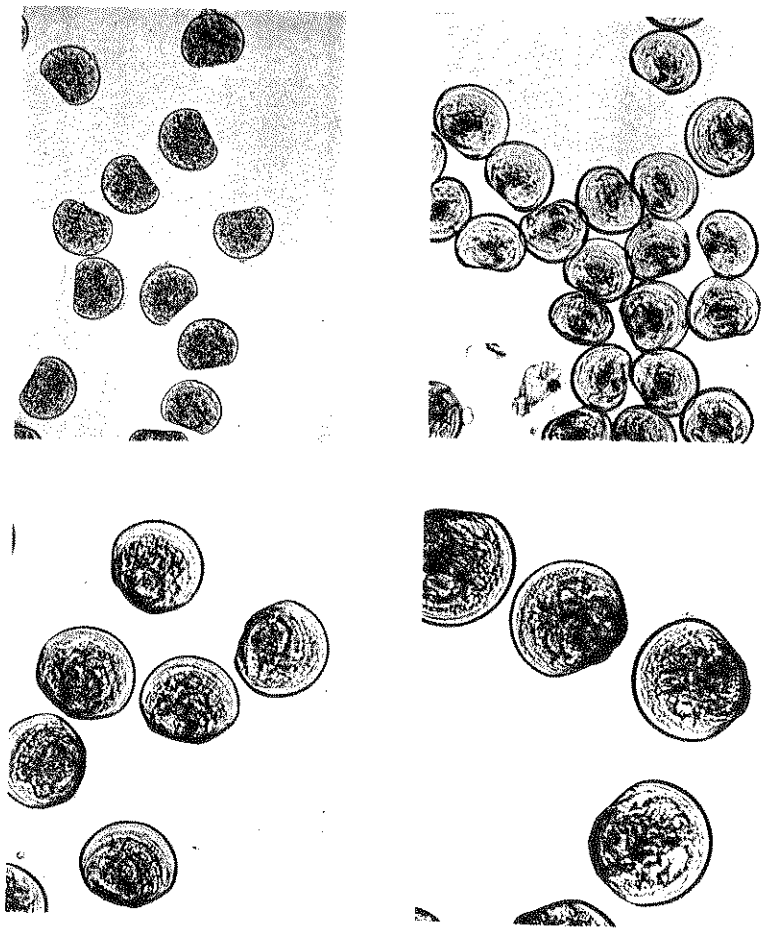

FIG. 30. Group photographs of different sizes of larvae of *Mercenaria mercenaria*. Smallest individuals of the youngest group are approximately 101 μ long, and the largest of the oldest, approximately 210 μ.

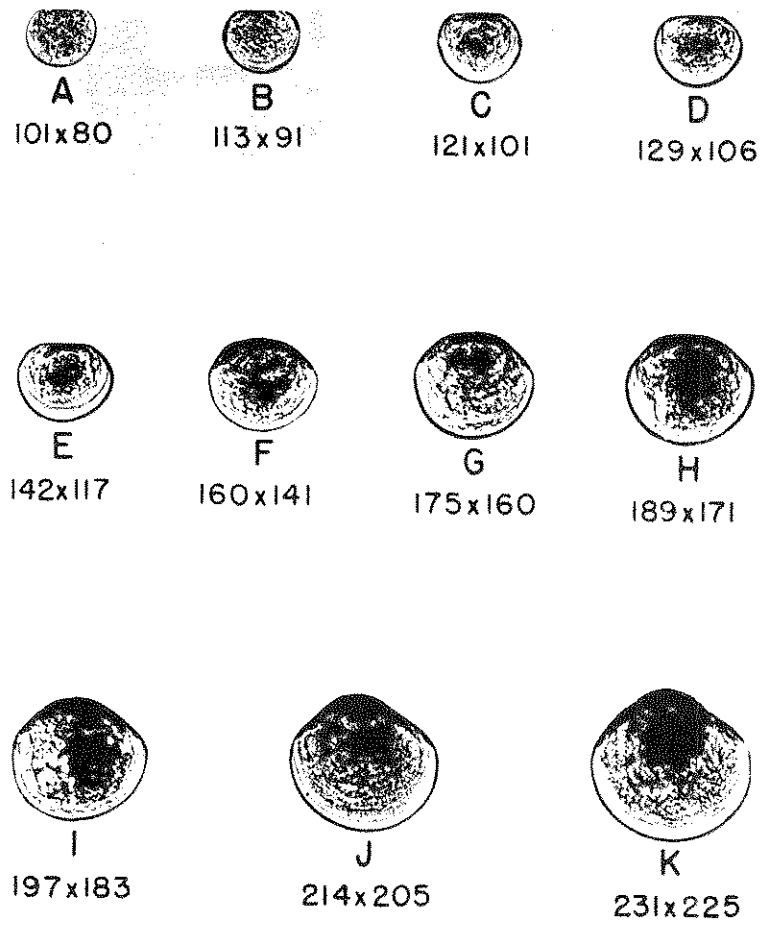

FIG. 31. Photographs of larvae of *Mercenaria mercenaria* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

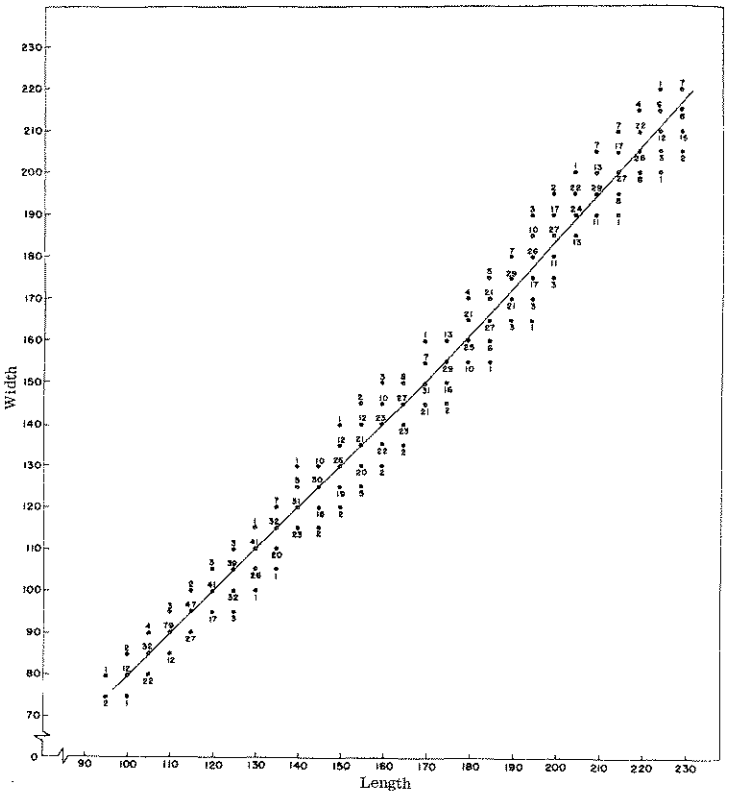

FIG. 32. Length-width relations of larvae of *Mercenaria mercenaria* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Gulf of St. Lawrence to Texas and is especially common south of Cape Cod.

The larvae of this clam have been described and illustrated by several investigators, including Stafford (1912), Belding (1912), Wells (1927), Sullivan (1948) and Carriker (1961). Until the larvae could be cultured from known parents under laboratory conditions, however, there was no assurance that the descriptions were really of this species. The first information of this nature was offered by Loosanoff & Davis (1950), who included in their article photomicrographs and measurements of the larvae from their early straight-hinge stage to metamorphosis. Later, many other investigators, including Turner & George (1955) and Carriker (1961), cultured the larvae successfully. Because of the numerous recent studies of larvae of this species no uncertainty exists as to their general appearance and dimensions (Loosanoff & Davis, 1963).

In our laboratory cultures only a few straight-hinge larvae were less than 100 μ long and most fully formed, straight-hinge veligers were approximately 105 x 80 μ (Figs. 30, 31, 32). Carriker (1961) also recorded comparatively small larvae, some of which were only 98 x 78 μ.

An umbo becomes visible when the larvae reach the length of approximately 125-130 μ (Figs. 30, 31). As the larvae continue to grow, their umbones become better defined but they are never as prominent as in such other bivalves as *Anomia*, *Crassostrea* and *Teredo*. Some larvae begin to metamorphose when they are only about 170 μ long. The most common length at metamorphosis is between 200 and 215 μ. Larvae 230 μ long or longer are uncommon. At metamorphosis, length is only 5-15 μ greater than width. Carriker (1961) reported that the largest clam veligers of Little Egg Harbor, New Jersey, ranged from 182-198 μ; thus, they metamorphosed at the same size as the larvae of *Mercenaria mercenaria* of Long Island Sound.

We disagree with Stafford's (1912) report indicating that the larvae of *Mercenaria mercenaria* grow to the size of 448 μ before setting. Sullivan (1948) also described larvae of a species other than *M. mercenaria*, because she reported the maximum size of the larvae as 320 μ, which is considerably larger than the size of fully mature larvae of this species. Sullivan later explained (personal communication) that she had confused larvae of *M. mercenaria* with those of another bivalve. Jørgensen (1946) found that metamorphosing veligers of the closely related species, *Venus gallina*, vary from 210-225 μ in length, a size similar to ours.

More recently, Ansell (1961, 1962) gave a comprehensive account of the appearance and functional morphology of the closely related species, *Venus gallina* (=*V. striatula*). According to Ansell the larvae of this species metamorphosed at approximately the same size as the larvae of *Mercenaria mercenaria*. Ansell cultured the larvae from known parents and under controlled conditions.

We have grown the larvae of *Mercenaria mercenaria* from parents from widely separated geographical areas, but size of larvae at metamorphosis did not differ in different groups. Moreover, the larvae reared at 5 different temperatures metamorphosed at about the same size.

11. *Mercenaria* (=*Venus*) *campechiensis* (Gmelin)

This clam, known as the southern quahog and closely related to *Mercenaria mercenaria*, is found on the Atlantic coast from Chesapeake Bay to Florida. Large numbers are also found in the Gulf of Mexico.

The larvae used in our studies originated from parents brought from the sandy beaches of Apalachicola, Florida, in the Gulf of Mexico. All stages of the larvae were identical to similar stages of *Mercenaria mercenaria* (Figs. 33, 34, 35). The lengths of early straight-hinge veligers ranged from 100-110 μ. Metamorphosis occurred most commonly within the length range of 175-215 μ.

As was already reported (Loosanoff & Davis, 1963), the spawning behavior of these 2 species was also virtually the same. Their larvae, when grown under identical conditions, including temperature, grew at the same rate and began to metamorphose at the same time and the same size. These observations contradict the conclusion (Thorson, 1950) that the eggs and larvae of the southern species, when grown at a certain temperature, develop more slowly than those of the northern species of the same genus. Reciprocal crosses of the 2 species produced viable larvae which grew to metamorphosis. These hybrids were fertile and their larvae were

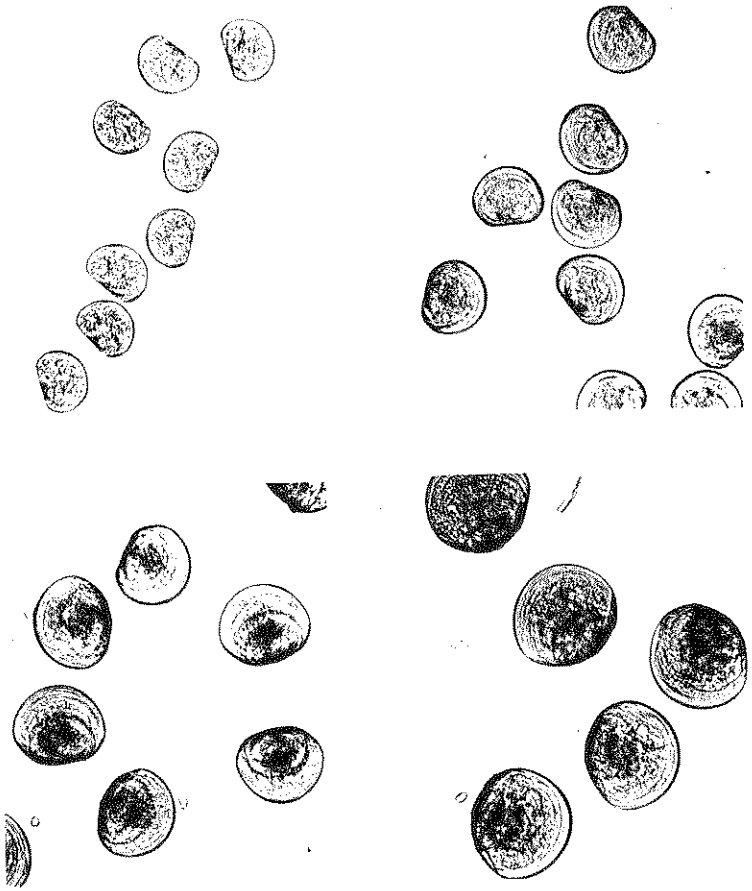

FIG. 33. Group photographs of different sizes of larvae of *Mercenaria campechiensis*. Small-individuals of the youngest group are approximately 100 μ long, and the largest of the oldest, approximately 185 μ.

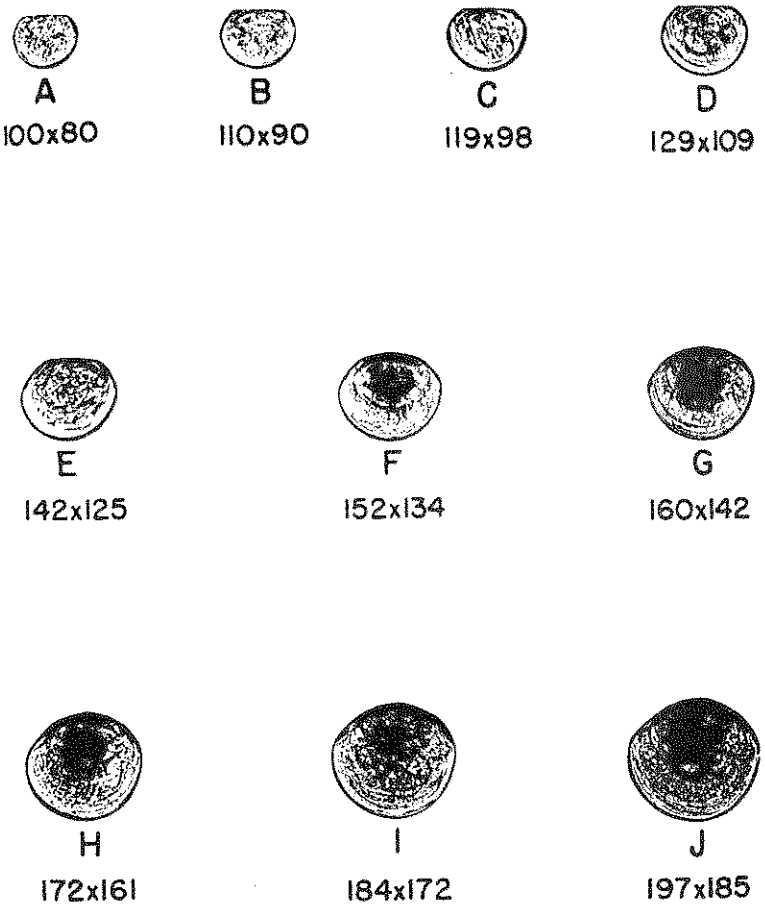

FIG. 34. Photographs of larvae of *Mercenaria campechiensis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (J). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

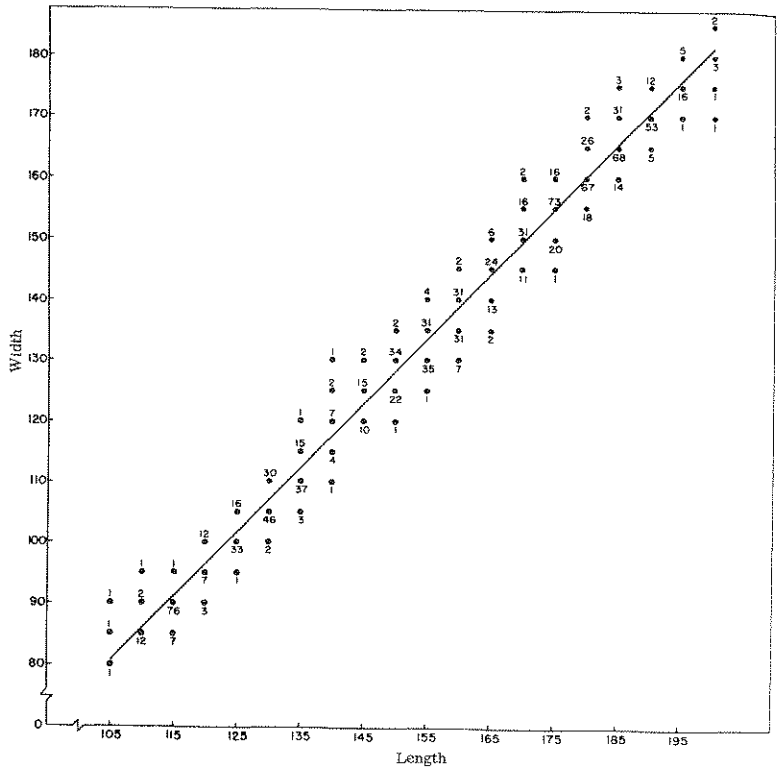

FIG. 35. Length-width relations of larvae of *Mercenaria campechiensis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

reared to adult stage.

We have seen no publications describing the dimensions or shapes of larvae of *Mercenaria campechiensis* or any aspects of the behavior.

12. *Mulinia lateralis* (Say)

This little clam occurs along the Atlantic coast from Canada to Mexico and is known by a variety of names, including Duck clam, Little Surf clam, Coot clam and sometimes Small Mactra. In some years *Mulinia lateralis* is common in Long Island Sound, both below and above low-water mark. They are usually found in the first half-inch of the bottom.

Larvae of this clam are extremely numerous in plankton samples, especially during the latter part of the summer. The smallest straight-hinge larva, a single animal, recorded in the cul-

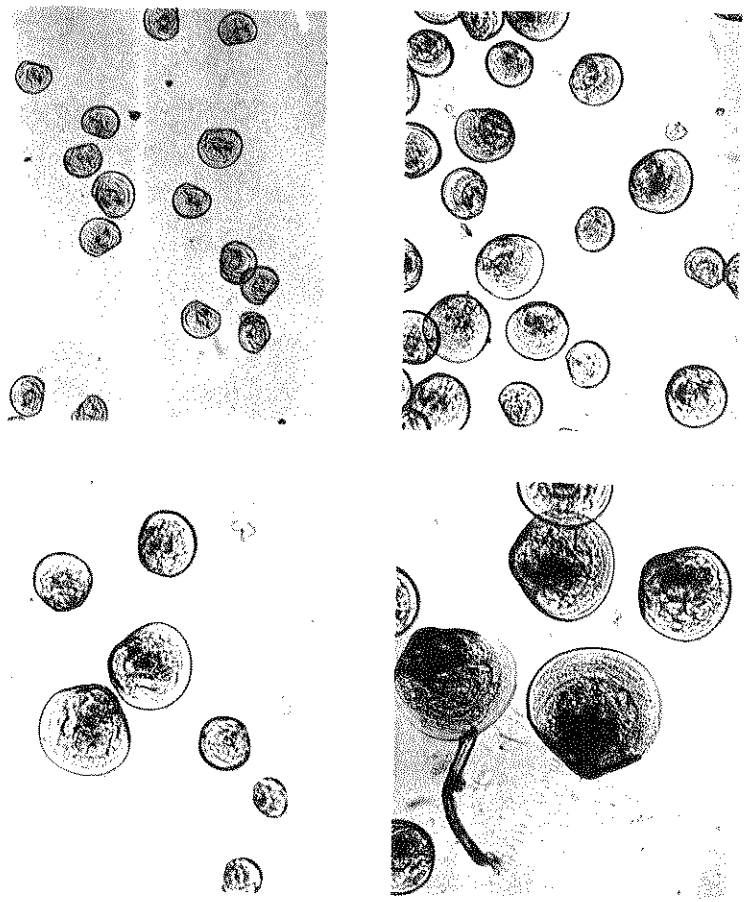

FIG. 36. Group photographs of different sizes of larvae of *Mulinia lateralis*. Smallest individuals of the youngest group are approximately 60 μ long, and the largest of the oldest, approximately 225 μ.

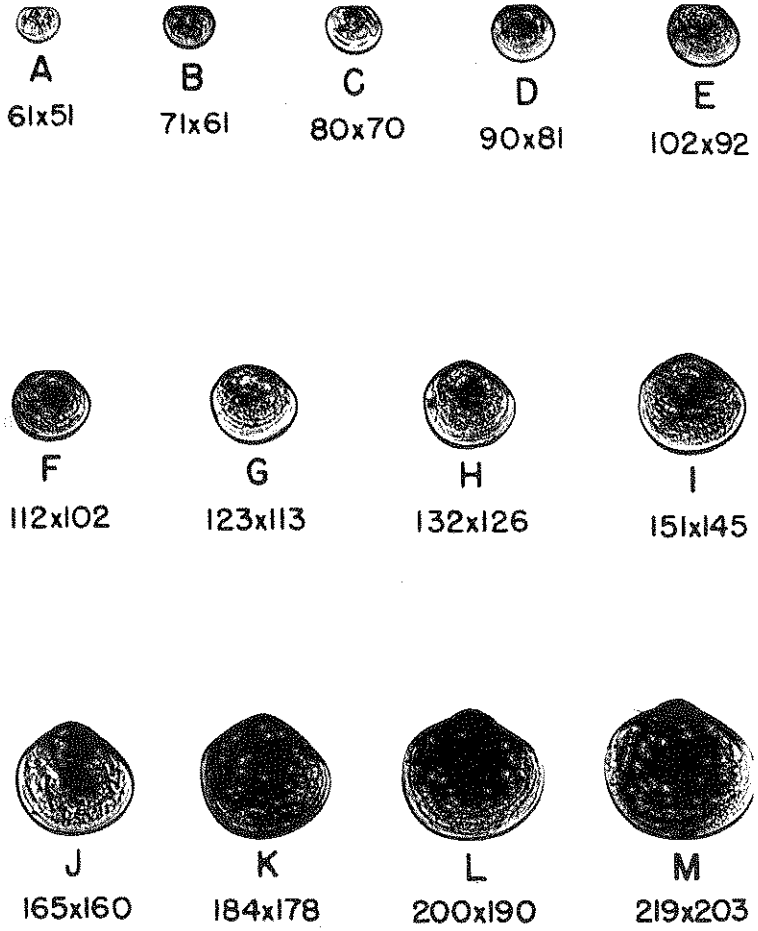

FIG. 37. Photographs of larvae of *Mulinia lateralis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (M). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

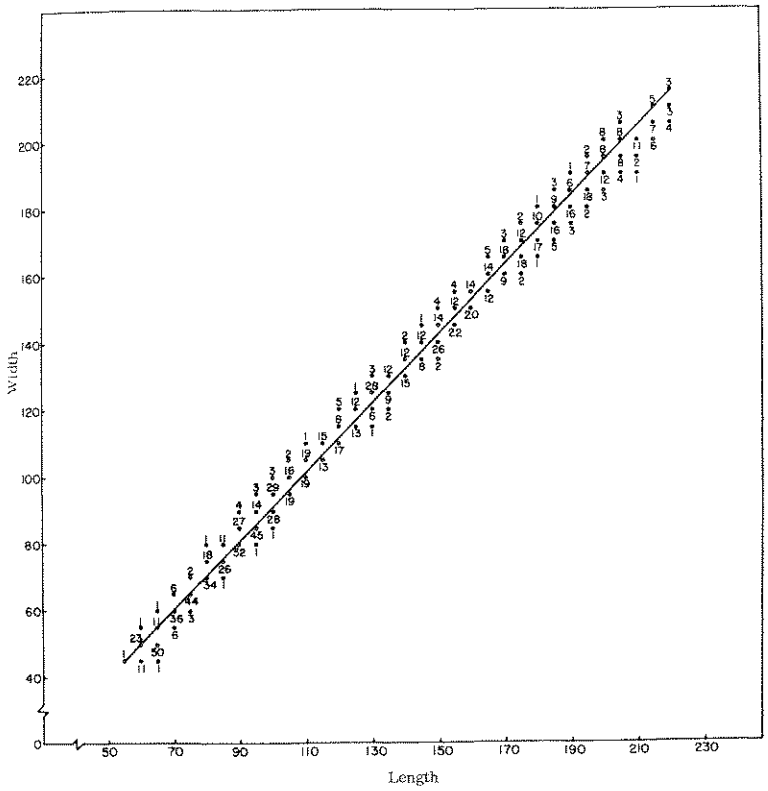

FIG. 38. Length-width relations of larvae of *Mulinia lateralis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

tures grown at our laboratory was only 55 μ long by 44 μ wide. Normal young straight-hinge larvae measure about 60 x 50 μ (Figs. 36, 37, 38). As is common among lamellibranch larvae, the widths of individuals of the same length vary considerably. For example, the widths of larvae 60 μ long may vary from 45-55 μ.

The early stages of *Mulinia lateralis* larvae, although somewhat smaller, closely resemble those of *Crassostrea virginica*. After the larvae reach the length of about 105 μ, however, their general appearance becomes distinctly different from oyster larvae; their umbones are much less pronounced than in the larvae of *C. virginica* of the

same size.

Most larvae undergo metamorphosis at lengths from 210-230 μ. Variation is considerable, however, because some individuals as small as 190 μ appeared entirely metamorphosed, whereas others as large as 235 μ were still swimming. Measurements of the prodissoconch portion of the shell of spat measuring 250-350 μ in length showed that the prodissoconchs ranged from 215-222 μ. These figures agree closely with the measurements of the average sizes of larvae approaching metamorphosis in our cultures. Width is usually about 10 μ less than the length throughout most of the developmental period but it may be 20-25 μ smaller in larvae more than 200 μ long. No evidence of "eye" spot or other distinctive marks was found in larvae as they approached setting.

Sullivan (1948) is the only author who offered descriptions and a series of photomicrographs of the larvae of *Mulinia lateralis*. The size range of her larvae, however, differed significantly from ours. Her minimum size, 85 x 75 μ, is about 25 μ larger than the young straight-hinge larvae recorded in our cultures. Her maximum size, 270 x 245 μ, exceeded the size of our largest larvae by about 35 μ. Sullivan stated further that the straight-hinge larvae were pale yellow and that their color became more intense, changing to a bright yellow as the larvae grew. We found that the young larvae are usually silvery and transparent, not yellow, and that even the old larvae do not become bright yellow.

13. *Tapes semidecussata* Reeve

This clam, accidentally introduced into the State of Washington with seed of *Crassostrea gigas* imported from Japan, is now common along our Pacific coast from Canada to California. In Japan it is one of the most important commercial species of clams (Cahn, 1951). In this country it is called the Japanese little neck, or Manila clam. It appears in literature under many names, including *Tapes japonica*, *Venerupis semidecussata*, *V. philippinarum* and *Paphia philippinarum*. Some authors, such as Quayle (1952), have preferred to use the generic name *Venerupis* instead of *Paphia* or *Tapes*. Abbott (1954), whom we follow, used *Tapes*.

Although some smaller individuals were seen occasionally in our cultures, fully formed, straight-hinge larvae were usually about 95 x 70 μ (Figs. 39, 40, 41). Throughout the larval development, widths of the larvae were about 15-25 μ less than the lengths. The umbo began to form at a length of about 120 μ and became prominent when the larvae were about 140 μ long (Fig. 40). In older larvae the umbones were somewhat more pronounced than in *Mercenaria mercenaria* but, in general, the larvae of *Tapes semidecussata* and *Mercenaria mercenaria* closely resemble each other, especially in the early straight-hinge stage.

The smallest larvae undergoing metamorphosis were about 175 μ long, but most of them metamorphosed at 200-220 μ. Occasionally, individuals as large as 235 μ were swimming and displayed a prominent, functional velum.

Yoshida (1953) gave the dimensions of fully grown veligers of *Venerupis* (=*Tapes*) *semidecussata* as 200 x 190 μ. These measurements agree with our observations on the dimensions of larvae at which metamorphosis may occur. Later, Yoshida (1960, 1964), working with *Tapes variegata*, which is probably the same form as *T. semidecussata*, reported that fully grown veligers measured from about 200 x 180 μ to 215 x 200 μ. Quayle (1952) gave the size of a mature larva of *Venerupis* (=*Tapes*) *pullastra* as 260 x 240 μ, about 25 μ longer than the largest swimming larvae we observed in our cultures. Rees (1950), who placed this species in the genus *Paphia*, gave the size of the mature prodissoconch as 240 μ, which is not much greater than our free-swimming larvae (Fig. 41).

14. *Pitar* (=*Callocardia*) *morrhuana* Gould

This species is found on our Atlantic coast from Prince Edward Island to Cape Hatteras. Its general appearance resembles that of *Mercenaria mercenaria* but it is considerably smaller and has a

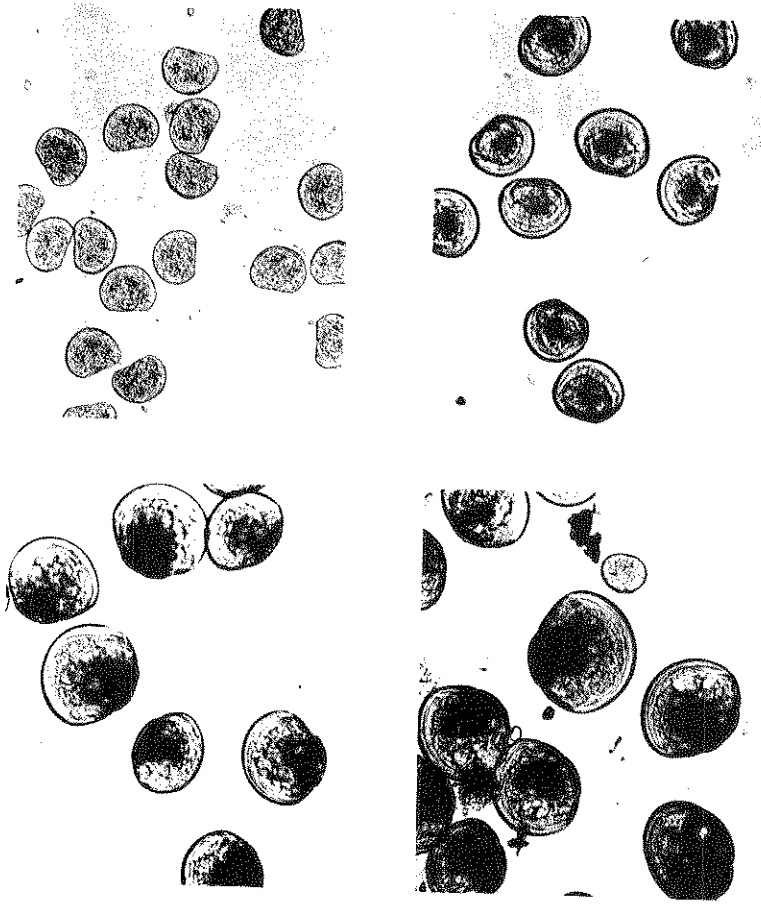

FIG. 39. Group photographs of different sizes of larvae of *Tapes semidecussata*. Smallest individuals of the youngest group are approximately 93 μ long, and the largest of the oldest, approximately 215 μ.

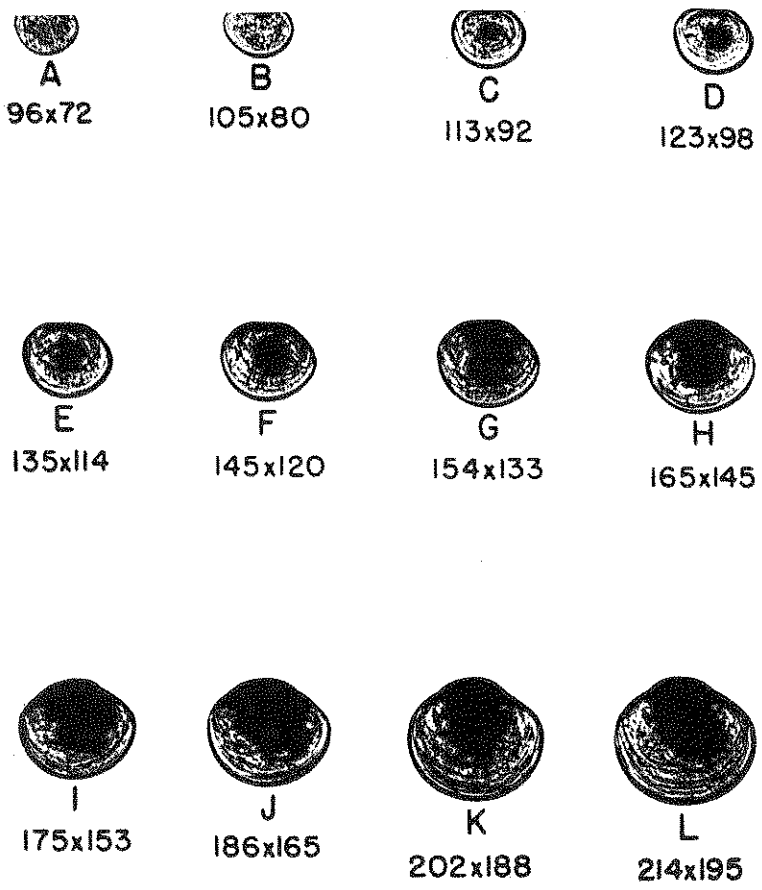

FIG. 40. Photographs of larvae of *Tapes semidecussata* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns: the first figure under a photograph indicates length, and the second, width of the larva.

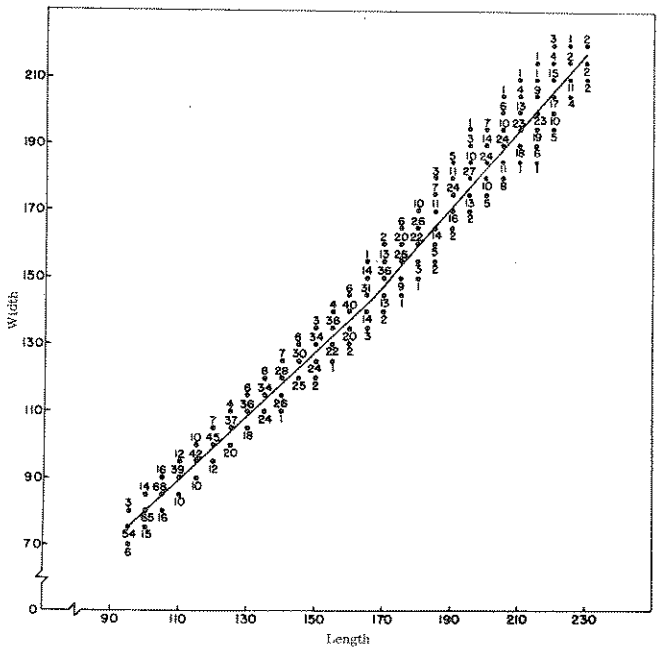

FIG. 41. Length-width relations of larvae of *Tapes semidecussata* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

lighter shell. References in the literature to the larval stages of this form are few. Sullivan (1948) offered a description and photomicrographs of what she assumed were larvae of this bivalve, and Costello *et al.* (1957) discussed the methods of obtaining fertilized eggs and gave a brief description of its early stages of development.

The smallest larvae of *Pitar morrhuana* measure about 70 x 55 μ, although some of them may not be fully formed. Most young straight-hinge larvae measure about 80 x 65 μ (Figs. 42, 43, 44). Upon reaching 125 μ, many larvae display a small umbo which becomes somewhat more prominent as they grow. Setting may begin at 160 μ and is common among larvae measuring about 180 μ. The largest free-swimming larvae were 192 x 179 μ. Even larvae approaching metamorphosis do not have an "eye" spot.

Sullivan (1948) reported that the smallest larvae of *Pitar morrhuana* were 120 x 95 μ, and the largest 220 x 210 μ. Sullivan's smallest larvae thus were about 40 μ larger than ours, and her largest exceeded the maximum size of our larvae by approximately 25 μ. Sullivan, who based her identification on larvae in plankton samples, applied the "indirect method". Later, in personal communication with us, she stated that she had confused the larvae of *Pitar* with those of another species (Loosanoff & Davis, 1950).

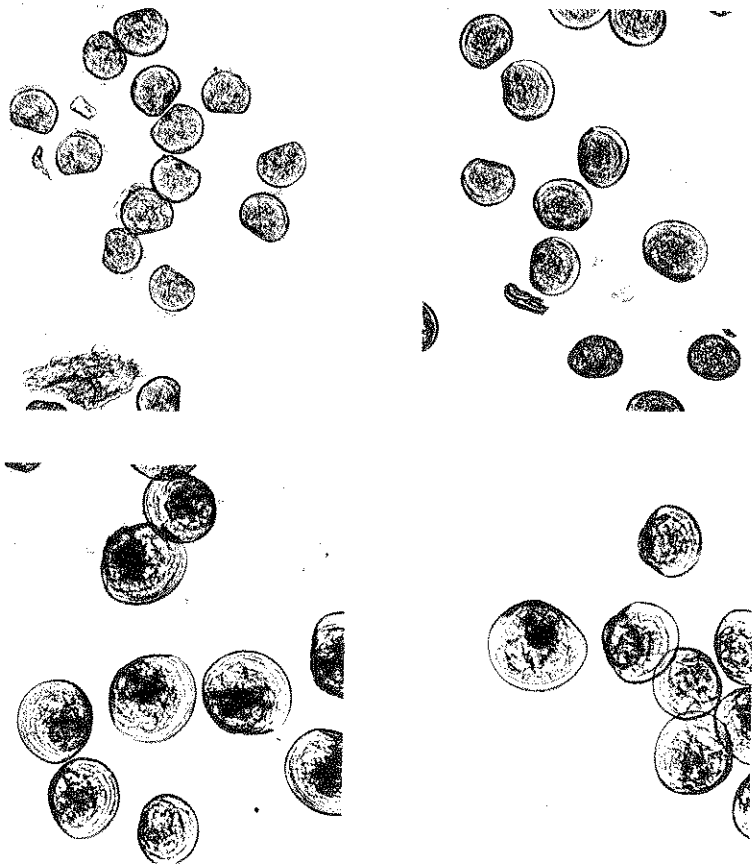

FIG. 42. Group photographs of different sizes of larvae of *Pitar morrhuana*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 170 μ.

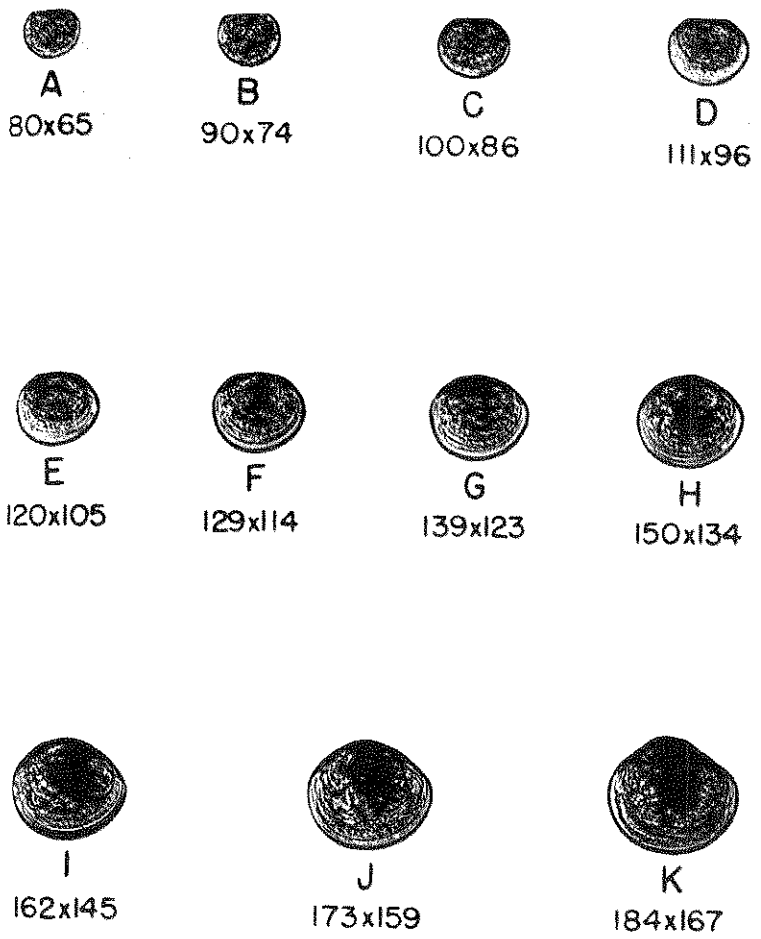

FIG. 43. Photographs of larvae of *Pitar morrhuana* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

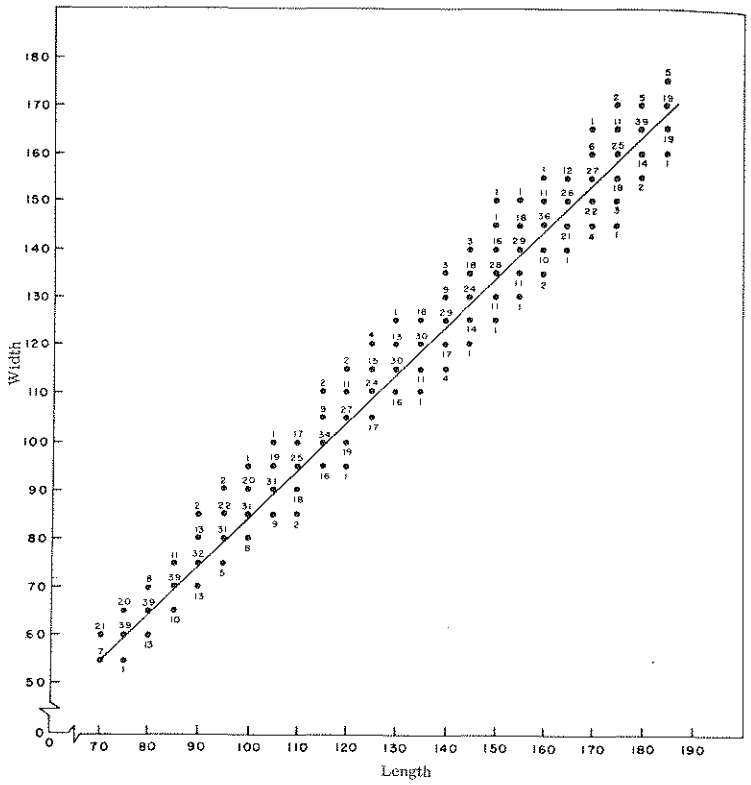

FIG. 44. Length–width relations of larvae of *Pitar morrhuana* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Again, we call attention to the differences in widths of larvae of the same length (Fig. 44). For example, even during the early stages when the larvae are only 90 μ long, their widths range from 70 to 85 μ. In larger larvae measuring 170 μ long, the widths may vary from 145 to 170 μ, a difference of 25 μ. These variations may be due, in part, to the positions of the larvae on the microscope slides but, nevertheless, the variations are real because even young, relatively flat larvae display them (Fig. 44).

15. *Petricola pholadiformis* Lamarck

This little clam, often called the Rock borer, ranges along our Atlantic coast

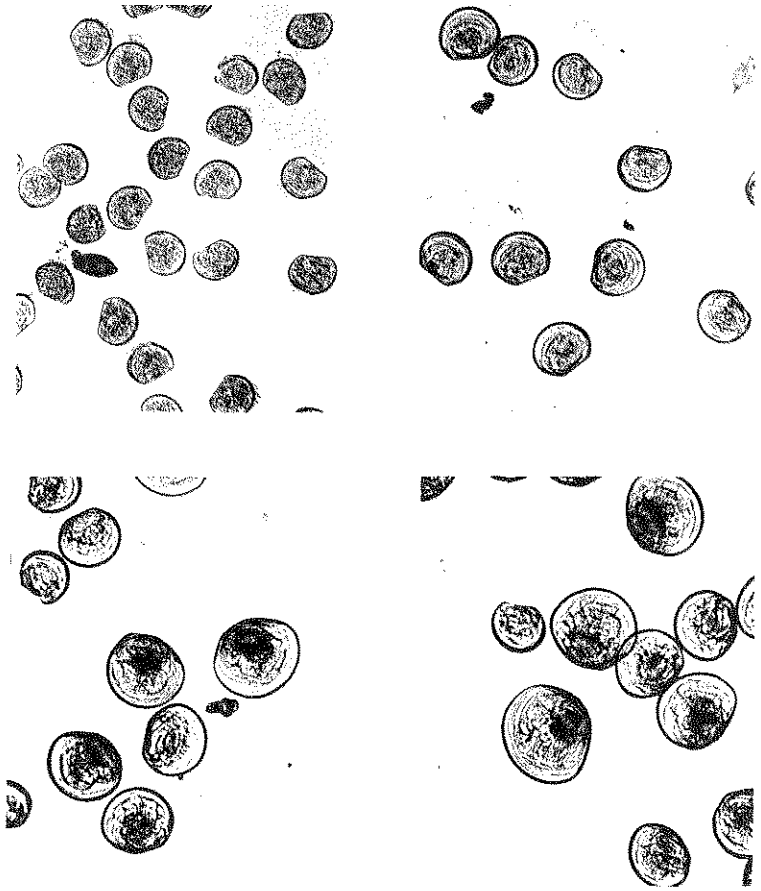

FIG. 45. Group photographs of different sizes of larvae of *Petricola pholadiformis*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 180 μ.

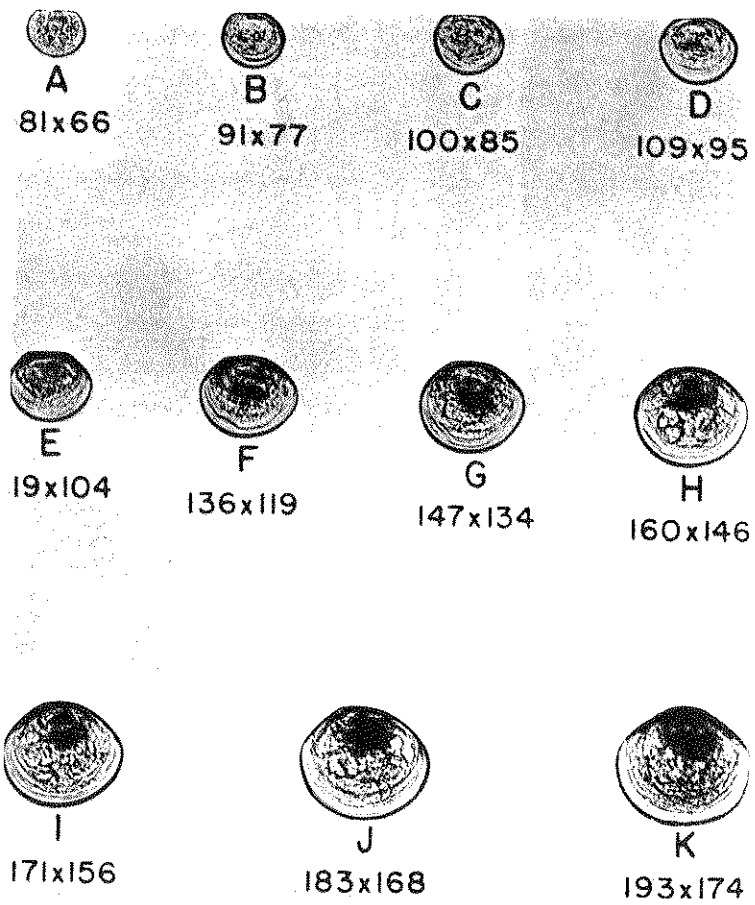

FIG. 46. Photographs of larvae of *Petricola pholadiformis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

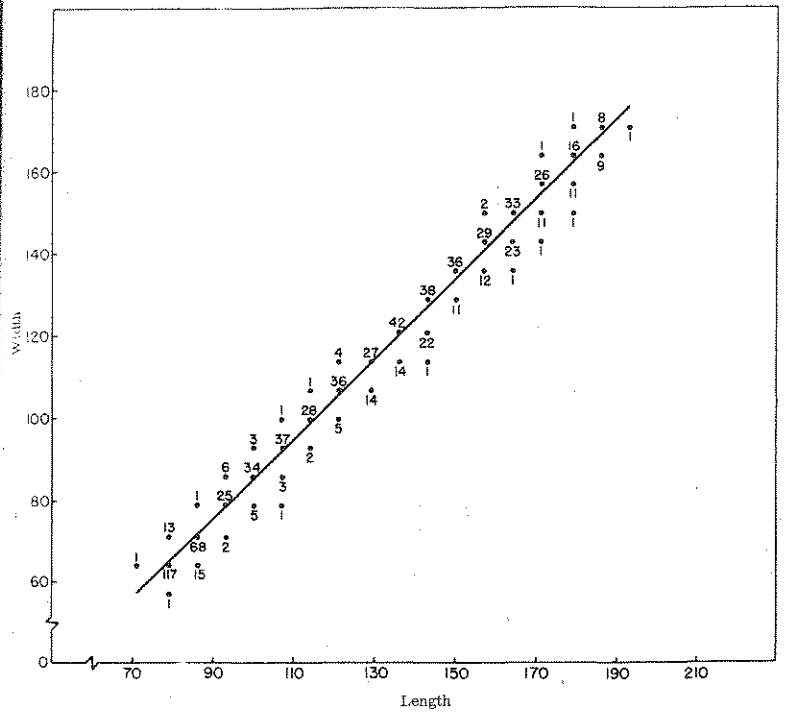

FIG. 47. Length-width relations of larvae of *Petricola pholadiformis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

from Prince Edward Island south and is also found in the West Indies and some areas of the Gulf of Mexico. Because this species occurs over such a wide range, its larvae should be common in plankton but, strangely enough, Sullivan (1948) and Loosanoff & Davis (1963) are the only authors who offer descriptions. Sullivan said that the larvae of this species appear in plankton in early summer and disappear from the waters of the St. Andrews, New Brunswick, area in early September.

In our laboratory cultures the larvae of *Petricola pholadiformis* measured about 80 x 65 μ at straight-hinge stage (Figs. 45, 46, 47). One or 2 smaller larvae, between 65 and 75 μ long, were seen. In general, our measurements of the straight-hinge larvae are considerably

smaller than Sullivan reported. According to her, straight-hinge larvae of this species are relatively large, 115 x 100 μ.

Many larvae begin to metamorphose at a length of about 185 μ, but larvae as large as 193 x 174 μ have been seen swimming in our cultures (Fig. 46). Sullivan's measurements of setting larvae were about 175 x 160 μ, which differs little from the sizes of the smallest metamorphosing larvae in our cultures.

Larvae of *Petricola pholadiformis* are, as a rule, more transparent than those of most other species that we cultured, with the exception of *Anomia simplex* and *Aequipecten irradians*. The early straight-hinge stages are especially transparent and they remain transparent until they metamorphose. According to Sullivan, straight-hinge larvae of this species are pale yellow, whereas older individuals are deep yellow. We do not share this opinion.

16. *Ensis directus* (Conrad)

Ensis directus, the common razor-shell clam of our Atlantic coast, is found in large numbers from Labrador to the Florida Keys. Regardless of its common occurrence, the shelled larvae have been studied only by Sullivan (1948) and Costello *et al.* (1957), who described the early stages of development. Loosanoff & Davis (1963) described the method of cultivation of the species under laboratory conditions.

At early straight-hinge stage the larvae of this clam measure about 92 x 78 μ, although some are occasionally smaller (Figs. 48, 49, 50). They are much more transparent than the larvae of *Mercenaria mercenaria*. The length of the larvae increases more rapidly than the width and at the time of metamorphosis may exceed the width by 40 μ.

The larvae begin to form an umbo when about 115 μ long; this umbo becomes well developed in veligers 130 μ long and longer (Fig. 49). The umbones do not acquire the prominence shown in some other mollusks, for example, the genus *Crassostrea*. The umbo is sufficiently large, however, to prevent larvae from lying flat on the microscope slides. Considerable variation may occur, therefore, in length-width ratios of larvae of the same size.

The smallest metamorphosing larvae in our cultures were only about 210 μ long but some larvae may reach a much larger size before they metamorphose. Several larvae of about 270 μ were still swimming, whereas many already metamorphosed larvae, with a well-developed foot, gills and syphons, measured only about 220 μ.

In most normal larvae of *Ensis directus* 120 μ long or longer a clear area can be easily distinguished around the edge of the shell. This area is noticeable to a length of about 185 μ, but it becomes less pronounced at still greater sizes. This character may be of diagnostic value.

The "eye" spot was not often found even in larger larvae. When it did appear it was not well defined. Sullivan (1948) did not refer to this structure in her studies of the larvae of *Ensis directus*. Werner (1939), working with a related species, stated that its larvae did not have "eye" spots. Jørgensen (1946) mentioned several references to other workers who studied the larvae of closely related forms but found nothing resembling the so-called "eye" spot.

Sullivan (1948) reported that the size range of *Ensis directus* larvae varies from 140 x 120 μ to about 320 x 280 μ. As can be seen from the measurements and photographs (Figs. 48, 49, 50), the sizes of early straight-hinge larvae in our cultures were much smaller than those presented by Sullivan, and our maximum sizes, similarly, were about 50 μ smaller than those observed by her.

Jørgensen (1946) and Rees (1950) gave the dimensions of larvae of several members of the Solenacea of European waters. The measurements of larvae approaching metamorphosis were considerably larger than ours. For example, Jørgensen reported that the largest lar-

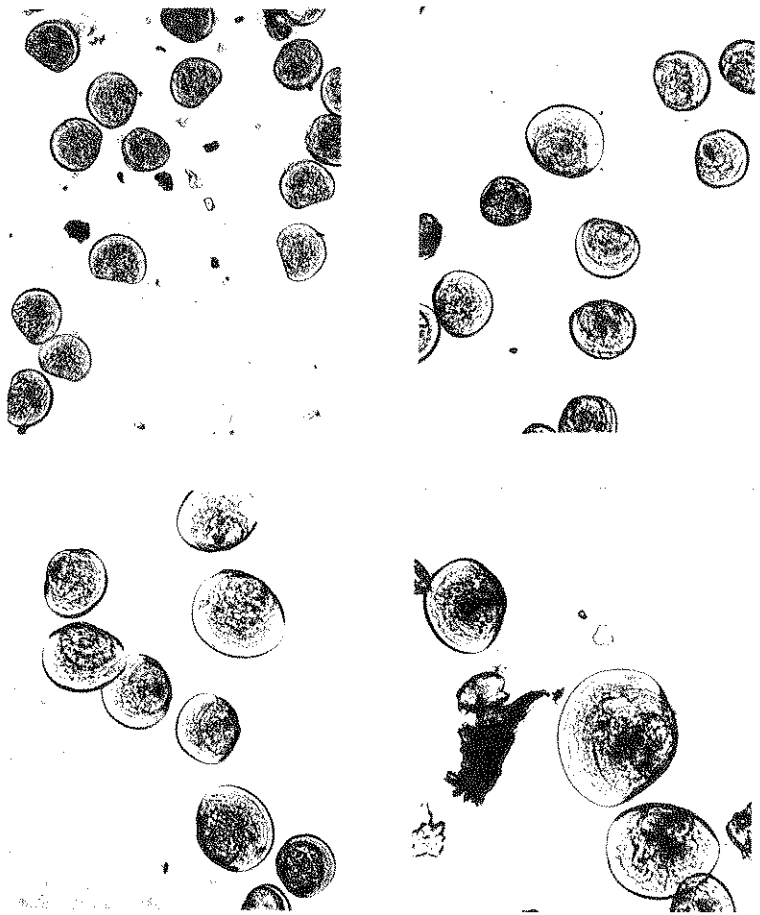

FIG. 48. Group photographs of different sizes of larvae of *Ensis directus*. Smallest normal individuals of the youngest group are approximately 90 μ long, and the largest normal individuals of the oldest approximately 235 μ.

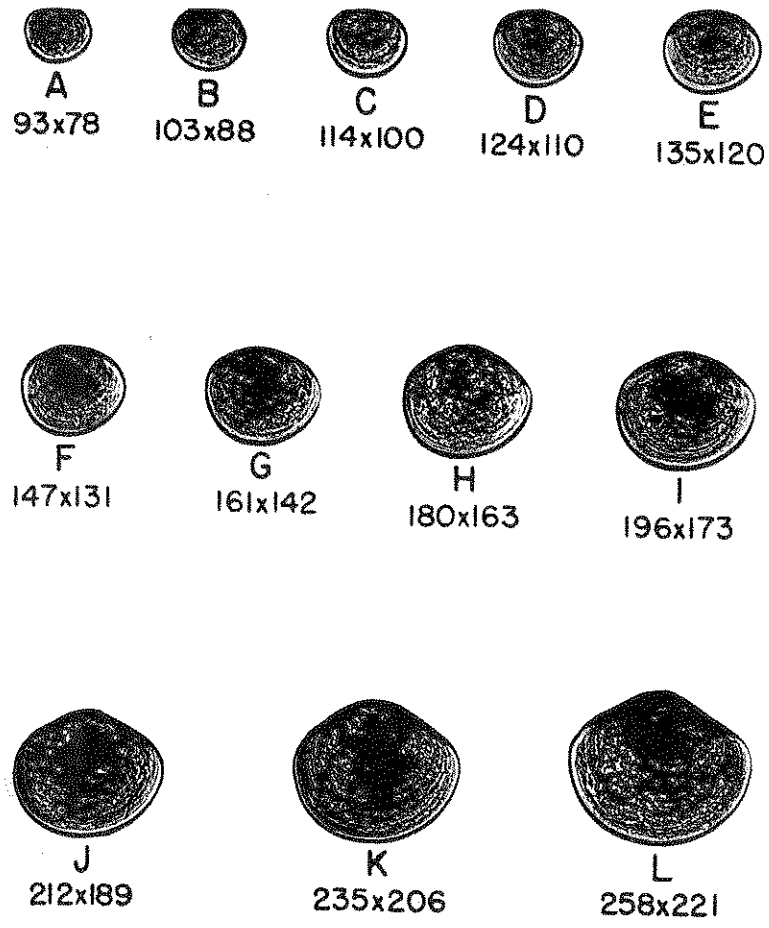

FIG. 49. Photographs of larvae of *Ensis directus* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

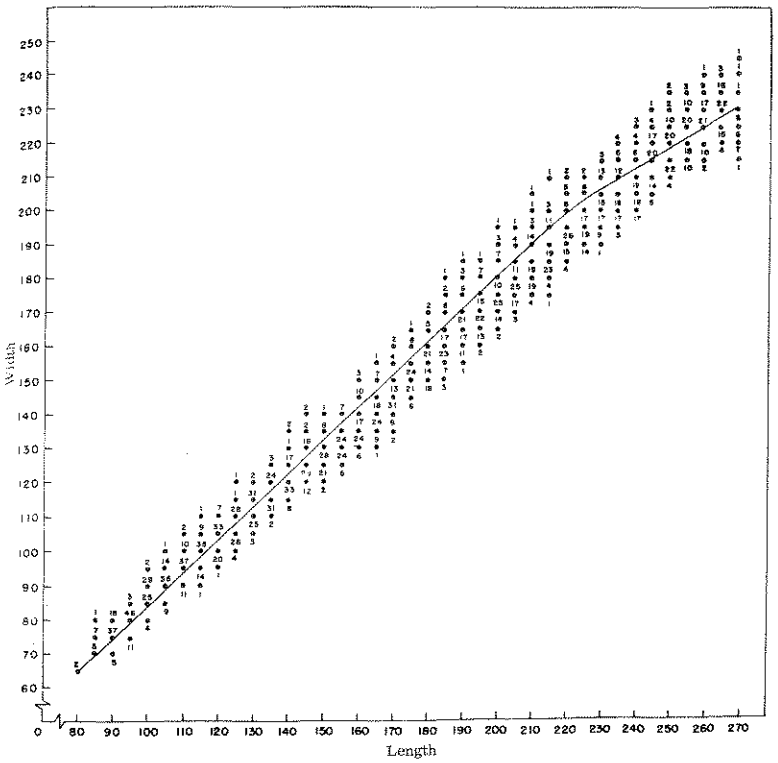

FIG. 50. Length-width relations of larvae of *Ensis directus* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

vae of *Cultellus pellucidus* were up to 360 μ long, and Rees stated that one larva of this species, about 400 μ long, was recorded. The lengths of the larvae given by these 2 authors are larger by about 100 μ than those in our cultures (Figs. 48, 49, 50). Another closely related species, *Ensis siliqua*, mentioned by Lebour (1938) may be about 350 μ long, also much larger than the larvae of our species, *E. directus*. We may add also that the largest larva of *E. directus* shown in the photograph given by Sullivan in her article appears somewhat different from our larvae, and that the 245 μ long larva of *E. ensis* in Rees' photograph has little resemblance to the larvae of *E. directus* of the same size grown at our laboratory (Fig. 49).

17. *Mactra* (=*Spisula*) *solidissima* Dillwyn

This mollusk, commonly called the

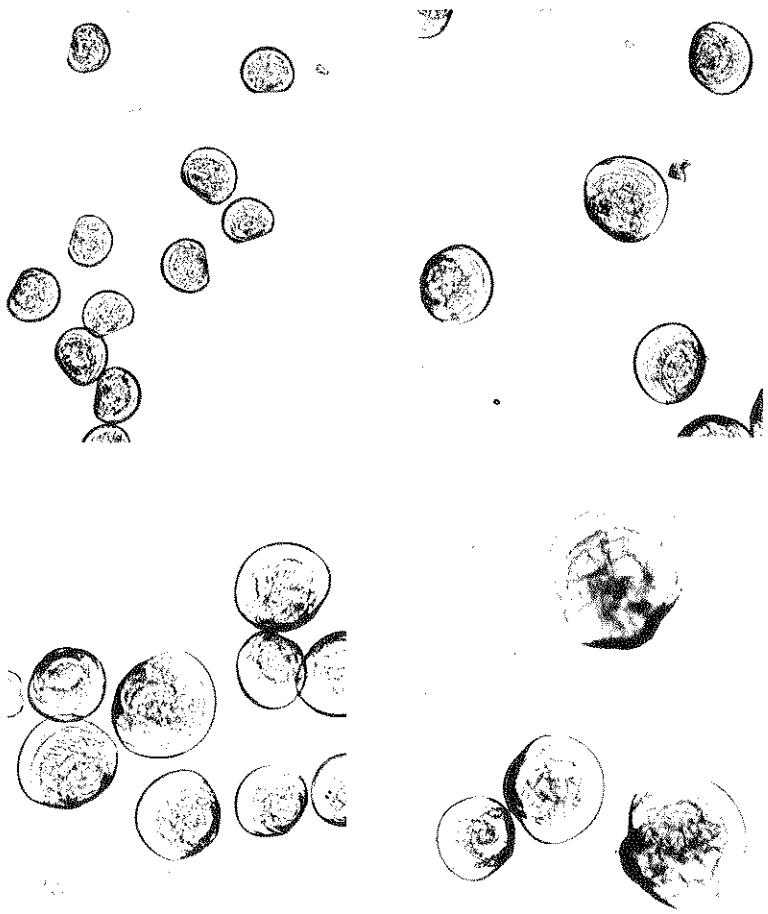

FIG. 51. Group photographs of different sizes of larvae of *Mactra solidissima*. Smallest individuals of the youngest group are approximately 72 μ long, and the largest of the oldest, approximately 218 μ.

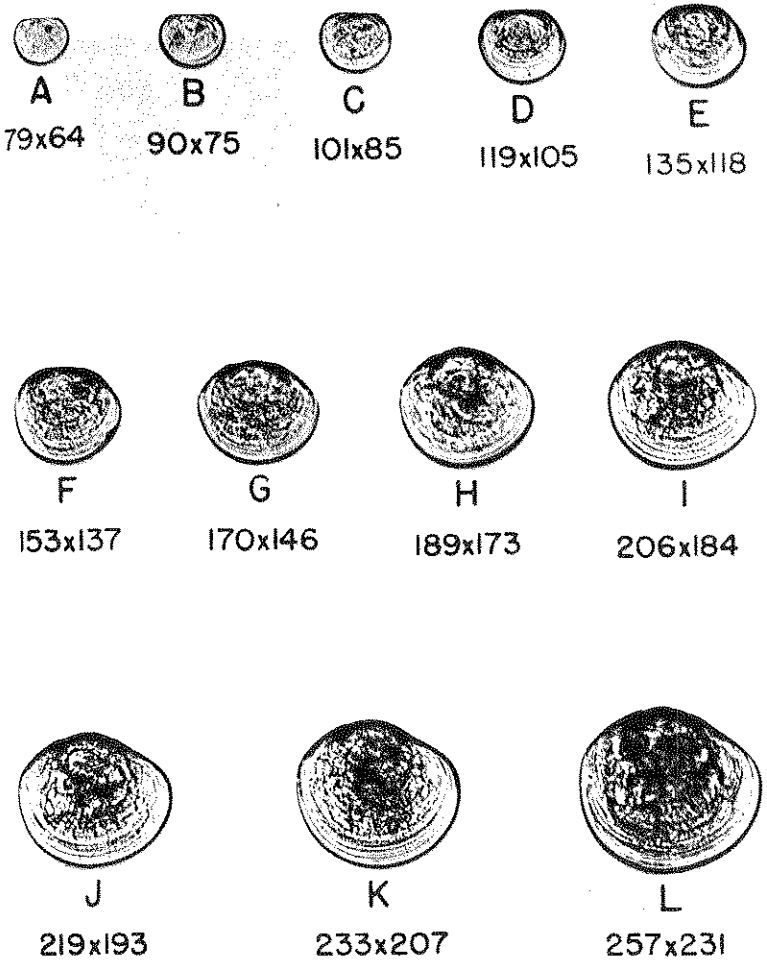

FIG. 52. Photographs of larvae of *Mactra solidissima* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

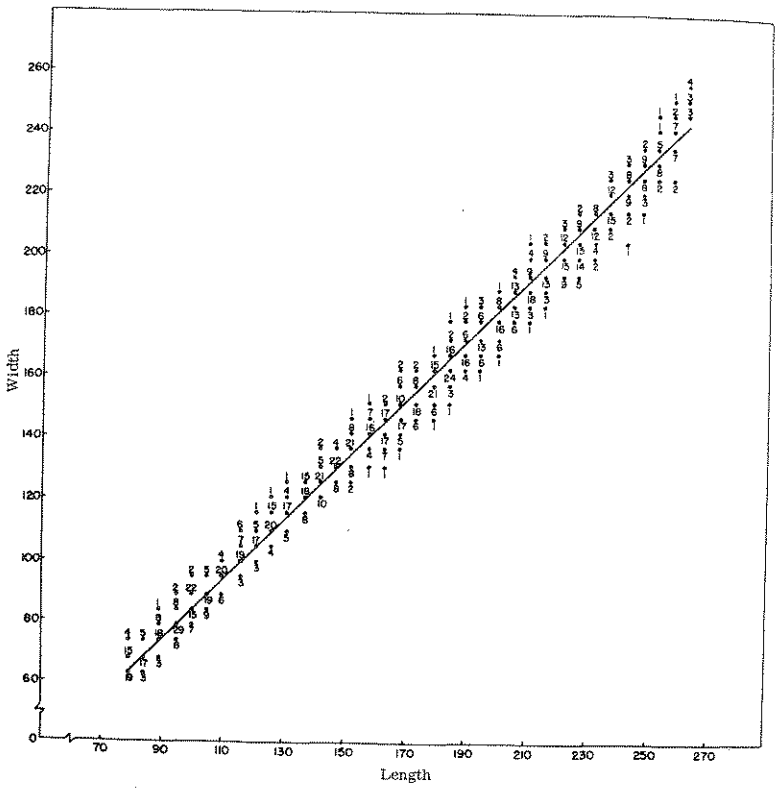

FIG. 53. Length-width relations of larvae of *Mactra solidissima* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Surf clam, is the largest bivalve of our Atlantic coast, sometimes measuring almost 7-1/2 inches in length. It is extremely abundant in some sections of its range, which extends from Labrador to Cape Hatteras.

The early normal straight-hinge larvae of this clam are approximately 80 x 65 μ (Figs. 51, 52, 53). Our cultures sometimes contained smaller larvae, but they usually showed some anatomical abnormality. As with several other species, the larvae of *Mactra solidissima* display considerable differences and variations in the sizes at which certain organs begin to be discernible or at which they begin to metamorphose. Some larvae may have a well-formed foot when

they are only 160-165 μ long although, as a rule, this organ appears when the larvae are near 215 μ long. When the length is about 240 μ, most larvae display a strong, functional foot.

A few individuals are fully metamorphosed when only about 220 μ long. Normally, however, a larva is between 230 and 250 μ long before it settles. Occasionally larvae measuring slightly over 260 μ long were still swimming in our cultures.

In general, our studies on the development and growth of larvae of *Mactra solidissima* closely agree with those of Imai *et al.* (1953b), who studied the development of a related species, *M. sachalinensis*. Both Imai's group and ours worked with larvae of known parents grown under controlled laboratory conditions. Sullivan (1948) gave the size range for larvae of *M. solidissima* from 95 x 80 μ to 270 x 245 μ. Thus, her smallest larvae were about 15 μ longer than ours; the maximum size was similar to ours.

Jorgensen (1946), describing *Spisula subtruncata*, a European form closely related to our clam, reported that metamorphsis in that species took place at the length of about 400 μ or more. This size is considerably larger than we observed among the larvae in our cultures and is also larger than the measurements given by Kändler (1926), who recorded the length of metamorphosing larvae of *S. subtruncata* as only 310 μ. Rees' (1950) measurements of larvae, which he considered as belonging to the family Mactracea, were also considerably larger than ours. Rees gave the length of advanced stages of larvae, presumably those of *Spisula solida*, as 360 μ and of *S. elliptica* as 355 μ. These measurements exceed by almost 100 μ the maximum length of the larvae of *Mactra solidissima* reared in our experiments and the larvae of *M. sachalinensis* grown by Imai *et al.* (1953b). The photomicrographs of *S. solida* offered by Rees in his article bear little resemblance to our larvae of *M. solidissima* because of the strongly pronounced concentric lines of the shell of the European species. His picture is obviously of a juvenile, not a larva. Moreover, the general shapes of older larvae of *S. subtruncata* offered in his photomicrographs do not closely resemble the outlines of the advanced stages of larvae of *M. solidissima* (Fig. 52). Moreover, the remarks by Rees in the discussion of the superfamily Mactracea indicate much uncertainty about the appearance and sizes of larvae of this group. Rees himself pointed out the wider disagreement about specific boundaries in this group than in any other. We agree on this point because of the differences in sizes of metamorphosing larvae studied by Imai *et al.* (1953b) and ourselves and of those described by Rees.

Some of Rees' statements are almost incompatible with our findings. For example, in his discussion of what he called "Mactrid E", characterized by *Mactra corallina*, Rees (1950) stated that the mactrid tooth, which is, presumably, characteristic of this entire group, is not formed even in larvae as large as 290 μ but appears later. None of our larvae nor those of Imai, Kändler or Sullivan measured 290 μ at the time of metamorphosis, a size that according to Rees was still characteristic of immature larvae without mactrid teeth.

18. *Mya arenaria* Linnaeus

This extremely common clam of our Atlantic coast ranges from the Canadian border to North Carolina. It has also been introduced with shipments of eastern oysters to the Pacific coast where it is now comparatively abundant.

Again, as with other pelecypods, it is difficult to indicate the smallest normal size of straight-hinge larvae. In our cultures straight-hinge larvae measuring only about 86 μ long were seen occasionally. Most fully formed larvae, however, were about 90 x 75 μ (Figs. 54, 55, 56). Throughout the entire growth the length of the larval shell

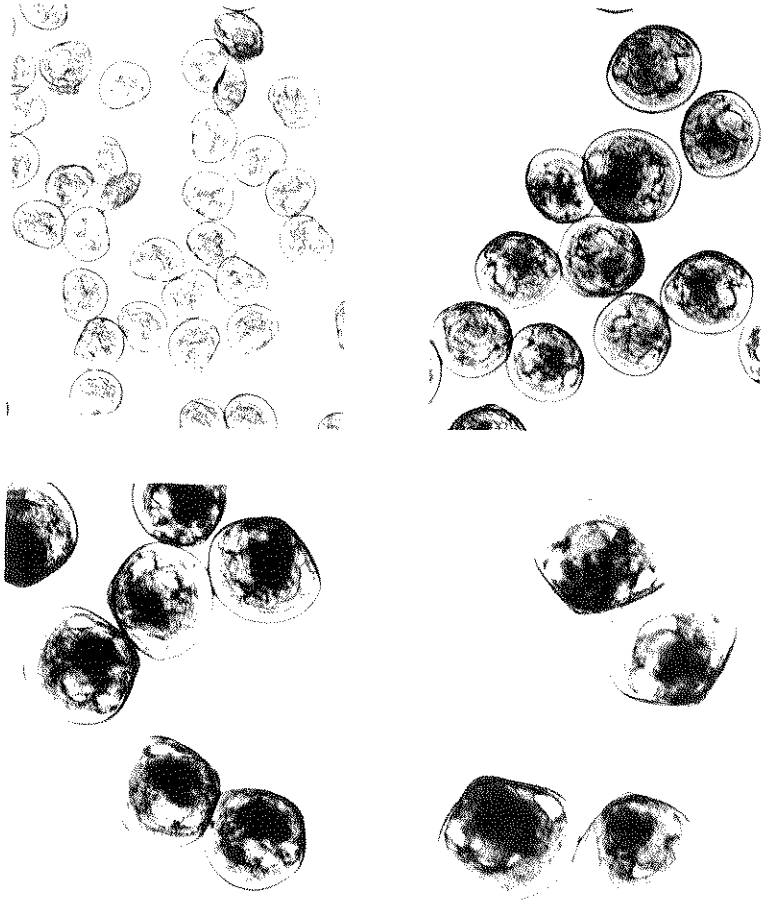

FIG. 54. Group photographs of different sizes of larvae of *Mya arenaria*. Smallest individuals of the youngest group are nearly 93 μ long, and the largest of the oldest group are approximately 230 μ; some of them are near, or in the process of metamorphosis.

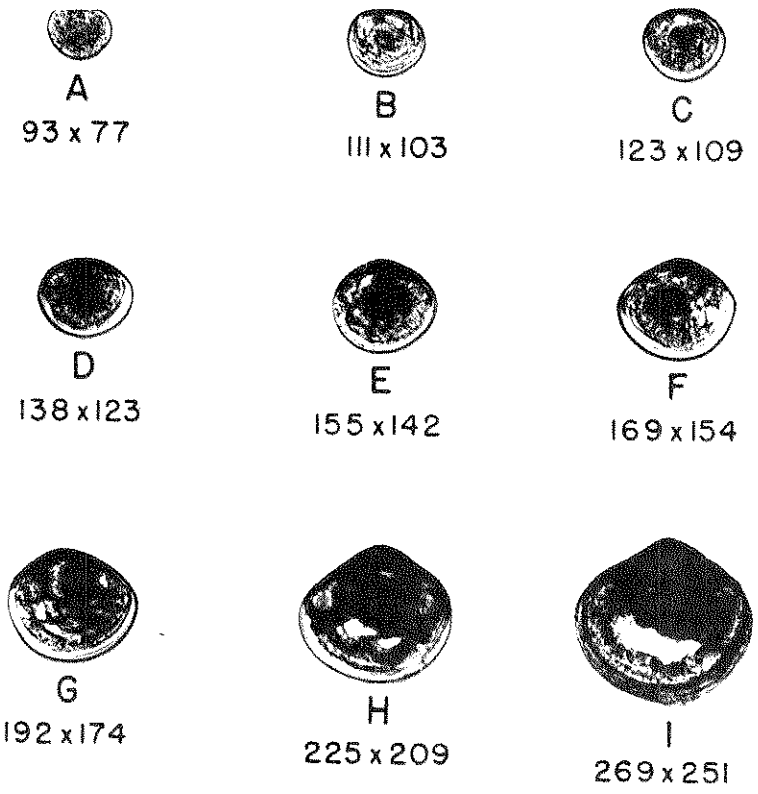

FIG. 55. Photographs of larvae of *Mya arenaria* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (H). The last figure (I) is that of a recently metamorphosed individual. Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

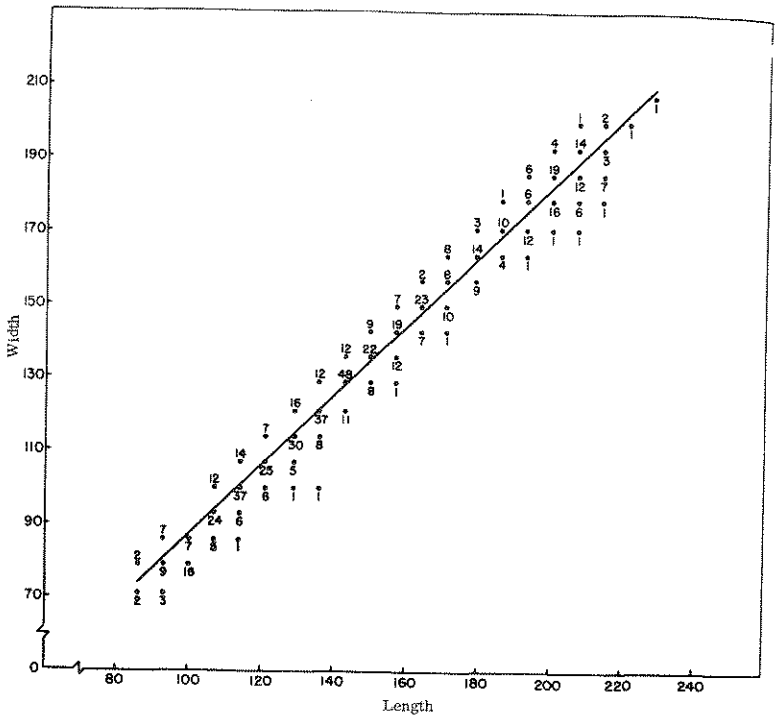

FIG. 56. Length-width relations of larvae of *Mya arenaria* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

remains greater than its width.

The larvae of *Mya arenaria* are light-colored, especially during early development (Fig. 54). When the larvae reach 110 μ their shells become somewhat darker. Larvae 175 μ or longer have irregular opaque spots, measuring 5-15 μ in diameter and located along the margin of the shells. Since these spots occur regularly, they may be characteristic of this species, especially of the late larval stages. Jørgensen (1946) also noticed the pigmented areas of the soft parts of larvae of *M. arenaria* over 200 μ long and believed that these spots may be a reliable character for identification.

The size range within which metamorphosis of the larvae of *Mya arenaria* occurred in our experimental cultures extended from about 170-230 μ; however the majority of the larvae began to metamorphose soon after they reached 200 μ. Almost the same observations were made by Stickney (1964), who studied the larvae of *M. arenaria* that came from widely separated areas of the Atlantic coast.

The smallest larva with a well-developed foot was about 165 μ long. The velum normally began to disappear after the length of 175 μ was reached, and, as a rule, the velum was already completely or almost completely resorbed in most individuals that measured over 200 μ. In some cultures, individuals only 175 μ long were crawling on the bottom of culture vessels and using their foot energetically. The otocyst could be seen in larvae approximately 175 μ long, and the byssus gland was easily discerned at approximately 200 μ.

Larvae assumed to be those of *Mya arenaria* have been described by several investigators. Stafford (1912) reported that the largest such larva he measured was 414 x 345 μ. These measurements are almost twice as large as those we made on metamorphosing individuals in our cultures. We suspect, therefore, that Stafford measured either the larva of a species other than *M. arenaria* or an individual that had metamorphosed some time earlier. Since, however, his measurements were consistently larger than ours for all species, it is possible that he erred in his measurements. Sullivan (1948) gave the size range of larvae of *M. arenaria* as extending from 105 x 90 μ to 250 x 230 μ. These figures, in general ral, are close to ours. Jørgensen (1946) reported that the size of metamorphosing larvae of *M. arenaria* is extremely variable, ranging from about 200-300 μ. Even though the maximum size of larvae given by Jørgensen is much larger than ours, we agree with him that the difference in sizes of larvae of *M. arenaria* at setting is considerable. In studies of a closely related species, *Mya truncata*, Jørgensen concluded that the maximum size of its larvae is about 320 μ, considerably larger than the maximum size of the larvae of *M. arenaria* grown under controlled conditions (Loosanoff & Davis, 1963; Stickney, 1964). Yoshida (1938) found that the size at which larvae of *Mya japonica* metamorphosed varied from 240 x 220 μ to 300 x 260 μ. The maximum sizes of the metamorphosing larvae offered by Yoshida, therefore, are approximately 70 μ larger than ours.

19. *Teredo navalis* Linnaeus

Teredo navalis, often called the common shipworm, is found along both coasts of the United States and also in Europe and Asia. It is a larviparous bivalve, releasing its larvae when they are already veligers in the straight-hinge stage.

In our laboratory the smallest larvae released measured 80 x 70 μ, whereas the largest larvae recently discharged or found in the mantle chamber of the mother mollusk were 90 μ long. This size is about 10 μ larger than was reported by Jørgensen (1946). In general, however, our observations on the size of recently released larvae of *Teredo navalis* (Figs. 57, 58, 59) are in agreement with those of Imai *et al.* (1950a), Sullivan (1948) and Jørgensen (1946). We disagree, though, with the observations of Lane *et al.* (1954), who stated that the larvae of *T. navalis* are about 250 μ long at the time they are released from the gill chamber of the mother.

The shells of even recently released larvae are heavy and thick, and are characterized by a dark band around the edge (Figs. 57, 58). Sometimes another light band may be seen clearly inside of the darker outside band. This band remains distinguishable until metamorphosis. As the larvae grow, the color of their shells gradually becomes darker.

Several fully metamorphosed young *Teredo* measuring only 190 μ in length were found on the bottom of our culture vessels. The largest swimming larvae in our cultures were only slightly longer than 200 μ (Figs. 58, 59). These measurements are similar to those of Sullivan (1948) and Imai *et al.* (1950a), although their maximum measurements exceed ours by about 10 μ.

The larvae of *Teredo* do not develop

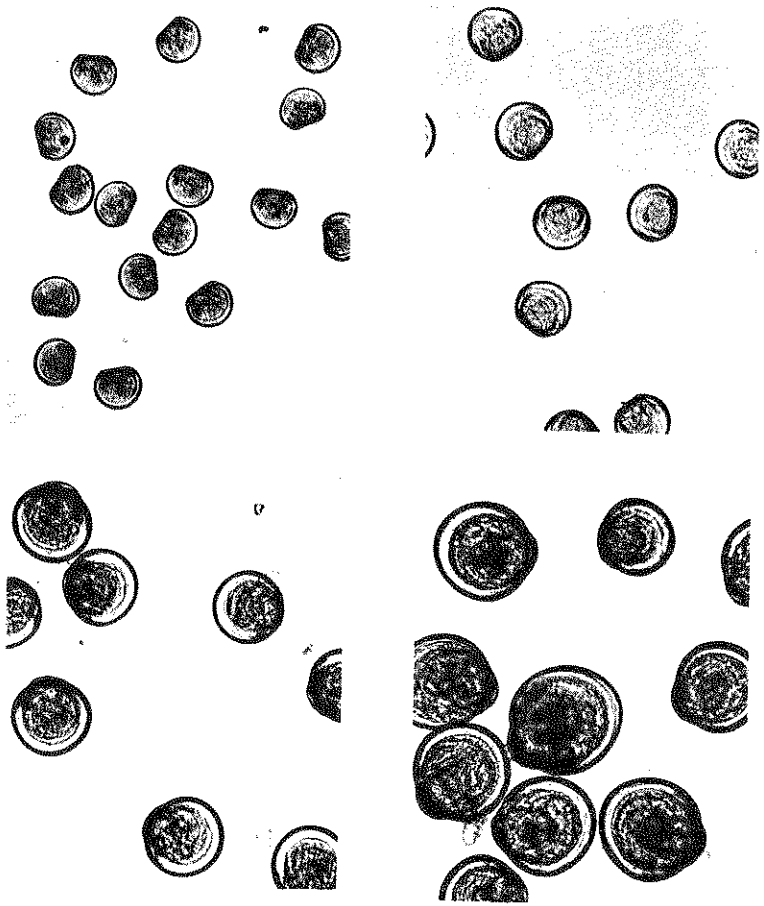

FIG. 57. Group photographs of different sizes of larvae of *Teredo navalis*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 185 μ.

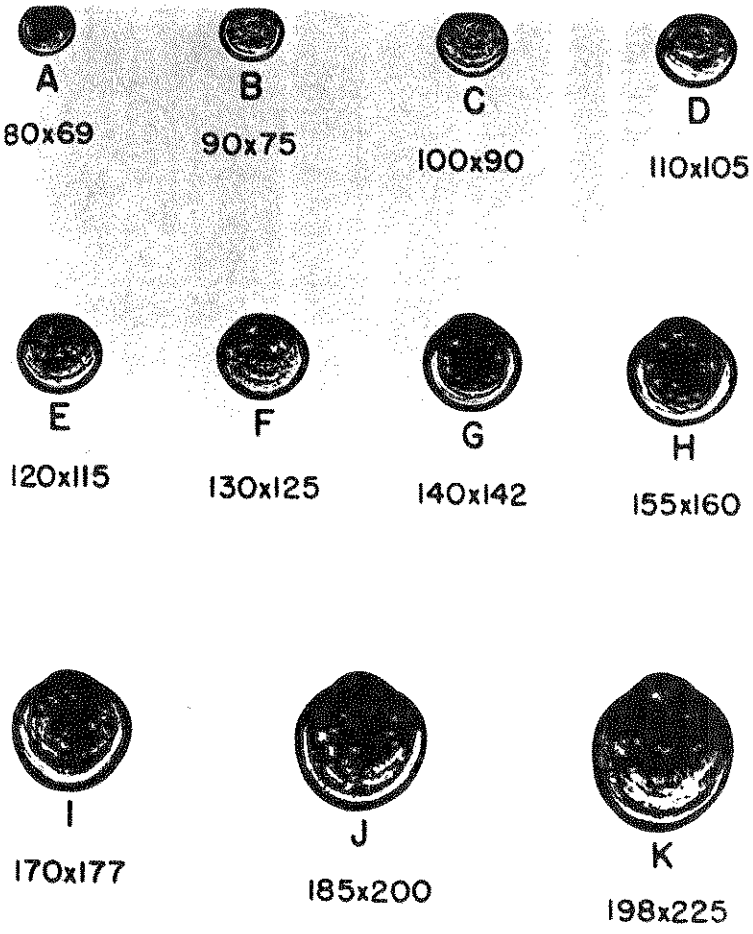

FIG. 58. Photographs of larvae of *Teredo navalis* from the time they are released in swarming by the parents (A) until the time of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of a larva.

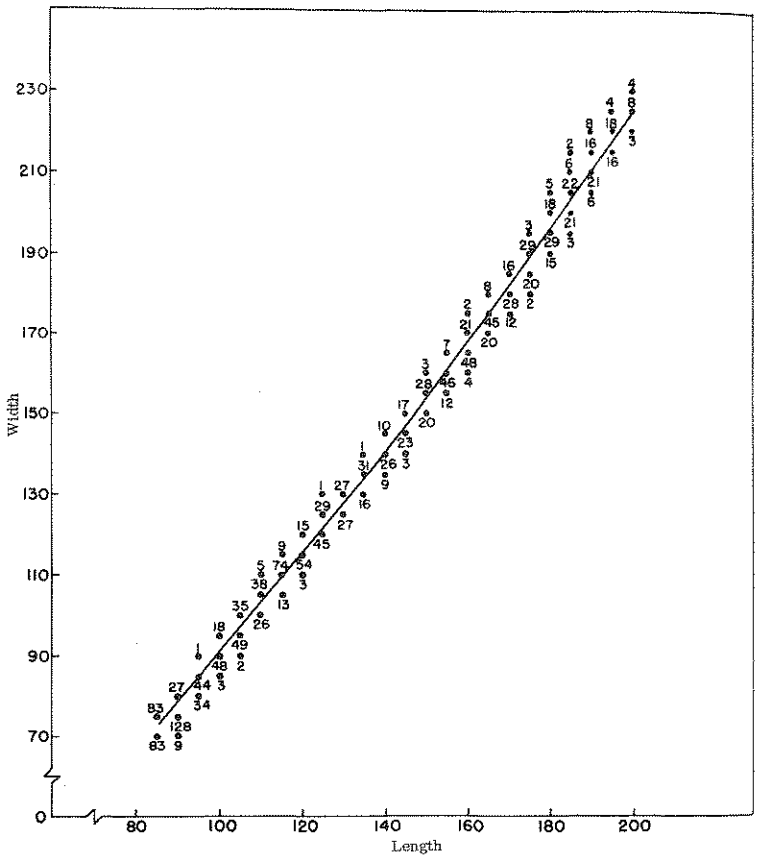

FIG. 59. Length-width relations of larvae of *Teredo navalis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

the "eye" spot that is found in mature larvae of some other species of bivalves. Details on the rearing of *Teredo* larvae under laboratory conditions and information about their behavior are given in the recent article of Loosanoff & Davis (1963).

Jørgensen (1946) offered information on the larvae of a closely related species of European waters, *Teredo norvegica*. According to him the oldest veligers of this species may be approximately 300 μ long and are almost circular; thus their shape differs from that of the larvae of *T. navalis* (Fig. 58). Furthermore, some veligers of *T. norvegica* possessed a black "eye" spot, a structure not found in *T. navalis*. The larvae of yet another species, *T. megotara*, described by Jørgensen, contained individual veligers up to about 330 μ long.

20. *Laevicardium mortoni* (Conrad)

This small bivalve, which is very abundant from Martha's Vineyard, Massachusetts, to New Jersey, U. S. A., is found from Nova Scotia to Brazil. It is known by several common names, including Morton's cockle. As far as we could determine, no description of the larvae of this species is found in the literature.

The smallest straight-hinge larva of this cockle in our laboratory cultures measured approximately 85 x 70 μ. Most larvae at this stage, however, were a few microns larger (Figs. 60, 61). Length of the larval shell increases more rapidly than its width, and at metamorphosis the length may exceed the width by more than 30 μ. The margin of the straight-hinge larval shell is outlined by a dark band resembling the band in *Teredo* larvae, but not so prominent. At almost all stages, especially near metamorphosis, one end of the larval shell is longer and somewhat more pointed than the other (Fig. 60). Soon after a length of about 135 μ is reached the umbo begins to appear; it becomes prominent when the shell length is about 160 μ. No "eye" spot was observed in the larvae, even in those reaching metamorphosis.

Some larvae already displayed a well-developed foot when only about 205 μ long. Several entirely metamorphosed individuals, with well-developed gills and syphons, were only 220 μ long. On the other hand, some larvae measuring 245 μ in length and with an apparently normal velum were still swimming. The largest swimming larva in our cultures was about 250 x 220 μ.

Sullivan (1948) stated for a related species, *Cardium pinnulatum*, that the size of larvae ranged from 90 x 80 μ, at the earliest straight-hinge stage, to 250 x 230 μ at metamorphosis. Her measurements of *C. pinnulatum*, therefore, closely resembled ours of *L. mortoni*. Jørgensen (1946) found that the larvae of *C. edule* metamorphosed at the size of about 275 to 335 μ, *i.e.* when considerably larger than the larvae of *L. mortoni* or *C. pinnulatum*. He found the larvae of *C. edule* extremely variable in the size at which they reached metamorphosis, a condition that agrees closely with our own observations on *L. mortoni* and the larvae of the majority of other species we reared.

Jørgensen offered a number of references on the studies of larvae of Cardidae in European waters. In his discussion of the sizes of the larvae of different species he mentions that *Cardium echinatum* reached about 480 μ at metamorphosis. The prodissoconch of young bottom stages of another species, *C. minimum*, measured between 330 and 400 μ and averaged approximately 365 μ. In another form, *C. fasciatum*, the largest stages in the plankton were about 300 μ long. Thus, all 3 of the above-mentioned species exceeded the maximum sizes of the larvae of *L. mortoni* in our cultures and the larvae of *C. pinnulatum* described by Sullivan, by at least 50 μ.

In still another species mentioned by Jørgensen, *Cardium exiguum*, metamorphosis appears possible at the length of only 250 μ, a size closely similar to ours. Nothing is known, however, about the possible variations in length of larvae of *C. exiguum* at the time of metamorphosis.

Rees' (1950) description of the larvae of Cardidae pointed out large differences among the larvae of the genus *Cardium*, although he maintained that they conform to a basic type. We cannot agree with the latter conclusion after examining the

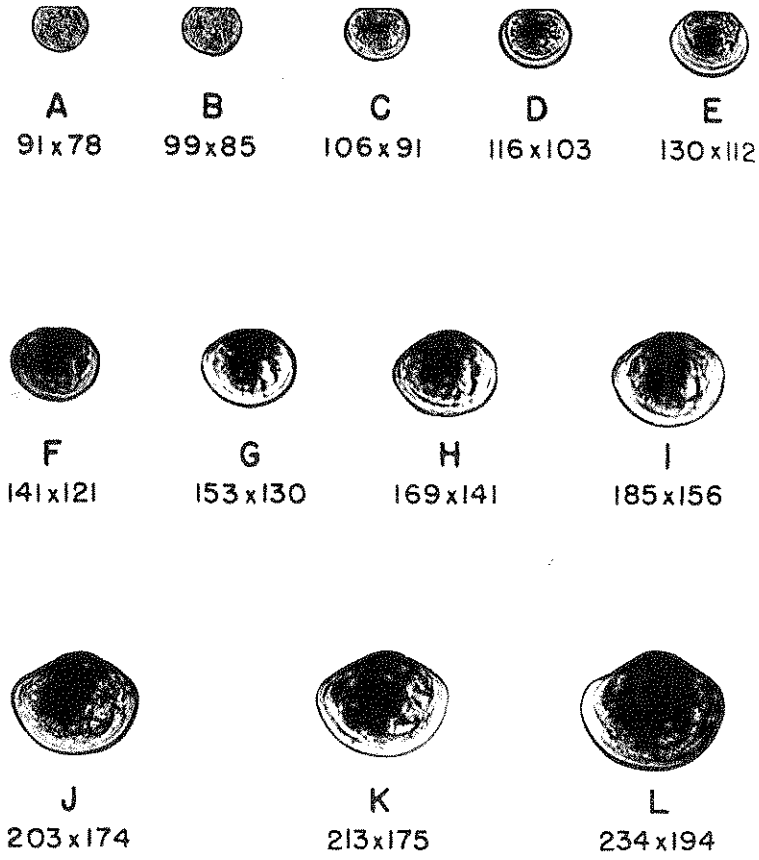

FIG. 60. Photographs of larvae of *Laevicardium mortoni* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

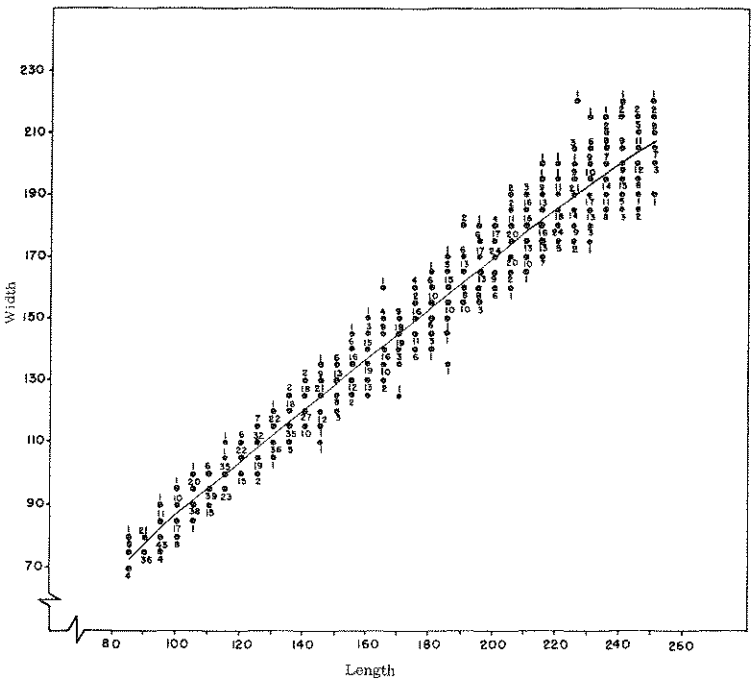

FIG. 61. Length-width relations of larvae of *Laevicardium mortoni* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

photomicrographs he published. Length-width measurements of this group also ran counter to his views.

If the maximum sizes of the larvae of different species of the family Cardidae differ so much, the above observations may be of considerable biological interest. No final conclusions regarding the matter can be formed, however, until the larvae of all the species of Cardidae discussed have been grown under identical laboratory conditions, where accurate observations can be made on their growth and minimum and maximum sizes. We emphasize, nevertheless, that during our long and varied studies we found that the minimum and maximum sizes of the larvae of closely related species of the same genus, for example, *Crassostrea virginica* and *C. gigas*, or *Ostrea edulis* and *O. lurida*, closely resemble each other.

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RESUMEN

DIMENSIONES Y FORMAS LARVALES DE ALGUNOS BIVALVOS MARINOS

Métodos de reciente desarrollo para la crianza de larvas de Bivalvos bajo condiciones controladas, ha hecho posible el cultivo de las siguientes especies: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria* (=*Venus*) *mercenaria, Mercenaria* (=*Venus*) *campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar* (=*Callocardia*) *morrhuana, Petricola pholadiformis, Ensis directus, Mactra* (=*Spisula*) *solidissima, Mya arenaria, Teredo navalis, Laevicardium mortoni.* Estas formas pasaron metamorfosis desde huevos o larvas de recien eclosión, de progenitores conocidos. Una serie de microfotografías y medidas de longitud-diámetro de las larvas, desde temprano estado hasta metamorfosis, se dan para cada especie. Agréganse descripciones de la forma general, prominencia de los umbones y otros caracteres morfológicos de las conchillas larvales durante el crecimiento. Se discuten problemas y dificultades en la identificación, especialmente de formas muy relacionadas entre sí, ofreciendo sugestiones para el mejoramiento de los métodos de identificación.

АБСТРАКТ

РАЗМЕРЫ И ФОРМА ЛИЧИНОК НЕКОТОРЫХ МОРСКИХ ДВУСТВОРЧАТЫХ МОЛЛЮСКОВ

Виктор Л. Лосанов, Гарри С. Дейвис и Павел Е. Чанлей

Последние усовершенствования методов выращивания личинок двустворчатых моллюсков в условиях лабораторного контроля, дали возможность вырастить культуры следующих 20 видов: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria mercenaria, Mercenaria campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar morrhuana, Petricola pholadiformis, Ensis directus, Spisula solidissima, Mya arenaria, Teredo navalis, Laevicardium mortoni.*

Эти виды были взрощены в стадиях после превращения личинки из яйца или же являлись личинками известных родителей. Для каждого вида даны серии микрофотографических снимков и размеры длины и ширины его личинок. Дополнительно к этим признакам, описаны общие формы, степень выпуклости вершушки и другие морфологические особенности личинковой раковины в процессе ее развития. Обсуждены проблемы и затруднения при определении видов, особенно среди родственных форм, и предложены методы для его улучшения.