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Advances in

MARINE BIOLOGY

VOLUME 1

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PREFACE

The very great expansion of marine research in recent years has resulted in a mass of published results scattered through a very wide range of periodicals. In consequence it is becoming increasingly difficult to obtain a general picture of the overall advance that is being made in our knowledge of the many aspects of life in the sea.

It is hoped that the production of this new serial publication will help biologists to keep abreast of knowledge in the different lines of research on the biology of marine organisms. It is intended that each annual volume shall contain comprehensive review articles summarizing the general position of our knowledge in individual fields. Attention will be given to recent advances in fisheries biology, the results of research in which are often published in periodicals that may not normally be available in the libraries of university biology departments. These investigations are, however, of very general interest since they usually concentrate on the biology and ecology of a few individual species in greater detail than for other marine organisms.

When possible shorter review articles may also be published drawing attention to new developments and growing points in marine biology.

General articles on the biology of marine organisms will include information on the environment only in so far as it is necessary for an understanding of their habits. Articles will not be published which relate only to the physical and chemical conditions in the sea in relation to water movements and deep-sea oceanography.

Any suggestions from readers on fields of research that need reviewing and might form subject matter for future volumes will be welcomed. Editorial correspondence should be addressed to me at Wardour, Derriford, Crownhill, Plymouth, Devon.

April, 1963 F. S. R.

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REARING OF BIVALVE MOLLUSKS

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I. Introduction

Until recently rearing of larvae and juveniles of marine bivalves, on a basis where repeatable results could be expected, was virtually impossible because of the lack of satisfactory, reliable methods. Thus, although culturing of larvae of bivalves was first attempted in the last century, few workers succeeded in rearing them to metamorphosis and, as a rule, they were rarely grown beyond early straight-hinge stage. Even though, in the twenties, Wells (1927) was able to rear the American oyster, *Crassostrea virginica*, from artificially-fertilized eggs to spat, and Prytherch (1924) raised larvae of the same species in large numbers, their results could not be consistently repeated by other investigators. The failures were usually due to poor culture methods and want of good food for the larvae, especially when they were grown in heavy concentrations. It is also possible that diseases, including those caused by fungi, were responsible for the persistent failures.

Attempts to rear larvae of bivalves were not confined, of course, to *C. virginica*. Cultivation of larvae of several other species was also tried by early workers. For example, Belding (1912) attempted to raise larvae of clams, *Mercenaria mercenaria* (formerly *Venus mercenaria*), but without success. He concluded that there was no practical method for raising clam larvae to straight-hinge stage because of the small size and delicate nature of the egg. Wells (1927), however, was more successful and carried the clam larvae in his cultures until they metamorphosed.

Even in more recent years the situation remained practically the same. This is well demonstrated by the work of Yoshida (1953) who, in his attempts to identify larvae of Japanese bivalves, had to depend upon obtaining the larvae from plankton, instead of trying to grow them from fertilized eggs under controlled laboratory conditions where their identity would be assured. The difficulties experienced as recently as 1953 by Nikitin and Turpaeva (1959), in their attempts to raise larvae of some bivalves of the Black Sea by using old methods, vouch for the inefficiency of these now obsolete approaches.

Obviously, as the general studies of marine organisms progress, the necessity for methods by means of which bivalve larvae can be reared successfully becomes more and more urgent. The availability of such methods would immediately offer the opportunity to study the effects of numerous environmental factors, singly and in combination, upon the growth of larvae, thus helping to determine the physiological requirements of these organisms. It would also offer the means for studying the genetics of bivalves and initiating properly controlled experiments on selective breeding of these mollusks. Moreover, by

growing larvae under different conditions their diseases and parasites could be studied and methods for their control developed. Finally, because the larvae of many species of bivalves are much alike in size and appearance, it was virtually impossible to identify them, with any degree of accuracy, in plankton collections. With the recent development of methods of rearing larvae in the laboratory, however, this difficulty should soon disappear because larvae found in plankton can now be easily and accurately compared with preserved samples and photomicrographs of larvae grown from known parents under controlled conditions.

By using successfully conditioning and rearing methods, many aspects of which were developed at Milford Laboratory (Loosanoff and Davis, 1950; Loosanoff, 1954) and are described in this article, larvae of approximately twenty species of bivalves have been cultured at Milford. Not all of these species are indigenous to New England waters or even to our Atlantic coast. Several are native to the Pacific and one species came from Europe. The non-indigenous forms were representatives of commercially important species in which we were interested. The bivalves, the larvae of which have been reared from fertilization to metamorphosis, included the transverse arc clam, *Arca transversa*; the ribbed mussel, *Modiolus demissus*; the common mussel, *Mytilus edulis*; the bay scallop, *Pecten irradians*; the jingle shell, *Anomia simplex*; the European oyster, *Ostrea edulis*; the native Pacific coast oyster, *Ostrea lurida*; the American oyster, *Crassostrea virginica*; the Japanese oyster, *Crassostrea gigas*; Morton's cockle, *Laevicardium mortoni*; the hard shell clam, *Mercenaria* (—*Venus*) *mercenaria*, and its relative, *Mercenaria* (—*Venus*) *campechiensis*; hybrids of these two species; the Japanese clam, *Tapes semidecussata*; the small clam, *Pitar* (—*Callocardia*) *morrhuana*; the rock borer, *Petricola pholadiformis*; the razor clam, *Ensis directus*; the surf clam, *Mactra* (—*Spisula*) *solidissima*; the soft shell clam, *Mya arenaria*; and the common shipworm, *Teredo navalis*.

Of the above species the larvae of *Crassostrea virginica* and *Mercenaria mercenaria* have been studied most intensively and, as a result, we have accumulated an extensive knowledge of their physiological and ecological requirements (Loosanoff and Davis, 1950; Loosanoff *et al.*, 1951; Loosanoff and Davis, 1952a; Loosanoff and Davis, 1952b; Davis, 1953; Loosanoff, 1954; Loosanoff *et al.*, 1955; Davis and Chanley, 1956a; Davis, 1958; Davis and Guillard, 1958; Loosanoff, 1958a; Loosanoff, 1958b; Loosanoff, 1959; and Davis, 1960). Several other species, such as the European oyster, *Ostrea edulis*, and the Olympia oyster, *Ostrea lurida*, have also received much attention.

Most of the other species, however, were studied less intensively, work on them being confined to culturing their larvae and observing the appearance and general behavior of the latter. Naturally, our knowledge of the requirements of larvae of such species is still fragmentary but, nevertheless, we shall present the information already available even though it is admittedly incomplete.

II. Equipment

The rearing of larval and juvenile bivalves requires an adequate supply of sea water of proper salinity and free of substances that may interfere with their normal development. The water used at Milford Laboratory is pumped from the Wepawaug River at a point about 100 yd from its entrance into Long Island Sound. Because the tidal rise and fall in this area is from 6 to 10 ft, the flushing rate of this comparatively narrow and shallow inlet is relatively high.

The sea water is pumped into a 6 000-gal wooden storage tank located in the laboratory attic. Because pumping normally takes place 1½ hr before and after the high tide stage, the salinity of the water is usually near 27 parts per thousand, which is virtually the same as in Long Island Sound, where the majority of the forms, the larvae of which are described in this article, exists. To assure a supply of water of high salinity the intake of the salt water system is located approximately 4 ft below the mean low water mark; therefore, it is at a safe distance from the surface layers which, after periods of heavy rains, may be greatly diluted.

The main pump providing the laboratory with salt water is rubber-lined. The intake and distribution lines, as well as the check and cutoff valves, are made of lead. The faucets, however, are of hard rubber. The storage tank is of cypress wood and is painted inside with asphalt paint.

We prefer lead pipes because, although pipes made of several new plastics are nontoxic, light and inexpensive, they possess several important disadvantages. One of them is that since it is often necessary to reduce fouling inside of the pipes by treating them with hot water or steam, this treatment, commonly used with lead pipes, cannot be employed in systems containing plastic parts as it may cause damage, especially at the joints of the pipeline.

Another serious disadvantage in using plastics is that they adsorb and absorb many chemicals, including insecticides, and once contaminated can themselves become a source of later contamination of the sea water. Moreover, since some plastics are permeable to insecticides and other compounds, these materials might enter from the sur-

rounding soil into pipes carrying sea water. Finally, some laboratories that have plastic sea water systems have complained that since these pipes are not electrically self-grounded, they present a serious element of danger in laboratories with wet floors.

We are finding an increasing usage for plastic pumps and pipes, especially in our temporary installations. We have also found that tanks made of Fiberglas, instead of wood, can be advantageously used, especially in areas where wood-boring organisms, such as *Teredo*, are common.

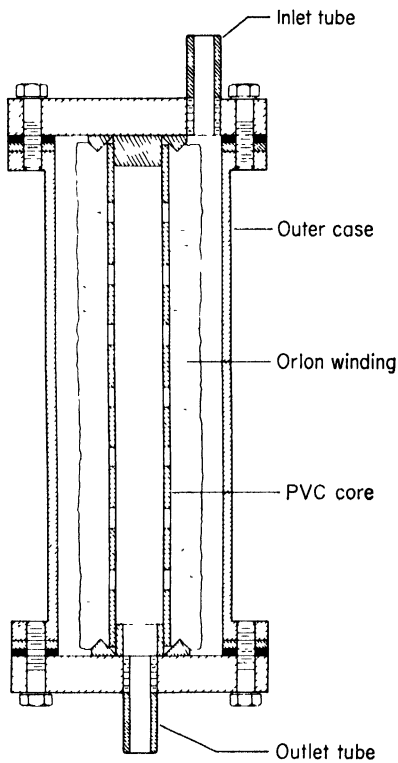


FIG. 1. Diagram of water filter designed to remove all particulate matter larger than 15 μ in diameter. Description in text.

Normally, in addition to small algae on which larval and juvenile mollusks feed, sea water contains many large diatoms, free-swimming crustaceans, gastropods, worms, etc., and their eggs and larvae. Many of these forms compete with bivalve larvae for food, prey on them or may even harbor diseases or parasites that could be transmitted to larvae. We prevent undesirable organisms of larger sizes from entering our larval cultures by filtering the water and later killing the smaller forms with ultraviolet light.

The filter element consists of a polyvinylchloride (PVC) core wound with Orlon. The complete unit (Fig. 1) is manufactured by Commercial Filters Corporation, Melrose, Massachusetts (filter no. CFXl-10-5

with an O15-R10X filter element). These filters, designed to remove all particulate matter larger than 15 μ in diameter, are made with a variety of core and winding materials. We chose the PVC core because it is nontoxic, and the Orlon winding because it is inexpensive, nontoxic and does not support bacterial growth.

To prevent fungus diseases in clam larvae and juveniles we began treating sea water with ultraviolet light in 1954 and, within a short time, had some evidence that such treatment, even of running, unfiltered sea

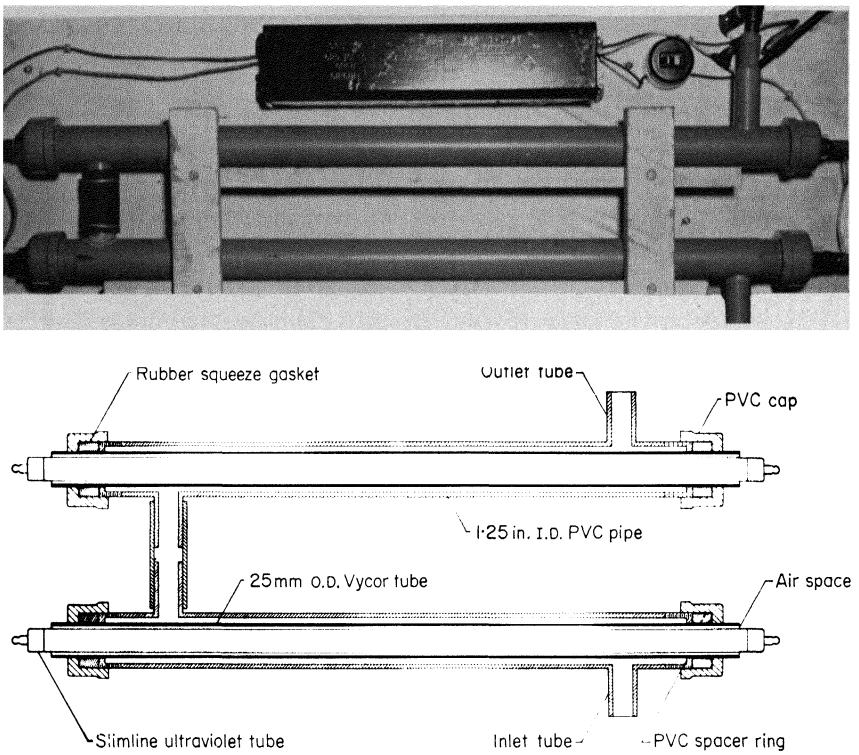


FIG. 2. Photograph (*above*) and drawing (*below*) of ultraviolet water treatment unit used at Milford Biological Laboratory. Description in text.

water, was helpful in preventing mortality of juvenile clams. In the summer of 1955 it was definitely demonstrated that larval cultures, receiving treated water and untreated phytoplankton from the outdoor mass culture, developed fungus, whereas larval cultures in which phytoplankton and sea water were both treated did not. Since that time, it has become a routine practice to treat with ultraviolet light all sea water used for our larval cultures and for keeping recently-set clams and oysters. Moreover, we are attempting to supply ultraviolet-treated running sea water to all containers in which later stages of juvenile clams are grown.

Ultraviolet treatment of sea water for purification of shellfish has been described by several workers in Japan (Sato, 1954; Satoh, 1960) and Wood (1961) in England. As is the practice in our laboratory, Waugh (1958) also used ultraviolet-treated sea water for rearing larvae of the European oyster, *O. edulis*. Several of these authors have described the equipment used but, because of certain considerations, we constructed our own units, a description of which is offered here.

The ultraviolet water treatment unit consists of a $1\frac{1}{4}$-in inside diameter PVC pipe, 30 in long, threaded at each end for caps (Fig. 2). A small ring of PVC is cut to fit inside of each end of this pipe and reamed to act as a spacer for a 25-mm Vycor tube. A squeeze gasket is used to make a water-tight seal between the Vycor tube and the end of the PVC pipe. An inlet tube is located on the side at one end of the PVC pipe and an outlet tube is located on the opposite side at the other end. The 33-in-long, slimline ultraviolet tube lays free in the $32\frac{1}{4}$-in-long Vycor tube and extends slightly beyond at each end.

In practice we use two such units connected in a series so that the water passes the length of both tubes. Since there is only about a $\frac{1}{8}$-in layer of water surrounding the Vycor tube, this apparatus, when used with filtered sea water, should give practically sterile water at the rate of flow of about 10 gal per min. With unfiltered sea water the efficiency is not expected to be as great, but our experience has shown that even then the treatment is of considerable help in reducing mortality of juvenile clams and in preventing fouling by tunicates, worms and bryozoa.

To condition mollusks for out-of-season spawning it is necessary to keep them in running sea water at temperatures of 18° to 20°C or sometimes higher. Warm sea water is also needed for rearing larvae and juveniles during the cold season. Since the water must not contact toxic metals, conventional water heaters cannot be used. Therefore, to heat the water we use a type of heat exchanger (Loosanoff, 1949). The sea water is heated as it passes through a coil of lead pipe immersed in hot fresh water, which fills the tank of a conventional gas water heater that has had the top removed to permit insertion of the lead coil (Fig. 3). However, because the thermostatic controls of a conventional water heater are not sufficiently accurate, the gas flame is controlled through a solenoid gas valve by a Minneapolis-Honeywell thermostat (T415A323XA3). The thermostat-sensing bulb is encased in a lead well in the warm sea water line and maintains the temperature at 37°C $\pm$ 0·5°C.

By mixing varied amounts of cold and heated sea water any temperature between that of the unheated water and 37°C can be main-

tained. In our winter work, when the temperature of the water in Milford Harbor is near freezing, we often simultaneously employ streams of water at 5°, 10°, 15°, 20°, 25°, 30°, and even 35°C. Of course, any other temperature within this range can also be maintained by using constant level jars of cold and warm water and regulating the

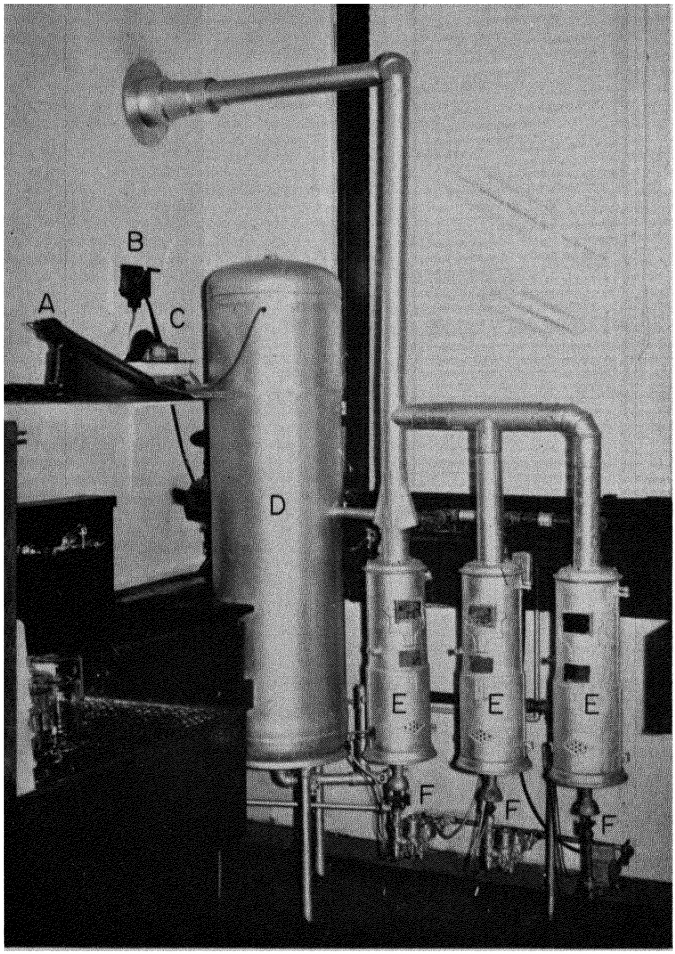


FIG. 3. Heat exchanger to provide laboratory with warm sea water. A, thermostat-sensing bulb; B, thermostat; C, air pump to prevent stratification of fresh water in tank; D, tank; E, gas water heaters; F, solenoid gas valves.

flow from these jars into a mixing chamber from which water of desired temperature flows into trays or aquaria where experimental animals are kept (Fig. 4).

To keep larval cultures at desired temperatures various constant temperature devices are used. Since a temperature of about 24°C is

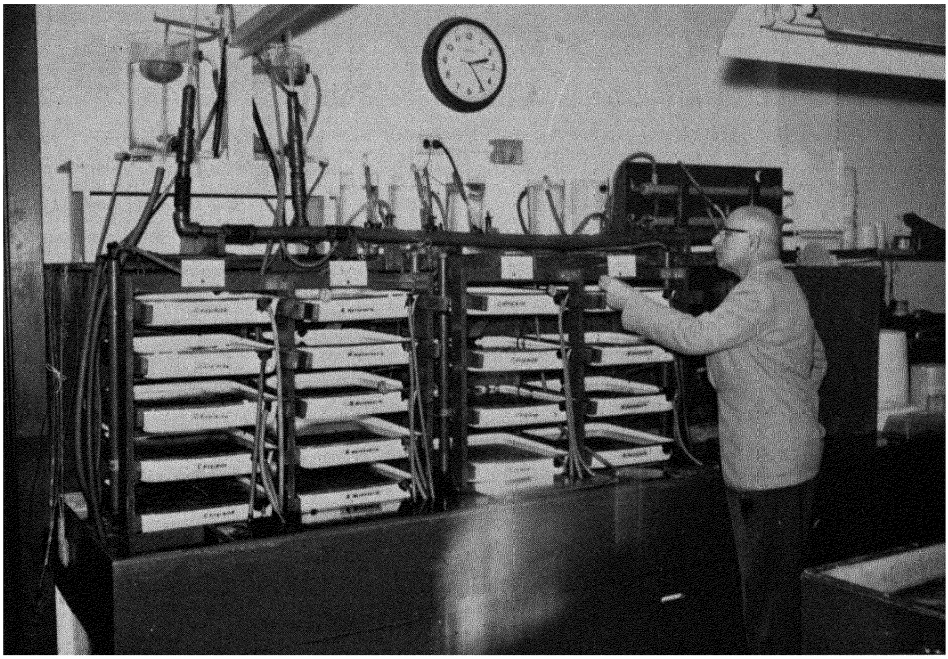


FIG. 4. Racks of trays for conditioning bivalves for spawning. Racks are provided with running sea water of different temperatures. Constant level jars for warm and cold water are seen in upper left corner. Water from these two jars is mixed in required proportions in the smaller glass jars located on lower shelf. Ultraviolet unit for treatment of water is located at right.

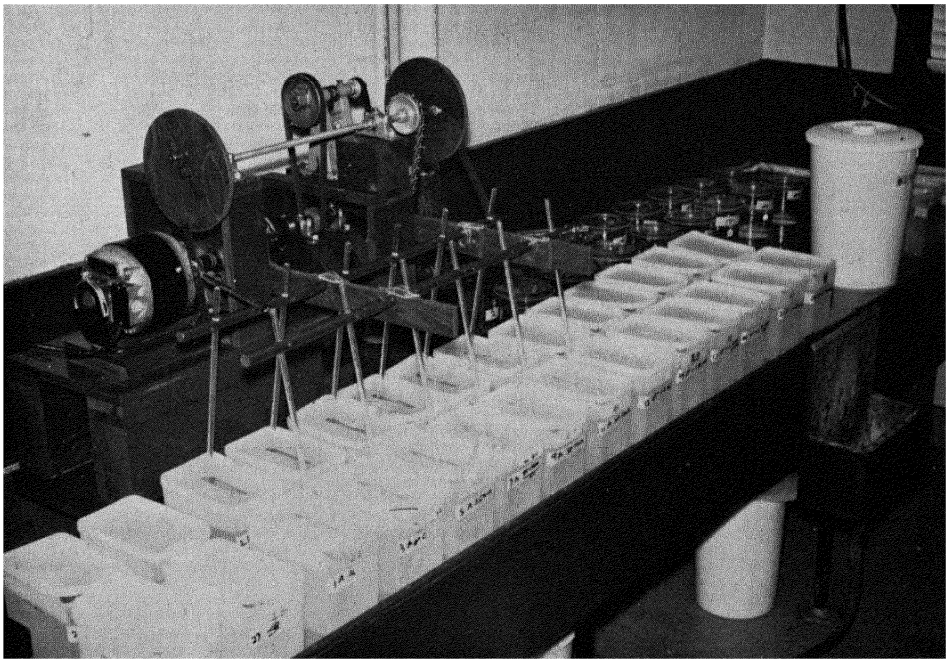


FIG. 5. Constant temperature water bath used to maintain desired temperature in culture vessels, which are partially immersed in water circulating in bath.

near the optimum for growth of algae, such as *Isochrysis galbana* (Ukeles, 1961), which are the best larval foods, this temperature level is often maintained. However, because 24°C is somewhat above normal room temperature, our simplest and most commonly used temperature control devices are lead-lined water tables, 3 ft × 12 ft, that serve as constant temperature water baths (Fig. 5). These tables are filled to a depth of 3 to 4 in with tap water, which is kept in constant circulation by a pump that takes water at one end of the table and discharges it

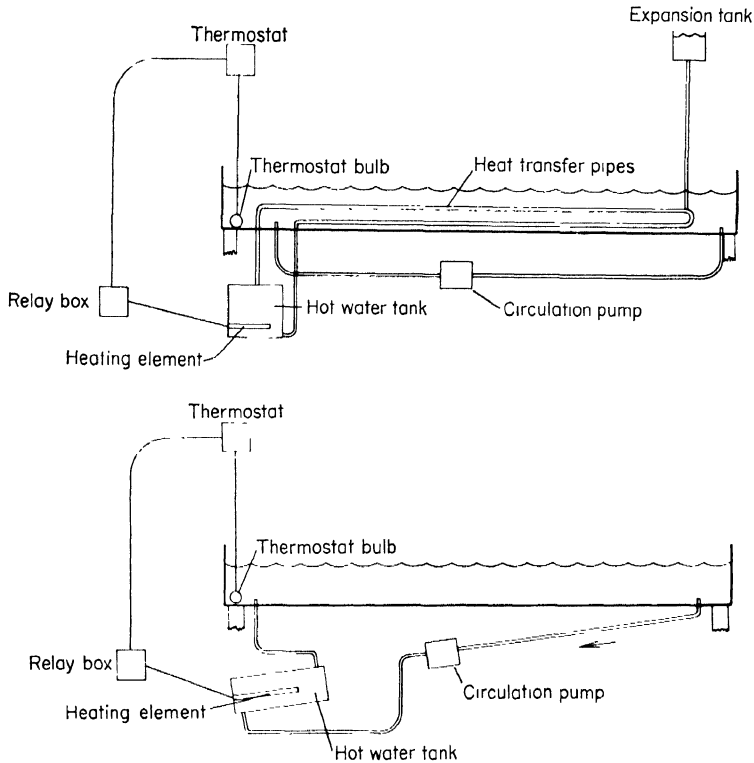


FIG. 6. Two methods of heating water for constant temperature baths. Diagram of closed system above, and open system below.

at the other end. A Minneapolis-Honeywell thermostat (T415A323XA3) with the sensing bulb enclosed in a lead pipe, immersed in the water on the table, controls a 1000- or 1500-W immersion heater. The heater may be either inserted in the pipeline, through which the circulating pump transfers water from one end of the table to the other (open system) or it may be inserted in a small hot water tank and the heat transferred to the water on the table by passage of the water from the tank through a lead coil or loop immersed in the water on the table (closed or heat exchange system) (Fig. 6).

Whenever the larval cultures are to be kept at about 24°C any type of container, the lower part of which is immersed in the bath, will maintain this temperature because convection currents within vessels prevent temperature stratification. Even in containers of

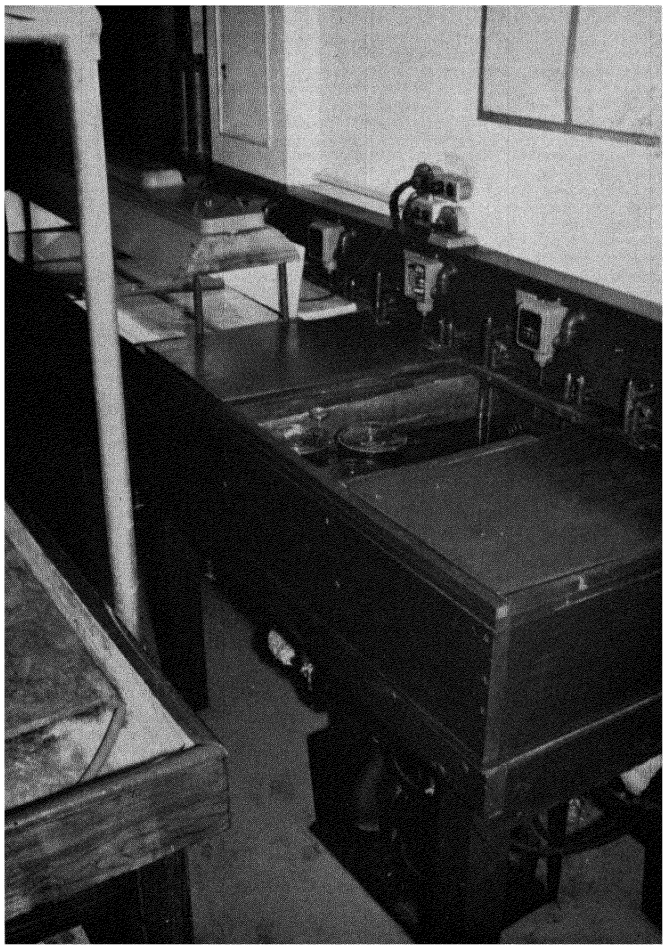


FIG. 7. Constant temperature apparatus consisting of 6 units. Temperature of each unit can be adjusted independently and maintained at any desired level within the range from 5° to 37°C. If necessary, all units may be maintained at the same temperature.

different sizes and shapes the temperature will vary only slightly, while in a series of individual containers of the same type the water will be maintained at almost precisely the same temperatures.

A similar arrangement can be used to maintain temperatures below that of the room by employing a liquid cooler, instead of a

heater. Units that combine a heater and cooler and will maintain temperatures above or below room temperature are also available. However, when cooling devices are used it is necessary to keep the water in cultures continuously agitated to prevent temperature stratification.

To study the effects of different temperatures on development of eggs and larvae of bivalves another apparatus was devised (Fig. 7). This apparatus, which can also be used for studies of many other forms, consists of a series of six lead-lined tanks, each 15 in wide by

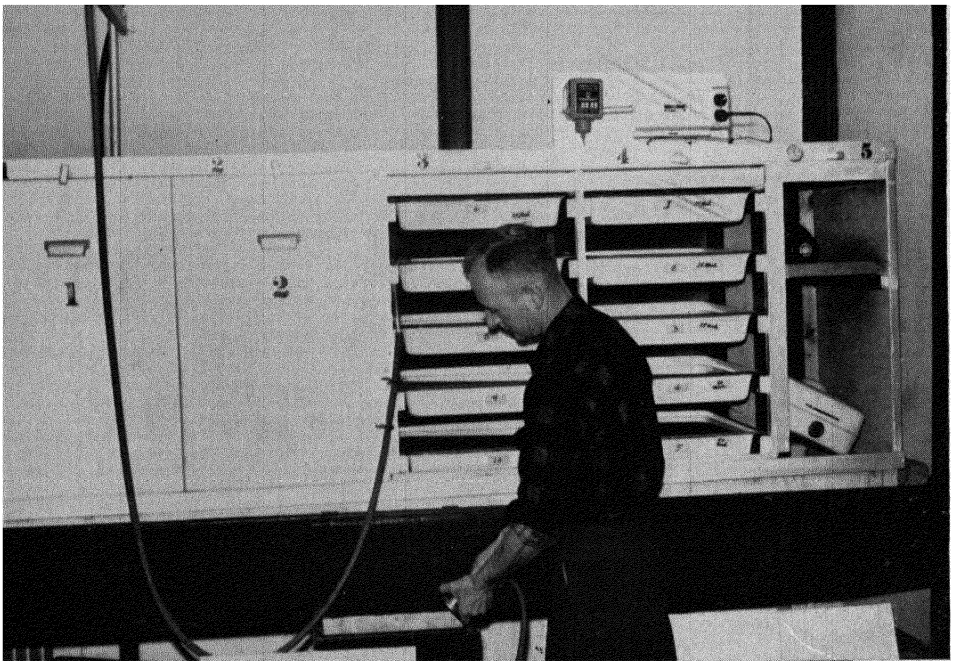


FIG. 8. Constant temperature air chambers in which trays or other containers with larval or juvenile mollusks are held. Electric heater and fan for circulating the air can be seen in right hand corner of unit.

26 in long and 13 in deep and filled with fresh water to a desired level. Vessels containing experimental animals are immersed in these tanks.

To maintain water in the tanks at desired temperatures each tank is equipped, along its walls, with loops of tubing to circulate cold and hot water. The amount of water passing through each of these tubes is controlled by double-action thermostats which activate solenoid valves so that if the temperature in any tank falls below the thermostat setting, the valve in the line, through which hot water circulates, opens, allowing hot water to flow through the loop. If, on the other

hand, the temperature exceeds that indicated by the thermostat, the solenoid valve in the cold water line opens, allowing circulating cold water to reduce the tank temperature. To have the entire mass of water at uniform temperature a circulator pump is employed. The temperature controls of the entire unit are so arranged that all tanks may be maintained at the same temperature, within the range from 5° to 37°C or, if necessary, at different temperatures.

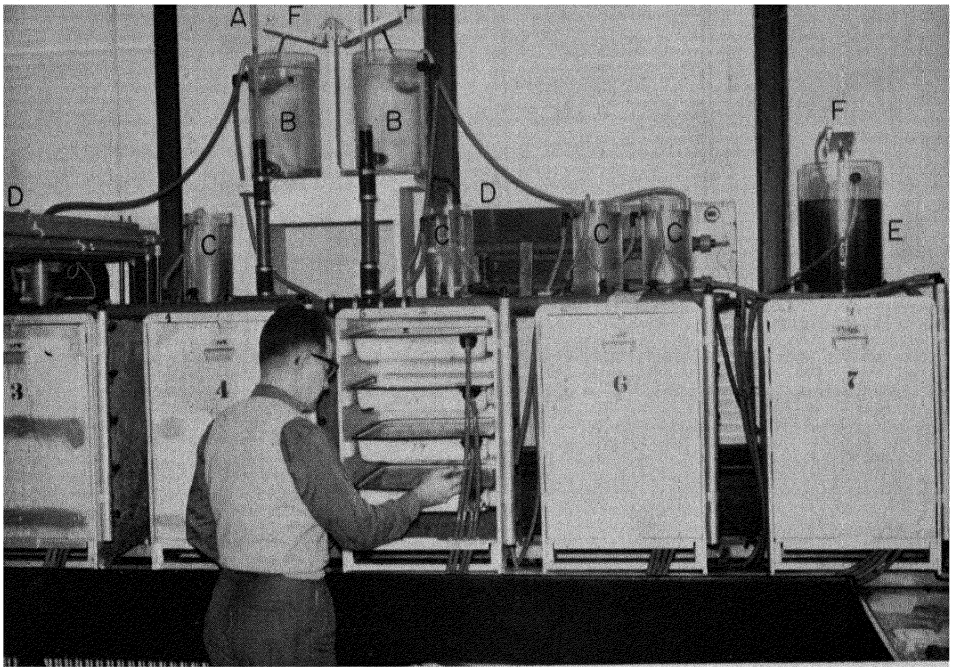


FIG. 9. Temperature apparatus for simultaneous studies of certain aspects of behavior of juvenile mollusks in running water of different but constant temperatures. A, escape tube for air trapped in sea water lines; B, cold and warm water constant level jars from which water in different proportions enters mixing jars (C). Each jar may be maintained at any temperature ranging from 5° (in winter) to 35°C; D, ultraviolet units through which all sea water passes to constant level jars; E, constant level jars from which phytoplankton is added at a definite rate to running sea water; F, floats controlling levels in constant level jars.

To control the temperature of the air chambers in which culture vessels are kept in some experiments thermostatically-controlled electric heaters are used. For example, in experiments, where a series of four banks of five trays each of standing water are used to hold juvenile clams, a uniform constant temperature is maintained by enclosing all twenty trays in a chamber where thermostatically-controlled electric heaters are installed (Fig. 8). When heated air is used, however,

special precautions are necessary to prevent its stratification. To achieve this in the enclosure where our racks of trays are kept a large fan forcing air through has been found sufficient.

Still another temperature apparatus is used at our laboratory for simultaneous studies of growth of juvenile mollusks in running water of different but constant temperatures (Fig. 9). The entire apparatus consists of seven independent units, each insulated so as not to be affected by outside temperatures. As many as five trays may be placed in each chamber. By mixing, in winter, different proportions of warm and cold sea water, temperatures ranging from about 5° to 35°C can be maintained quite accurately.

The amount of water entering each tray can be adjusted to a desired rate and, when necessary, the trays in all seven chambers may receive the same quantity of water and plankton food per hour. As a rule, sea water and food, before entering trays containing juvenile mollusks, are passed through the special unit where they are sterilized by ultraviolet rays.

In addition to various apparatus and devices discussed in this section there are several others that have been used in special studies. A description of these will be given elsewhere.

III. Conditioning Mollusks for Out-of-Season Spawning

Before the present method of providing laboratories with warm water in winter was developed, experiments on most of the bivalves and, especially, their larvae were confined, in New England waters and similar areas, almost exclusively to the short periods of natural propagation, usually lasting for only the $2\frac{1}{2}$ or 3 summer months. However, since it was found that in many bivalves, by using proper conditioning methods, normal development of gonads can be stimulated and spawning induced during late fall, winter and spring, the experimental period has been greatly expanded (Loosanoff, 1945).

Conditioning of bivalves to develop mature gonads during the cold part of the year is relatively simple. It consists of placing mollusks, brought from their natural environment where water temperature may be near freezing, into somewhat warmer water and then gradually increasing the temperature several degrees each day until the desired level is reached (Loosanoff and Davis, 1950). Sometimes, especially towards the spring, instead of a gradual conditioning the mollusks can be placed directly in water of about 20°C. As a rule, the gametes obtained from these mollusks were no less viable than from those conditioned gradually. We have often employed this more rapid

approach, thus shortening by several days the length of the conditioning period which, for oysters kept at 20°C, is approximately 3 to 4 weeks.

The conditioning period can also be shortened by keeping mollusks at temperatures higher than 20°C (Loosanoff and Davis, 1952b). For example, *Crassostrea virginica* kept at 25°C developed ripe spermatozoa and fertilizable eggs by the 5th day, and light spawning could be induced on the 7th day. When kept at 30°C ripe spermatozoa and fertilizable eggs were found in oysters which, only 3 days before, were brought from the ice-covered harbor where they were hibernating. Some oysters of this group were induced to spawn on the 5th day.

Obtaining spawn from another common bivalve, the hard shell clam, *Mercenaria mercenaria*, is also relatively simple in summer. It is often accomplished merely by raising the water temperature a few degrees and by adding a sperm suspension (Loosanoff, 1937a). Previously, as already mentioned, this could be accomplished only during a short period, whereas, using our recently-developed methods, it is now possible to obtain ripe gametes and raise larvae of this species on a year-round basis (Loosanoff and Davis, 1950, 1951).

The method for conditioning clams for spawning in winter is the same as that described for oysters. The entire conditioning period takes approximately 2 to 3 weeks, but can be made even shorter towards or during spring. On several occasions clams brought directly from natural beds during early spring could be induced to spawn without any preliminary conditioning. However, this method often failed and cannot be considered reliable. Usually, only males responded on such occasions. As a rule, some conditioning of clams is necessary, even towards spring, to have a reliable source of eggs and sperm.

Our studies have demonstrated that bivalves can be conditioned for late fall and early winter spawning only after they recover from the natural spawning activities of the preceding summer. This recovery consists of many complex physiological processes leading, in general, to accumulation of reserve materials, of which glycogen is probably the most important (Loosanoff, 1937a, 1942). Since many species of bivalves of Long Island Sound, including oysters and clams, sometimes continue to spawn until late August or even the middle of September and are not completely recovered from these activities until the end of November, they cannot be conditioned for spawning during these months.

We solved the problem of supplying ripe mollusks during the period from late August to late November by delaying their gonad development and spawning until late fall (Loosanoff and Davis, 1951). Clams,

M. mercenaria, and oysters, *C. virginica*, are taken from Long Island Sound early in the season, usually late in May, long before the beginning of their natural spawning, and transplanted to the waters of Maine, where the summer temperature averages about 7° lower than in our waters. This temperature, while permitting slow development of gonads, is, nevertheless, low enough to prevent spawning. Thus, when oysters and clams in Long Island Sound are already spent, those transplanted to Maine still retain their spawn. In the fall, small groups of these mollusks are routinely shipped back to our laboratory, where they are easily induced to spawn, providing normal gametes which are unobtainable locally during that time of the year.

By using the above method spawning of *C. virginica* can be postponed only for 6 or 8 weeks after oysters of Long Island Sound are completely spent. After that period the oysters, even if they are still kept in the waters of Maine, begin to resorb undischarged gonad material and, thereafter, become useless as spawners. We overcame this difficulty by developing another useful method, which postpones early gonad resorption. It consists of conditioning oysters early in the spring and spawning them at Milford by early June. After that they are transferred to the colder waters of Maine. Oysters treated in this manner must resorb old gonads and build up glycogen before developing new gonads. Because they are compelled to go through these processes, these oysters reach ripeness much later in the season than those that are planted in Maine without spring conditioning and spawning and, as a result, they do not begin to resorb gonad material as early as do unspawned oysters transferred to Maine at the same time. Taking advantage of this situation we have been obtaining normal larvae from October to January from spawn of oysters so treated.

Because *M. mercenaria* does not resorb undischarged gonad material in the fall, as oysters do, transferring them to the colder waters of Maine in the spring proved to be a highly satisfactory method of delaying spawning. Under these conditions the clams retain sperm or eggs throughout the summer and, as a result, can be induced to spawn throughout the next fall, winter and even during the following spring, always producing gametes which develop into normal larvae.

We have also delayed spawning of clams and oysters by taking these mollusks early in the summer from their natural habitat and keeping them in insulated boxes through which mechanically-cooled sea water flowed. Usually, only a comparatively small number of adult mollusks could be conveniently kept under these conditions and, as a rule, bivalves so treated were in much poorer condition than those kept under natural surroundings in the waters of Maine. More-

over, a failure of the artificial refrigeration system may cause the entire stock to spawn prematurely.

By combining our two methods, one consisting of conditioning mollusks for spawning during the cold periods and the other of delaying gonad development and preventing spawning during their normal reproductive season, ripe bivalves may now be available throughout the entire year.

We have also found (Loosanoff and Davis, 1952a) that *C. virginica* and *M. mercenaria* are able to reproduce several times a year, provided that changes in ecological conditions, especially temperature, are so controlled that these mollusks can rapidly recover from spawning, accumulate in their bodies material needed for gonad development, and begin the cycle again. As a result of the discovery of these new approaches and methods, as much can now be accomplished in one year in certain fields of the biology of bivalves as could formerly be done in three or four.

It should be emphasized that our conditioning methods are not equally successful or applicable to all groups of oysters, *C. virginica*, and, perhaps, certain other species of bivalves of our Atlantic and Gulf coasts. This is probably because populations of these species are not genetically homogeneous, but consist of different physiological races. We began to suspect the existence of such races in *C. virginica* as early as 1937 (Loosanoff and Engle, 1942). Stauber (1950), in reviewing the literature on spawning of the American oyster, also came to the conclusion that oysters from different areas along our Atlantic coast may belong to different geographical races. Our experiments in this field strongly supported this assumption by demonstrating that, even though all these oysters belong to the same species, the temperature requirements for gonad development and spawning of the northern populations are definitely lower than those of the southern groups (Loosanoff and Nomejko, 1951).

The results of our later, more extensive studies, in which several thousand specimens representing populations of different areas of the oyster-producing belt extending from the Gulf of Mexico to Cape Cod were used, fully supported our original conclusions (Loosanoff, 1958a). The oysters used in these experiments and observations were from Florida (Gulf of Mexico), South Carolina, Virginia, New Jersey and New England. They were received in the fall, after they had completely spawned in their native environment, and were kept in Milford Harbor throughout early winter. Some time in January the first groups of these oysters were transferred to the laboratory to be conditioned for spawning.

We employed two criteria to evaluate ripeness of the oysters. The first was to ascertain the number of days needed for 50% of the oysters constituting a sample to develop active spermatozoa or fertilizable eggs. Secondly, we had to determine the length of the conditioning period before spawning in 50% of the oysters could be induced by our usual method. Each sample contained fifty adult individuals.

The experiments showed conclusively that Long Island Sound oysters develop gonads and can be induced to spawn after considerably shorter conditioning periods than those required by southern oysters. When kept at the same temperatures oysters from New Jersey, although slower than those of Long Island Sound, showed, nevertheless, much faster gonad development than oysters of Virginia, South Carolina and Florida. In averaging the results of the experiments it was found that 50% of Long Island Sound oysters, conditioned at 21°, 24° and 27°C, contained mature gametes after only 15, 8 and 5 days, respectively. The corresponding groups of New Jersey oysters reached this stage only after 55, 32 and 22 days, thus requiring three or four times as long at the three above-mentioned temperatures as did the northern race.

In certain experiments we were able to induce spawning in 50% of Long Island Sound oysters after only 18 days of conditioning at 21°C. To achieve the same results with New Jersey oysters 78 days were needed. The more southern groups kept under the same conditions failed, as a rule, to produce 50% spawners.

The most striking differences were noticed when oysters of different geographical regions were kept at relatively low temperatures. For example, after 68 days of conditioning at 12°C, 67% of Long Island Sound oysters contained mature eggs or spermatozoa. In this group we were able to induce spawning in one male and, 10 days later, in one female. Oysters of the other groups kept at the same temperature contained not a single individual with mature gonads, even after 78 days. Moreover, in the majority of New Jersey and Virginia oysters and in all of those from South Carolina and Florida the gonads were so poorly developed that the sexes could not be distinguished, even by microscopic examination of the raw gonad material.

The method of inducing spawning of oysters and clams in summer has already been described in detail (Galtsoff, 1930, 1932; Loosanoff, 1937a, 1954). The same method, as a rule, has also been used to induce spawning in other bivalves. In general, our present method can be described as follows: After the proper conditioning period ripe bivalves are placed in glass spawning dishes, each containing approximately 1 liter of sea water of the same temperature as that at which mollusks



FIG. 10. Ripe oysters in spawning dishes. Male oyster is shown spawning in center dish.



FIG. 11. Inducing spawning of clams, oysters and other bivalves by immersing dishes of sea water containing animals in warm water on spawning table.

were conditioned (Fig. 10). These dishes are partly immersed in a large tray or sink, which is filled with hot water, thus quickly raising the temperature in the dishes to the desired level (Fig. 11).

In some instances thermostimulation alone is sufficient to induce spawning. In other cases, however, mollusks need additional stimulation, which consists of adding to the water small quantities of sperm or egg suspension made from gonadal material of ripe individuals of the same species. Many forms quickly respond to combined thermal and chemical stimuli; others, such as the common mussel, *Mytilus edulis*, do not usually respond to this method but can, nevertheless, be induced to spawn by other means, which will be discussed later.

In a special series of experiments we tried to cause artificial discharge of reproductive elements by injecting weak solutions of Mn_4OH and other chemicals into the bodies of bivalves that could not be spawned by other means. The results were usually not gratifying, except in the case of *M. edulis*, when injection was made in its adductor muscle.

At the time of our experiments to induce spawning in ripe bivalves we were already aware of the success of Japanese workers in inducing spawning in mussels by giving them a mild electric shock. We repeated these experiments but, unfortunately, with indifferent results.

In still other species, for example, *Modiolus demissus*, all our methods, including those that were successful in the case of *Mytilus edulis*, proved to be ineffective in inducing spawning. Therefore, unless ribbed mussels spawn naturally, thus providing normally fertilized eggs, no other means, except perhaps stripping, are left for obtaining their spawn.

Fertilizable eggs of many species, including those of *C. virginica* (Brooks, 1880), can be obtained by stripping mature females but, since many of these forms spawn so readily in response to chemical and thermal stimulations, it is seldom necessary to resort to this means. However, when working with other species, especially those that cannot be spawned by conventional methods, stripping may be the only way to obtain ripe eggs. It is a simple process and is carried on as follows: After removing the outer membrane that covers the gonads, the mollusk is gently rinsed in sea water. This action separates from the gonad large numbers of eggs without serious injury to them. Using a series of sieves of proper size mesh the eggs are later freed of blood cells, pieces of tissue, etc., and then placed in sea water to which sperm is added. The fertilized eggs can then be placed in culture vessels.

This approach is possible only for eggs of those forms in which the germinal vesicle dissolves after stripping. In many species, however,

including *Mercenaria mercenaria* and *Pitar morrhuana*, attempts to fertilize stripped eggs usually fail because in these eggs the germinal vesicles remain intact and, as a result, fertilization does not occur. Under normal conditions the germinal vesicles in eggs of such species dissolve while they are still in the ovaries of the female, just before they are discharged in the process of spawning. Upon dissolution of the germinal vesicle the germinal spindle is formed and the discharged egg is ready for fertilization (Loosanoff, 1953).

Recently, following the suggestion of Mr. David Tranter of Australia, we used a weak solution of ammonium hydroxide to break the germinal vesicle of eggs of certain bivalves. By employing this method we succeeded in raising normal larvae from eggs stripped from *Mercenaria mercenaria*, *Tapes semidecussata* and several other species.

After the eggs were washed from a gonad they were passed through a coarse, 50-mesh screen to remove debris, large pieces of tissue, etc. Later, they were washed on a 325-mesh screen which retained the eggs but let pass the body fluids that might pollute the water in culture vessels. After that, 3 ml of 0·1 normal solution of ammonium hydroxide were added to every 100 ml of the prepared suspension of eggs in sea water. After the eggs were in this solution for some time they were washed again on a 325-mesh screen, being finally ready for fertilization. A more detailed description of handling fertilized eggs will be given in the section on methods of cultivation of eggs and larvae.

The length of exposure to the solution of ammonium hydroxide may vary somewhat from species to species. The following table shows the ratio between length of exposure and percentage of normally developing eggs of *M. mercenaria*:

15 minutes—32%
30 minutes—16%
45 minutes— 9%
60 minutes— 3%
75 minutes— 2%
90 minutes— 0%

Even after 90 minutes of exposure to the solution of ammonium hydroxide some eggs became fertilized, but their development was not normal.

The percentage of normal larvae obtained from chemically-treated eggs was low compared to that of naturally spawned eggs but, nevertheless, it was high enough to permit successful culturing of larvae of those species in which we were not able to induce spawning. Perhaps by changing the concentration of ammonium hydroxide, using other

chemical agents, or by improving the methods of stripping even better results may be obtained.

Finally, there were several species of bivalves which we could neither spawn artificially nor collect their normally discharged eggs. Moreover, eggs stripped from some of these forms could not be fertilized regardless of various preparatory measures, which included the chemical treatment described above.

Fecundity of many lamellibranchs, especially those of commercial importance, has been speculated upon for a long time. Brooks (1880) estimated that *C. virginica* could produce between 18 750 000 and 125 000 000 eggs. He based his estimate upon volume of material removed from the ripe female, but stated that this figure should be reduced by approximately 50% because of other matter that was measured together with eggs. Churchill (1920) stated that a large oyster may discharge 60 million eggs, while Galtsoff (1930) estimated that the number of eggs released in a single spawning may range between 15 and 115 million. He concluded that the maximum number of eggs that can be released by a single female during the entire spawning season is approximately half a billion. Burkenroad (1947), without offering any experimental observations of his own, suggested that Galtsoff's estimate was approximately ten times too high. Belding (1912) estimated that *M. mercenaria*, $2\frac{1}{2}$ in long, produces an average of 2 million eggs, a figure not substantiated by experimental studies.

Since reliable information on the fecundity of even the most commonly studied pelecypods was unavailable, experiments were undertaken by Davis and Chanley (1956b) to determine total numbers of eggs actually produced by individual oysters, *C. virginica*, and clams, *M. mercenaria*, under natural and artificial conditions.

The first series of observations was made on seventy-five oysters, measuring from $3\frac{1}{2}$ to $4\frac{1}{2}$ in long, and on the same number of clams approximately 3 to 4 in long.

The experiments were conducted in the laboratory during the winter, a most convenient period for proper conditioning of both clams and oysters. Each bivalve was individually numbered and a complete record was kept of its behavior during the entire experiment. The first group of oysters composed of twenty-five individuals was spawned at 3-day intervals, the second group at 5-day intervals and the third at 7-day intervals. In clams, which were also divided into three groups of twenty-five individuals each, spawning was induced at 3-, 7- and 14-day intervals. Spawning of these groups of clams and oysters was continued at the specified intervals for more than 2 months.

Experiments have shown that, as a rule, an individual oyster or clam does not discharge all its eggs or sperm in a single spawning, but will continue to spawn at intervals over extended periods. One female oyster spawned on sixteen occasions and a clam, eleven times. The number of spawnings per female oyster ranged from two to sixteen. The highest number of eggs was produced by an oyster that spawned nine times, while a female that spawned sixteen times ranked second. The lowest total number of eggs released by an oyster was by an individual that was induced to spawn seven times.

No significant difference was observed in the average number of eggs released during the entire experimental period, whether the oysters were induced to spawn at 3-, 5- or 7-day intervals, although the average number of spawnings per female oyster decreased progressively as the intervals between spawnings were increased. It was also determined that female oysters having larger numbers of eggs tended to spawn more frequently than did females with smaller numbers.

The highest number of eggs released by any female clam in a single spawning was 24·3 million and the total number released by individual clams during the entire experimental period of about 2 months ranged from 8 million to 39·5 million, with an average of about 24·6 million.

There was no significant difference in the average number of eggs released in a season, whether the clams were spawned at 3-, 7- or 14-day intervals. It was also found that correlation between the number of times a female clam spawned and the number of eggs produced was not significantly different from zero.

An auxiliary experiment consisted of observations on spawning of fifty oysters taken from Milford Harbor early in April, brought into the laboratory and placed in conditioning trays at temperatures of about 20°C. Three weeks later these oysters were induced to spawn daily for 5 consecutive days, and seventeen females and twenty-four males responded during the first day. Altogether, this group contained twenty-four females and twenty-six males. Of the twenty-four females, fourteen spawned on 2 or more consecutive days, eight spawned on 3 or more consecutive days, five spawned on 4 or more consecutive days, and three females spawned on each of the 5 days of the experiment. Eight males spawned each day.

The important contribution of this experiment was the clear-cut demonstration that there is no 2- to 5-day refractory period during which female oysters cannot be induced to spawn, as maintained by Galtsoff (1930). On the contrary, the results suggest that upon proper

stimulation both male and female oysters can spawn any time they have physiologically-ripe sex cells to discharge.

The final experiment consisted of observations on nine female oysters developing gonads under normal conditions in Long Island Sound and induced to spawn at the end of June. The total number of eggs discharged by these oysters ranged from 23·2 million to 85·8 million and averaged 54·1 million eggs per female. Thus, both average number of eggs and maximum number per female of the summer



FIG. 12. Representatives of three groups of oysters of different ages and sizes used in studies to determine viability of their gametes. Members of oldest group were estimated to be between 30 and 40 years.

spawning group were about 20 million higher than found in the winter experiment. Nevertheless, none of these oysters discharged as many as half a billion eggs, as suggested by Galtsoff (1930). The larger number of eggs developed by oysters of this group, as compared with production of eggs by oysters conditioned in the laboratory during early winter, may be ascribed to larger reserves of glycogen possessed by oysters developing gonads under natural conditions.

A question that had long been of interest to biologists was, At what age do oysters and clams produce the best, most viable sexual products? Until recently, no answer could be given because no reliable methods

were available to conduct critical experiments on development of eggs and growth of larvae to setting or post-setting stage. Since development of these methods, such studies have become possible and recently were undertaken at our laboratory.

Three groups of oysters of different ages and sizes were conditioned for spawning (Fig. 12). The average age of individuals of the oldest group was estimated to be between 30 and 40 years, some of them being over 9 in long and over 4 in wide. The intermediate group of oysters of marketable size was from 5 to 7 years old, while the youngest group was composed of small oysters approximately 2 years old. These groups were conditioned and induced to spawn under controlled conditions, their larvae grown to setting stage, and rates of survival and growth of larvae from the three size groups compared.

The results showed no significant difference between oysters of the different age groups in the time needed to develop ripe gonads. We were somewhat surprised, however, to find that oysters of the oldest group responded to spawning stimuli more rapidly than individuals of the two younger groups.

There was also no significant difference in percentage of fertilizable eggs because almost 100% of the eggs of all three groups became fertilized. Furthermore, the percentage of fertilized eggs developing to straight-hinge larval stage showed no consistent variation that could be ascribed to size or age of parent oysters. Finally, no consistent difference was found either in the sizes of the early straight-hinge larvae originating from eggs of different age-group oysters or in survival and rate of growth of their larvae.

Similar studies on hard shell clams, *M. mercenaria*, measuring from 37 to 110 mm in length, also showed that there was no significant difference in viability of spawn produced by clams of different sizes and ages. Often the differences between the progeny of individuals of the same size groups were as great as the differences between those of different ages and sizes. Larvae grown from eggs of clams of all three sizes were successfully carried to setting stage.

On the basis of the above-described experiments we came to the conclusion that since there was no significant difference in the quality of spawn developed by individuals of different ages or sizes, mature oysters and clams of all age groups may be safely used as spawners.

Of special biological interest was the observation that the sexes among the oldest oysters were about evenly divided. This discovery was contrary to the old conception that in the oldest groups females should decidedly predominate in numbers. We also noticed that many of the largest and oldest oysters, while kept in the laboratory to be

conditioned for spawning, formed normal, new shell growth, thus indicating that even at that age and size the oysters did not lose their ability to grow (Fig. 12).

IV. Cultivation of Eggs and Larvae of Bivalves

A. *General description of the development*

Eggs of bivalves differ in many respects, including their size, color and specific gravity. They also differ in thickness of the membrane surrounding them (Costello *et al.*, 1957). In oysters and certain other forms this membrane is only a few microns thick. In others, however, such as *M. mercenaria*, the egg proper measures only 70 to 73 μ, while the total diameter of the egg and surrounding gelatinous membrane is about 170 μ. This membrane, in many instances, continues to surround the embryo past blastula stage and, on some occasions, until late trochophore stage is reached (Loosanoff and Davis, 1950).

We shall describe specific characteristics of the eggs later on, when discussing each of the species studied. Here, because the description of a typical bivalve egg and its development to straight-hinge stage or, as it is often called, early veliger has been given on many occasions, including Brooks (1880), MacBride (1914) and others, we shall present only a general picture of changes occurring from the moment the egg is discharged, or stripped, until it becomes a straight-hinge larva. This description is based upon observations made on eggs and early embryos of *Mactra* (= *Spisula*) *solidissima*, the surf clam, which is the largest bivalve of our Atlantic coast. It measures up to 7½ in long and can be found in considerable numbers from Labrador to Cape Hatteras. Additional information on spawning of these clams and rearing of their larvae is included in the section dealing with rearing of larvae of different species.

The diameter of a mature egg of *M. solidissima* averages 56·5 μ (Fig. 13*a*). Costello *et al.* (1957) give the diameter of the unfertilized ovum of the same species as ranging between 53 and 56 μ, thus agreeing with our measurements. According to Cahn (1951), who bases his conclusions on the work of the Japanese investigators, Kinoshita and Hirano (1934), whose paper was not available to us for consultation, the diameter of the egg of a closely related form, *Spisula sachalinensis*, is only 50 μ. Another group of Japanese workers (Imai *et al.*, 1953), studying the same species reports that the diameter of the mature egg of this clam varies from 70 to 75 μ, thus being considerably larger than the size given by Cahn. Jørgensen (1946) states that eggs of *Spisula subtruncata* of European waters vary in diameter from 50 to 55 μ.

Early development of the egg of *M. solidissima* is basically the same as that of many other bivalves. After dissolution of the germinal vesicle (Fig. 13*b*) the size and shape of the egg remain the same. If

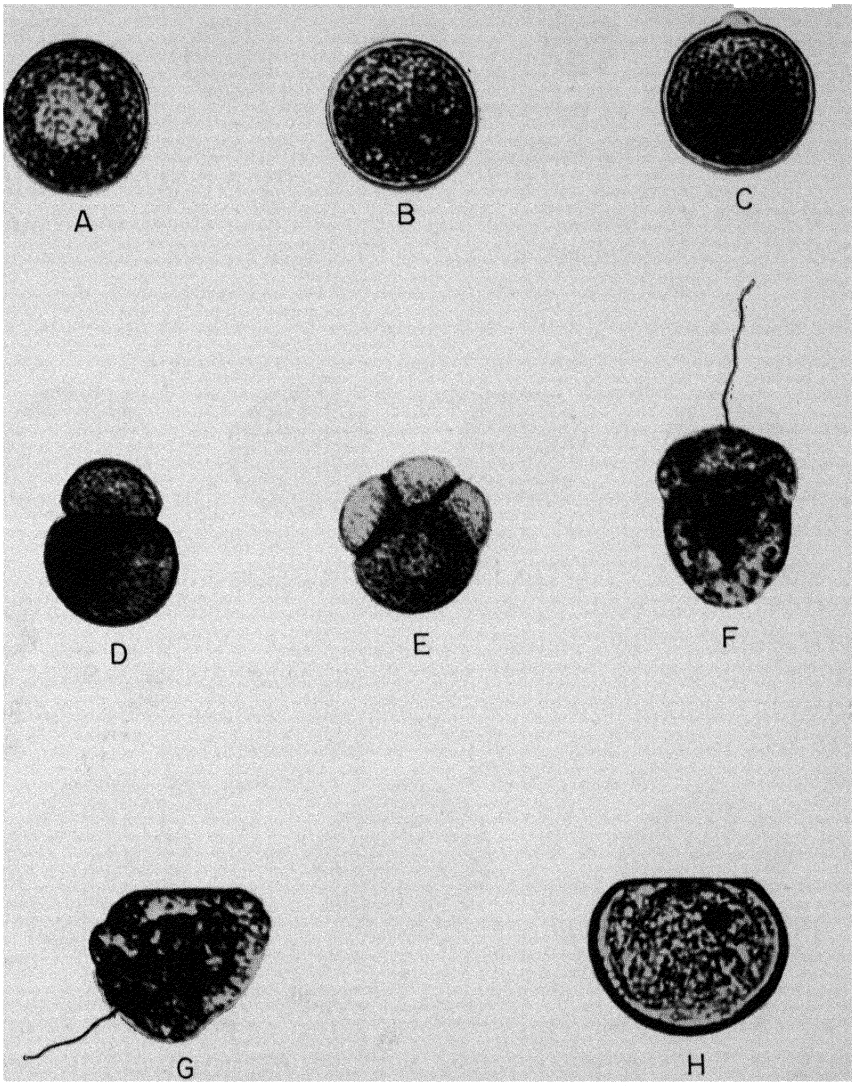


FIG. 13. Development of *Mactra* (= *Spisula*) *solidissima* from unfertilized egg (A) to straight-hinge larva (H). Diameter of egg is about 56 μ, while length of early straight-hinge larva is about 79 μ. Detailed description in text.

the fertilized egg is kept in water of about 20°C, the polar body is formed in about 45 min (Fig. 13*c*) and the two-cell stage, measuring about 65 μ along the longest axis, is reached in 90 min (Fig. 13*d*).

Development of the egg of a bivalve, as described above, is typical only of a group in which the germinal vesicle breaks upon discharge

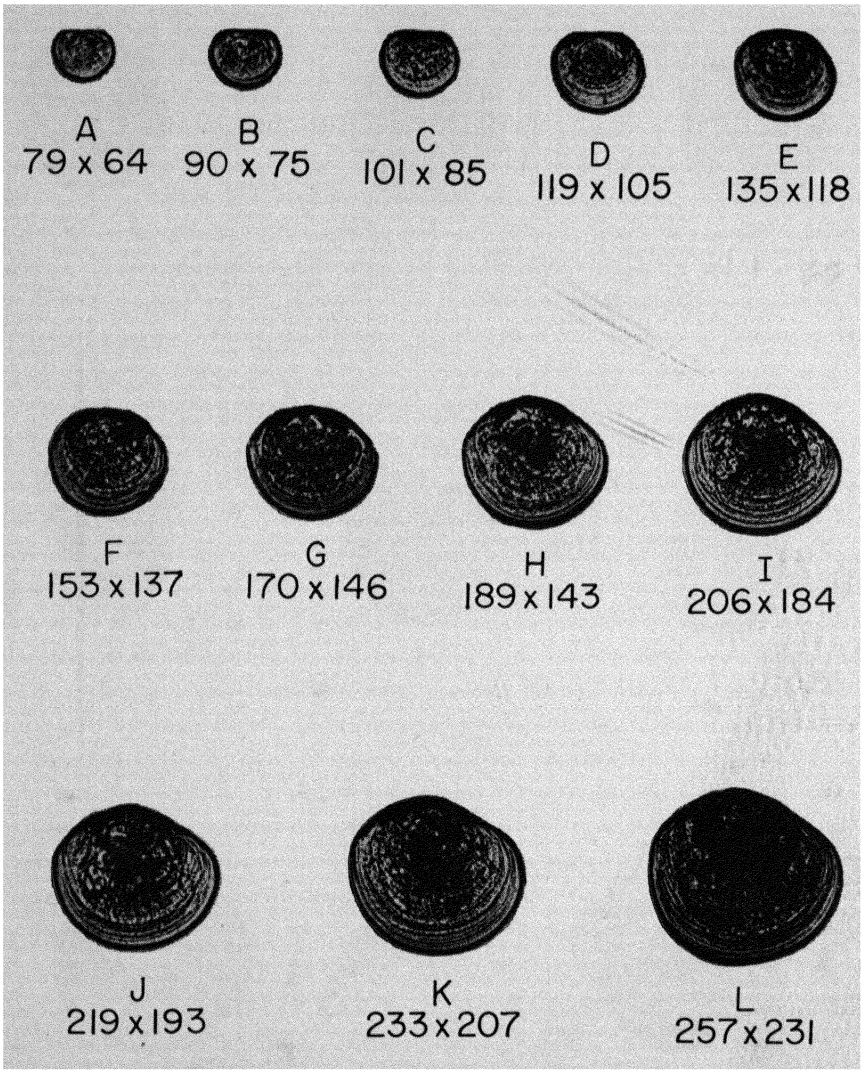


FIG. 14. Development of *Mactra* (= *Spisula*) *solidissima* from straight-hinge stage (A) to metamorphosis (L). Measurements of length and width of larvae of different stages are given in microns.

or upon stripping, thus rendering the egg ready for fertilization. Eggs of *Crassostrea virginica* and many other species belong to this category. In the other group stripped eggs continue to retain their

germinal vesicles intact and fertilization does not occur. However, as already mentioned, eggs of such species can be chemically treated and thereby become ready for fertilization.

As cleavage progresses and more micromeres are formed (Fig. 13*e*), the embryo gradually develops into a swimming, ciliated larva which eventually reaches trochophore stage (Fig. 13*f*). Under favorable conditions this stage may be reached in 12 to 16 hr, depending upon the original condition of the eggs, culturing methods and, of course, water temperature.

During late trochophore stage (Fig. 13*g*) the cell gland begins to secrete the shell. When the shell completely encloses the soft parts the larva has reached early straight-hinge stage (Fig. 13*h*).

Development of larvae of *Mactra solidissima*, from early straight-hinge stage until metamorphosis, and their length—width measurements during this entire period are shown in Fig. 14. Very early, normal straight-hinge larvae measure only about 79 μ in length and usually between 63 and 65 μ in width. In some cultures, composed mostly of abnormal individuals, somewhat smaller, slightly deformed straight-hinge larvae can be seen occasionally, but it is doubtful that they survive to metamorphosis.

Individual larvae of *M. solidissima* display considerable variations as to the size at which certain organs of their bodies begin to develop and at which metamorphosis occurs. For example, in some individuals the foot can be seen when they are only about 160 μ long. Approximately 80% of the larvae show a well-developed foot by the time they are 215 μ long, and at a length of 240 μ practically all possess this organ.

Disappearance of the velum is another step in larval development that is not strictly correlated with a definite size. In some larvae measuring only 219 μ in length the velum was already completely resorbed, while in extreme cases a diminishing, but still functional velum was seen in larvae about 257 μ long.

A few larvae begin to metamorphose when they are about 220 μ long, but the majority are between 230 and 250 μ before metamorphosis occurs. At this time the velum is resorbed, rudimentary gills develop, and a powerful ciliated foot, which when expanded is as long as the young clam itself, serves as the only means of locomotion. Individuals measuring 262 μ in length were the largest true larvae recorded. In this respect our observations are in agreement with those of Imai *et al.* (1953), who found that in *Mactra sachalinensis* the foot begins to develop at a length of about 200 μ and that larvae set at about 270 μ.

B. *Abnormal eggs and larvae*

Abnormal development of eggs and larvae of bivalve mollusks may be due to any one of a variety of factors or to a combination of such factors. It is our practice, however, to discard cultures in which less than 50% of the eggs develop into normal straight-hinge larvae. This is done because batches of eggs giving a low percentage of larvae may be abnormal in some respects, and these abnormalities may lead to aberrant experimental results and wrong conclusions. We do not know, as yet, what factors are responsible for poor eggs and feeble embryos. In some instances abnormal larvae, or failure of eggs to develop to straight-hinge larval stage, may be the result of incompatible genetic combinations. Our experience indicates, however, that such combinations are comparatively rare.

Some abnormalities of larvae may be ascribed, no doubt, to the poor physical condition of spawners. Several investigators have believed that eggs released late in the season were less viable and produced less vigorous larvae than those from earlier spawnings. Loosanoff and Davis (1950) were under the impression that the last batches of eggs discharged by virtually spent females gave feeble larvae that grew slowly and showed high mortality. Cole (1941) offered evidence that the brood strength of *Ostrea edulis* may decline during the course of a breeding season and he believed that this was due to a depletion of food reserves in the bodies of parent mollusks. Walne (1956) thinks that the lack of " vigour " in larvae may result from poor condition of the parent oyster and believes it possible that the vigour of larvae may be affected by the quantity of food reserves laid down in the eggs.

More recently, Davis and Chanley (1956b) have shown conclusively that the last batches of eggs of both clams, *M. mercenaria*, and oysters, *C. virginica*, discharged by virtually spent females were cultured with no apparent diminution of either percentage of eggs developing into straight-hinge larvae or rate of growth of these larvae. Accordingly, we now believe that abnormal or feeble larvae do not occur more frequently in later spawnings than in other spawnings throughout the season. As has already been mentioned, our experiments have shown that there is no correlation between viability of spawn and age of parents.

There is evidence that bivalves can be induced, by strong chemical and thermal stimulations, to abort eggs even though they are not fully ripe (Fig. 15). In some cases such spawnings appear to be quite normal and a large number of eggs may be released. More often, however, comparatively few eggs are shed. In the case of *C. virginica* immature oyster eggs usually develop only to late gastrula or early

trochophore stages, and then become so " sticky " that they adhere to each other and to the walls of the containers, particularly at the

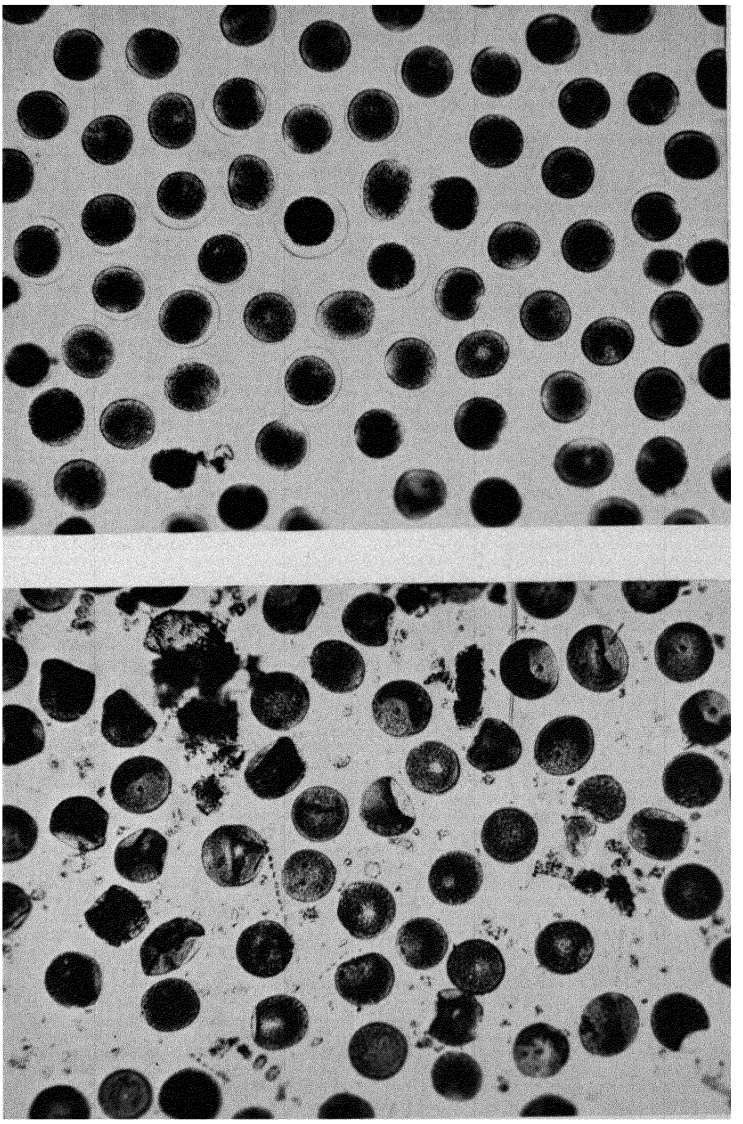


FIG. 15. Largely normal (*above*) and abnormal (*below*) eggs of *Ensis directus*. Abnormal eggs were discharged by a female compelled by strong stimulation to spawn before eggs were ripe. Normal eggs vary from 64 to 73 μ in diameter.

air-water-glass interface where they normally congregate in large numbers.

With somewhat more advanced, but still not entirely ripe, oyster

eggs the larvae develop more normally but are quite small, measuring only 60 to 70 μ at the 48-hr stage (Davis, 1949). Finally, in induced spawning of oysters late in the season after resorption of their gonads has begun, embryonic development of eggs is frequently abnormal and only a low percentage of them develop into healthy straight-hinge larvae.

Subjecting eggs and spermatozoa to temperatures higher than 30°C may injure or even kill them. Maintaining recently discharged eggs in heavy concentrations, a condition that leads to formation of a thick layer of them on the bottom of rearing vessels, may result in a sufficient

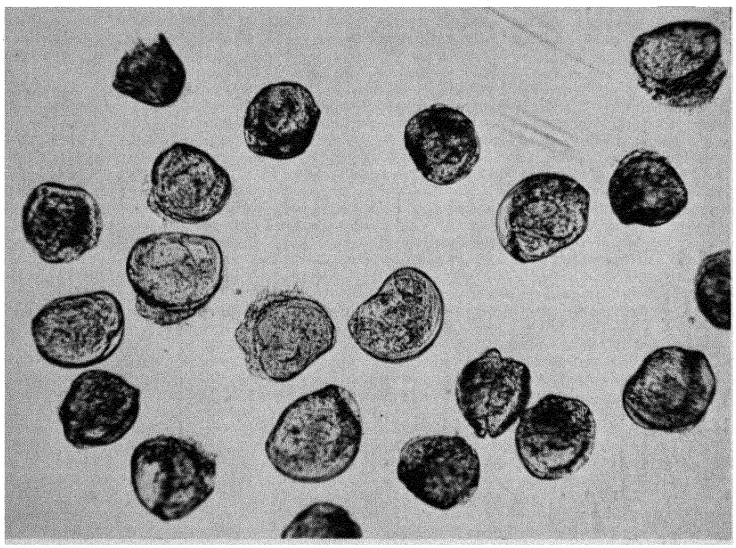


FIG. 16. Abnormal 4-day-old larvae of *Mercenaria mercenaria* from crowded culture. Largest larvae in photomicrograph are approximately 105 μ long.

depletion of oxygen and accumulation of catabolic products that will affect the eggs and their further development. If zygotes and early embryos are badly overcrowded, their shell development usually proceeds only as far as the shell gland stage. Thus, instead of shells being fully formed 48 hr after fertilization, as occurs in normal larvae which, at that time, can retract their soft bodies completely within the new shell, overcrowded larvae have a small, dark oval area denoting the position of the shell gland or a small band of shell material not more than twice the diameter of the shell gland.

In less-crowded cultures larvae form enough shell to protrude from their bodies to give the appearance of small wings (" winged larvae "). Under somewhat better conditions a larger, but still incomplete shell

is formed, but the hinge line, instead of being straight, is concave, characterizing "saddleback larvae", or convex, typical of "humpback larvae" (Fig. 16). In both of these abnormalities much of the ventral portion of a larva's body will extend beyond the shell. The results of overcrowding on development and growth of larvae will be more fully described in a later section of this article.

Occasionally, in some cultures many larvae have abnormally small vela. This abnormality may, sometimes, be due to mechanical injuries to the velum when larvae are screened before their shells are fully developed to protect the soft parts. In other cultures it has been associated with the presence of numerous ciliates. It is possible that velar deformities in these cases were the results of injuries by ciliates, but it is more probable that the ciliates were feeding on particles of vela cast off by larvae in response to adverse conditions, such as artificially-created concentrations of certain chemicals.

The same type of abnormalities, as observed in overcrowded cultures, occurs when eggs are cultured in sea water in which adult oysters have previously been kept. Probably because of the same reason, eggs carried along with water from tanks or trays in which a mass spawning has occurred seldom develop into normal larvae unless the original water is greatly diluted with fresh sea water.

Failure of larvae to develop normal shells when overcrowded, or when grown in water in which adult oysters had previously been kept, may indicate a depletion of certain substances, normally present in sea water, that are needed for shell formation. In experiments devised to verify this possibility some of the eggs discharged by a single female were placed in fresh sea water, while others, fertilized with sperm from the same male, were placed in sea water taken from an aquarium in which adult oysters had been kept. The latter group of eggs gave a much lower percentage of normal larvae.

One interesting class of abnormal larvae consists of those that do not feed, even though they do not show clear-cut anatomical malformations. These apparently normal larvae, which developed to straight-hinge stage under our standard conditions and are kept in the same cultures with other larvae which are feeding and growing normally, seem unable to feed, do not grow, and eventually die. Before death, the larvae become emaciated so that most of the space inside their shells is empty with only the retractor muscles, a small velum and a shrunken visceral mass remaining. In some cultures this abnormality is found in more than 25% of the larvae.

In several experiments this type of abnormality has been associated with the kind of food given. In these instances approximately 50%

of larvae of *M. mercenaria* receiving *Chlamydomonas* sp. displayed this abnormality, while the remaining 50% fed and grew at a normal rate, as did all of the sibling larvae in other cultures receiving other foods. A similar phenomenon was observed in American oyster larvae fed *Phaeodactylum tricornutum* (Davis and Guillard, 1958).

While some anatomical abnormalities may interfere with the ability of larvae to gather or ingest food, resulting in poor growth and eventually death, other abnormalities, such as badly deformed shells, may still permit larvae to feed and grow. Sometimes, as they grow, such larvae gradually become more normal in appearance, but usually remain distinguishable even when they are nearing metamorphosis.

Experiments on tolerance of eggs and larvae of bivalves to such factors as turbidity and salinity, and to chemicals, such as pesticides, antibiotics, and bacteriostatic compounds, have also shown that if any one of these falls outside of the tolerated limits, embryonic development becomes affected, resulting either in death of the zygotes or in abnormal larvae. These matters will be discussed in more detail later in the article.

Some of the larvae, particularly those of the clam, *M. mercenaria*, that are abnormal because of overcrowding, exposure to low temperatures or high turbidity during early stages of development often grow to metamorphosis if returned to favorable conditions and given good food.

Dense algal blooms may also cause abnormal development. We have frequently observed, during blooms of dinoflagellates in Milford Harbor, that in our laboratory cultures only a small percentage of clam or oyster eggs developed into normal straight-hinge larvae. Eggs placed in water from which algae were removed by Millipore filters showed only a slightly higher rate of normal development than eggs grown in unfiltered water containing dinoflagellates. Eggs from the same spawnings but cultured in sea water collected prior to the bloom gave considerably higher percentages of normal larvae (Davis and Chanley, 1956b).

It may be added that plankton samples collected in Long Island Sound during or immediately following heavy algal blooms are usually characterized by the scarcity or even complete absence of early straight-hinge stages of bivalve larvae (Loosanoff, 1958a). We believe that reduction in numbers of normally developing bivalve eggs and larvae in the above instances is primarily caused by highly toxic metabolites of algae that may persist for several days after the blooms have ended. It is possible, however, that this phenomenon is due, at least in part,

to removal by algae of certain chemicals from sea water that are essential to larval development.

C. *Methods of cultivation of eggs and larvae*

Methods of culturing eggs and larvae of bivalves under laboratory and small-scale hatchery conditions have been tested by many workers for over 100 years. Costé, a Frenchman, was probably the first to attempt this around 1858. In the United States a number of extremely capable men, including Brooks (1880), Ryder (1883) and Winslow (1884), continued these efforts on *C. virginica*, but were unsuccessful. Perhaps the best summary of these efforts is given by Winslow, who states, " But after my experience of the past spring and summer I am convinced that it will require a series of painstaking experiments, extending over considerable time and conducted under many dissimilar conditions, before the artificial production and culture of the oyster is made a matter of practical importance."

Interest in artificial propagation of bivalves was revived when Prytherch (1924) and Wells (1920, 1927) succeeded in carrying oyster larvae to metamorphosis. This success was probably due to the practice of renewing the water in which oyster larvae were kept. Wells used a milk separator for this purpose, while Prytherch used filtros plates. Other successful workers in this field included Hori and Kusakabe (1926), Cole (1936), Bruce *et al.* (1940), Lindsay and Woelke (1960), Woelke (1960) and, especially, Imai *et al.* (1950b). In our case some oysters were carried to metamorphosis as early as 1932, but efforts to repeat this success usually failed until about 1946–1947 when we began to develop and improve the methods used at our laboratory (Loosanoff and Davis, 1950; Davis, 1953; Loosanoff, 1954).

It is our practice to fertilize eggs as soon as they are discharged. Usually it happens automatically because since we use a sperm suspension to stimulate spawning, spermatozoa are already present in the water when females begin to discharge eggs. Fresh, actively-moving sperm are used to assure normal fertilization of eggs and development of zygotes. Sufficient quantities of sperm are always added, but when working with small eggs, such as those of *C. virginica*, which cannot be retained even by fine screens, we limit the quantity of suspension. In this way excessive quantities of sperm are not carried into our culture vessels, and the undesirable effects of decomposing sperm on developing eggs are avoided.

The bivalves are usually spawned in Pyrex glass dishes containing about 1·5 liters of water (Figs. 10 and 11). As has already been mentioned, to separate the eggs from the debris and, later, from the excess sperm,

blood cells and body fluids accompanying the spawning, we use a series of stainless steel sieves with screens containing different numbers of meshes per linear inch (Fig. 17). The finest screen that was found practical in our operation has mesh openings averaging 44 μ, but since many meshes are actually larger and exceed the diameter of an oyster egg, which is about 50 μ, many eggs pass through the sieve. It is true that by using No. 25 bolting silk a smaller size mesh is available but in that case the openings are so small that they easily get clogged,



FIG. 17. Screening bivalve eggs through 100-mesh sieve to remove detritus. Similar screens, of 3 in diameter and of smaller mesh opening, are used to collect bivalve eggs and to retain larvae during changes of sea water in culture vessels.

rendering the sieves useless. As a result, in our practice we use a series of sieves, the finest of which has a nominal opening of about 44 μ, followed, when necessary, by any of the coarser screens with openings of 53, 62, 74, 88, 120, 125, 149 and 177 μ.

In species having eggs too small to be retained even by our finest screen, the eggs can be partially freed of body fluids, sperm, etc., by letting the eggs settle on the bottom of a dish and then syphoning or decanting most of the fluid. By repeating this procedure several times most of the undesirable substances that are dissolved or suspended in the water will be discarded.

We have used a variety of containers to culture larvae. Some of them were large glass vessels, including Downing and McDonald jars used in fish hatcheries for incubation of semi-buoyant eggs, lobster jars, 5-gal earthenware jars, and 75-gal polyethylene and Fiberglas containers. We have also grown larvae in large, outdoor, concrete tanks containing several thousand liters of sea water (Loosanoff, 1954). In all these instances the larvae were grown successfully.

For precise experimental work Pyrex glass beakers of 1000- to 1500-ml capacity are perhaps the most satisfactory because they are not toxic and are readily cleaned and sterilized (Fig. 5). Polyethylene and other plastic containers are also convenient and non-breakable and some can be sterilized. However, some of them are permeable to certain insecticides and, perhaps, to other substances and are known to adsorb a variety of toxins. Because of these considerations polyethylene and some other plastic containers, while convenient as culture vessels, cannot be used in experiments involving certain toxic substances, such as insecticides.

New, soft glass vessels may contain substances which are toxic to eggs or larvae of oysters and clams. Even though these vessels are conditioned in sea water for several days, culturing larvae in them is always haphazard because, although larvae in different vessels are presumably grown under identical conditions, their rates of growth are often distinctly different and they show mortalities unrelated to the treatment. At the same time sibling larvae grown in earthenware jars or Pyrex glass containers suffer no mortality and different cultures receiving the same treatment show good duplication in their rate of growth.

Although we could not identify the substances responsible for poor growth of larvae grown in soft glass jars, we found, nevertheless, that young bivalve larvae, especially those of *C. virginica*, are sensitive to presence in the water of even minute quantities of certain chemicals. For example, we noticed that washing of glassware and other implements with tap water that passed through a pipeline containing copper unfavorably affected larval development. Apparently, even minute quantities of these metals are sufficient to interfere with normal development of eggs and larvae.

Our experience in growing bivalve larvae has shown that they cannot be kept in recently-built concrete tanks and that, usually, it is necessary to age the tanks with sea water for a long time before this can be done.

Since most of our studies are quantitative, as well as qualitative, definite numbers of eggs or larvae per ml of culture are needed from the start. This is achieved in the following manner: eggs are placed

in a tall, narrow glass jar and the water in it is thoroughly agitated with a perforated plastic plunger to distribute the eggs uniformly. A sample is then taken with a volumetric pipette, and the number of eggs or larvae per ml is determined by counting them on a Sedgwick-Rafter cell. After that the eggs or larvae are again agitated, to ensure their even distribution in the vessel, and the necessary volumes of water carrying larvae are transferred to culture vessels.

We usually begin our experiments with 10 000 to 15 000 straight-hinge larvae per liter of sea water. However, because not all fertilized eggs develop into normal larvae, it is our practice to place approximately twice this number of eggs into each culture vessel to produce a sufficient number of larvae. Accordingly, about 30 000 eggs per liter are used in starting cultures. These eggs are placed in containers filled with sea water that is first filtered through an Orlon filter and then subjected to the sterilizing action of ultraviolet rays. The eggs are then left to develop undisturbed for 48 hr and no food is added during this period.

All culture vessels are immersed in a common water bath table, the temperature of which is controlled within $\pm$ 1·0°C (Figs. 5 and 6). Usually, neither aeration nor mechanical agitation is employed because we have established that clean, well-attended cultures do not require aeration if the water is changed every second day. In special experiments requiring mechanical agitation we use a number of devices, including a rotating wheel, paddle-agitator (Fig. 5), or regular shaking machine.

At the end of 48 hr young larvae, now protected by fully formed shells, are collected by screening the cultures through sieves having 325 meshes per lineal inch (44 μ opening). Larvae retained by the screen are gently washed and placed in a tall jar. Using the same method as that employed with eggs, the number of larvae per ml is determined, and the appropriate volumes of water containing larvae are placed in each culture jar to create desired concentrations.

Samples of larvae are taken whenever needed, usually at 2-day intervals. This is again accomplished by collecting all larvae from a container on a 325-mesh screen and then transferring them to a graduated cylinder of 1-liter capacity from which, after proper agitation, required samples are taken, while the remaining larvae are returned to the culture vessel.

D. *Larval period*

Rate of growth of veligers from straight-hinge stage to metamorphosis is affected by many conditions. In our laboratory work

the chief controlling factors have been food and temperature. The role of these conditions will be more fully discussed in special sections later on, and also in the sections dealing with development and growth of larvae of different species; therefore, here it will be sufficient to mention only general observations.

Our experiments have shown that larvae of different bivalves display different food requirements (Loosanoff and Davis, 1951). Until they reach a length of about 125 μ larvae of *C. virginica*, for example, are quite restricted in types of food they can utilize (Davis, 1953). Certain naked flagellates are the only organisms, thus far tested, that may be included in this category. *Chlorella* is one of the many genera of algae having thick cell walls that oyster larvae either cannot utilize or utilize only to a very limited extent during early stages, although it seems to be quite a satisfactory food for older larvae (Davis and Guillard, 1958). Thus, if during the early stage of development of oyster larvae specific food organisms are either entirely absent or are uncommon, the larval free-swimming period may be greatly prolonged or the larvae may never reach metamorphosis. For example, during our earlier efforts of raising larvae of *C. virginica*, when little was known about their food requirements, approximately 50 days were required before the most advanced individuals began to metamorphose in some cultures. In similar cases, with larvae of *C. gigas*, the cultures were discarded after 53 days because the largest larvae at the time measured only about 100 μ. Now, using good food organisms, such as *Isochrysis galbana* and other naked flagellates, and maintaining the temperature at about 23°C, larvae of *C. virginica* have been reared to metamorphosis in our laboratory in 18 days. This is, probably, the approximate time required by larvae to grow to setting size under natural conditions in Long Island Sound (Loosanoff and Engle, 1947). At 30°C well-fed oyster larvae, grown under laboratory conditions, began to metamorphose 10 days after fertilization.

The importance of the second factor, water temperature, on length of larval period of bivalves has also been well demonstrated in our studies of larvae of *M. mercenaria* (Loosanoff *et al.*, 1951). These studies showed that, under identical conditions, larvae kept at a temperature near 30°C began to set as early as the 7th day after fertilization, while cultures maintained at 18°C contained the first metamorphosing individuals only after 16 days.

In the case of larvae of all the species we reared it has been clearly demonstrated that even though larvae originate from the same spawning and, sometimes, from the same parents, and are kept in the same vessel under identical conditions, individuals grow at widely

different rates and, therefore, metamorphose at different times (Fig. 18). For example, in a recent experiment a healthy culture of larvae of *C. virginica* fed a mixture of *I. galbana* and *Monochrysis lutheri* and kept at about 23·5°C began to set 18 days after fertilization. Setting gradually increased in intensity and remained heavy for the first 17 days, but some larvae continued to swim, before metamorphosing, for another 10 days. Thus, setting of this, presumably, homogeneous culture continued uninterrupted for a period of 27 days.

A number of similar observations on larvae of *M. mercenaria* obtained from the same parents and grown under identical conditions, but showing considerable individual variations in rate of growth and in

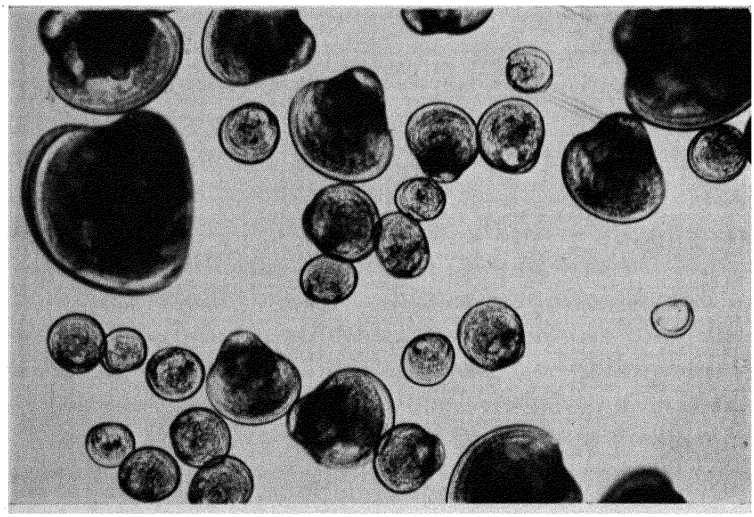


FIG. 18. Differences in sizes of larvae of *Crassostrea virginica* of the same age and grown under identical conditions in the same culture vessel. Some of the largest larvae are approximately 295 μ long and are nearing metamorphosis.

time needed to reach metamorphosis can be given. Perhaps the most detailed description of this phenomenon appears in the paper of Loosanoff *et al.* (1951) on growing clam larvae at five constant but different temperatures. These authors gave the minimum and maximum sizes of larvae recorded in each culture every 2nd day from time of fertilization until the majority of the larvae metamorphosed. During the early life of a culture, on the 2nd or 3rd day, the larvae differed in size by only a few microns, but several days later, depending upon the temperature, the size ranged from small straight-hinge larvae of approximately 100 μ long to full grown, ready-to-metamorphose individuals. For example, sizes of larvae grown at 30°C ranged on the 8th day from 107 to 226 μ. In a culture kept at 21°C the minimum and

maximum sizes recorded on the 21st day were 107 and 221 μ. Our colleagues working in the same field, especially Imai *et al.* (1954), fully share our experiences.

At present, no well-based explanation can be advanced for these differences. Perhaps, as has been suggested in connection with survival and growth of certain fish, vitality of the individual eggs and larvae that emerge from them depends to some extent upon the position of the eggs in the ovaries and the amounts of nutritive materials that have been stored in the individual eggs before they are discharged.

Chanley (1955) assumed that differences in sizes of larvae in the same cultures must be due, at least in part, to inherited characteristics. He also reported evidence of significantly different rates of growth of larvae originating from eggs of the same female crossed with different males and larvae grown from eggs of two females individually crossed with the same male. He tentatively concluded that inherited differences from either parent may be responsible for differences in rate of growth of different larvae.

In some cultures, especially those kept at comparatively high temperatures, the range of larval sizes usually diminishes several days after beginning of metamorphosis. This is due to the disappearance of larger individuals because of setting and, partly, because abnormal, undeveloped, slow-growing larvae are rapidly dying.

There were periods in our practice, for example, in growing larvae of *Ostrea edulis*, when regardless of all efforts they would not grow at all or ceased growing soon after reaching a size of about 220 μ. The reasons for cessation of growth still remain an enigma because, at times, these larvae refused to grow even when given foods on which, in previous experiments, they grew well.

E. *Hardiness of eggs and larvae*

According to Nelson (1921) larvae of *C. virginica* are extremely sensitive to a sudden change in water temperature. A drop of only 3° to 5°C within 24 hr may be followed by the disappearance of a majority of the larvae. According to the same author rain storms, as well as strong winds, cause death of large numbers of bivalve larvae. Nelson, however, failed to offer experimental evidence to support his contention of the unusual sensitivity of bivalve larvae to relatively minor changes in their environment. Our observations, reported partly in this section and partly in the sections to follow, lead us to disagree with Nelson's point of view because they have clearly demonstrated that bivalve eggs and larvae, if protected against disease-causing organisms and toxic substances, are rather hardy.

Laboratory and field observations lead us to believe that oyster eggs that are still in the ovaries are hardy and capable of withstanding sharp physical changes in their environment. For example, on several occasions oysters with mature gonads have been kept for various periods of time in the refrigerator at about 2°C to delay their spawning. Some of them, kept at this low temperature for 7 days, have spawned copiously later on, when subjected to proper stimulation, and larvae from these spawnings have been reared to metamorphosis. Other groups kept in the refrigerator for 15 days also spawned normally and produced healthy larvae. However, oysters that were kept in the refrigerator for 30 days spawned feebly, and only a portion of the eggs developed into normal larvae. This semifailure was probably due to severe dessication of the oysters and their gonadal tissue. This conclusion is supported by the observation that the best spawnings occurred when refrigerated oysters, prior to attempts to spawn them, were kept in running sea water at room temperature for at least 6 hr. During this recuperation period they probably restored their water loss.

Another experiment on effects of low temperature upon ovarian eggs of *C. virginica* of Long Island Sound was performed only last winter (1961–62). Oysters measuring from 3 to 6 in long were brought into the laboratory early in January from their natural beds and placed in conditioning trays to be ripened for spawning. After conditioning at about 20°C for about 1 month, these oysters, now ripe, were transferred to outdoor tanks where the water temperature was near 0°C and where, at times, a layer of ice was formed.

Twenty days later, on 26 February, the first group of oysters was returned to the laboratory and placed in water of the same temperature as that outdoors. Then the temperature was slowly raised to about 17°C for 2 days. Following this recovery period fifteen oysters were placed in spawning dishes and our usual method of inducing spawning was applied. Eight of fifteen oysters responded, of which five were females and three were males. Spawnings were light to medium with a total of 27 million eggs released. These eggs were cultured by our usual method, but only a comparatively small number of larvae developed to straight-hinge stage.

On 6 March another group of the oysters was brought into the laboratory from the outdoor tanks and later induced to spawn. Four out of eight oysters spawned, three of which were females. The total number of eggs discharged by these females was 57 800 000. The majority of the eggs were normal in appearance, although a few were deformed and some were small.

In one of the containers, in which 375 000 eggs from this spawning

were placed in 5 gal of water, a count of straight-hinge larvae was made 48 hr later and showed that the culture contained 155 000 normal, straight-hinge larvae, 11 000 abnormal ones and 2 000 dead individuals. Therefore, approximately 168 000, or about 45% of the eggs placed in the culture developed into larvae. In another culture, where approximately 750 000 of these eggs were placed in 10 gal of water, the count made 48 hr later gave 424 000 normal, 46 000 abnormal and 32 000 dead larvae; therefore, approximately 502 000, or 67% of all the eggs that were originally placed in the culture developed to straight-hinge stage. From then on, however, larval development was poor, showing high mortality.

On 19 March, 43 days after the ripe oysters were placed in the icy water, another group was brought in and, after being kept for 4 days in running sea water at a temperature ranging between 14° and 17°C, was induced to spawn. Both males and females spawned. One of the females released 18 million and another, 27 million eggs. Larvae obtained from eggs of one of the females grew well, increasing approximately 10 μ in length per day.

This experiment demonstrated the remarkable fact that oysters artificially ripened in the middle of winter can be transferred abruptly from warm to freezing water, retained there for over 40 days, and then returned to warm water and induced to spawn, producing viable eggs and sperm that eventually develop into normal straight-hinge larvae. Even though mortality among larvae obtained in this unusual manner was relatively high and many larvae were abnormal, the experiment demonstrated, nevertheless, the remarkable power of oysters to retain their ripe sex cells under extremely adverse conditions. Results of histological studies of gonads of oysters involved in these experiments will be described later in a special publication.

Regardless of the ability of ovarian eggs of *C. virginica* to withstand exposure to low temperatures for long periods, recently fertilized eggs, in the polar-body stage of development, do not display the same tolerance. This was demonstrated by an experiment in which eggs, within 1 or 2 hr after fertilization, were placed in a refrigerator maintained at a temperature of about 2°C, and kept there for 6, 24 and 48 hr. Samples were then returned to room temperature and further development of the eggs subsequently observed. In all samples a few eggs developed into abnormal ciliated blastulas, but practically all of them failed to develop further and soon disintegrated.

Healthy shelled larvae of oysters, *C. virginica*, are, nevertheless, capable of withstanding sharp changes in temperature of the surrounding water. In a special series of experiments, designed to verify Nelson's

conclusion of extreme sensitivity of these larvae to temperature changes, beakers of 1-liter capacity containing larvae grown at a temperature of about 22°C and measuring about 200 μ in length were placed in a refrigerator at 2°C and returned to room temperature following 6, 12 and 24 hr of refrigeration. Within a few hours the predominating majority of larvae exposed to the low temperature for 6 and 12 hr were swimming and feeding normally. However, many of the larvae which were refrigerated for 24 hr lost a portion of the velum and eventually died. The mortality in each of the above groups at the end of one week after return to room temperature was: control, 4·2%; 6-hr chilling, 6·5%; 12-hr chilling, 4·9%; and 24-hr chilling, 44·9%. Thus, even though exposed to a near freezing temperature for a 24-hr period, more than half of the larvae survived and continued to develop.

In still another experiment oyster larvae lived and grew when subjected every 48 hr to a sharp drop in temperature, from 20° to 10°C, for periods of 15 to 30 min, followed in a few minutes by an equally abrupt return to 20°C. A majority of these larvae subsequently reached metamorphosis. It would seem unlikely, therefore, as claimed by Nelson (1921), that ordinary short-term temperature fluctuations of only a few degrees, occurring in natural waters, could be responsible for an appreciable, sometimes total mortality of larvae.

It is also certain at this time that bivalve larvae may survive long periods with little or no food. In many of our experiments several control cultures survived from 2 to 3 weeks with little or no mortality, even though they did not receive any food except that which was present in the filtered sea water where they were kept. Moreover, in our earlier experiments, before such good food forms as naked flagellates became available, many oyster larvae cultures were kept for more than 40 days, although they did not show any growth. As already mentioned, in some of these cultures setting began only after 50 days. These observations demonstrate that bivalve larvae may tolerate comparatively long periods of semi-starvation and some may even reach setting size and metamorphose regardless of poor feeding conditions. It is improbable, therefore, that under natural conditions larval populations of such mollusks as oysters will die within 2 or 3 days because of a lack of sufficient quantities of food. It is clear, however, that lack of food will prolong the larval period, thus increasing the loss of larvae because of predation and dispersal.

Larvae are also able to tolerate very low oxygen concentrations, at least for short periods. For example, on several occasions a number of

larvae were accidentally left overnight in a small pipette of sea water, yet they were found alive and healthy the following day.

Recent studies of Davis (1958) have clearly demonstrated that eggs and larvae of at least some estuarine species, such as *C. virginica*, can endure sharp changes in salinity. This matter will be discussed more extensively in the section dealing with the general aspects of changes in salinity upon development of eggs and larvae.

Studies of effects of turbidity upon eggs and larvae of *C. virginica* (Davis, unpublished) and those of *M. mercenaria* (Davis, 1960), which will be discussed later in greater detail, have demonstrated that larvae of these two species can endure and even continue to grow in water that is quite turbid. For example, Davis has shown that larvae of *C. virginica* may survive for at least 14 days in a concentration of 2 g of silt per liter of sea water. Such a heavy concentration seldom occurs in nature.

Fertilized eggs and larvae of many bivalves can also withstand vigorous mechanical disturbances without ill effects. For example, to obtain a representative sample of the population from our culture vessels, the water is strongly agitated by means of a plunger to assure a homogeneous distribution of larvae. Such relatively rough treatment, usually performed every day or every second day, does not cause an increase in mortality or decrease the rate of growth of larvae. Observations on the behavior of larvae in nature also support this conclusion because, as shown by our studies of plankton samples and by observations on intensity of setting of oysters on natural beds, it has been definitely established that strong winds accompanying New England hurricanes and churning the water of Long Island Sound steadily for several days do not noticeably diminish larval populations. This was especially well demonstrated in August 1955, when a marked increase in intensity of setting of oysters occurred immediately after hurricane "Connie". This increase continued for 2 weeks, thus showing that larvae of all ages survived the hurricane. It is also of interest that setting of oyster larvae occurred during the hurricane, thus indicating that strong water turbulence does not easily destroy larvae or seriously interfere with their metamorphosis.

Recent studies have repeatedly demonstrated the sensitivity of bivalve larvae to traces of certain substances in the water. These observations showed that sea water, in which our larval cultures are grown, sometimes contains substances, so far unidentified, which determine whether larvae will grow normally (Loosanoff *et al.*, 1951; Davis, 1953). Wilson (1951) found similar differences between natural sea water collected from widely separated areas of the ocean. We are

still not certain whether it is the presence of deleterious materials or absence of growth-promoting substances in sea water that slows growth or prevents normal development of larvae.

We have observed that some substances which interfere with normal development of larvae may originate from sources to which we have previously paid little attention. Under certain conditions these substances may be released mechanically from bottom soil. This was noticed during a winter when a deep channel was dredged in Milford Harbor, from which our laboratory obtains its water. During that period the water acquired certain properties which strongly interfered with normal development of eggs and larvae. These substances were apparently in solution or in fine colloidal suspension because they were still present in the water after it was filtered. Neither aeration nor ageing appreciably improved the quality of the water.

Sensitivity of eggs and larvae to different substances dissolved in sea water was further demonstrated by Davis and Chanley (1956b) in a series of experiments which showed that, while low concentrations of antibiotics may increase rate of growth of larvae, even a slight excess of them reduces rate of growth. Progressively increasing concentrations of these substances correspondingly decrease rate of growth of larvae and eventually cause their mortality. This matter will be discussed in greater detail in the section devoted to larval diseases and their treatment.

Recently, extensive studies on effects of numerous insecticides, weedicides, oils, organic solvents and detergents on mollusks have been undertaken at Milford Laboratory. While these studies are still in progress, it has already been found (Davis, 1961) that within each group of these compounds there are great differences in toxicity of individual chemicals to eggs and larvae of bivalves. For example, DDT was found to be one of the most toxic of the commonly used insecticides because even at a concentration of 0·05 parts per million it caused almost total mortality of oyster larvae. On the other hand, another common insecticide, Lindane (1, 2, 3, 4, 5, 6 hexachlorocyclohexane), even at a concentration of 10 ppm, which is essentially a saturated solution in sea water, caused no appreciable mortality of larvae. On the contrary, growth of clam larvae in 5 ppm of Lindane was somewhat faster than that of larvae in control cultures.

Certain concentrations of phenol, chloramphenicol and Dowicide "A", among the antibiotic, bactericide and disinfectant compounds also appreciably improved rate of growth of bivalve larvae. This is attributed to the action of these compounds which inhibits growth of

bacteria toxic to larvae. Other compounds which, in certain concentrations, probably improve rate of growth of larvae by partially inhibiting growth of toxic bacteria are acetone and trichlorobenzene among the organic solvents, Monuron and Fenuron among the weedicides, and Guthion among the insecticides. Davis (1961) appropriately suggested that, in some phases of shellfish culture, a sufficient concentration of such insecticides as Lindane may be maintained to destroy all undesirable crustaceans, while not affecting growth of bivalve larvae or their food organisms.

Our laboratory and field observations have shown that metabolites released by some microorganisms, especially dinoflagellates, seriously affect not only adult bivalves (Loosanoff and Engle, 1947), but also development of their eggs and larvae (Loosanoff *et al.*, 1953). Such toxicity of external metabolites and their physiological effects on aquatic organisms have been recognized by many biologists, some of these studies having been summarized by Lucas (1947, 1961) and Korringa (1952). More recently, Loosanoff (1955) reported that a heavy bloom of dinoflagellates in Milford Harbor caused abortion of embryos and immature larvae of gravid European oysters, *O. edulis*. Davis and Chanley (1956b) found that a dense bloom of dinoflagellates caused abnormal development of eggs and larvae of the clam, *M. mercenaria*, and oyster, *C. virginica*. Under these conditions only a few developed into shelled veligers. During that summer concentrations of dinoflagellates in some areas of Milford Harbor were as high as 300 000 cells per ml. Placing eggs of clams or oysters in this water, even after it was passed through a Millipore filter to remove dinoflagellates, resulted in only a slight increase in the percentage of clam or oyster eggs that developed normally.

Although we assume that the effects noted above were due to external metabolites emitted by dinoflagellates, it is possible that they were caused by removal from sea water, by these cells, of certain substances necessary for normal development of clam or oyster eggs and larvae. Another possibility is that the presence of a certain substance, favoring rapid growth of dinoflagellates and preventing normal development of larvae, was simultaneously responsible for both phenomena.

F. *Effects of temperature on eggs and larvae*

Certain observations and experiments devoted to studies of effects of sudden and extensive changes in temperature on eggs and larvae of several bivalves have already been described in the preceding section.

Here, we shall briefly discuss the results of observations on effects of temperature within a much more limited range.

Larvae of most of the species cultured at our laboratory were grown under routine conditions, i.e. at room temperature, which was normally near 20°C. Because of this no extensive information is available as to temperature ranges within which larvae of different species may survive or their optimal growing temperatures. In a few species, nevertheless, rather extensive observations on effects of temperature on development of their eggs and on growth of the larvae were undertaken. Studies of this nature on *M. mercenaria* and *C. virginica* have been the most complete.

M. mercenaria has been grown from egg to metamorphosis at constant temperatures ranging from 18° to 30°C (Loosanoff *et al.*, 1951). If, within 3 hr after fertilization, eggs of these clams were placed in water of 15°C, virtually none of them developed normally to straight-hinge stage. If eggs were kept at room temperature from 6 to 9 hr after fertilization and then subjected to a temperature of about 15°C, some developed into straight-hinge larvae. The majority of these larvae, however, were abnormal and many of them soon died, although some continued to grow at a very slow rate.

If eggs and, later, larvae developing from them were kept at room temperature for the first 2 days after fertilization, until straight-hinge stage was well formed, and then placed in water of 15°C, some of the larvae survived for 12 days or even longer. It is possible that if given good food, some of the individuals might eventually reach metamorphosis. However, if larvae grown at room temperature for the first 2 days of their existence were placed in water of 10°C (Fig. 19), they would not grow.

At the other end of the temperature range, at about 33°C, abnormal development and heavy mortality usually occurred if recently fertilized eggs were transferred to water of this temperature. However, if eggs and, later, larvae developing from them were kept at room temperature for the first 48 hr after fertilization and then transferred to water of 33°C, rapid normal development, similar to that observed in cultures kept at 30°C followed. Thus, our observations on development of eggs and growth of larvae of *M. mercenaria* at temperatures from 15° to 33°C support the view expressed by Pelseneer (1901) that normal early cleavage stages of molluscan eggs are limited to a narrower temperature range than can be tolerated by more advanced stages of the eggs or larvae.

Larvae of *M. mercenaria*, developing from eggs within the temperature range of 18° to 30°C, grew to metamorphosis, growth being

generally more rapid at higher temperatures. At 30°C larvae began to set as early as the 7th day after fertilization. Sometimes, the entire population grown at this temperature would metamorphose within

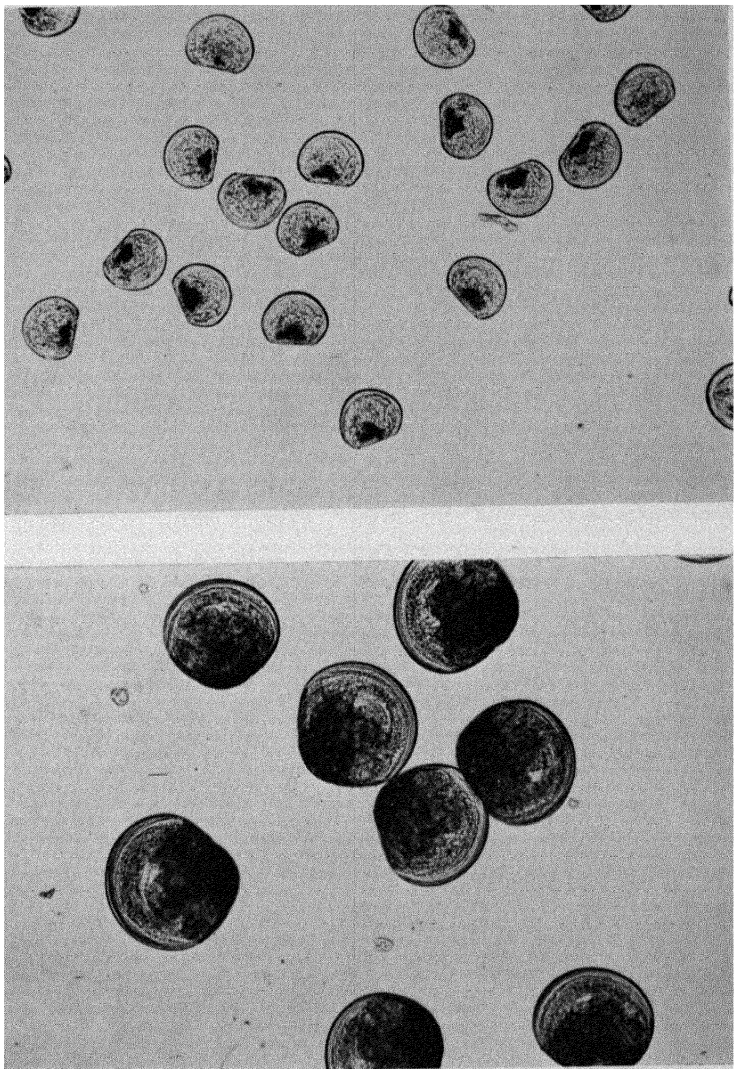


FIG. 19. Differences in sizes of 12-day-old larvae of *Mercenaria mercenaria* grown at 10°C (*above*) and 30°C (*below*). Average lengths of larvae were 105 and 195 μ, respectively.

5 to 7 days. When grown at 18°C the first metamorphosing individuals were noticed 16 days after fertilization, although in some cultures this event did not occur until after 24 days. Other factors, such as quantity and quality of food, density of larval population, etc., are no doubt

responsible for these variations. However, by maintaining the cultures at a constant temperature of 24°C and providing the larvae with good food, such as *Isochrysis galbana*, we consistently bring cultures of

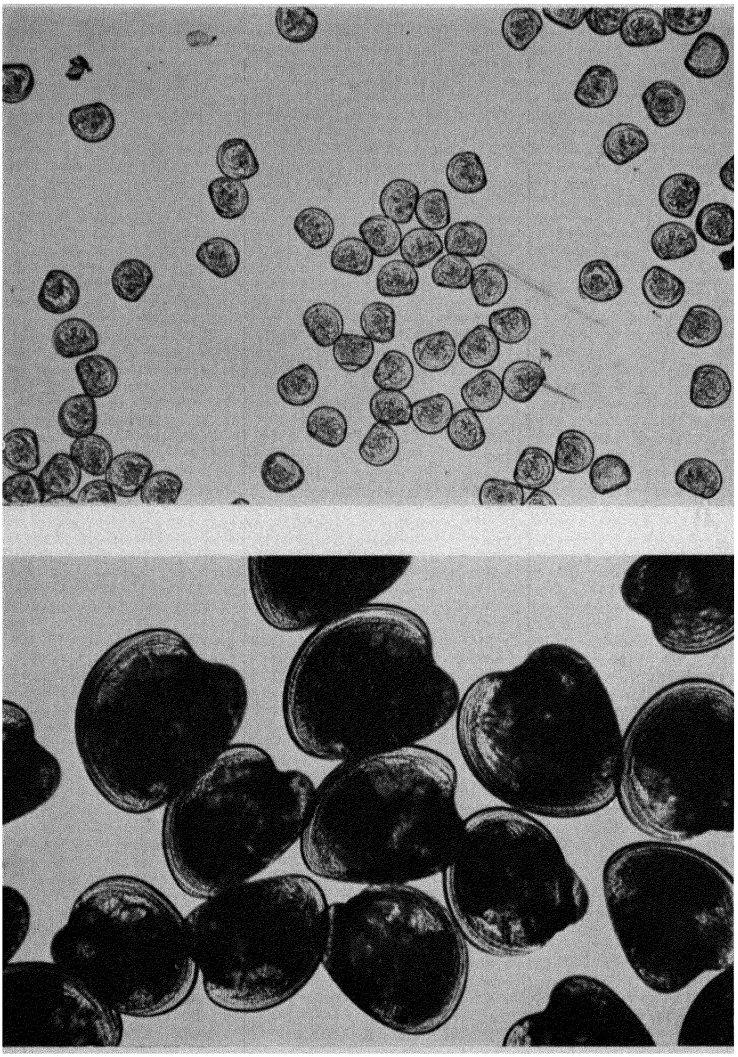


FIG. 20. Differences in sizes of 12-day-old larvae of *Crassostrea virginica* grown at 10°C (*above*) and 33°C (*below*). Average lengths of larvae of cold and warm water groups were 77 and 203 μ, respectively.

M. mercenaria to the beginning of setting 12 days after fertilization.

In experiments designed to determine temperature limits for development of eggs of *C. virginica* it was found that at 17·5°C as many as 97% of the eggs may develop to normal straight-hinge stage.

At 15°C, however, none of the eggs reached this stage although a few developed as far as early shelled larvae.

In some experiments 100% of recently fertilized oyster eggs transferred directly to 30°C developed into normal straight-hinge larvae, but, at 33°C, only 48% or less reached this stage. The abnormal larvae of this group were unable to feed or grow even when returned to a temperature of 24°C.

Although 2-day-old larvae placed in water at constant temperatures of 10° and 15°C for 12 days did not grow (Fig. 20), their rate of mortality during this period was comparatively low. The larvae kept at 10°C for 12 days could not feed even after being returned to a temperature of 24°C. However, some of the larvae kept at 15°C for the same length of time and then returned to 24°C fed, but their growth was negligible. Larvae kept at 17·5°C took some food, but also showed little growth. The majority of these larvae, however, began to grow rapidly when returned to water of 24°C.

At temperatures of 20°C and higher growth of oyster larvae was, to a large extent, dependent upon the food given. When fed *Chlorella* sp. (580), which is a relatively poor food, the larvae grew less rapidly than they did at the same temperatures when given better foods. Nevertheless, even when fed *Chlorella* sp. growth of larvae within the range from 20° to 33°C increased progressively with each increase in temperature.

Recent experiments suggest that one of the ways in which low temperature may affect growth of bivalve larvae is through inactivation of certain enzymes. For example, clam larvae kept at 10°C can ingest food organisms but are apparently unable to digest them. This is well shown in the upper photograph of Fig. 19. Larvae kept at 15°C can digest and assimilate naked flagellates and grow slowly, but are unable to utilize *Chlorella* sp. Those kept at 20°C were able to utilize both the naked flagellates and *Chlorella* sp. Similarly, larvae of *C. virginica* kept at a temperature of 20°C or lower cannot utilize *Chlorella* sp. However, at 25°C these larvae receiving *Chlorella* sp. showed some growth and at 30°C they were apparently able to utilize *Chlorella* sp. much more efficiently and, as a result, grew quite rapidly.

Larvae receiving *Dunaliella euchlora*, a moderately good food organism, showed a sharp increase in growth between 20° and 25°C. However, within the temperature range from 25° to 33°C the rate of growth remained virtually the same.

Larvae given a mixture of our best food organisms, *M. lutheri* and *I. galbana*, together with *Dicrateria* sp. (BII) and *Chlorella* sp. (580), grew better at the same temperatures than when fed only *Chlorella*

sp. (580) or *Dunaliella euchlora*. In general, through the range from 20° to 30°C growth increased parallel with the increase in temperature. At 30° and 33°C, however, the larvae grew virtually the same and metamorphosis at both temperatures began consistently between the 10th and 12th days.

G. *Effects of salinity on eggs and larvae*

Bivalves, even though they belong to the same class of mollusks, display extremely wide differences in their salinity requirements and in ability to withstand sharp or gradual changes in salt content of sea water. Therefore, in determining minimum, maximum and optimal salinities for their existence each species, especially those populating estuarine regions, must be studied individually. For example, deltas of rivers, where salinities are relatively high most of the time, may be populated by both *C. virginica* and *M. mercenaria*, while a short distance above this line, where the salinity of the water is considerably lower than 20 parts per thousand, only oyster beds can be found because clams are unable to survive under such brackish conditions. To demonstrate the differences that may exist between two species that often may be found in the same environment, we shall briefly discuss the differences in salinity requirements of larvae of *C. virginica* and *M. mercenaria*.

Loosanoff (1952) found that the lowest salinity at which normal development of gonads of *C. virginica* of Long Island Sound may proceed is near 7·5 ppt. Continuing the study of various aspects of variations in salinity on propagation of American oysters, Davis (1958) demonstrated that 22·5 ppt was the optimum salinity for development of eggs of oysters that had grown in Long Island Sound and had developed gonads at a salinity of about 27 ppt. Some normal larvae developed, nevertheless, in salinities as low as 15 ppt and as high as 35 ppt. At salinities below 22·5 ppt the percentage of eggs that developed to straight-hinge larval stage steadily decreased until, at 15 ppt, only 50 to 60% of the eggs developed normally. At 12·5 ppt practically none of the eggs developed into normal shelled larvae.

In another experiment Davis used Maryland oysters that had grown and developed gonads in the upper parts of Chesapeake Bay where the salinity, at the time the oysters were collected, was only 8·7 ppt. These oysters were spawned at Milford Laboratory in salinities of 7·5, 10 and 15 ppt. Under these conditions some eggs developed into normal larvae even at 10 ppt and 7·5 ppt although, in the latter, slightly smaller than normal larvae were common. In general, the optimal salinity for normal development of eggs of these oysters from

very brackish water was between 12 and 15 ppt, while a salinity of 22·5 ppt was the upper limit.

When oysters that had developed gonads at a salinity of 27 ppt were used as parents, the optimal salinity for growth of their larvae, after they had reached straight-hinge stage, was 17·5 ppt. Good growth was also recorded at a salinity of 15 ppt, but at 12·5 ppt growth was appreciably slower, although some larvae grew to metamorphosis. At 10 ppt growth was practically at a standstill and it is doubtful that any larvae could reach setting stage at this salinity. The older the larvae, however, the better they withstood the salinity of 10 ppt. Larvae that were reared almost to setting stage at our normal salinity of about 27 ppt continued to grow and even metamorphosed when transferred to a salinity of only 10 ppt.

Davis (1958) also showed that the optimal salinity for development of eggs of *M. mercenaria* of Long Island Sound was about 27·5 ppt. No normal larvae developed at salinities of 17·5 ppt or lower. The upper salinity limit for development of clam eggs was 35 ppt, but only an occasional normal larva developed at that concentration of salt.

Straight-hinge clam larvae grew reasonably well at 17·5 ppt and many reached metamorphosis, but at 15 ppt none of them reached that stage, although some lived for 10 or more days and showed a slight increase in size. At 12·5 ppt straight-hinge clam larvae showed no growth and all were dead by the 10th day.

As can be seen from this brief comparison, eggs and larvae of *C. virginica* can normally develop and grow to metamorphosis in a much lower salinity than those of *M. mercenaria*. Undoubtedly, using present methods of cultivation of larvae, similar studies will soon be performed on other species of bivalves and prove to be as informative and useful as those reported in the recent article by Davis and Ansell (1962) on development of eggs and growth of larvae of *O. edulis* in water of different salinities.

H. *Effects of turbidity on eggs and larvae*

One of the least studied factors of molluscan environments is that of turbidity (Loosanoff and Tommers, 1948; Jørgensen, 1949; Loosanoff, 1962a). A review of the literature in this field (Jørgensen, 1960) shows that even though some work has been performed on adult mollusks, until the recent contributions of Davis (1960, and unpublished), virtually nothing was known of the ability of bivalve eggs to develop or larvae to survive in turbid waters. Davis employed a rotating wheel, to which culture vessels were attached, to maintain turbidity at definite constant levels. The turbidity-creating substances

used in his experiments were the same as those employed by Loosanoff and Tommers (1948) in their studies on behavior of adult oysters. They were fine silt collected from tidal flats, kaolin (aluminium silicate), powdered chalk and Fuller's earth.

Davis showed that silt was considerably more harmful to eggs of oysters, *C. virginica*, than to those of clams, *M. mercenaria*. For example, in concentrations of 0·25 g/l of silt only 73% of oyster eggs survived, while more than 95% of clam eggs developed to straight-hinge stage. Practically all clam eggs developed to straight-hinge stage in concentrations of 0·5 g/l of silt, while only 31% of oyster eggs survived.

In a suspension of kaolin and Fuller's earth, on the other hand, clam eggs showed much higher mortality than eggs of oysters. Thus, in concentrations of 1 g of these substances per liter of sea water, practically all oyster eggs developed to straight-hinge stage, while only 37% and 57% of clam eggs survived.

Strangely enough, of the materials which were tested in these experiments, silt, a natural substance, was more harmful to oyster eggs than either kaolin or Fuller's earth. While practically none of the eggs exposed to 1 g/l of silt reached straight-hinge stage, some eggs developed normally even in concentrations as heavy as 4 g/l of kaolin or Fuller's earth.

As in the case of eggs of these two species, silt was more harmful to oyster larvae than to clam larvae. At a concentration of 0·75 g/l of silt growth of oyster larvae was markedly decreased while, as a striking contrast, clam larvae grew normally even in 1 g/l of silt. Moreover, the majority of the clam larvae survived for 12 days and even showed some growth in 3 and 4 g/l although it is doubtful that they could reach metamorphosis under these conditions.

Kaolin and Fuller's earth were considerably more harmful to clam larvae than to oyster larvae. Concentrations of 0·5 g/l of kaolin caused about 50% mortality of clam larvae in 12 days and, while practically no clam larvae survived in concentrations of 1 g/l of either kaolin or Fuller's earth, growth of oyster larvae was not appreciably affected by 1 g/l of kaolin. Davis also found that some oyster larvae may live as long as 14 days in concentrations of 2 g/l of silt and up to 4 g/l of either kaolin or Fuller's earth. These observations demonstrated an unusual ability of larvae of *C. virginica* to withstand highly turbid water, a situation often existing in summer at or near mouths of rivers where natural oyster beds are found.

In several experiments, where small quantities of turbidity-creating materials were added to water containing straight-hinge larvae

of oysters or clams, growth of these organisms was stimulated, often becoming considerably more rapid than in control cultures. Possibly, this was a result of adsorption, by particles of such materials, of toxic substances formed in larval cultures. It is also possible that some of these materials that were added to the water contained a positive growth factor, as do certain soil solutions.

In summarizing the observations on the effect of turbidity on oyster and clam larvae, it may be concluded that larvae, as well as adults, are affected by turbidity-creating substances, although larvae seem to display a considerable tolerance towards some of these materials. Moreover, larvae of different species react differently, one species may be more tolerant or less resistant to the same material under the same conditions. It is significant, nevertheless, that in some instances comparatively light concentrations of common silt may strongly interfere with normal development of eggs of some bivalves.

I. *Effects of foods on growth of larvae*

In any laboratory, where large numbers of adult and juvenile mollusks are kept, these animals, because of limited space, are often crowded, receiving insufficient quantities of water and, therefore, food. To improve these conditions we add large quantities of artificially-grown plankton to the water flowing through troughs and trays.

Because of the scope of our work several hundred gallons per day of relatively rich phytoplankton are often needed. Obviously, it is impractical to grow such large quantities of plankton in glass flasks using common laboratory techniques. Fortunately, by merely adding complete commercial fertilizers to sea water, rapid growth of phytoplankton can be initiated and later maintained in heavy concentrations. Our experiments have shown that fertilizers designated by formulas 5-3-5 and 6-3-6, both used by Connecticut tobacco growers, gave the best results, although lawn fertilizer, 10-6-4, was also good (Loosanoff and Engle, 1942). Using these fertilizers, mass cultures of rich, mixed plankton have been continuously grown at our laboratory since 1938. A wooden, 2000-gal oval tank is used for this purpose, although on several occasions the cultures have been grown in outdoor, concrete, 10000-gal tanks. The sea water used in these tanks was passed through a sand filter.

To supply the laboratory in winter with a sufficient quantity of plankton we designed a special enclosure, resembling a greenhouse, in which a plankton-containing tank is installed (Fig. 21). By providing artificial light, when needed, and maintaining the temperature of the

enclosure at the desired level, the laboratory is now supplied with rich, mixed phytoplankton on a year-round basis.

A common difficulty experienced in growing phytoplankton in open tanks of several-thousand-liter capacity, as is done at Milford, is invasion of these cultures by zooplankton organisms. In our mass cultures the most common offenders are crustaceans, especially copepods. These forms multiply so rapidly in rich phytoplankton that they soon consume most of the plant cells, rendering the culture useless.

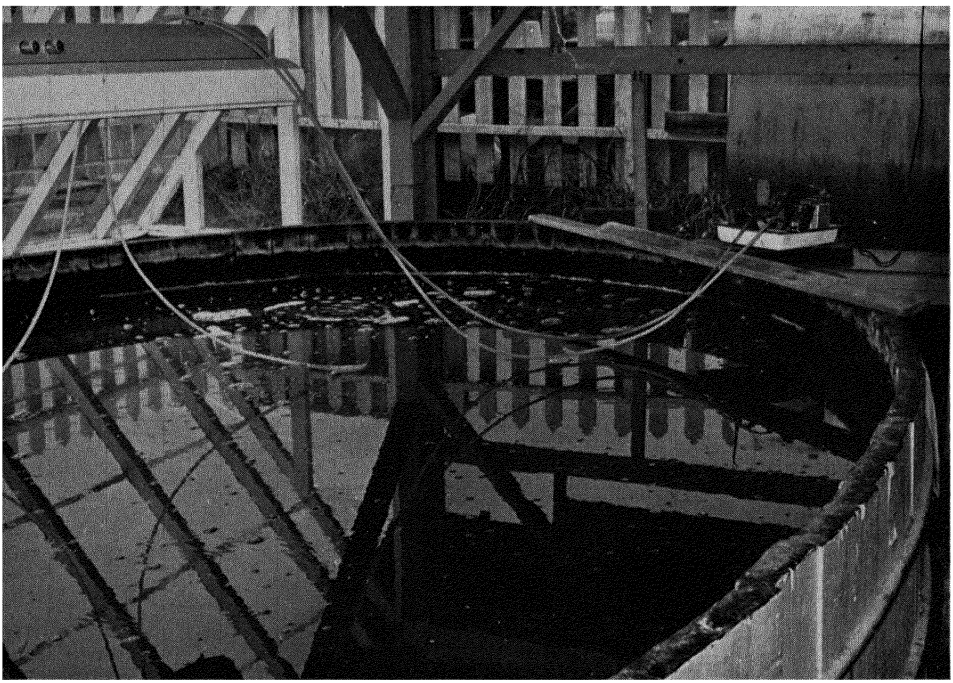


FIG. 21. Mass culture of mixed phytoplankton grown in large wooden tank of about 2 000-gal capacity under semi-outdoor conditions. Description in text.

In the past, several methods were tried to prevent such contamination of open-air algal cultures, but they usually were unsuccessful because some crustacean eggs were always left behind and eventually hatched, reinfesting the cultures. Recently, we developed an extremely simple and safe method to control these infestations by merely adding to our cultures, when necessary, small quantities of insecticides (Loosanoff *et al.*, 1957). Several of these substances have been tried and found successful in concentrations as low as 0·1 ppm. At present, we use a commercial preparation known as TEPP, which contains 40% of tetraethyl pyrophosphate. The advantages of using TEPP are

that it hydrolyzes within 24 to 48 hr and it has no permanent effect on algae; therefore, it does not impair the usefulness of the culture as a food for mollusks.

The mass culture grown in our tank is not a single species but a mixture, the composition of which varies from day to day or even hour to hour. This culture usually contains various species of *Chlorella*-like organisms, but because *Chlorella* is not one of the best foods for larval

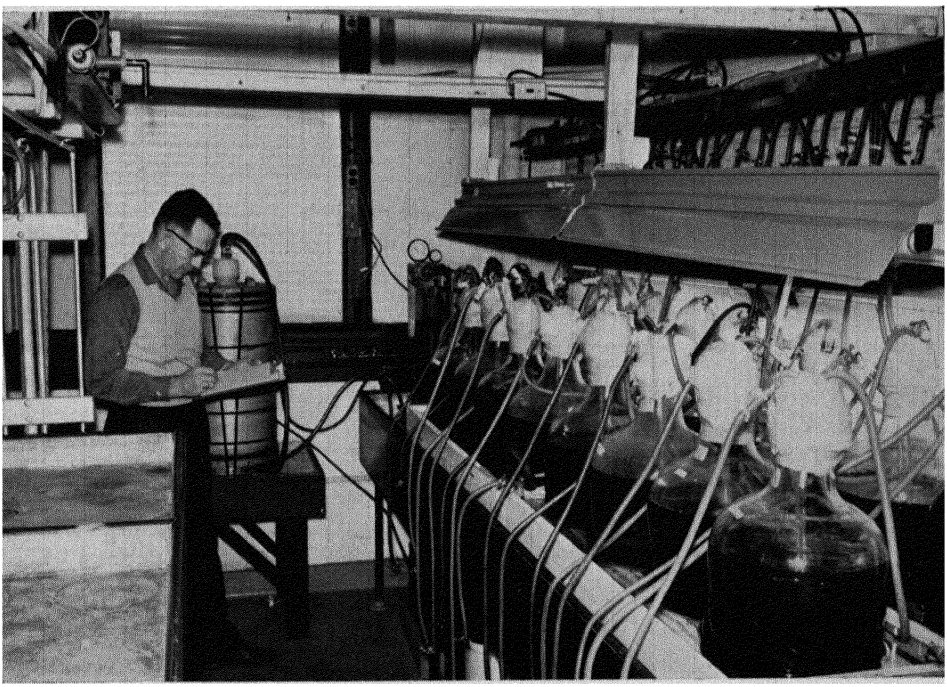


FIG. 22. Battery of specially-fitted, 5-gal Pyrex carboys serving as growth chambers for mass culture of photosynthetic microorganisms. Description in text.

and juvenile mollusks, it has become necessary to grow on a large scale such forms as have been recently found to assure good growth and low mortality of larvae. Moreover, because it was found by our European colleague (Walne, 1956, 1958) and at our laboratory (Davis, 1953; Davis and Guillard, 1958) that bacteria in sea water, especially in algal cultures, may seriously affect lamellibranch larvae, sometimes not only slowing their growth but causing complete, or almost complete mortalities, we made special efforts to develop a method by means of which virtually bacteria-free algal cultures can be grown. To achieve this an apparatus was devised and placed in operation at our laboratory

approximately 3 years ago and has since consistently given satisfactory results (Davis and Ukeles, 1961).

The culture apparatus consists of sixteen 5-gal Pyrex carboys as growth chambers (Fig. 22). Vigorous agitation, by bubbling a mixture of air and CO_2 through the cultures, keeps the contents of the chambers thoroughly mixed. This prevents stratification and helps to expose all cells to equal periods of strong illumination. The carboys are immersed to a depth of 3 or 4 in in a water bath kept at a desired temperature, usually 19° ± 1°C. About 3 liter of the algal culture from each growth chamber are harvested each day, yielding about 1·5 ml of packed wet cells. The present system, thus, produces daily approximately 50 liter of algal suspension, averaging 0·5 ml of packed cells per liter.

A volume of sea water, nutrient salts and antibiotics, equal to the volume of culture drawn off, is added daily to each growth chamber. The sea water used is first passed through Orlon filters, previously described, to remove larger particles. Nutrient salts are then added and this solution is forced through a ceramic bacteriological filter (Selas No. FP-128-03, maximum pore size 0·6 μ) into the growth chambers. Recently, we have been adding to the sea water and nutrient salts, prior to final filtration, 0·002% Acronize (approximately 10% chlorotetracycline) to reduce bacterial growth on the ceramic filters. This concentration of Acronize does not interfere with algal growth and helps prolong the life of the cultures.

Although *Chlorella* sp. and a number of other algae will grow on a media made from 5-3-5 or 6-3-6 fertilizers, a more elaborate media is needed for our bacteria-free cultures. Since the requirements of each of the more than eighty species of marine algae maintained at our laboratory have not been determined, we use the following as " universal " media, although it is recognized that the necessity for the various ingredients has not been ascertained. Two stock solutions of nutrient salts are prepared and 1 ml of each is used per liter of sea water.

Solution A

Dissolve in 1 liter of distilled water	
NaH_2PO_4	20·0 g
Thiamine HCl	0·2 g
Biotin	0·001 g
B_{12}	0·001 g
Pyradoxine HCl	0·1 g
Calcium pantothenate	0·2 g

Solution B

Dissolve in 1 liter of distilled water

$NaNO_3$	150·0 g
*NH_4Cl	50·0 g
Ferric sequestrine	10·0 g

* Media for *Isochrysis galbana* should omit the NH_4Cl.

Experiments conducted at our laboratory have shown that some species of bacteria are harmless, others are strongly pathogenic, and still others produce toxic metabolites. It is quite possible, therefore, for some bacterized cultures of algae to be good larval foods, while the same algae, with a different bacterial population, may be acutely toxic. Consequently, for critical evaluation of any phytoplankton organism as a food for larvae it is necessary to use a bacteria-free culture of it. Furthermore, in using mass cultures of algae, where there is always danger of bacterial contamination, it should always be ascertained that the cultures have not become contaminated with toxic or pathogenic bacteria.

As already mentioned, certain species of algae also produce metabolites that are toxic to bivalve larvae, while other species produce little or none (Fig. 23). Some of the algae produce so much toxic material that they are useless as foods because their toxins kill larvae even when concentration of algal cells is too light to satisfy larval demand for food. Others, such as *Chlorella* (580), produce some toxic products but are still usable foods, provided that their concentrations are not too high.

Recently, Davis (1953) and Davis and Guillard (1958) concluded that presence and thickness of cell walls and degree of toxicity of metabolites are important factors in determining usability of photosynthetic microorganisms as larval food. They showed that the naked flagellates, *I. galbana* and *M. lutheri*, were of approximately equal value as food for larvae of the American oyster and induced more rapid growth than any of the other species tested. Davis also believes that *I. galbana* and *M. lutheri* produce little, if any, toxic external metabolites which unfavorably affect larvae. This is supported by his observations that the optimal concentrations of the two forms for either clam or oyster larvae were at least double the optimal concentrations of *Chlorella* sp. (Lewin's isolate).

The food value of microorganisms also depends, in part, upon how completely they meet the food requirements of larvae. It was found, for example, that a mixture of *I. galbana*, *M. lutheri*, *Platymonas* sp. and *Dunaliella euchlora* induced more rapid growth of both clam

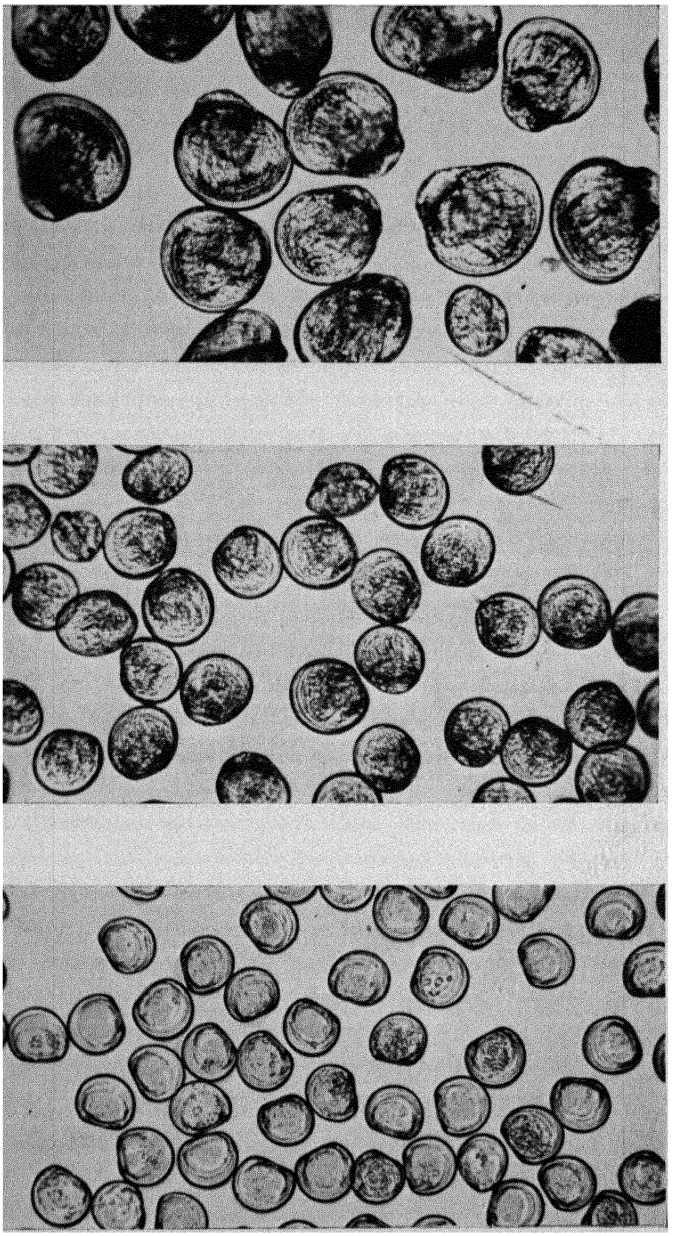


FIG. 23. Twelve-day-old larvae of *Crassostrea virginica* given different algae as food. Group fed *M. lutheri* (*upper photograph*) averaged 169 μ in length, while the middle group, serving as control and receiving no supplementary food, averaged 96 μ. The lower group, containing only dead larvae, was given *Stichococcus* sp. isolated from Great South Bay, Long Island, New York, which produces toxic metabolites.

and oyster larvae than did equal quantities of any of these foods separately.

D. euchlora and *Dunaliella* sp., both naked flagellates, as are *I. galbana* and *M. lutheri*, also induced better growth of oyster larvae during the first 6 days of their development than did any of the forms having cell walls. Thus, Davis concluded that, with the exception of *Prymnesium parvum*, which is toxic, even the poorest of the naked flagellates is a better food for young larvae of *C. virginica* than any of the organisms with cell walls. This conclusion supports the earlier one of Cole (1939) and Bruce *et al.* (1940), that nanoplankton may differ in their value as food for larvae of *O. edulis*. Davis found, nevertheless, that *Chlorella* (580), *Platymonas* sp., *Chlorococcum* sp., and *Phaeodactylum tricornutum*, all forms having cell walls, were utilized by larvae of *C. virginica*, but growth, particularly of younger individuals, was slow and might have occurred because of presence in the water of other food materials.

Observations on behavior of larvae of approximately twenty different species of bivalves grown at our laboratory have shown that, in general, as far as their qualitative food requirements are concerned, they can be roughly divided into two or, perhaps, three groups. The first group, well-represented by larvae of oysters of the genus *Crassostrea*, is able to utilize, during early straight-hinge stages, only a few of the many food forms (Davis, 1953; Davis and Guillard, 1958). The second group includes larvae of such species as *Mercenaria mercenaria* and *Mytilus edulis*, which seem to be able to utilize most of the microorganisms, provided that they are small enough to be ingested. The third, an intermediate group, also can be tentatively recognized. This group includes such larvae as those of larviparous oysters of the genus *Ostrea*, which are much less restricted in their qualitative food requirements than larvae of the genus *Crassostrea*, yet they are unable to grow quite as well on some of the foods as larvae of *M. mercenaria*.

The food requirements of the two marginal groups were clearly shown in our experiments where larvae of the oyster, *C. virginica*, and clam, *M. mercenaria*, were placed simultaneously and kept together in the same laboratory culture vessels or in large outdoor tanks. All cultures were given the same food, which consisted of mixed phytoplankton in which small, green algae, such as *Chlorella*, normally predominated. Under these conditions larvae of *M. mercenaria* grew rapidly and metamorphosed approximately in 12 days, while larvae of *C. virginica*, after attaining straight-hinge stage, showed virtually no growth and eventually died. The results of these early experiments were confirmed by Davis (1953), who showed that while young larvae of

C. virginica are unable to utilize forms having cell walls, such as *Chlorella*, older larvae of the same species become able to do so after they reach a larger size of approximately 110 μ.

In general, these studies have demonstrated several important points. One of them is that larvae of *M. mercenaria* can live and grow to metamorphosis on a very restricted diet, consisting of a single species of algae, such as *Chlorella*, and that unlike larvae of *C. virginica*, they can utilize these algae during all stages of development. Our conclusions, therefore, disagree with those of Cole (1936) who maintained that bivalve larvae, in general, do not possess the enzymes needed for digestion of cellulose, of which the cell walls of algae, such as *Chlorella*, are made.

As our techniques improved and we were able to evaluate the food value of different forms of phytoplankton, we found that larvae of *M. mercenaria* can be grown not only on a pure culture of *Chlorella*, reaching metamorphosis in some cases in 12 days, but that they can also be grown to metamorphosis on pure cultures of any one of the following three flagellates: *Chlamydomonas* sp., *Chromulina pleiades* or *I. galbana* (Davis and Loosanoff, 1953).

Our studies have also shown that organic detritus, at least of the types tested, cannot be utilized by larvae of clams, *M. mercenaria* (Loosanoff *et al.*, 1951), or oysters (Davis, 1953).

Larvae of *M. mercenaria* seem to be capable of both mechanical, or quantitative, and chemical, or qualitative, selectivity in feeding. They are able to regulate the amount of food ingested and thus survive in heavy concentrations of food cells, often containing less food in their stomachs than larvae kept in lighter food concentrations. Apparently, clam larvae are not merely mechanical feeders, but possess a mechanism by means of which they can control the food intake by rejecting algal cells, when necessary. However, if kept in heavy concentrations of algae for a long time, the larvae lose this regulating ability, become choked with food cells and, eventually, die.

We also observed that larvae can select certain food organisms from a mixture of several forms of phytoplankton. For example, when given a mixture of *Porphyridium* sp. and *Chlamydomonas* sp. larvae of *M. mercenaria* ingested the much larger cells of *Chlamydomonas*, while rejecting the cells of the smaller *Porphyridium* (Loosanoff *et al.*, 1953).

An important problem faced in connection with cultivation of bivalves was to ascertain the effects of different concentrations of food organisms upon larval survival and rate of growth. The first series of experiments was conducted with larvae of *M. mercenaria* in

concentrations of approximately seven larvae per ml, but fed different quantities of food, consisting principally of small *Chlorella* measuring only about 3 μ in diameter. These cells were fed to larvae in concentrations ranging from 6 500 to 1 million cells per ml of water in culture vessels. Simultaneously, another series of larval cultures was fed a unialgal strain of another *Chlorella*, the cells of which were about 8 μ in diameter (Loosanoff *et al.*, 1953).

Results showed that optimal concentrations of food cells clearly depended upon their size. When large *Chlorella* was given, the optimal concentration of this form for best survival and growth of larvae of *M. mercenaria* was approximately 50 000 cells per ml, while approximately 400 000 cells per ml of the smaller *Chlorella* were needed to achieve the same results. This suggests that the food value of 400 000 small *Chlorella* cells closely approached that of 50 000 cells of the larger form, both concentrations being near optimum. If the cells are considered as perfect spheres, the volume of 400 000 cells, 3 μ in diameter, is approximately equal to the volume of 50 000 cells, 8 μ in diameter.

A concentration of approximately 750 000 cells per ml of small *Chlorella* was already above the optimum because, when given so much food, the larvae grew more slowly than when given only 400 000 cells per ml of small *Chlorella*.

Larvae of *M. mercenaria* and many other bivalves can be killed if concentrations of food cells, such as *Chlorella*, become too heavy. Again, these concentrations depend upon the size and kind of cells. For example, approximately 90% of clam larvae were killed within a few days and those that survived grew very slowly or not at all when given approximately 300 000 cells of large *Chlorella* per ml of water. When the concentration was increased to 500 000 or more cells per ml, all clam larvae were killed within 24 hr. However, when given the much smaller form of *Chlorella*, which measured only about 3 μ, the larvae grew comparatively well in concentrations as high as 750 000 cells per ml.

It is of interest that larvae that managed to survive in heavily overfed cultures usually displayed certain anatomical abnormalities which, probably, made the larvae unable to ingest food. Perhaps these abnormalities were responsible for survival of these larvae under the conditions where normal individuals were killed.

We realize that, in studying the food requirements of bivalve larvae, the quantity of algal cells in the surrounding water constitutes only one factor needed to determine the adequacy of a food because this value may be subject to considerable variations according to the

age of the algal cultures, their density, chemical composition, bacterial flora and, of course, the media in which they are grown. These difficulties have been eliminated, to some extent, in our more recent experiments where production of food cells has been standardized (Davis and Ukeles, 1961).

As has previously been shown for adult bivalves (Loosanoff and Engle, 1947), their larvae can be killed either by a heavy concentration of algal cells alone, by the filtrate of algal cultures or by a combination of the two (Loosanoff *et al.*, 1953). In other words, dense concentrations of certain food organisms, such as *Chlorella*, affect larvae of *M. mercenaria*, as well as those of several other species, both mechanically, by interference of food cells with larval swimming and feeding mechanisms, and chemically, by producing external metabolites which are toxic to larvae. As an illustration, the larvae grew comparatively well when control cultures received approximately 100 000 cells per ml of large *Chlorella*, even though this concentration was somewhat above the optimum for this strain of algae. However, cultures of larvae receiving cells of *Chlorella*, that had been removed from the culture medium by Millipore filters and later resuspended in sea water at the rate of 1 million cells per ml, were rapidly killed. Similarly, larvae receiving the filtrate only from a certain volume of algal culture originally containing one million cells of *Chlorella* per ml also quickly died. These studies further showed that a filtrate containing heavy concentrations of metabolites of *Chlorella* cells may be even more detrimental to larvae than heavy concentrations of the resuspended cells themselves. As has already been mentioned, the ecological effects of external metabolites have long been recognized by aquatic biologists (Lucas, 1947).

Recently, Davis and Guillard (1958) conducted extensive experiments to determine the relative value, as larval food, of representatives of ten different genera of microorganisms. *I. galbana* and *M. lutheri* were the best foods and were approximately of equal value. In some experiments, nevertheless, *Chlorococcum* sp. was the best food for larvae of *M. mercenaria*. Clam larvae were also able to utilize several species of *Chlorella*, *Dunaliella euchlora*, *Dunaliella* sp., *Platymonas* sp., *Chlamydomonas* sp. and *Phaeodactylum tricornutum*. However, they could not utilize one species of *Stichococcus* or *Prymnesium parvum*.

Experiments also demonstrated that, as in the case of larvae of *C. virginica*, a mixture of *I. galbana*, *M. lutheri*, *Platymonas* sp. and *D. euchlora* promoted somewhat more rapid growth of clam larvae than did equal quantities of any of these foods separately.

Some of the algae tested at Milford Laboratory are given below with

the species listed in their approximately descending order of value as foods for larvae of *M. mercenaria* and *C. virginica*. Several other species tested are not listed here because they were either poor foods or were toxic.

M. mercenaria	*C. virginica*
A. Good Foods:	A. Good Foods:
Monochrysis lutheri	*Monochrysis lutheri*
Isochrysis galbana	*Isochrysis galbana*
Dicrateria sp. (B II)	*Chromulina pleiades**
Chlorococcum sp.	*Dicrateria inornata**
Platymonas sp. (1)	*Pyramimonas grossi**
B. Medium Foods:	*Hemiselmis refescens**
Carteria sp.	B. Medium Foods:
Chlamydomonas sp.	*Dunaliella euchlora*
Cyclotella sp. (O-3A)	*Platymonas* sp. (1)
Chlorella sp. (580)	*Cyclotella* sp. (O-3A)
Stichococcus sp. (O-18)	*Dunaliella* sp.
Phaeodactylum tricornutum	*Chlorococcum* sp.
Skeletonema costatum	*Chlorella* sp. (UHMC)
Chlamydomonas sp. (D)	*Phaeodactylum tricornutum*
Rhodomonas sp.	*Cryptomonas* sp.
Dunaliella sp.	
Olisthodiscus sp.	
Dunaliella euchlora	

* Not tested on clam larvae.

The most recent contribution to our knowledge of food requirements of the European flat oyster, *O. edulis*, was made by Walne (1956) who also reviewed efforts in this field by earlier investigators. Walne conducted over 200 tests using many species of algae. Although he states that many of his experiments were failures, often for no apparent reason, his results showed that the Chrysophyceae, especially *Isochrysis galbana* and *Chromulina pleiades*, gave good results, notwithstanding that *P. parvum* was toxic to larvae. Members of the Chlorococcales, which have a thick cell wall, were found to be poor food for the larvae of *O. edulis*. Of the Chlorophyceae, only *Pyramimonas grossi* was a good food.

In our experiments we found that larvae of *O. edulis* can be grown on a species of *Chlorella*, even though it has a thick cell wall. In this respect our results disagree with those of Walne and some of the earlier investigators. We agree, however, that naked flagellates,

especially *I. galbana* and *M. lutheri*, are the best foods for larvae of this oyster.

Imai *et al.* (1953) mentioned in several articles the successful use of the colorless naked flagellate, *Monas* sp., as a food for oyster larvae. Through the kindness of Dr. Imai we received a sample of a culture of this organism and grew it on a large scale. However, we have consistently been unable to raise larvae on a diet of this flagellate alone. In our controlled experiments larvae of *M. mercenaria* and *C. virginica* grew and survived better in unfed controls than when given 4 000 cells of *Monas* sp. per ml of water in culture vessels. Use of the same flagellate by oyster biologists of the State of Washington (Lindsay, personal communication), who also obtained these flagellates from Dr. Imai, always resulted in failure. Our conclusion that colorless flagellates are not a good food for bivalve larvae is also supported by recent observations of Walne (1956), who could not raise larvae of *O. edulis* by using another colorless flagellate, *Bodo* sp.

Growing of algal food for larval or juvenile mollusks, even if these cultures do not need to be kept unialgal and bacteria-free, presents a number of difficulties and, naturally, an easier method of producing food for bivalves, including adults, is desirable. Our experience, in the late 'thirties, in attempting to increase the glycogen content of adult oysters by feeding them pulverized dried algae, such as different species of *Ulva* and *Laminaria*, led us to try the same approach in feeding larvae with dried algae. In the initial experiments dried and pulverized *Ulva*, which we preserved and kept in a glass jar for over 20 years, was used. Surprisingly enough, many cultures of larvae of *M. mercenaria*, given this food, grew to metamorphosis. However, several problems were encountered in connection with this method. First, it was found difficult to grind these algae into particles small enough to be ingested by larvae. Secondly, the material quickly settled on the bottom, thus becoming unavailable to swimming larvae. Finally, because of rapid decomposition of unconsumed algae, the larval cultures became fouled and the bacterial flora in them quickly increased.

Fortunately, we have been able to overcome these difficulties. Through the courtesy of Dr. Hiroshi Tamiya of The Tokugawa Institute for Biological Research in Tokyo, Japan, and Dr. Hiroshi Nakamura of the Japanese Nutrition Association, we received samples of dried *Scenedesmus* sp. and *Chlorella* sp. Because the average size of the individual cells of both of these algae is small, they can be easily ingested by larvae. By feeding proper quantities of dried, ground *Scenedesmus* in larval cultures, which are continuously agitated by

plungers or horizontal-action paddles (Fig. 5), and by controlling the bacterial flora in the cultures by the addition of Sulmet, our associate, H. Hidu, to whom these studies were suggested, has been

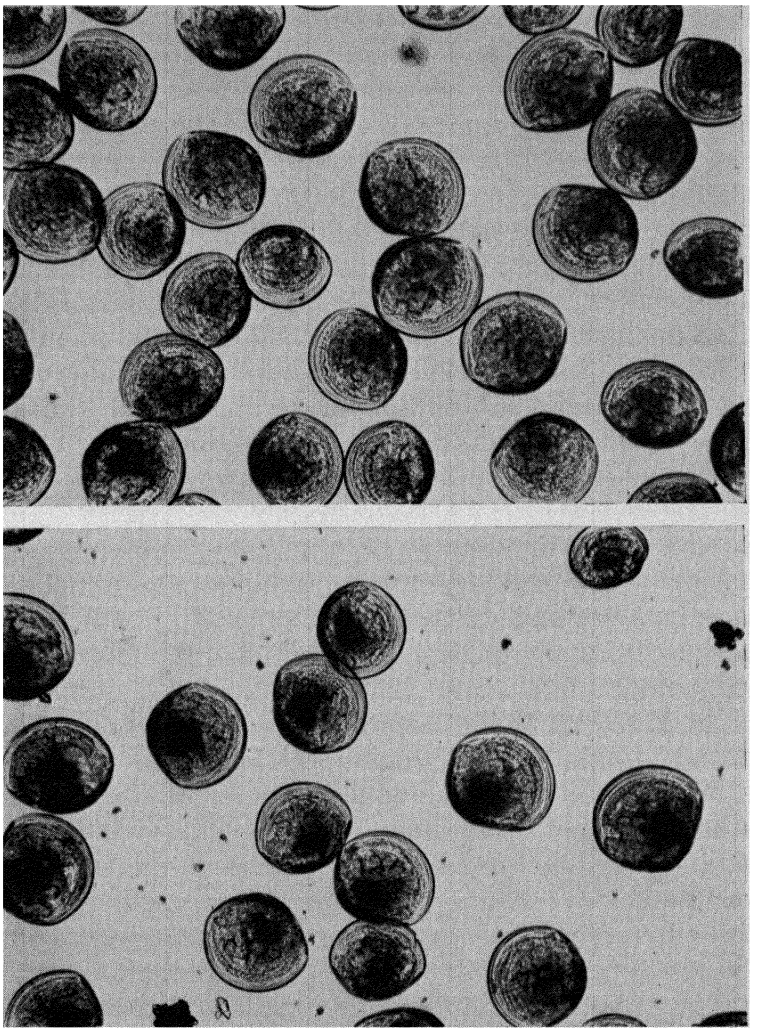


FIG. 24. Twelve-day-old larvae of *Mercenaria mercenaria*. Larvae shown in upper photomicrograph were fed freeze-dried cells of *Isochrysis galbana*, while those in the lower picture were given the same quantities of live cells of the same algae. Largest larvae are about 215 μ long.

able to grow larvae of *M. mercenaria* almost as effectively as when they are fed our best live food organisms, such as naked flagellates. In some experiments clam larvae fed freeze-dried *I. galbana* grew as rapidly as larvae in the control cultures given the same quantities of live cells of the same form (Fig. 24).

When fed *Scenedesmus* clam larvae grew best in concentrations of 0·02 ml packed food per liter of water per day. However, dosages as low as 0·005 ml packed food per liter gave just as good results in feeding larvae during their first 4 days of existence (Hidu, personal communication). Agitated cultures treated with Sulmet gave 50 to 100% better growth of larvae than identical unagitated cultures. The type of motion and size of agitating devices appeared to be of little significance to larval growth and survival. Mortality in all agitated cultures was negligible. In some situations, nevertheless, agitation may not be desired.

Experiments on growing larvae of American oysters on dried *Scenedesmus* have been unsuccessful thus far. We are, however, continuing experiments in this field using, at present in a dried state, such organisms as *I. galbana* and *M. lutheri* which, when alive, are readily utilized by larvae of *C. virginica*. Results of these and related studies will be reported in the near future by Mr. Hidu. It should be realized, nevertheless, that this sphere of research is now only in its initial phase and, therefore, it is too early to form general conclusions. We hope, however, that it will be extremely productive.

In discussing larval foods we would like to emphasize that color of the larvae themselves depends, to a large extent, upon color of food consumed. By feeding larvae differently colored food organisms we were able, especially during early straight-hinge stages, to change their color within a few hours.

Although the color of the shell proper was not always affected, the soft parts of the body quickly changed their coloration which, of course, reflected on the color of the larvae as a whole. It may also be added that according to our observations even the color of shells of recently set oysters growing in running water is darker than that of oysters of the same age that are kept in filtered sea water and fed naked flagellates. However, if these pale young oysters are transferred to natural water containing color-carrying phytoplankton, they quickly develop a much darker color. It seems logical to expect that in nature, where combinations of forms constituting phytoplankton change frequently, correspondingly frequent and rapid changes in the general color of larvae may also occur. We disagree, therefore, with workers who maintain that color is a dependable criterion for identification of bivalve larvae.

J. *Effects of crowding*

An important problem that faced us in early attempts to rear molluscan larvae was to determine maximum concentrations at which

they could survive and optimal concentrations for their growth. We expected these concentrations to depend upon species and quantity and quality of food, but soon found that such hardy varieties as *M. mercenaria* could be grown in concentrations of 50 to 100 larvae per ml of water. If these cultures were properly attended and fed, the majority of the larvae survived and, despite their slow rate of growth, they could, nevertheless, be reared to metamorphosis.

Although these were much heavier concentrations than those advocated by other investigators, who usually emphasize the danger of overcrowding, we sometimes reared larvae to metamorphosis even under more crowded conditions. However, since these observations were of a general nature, special quantitative experiments were undertaken (Loosanoff *et al.*, 1955). In these experiments larvae of *M. mercenaria* were grown in concentrations of about six, thirteen, twenty-six and fifty-two individuals per ml. Each culture received the same quantity of food, namely, 100 000 cells of a small strain of *Chlorella* per ml of water in the rearing vessels.

Larvae in all cultures showed good survival and grew to metamorphosis, although the mean rate of growth in the different cultures had an inverse relationship to population density. For example, on the 10th day the mean length of larvae in the series of cultures containing six, thirteen, twenty-six and fifty-two individuals per ml was 162, 156, 151 and 144 μ, respectively. Experiments showed that, as reported earlier (Loosanoff *et al.*, 1951), overcrowding clam larvae may not be as dangerous as formerly believed but, nevertheless, rate of growth in overcrowded cultures is slower and time of metamorphosis is correspondingly delayed.

Slower growth in the more crowded cultures may be attributed, in part, to more frequent collisions between the larvae and, in part, to the deleterious effect of greater concentrations of excretory products of larvae. Finally, the fact that there was less food per larva in the more heavily populated cultures was suspected as the most probable cause of slower growth. If this were true, rate of growth of larvae in densely populated cultures should be brought up to normal by a proportional increase in amount of food supplied. Accordingly, a new series of experiments was conducted in which number of cells of *Chlorella* was increased in proportion to increase in larval population. This was achieved by adding daily to the culture vessels containing six, thirteen, twenty-six and fifty-two larvae per ml of water, approximately 100 000, 200 000, 400 000 and 800 000 cells of *Chlorella* per ml.

After 10 days larvae in the least crowded culture averaged 162 μ in length, while larvae in the culture containing thirteen larvae per ml

averaged only 148 μ. The two other cultures, containing twenty-six and fifty-two larvae and given 400 000 and 800 000 *Chlorella* cells per ml, died within a few days. This and similar experiments showed, therefore, that crowding of larvae beyond certain limits cannot always

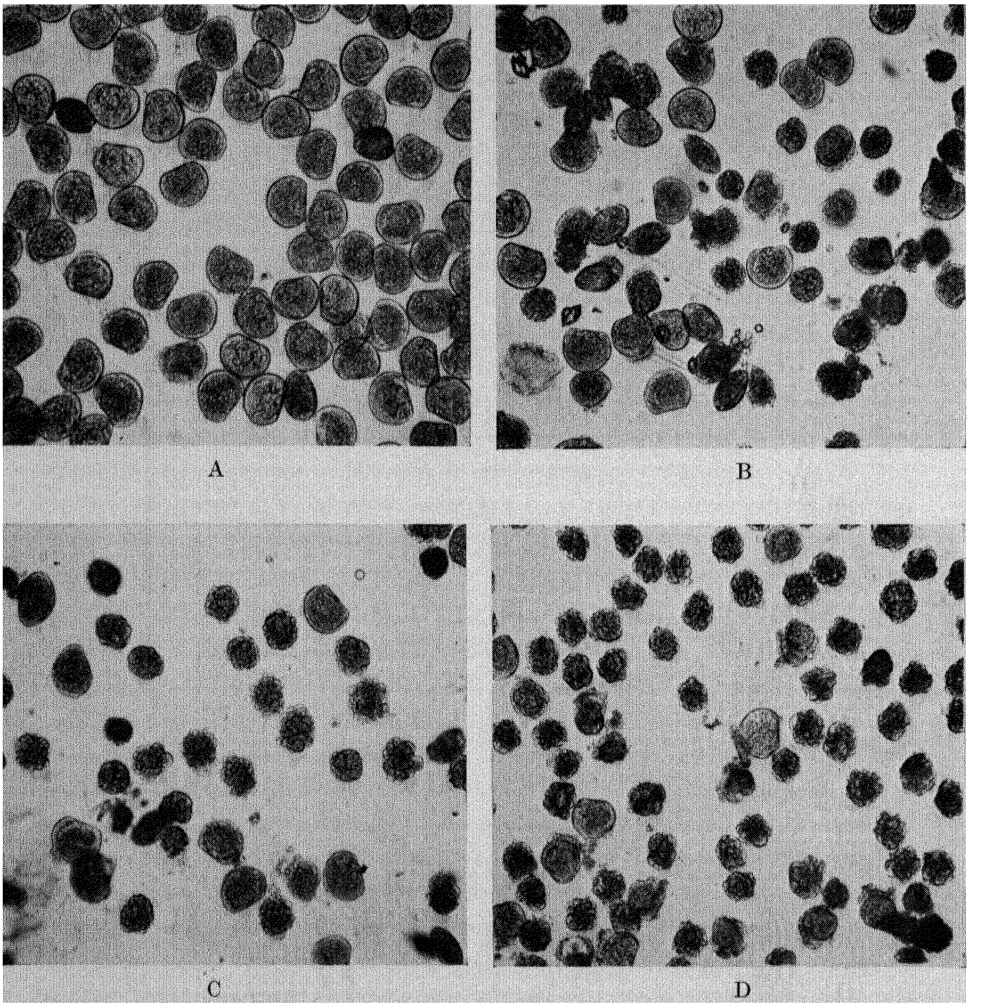


FIG. 25. Forty-eight-hour larvae of *Mercenaria mercenaria* developing from eggs cultured at different densities. A, 250 eggs per milliliter of water; B, 500 eggs per ml; C, 1000 eggs per ml; and D, 3000 eggs per ml.

be remedied by a proportional increase in quantity of food. It was also demonstrated that lethal concentrations of food organisms, as was the case when 400 000 and 800 000 cells of *Chlorella* per ml were given, cannot always be reduced to a safe level by the large number of larvae that presumably would rapidly consume these cells.

Still another experiment showed that eggs and larvae of *M. mercenaria* can develop under even much more crowded conditions than we have indicated thus far. In this experiment cultures were begun by placing in rearing vessels 250, 500, 750, 1000 and 3000 eggs per ml of water. The cultures were incubated at a temperature of about 24°C and examined at the end of 48 hr. The majority of eggs reared at a density of 250 per ml developed into normal straight-hinge larvae (Fig. 25), while in cultures that were begun with 3000 eggs per ml, most of the eggs failed to develop past morula stage and those few that managed to develop to shelled stage were abnormal. In intermediate concentrations of 500, 750 and 1000 larvae per ml some eggs managed to develop into normal straight-hinge larvae but their numbers decreased proportionally with each increase in the initial concentration of eggs.

Experiments on effects of crowding on growth of larvae of the American oyster, *C. virginica*, were described by Davis (1953). He used 640, 2 785, 18 518 and 32 918 48-hr-old larvae per liter and gave all of these cultures the same quantity of food, namely, 50 000 cells of *Chlorella* per ml of water. At the end of 14 days larvae from all cultures were examined and measured. Results showed that there was an inverse relationship between concentrations and rates of growth of larvae. Thus, observations on larvae of *C. virginica* were in agreement with similar observations on clam larvae.

On the basis of our results we can conclude that the danger from overcrowding larvae in well-maintained cultures may not be as acute as believed. Nevertheless, crowding is undesirable because it decreases rate of growth of larvae and, obviously, overcrowded larvae are more susceptible to diseases than are larvae in less densely populated cultures.

K. *Metamorphosis*

In such forms as oysters the end of the free-swimming and crawling periods is clearly terminated by attachment of larvae to some clean, hard surface. However, in most of the other bivalves, whose larval development has been studied at our laboratory, the precise or, often, even approximate moment of metamorphosis is difficult to determine because metamorphosis in such forms as *M. mercenaria*, as we have already indicated (Loosanoff *et al.*, 1951), is a gradual process. It is preceded by a stage in which advanced larvae have both a functional velum and a foot, and alternately swim about and crawl on the bottom. This stage, which has been appropriately termed " pediveliger " by Carriker (1956), may last, under certain conditions, for several hours

or, perhaps, even days. This opinion is indirectly supported by the suggestion of Thorson (1946), Wilson (1958) and other investigators that pediveligers of many bivalves are able to postpone metamorphosis if conditions of environment are unfavorable for completion of this important stage.

Literature contains few references to anatomical changes accompanying metamorphosis of bivalves. This is understandable because, until recently, few forms were successfully and repeatedly grown to this stage. Prytherch's (1934) description of metamorphosis in *C. virginica*, Cole's (1938) in *O. edulis* and, especially, Quayle's (1952) in *Venerupis pullastra* should be mentioned as contributing to our knowledge in this field. However, since a description of the major anatomical changes occurring during metamorphosis does not constitute a part of this paper, no references will be made to the details of this phenomenon in larvae of the mollusks studied by us.

As already mentioned, the number of days required for larvae of the same species to reach metamorphosis depends upon a complex combination of ecological factors, of which temperature and quantity and quality of food are the most important. Each species, of course, has its optimal temperature range for larval development, as well as minimum and maximum levels within which development is possible. Since all species that we cultured were grown to metamorphosis at room temperatures ranging from 18° to 24°C, it is quite certain that this part of the temperature range is comparatively favorable for development of most bivalves of our waters, as well as some of the exotic species with which we worked. However, information as to complete temperature range within which development of each of these species is possible is still lacking in most instances.

We have obtained such data for some species. For example, as already mentioned, in the case of *M. mercenaria* it has been ascertained that larvae grown at 18°C began to metamorphose 16 days after fertilization and continued to set as late as the 30th day. Thus, at this temperature, the period between beginning and completion of metamorphosis of larvae of the same cultures extended for 14 days. At a temperature of 24°C the earliest metamorphosing larvae were noticed on the 11th day, and the latest, 22 days after fertilization. At the considerably higher temperature of 30°C setting of clam larvae began as early as the 7th day after fertilization and was normally completed within 5 to 7 days, or by the 14th day, although in some of the more erratic cultures the last setting larvae were observed on the 16th day after fertilization (Loosanoff *et al.*, 1951).

Similar observations on larvae of *C. virginica* showed that, at a

temperature of 30°C setting usually began on the 10th or 12th day but, again, it extended for several days, as was the case with clam larvae. At lower temperatures the beginning of setting was delayed and its duration prolonged. For example, in one culture kept at a temperature of 24°C the larvae metamorphosed continuously for 27 days.

The number of days needed for larvae of the same cultures to reach setting stage is, therefore, not sharply defined even for a culture reared under standard, well-controlled conditions. In poorly fed, crowded or generally neglected cultures the beginning of setting is usually delayed and the time difference between beginning and end of setting is considerably extended. Sometimes, in cultures kept under poor conditions, towards the end of the experiment large numbers of larvae were found which were apparently unable to grow beyond a certain stage and eventually died without metamorphosing.

In earlier studies (Loosanoff and Davis, 1950) we were already aware that at the time of metamorphosis the size of larvae varied, even among those of the same species. At first, the smallest metamorphosing larvae of *M. mercenaria* were thought to be 210 μ long but, later, larvae measuring only about 175 μ but already going through this process were seen in the cultures. However, setting occurs most commonly when larvae measure between 200 and 210 μ in length.

The largest larvae do not always metamorphose first. Often, in the same cultures comparatively small individuals only about 180 μ in length will complete metamorphosis, while many larger larvae, exceeding 220 μ in length, still continue to swim.

Since there are several suggestions in the literature that invertebrate larvae reach a larger size before metamorphosis if they develop at low temperatures, we conducted a number of experiments to verify these suggestions (Loosanoff, 1959). This information was desired because if it were true that there was a definite relationship between setting size and temperature at which the larvae were grown, then it should be possible to devise a formula to predict setting size for each temperature.

The studies were conducted with larvae of *M. mercenaria* at temperatures ranging from 18° to 30°C. Within this temperature range there were no significant differences with respect to *mean lengths* of larvae at time of setting. Thus, although larvae grown at lower temperatures required more time before reaching metamorphosis, in all cases the larvae attained approximately the same mean lengths before setting. Furthermore, there was no apparent relationship between

maximum lengths of larvae at time of setting and water temperature. Finally, no relationship was found between shape of larvae (ratio of mean lengths to mean widths) at the time of setting and water temperature.

Incidentally, these studies gave us an opportunity to verify the opinion expressed by some authors that forms living in warmer waters have just as long a pelagic life as related species living in northern waters, and that eggs and larvae of southern species develop more slowly than those of northern species of the same genus if both species are kept under identical temperature conditions. We conducted these studies with *M. mercenaria* of Long Island Sound and *M. campechiensis* imported from the Gulf of Mexico. Both groups were ripened in our laboratory under identical conditions and induced to spawn by the usual methods. Eggs and larvae of both species were grown at a temperature of 21°C in triplicate cultures, and random samples of 100 larvae from each culture were taken for length and mortality measurements every two days from fertilization to metamorphosis.

Results clearly indicated that rates of growth and mortality of larvae of the two species were practically identical and that setting of larvae of both groups began simultaneously. On the basis of these observations we may conclude that the belief that eggs and larvae of southern species, when grown at the same temperatures, develop more slowly than those of the northern species of the same genus is not true in all cases.

As has already been mentioned, in some bivalves the beginning of metamorphosis may be delayed because of unfavorable conditions. In addition, in at least one case, namely, that of *Anomia simplex*, we observed what appeared to be partial or interrupted metamorphosis (Loosanoff, 1961). While in larvae of this species metamorphosis commonly occurs at a length of approximately 200 μ, hundreds of individuals considerably larger than 215 μ were seen in some cultures crawling on the bottom by means of a powerful ciliated foot. One of these individuals measured 577 $\times$ 514 μ.

Partial metamorphosis was characterized by disappearance of the velum but retention of a functional foot. Moreover, examination of these crawlers showed another common characteristic, namely, a definite narrow band on their shells, which probably indicated the edge of prodissoconch, or larval shell, and the beginning of dissoconch, or post-larval shell. We assume that the band dividing the two portions of the shell was formed during an important event in the life of the young mollusk, possibly when the velum had entirely disappeared or some other equally important anatomical or physiological change

had taken place. This conclusion is supported by measurements of the inner prodissoconch shells surrounded by the band, which were usually approximately 200 μ in length. This is the size at which setting of the majority of normal larvae of *A. simplex* occurred.

L. *Diseases of larval and juvenile mollusks and their treatment*

Even under the best conditions that can now be maintained in the laboratory there have been occasional heavy mortalities of larval and juvenile mollusks that cannot be accounted for by experimental treatment or errors in technique. Although in most instances this mortality was light, weak or dying larvae could usually be seen harboring heavy populations of bacteria or protozoans; in some cases the mortality was epizootic, killing nearly all young bivalves within a few days.

The field of diseases and parasites of larval and juvenile mollusks is entirely new because studies of this nature were impossible until successful methods for rearing larvae were developed. No information was available, therefore, as to whether the bacteria, protozoans, etc., observed in weak and dying larvae, were the primary cause of their death or merely secondary invaders and, perhaps, only scavengers. Although Davis (1953), in attempts to feed oyster larvae on bacteria, had shown that bacteria retarded growth of larvae and eventually killed them, it was not until 1954 that a fungus, *Sirolpidium zoophthorum* (Fig. 26), was found responsible for some of the epizootic mortalities in our cultures of clam larvae (Davis *et al.*, 1954; Vishniac, 1955). So far, fungus has been found to affect larvae of *M. mercenaria*, *M. campechiensis*, the hybrids of these two species, *Teredo navalis*, *Pecten irradians*, *Tapes semidecussata* and *C. virginica*. However, since it was observed and identified only recently, we have not established whether it can infect larvae of those bivalves which were reared at our laboratory prior to its discovery.

Not all of the forms mentioned above are equally susceptible to fungus. For example, while larvae of *M. mercenaria* and *Teredo navalis* are easily infected, the infection often assuming epizootic proportions, infection of larvae of *C. virginica* is extremely rare. The only case of this type occurred when a large number of fungus-infected clam larvae was introduced into a vessel containing young oyster larvae. Larvae of other forms, such as the bay scallop, *Pecten irradians*, and the Japanese clam, *Tapes semidecussata*, frequently became infected, but the disease seldom reached epidemic proportions.

In *M. mercenaria* and several other species, larvae of all ages, from very early free-swimming stage to those ready to undergo metamorphosis, can be parasitized by fungus. Juvenile clams up to 400 μ in

size have also been found severely infected. On many occasions hundreds of thousands of young clams of this size were found dead or dying within a day or two after the first signs of infection were noticed.

Our observations indicate that fungus is introduced into larval cultures with untreated sea water or, perhaps, more often with food organisms, such as phytoplankton grown in our outdoor tank in which the media is not sterilized. It may be the same organism that infects and kills small crustaceans, such as copepods, which are sometimes present in our outdoor cultures of phytoplankton.

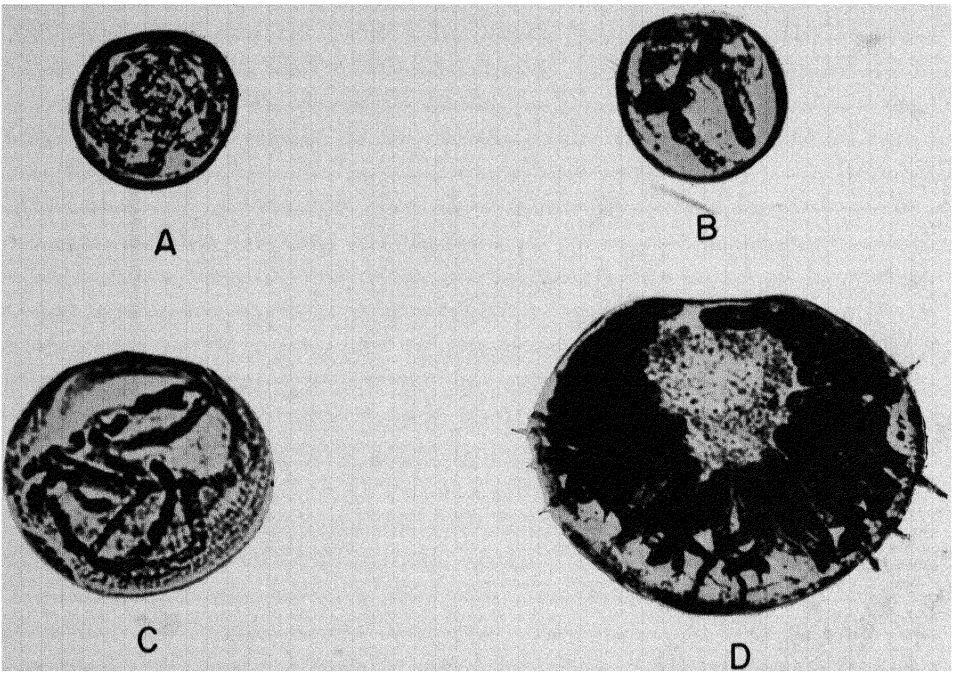


FIG. 26. Larvae infested with fungi. A and B, young larvae of *Crassostrea virginica* stained with Neutral Red; C, young larvae of *Mercenaria mercenaria* stained with Neutral Red; D, old larvae of *Mercenaria mercenaria* stained with Cotton Blue. × 225.

In seeking a method to control fungus infections in our larval cultures we studied the effects of many fungicides, including most of those used in fish hatcheries. So far, not a single promising compound has been found. As a rule, the chemicals unfavorably affected the larvae at concentrations lower than those at which the fungus was affected. However, precautionary measures, consisting largely in maintaining a general cleanliness of all utensils coming in contact with larvae and in using germicidal ultraviolet rays to treat all water, gave promising results. Plankton food, if it comes from impure mass

cultures, should also pass over the ultraviolet tubes. This measure, in addition to controlling the fungus, also protects larval cultures against invasion by undesirable forms, such as small crustaceans, larvae of different worms, rotifers and protozoa, which compete with bivalve larvae for space and food. In some instances raising the water temperature to approximately 32·5°C for several hours may kill fungus without causing serious injury to young mollusks.

Ultraviolet treatment of sea water for purification of shellfish has been described by several workers in Japan, and by Wood (1961) in England. Waugh (1958) and Walne (1958) also used ultraviolet-treated sea water for rearing larvae of *O. edulis*. To prevent fungus diseases of young clams we began using ultraviolet light in 1954 to treat sea water and soon found that this treatment was helpful in preventing mortality of juvenile clams kept in trays of running water. In the summer of 1955 it was found that larval cultures receiving ultraviolet-treated sea water, but untreated phytoplankton from the outdoor tank, developed fungus, while cultures receiving the same phytoplankton and sea water, both of which were treated, did not become infected.

Because of these observations and because it had long been recognized at our laboratory that many mortalities in larval cultures were caused by bacteria (Loosanoff, 1954; Davis and Chanley, 1956b), it became our standard practice, since the summer of 1955, to use filtered and ultraviolet-treated sea water in all larval cultures and in standing water trays containing recently set clams.

Walne (1958) also reported that bacteria may seriously affect larvae and Guillard (1959) demonstrated, while working at our laboratory, that certain bacteria produce toxins that can retard growth of larvae or kill them. Guillard isolated two virulent clones, one of which appeared to be a species of *Vibrio*, and the other, of *Pseudomonas*. His experiments showed that larvae of *M. mercenaria*, when exposed to virulent bacteria and treated simultaneously with antibiotics, such as penicillin and streptomycin sulfate, remained as healthy as the control cultures. High temperature, near 30°C, favors growth of bacteria, thus emphasizing some of the disadvantages of growing larvae at comparatively high temperatures. Bacterial metabolites, when present in high concentrations, may stop larval growth entirely. Guillard also noticed that bacterial contamination of algal food cultures sometimes caused a sharp decrease in growth of larvae without, however, causing immediate extensive mortality.

More recently our associates, Chanley and Tubiash, again isolated bacteria from moribund and dead clam larvae. When these pathogens were seeded into cultures of clam or oyster larvae they caused almost

complete mortality of larvae within 12 hr (Fig. 27). Later, these strains were reisolated from moribund larvae to satisfy Koch's postulates. These studies are still in progress and it appears that the recent isolation deals with different clones from those observed by Guillard.

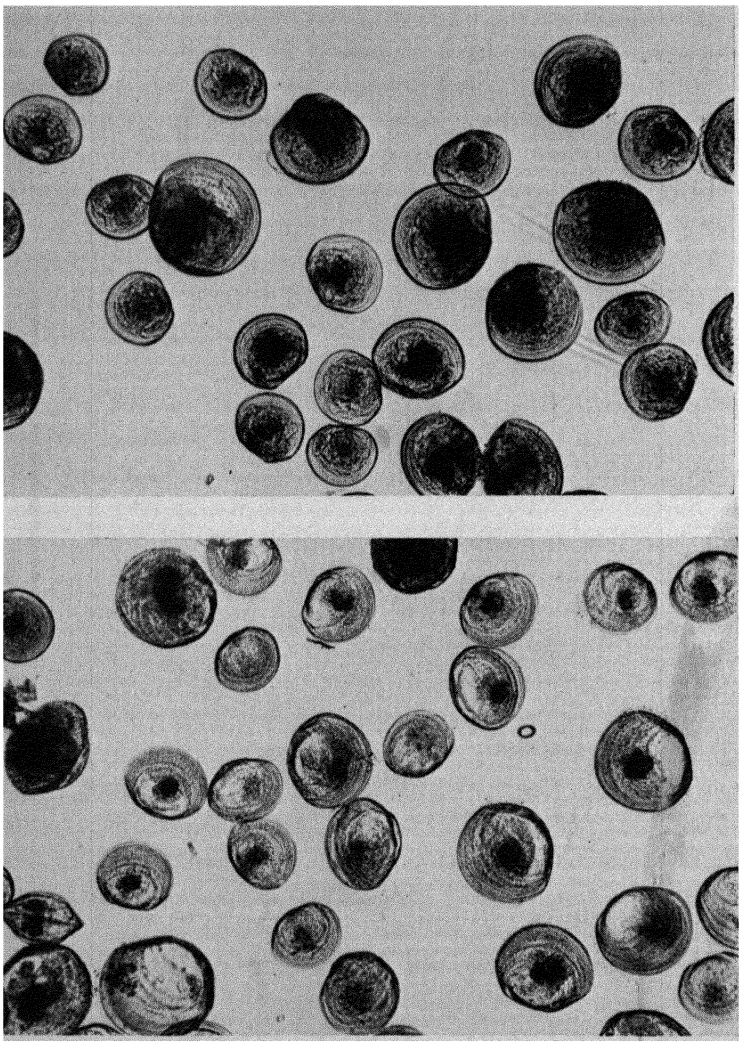


FIG. 27. Effect of pathogenic bacteria upon larvae of *Mercenaria mercenaria*. Healthy larvae (*above*); larvae from the same culture 12 hr after inoculation (*below*). Largest larvae in this photomicrograph are approximately 150 μ long.

Following recognition of the pathogenicity of fungi and bacteria we began testing a number of antibiotics and fungicides, in addition to using physical measures for prevention of diseases, to determine their effects on survival and growth of larvae (Davis and Chanley,

1956b). It was found that at low concentrations streptomycin, aureomycin, Combistrep (a mixture of dihydrostreptomycin and streptomycin sulfate), and Sulmet (sulfamerazine) increased the rate of growth of clam larvae but that, as concentrations were increased beyond certain limits, the rate of growth was retarded and, at still higher concentrations, the larvae were killed.

The most rapid growth of clam larvae occurred in cultures containing about 100 ppm of streptomycin or Combistrep, in about 33 ppm of Sulmet and in only 3 ppm of aureomycin. The increase in rate of growth of clam larvae in cultures receiving 3 ppm of aureomycin was not as great as in cultures receiving optimum concentrations of other antibiotics, such as streptomycin, Combistrep or Sulmet. The commercial preparations of terramycin, sulfathiazole and sulfanilamide were somewhat toxic in minimum concentrations tested and retarded growth of larvae. Combistrep, even at 100 ppm, which is the optimal concentration for clam larvae, retarded the rate of growth of oyster larvae.

In some tests streptomycin did not reduce larval mortalities but, for certain pathogens a closely related compound, Combistrep, in concentrations ranging from 125 to 200 ppm has proved to be quite effective. Acronize (chlorotetracycline HCl) at 10 ppm and chloromycetin at 20 ppm have also been found effective for certain pathogens. Furthermore, cultures of clam or oyster larvae, routinely receiving 33 ppm of Sulmet with each change of water, consistently showed either better survival or more rapid growth, or sometimes both, than larvae in cultures receiving no treatment. Although at this concentration Sulmet did not appreciably decrease the number of bacteria, in some instances, where larvae in untreated cultures grew poorly, treatment with Sulmet improved their growth remarkably. In these cases, we believe, poor growth of larvae in untreated cultures was caused by toxins produced by bacteria introduced with food cultures. The much better growth of Sulmet-treated larvae, therefore, must have been due either to a reduction in number of the bacteria that produced the toxins or to a removal of the toxin from solution by forming a nontoxic complex with the Sulmet.

We find that, in addition to antibiotics, several substances, including such unrelated compounds as phenol, the insecticides Lindane and Guthion, the weedicide Endothal and such presumably inert substances as silt and kaolin, when present in proper concentrations cause a similar improvement in rate of growth of larvae. We suspect that it is the result of removal of toxins from the water in larval cultures. This is, probably, accomplished either by adsorption on particles, such as

non-hybrids. Moreover, neither group of hybrid larvae could be reared to metamorphosis, while under the same conditions non-hybrid larvae of *C. virginica* and *C. gigas* grew to setting stage. In both hybrid crosses fertilization and early larval development apparently progressed normally but about 5 days later, after reaching straight-hinge stage, the larvae died.

More recently, Imai and Sakai (1961) presented results of their extensive studies of crossing different strains of Japanese oysters, *C. gigas*. According to these authors the hybrids displayed a greater adaptability to environmental conditions than the inbred strains. Imai and Sakai also reported that hybrid oysters can be grown from crosses of *C. gigas* and *C. angulata*, while in the case of crossing *C. gigas* with *C. virginica*, *C. echinata* or *C. rivularis*, cross-fertilization might take place but hybrid larvae will not survive.

It has also been demonstrated that two closely related species of the hard shell clam, *M. mercenaria*, of Long Island Sound and *M. campechiensis* from the Gulf of Mexico can be successfully crossed (Loosanoff, 1954). Larvae resulting from these crosses were often grown to metamorphosis, perhaps as a result of hybrid vigor, at a faster-than-normal rate.

Many thousands of juvenile clams from these crosses, after they reached sizes ranging from $\frac{1}{8}$- to $\frac{1}{4}$-in, were distributed to a number of marine laboratories along our Atlantic and Gulf coasts for observations on their survival, behavior and growth under different conditions. Usually, together with the two groups of hybrids, non-hybrid juveniles of *M. mercenaria* and *M. campechiensis* of the same age as the hybrids were also included. A number of papers, including those of Haven and Andrews (1957), and Chestnut *et al.* (1957), described the observations on survival and growth of these four groups of young clams.

Chanley (1961) using the techniques for rearing larvae from crosses of selected clams showing certain peculiarities demonstrated that shell markings of *M. mercenaria notata* were inherited as a simple Mendelian character with incomplete dominance. In another series of experiments he crossed two unselected clams and used the faster growing offspring obtained from that cross as parents for the next generation. He compared growth of progeny of these clams with growth of progeny of two randomly selected individuals. When grown under the same conditions for 15 months progeny of the fast growing individuals were 60% larger than progeny of the randomly selected individuals.

V. Rearing of Different Species

Since much of the material discussed earlier in this article was

based on our observations and experiments on larvae of *C. virginica* and *M. mercenaria*, these species will be considered first. However, to avoid repetition of the material already discussed, information on rearing of larvae of these two bivalves will be presented in the form of a comparatively brief review.

A. *Crassostrea virginica* (Gmelin)

A discussion of the literature on various aspects of propagation of this species has already been given in the earlier part of this article.

By using different methods these oysters can be conditioned for spawning throughout the year and, if necessary, several times annually (Loosanoff and Davis, 1952a). Spawning is induced by raising the temperature within the range from 20° to 32°C, depending upon the previous temperature régime. Addition of suspensions of sex products helps to stimulate the spawning. Eggs can be stripped and fertilized.

Eggs of *C. virginica* vary in size from 45 to 62 μ, but the majority measure between 50 and 55 μ. Costello *et al.* (1957) stated that the size of the oyster egg varied between 45 and 54 μ. The size of the egg is not influenced by the size of the mother oyster. For example, eggs discharged by females 30 to 40 years old and over 9 in long averaged 50·4 μ and ranged between 48 and 54 μ in diameter, while the eggs from much younger and smaller females, approximately 6 years old and 4 in long, averaged about 51 μ, the difference being insignificant.

Under favorable conditions 90 to 95% of ripe, properly handled eggs can develop within 24 hr to shelled veliger stage. The smallest normal straight-hinge larvae measure approximately 68 $\times$ 55 μ. In 48 hr, at a temperature of about 22°C, the larvae measure about 75 $\times$ 67 μ. At this stage they already begin to take in particulate food.

The length of the larvae, measured parallel with the hinge line, continues to be approximately 5 to 10 μ greater than the width, measured from the hinge to the ventral edge of the shell, until the larvae reach the size of 85 $\times$ 80 μ. At 95 to 100 μ the length and width are approximately equal, but after that stage the increase in width is more rapid. When the length reaches 125 to 130 μ the width already exceeds it by about 10 μ. This 10 μ disparity between the two measurements remains virtually constant until the larvae reach metamorphosis.

The length–width ratio of larvae of *C. virginica* is almost linear, except for the section roughly confined to the length between 105 and 130 μ where it displays a tendency to form a flat curve. It is of interest that the length–width curve of the closely related species, *C. gigas*, the Japanese oyster, clearly shows the same tendency.

The majority of larvae of *C. virginica* metamorphoses between 275 and 315 μ in length, but occasionally free-swimming larvae may be 355 μ long. Larvae were grown to metamorphosis at temperatures ranging from about 17° to 33°C; at the latter temperature some larvae metamorphosed in about 12 days. Naked flagellates, such as *I. galbana* and *M. lutheri*, are the best foods, whereas some of the green algae with thick cell walls, such as certain *Chlorella* species, are not readily utilized by early veligers, especially at comparatively low temperatures.

Stafford (1912), in his paper on recognition of bivalve larvae in plankton collections, offered a description and drawings of larvae of *C. virginica* of different stages. His description and, especially, the length–width relationships of the larvae are widely different from ours. For example, Stafford gives the following length–width (depth) measurements, in microns, as typical for oyster larvae: 82·8 × 69·0; 110·4 × 96·6; 124·2 × 110·4; 151·8 × 131·1; 165·6 × 144·9; 207·0 × 193·2; 310·5 × 276·0; and 345·0 × 303·6. A comparison with our data shows that the majority of the above length–width ratios cannot apply to larvae of *C. virginica*. For example, we found that among the 130 of our larvae measuring 110 μ in length the width varied only from 105 to 125 μ. In other words, none of these larvae were only 96·6 μ wide, as indicated by Stafford. His discrepancies in length–width ratio are even greater when he gives measurements of larger larvae. Finally, his larvae always measure more in length than in width (depth) although, as has already been mentioned, when a length of about 125 μ is reached, the width of the larvae begins to exceed the length by about 5 to 10 μ and continues to do so until metamorphosis. Sullivan's (1948) measurements and photomicrographs of larvae of *C. virginica* are quite accurate.

The color of larvae varies somewhat with the food, but healthy larvae are usually a golden brown, particularly in the area of the digestive diverticulum. Young larvae are usually pinkish-orange *en masse*, but this color changes to brown and, later, to almost black as the larvae grow larger.

Larvae are highly active and remain in suspension throughout the free-swimming period. Large larvae, 200 μ or more in length, have a tendency to gather on the surface of the water and may appear as small " rafts " floating just beneath the surface. A pronounced " eye " spot develops, when larvae are about 270 μ in length, and is present throughout the remainder of the free-swimming period.

Larvae of *C. virginica* may be affected by fungus, *Sirolpidium zoophthorum*, and die, but they are much less susceptible to this disease than larvae of *M. mercenaria* and some other forms.

B. *Mercenaria* (= *Venus*) *mercenaria* (Linné)

Literature pertaining to the natural history and propagation of this species has already been reviewed.

These clams can be conditioned and induced to spawn throughout the year. As in the case of oysters, both chemical stimulation, by the addition of suspensions of sex products, and physical methods, by increasing the water temperature, are effective. However, stripped eggs, if not treated with certain chemicals, cannot be fertilized.

Eggs proper of these clams measure between 70 and 73 μ in diameter and differ from eggs of some other lamellibranchs in that they are surrounded by a thick membrane, the diameter of which ranges from

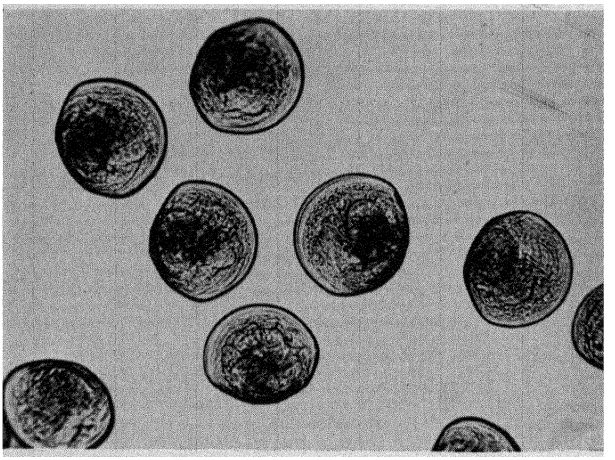


FIG. 28. Larvae of *Mercenaria mercenaria* approaching metamorphosis. Largest individuals in this group are about 200 μ in length.

163 to 170 μ. These clams are prolific. A single female was recorded to produce about 24 million eggs in one spawning.

The smallest but apparently normal straight-hinge larva measured 86 $\times$ 64 μ, although, usually, the size of early veligers is considerably larger, being approximately 105 $\times$ 80 μ and, at a favorable temperature, the majority of normal larvae are from 110 to 115 μ in length.

The size at which metamorphosis occurs varies considerably. Larvae ranging from 175 to 240 μ were seen at this stage. Nevertheless, metamorphosis occurs most commonly when larvae are between 200 and 215 μ in length (Fig. 28). Jørgensen (1946) found that metamorphosing veligers of the closely related species *Venus gallina* are from 210 to 225 μ in length. In our case, as indicated above, variations in the maximum size of prodissoconch of *M. mercenaria* are even greater than those indicated by Jørgensen. However, in our extensive experi-

ence larvae of these clams have never approached the size of 320 μ, as reported by Sullivan (1948). In a letter to us Miss Sullivan explained that she had confused larvae of *Pitar morrhuana* with those of *M. mercenaria* and ascribes the error to the circumstances that newly set spat of both species were present in her collection (Loosanoff *et al.*, 1951).

Our observations on maximum size of larvae reached before metamorphosis also show that it is highly improbable that Stafford (1912) was actually describing larvae of *M. mercenaria* because he stated that veligers of this clam grew to a size of 448·5 μ before setting. Furthermore, when the shapes of the larvae shown in Stafford's figures are compared with those of larvae grown from eggs at our laboratory, it becomes clear that Stafford mistook larvae of some other bivalve for those of *M. mercenaria*.

Food requirements of larvae of *M. mercenaria* are less restricted than those of some other species, such as *C. virginica*. Clam larvae can be grown to metamorphosis on a diet consisting almost exclusively of a unialgal culture of *Chlorella* sp. However, such foods as *I. galbana* and *M. lutheri* promote better growth.

Larvae have been grown at temperatures ranging from 15° to 33°C. At the latter temperature setting occurred 6 to 8 days after fertilization.

During early stages the color of the larvae can be significantly changed by differently colored foods. However, as the larvae grow and their shells become darker, this effect becomes less noticeable. Larvae of the same cultures greatly differ in size, especially if they are not properly attended or are too crowded.

Larvae of *M. mercenaria* are not too selective with regard to the substratum on which their metamorphosis is completed. They metamorphose in containers made of a variety of substances, including glass, plastics, earthenware, Plexiglas, concrete and several other materials. This is contrary to observations on other forms, such as echinoderms (Mortensen, 1938) and polychaetes (Wilson, 1948), where it was found that mature larvae postponed metamorphosis until they located a substratum possessing the necessary physical and chemical characteristics. In our cultures setting usually began when some larvae were approximately 180 μ in length, regardless of the size of containers or material of which they were made.

Setting of clam larvae occurred at approximately the same time, whether they were grown in containers from which all light was excluded or in transparent glass vessels. Turner and George (1955) found that clam larvae were rapid swimmers capable of moving upward at the rate of 8 cm/min. However, they showed no detectable reaction to light.

C. *Arca transversa* Say

No description of larval development of *A. transversa* or any references to its spawning could be found in the literature.

Our attempts to condition and spawn *A. transversa* in winter met with failure or only partial success. Later in the season, about the middle of May, some of the " arks " brought in from Long Island Sound and placed directly in water of 20°C spawned lightly within 2 or 3 hr. No normal larvae, however, could be grown from these eggs. Nevertheless, by placing the same " arks " in running sea water at 15°C from 3 to 7 days to condition them, spawning was easily induced by raising the water temperature to 27° or 28°C. Both males and females

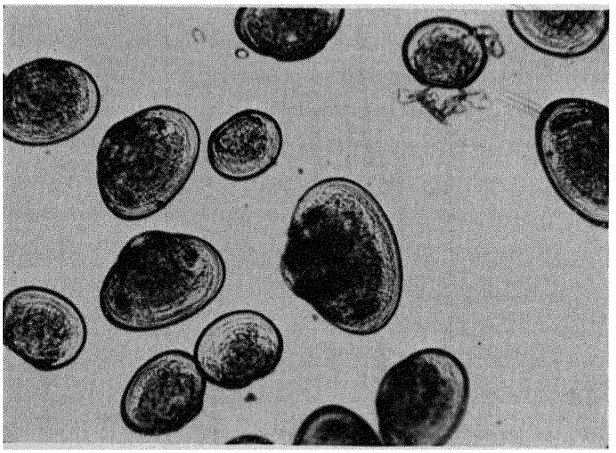


FIG. 29. Larvae of *Arca transversa*. Largest larva, approximately 230 μ in length, may be approaching metamorphosis. Note differences in sizes of larvae, all of which are of the same age.

spawned profusely, releasing gametes in streams similar to streams of sperm ejected by male American oysters.

The eggs of *A. transversa* are pinkish-orange in color and average approximately 52 μ in diameter. They are surrounded by a very thin, almost indistinguishable membrane. The sperm head is roughly triangular in shape, with a broad centerpiece. The anterior part of the head is " pinched " off in a short, nose-like structure. The head and centerpiece of the spermatozoa are between 3 and 4 μ in length, while the tail is from 47 to 55 μ long.

Larvae were grown at room temperature, which was approximately 20°C, and fed mixed phytoplankton composed principally of *Chlorella* and closely related forms. Under these conditions the larvae set from 27 to 37 days after fertilization.

Larvae of *A. transversa* are quite distinctive in appearance resembling, in general, their adults, particularly as they grow larger. The smallest normal straight-hinge larva measured 70 μ long and 55 μ wide. Thus, even in the youngest larvae, the difference between length and width is quite considerable. However, when larvae are near setting, the length may exceed the width by about 70 μ (Fig. 29).

The larvae are dark brown in color. As they grow larger, their color becomes darker and one end of their shells becomes more pointed than the other. Under the microscope larvae appear quite variable in outline because their odd shapes cause them to rest in a variety of positions.

The first indication of an umbo begins to appear soon after the larvae pass 105 μ in length, and at 130 μ it usually is quite conspicuous. When the larvae reach approximately 140 μ in length the pointed, or less rounded end of the shell becomes distinctly reddish-brown, while the opposite, more rounded end remains almost brown. This color difference is quite pronounced in many individuals.

An " eye " spot appears when the larvae are approximately 225 μ long. In some individuals this spot is not too conspicuous at first, but as the larvae approach metamorphosis it becomes quite prominent. Slow-growing larvae may develop the " eye " spot at a much smaller size. For example, in at least one case it was observed in larvae that were only 205 μ in length.

As is usual in rearing larvae of bivalves, considerable variation was noticed in setting sizes. The smallest, virtually metamorphosed individuals measured only 215 μ in length, while one larva in the same culture measured about 310 μ and, although it had a large foot, was observed actively swimming. This may have been a somewhat abnormal individual because a majority of the normal larvae in our cultures set when only 240 to 260 μ long.

Upon reaching metamorphosis recently set clams develop a strong byssus by which they attach to particles of sand, shells or other material.

Unlike larvae of *M. mercenaria* and several other species, which are easily affected by fungi, no epizootics that could be ascribed to these organisms were observed in our cultures of *A. transversa*.

D. *Modiolus demissus* (Dillwyn)

M. demissus, the common ribbed mussel of our waters, is also referred to by some authors as *Volsella demissa*, *Volsella plicatula* and *Modiolus plicatulus*. A review of the literature shows that, except

for Sullivan's (1948) article, there are no other references to larval development of this species. Considerable literature, nevertheless, exists on larvae of *Modiolus modiolus* and closely-related forms. These references can be found in the papers of Jørgensen (1946) and Rees (1950).

Various methods used to stimulate spawning of other bivalves proved unsuccessful for ribbed mussels. On two occasions, however, mussels kept in aquaria spawned without artificial stimulation. In both cases spawning occurred at night and, when the eggs were found in the morning they were already undergoing segmentation. Thus, no measurements of recently discharged eggs were made. Jørgensen

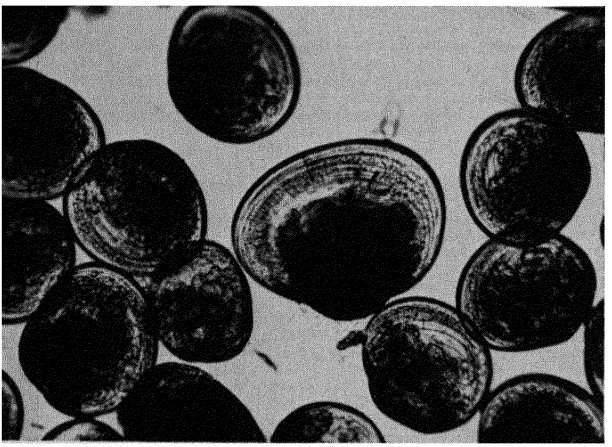


FIG. 30. Larvae of *Modiolus demissus*. Note differences in sizes of larvae that originated from the same group of eggs and were reared in the same vessel. Largest larva in center is approximately 300 μ long.

(1946) states that the diameter of an egg of a closely related species, *Modiolus modiolus*, is about 100 μ.

Larvae developing from eggs released during two normal spawnings were reared to metamorphosis. At room temperature straight-hinge stage was reached in about 24 hr. The majority of the larvae at that time measured from 110 to 115 μ in length and 85 to 90 μ in width. The smallest normal straight-hinge larva was only 105 μ long.

If kept at a temperature of about 22°C and given good food, such as *I. galbana*, many larvae reached a length of 200 μ by the 10th day. A few, upon reaching this size, developed a prominent " eye " spot and functional foot. Nevertheless, although completely metamorphosed juveniles of a size slightly above 220 μ in length were observed in some cultures, the majority of the larvae did not lose their vela until they

reached 275 μ, and a few individuals measuring between 295 and 305 μ in length still retained a functional velum.

While some larvae metamorphosed in about 12 to 14 days after fertilization, many others in the same cultures were still free-swimming when the experiment was discontinued after 43 days (Fig. 30). In one of these cultures, while there were still free-swimming larvae from 250 to 295 μ long, there were also several thousand completely metamorphosed juvenile mussels that ranged up to 1 mm in length. Why so many of the larvae were still in the free-swimming stage, while others in the same cultures had metamorphosed and showed considerable post-larval growth, remained unexplained.

According to Sullivan (1948) the smallest straight-hinge larvae of *M. demissus* measure approximately 112 $\times$ 90 μ. This size quite closely agrees with our measurements. However, the maximum size given by Sullivan, 205 $\times$ 180 μ, is considerably smaller than that observed in our cultures, which was about 303 $\times$ 260 μ. We also differ with Sullivan on the color of ribbed mussel larvae because she states that these larvae are a deep yellow in the early stages, whereas we found that throughout their development they are brown.

Jørgensen (1946) discussed larvae of closely-related species. In his references to *Modiolus modiolus* Jørgensen stated that larvae of this species have not been identified with certainty in plankton samples taken in Danish waters. He thinks that this is probably due to the very close resemblance of this species to veligers of *Mytilus edulis*. We disagree with Jørgensen since, in our studies of larvae of these two species, we found them to be distinctly different in their length–width measurements. Furthermore, the difference in their general appearance, especially during later stages of development, is too great to confuse these two groups of veligers.

Rees (1950) stated that in the smallest veligers of *Modiolus* and *Mytilus* the shape is similar, although in the former the narrow end is less pointed. Nevertheless, in later stages the shapes of the two genera become more differentiated. Rees also thought that the small specimens of the two mussels are distinguished more easily by their texture than by their shape. He concluded that Jørgensen's drawing (Fig. 167d) is probably of *Modiolus modiolus*, instead of *Mytilus edulis*, as claimed by Jørgensen. However, examination of the photomicrographs of, presumably, *Modiolus modiolus* offered by Rees clearly shows that their shape significantly differs from that of *Modiolus demissus* grown in our cultures from known parents. This is especially true of his larvae, approximately 250 μ in length, which have very little resemblance to our larvae of the same length.

E. *Mytilus edulis* Linné

A study of the literature on lamellibranch larvae shows that veligers of *M. edulis* have been described more frequently than those of other bivalves. Borisjak (1909) was probably the first to describe these larvae while, more recently, descriptions of presumably the same veligers were given by Jørgensen (1946), Sullivan (1948), Rees (1950) and others.

Mussels with apparently morphologically-ripe gonads are found in our waters in early spring, but under laboratory conditions, using our method of maturing animals in warm water, ripe mussels can be made available in January.

Field (1922) reported that rough handling of mussels, such as shaking them in a dish of sea water, will induce spawning within an hour, but Costello *et al.* (1957) found this method unsuccessful. In our case, during studies conducted for 3 yr, except for brief periods in April and early May, all efforts usually employed to stimulate bivalves to spawn failed to work with *M. edulis*. These included sharp increases or decreases in temperature, addition of sex products to the water, keeping mussels in air overnight, placing them in refrigerators for various periods, increasing or decreasing salinity of the water, and even applying light electrical shocks. This was true also of mussels that were conditioned in the laboratory for a considerable time and whose gonads appeared to be morphologically ripe.

Fortunately, it was noticed by two of our associates, first, W. Arcisz, and several years later, J. Uzmann, that some ripe female mussels released large numbers of eggs after their adductor muscles were cut.

These observations suggested a number of experiments on inducing spawning in mussels. The first attempt consisted of opening a large number of these mollusks and placing each individual in a separate vessel. The results were rather gratifying because, in the majority of cases, the mussels discharged large quantities of normal sex products. The method worked even on mussels that were not laboratory conditioned. For example, on 26 April 1951, mussels were brought in from Milford Harbor, where the water temperature was 8°C. The adductor muscles of twelve females were severed and the mussels were placed in water at room temperature. The first two females spawned within 12 hr; four others deposited masses of eggs within 24 hr, and six remaining females released eggs toward the end of the 48-hr period. This experiment was repeated on several occasions giving virtually the same results.

Eggs released by females with severed muscles were usually discharged in " strings ", as occurs in normal spawning. The majority

of the eggs released appeared normal, but many abnormal larvae were found later (Fig. 31). However, such larvae were also common in cultures grown from eggs discharged in normal spawnings. Mussel eggs are orange-yellow in color. They are quite heavy and usually settle quickly on the bottom.

We also noticed that mussels which were dying from some undetermined cause often spawned soon after they relaxed their shells, even when their muscles were not cut. This observation suggested that the stimulating center, which induces discharge of eggs or sperm, is probably located in the adductor muscles. If these muscles are abnormally relaxed or stimulated, spawning follows. This reasoning led to another series of experiments designed to obtain eggs and sperm from ripe

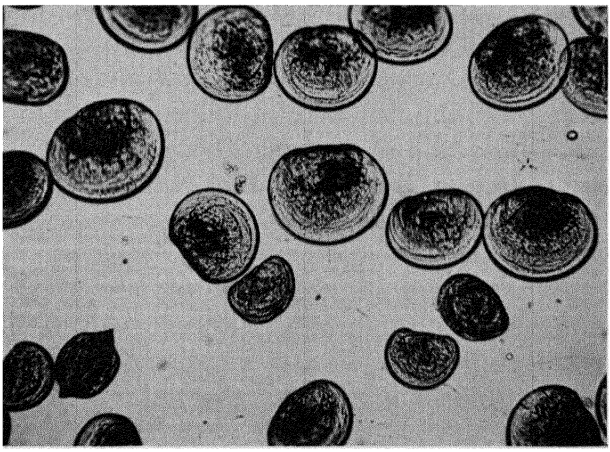


FIG. 31. Larvae of *Mytilus edulis*. Largest larvae are approximately 170 μ long. Several small, abnormal individuals can be seen in lower right corner.

mussels without killing them by cutting their muscles. This modification of the method would prevent fouling of eggs with blood cells, decomposition products, large numbers of bacteria, etc., that usually accompanies collection of eggs from females whose muscles are cut.

The new method consisted of inserting a small wooden wedge between the mussels' shells, thereby stretching the adductor muscle so that the two shells would be forced open about $\frac{1}{8}$- to $\frac{1}{4}$-in. In experiments where this principle was used the majority of pegged mussels spawned, while control mussels kept under identical conditions did not. Some began spawning within 2 hr after pegs were inserted and several spawned three times during a single week.

No mortality was noted among pegged mollusks, even when the pegs remained between the shells for 10 days. Mussels fed in an

apparently normal way, forming true feces and pseudo-feces. Mussels that were placed together in large trays with running sea water eventually attached to each other by their byssus.

Since the second series of experiments has also showed that discharge of spawn in mussels of both sexes can be induced by stretching the posterior adductor muscle, it became more certain that the nerve locus causing the discharge is located there. Accordingly, it was decided to stimulate this region, by touching or pricking it with a sharp needle, and note whether this type of stimulation would also induce spawning reaction.

In the middle of March two groups of mussels, each composed of ten individuals, were placed in running water at a temperature of 19°C. The first group, the control, contained individuals that were not stimulated. In the second group each individual was gently stimulated by pricking the muscle. The first male in the stimulated group spawned in about 2 hr. An hour later the first female spawned and continued to discharge eggs for almost 75 min. The eggs were discharged in orange-colored rods, 3 to 4 mm long. These rods were often expelled with such force that they travelled 4 to 5 in away from the spawning female.

Seven hours after the stimulation another male spawned, and after 9 hr two more females began to discharge spawn. Within 12 hr every individual in the stimulated group had spawned, while none in the control group had done so. Thus, it was demonstrated that needling the adductor muscle is an effective method of inducing spawning in *M. edulis*.

All mussels that had spawned were later placed in running sea water to see whether they would survive the stimulation treatment. All of them lived for over a month and were then discarded.

Although the previously-described experiment had demonstrated that pricking of the adductor muscle stimulated spawning of mussels, the fact that all ten animals were kept in the same dish left some doubt as to the exact conditions that caused spawning during the latter part of the experiment. This doubt existed because toward the end both sperm and eggs were present in the water and, therefore, might have helped to stimulate the mussels that had not yet spawned. To clarify this matter another experiment was designed in which we kept each mussel in a separate dish. Again, ten mussels were used in the control group and ten in the group that was stimulated. The first male spawned 30 min after stimulation and the first female began to discharge eggs 1 hr after its muscle had been gently touched several times with the point of a needle. The second female spawned only

2 or 3 min after the first one. Both individuals discharged eggs in large numbers for a considerable period. Within 12 hr eight of ten stimulated mussels spawned, while none of the control group discharged any sex products.

The experiment was repeated four times involving, altogether, 120 mussels. Of the sixty stimulated mussels, fifty-four responded, while none of the sixty control animals spawned. All mussels of the stimulated group remained alive for at least 2 weeks, after which they were discarded. Thus, a very simple method for stimulating ripe mussels to spawn has been developed. To make the method even easier we filed a small notch at the edge of the shell through which the needle was inserted.

According to Jørgensen (1946) one of the most remarkable peculiarities of larvae of *M. edulis* is " its excessive variability both as regards the color of the shell, its shape, and stage of development as compared with larval size, in which respects it is not surpassed by any of our other common Lamellibranch veligers " (p. 287).

Our cultures of *M. edulis* were grown during the early period of our studies of molluscan larvae; in other words, before the good food organisms, *I. galbana* and *M. lutheri*, became available to us. The larvae were fed an algal mixture, consisting chiefly of *Chlorella* and other green forms, and grew remarkably well. Strangely enough, it was virtually impossible to injure them by adding to the water large quantities of food microorganisms, a situation that often arises in culturing larvae of other species, such as clams and oysters.

The smallest normal straight-hinge larvae measured approximately 93 $\times$ 64 μ, and the largest, about 300 $\times$ 286 μ. Thus, our measurements are very different from those given by Sullivan (1948), who stated that larvae of *M. edulis* range in size from 155 $\times$ 120 μ to approximately 355 $\times$ 320 μ. The smallest size given by Sullivan is, therefore, almost 60 μ greater than that of the smallest larvae in our cultures, and the maximum size is considerably larger than that which we ever recorded among swimming larvae.

Jørgensen also apparently mistook other larvae for advanced stages of *M. edulis* because he speaks of individuals which are 400 μ long. Werner (1939), whose length and width measurements of larvae of *M. edulis* somewhat resemble ours, still fails to give correct measurements for the smallest straight-hinge stage larvae. In his growth curve for these organisms he gives the size of the smallest larvae as approximately 112 μ long and 84 μ wide, which is considerably larger than the size of the smallest larvae ordinarily found in our cultures.

The so-called " eye " spot usually begins to appear in larvae when

they reach 215 μ in length. This spot is usually located approximately in the center of the larvae and measures from 5 to 7 μ in diameter. In one individual measuring only 205 μ in length a well-defined " eye " spot was found, but this was the only case of an " eye " in such a small larva recorded after examining thousands of individuals. When a length of 230 μ was reached the " eye " spot was present in all larvae.

The size at which mussel larvae metamorphosed varied by almost 90 μ. The smallest metamorphosed individual, attached by a byssus to an oyster shell laid in one of our culture jars, was only 215 $\times$ 201 μ. Individuals measuring 225 μ in length, but fully metamorphosed and attached by a byssus, were not uncommon. On the other hand, some larvae continued to swim until they were almost 300 μ in length. Large variations in the size of *M. edulis* larvae at the time of metamorphosis were also recorded by Jørgensen (1946). He thinks that variable size at metamorphosis is not entirely due to the fact that veligers may pass into the bottom stage after attaining a different stage of organization, but also because of the varying ratio between the rate of differentiation of the tissues and rate of growth in different individuals.

The factors which govern appearance of the foot and disappearance of the velum in larvae of *M. edulis* are rather baffling. In some instances a well-developed foot was observed in animals as small as 185 μ in length. Such cases, however, were not too common and, usually, the appearance of a developing foot occurred as the larvae approached 210 μ in length. Most larvae possessed a well-developed foot by the time they reached 230 μ in length, but a functional velum has been observed in larvae as large as 288 μ.

The great differences in the state of organization attained at a certain size by larvae of *M. edulis* are also emphasized by Jørgensen. He gives examples of larvae measuring 250 μ long and nearing metamorphosis with well-developed gills and foot and with a velum in a reduced condition, while in other cases larvae of the same size will have only a vestige of a foot but a large velum, thus indicating that they are still far from metamorphosing.

The variation in size of larvae at the time of metamorphosis suggested a more critical analysis of the data on growth of larvae in the same cultures. Fortunately, among our cultures there was one in which all larvae originated from eggs of the same female and were fertilized by sperm of the same male. Regardless of this, 2 days after fertilization the larvae varied in length from 93 to 120 μ, with an arithmetic mean of 106 μ. When the culture was 8 days old the length varied from 107 to 162 μ, the average being 130 μ. At 14 days some of the

larvae were already metamorphosing and the mean length was 181 μ, but some larvae only 128 μ long were still present.

This experiment demonstrated, as we have pointed out on many occasions, that it is obviously incorrect to relate the size of larvae to their age because variations in size, even among larvae that originate from the same parents, are of considerable magnitude. In cultures that are grown at different temperatures and fed different foods these differences are usually even more striking.

Some workers explain variations in size of larval fish originating from eggs produced by the same female as dependent upon development of these eggs while still in the ovaries, including proximity of an egg to large blood vessels which provide the best feeding conditions for a single egg. Others explain the different rates of survival and growth of fin fish larvae as dependent upon quantities of yolk in different eggs. Possibly, the same considerations hold true and, in part, explain variations in rate of growth of bivalve larvae that originate from eggs discharged by the same female in the same spawning.

As is usually the case with larvae of most bivalves, their color varies greatly in accordance with the color of the food microorganisms that they are able to obtain from water. Larvae of *M. edulis* given heavy doses of purple bacteria rapidly acquired a pinkish color, which was most pronounced in the area of their digestive organs. If these larvae were later fed green *Chlorella*, their coloration changed to a greenish tint and the livers became dark green. Contrary to Sullivan's (1948) contentions, no purple tint was observed around the shoulders of the shell, even in advanced larval stages.

F. *Anomia simplex* D'Orbigny

A. simplex is a common bivalve of Long Island Sound, where it propagates at approximately the same time as *C. virginica*. Because of its more rapid growth immediately after setting, however, this mollusk is a dangerous competitor, since it overgrows and completely covers large numbers of recently set oysters (Loosanoff and Engle, 1941).

Descriptions of larvae of several species of *Anomia* are given by students working in widely separated parts of the world. Stafford (1912) gave a description of *A. aculeata*; Miyazaki (1935) described the larvae of the Japanese species, *A. lischkei*, and Lebour (1938), as well as Jørgensen (1946), described those of *A. squamula*. More recently, Sullivan (1948) also described larvae of *A. aculeata*, while Rees (1950) made a brief reference to three species of *Anomia*. One

of these, *A. ephippium*, is a synonym for *A. simplex*. Other references can be found in the above-mentioned articles of Jørgensen and Sullivan.

Large *A. simplex* can be conditioned in December and induced to spawn during the first part of January. Some conditioned groups were induced to spawn several times between the middle of January and the beginning of August. To induce spawning presented no problem because, usually, ripe animals began to spawn as soon as the temperature of the water was raised only a few degrees above 20°C. Even in summer it was not necessary to raise the temperature much above 25°C. In many instances spawning began without addition of any sex products, a circumstance which is unusual in our experiences with spawning of other bivalves.

Artificial fertilization of *A. simplex* eggs is possible. Stripping can be easily accomplished by gently washing the light yellow gonad tissue of a female in sea water. The eggs separate easily and many remain uninjured. Therefore, a high percentage of them ordinarily develop into normal larvae.

Compared with eggs of other bivalves, eggs of *A. simplex* are comparatively small, ranging only from 42 to 45 μ in diameter. Because of their small size the eggs are difficult to handle, as they easily pass through the mesh of the smallest screen used for egg retention. Because eggs and early larvae cannot be strained and, thus, separated from the surrounding water, as is done with larger eggs, in fertilizing eggs of *A. simplex* care should be taken not to use too much sperm so as not to pollute later cultures of developing eggs and early larvae.

In our cultures of *A. simplex* the smallest larva with completely formed shells measured approximately 58 $\times$ 47 μ. Young larvae are more fragile and transparent than those of *C. virginica* of corresponding stages. The " straight-hinge " is actually sloped about 5° so that it is somewhat convex. This is difficult to observe under a microscope unless larvae are seen precisely in profile.

The most common size at which larvae of *A. simplex* metamorphosed was at a length of 195 to 210 μ. The largest swimming larvae measured approximately 215 $\times$ 220 μ. We cannot compare the dimensions and shapes of our larvae with those given by Stafford (1912) because his drawings and measurements bear little resemblance to the larvae of *A. simplex* in our cultures.

Sullivan (1948) gave the smallest size of *A. aculeata* as 110 $\times$ 100 μ, and the largest as 285 $\times$ 280 μ. Jørgensen (1946), in referring to his own observations on *A. squamula*, reported that the smallest larvae measured 65 to 75 μ in length, and the largest attained a length of

250 to 270 μ. Lebour (1938) stated that *A. squamula* may metamorphose at a length of only 180 μ, which coincides with our observations on *A. simplex*, while Stafford maintained that the veliger of *A. aculeata* is still pelagic at about 350 μ.

The size of larvae of *A. simplex*, when the " eye " spot appears, is difficult to indicate. In a few cases the " eye " was observed in individuals measuring only 136 μ in length although, as a rule, it appeared when the larvae were near 160 μ. The " eye " seems to be composed of from four to six dark bodies grouped together. In many individuals, including some that were near setting, no " eye " spot could be distinguished.

Even in early straight-hinge stages there is considerable difference in the shape of the two shells. The right shell, or the one that will

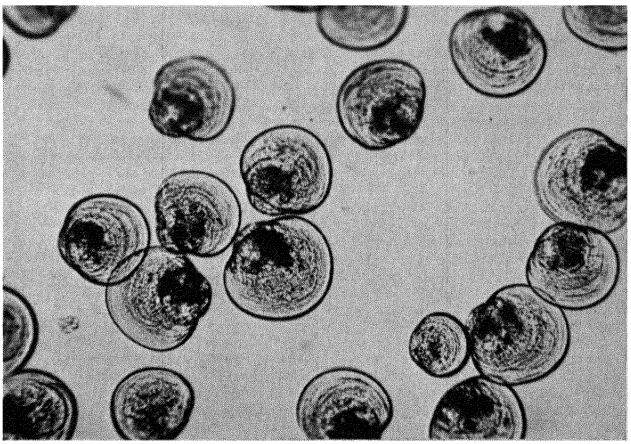


FIG. 32. Larvae of *Anomia simplex*. Largest larvae in photomicrograph are about 160 μ long. Note transparency of larval shells.

eventually be the upper, is conspicuously rounded, while the left, or the one that will become the lower shell is virtually flat. This distinction remains throughout larval development. Jørgensen (1946) reported that in *A. squamula* the umbo of the right shell is not developed. We made the same observation on the shell of *A. simplex*.

An observation made during the rearing of larvae of *A. simplex* concerned the inconsistency of the appearance on its shell of the indentation known as the byssus notch which, presumably, is diagnostic of larger larvae of this species. Since this was one of the features which we expected to be rather prominent and to appear in all older larvae, we were somewhat perplexed not to find this notch in many individuals. It is true that in some individuals this notch was present

in larvae only about 180 μ long, but often it was only a thickening of the shell edge on the side opposite the foot. In our extensive studies of living material and numerous preparations of larvae imbedded in balsam, in permanent slides, we were unable to find such " deformed " larvae as those shown by Sullivan (1948).

Early larval stages of *A. simplex* are very light, almost transparent in color (Fig. 32). Even larvae nearing metamorphosis remain silvery transparent except, of course, their digestive organs which, as a rule, take on the color of the food that they contain. In this respect our observations are rather different from those of Sullivan (1948), who stated that, at first, *Anomia* larvae are pale yellow but, later, become deep yellow, except for the viscera, which are dark gray.

Since larvae of *A. simplex* may be mistaken for those of oysters, especially in advanced stages when umbones in both species are quite prominent, one way to distinguish the two species is to remember that in *A. simplex* the digestive organs are situated much higher, lying almost under the umbones.

In the early stages of our work on cultivation of *A. simplex* larvae, which was conducted in 1950 and 1951, the only food that was regularly available was a mixture of green algae composed largely of *Chlorella*. Although the larvae reached metamorphosis when fed this food, their growth, as a rule, was slow and mortality heavy. Later, when cultures of *I. galbana* and *M. lutheri* became available, the larvae responded well to the new food, growing much faster and showing lower mortality. When fed these flagellates at room temperatures, many larvae of *A. simplex* began to metamorphose after the 12th day although, in the same cultures, some larvae were still swimming 33 days after fertilization.

As already mentioned, one of the most interesting observations made on cultures of *A. simplex* was what appeared to be partial metamorphosis, or metamorphosis without attachment to substratum (Loosanoff, 1961). Partial metamorphosis was characterized by disappearance of the velum, but retention of a functional foot. Moreover, these partially metamorphosed individuals were unable to attach to the substratum, and their shells showed a distinct demarcation line between larval and post-larval portions.

G. *Pecten irradians* Lamarck

The early embryonic development of the bay scallop, *P. irradians*, also called *Aequipecten irradians*, has been described by a number of authors, including Fullarton (1890), Drew (1906), Belding (1910),

Gutsell (1930) and, more recently, by Costello *et al.* (1957). The later development of the larvae, beginning with the formation of the straight-hinge stage, however, has never been adequately described because virtually no one succeeded in growing these larvae to metamorphosis. The only exception was Wells (1927), who grew scallop larvae past setting stage, but gave only a superficial description of them, although he supplied good photographs showing the different stages of development.

Descriptions of eggs and early stages of several European Pectinidae were offered by Jørgensen (1946). However, as in the case of the American bay scallop, virtually none of the European workers, except Odhner (1914), gave photomicrographs of older veliger stages that may be helpful in identifying the larvae.

The scallops used in our studies were brought, in February, from Long Island, where they are found in a number of bays, harbors and inlets. They were placed in running sea water, the temperature of which was increased within a few days to 20°C. The first spawning was attempted after 23 days of conditioning. The scallops responded readily to a temperature stimulus of about 30°C and spawned profusely.

Scallops usually spawn first as males and, later, as females. During one spawning, fourteen scallops started spawning as males. However, 10 or 15 min later seven of these fourteen individuals began to discharge eggs, but within a few minutes two of these seven again reverted to spawning as males, releasing large numbers of spermatozoa. On one occasion the same scallop was observed releasing sperm and eggs simultaneously.

Scallop eggs obtained in our experiments measured from 55 to 65 μ in diameter, the average size being near 60 μ. Belding (1910) and Gutsell (1930) gave the size of the scallop egg as 63 μ. Fullarton (1890) reported that the egg diameter of a related European species, *Pecten opercularis*, is 68 μ. The scallop egg is surrounded by a thin membrane and is usually of a pale orange color. Brief remarks on fertilization, cleavage and rate of development of the fertilized ovum were given by Costello *et al.* (1957), who based his descriptions on the works of Belding (1910) and Gutsell (1930).

The smallest straight-hinge scallop larvae observed in our cultures were 80 μ long and 65 μ wide, and the largest swimming individuals, approximately 200 $\times$ 195 μ. Some larvae metamorphosed upon reaching 175 μ in length. Jørgensen (1946) stated that the largest planktonic stage of the European scallop, *P. opercularis*, is approximately 250 to 260 μ long, while the larvae of another European scallop, *Pecten striatus*, approaching metamorphosis may be only 200 to 210 μ

in length, which is in close agreement with the measurement of larvae of our species.

Scallop larvae were grown at room temperatures varying between 20° and 23°C. They were fed either mixed cultures of plankton consisting principally of *Chlorella*-like forms or a mixture of flagellates, such as *I. galbana* and *M. lutheri*. They grew well on either diet, but cultures fed flagellates grew better. When well fed the growth of larvae is comparatively rapid, averaging more than 10 μ per day. In some of our cultures setting began 14 days after fertilization.

Larvae are susceptible to fungus diseases, but fungus does not appear to be as devastating to scallop larvae as it is to larvae of

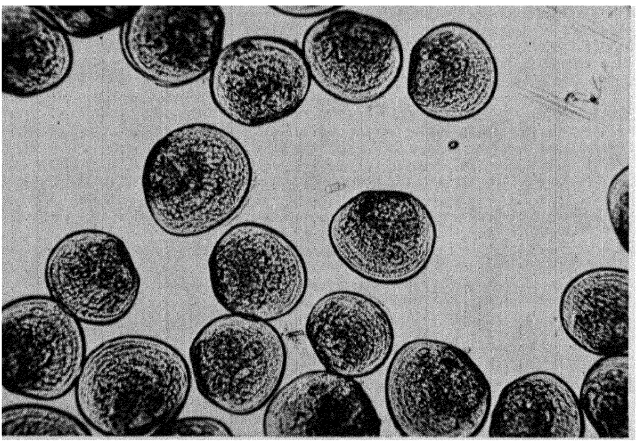


FIG. 33. Larvae of *Pecten irradians*. Largest larvae are about 180 μ long.

M. mercenaria or *T. navalis*. Larvae are also highly susceptible to bacterial infections.

Scallop larvae are quite pale and, although the color changes with the food contained in their digestive system, normal scallop larvae are invariably paler than those of *M. mercenaria*. At all stages they appear slightly asymmetrical, this condition becoming more pronounced in larger and older larvae (Fig. 33). In those measuring over 125 μ in length a slight notch is evident at the base of the shell, on the less pointed end of the larvae. Although this mark is not too conspicuous, it does appear to be characteristic.

Healthy larvae are active and energetic swimmers. Some of them display a small inconspicuous " eye " spot when they reach about 150 μ in length. Although the " eye " can be seen in most larvae about 170 μ in length, in larger larvae this spot is virtually invisible, probably because of the thickening of the shell.

H. *Ostrea edulis* Linné

We are interested in this species because its northern races propagate at somewhat lower temperatures than the American oyster, *C. virginica*. Because of this we imported *O. edulis* into the United States in 1949 in the belief that certain areas along the shoreline of Maine and our Pacific coast states were promising for natural propagation of these oysters (Loosanoff, 1951, 1955, 1962b). Since then, *O. edulis* have grown and propagated naturally in New England waters and have become established in Maine. Young oysters reared at Milford, Connecticut and sent to the State of Washington have also grown well there.

Literature on the sexuality and propagation of the European flat oyster, *O. edulis*, has been well reviewed by Orton (1937), Korringa (1941), Walne (1956) and Yonge (1960) and, therefore, need not be discussed here in detail. Using our methods for ripening mollusks out of season we have obtained larvae of *O. edulis* from the end of January to the end of the normal spawning period which, in Milford Harbor, extends into September. Our attempts to induce spawning of ripe oysters were not always successful. On several occasions, nevertheless, by raising the temperature of the water containing conditioned oysters and simultaneously adding a suspension of gonad material, spawning has been initiated in both sexes. This was ascertained by finding sperm balls or recently discharged eggs on the bottom of the aquaria. Well-developed eggs ranging in size from 114 to 126 μ were often lost when, during the process of spawning, they were released from the gonad to enter the gill chamber where, normally, they are incubated until larvae are released at swarming.

The manner in which eggs are lost was observed on several occasions during normal spawnings. These eggs were released from the exhalant chamber in a thin stream, almost in "single file". Because only a weak current was carrying them, the eggs settled next to the shells of the mother oysters, eventually forming a small mound. By a gentle moving of the spawning oysters from one area of the aquarium to another and observing the formation of new piles of eggs, it was established that a spawning female may continue a steady discharge of eggs for as long as 4 hr.

Since we could not always induce spawning in conditioned oysters, we depended quite often on unprovoked normal spawnings and subsequent release, or swarming of the larvae. Therefore, when a gravid female was detected, by the presence of a small pile of eggs near its excurrent side, it was placed in a separate aquarium with aerated standing water and kept there until larvae were released. The

water was changed daily and the oysters were given sufficient quantities of food to keep them and the larvae alive.

At room temperatures swarmings took place from 6½ to 10 days after spawning. The size of larvae released by a single female in the same swarming varied considerably. On one occasion samples of 100 larvae were collected from swarms released by each of six females which had been kept in separate aquaria. Larvae released by female (A) ranged in length from 142 to 199 μ, with a modal size of 186 μ; by female (B), from 164 to 192 μ, with a modal size of 184 μ; by female (C), from 164 to 203 μ, with a modal size of 188 μ; by female (D), from 149 to 203 μ, with a modal size of 187 μ; by female (E), from 164 to 192 μ, with a modal size of 180 μ; and female (F), from 164 to 195 μ, with a modal size of 183 μ. Occasionally, broods of smaller larvae measuring 175 $\times$ 160 μ were released. The average size of such broods closely resembled those reported by Boury (1928), Voisin (1931) and Korringa (1941).

In rare cases the modal sizes of larval broods were unusually large, over 200 μ in length. Because all female oysters incubating larvae were kept at the same temperature, it is improbable that the difference in size of the liberated larvae of the different broods was governed by the temperature at which incubation occurred. It seems more reasonable that size of larvae at liberation depends upon how long larvae are retained in the mantle cavity. This may be governed by the physiological condition of the parent oysters or the conditions in the water in which oysters are kept, the larvae being retained longer and, hence, are larger at time of release when these conditions are not at their optimum. This is supported by observations on liberation of larvae by two females that appeared sick. The first was used in an experiment where induced spawning was attempted by quickly raising the temperature to 37°C. The oyster did not spawn but was apparently injured by this treatment because it gaped for several hours after its return to sea water at room temperature. It did spawn the next day, however, but the spawning was not normal because too many eggs were found on the bottom of the aquarium near the oyster. The eggs, nevertheless, were fertilized.

Ten days later this oyster discharged, simultaneously, a brood of larvae and many empty larval shells, indicating that many larvae had died within the mantle cavity during incubation. There was also a considerable number of abnormal larvae with defective vela. Normal larvae, which still were in the majority, measured from 199 to 212 μ in length, with a modal size of about 208 μ. Regardless of some abnormality observed in the development of this brood, the larvae were reared to metamorphosis.

The second release of larger-than-average larvae, measuring between 200 and 210 μ in length, was also observed in an oyster that was kept at high temperature for several hours and was probably injured by this treatment.

Another possibility is that the size upon release may be governed by the number of incubating larvae in the mantle cavity, with the larvae growing faster if the number is small.

Swarming or, more correctly, release of larvae by parent oysters was observed on numerous occasions. In general, it resembled discharge of eggs by a spawning female of *C. virginica*. The larvae were expelled in cloud-like masses by a forceful closing motion of the shells. Discharge of larvae by a single female may continue for 3 or even 4 days. Usually, during the 1st day only a few larvae are released. The chief masses of larvae are expelled during the 2nd day and then the number of newly released larvae sharply decreases. Larvae that had just been released usually contained in their stomach large quantities of algal cells which had been added to the water during their incubation.

In many of our experiments, including the early one when larvae were fed phytoplankton composed principally of *Chlorella*, the veligers grew and survived well. At temperatures ranging between 18° and 20°C " eyed " larvae measuring approximately 270 μ, with a prominent pigmented spot, began to appear about the 9th or 10th day. Setting usually began on the 15th or 16th day, although in several cases, when fed *I. galbana* and *M. lutheri*, the larvae began to set between the 7th and 8th days.

Setting size of the larvae in our cultures was most commonly between 280 and 300 μ. In this respect our observations agree with those of Cole (1939), who reported that metamorphosing larvae in his experiments measured from 290 to 310 μ. However, we have never observed larvae as large as 350 μ which Cole found in some of his tanks. Imai *et al.* (1953) reported that none of the larvae of *O. edulis* in their cultures reached 300 μ in width, and most of the individuals in Walne's (1956) broods also set before reaching 300 μ.

Throughout the experiments the rate of growth of individual larvae of the same broods showed considerable variations. For example, at the time of setting, when some larvae in a culture already measured 300 μ in length and were undergoing metamorphosis, other larvae still measured only about 175 μ, thus being of approximately the same size as many larvae at the time of swarming.

When recently released larvae were placed in culture jars many of them ascended to the surface and formed large, brown, floating masses,

often measuring several square millimeters in area. This congregating tendency apparently did not unfavorably affect larvae. If these masses of larvae were disturbed, the larvae would separate and continue to swim for some time but, later, would again form floating groups. Similar floating masses of larvae are frequently observed among older larvae of other species, including *C. virginica*.

I. *Ostrea lurida* Carpenter

The native oyster of our Pacific coast is the Olympia oyster, *O. lurida*. It is considerably smaller than its close relative, *O. edulis*, or the Atlantic coast oyster, *C. virginica*, seldom exceeding a length of $2\frac{1}{2}$ in. Unlike *C. virginica* which, when adult, are of separate sexes, the Olympia oyster is hermaphroditic. Its reproduction is also different from *C. virginica* in that the eggs are not discharged directly in the water but, as in *O. edulis*, they remain within a special brood chamber in the mantle cavity of the mother oyster.

Gonad development and spawning of *O. lurida* can be induced out of season by keeping them in water at about room temperature for several weeks. Spawning can be detected, as in *O. edulis*, either by clouding of the water with discharged sperm or by presence on the bottom of a few eggs that were lost during spawning. The eggs measure from 100 to 110 μ in diameter.

According to Coe (1931) Olympia oysters begin to spawn when the temperature reaches 16°C. Hori (1933) indicated the temperature as 14°C and Hopkins (1937) thought that spawning occurred soon after the minimum daily water temperature reached 13°C.

In our experiments the incubation period lasted from 7 to 9 days after which swarms of larvae were discharged in the water. Stafford (1914) estimated that in *O. lurida* the period between spawning and swarming was $16\frac{1}{2}$ days. Coe (1931) reported this period as 10 to 12 days, and Hopkins (1937), as about 10 days. The difference in time is probably due to environmental conditions, especially temperature, under which the different observers conducted their studies.

We were unable to rear successfully recently fertilized eggs that were occasionally lost by females. However, embryos that were lost after they had reached the ciliated blastula stage were cultured to straight-hinge stage.

In one of our experiments larvae as small as 160×149 μ were released at swarming, but these larvae appeared immature as they were too transparent and unable to withdraw the velum completely. It was possible, nevertheless, to rear even these small larvae to metamorphosis.

The size of normal larvae, at the time of swarming, was about 185 μ, but on several occasions groups of smaller larvae, measuring from 165 to 170 μ were released. Hori (1933) reported that larvae at the time of release are between 175 and 185 μ. Hopkins (1937) gave 180 μ as the average. Imai *et al.* (1954), in culturing *O. lurida* in Japanese waters, found that the length of larvae immediately after swarming ranged from 174·6 to 189 μ. In general, all these figures closely agree with ours.

The larvae are quite dark, even when first released, and appear black when seen *en masse* (Fig. 34). When given good food and kept at a temperature of about 24°C growth of these larvae is quite rapid, some of them beginning to set only 7 days after swarming. At 18°C,

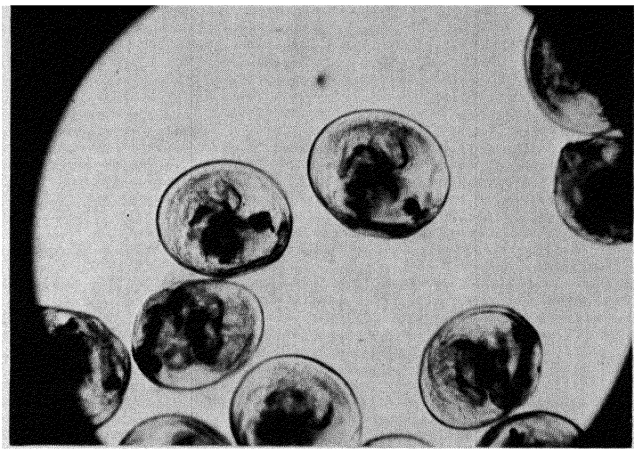


FIG. 34. Larvae of *Ostrea lurida*. Largest larva, near center, is 204 × 185 μ.

however, setting does not begin until the 16th day (Davis, 1949). Imai *et al.* (1954) reported that in their best cultures setting began on the 10th or 11th day at temperatures averaging 21·8°C.

Unlike larvae of the genus *Crassostrea*, larvae of *O. lurida* can utilize *Chlorella* from early straight-hinge stage and, in general, appear to be less restricted in types of phytoplankton organisms that they can utilize as food.

Larvae of *O. lurida*, particularly the larger ones, when seen under a microscope appear as thick wedges. Individuals 250 to 300 μ in length may measure as much as 200 μ in thickness if measurements are taken near the hinge, tapering rapidly to the sharp ventral or " bill " side. This makes it difficult to obtain accurate width measurements.

The setting size of larvae grown in our laboratory cultures was approximately 300 μ, which is not significantly different from setting

sizes of larvae of *C. virginica* and *C. gigas*. No free-swimming larvae measuring more than 312 μ in length were observed. Growth after metamorphosis was, for a short period, somewhat faster in *O. lurida* than in *C. virginica*.

J. *Crassostrea gigas* (Thunberg)

C. gigas, the common commercial species of Japan, was introduced to the waters of the State of Washington in 1902. During the last few decades it has become one of the most important mollusks of our Pacific northwest. Although the industry still depends largely upon seed oysters imported from Japan, a natural set of *C. gigas* occurs occasionally in such areas as Quilcene, Willapa and Dabob Bays and Hood Canal.

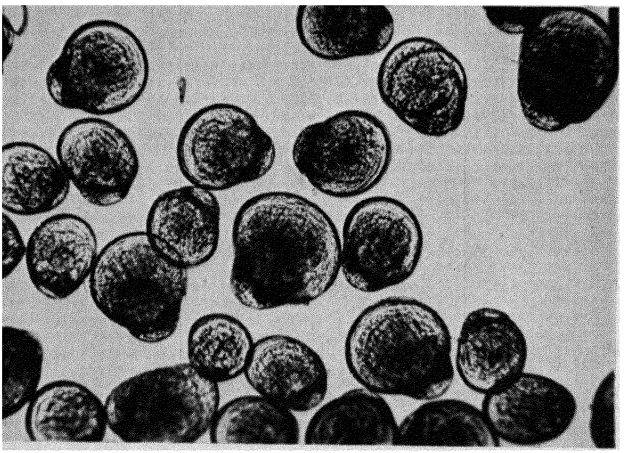


FIG. 35. Larvae of *Crassostrea gigas*. Largest larva, near center, is approximately 175 μ long.

Extensive studies conducted by Japanese workers on early development and propagation of *C. gigas* are reviewed at length by Cahn (1950). We may add to this review the articles of Hori and Kusakabe (1926) describing their successful efforts in growing larvae of *C. gigas*. More recently, Imai and Hatanaka (1949) and Imai *et al.* (1950b) grew larvae of these oysters on a much larger scale.

Our experience with *C. gigas* received from the State of Washington showed that their spawning behavior, egg development and the shapes of their larvae seem to be identical to those of *C. virginica* (Fig. 35). The similarity in shapes and sizes of the larvae of these two species is so great that we doubt if even an experienced investigator, familiar with both species, would be able to differentiate them in a mixed sample.

The general behavior, food requirements and growth rate of larvae of *C. gigas* also appear to be identical to those of larvae of the American oyster. Even the size of the eggs and the size at which larvae of the two species begin to metamorphose are alike. A comparison of the length–width relationship of larvae of the two groups will still further indicate their similarity. Yet, regardless of this similarity, the attempts of Davis (1950) and Imai *et al.* (1950b) to hybridize these two species were unsuccessful. Although fertilization occurred and the larvae developed into veligers, they all died before reaching metamorphosis.

Gonad development and spawning of Japanese oysters kept at Milford have not been as thoroughly investigated as those of the American oyster. Nevertheless, there appear to be several important differences. First, Japanese oysters require higher temperatures to begin spawning. Groups of these oysters kept in the laboratory all summer did not spawn, although the temperature at times was over 25°C. Furthermore, *C. gigas* either does not resorb the gonad material that remains undischarged at the end of the spawning season or does so at a much later date and at lower temperatures than *C. virginica.* Japanese oysters, brought to Milford from Puget Sound in October with undischarged gonads, held this material far into the winter and active sperm was found in some oysters late in December.

In our waters growth of post-setting stages of Japanese oysters is much more rapid than that of the local species. *C. gigas* that set in the laboratory in the spring and then were planted in Milford Harbor were $2\frac{1}{2}$ to 3 in long by the end of the growing season, while native oysters, which had set at the same time and were grown under identical conditions, were only 1 to $1\frac{1}{2}$ in long.

K. *Laevicardium mortoni* (Conrad)

This bivalve, which is called *Cardium mortoni* by some authors and is also known as Morton's cockle, is quite common in the comparatively shallow waters of Long Island Sound. If brought into the laboratory in late January and conditioned at temperatures between 15° and 20°C for several weeks, these cockles are easily induced to spawn by temperature stimulation alone. On several occasions spawning of ripe cockles began in less than 5 min after the water temperature was raised only 1° or 2° above 20°C. The majority spawned within $\frac{1}{2}$ hr and, as a rule, all began spawning before the water reached 30°C. Some cockles spawned at least three times during a single week.

The hermaphroditic cockles often acted first as males and then as females in the same spawning. Sometimes, after first discharging sperm, they released large quantities of eggs and finally ejected sperm

again. Probably because of this condition, which resulted in large quantities of sperm in the spawning dishes, many cases of polyspermy were seen.

The eggs of *L. mortoni* measure from 60 to 65 μ in diameter. Lovén (1848) reported that eggs of the related species, *Cardium exiguum*, have a diameter of 64 μ and are deposited in a thick gelatinous mantle within which development goes on until the shell-bearing veliger has attained a length of 90 μ. Orton (1924), who performed successful artificial fertilization of a closely related species, *Cardium fasciatum*, and Jørgensen (1946) reported that eggs of that bivalve measure about 80 μ in diameter, thus being considerably larger than those of our species. In still another closely related form, *Cardium edule*, according to Lebour (1938), the egg diameter is only 50 μ.

The smallest normal straight-hinge larvae in our cultures measured about 85 $\times$ 70 μ. Sullivan (1948) stated that very small larvae of *Cardium pinnulatum* are 90 $\times$ 80 μ, a size closely corresponding to our smallest normal larvae. In early stages the margin of the larval shell is outlined by a dark band, similar to that seen in *Teredo* larvae, but not quite as prominent. Usually, one end of the shell is slightly more pointed than the other.

The umbo begins to appear when larvae are between 135 and 150 μ in length and is usually quite prominent when a length of about 160 μ is reached.

The larvae were grown at room temperature of about 20°C and fed a mixture of *I. galbana* and *M. lutheri*. The first metamorphosing individuals were observed 8 to 10 days after fertilization. The smallest individual, having a definite foot but no velum, measured only 205 μ, while the largest swimming larvae with a still well-developed velum measured 245 μ. Some metamorphosed cockles with well-developed gills and a siphon were only 220 μ long. No " eye " was observed in any of the larvae.

The size of the largest swimming larva ever recorded in our cultures was 250 $\times$ 220 μ, but only one such individual was seen. The maximum size of our larvae, therefore, closely agrees with that described by Sullivan (1948) for *C. pinnulatum*, which measured 250 $\times$ 230 μ. Jørgensen (1946) mentioned that Lebour grew larvae of *Cardium echinatum* which, at metamorphosis, measured about 480 μ in length. We accept this figure with considerable reservation. Jørgensen also assumed that the maximum length of larvae of *C. exiguum* is about 250 μ, although he never observed this veliger with certainty in the Sound, where he carried on his experiments. His observation on *C. fasciatum* indicated that the largest larval stages

of this species found in plankton were about 300 μ long. However, he added that the veliger may leave the plankton at a length of about 255 μ, which is not too different from our maximal size.

Jørgensen (1946) also offered extensive observations on the length of larvae of *C. edule*. He stated that in rearing experiments at Kristineberg the length at metamorphosis varied from about 275 to 345 μ. Length measurements of prodissoconchs in oyster ponds near Limfjord varied from 200 to 275 μ, averaging 240 μ. Jørgensen was under the impression that larvae of this species are distinguished by an excessive variation in size at the time of metamorphosis. This condition coincides with our observation that usually in cultures of larvae approaching metamorphosis there is a great variation in size. For example, in our

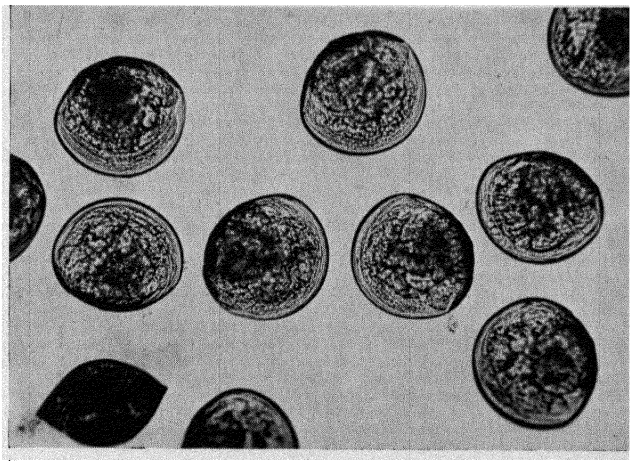


FIG. 36. Larvae of *Mercenaria campechiensis*. Largest larvae are approximately 185 μ long.

cultures of *L. mortoni*, while some of the larvae had already set and others approaching metamorphosis measured 245 $\times$ 205 μ, the smallest individuals in the same culture, grown under identical conditions, were only 140 $\times$ 120 μ.

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

These clams, commonly known as southern quahogs, were brought to Milford from the Gulf of Mexico, near Apalachicola, Florida. Although they appear to differ somewhat from northern quahogs, *Mercenaria* (= *Venus*) *mercenaria*, their spawning behavior and appearance of their eggs and larvae are identical and, therefore, they will not be described (Fig. 36).

On several occasions groups of *M. mercenaria* and *M. campechiensis*

were conditioned for spawning and later induced to spawn simultaneously but in separate dishes. The eggs obtained from these spawnings were cultured under identical conditions. Observations showed that egg development and rate of growth of larvae of these two species were virtually identical throughout the experiment and that metamorphosis in both groups began at the same time.

Reciprocal crosses of the two species produced viable larvae, which grew to metamorphosis; at times these hybrids showed somewhat more rapid growth, possibly as a result of hybrid vigor. Many of these hybrids have been grown to maturity in several locations along our South Atlantic coast and also in the Gulf of Mexico, but not in cold areas, such as Milford Harbor, where the low water temperature in winter usually caused their death.

M. *Tapes semidecussata* Reeve

T. semidecussata is one of the most important commercial species of clams in Japan, where it is known under the common name of Asari. It was accidentally introduced to our Pacific coast when Japanese oysters, *C. gigas*, were brought there early in the century. It spread rapidly and is now one of the most important species of clams in the State of Washington, where it is called the Japanese little neck, or Manila clam. In the literature *T. semidecussata* appears under a variety of names, including *Venerupis semidecussata*, *Venerupis philippinarum*, *Paphia philippinarum*, *Tapes japonica*, and others.

The first group of *T. semidecussata* was received in Milford from Puget Sound in December 1955. Upon arrival the clams were conditioned at about 20°C for 2 to 3 weeks and then induced to spawn. Cultures of larvae were successfully grown from January until the end of the summer. According to Cahn (1951) the spawning period of *T. semidecussata* of the Hokkaido region of Japan extends from June to late August, when the water temperature is between 20° and 23°C.

In our spawning experiments ripe clams quickly opened and pumped vigorously when the temperature of the water was increased to about 25°C. However, raising of the temperature even to 30°C was often insufficient to induce spawning, and addition of sperm or egg suspension was usually necessary. Even then, on some occasions, although their gonads were filled with mature gametes, the clams did not respond to the combination of stimuli.

Spawning usually occurred at temperatures between 20° and 27·5°C. The act of spawning closely resembled that of *M. mercenaria*.

Sperm or eggs were released in a constant stream from the excurrent siphon, sometimes continuously for 30 min or longer.

Eggs of *T. semidecussata* range from 60 to 75 μ in diameter, including the transparent membrane around the eggs that measures from 5 to 10 μ in thickness. The average diameter of the egg, including the membrane, is approximately 69·6 μ. According to Cahn (1951) Japanese workers found that eggs of this clam measured between 63 and 66 μ in diameter with a perivitelline space measuring from 3·3 to 4·6 μ in width and surrounded by a gelatinous coating approximately 23 μ in thickness.

Most of the cultures of *T. semidecussata* were grown at room temperature. They were fed a variety of algal cultures, but no systematic

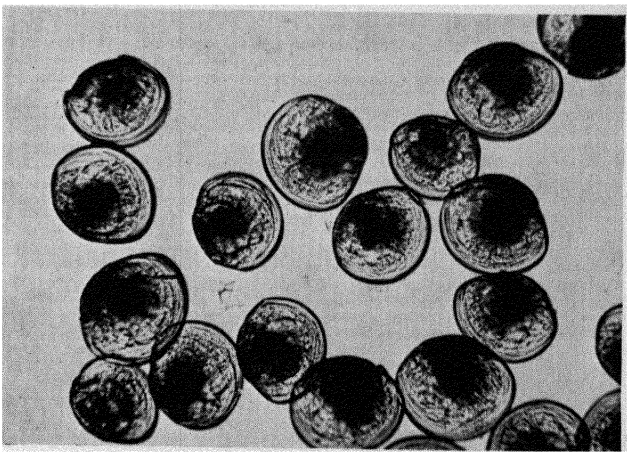


FIG. 37. Larvae of *Tapes semidecussata*. Largest larvae in photomicrograph are approximately 175 μ long.

studies of their food preference were made. Nevertheless, it was noticed that, while sometimes they grew well on mixed green algae consisting mostly of *Chlorella*, at other times, when given practically the same food, growth was poor. When given a mixture of *Chlorella* sp. and *P. tricornutum*, their growth also varied on different occasions. When fed *Chlorococcum* sp. the larvae usually grew well. Best growth was achieved when they were given *I. galbana* or *M. lutheri*.

Very early stages of straight-hinge larvae of *T. semidecussata* are remarkably similar to those of *M. mercenaria*. Some of the smallest straight-hinge larvae in our cultures were only about 90 μ long, but such individuals were uncommon; the majority measured approximately 95 $\times$ 70 μ. The umbo begins to develop when the larvae are approximately 120 μ long and becomes fairly prominent by the time

the larvae are about 140 μ in length although, even then, the hinge line may appear straight when seen from certain angles. As the larvae grow, the umbo becomes more prominent and in older larvae it is somewhat more pronounced than in *M. mercenaria* (Fig. 37).

When fed *Chlorella* sp. larvae reached metamorphosis in about 2 weeks. However, by giving them better food, such as naked flagellates, and by increasing the temperature of the water, setting size could be reached several days earlier.

The smallest metamorphosed individuals with a large, functional foot and fully resorbed velum measured about 175 μ in length, or about the same as that reported for *M. mercenaria*. The majority of the larvae metamorphosed when they were between 200 and 220 μ in length, but some much larger larvae measuring about 235 μ in length still possessed a functional velum and were able to swim. Yoshida (1960) gave the size of fully grown veligers of *T. variegata* as 215 $\times$ 195 μ.

As in most of our larval cultures, the color of the larvae depended, to a large extent, upon the food given. Furthermore, differences in size among larvae of the same cultures were of about the same magnitude as in cultures of other species. It has also been definitely established that larvae of *T. semidecussata* are susceptible to fungus diseases.

Because of our prolonged studies of *T. semidecussata* we have had an opportunity to observe their adaptability to changes in their surroundings. These clams were able to survive considerable variations in temperature and salinity, which occur over the tidal flats of Milford Harbor in front of our laboratory. During one winter, when the temperature of the water remained below zero for several weeks and the shores were covered with a thick layer of ice, only about 3% of the clams planted on the flat, near the mean low water level, died. The clams also survived periods of freshets, such as were caused by hurricane "Donna" in 1960, when salinity of the water in Milford Harbor was reduced almost to zero and remained low for several days.

The clams spawned and their larvae set normally in our experimental ponds. The small clams grew to a size of about 1 cm by the middle of September.

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

This small mollusk, which somewhat resembles *M. mercenaria*, is found along the northern section of our Atlantic shore, roughly from Prince Edward Island to Cape Hatteras. In some sections of this range, as in Narragansett Bay, it is quite numerous.

Recent literature contains few references to propagation or larval

stages of *P. morrhuana*. Sullivan (1948) is virtually the only author to devote some attention to veligers of this bivalve. Costello *et al.* (1957), calling the same form *Callocardia convexa*, gave a good description of procuring gametes of these mollusks.

Our own experience with *P. morrhuana* has been extensive but not always satisfactory because this clam is one of the few bivalves that we could not induce to spawn. All the methods known to us, including increasing of the water temperature, addition of ripe sex products, changes in pH or salinity, and use of mechanical and electrical stimulation failed to induce spawning. Moreover, we have never observed natural spawning among the hundreds of these clams that have been kept in our laboratory under different conditions, sometimes for periods of several months.

Animals brought into the laboratory from their natural beds in January already contained what appeared to be morphologically-ripe gametes. The color of the female gonad was usually creamy white and that of the male a light yellow. Even this early in the season active sperm could be taken from male gonads. The spermatozoa resembled those of *M. mercenaria* in shape. Eggs could be easily obtained by stripping, but they could not be fertilized so early in the season. This was true even when *P. morrhuana* was slowly conditioned in the laboratory by day-by-day increases in temperature. However, as the season progressed, the eggs became more responsive and the germinal vesicle in some of them dissolved soon after introduction of spermatozoa.

Our larval cultures were grown from eggs obtained by stripping. The size of the eggs taken from females with well-developed gonads ranged in diameter from 49 to 60 μ, with the modal size-group between 50 and 55 μ. These measurements, however, refer only to the egg proper; if the entire diameter of the ovum, including its thick, gelatinous membrane were measured, it would vary between 92 and 128 μ, with the modal class near 117 μ.

On several occasions we tried to improve the condition of stripped eggs by adding 3 ml of 0·1 N ammonium hydroxide to every 100 ml of egg suspension. After 25 min of this treatment the eggs were screened to discard the fluid. The eggs were then rinsed with sea water, resuspended, and spermatozoa added in proper quantities. In some instances, after this treatment about 40% of all eggs underwent cell division, but usually not more than 5% developed to normal straight-hinge larvae.

Early development of eggs and larvae of *P. morrhuana* is virtually identical to that of other mollusks of the same group. Progress of development, as usual, depends upon the temperature at which the

organisms are grown. In some cases straight-hinge larvae were formed after 24 hr at a temperature of about 21°C.

The size of the smallest normal straight-hinge larvae was approximately 78 × 64 μ. Several smaller larvae measuring only 75 μ in length were also observed, but appeared to be abnormal. Some larvae began developing an umbo when 95 μ long, and the majority possessed a well-developed umbo by the time they reached a length of 125 μ. No " eye " spots were observed in either larvae or recently set juveniles. Larvae of *P. morrhuana* closely resembled those of *M. mercenaria*, but were considerably less active (Fig. 38).

Metamorphosis occurred when the larvae were still comparatively small. The smallest young clam possessing a functional foot and

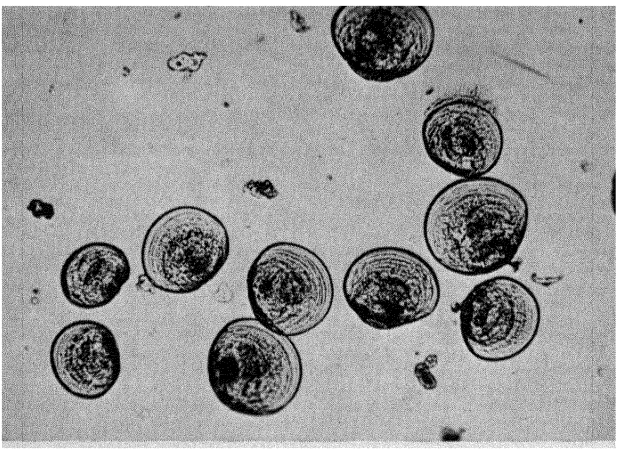


FIG. 38. Larvae of *Pitar morrhuana*. Largest larvae shown are approximately 150 μ long. Small, abnormal larvae can be seen in the group.

attached by a byssus thread measured only 160 μ. However, a majority of the larvae did not begin to metamorphose until reaching a length of approximately 180 μ. The largest free-swimming larvae still possessing a functional velum measured 192 × 179 μ.

According to Sullivan (1948) the smallest larvae of *P. morrhuana* were 120 × 95 μ. This size is considerably larger than that of the smallest larvae in our cultures. The maximum size offered by Sullivan, 220 × 210 μ, was much larger than ever recorded in our cultures. It seems improbable, therefore, that the larvae considered by Sullivan to be those of *P. morrhuana* were actually of this species.

Growth of larvae in different cultures varied considerably, depending upon temperature and quality of food given. The majority of the cultures fed a mixture of plankton, composed mostly of several species

of *Chlorella*, and kept at room temperature began to set about 14 days after fertilization. Probably if given better foods, such as *I. galbana* and *M. lutheri*, which at the time of rearing *P. morrhuana* were not available at our laboratory, a better rate of survival and growth could have been achieved.

Many cultures suffered mass mortality, which usually occurred during the late stages of larval growth. These mortalities were probably caused by the same fungi that were later found responsible for heavy mortalities of larvae in cultures of *M. mercenaria* and several other species.

O. *Petricola pholadiformis* Lamarck

Even though the range of this clam extends from Prince Edward Island to the West Indies and Texas and their larvae should be common in plankton samples during the reproductive period, Sullivan (1948) seems to be the only author who has described them. According to this author the first larvae of *P. pholadiformis* normally appear in the waters of Malpeque Bay, Prince Edward Island, about the 2nd week of July and, after reaching peak numbers in early August, disappear from plankton in early September.

In our laboratory, groups of *P. pholadiformis* were conditioned for spawning from the middle of December until summer. In the early winter these efforts were not as successful as later in the season and conditioning required a much longer time. For example, clams placed in conditioning trays at about 20°C in December required 4 to 6 weeks before the majority responded to stimulation and spawned. In the middle of April, however, only a week of conditioning at about 20°C was sufficient to bring these clams to spawning condition.

Conditioned clams were induced to spawn by our usual method, consisting of subjecting them to a quick increase in the water temperature from about 20° to 27°C and by the addition of a sperm suspension. Later in the season spawning, especially of males, could be induced on some occasions at a temperature as low as 15°C. Raising the water temperature to about 32°C always affected clams unfavorably.

Early in the season several hours at the increased temperature were often required before the first individuals, usually males, would respond, whereas late in March and in April spawning was usually provoked within the first hour. Even young clams, less than 1 yr old, and individuals with partially damaged shells responded to stimulation and discharged large quantities of spawn. Often the same individual would spawn for a while, cease spawning and then resume it. Many individually-marked clams spawned several times during the season.

Attempts at artificial fertilization of eggs of *P. pholadiformis* were partially successful, indicating that this can be done. As usual in these cases, the majority of stripped eggs were somewhat injured.

Ripe eggs measured immediately after discharge varied in diameter from 51 to 58 μ, but the modal size was quite clearly defined at 52 μ. No special studies were made as to the number of eggs produced by a single female during the season. However, in one case a large female discharged approximately 1 125 000 eggs in a single spawning.

According to Sullivan (1948) straight-hinge larvae of *P. pholadiformis* are quite large, measuring 115 $\times$ 100 μ. We found, however, that young straight-hinge larvae are considerably smaller than reported by Sullivan. With the exception of one, apparently an abnormal larva

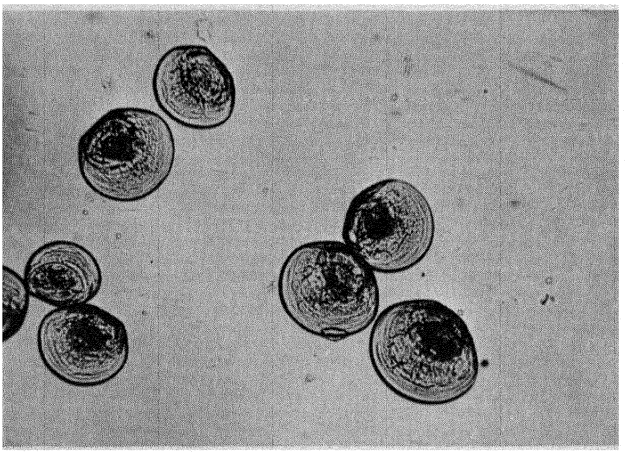


FIG. 39. Larvae of *Petricola pholadiformis*. Largest larva in this photomicrograph is about 164 $\times$ 143 μ.

which measured approximately 71 $\times$ 67 μ, the majority of normally formed young larvae were 79 $\times$ 65 μ in size. The largest free-swimming larva was about 193 $\times$ 174 μ, although many underwent metamorphosis before reaching this size, being approximately 186 $\times$ 164 μ (Fig. 39). These dimensions are somewhat larger than indicated by Sullivan (1948).

Early straight-hinge larvae are very light in color and even their digestive organs are comparatively pale. In general, they are more transparent and thinner than larvae of most of the species described in this paper. Some of them remain transparent up to the time of metamorphosis. However, when given purple sulphur bacteria belonging to the genus *Chromatium*, larvae quickly acquire a pinkish color. If they are given such foods as *Chlorella*, their digestive glands rapidly become a greenish color.

Since studies on larvae of this species were carried on when good food organisms, such as the naked flagellates, were not available, the larvae were fed mixed cultures of microorganisms in which *Chlorella* was usually the predominating form. Larvae grew well on this alga, although it is quite certain that they would have grown faster if given better foods.

Larvae of *P. pholadiformis* were grown at temperatures ranging from 18° to 30°C. The best cultures were observed at room temperatures ranging from 20° to 25°C. At somewhat lower temperatures, between 17° and 18°C, eggs developed and larvae grew, but growth was slow. At 30°C egg development was rapid, but larvae were feeble and the majority died within 2 to 4 days. Perhaps mortality was not due exclusively to temperature alone, but to the heavy bacterial flora that quickly established itself under these conditions.

The shortest period from fertilization of the egg to metamorphosis at room temperature was 13 days. In several instances, however, the larvae of these cultures did not begin to set until the 20th or 21st day. The differences were probably due to variations in quality and quantity of food.

Two characteristics were noticeable in young clams soon after metamorphosis. First, the color of their shells becomes much denser and, secondly, the edges of the shells opposite the umbo acquire a serrated, roughened appearance.

P. *Ensis directus* (Conrad)

The general characteristics of larvae of *E. directus* were given recently by Sullivan (1948). Costello *et al.* (1957) gave a brief description of early stages of egg development, while Lebour (1938) had studied larvae of *Ensis siliqua*. In general, however, larvae of *E. directus* have been less intensively studied than those of other common bivalves of our coast.

In our laboratory, observations on *E. directus* and its larvae were conducted for three winters. Each year these clams were brought from the field and placed in conditioning trays in late December. It was found, however, that when these clams are removed from the soil they soon begin to die because the powerful hinge pulls the clam shells apart. This can be prevented by placing tight rubber bands around each clam to counteract the action of the hinge and keep its shells closed. Using this simple method these clams have been kept alive without any soil for periods as long as 6 months.

Attempts to induce spawning of *E. directus* were made during the middle of January after 2 or 3 weeks of conditioning. Although at

that time their gonads contained some eggs that appeared morphologically ripe and active sperm, the clams would not spawn. Even after 6 or 8 weeks of conditioning, attempts to spawn these bivalves often met with failure. In those cases, however, when stimulation was successful, spawning proceeded normally. Some females were observed spawning almost continuously for a period of approximately 45 min, and males that spawned for periods sometimes as long as 2 hr were common.

When the clams were ripe they usually spawned within an hour after the temperature was increased to about 25°C. Males continued to spawn profusely even after being returned to water of only 13°C. Clams became sluggish at 30°C but, nevertheless, would spawn even

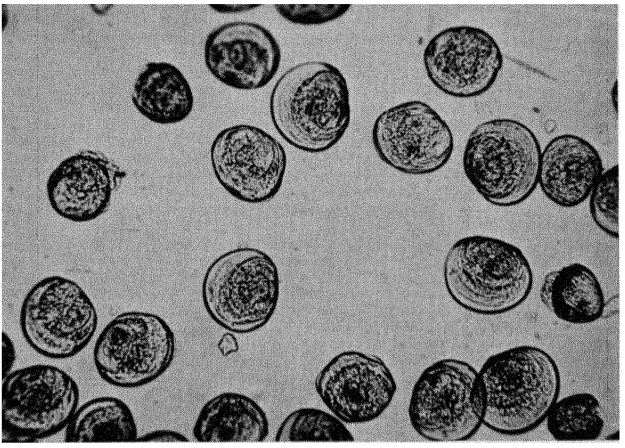


FIG. 40. Larvae of *Ensis directus* grown from eggs obtained by stripping. Note that many larvae are abnormal. Largest normal larvae shown are about 125 μ long.

at this temperature. Spawning activity was definitely accelerated by the presence of sperm. Both males and females released gametes in a thin, steady stream from the excurrent siphon.

Several clams spawned at least three times, at weekly intervals. The greatest number of eggs released by one female in a single spawning was 12585000. The greatest number of eggs released by one female in three spawnings was 20535000.

Unprovoked spawning of razor clams kept in conditioning trays occurred on many occasions. It took place at temperatures ranging from about 15° to 22°C. It has not been determined what stimulus induced spawning in those instances. Histological studies showed that on many occasions gonads were almost completely spent in a single spawning effort.

Success of fertilizing eggs stripped from conditioned females depended upon the degree of their ripeness. Early in the season, when the largest of the eggs were only 66 μ, none were fertilizable. Later, when the clams were riper, a large percentage of stripped eggs underwent cleavage but, as is often the case in using eggs obtained in this manner, most of the larvae were abnormal (Fig. 40). Costello *et al.* (1957) also reported that eggs of *E. directus* can be fertilized artificially and they remain fertilizable for about 5 hr.

The egg of a razor clam is surrounded by a narrow perivitelline space enclosed in a thin vitelline membrane. Measurements of eggs discharged in a normal spawning showed that they varied in diameter from about 64 to 73 μ, the majority being 71 μ, thus indicating that this is the modal size of normal eggs. Lebour (1938) gave the diameter of eggs of *Ensis siliqua* as about 70 μ, which closely resembles measurements of eggs of our species. Jørgensen (1946) gave references to other workers who studied eggs and larvae of *Ensis* and related forms.

Eggs and larvae were usually cultured at about 22°C. The smallest straight-hinge larvae were 80 μ in length, but only two individuals this small were observed. Even larvae as small as 85 μ in length were scarce, while those measuring approximately 92 $\times$ 78 μ were common. This size is considerably smaller than the 140 $\times$ 120 μ indicated by Sullivan (1948) as the smallest larvae of this species.

The larvae are light in color and more transparent than those of *M. mercenaria*. The umbo appears in larvae only 115 μ in length and becomes well developed in larvae 135 μ long. Larvae of this size have definitely passed the straight-hinge stage. The umbo is so pronounced in larger larvae that it is impossible for them to lie flat. As a result, considerable variation in the length–width ratio is obtained when large larvae are measured under a microscope.

Setting of *E. directus* began soon after some larvae reached a length of about 210 μ. At 24°C this often occurred only about 10 days after fertilization. However, some larvae remained swimming until they reached a much larger size before undergoing metamorphosis. For example, in one culture fed *Chlorella* sp. larvae measuring 250 to 260 μ in length were still swimming 27 days after fertilization and possessed both a powerful velum and a well-developed foot. The largest swimming larva measured 270 μ, while in the same culture many fully metamorphosing individuals showing a well-developed foot, gills and siphons were only 220 μ long.

The appearance of the " eye " was irregular and it was not located where this structure is usually found in most bivalve larvae. The smallest individual possessing this structure was only 126 μ long, but

many other larvae, even those nearing metamorphosis, did not display it. Sullivan (1948) did not mention the presence of an " eye " in *E. directus* larvae and Werner (1939), working with a species that he called *Cultellus pellucidus*, a form closely related to *Ensis*, stated that its larvae do not possess " eyes ". This observation is quite important because, according to Rees (1950), the description by Werner of *C. pellucidus* was really that of *Ensis*. Our observation that the " eye "-like structure is sometimes present in larvae of *E. directus* and Werner's, that it is always absent in the species that he studied, may indicate that Rees' assumption is not correct and that the *C. pellucidus* of Werner was not an *Ensis*.

One of the characteristics of larvae of *E. directus* which may be of diagnostic value is the presence of a clear area around the edge of the shell. This area, which does not occur in larvae of other species that we have studied, is well defined and clearly seen. It appeared in larvae of about 120 μ long and persisted until they reached a length of 180 to 190 μ. Later this area became less definite and more or less merged with other parts of the shell. Near setting, however, a purple cast became apparent along the edge of the larval shell.

In rearing of *E. directus* the presence of many abnormal larvae was quite common, not only in cultures that were started from stripped eggs, but also in those that were grown from normally discharged ones.

In several cultures, usually those where larvae were approaching setting stage, mortalities on an epizootic scale were recorded. In several instances practically all of the larvae died within a short period, usually less than one day. Since this happened before we learned the devastating effect of larval diseases caused by fungi or bacteria, we did not establish the cause of death of these larvae but strongly suspect that these mortalities were principally the result of fungus infestations.

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

The clams used in these studies were taken from the sandy beaches of the south shore of Long Island, New York. They were shipped to Milford and kept for many months, either in the laboratory or in the harbor, without any appreciable mortality, although the salinity at Milford is about 27 ppt, or approximately 8 ppt lower than in the areas where the clams were dredged. The clams survived equally well whether they were allowed to dig into sand or were kept in wire baskets containing no soil. To prevent mortality, however, it was necessary to expel bubbles of air which were trapped inside the clams while they were out of water. Clams placed on their sides cannot expel these bubbles and, eventually, die.

Our experience in growing larvae of *M. solidissima* was confined to the period from the middle of January to the end of June. During that time morphologically-ripe eggs and spermatozoa were always present in the gonadal follicles. Possibly, equally well-developed sex cells could have been found in the gonads several weeks earlier than January because, apparently, the most important period of gametogenesis in *M. solidissima* begins immediately after the end of spawning, as in *M. mercenaria*, in which gonads of both sexes present a ripe appearance in December (Loosanoff, 1937b). Allen (1953) obtained ripe eggs of *M. solidissima* from early spring until late autumn.

Spermatozoa, taken from clams brought from their natural beds early in January, when placed in a drop of water at room temperature quickly began to move. However, eggs taken from clams of the same groups usually could not be fertilized, probably because they were not physiologically ripe. Nevertheless, placing female clams in water of about 15°C for only a few days was sufficient to ripen them. Later in the season, when the temperature of the water in Milford Harbor increased to 12°C, no conditioning was needed.

Fertilizable eggs could be obtained either by stripping or by inducing spawning. Sometimes, stripped eggs obtained from a ripe female were as viable as those discharged during a normal spawning. More often, however, a culture started with stripped eggs contained many abnormal individuals. Costello *et al.* (1957) suggested a different method of obtaining gametes, which consisted of straining the eggs through a cheesecloth.

Spawning was induced by the usual method of thermal and chemical stimulation. On several occasions thermal stimulation alone was sufficient. Normally, addition of a suspension of sex cells was required and, even then, many conditioned clams did not spawn.

Spawning was induced at temperatures ranging from 18° to 25°C. Temperatures of 30°C and over unfavorably affected the clams. They gaped and abnormally extended their feet which, like the rest of their bodies, became limp and soft. If, after exposure to such high temperatures the clams were quickly returned to cooler water of about 25°C, they often began to spawn, but the eggs obtained in such a manner did not develop past the formation of polar bodies. Apparently, exposure of clams to temperatures over 30°C caused serious injuries to their eggs. Our observations in this respect agree with those of Imai *et al.* (1953) who, while working on a closely-related species, *Mactra sachalinensis*, found that at a temperature of about 32°C none of the eggs underwent normal cleavage.

Observations were made on the growth of larvae of *M. solidissima*

at two different temperatures. Eggs obtained from several females and fertilized with spermatozoa of three ripe males were mixed together and then divided into two groups, one to be grown at a temperature of about 22°C and the other at 14°C. The concentration of eggs per ml of water was the same in both cultures. During the experiment the larvae were fed equal quantities of phytoplankton composed largely of *Chlorella* sp.

Eggs placed in water at 14°C were in the trochophore stage at the end of 40 hr. After 72 hr the culture contained normal and active straight-hinge larvae averaging 85 μ in length, which were quite uniform in size and appearance. At 22°C this stage was reached after only 28 hr. Young straight-hinge larvae of *M. solidissima* were usually

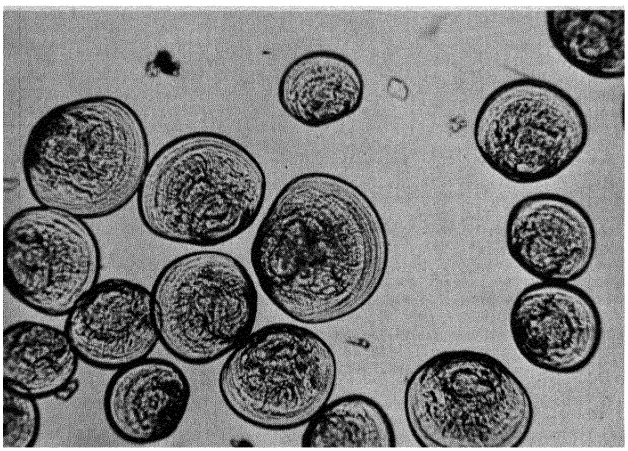


FIG. 41. Larvae of *Mactra solidissima*. Largest larva, 219 μ long and 193 μ wide, is approaching metamorphosis. Note differences in sizes of larvae that originated from the same group of eggs and were reared under identical conditions.

almost transparent and had a granular appearance with the internal organs at this time not too well defined. Later, as in the case of most larvae, the color began to deepen.

On the 19th day, when larvae in the warmer culture began to metamorphose, the length of the modal class of larvae grown at 14°C was only 117 μ, and the larger individuals in the cultures were only 153 μ long. The first metamorphosing clams were observed in this culture after 35 days. When the experiment was discontinued on the 50th day the remaining larvae showed a wide range in size, the smallest being only 109 μ long (Fig. 41).

A partial description of development and dimensions of larvae of *M. solidissima* was given earlier in this article. Here we may add

that the most recent description of what were assumed to be larvae of *Mactra* (= *Spisula*) *solidissima* was reported by Sullivan (1948). She gave the minimum size of straight-hinge larvae as about 95 × 80 μ, which is approximately 15 μ longer than usually found in our cultures, while the maximum size of 270 × 245 μ closely agreed with our measurements. In both instances the length–width relationship given by Sullivan falls near the median line of length–width relationships which we found for larvae of *M. solidissima*.

In describing larvae of a related form, *Spisula subtruncata*, Jørgensen (1946) reported that veligers are about 400 μ at the time of metamorphosis. Kändler (1926) stated, however, that the length of this species at metamorphosis is only 310 μ. Considering that Imai *et al.* (1953) found the maximum size of larvae of *Mactra* (= *Spisula*) *sachalinensis* to be about 270 μ, virtually the same as we found for *M. solidissima*, and because Imai's conclusions and ours are based on measurements of larvae of a known origin, we think that Kändler's measurements are more realistic than Jørgensen's and that the latter was probably describing larvae other than those belonging to the genus *Mactra* (= *Spisula*). The same consideration leads us to believe that the descriptions and measurements offered by Rees (1950) of advanced stages of larvae presumably of the superfamily Mactracea, including *Spisula solida* (360 μ) and *Spisula elliptica* (355 μ), are really those of some other species.

R. *Mya arenaria* Linné

Our efforts to induce spawning of *M. arenaria* were confined largely to the period extending from March until the middle of July. Several groups of these clams were also conditioned and spawned in winter. Moreover, to induce spawning of even well-conditioned and apparently ripe *M. arenaria* is difficult, nevertheless.

In developing a method to induce spawning of these clams we tried many approaches, including sudden and gradual changes in water temperature, changes in pH, salinity, hydrostatic pressure, light intensities and the addition of sex products. Usually, none of these worked. The only method that proved to be successful with some regularity consisted of subjecting ripe clams to water of relatively high temperature, of about 26° to 28°C, for long periods often extending from 6 to 8 hr and adding, during this time, a suspension of sex products. Many clams spawned profusely when this method was employed and discharged a large number of eggs, but a high percentage of these eggs usually developed into abnormal larvae.

Belding (1931) reported the diameter of the average egg of the

soft shell clam as 62·5 μ, while Battle (1932) gave the egg size as varying from 70 to 80 μ. Our measurements of hundreds of eggs discharged by different females and on different occasions showed that the majority were between 68 and 73 μ in diameter, with a modal size of 70·5 μ.

Belding (1931) expressed the opinion that artificial cultivation of *M. arenaria* is virtually impossible because the eggs either fail to develop normally or else never pass the young veliger stage. Nevertheless, Belding was able to show that, unlike other pelecypods, eggs stripped from *M. arenaria* can be artificially fertilized.

The smallest normal straight-hinge larvae recorded in our cultures measured only about 86 $\times$ 71 μ. These were, however, extremely uncommon and normal, fully-formed straight-hinge larvae were usually about 93 $\times$ 77 μ. As in most pelecypod larvae, they were light in color at this stage and their internal organs were not well defined. They remained quite light, almost transparent, until a length of about 110 μ was reached. As the larvae grew, they became darker. Nevertheless, as mentioned on several occasions, these larvae do not possess characteristic colors that would help to distinguish them from members of other genera or species of bivalves. In our experiments, where larvae of this species were fed different foods, their color ranged from a dark reddish-brown to dark green. We cannot, therefore, agree with Sullivan (1948) that brown pigmentation in large larvae of *M. arenaria* is diagnostic of that species.

In older larvae measuring about 175 μ and longer we noticed the presence, in the margins of the mantle, of irregular opaque spots varying in size from 5 to 15 μ. These granules occurred with such regularity that we are inclined to consider them as characteristic of the species, at least during late larval stages. Jørgensen (1946) noticed a somewhat different pigmentation of the soft parts of larvae of *M. arenaria* measuring about 200 μ and larger. He also suggested that this may be a reliable specific character.

The size of larvae of *M. arenaria* at setting is extremely varied. Metamorphosis may occur at any length from 170 to 228 μ. The latter is the size of the largest free-swimming larva ever recorded in our cultures. The majority metamorphosed at a length between 200 and 210 μ.

The smallest larva in which the foot was present was about 165 μ long but many of the larvae had a well-developed foot by the time they reached 175 μ in length. The presence of a large foot does not necessarily indicate that the velum has already become non-functional. Larvae as long as 210 μ have been seen at times swimming about using both the velum, which still appeared to be of normal size, and also

the large foot. However, the velum normally begins to disappear soon after a length of 172 to 175 μ is reached and sometimes even earlier. In most individuals 200 μ in length the velum is already resorbed. Some larvae measuring only 175 μ in length, and having no velum, were seen actually crawling, using their feet.

The balancing organ, the otocyst, can be clearly seen at the base of the foot of larvae measuring about 175 μ in length. The byssus gland also can be seen in larvae less than 200 μ in length, and the gills may be clearly discerned in some individuals of about the same size. The byssus thread is strong, and our attempts to break it by directing a strong jet of water from a pipette caused the larvae to sway from side to side, but did not break the thread.

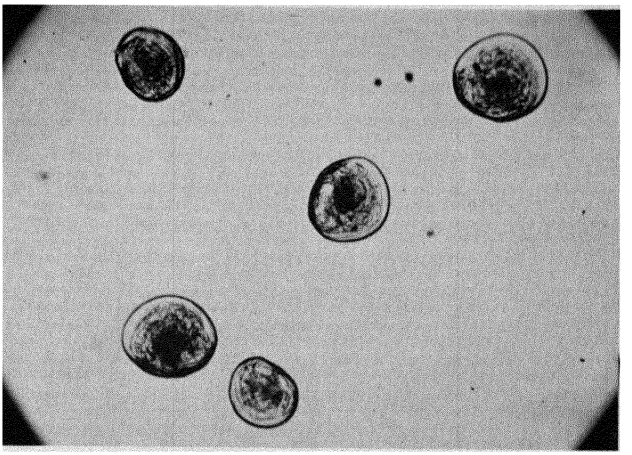


FIG. 42. Young larvae of *Mya arenaria*. Largest larva shown is about 140 μ long.

No systematic studies on the rate of growth of larvae of *M. arenaria* at different temperatures, such as those conducted with larvae of *M. mercenaria*, were made. Our attempts to grow larvae at low temperatures ranging from 12° to 15°C were usually unsuccessful because of slow growth. For example, at a temperature of about 14°C larvae, even after 15 days, were only about 110 to 115 μ long. Larvae grown at low temperatures, probably because of the slow rate of growth, were usually of extremely uniform size.

Most of our cultures were grown at room temperatures which ranged from about 19° to 24°C. Under those conditions the rate of growth was quite rapid, although it varied, of course, from culture to culture, depending upon the temperature, concentration of larvae, and quality and quantity of food given. At about 23°C the average length of larvae 2 days after fertilization was approximately 109·5 μ

and the maximum 117 μ. After 5 days larvae averaged 120 μ in length and the largest individuals were 140 μ long (Fig. 42). After 10 days some of the largest larvae approached a length of 180 μ at which setting is possible. By the 15th day many individuals had already set, and the average size of the larvae in the cultures had increased to about 175 μ. A few large larvae, measuring about 225 μ in length but still free swimming, were also found in our samples. In some cultures setting began when the larvae were about 10 days old and continued until the end of the 35th day.

As has already been mentioned, the smallest straight-hinge larvae of *M. arenaria* in our cultures measured about 86 $\times$ 71 μ. The largest free-swimming individuals were 228 $\times$ 207 μ, although most of them metamorphosed before that size was reached. Our measurements, therefore, differ from those given by Stafford (1912), who stated that the smallest straight-hinge larva of *M. arenaria* that he found was only 75·9 $\times$ 62 μ, while the largest measured 414 $\times$ 345 μ. Of the latter he said, "The largest measurement I have is 64 $\times$ 53, and I have seen them attached by a byssus-thread, their siphons protruded, and the big hinge-tooth on the left valve." Since, according to Stafford, each unit of his measurements was equal to 6·9 μ, the dimensions of his larvae were as given above. It is quite possible, if his measurements were correct, that Stafford was working with larvae of a species other than *M. arenaria* and, possibly, his large individuals were already juvenile mollusks and not free-swimming larvae. Another possibility is that Stafford's microscope was not correctly calibrated.

The dimensions of larvae in our cultures were not too different from Sullivan's (1948). Nevertheless, her smallest size of 105 $\times$ 90 μ is considerably larger than we found and her largest, 250 $\times$ 230 μ, also somewhat exceeds ours. Yoshida's (1938) observation that larvae of *M. arenaria* in Japanese waters metamorphose upon reaching a size ranging from 240 to 300 μ also disagrees with ours because, while the length of 240 μ does not differ radically from the measurements of our largest larvae, the maximum size of 300 μ given by Yoshida exceeds ours by about 70 μ.

The length of early straight-hinge larvae of *M. arenaria* given by Jørgensen (1946) is similar to ours. This is to be expected because his early larvae were laboratory-reared, as were ours, and, therefore, there is no doubt that we and Jørgensen were working with the same species. However, we disagree with Jørgensen that larvae of *M. arenaria* may reach 300 μ in length before metamorphosis. His conclusion regarding the setting size is based not on laboratory-reared *M. arenaria*, but on specimens collected in the field and only assumed to be this

species. The fact that Jørgensen stated on several occasions that metamorphosis of *M. arenaria* may occur upon attainment of a much smaller size than 300 μ strongly supports our opinion. For example, Jørgensen mentioned that in Ringkbing Fjord the size of larvae at metamorphosis in shallow water varies between 200 and 225 μ, thus being within the size range observed in our cultures.

S. *Teredo navalis* Linné

Larvae of *T. navalis* have been described by many authors, including Jørgensen (1946), Sullivan (1948) and, also, Imai, Hatanaka and Sato (1950), who gave a good description of the method of rearing them.

In our laboratory adult *T. navalis* were conditioned to spawn as early as the first part of December. This was done by placing pieces of wood, containing wood-borers, in sea water maintained at a temperature between 15° and 20°C. Spawning occurred at temperatures of 14°C and higher, and larvae were released at temperatures ranging from about 16° to 20°C. Grave (1928) reported that spawning of *T. navalis* began when the water temperature reached 11° to 12°C. Imai *et al.* (1950b), however, found that spawning begins when the water temperature reaches 18°C. Sullivan's (1948) data closely agree with ours, that spawning and swarming may occur at approximately 15°C.

Although *T. navalis* is naturally larviparous, both recently-fertilized eggs and immature larvae removed from the gill chambers of the parents developed normally past metamorphosis. The diameter of unfertilized eggs varied between 50 and 60 μ, agreeing with measurements given by Jørgensen (1946) and Costello *et al.* (1957). In the dissected adults, however, most of the eggs found were either already fertilized or immature, thus presenting difficulty in obtaining reliable egg measurements.

The smallest larvae released in natural swarmings at our laboratory measured only 80 $\times$ 70 μ, while the largest larvae found in the gill chamber of the mother were 90 μ long, or approximately 10 μ longer than reported by Jørgensen (1946). Evidently, the length of larvae at the time of release may vary by at least 20 μ. Imai *et al.* (1950b) indicated that the mean size at the time of release is 85 $\times$ 72 μ. Our observations that the average size of just-released *Teredo* larvae is between 85 and 95 μ are in agreement with those of Sullivan (1948), Jørgensen (1946) and Imai *et al.* (1950a). We cannot, however, accept the conclusion of Lane *et al.* (1954) who maintained that larvae are about 250 μ in size when released from the gill chamber.

Eggs, in early stages of development, taken from the gill chamber

of a female *Teredo* were cultured to metamorphosis in 28 days at a temperature of about 20°C. Grave (1928) thought that the entire period of development of *Teredo* from the moment of fertilization to metamorphosis takes about 5 weeks. Judging by data offered by Imai *et al.* (1950a), setting in their cultures occurred between the 24th and 34th days.

A brief description of early stages of development of eggs and larvae of *T. navalis* are given by Costello *et al.* (1957) and of later stages, by Sigerfoos (1908). Imai *et al.* (1950b) gave a good account for all stages. In our cultures the shells of straight-hinge larvae appeared heavy and thick. The larvae were also characterized by a dark band

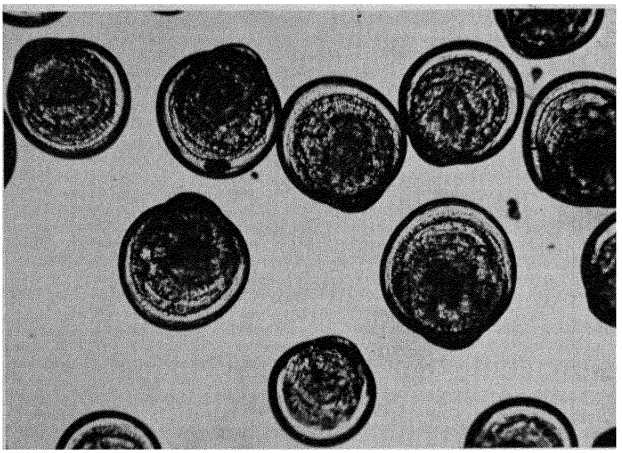


FIG. 43. Late larval stages of *Teredo navalis*. Largest larva in the group is about 185 μ long and 200 μ wide. Note dark band around edge of shell characteristic of larvae of this species.

around the edge of the shell from one end of the hinge to the other (Fig. 43). A light band was quite conspicuous inside of this dark band. Although these bands are probably optical illusions resulting from curvature of the shell seen under the microscope, they are well pronounced. The bands are quite narrow and less conspicuous in larvae smaller than 90 μ in length but, nevertheless, they are present even in these small individuals. As larvae approach setting size, the bands become less sharply delineated, although they remain quite prominent.

The color of larvae begins to darken soon after they reach 100 μ in length. Imai *et al.* (1950a) also came to the same conclusion. However, while Imai reported that neither the foot, otocyst or gill filament appears before larvae reach the size of 200 $\times$ 215 μ, we observed their appearance in larvae at least 15 μ smaller.

Imai *et al.* (1950b) gave a table showing growth of *T. navalis* larvae from day to day, indicating length–width relationships during different stages of growth. These data closely resemble ours. Other observations of these authors on appearance and behavior of larvae are also in close agreement with ours.

Larvae of *T. navalis* are extremely active and usually swim vigorously and virtually continuously. This is particularly true of younger stages. We noticed that the larvae have some substance on the outside of their shells by means of which they adhere readily to glassware and, as a result, it is extremely difficult to rinse them from beakers, pipettes, slides, etc.

Larvae began to metamorphose soon after a length of 200 μ was reached. However, several fully-metamorphosed individuals measuring only 190 μ in length and 206 μ in width were seen. The largest swimming larvae were approximately 200 $\times$ 231 μ. Our maximum size of free-swimming larvae of the wood-borer is, therefore, somewhat smaller than the 220 $\times$ 250 μ reported by Sullivan (1948), but closely approaches that given by Imai *et al.* (1950).

Larvae of advanced stages do not develop an " eye " that is characteristic of larvae of corresponding stages of other species, such as *C. virginica*. The foot of recently set borers is extremely slender and worm-like. The set attach themselves to the substratum by means of a byssus.

The time required for larvae in our cultures to reach metamorphosis varied. Early in our work, before good food organisms became available, the first metamorphosing larvae were observed 20 days after swarming, when grown at room temperature. If better growing conditions were provided, the free-swimming period could undoubtedly be shortened. Nevertheless, we strongly disagree with the conclusions of Lane *et al.* (1954) that the normal free-swimming period of *Teredo* larvae does not exceed 4 days.

Teredo larvae are quite susceptible to fungus diseases. Such infections were observed on numerous occasions and were probably responsible for the complete mortalities of *Teredo* larvae in some of our cultures.

VI. Acknowledgments

Our studies, which provided most of the material for this article, have been continuous since 1944 and, naturally, during this time many people have participated either directly or indirectly. We want to express our appreciation to all biologists of our laboratory, especially to Mr. Paul E. Chanley, who grew larvae of the several species of

bivalves discussed in this article; to Mr. Herbert Hidu, who contributed a great deal of information on utilization of dried algae as larval food; to Miss Phyllis B. Smith, who assisted us in a number of the earlier experiments; and to our microbiologists, Dr. Ravenna Ukeles and Dr. Robert R. Guillard, who provided the phytoplankton for our feeding experiments. We are grateful to Dr. F. S. Russell and Dr. Mary Parke of Plymouth Laboratory, England, for sending us inocula of algae, several of which were extensively used in our studies.

We also want to acknowledge the technical help of our Laboratory Mechanic, Mr. Joseph F. Lucash, whose ingenuity in designing and building various apparatus for our experiments made possible the successful completion of many of our physiological studies. Miss Rita S. Riccio and Mrs. Florence S. Munz were extremely helpful in preparing and editing this manuscript, while to Messrs. Manton Botsford and Charles Nomejko we are indebted for preparation of the photographs and other illustrations.

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THE BREEDING OF THE NORTH ATLANTIC FRESHWATER-EELS

The late ANTON F. BRUUN

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Editor's Note

In August 1961 I wrote to Anton Bruun asking whether he would prepare an article for the first volume of "Advances in Marine Biology". I saw him in Copenhagen the following October and he told me that he had nearly finished a manuscript in support of Schmidt's theory on the migrations of the eel. A few weeks later he died. In March 1962 the manuscript was sent to me from Copenhagen by Torben Wolff.

I am indebted to E. Bertelsen for the following information. It was originally intended that the paper should be under the joint authorship of Bruun and Bertelsen, but subsequently it was decided that there should be one author. The manuscript was in the form of draft sections which Bruun had intended to knit together and round off with a concluding section.

It was obviously unfinished, but nevertheless since Anton Bruun was one of the foremost authorities on the subject and had worked side by side with Johs. Schmidt I felt that it should be published if possible. The manuscript was then seen by N. B. Marshall, who agreed.

No alterations have been made to the original text other than minor grammatical amendments to the English. Bruun was a master of languages and the paper has been left much as his friends would have liked to hear him say it.

It is a pleasure to be able to publish this posthumous work as a tribute to a great zoologist and oceanographer who had the esteem and affection of so many in all parts of the world.

I wish to thank Dr. E. Bertelsen, Dr. Torben Wolff and Mr. N. B. Marshall for their assistance. Mr. J. Boëtius kindly helped in the preparation of the list of references.

F.S.R.

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I. INTRODUCTION

Since the publication of "The Breeding Places of the Eel" by Johs. Schmidt (1925), and even before that, no serious objections have been raised against Schmidt's well-founded conclusions from 20 years of extensive and intensive observations, until D. W. Tucker (1959a) put

forward "A New Solution to the Atlantic Eel Problem". In this article Tucker (p. 496) rejects Schmidt's assumption that the European freshwater eel (*Anguilla anguilla* L.) returns to the Sargasso Sea and " proposes a new and drastically different interpretation of the observed phenomena, namely: (1) That the European eels need not and do not succeed in returning to the ancestral spawning-area, but perish in their own continental waters. (2) That the American and European eels are not distinct species, but merely eco-phenotypes of *Anguilla anguilla*, their apparent distinguishing characters being environmentally determined (in the manner of numerous precedents) by demonstrable differences in temperature conditions encountered during the ascent from different parts of the American eels' spawning area to the surface, and their distribution by demonstrable coincident differences in the subsequent transport of the surface water-masses. (3) That the populations of the so-called ' European ' eels, *A. anguilla*, are therefore entirely maintained by reinforcements of larvae of American '*A. rostrata* ' parentage."

Tucker's hypothesis thus leaves us with the implication " that Europe and North Africa are regularly colonized by eels of American ancestry doomed to perish in a fruitless suicide-migration."

No wonder this statement has had a great appeal to the general public and has been very widely spread by magazines and newspapers. With Dr. D. W. Tucker's background, the British Museum (Natural History), it is quite natural if teachers of biology have come to doubt whether Schmidt was right in his solution of the problem about the breeding places of *A. anguilla.* They may think this is still a problem in which two hypotheses are possible; for Tucker claims at least parity with Schmidt. But I propose to provide sufficient evidence to prove that this is far from being the case.

Three scientists have already put forward good arguments against Tucker's ideas (D'Ancona, 1959; Jones, 1959; Deelder, 1960). In each case Tucker (1959b, 1959c, 1960) has fully maintained and extended his own ideas. I shall restrict myself to discussing what Tucker himself has put forward. I have found it impossible to include reviews in general even if they have been in favour of Tucker's ideas (*fide* Tucker, 1959c, p. 1283).

Tucker has founded his hypothesis on part of the existing literature without any new observations of any kind; so although I have been working with Schmidt and Schmidt's collections since 1924 I shall not use anything unpublished from this material; but will only mention that any new observations which may have been made or old observations studied in more detail than already published by Schmidt, have only given further support to Schmidt's conclusions.

II. *Anguilla anguilla* L.—*A. rostrata* Le Sueur

The Taxonomic Situation

Ege (1939) has shown that the two species are more closely allied in every respect than either is even to *A. japonica* Temminck and Schlegel, which is quite closely related to both. The two Atlantic species are most easily distinguished by the number of vertebrae. Schmidt (1913) examined sixteen samples between Iceland and Cyprus, altogether 2775 specimens of *A. anguilla*, and found from 110 to 119 vertebrae, average 114·7, only one having 110 and seventeen 111 vertebrae. Furthermore in four samples of *A. rostrata* between St. Laurence and St. Croix, Virgin Is., 361 specimens had vertebral complements varying between 103 and 110, average 107·1 vertebrae; twelve had 110 vertebrae. Later on Schmidt (1915, p. 6) and Ege (1939) added further material of *A. rostrata*, so that 962 specimens have been examined, showing a variation of from 103 to 111 vertebrae, average 107·2: thirty-three had 110 and three had 111 vertebrae.

The differences in the average numbers of fin rays and branchiostegals are too small to be useful in identification. While Schmidt was fully aware of the fact that the numbers of vertebrae and fin rays may vary to a certain extent under the influence of the environment, this has not been shown for one character, the dentition, which Schmidt also used. Ege (1939, p. 122) has studied the proportion between the length of the intermaxillary-vomerine band from the foremost point to the hindmost tip, and the length from the same foremost point to the posterior end of the right maxillary band. This character varies to a certain extent according to sex and the total length of the fish. Out of Ege's detailed analysis we may select as an example the females of a length between 30 and 40 cm. The percentage values are, for *A. japonica* 77·7, *A. rostrata* 69·0 and *A. anguilla* 76·1.

When Schmidt (1927, 1928) divided *A. australis* Richardson into two subspecies he had a similar case, later studied in detail by Ege (1939). Here the total number of vertebrae is 112·6 in *A. australis australis* and 111·7 in *A. australis schmidti*. Using the same character of the dentition (Ege, 1939, p. 184) as above for *A. anguilla* and *A. rostrata*, corresponding values of specimens measuring 50–60 cm are 69·3 and 71·2, thus indicating a much smaller difference, if any, than that between *A. rostrata* and *A. anguilla*.

Tucker treats *A. anguilla* and *A. rostrata* as though they are distinguished only by the number of vertebrae. It should, however, not be forgotten that Johs. Schmidt made a close study of the taxonomy of the genus *Anguilla* Shaw. This was brought together in a monograph

by Ege (1939) after Schmidt's untimely death in 1933, and it may very well be maintained that no genus of fish has been treated taxonomically in so thorough a way. I may briefly summarize some observations from Ege and at the same time mention *A. japonica*, which is so closely related to the two North Atlantic eels.

TABLE I*

	Anguilla anguilla	*A. rostrata*	*A. japonica*
Preanal length as % of total length	41·56–42·83	42·73–43·90	38·85–40·03
$\frac{\text{Preanal length} - \text{head length}}{\text{total length}}$ as %	28·33–30·40	29·79–30·10	26·54–26·94
Distance from origin of dorsal fin to anus as % of total length	10·31–11·52	8·80–9·63	9·01–9·35
Predorsal length without head as % of total length	17·93–19·32	20·23–21·01	17·52–17·72
Head length as % of total length	11·20–13·39	12·90–13·78	12·24–13·16
Length of gape as % of head length	22·73–26·51	25·88–27·23	23·95–27·53
Position of eyes (Distance from perpendicular through eye centre projected to margin of upper jaw to angle of gape as % of gape length)	♂2·64–10·99 ♀2·96–12·93	♂7·7 ♀12·29–15·14	♂8·90–16·05 ♀16·27–21·41
Length of band of vomerine teeth as % of length of band of maxillary teeth	71·87–79·89	65·10–69·67	77·73–83·80
Numerical characters			
Prehaemal vert.	44–45·2–47	41–42·8–45	42–43·6–45
Total vertebrae	110–114·7–119	103–107·2–111	112–115·8–119
Branchiostegal rays	10·8	11·0	11·4
Pectoral rays	17·4	16·7	17·3

* In his manuscript Bruun had used the expressions "high" and "low". Numerical data have been given by N. B. Marshall instead. For further details see Ege (1939).

Altogether I find that Schmidt had very good reasons for assuming two breeding populations of the North Atlantic eels, whether they be called two distinct species or geographical races. He made these investigations before he knew the location of the breeding places, but it explained to him why he had failed in finding any early larval stages of *A. anguilla* in the Mediterranean on his two expeditions 1908–1910.

III. The Distance to Cover During the Migration

The central area for the distribution of *A. anguilla* is the British Isles and the coasts of the Bay of Biscay, judging from the mass occurrence of elvers ascending the rivers (Schmidt, 1906, p. 196–213). So Tucker (1959a, p. 496) is correct in giving the distance for this area from the breeding places as at least 3500 miles on a great circle course. But in his argument against Jones (1959, p. 1281), who thinks that *A. anguilla* is able to cover this distance, he overlooks the fact that the Azores have a population, about which Schmidt (1909, p. 139) had the information that *A. anguilla* is common in all the islands. This reduces the distance to cover for the eel of the Azores to about 2000 miles, or no more than *A. rostrata* from the New England states and Canada have to cover.

As is known (Bruun, 1937, p. 26), a single *A. rostrata* has been found in northern Spain; it was found among several hundred *A. anguilla* of which the number of vertebrae were counted. Rather a few specimens only of eel from the Azores have been examined, altogether 131 (Schmidt, 1913, p. 11) and they were all *A. anguilla*. It would, in fact, be very interesting to have several hundreds examined to see whether *A. rostrata* might reach the Azores more often than hitherto supposed. Tucker (1959a, p. 495) in referring to Vaillant (1898) maintains that "*Anguilla* adults have yet to be taken in the open ocean (one from the stomach of a cachalot off the Azores is obviously suspect of local provenance)." It may very well be of local provenance, but it is nevertheless a proof that a ripening eel has been observed in the open ocean, over very deep water, where the spermwhale is hunting other fast-swimming creatures like the squids (Clarke, 1956).

If we suppose that there is one single ancestral species of *Anguilla* in the North Atlantic and that this has a distribution more or less like that which *A. rostrata* now has, then the North Atlantic islands, first the Azores, and later on Madeira and the Canaries, may very well have served as stepping stones towards the development of *A. anguilla*; Jones (1959, p. 1281) is therefore right in assuming " intense selection in favour of eels which found the ' right ' spawning ground." Such

selection must have been at work, and probably still is, especially in *A. rostrata*. From the known distribution of the *A. rostrata* leptocephali it may be concluded that a considerable number fail to reach the coasts, especially those found north of 40° N. lat. and east of 55° W. long. But even some of these do reach Europe as mentioned above.

IV. How Does *A. anguilla* Reach the Breeding Place?

As already mentioned Tucker is of the opinion that *A. anguilla* cannot reach the breeding places. He then asserts (Tucker, 1959a, p. 497): " The east-coast American migration, by contrast, presents little difficulty. Along that coast the coastal water and immediately adjacent slope water are moving in a south-westerly direction (Fig. 3). Recent Discovery II work (Swallow, 1957) has confirmed the hypothesis of Stommel and proved the existence, 150 miles off South Carolina, of a strong south-going current (up to 8½ miles a day) deep under the Gulf Stream. This system provides a simple, rapid and direct path, and without demanding any differences of behaviour among the different eastern groups of American eels. Temperature and salinity gradients encountered on this route (Sverdrup *et al.*, 1942) are such that active migration would reinforce passive transport. The fate of the Mississippi eels need not concern us.

" We may here meet Bertin's demand (1956) for a migration theory containing all the observed phenomena of physiology and behaviour."

We do know that the European eel shows positive reactions to higher temperature, as Tucker (1959a, p. 497) states on the authority of Bertin (1956). This is well known to all fishermen and biologists who have studied the eel. The last silver eels are caught in Denmark when the season with frost starts, but the great majority are caught during the dark nights of the interlunar periods of August, September and October, and male silver eels may start migration as early as in the interlunar periods from June onwards (Otterstrøm, 1948, p. 296). In the spring the fishermen cannot use baited hooks for catching yellow eels until the water temperature reaches about 10° C, simply because the eel does not eat at lower temperatures (Otterstrøm, *loc. cit.*).

According to Matsui (1952, p. 242) the Japanese eel becomes inactive and loses its appetite when the water temperature falls below 15° C, and he advises that the feeding of stocks in eel-ponds should be stopped at temperatures below 10° C. This is in good agreement with the fact that twelve of the seventeen species of *Anguilla* are tropical and subtropical in distribution, and all of them breed in tropical or subtropical seas.

We do not know exact temperatures in relation to the behaviour of *A. rostrata*, but Bigelow and Schroeder say (1953, p. 152): " Eels tolerate a wide range of temperature. But it is common knowledge that those inhabiting the salt marshes and estuaries of our Gulf, and its tributary streams, mostly lie inactive in the mud during the winter." On the basis of this statement I feel myself justified in concluding that the reaction of *A. rostrata* towards temperature is much the same as that of the two other northern temperate eels, the Japanese and the European.

First I may mention then that temperature conditions in the Kattegat (Danish waters) as shown by Tucker (1959a, p. 496, Fig. 2) have no relation whatsoever with the migration of the European silver eels, because they do not migrate at all at the temperatures shown, 0° to 5° C.

But, most important, Tucker, maintaining that there can only be one inherited pattern of behaviour, uses this postulate in his arguments about the European eel, but forgets all about it when he speaks about the American eel.

His sentence that the fate of the Mississippi eels need not concern us makes one ask why Tucker uses so much space in arguing about the Mediterranean stock when considering the European eel; even if the observations on p. 497 should be of minor importance in the light of new and well-established facts in favour of Ekman's (1932) and Tucker's hypothesis, it might just as well be stated that the fate of the Mediterranean eels need not concern us.

But as regards the simple, rapid and direct path of the East American eel, leading to the breeding places, I fail to see its simplicity, keeping in mind that the breeding must take place above the oceanic thermocline, probably not deeper than 500 m, at temperatures of about 15°C. The deep countercurrent of the Gulf Stream off South Carolina is a true abyssal current. Instead of referring to Swallow (1957), as Tucker does, I may be allowed to cite Swallow and Worthington (1959), which was published well before Tucker's last article (1960). Swallow and Worthington write (1959, p. 444): " Southerly velocities of between 2 and 9 cm/sec were measured at a depth of 2580 m and between 9 and 18 cm/sec at 2840 m.

" The level of no motion was determined from the floats on five occasions. It fell between 1640 and 2150 m and between the potential temperature surfaces 3·43° and 3·68°. "

So Tucker, assuming that the American eel, like the European, shows positive reactions to high temperature and salinity, disregards the fact that the American eel, in order to take advantage of the deep

countercurrent of the Gulf Stream, will have first to head for higher temperature and salinity, then to dive to abyssal depths with a very low temperature and salinity, and finally to rise again to the level about 500 m below the surface with water of a higher temperature and salinity.

I do not intend to discuss fully how the American and European eels may find their breeding places, but will only refer to Hasler's excellent review (1956). After mentioning his experiments with the minnow which can smell the difference between water from Georges Bank and samples from the Sargasso Sea, he writes (p. 461): " Salinity, gases, or odors at any one place at sea seem to me to be signals that would be more meaningful as appropriate cues for informing the fish it is, for example, in a place to spawn, and not for directional orientation. To help in reaching a distant goal, the edge (sheer) effect presumes that the fish might follow the border of two water masses, but it leaves unexplained what might direct it straight ahead or the reverse." In the case of the eel he says (p. 462): " It might be conceivably stimulated by differences in sheer between the Gulf Stream and the water masses on each side. But more likely a chemical difference might also serve as signals, in which case by swimming straight ahead, with the odor of the Gulf Stream on the left, it could arrive in the vicinity of the spawning grounds of the Sargasso Sea."

I would also like to call attention to Waterman's (1959) paper on animal navigation in the sea. He reminds us (p. 253) of experiments showing that aquatic animals can use the Sun and perhaps the Moon for determining compass directions, as do many terrestrial animals, and he also mentions the possibility of an addition to the direct effect of the Sun's image from the polarization of natural underwater illumination; furthermore that laboratory studies yielded good evidence that the fish's directional sense is regulated by an internal clock mechanism which compensates for the Sun's movement through the sky as in many terrestrial forms.

Määr (1947) has given a detailed analysis of marking experiments on silver eels, or as he very properly calls them, Wanderaale, migrating eels. A total number of 882 were marked and no fewer than 157 or 17·7% were recaptured. Määr does not study the migration speed, but a few calculations of migrations longer than some 500 km support the views of Jones (1959) and Deelder (1960) of a considerable speed, much higher than those accepted by Tucker. Tucker's low estimates may have several reasons; only one may be mentioned here, that the silver eel does not migrate between sunrise and sunset in shallow water. In the open Baltic or in the Atlantic Ocean, however, the eel

may find its preferred layer of illumination and migrate continuously day and night.

Besides discussing his own results in comparison with all earlier experiments, Määr pays special attention to the question whether the silver eel is guided by some sense of direction, and his answer is convincingly in the positive; the migration is essentially directed towards the west as seen in the open Baltic, " in der Eigentlichen Ostsee hat sie im freien Wasser immer eine westliche Richtung gehabt, mit einer gewissen Tendenz nach dem Süden " (Määr, 1947, p. 33). Naturally the migrating eel from the Baltic must at some point turn to the north for some time to get out of Danish waters, but here salinity, temperature, currents and, perhaps, the smell of oceanic water may interfere with the directional sense.

We would like to see many more experiments carried out on the silver eel, either in aquaria or by marking experiments and other observations in free waters. But with the evidence at hand it is not too difficult to see a pattern of the migration leading to the Sargasso Sea. A directional sense towards the west with a deviation towards south; a preference for a small amount of dim light, which is indicated by the behaviour of the migrating fish and by the change of visual pigment in the eye from a mixture of rhodopsin and porphyropsin in the yellow eel to deep-sea rhodopsin in the silver eels (Wald, 1958, p. 1487, with further references); a preference for a temperature of about 15°C and the hydrostatic pressure at 500 m; these factors combined can be found only in the Sargasso Sea, which in addition may attract the eel by its smell long before it reaches there.

The olfactory sense of the apodal fishes is well known to be highly developed, even to the extent that Gosline (1959, p. 161) asserts: " As to sensory systems, the eels have undoubtedly the largest olfactory surface relative to body size of any fishes, and their sense of smell is notorious." By " eels " Gosline in this connection means apodal fishes in general.

V. Why Have No Migrating Eels Been Caught in the Strait of Gibraltar?

Tucker (1959a, p. 496) writes: " The expected passage of the vast Mediterranean populations through the sharp focus provided by the Strait of Gibraltar has never been witnessed, despite much study "; Jones (1959, p. 1281) replies to this: " It is no cause for astonishment that eels are not caught in the Strait of Gibraltar, for no commercial fishing gear in use there can be expected to catch eels." Then Tucker

(1959c, p. 1282) continues: " A surprising variety of fishes, including other Apodes, have been taken in deep-sea trawls by scientific expeditions; I have before me 29 *Synaphobranchus* from a single haul of an Agassiz trawl at 1300 metres." And further: " I did not write of ' commercial fishing gear ' in the Strait of Gibraltar but of an ' intensive study '; still more explicitly, scientific investigations by Danish, French, and Monagasque expeditions."

With an intimate experience of the gear used by the Danish expeditions and having been on board when they were used in the Strait of Gibraltar on four occasions I can state that no one on board ever dreamt about catching migrating eels in the stramin-nets intended for catching eel larvae, and that no other gear was used. Nor does any French or Monagasque publication indicate that suitable gear was ever used.

In fact a trawl which could catch the migrating eel in the Danish waters has still to be invented. The fishing of the bottom-dwelling yellow eel is a characteristic feature of the Danish eel fishery, but all experiments aimed at catching the pelagic migrating eel with a kind of trawl have been failures; such eels are taken in all sorts of traps.

Ehrenbaum (1930, p. 171) has commented on this problem (translated from German): " Outside the Skaw no marked eels have been recaptured, as in general the capture of eels in the open North Sea, not to speak of the ocean, is extremely rare.

" Probably the migrating eel swims at moderate or changing levels above the bottom. In recent years, when German trawlers have used a trawl, which only lightly touches the bottom, for catching the herring, eels are occasionally caught; thus e.g. on 18 November 1924, N. of the Skaw in 90 and 180 m of depth, and on 20 December 1924 not far from the Swedish coast off Vinga."

Using the same kind of gear as used for catching the yellow eels in Danish waters, but in bathyal and abyssal depths it is easy to catch the bottom-dwelling *Synaphobranchus*, as I have experienced also in the Indian and Pacific Oceans. So Tucker's reference to the capture of twenty-nine *Synaphobranchus* is no surprise, but not to the point, because so far there is no evidence that a trawl, which was not towed along the bottom, ever brought up a single *Synaphobranchus*.

If the silver eel migrates at depths of 180 m, as the German observation may indicate, it may even be carried out of the Mediterranean by the out-flowing current in the Strait of Gibraltar (Schott, 1928, p. 158, Fig. 10).

VI. The Return of the European Eel to the Sea

Tucker's statement (1959a, p. 496): " Differences between morphological and physiological states of the European and American eels on their descent to the sea are remarkable in a context quite apart from taxonomy. The European eel is already well advanced towards being a reproductive oceanic fish, and this despite the long journey which supposedly lies before it. The American eel, with a much smaller distance/time to go, is yet relatively retarded. The two conditions are the reverse of what any reasonable consideration of adaptive characters and natural selection would predict."

In support of this, Tucker firstly claims that the American eel is on average a larger and four-times heavier fish.

Tucker cites only Vladykov (1955), who has studied the female eels from the province of Quebec, Canada, one of the northernmost ranges, where the American eel is fairly frequent (Schmidt, 1909, p. 125). Vladykov has seen a female of 13 lb 5 oz, but also gives the average weight of 1500 adult females as close to 3½ lb (1585 g), with an average length of 36 in (91 cm). These are certainly large eels, but they do not represent any typical population; it is much more likely that this is the case with specimens from the Gulf of Maine or Chesapeake Bay. Hildebrand and Schroeder (1928, p. 115) have given the length and weight in a series of which the two largest eels are 30 in (76 cm), 44·5 oz (1276 g) and 30·1 in (76 cm), 33·9 oz (960 g).

But without entering into too many details I would just like to cite Bigelow and Schroeder (1953, p. 151): " Eels are said to grow to 4 ft (122 cm) in length and to 16½ lb (7460 g) in weight. Full-grown females average only 2 to 3½ ft (61 to 107 cm), however, and males are smaller. Any eel more than 18 in (46 cm) long would probably be a female, and one more than 24 in (61 cm) in length would certainly be one. The smallest males are about 11 to 12 in (28 to 31 cm) long, females about 18 in (46 cm)." (The metric values added by me.)

This may be compared with the conditions of *A. anguilla* in Denmark; Otterstrøm (1914, p. 308) says (translated from Danish): " The eel is said to reach a length of 150 cm and perhaps even a little more and a weight of about 6 kg. Eels larger than 120 cm, 3 kg, are rare, at least in Denmark (Saltbaekvig, 1909, 123 cm, about 4 kg). The full-grown females are at least 42 cm; usually they are 40 to 90 cm and weigh 1 to 1½ kg; males are very rarely longer than 50 cm (the largest known was 51 cm) and weigh at most 250 g; the smallest full-grown males observed were 29 cm."

Some figures from the Mediterranean may be mentioned. Heldt

(1931), speaking about the silver eel, writes (p. 21): " Pour le lac de Tunis, par exemple, on est sûr d'avoir, en début de saison, une grande majorité de petits exemplaires: anguilles de 30 à 40 cm, d'un poids de 50 à 100 g, et qui constitueront aussi la presque totalité des prises. Puis des individus plus grands sont capturés: 40 à 60 cm, 100 à 400 g, et enfin de très gros sujets, long d'un mètre et plus et pesant 1 ou 2 kg. En Algérie, par contre, le lac Fezzara, en communication avec la mer par la Seybouze, fournit presque exclusivement de grosses anguilles d'un kg et plus; le lac Melah donne regulièrement 50% d'anguilles moyennes d'environ 300 g et 50% de grosses anguilles de 80–90 cm, d'environ 1 kg."

In lake Tunis the smallest group comprises mostly males, and it is interesting to note that the small males depart before the bigger females, and that the biggest females are the last to leave for the ocean; this is in very good agreement with Tucker's argument (1959c, p. 1282) that larger individuals are faster swimmers, except that he uses it about *A. anguilla* versus *A. rostrata*, under the wrong supposition that *A. rostrata* is essentially larger than *A. anguilla*. For comparison of length–weight I cite some figures from Gandolfi-Hornyold (1930, p. 34): 96 cm—1675 g; 99 cm—1620 g; 99 cm—2210 g: 100 cm—2190 g; 101 cm—1780 g; 101 cm—1890 g. These figures also show a very great variation of weight of fish of the same length.

Much more material has been published, but I have only wanted to show that there is no very great size difference between the two species, and that Tucker has also neglected to discuss the fact that *A. rostrata* males are just as small as the European.

Next, Tucker is totally wrong about what the terms silver eel and bronze eel mean when he thinks that in *A. anguilla* the silver eel is more advanced than the bronze eel. My own experience only confirms Svärdson's (1949) and Rasmussen's (1952) observations, which clearly state that it is just the opposite; or as Svärdson sums it up, we should distinguish between four different stages of the eel:

1. Larval stage (Leptocephalus stage)
2. Yellow stage
3. Silvery stage
4. Nuptial stage

Svärdson has observed two females and two males in what he calls partial nuptial dress, and Rasmussen reports on two females. Naturally, nobody knows so far what is really the nuptial dress, the more so because in none of them were the gonads essentially more advanced than in the normal silver eel. In any case these large-eyed bronze eels

are very striking in appearance and therefore reported by the fishermen, so we can safely conclude that they are extremely rare, considering the thousands of tons of silver eel caught in the Baltic area every year.

Vladykov (1955) assumes that the bronze eel stage in North America corresponds to that of the silver eel for the European species. I would suggest rather that it is more advanced, but no decision can be made without a study of the egg-diameter in relation to the change of colour before and during the migration. I have seen ten live bronze eels, received through the kind assistance of Dr. Vladykov, and they certainly were more advanced than the European silver eel. The egg-diameters were from 0·20 to 0·35 mm in four specimens, which died within 27 days after their arrival from Canada, while those of the European silver eel very rarely exceed 0·20 mm.

Tucker (1959a, p. 496) mentions that the eel shows positive reactions to higher temperature and salinity and continues: " there can be only one common inherited pattern of behaviour, yet this has hitherto been assumed adequate to direct the return journeys of eels leaving points all over Europe and North Africa and successfully traversing a great variety of conditions to a common oceanic terminal."

We may agree with Tucker that there can only be one inherited pattern of behaviour; but it may very well be much more complicated than we think.

As has been long known, the elvers (glass eels) work their way towards brackish or fresh water and against the currents; this may be observed anywhere in the world where *Anguilla* occurs. Later on, when the yellow eel has turned into the silver eel, they leave the brackish water or fresh water and go for oceanic salinities. But not always so: Nature has made the great experiment of testing the eel towards higher salinities than those of the ocean. We may cite Heldt and Heldt (1928, p. 7): " En ce qui concerne le lac de Tunis, les conditions hydrologiques sont tout autres. Aucun apport d'eau douce ne se fait dans ce lac où, par contre, l'évaporation concentre en sels une masse d'eau peu profonde etalée sur une grande superficie." But lake Tunis produces every year up to 110 tons of silver eel (Gandolfi-Hornyold, 1930, p. 6), and Heldt and Heldt (1930) have shown how the elvers enter (p. 7): " La plus frappante est que, normalement, les civelles marchent dans le sens du courant, soit qu'il entre, soit qu'il sorte. Elles se laissent porter par lui. Il est rare qu'elles se présentent debout au courant que leur vigueur pourrait aisément remonter. Nous n'avons noté le fait qu'à de rares occasions et particulièrement lors de nos premières observations, ce qui nous fit prendre d'abord l'exception pour la règle générale.

" Il est en outre très net que, si les courant qui entrent portent souvent des civelles en grand nombre, il est exceptionnel d'en trouver en quantité notable, aux abords du lac, par courant sortant." On several occasions Heldt and Heldt caught from 2000 to 4000 elvers in 2 to 3 hr, and once 10 000 in 1½ hr, but with an outgoing current they most often caught none at all, and only on two occasions more than 50, namely 300 and 400.

I have repeatedly visited lake Tunis and been shown the elvers by Dr. Heldt and Madame Dr. Heldt, who also demonstrated how literally every single silver eel was caught when the elvers had grown up. Heldt (1931, p. 23) describes the departure: " Dans les lacs côtiers, commes aux estuaires, l''appel du large' est nécessaire pour décider les reproducteurs à prendre la mer. Il faut que l'eau de l'Océan les vienne baigner, les sollicite, les dirige. Il faut du gros temps, une nuit obscure et un courant de flot. Si ces conditions se produisent au moment favorable, la passe sera bonne. Des lacs se vident ainsi en quelques nuits de toutes leurs anguilles matures. C'est par centaines de tonnes qu'on les capture alors dans nos lacs de l'Afrique du Nord."

If for nothing else these observations, together with the well-known fact that the majority of males grow up only in waters of a salinity higher than about 10 parts per thousand, should have made Tucker hesitate writing (1959a, p. 498): " The evidence shows that the debility of the (European) eel which is obliged to drift passively downstream in the current is due to demineralization of the starving body at the inception of gonadial and other hormone activity, and that re-mineralization and resumed liveliness occur when the eel reaches the sea."

I have seen thousands and handled hundreds of silver eels, from fresh water, brackish water and sea water as well, and can fully confirm the statement of D'Ancona (1959, p. 1405) and J. W. Jones (1959, p. 1281) that the European silver eel is " vigorous, extremely energetic and in good condition." But Tucker (1959, p. 1282) is not " subdued by Dr. Jones's experience with thousands of eels. The great curse of the voluminous work upon eels, upon the Salmonidae and upon sundry other animals, has been that too much of it has been mechanical and repetitive, replete with experiments unintelligently planned and mountains of data inadequately pondered, parochial alike in the range of its geographical experience and in its isolation from relevant literature from alien countries and related disciplines."

This is just after citing Keys (1933) whose experimental results are used as a support for Tucker's ideas, but Krogh (1939, p. 150) has called attention to the fact that Keys unfortunately did not pay any

attention to the urine production, when discussing the change in weight taking place in eels transferred from fresh to salt water.

Apart from the facts from lake Tunis and the male silver eels in brackish water, experiments—which I find intelligently planned—have definitely shown that neither a dehydration nor a demineralization of the female silver eel in fresh water is a fact in the normal play of Nature (Koch, 1949; Fontaine and Koch, 1950). In passing I have been permitted to cite Prof. Koch's recent letter to me: " Not a single one of the silver eels that I manipulated in Denmark did show any sign of weakness. Some of the specimens came from the fresh-water of the lake Furesö, other ones were caught in the Baltic. Afterwards I had many specimens caught in the Meuse and Scheldt in Belgium and they too were very vigorous. The same remark was made to me for fresh-water silver eels by Miss W. Frost (Windermere) and Miss R. M. Lowe who at Windermere (in the English Lake District) manipulated a very large number of specimens caught in the Lake District on their down-stream migration. Even after having been kept without food for months in fresh water, silver eels are still very strong, as I saw myself in Belgium."

It is also important to note that the European eel sometimes starts its migration towards the sea before it is in the typical silver phase (Frost, 1946, pp. 47–48). Frost has made observations on all eels caught in a trap fishing the whole width of a stream which is the outflow of a lake: " Some of the eels caught, although clearly seaward migrants, had not developed fully these characteristics but were turning from the yellow to the silver phase. When the trap was first used no distinction between the fully silver and the transitional form was made, although later the two forms were distinguished, with the result that of the 60 migrants containing food 21 (18♀ and 3♂) may be taken as silver eels, the remainder being in the transitional forms, although probably including some silver specimens."

This does provide some evidence that the silver eel takes food on its migration towards the sea, and, therefore, this is another proof that it is not in a state of debility as Tucker (1959a, p. 498) asserts.

Tucker (1959a, p. 500) cites Callamand and Fontaine (1942) in support of his view that the debility of the female silver eel is due to demineralization. This is only possible if Tucker can prove that Koch (1949) is wrong when he shows that the apparent dehydration is only due to the deposition in the muscles of an increasing amount of fat which is a non-solvent phase for water. If the degree of hydration is calculated relative to the amount of protein present in the muscles, there is no difference between a yellow and a silver eel, whether from fresh water or

sea water. Nor did Koch find any sign of demineralization in the female silver eel, when leaving fresh water and freshly caught.

Fontaine and Callamand, in fact, reviewed the problem about demineralization on the female silver eel in a paper (1948, p. 318) of which it is sufficient to cite their comparison of new experiments with earlier ones: " Toutefois l'intensité de la déminéralisation du milieu intérieur nous était apparue, sur ces séries, en liaison directe avec développement pondéral des ovaires. Ce n'est cependant pas là une règle générale. En effet, au cours de l'hiver 1947–48, nous avons reçu du lac de Grand Lieu des Anguilles jaunes et des Anguilles argentées sans qu'apparaissent des différences significatives entre les unes et les autres. Les chlorémies étaient assez variables, comprises entre 4 et 7 grammes ‰ (Toutes les valeurs sont exprimées en NaCl ‰), mais les valeurs obtenues sur les Anguilles jaunes et les Anguilles argentées étaient étroitement mêlées. Ainsi, l'hypochlorémie n'est pas une caractéristique biochimique obligatoirement liée à l'argenture de l'Anguille et à sa transformation en Anguille argentée."

Again, if Tucker had cited only just the last sentence, all his arguments about this problem would have given his readers a more correct impression about the facts.

Fontaine and Koch (1950, p. 302) also explain the findings of Callamand and Fontaine (1940) and Callamand (1943). Fontaine and Koch also found a demineralization, when female silver eels are kept in fresh water without food for 4 to 5 months. But, as they point out, this is the situation first observed by Fontaine and Callamand, a consequence of two factors working towards the same result:

1. The absence of alimentary contribution of mineral matter because of the starvation.
2. The non-existence in the eel of an extra-enteral mechanism for the absorption of mineral ions (Krogh, 1937).

Tucker (1959b, p. 1406) finds important support from Schnakenbeck's (1934) and Berndt's (1938) descriptions of autolysis and phagocytosis of the gut. The fact is, however, that nobody has ever found a high mortality of silver eels which could be ascribed to malfunction of the gut as an osmo-regulatory mechanism in salt water.

As Tucker (1959a, p. 497) points out, mass-mortalities of eels have been observed; but instead of mentioning a case from 1655 (Nicoll, 1836, **2**, p. 234, *fide* Tucker) and 1914 (Mazzarelli, 1914) it seems to me that some of the many later cases where the cause was examined should have been included. In 1655 very little was known about the biology of the eel, but we now know that cold winters may kill immense num-

bers of eels (Johansen, 1929). The eel is simply the species of the Danish salt-water fishes which suffers most from severe winters; several other species, like *Gobius niger* L., *Coryphopterus flavescens* (Fabricius), *Solea solea* L. and others, may also suffer, but the important point is that *among the eels both silver eels and yellow eels are killed.*

Furthermore, bacterial diseases quite often cause mass kills, and great losses to the fishermen (Bergmann, 1909, 1912; Schäperclaus, 1927, 1934; Bruun and Heiberg, 1932, 1935; Nybelin, 1935).

Tucker (1959a, p. 497; 1959b, p. 1406) seems to assume that the European eel dies off mass-wise not very far from the coasts; Schnakenbeck's (1934) specimen, with complete occlusion of the vent, from the North Sea " is to be taken as representing the state attained in European continental waters by eels which survive thus." In view of the many marking experiments, showing recaptures of eels which have migrated 500–600 nautical miles, this seems a rather sweeping statement, also because Schnakenbeck's specimen was only one out of four, and that nobody else ever reported on a similar specimen.

If there really were a mass-mortality in European continental waters, not least in the North Sea and the English Channel, such a yearly occurring phenomenon would certainly have been observed. In nature weaklings and dead animals are rarely left to rot on the sea-floor; they are eaten. This has, in fact, also been reported after cold winters in Denmark. Johansen (1929, p. 91) reports a remarkable case of a cod (*Gadus morrhua* L.), 89 cm long, containing eight large eels; this is remarkable because the cod generally cannot catch large eels, so they must have been weakened by the cold. Johansen also cites a letter from a fisherman, who states: " The eel is the fish which suffers most here during ice-periods. When fishing operations are carried on with the Danish seine or otter seine on the last few days before the water is covered with ice, the cod which are caught are full of eels, and feeble eels are now and then taken up with the seines. The same occurs just after the ice has gone."

The sperm-whale is no scavenger so even if Vaillant's observation (1898) is unique so far, it is not contrary to the idea that healthy silver eels do occur in the open Atlantic, in this case in the vicinity of the Azores.

Another observation pointing to a pelagic life of the silver eel is found in the classical paper of Grassi and Calandruccio (1897, p. 427), here translated from the German: " Eels . . . are also found in the stomachs of sword-fishes, caught in the Straits of Messina. They even seem to be their favourite food."

VII. Schmidt's Collections of *Anguilla* Leptocephali

Tucker (1959a, p. 499) gives the following statement: " In fairness to Schmidt, it must be said that he lacked much of the information now available and that his terms of reference from his Government were to locate the birthplace of the European eel. The '*A. rostrata* ' larvae were, to him, an unexpected nuisance. In the area now suggested as the source of the '*A. rostrata*' phenotypes the Danish Expeditions took only a score of stations (Schmidt, 1919); those of the R. V. Margrethe were worked in during November-December 1913, too late in the year, while the remainder, at miscellaneous dates and shallow depths, were worked by amateurs from commercial vessels, in a region of rapid currents and, on my hypothesis, minute deep-lying prelarvae. Closing nets were not used.

" It may be objected that '*A. rostrata*' is said to breed during January-February, *A. anguilla* during February-March (Schmidt, 1922; Tåning, 1938). Against this simple statement must be balanced the fortunes of collecting, the lengths of overall journeys from various starting-points, disparities in sexual maturation, velocities of currents at various possible migration-depths, duration of spawning periods and annual variations in all these; effects of temperature on rates of hatching and early development and rates of ascent of larvae over different parts of the spawning area. The criticism is more easily answered than made."

But Schmidt (1925, p. 307) has really given some of the answers. He was very much aware of the lack of material from the early months of the year; therefore the Dana expedition 1920-21 and the Dana II expedition 1921-22 were sent out with the following result (Schmidt, 1925, p. 307):

Table II

Leptocephali of	*A. rostrata*	*A. anguilla*
Captain Andrea (about 1865)	1	2
Trading vessels (1911–1915)	3	120
Margrethe 1913	24	714
U.S.S. Bache 1914	6	31
Dana 1920–21	1868	6446
Dana 1921–22	>400	>4500

Thus Tucker's statement gives the impression that Schmidt had only thirty-four *A. rostrata* leptocephali and 867 *A. anguilla* leptocephali from the Atlantic whereas he really had more than 2200 *A. rostrata* and more than 11 800 *A. anguilla*. In these figures are not

included the numerous *A. anguilla* leptocephali which Schmidt collected on his Thor expeditions in the Mediterranean and the adjacent seas in 1908–10 and earlier. Details of the stations of the two Dana expeditions were given by Schmidt (1929), a paper which is included in Tucker's references (1959a, p. 501).

In any case the background for Schmidt's considerations about the breeding of *A. rostrata* is that he had seen tiny larvae among the more than 2200 leptocephali examined. So he could write (Schmidt, 1925. p. 309): " The early tiny larvae, 7–8 mm long, of *Anguilla rostrata* were taken in February. In April the average length was about 20–25 mm, in June about 30–35 mm, in July about 40 mm, and in September 50–55 mm (cf. Fig. 14). Toward the end of the year the larvae have attained their full length, about 60–65 mm; metamorphosis takes place during the winter months, and in the spring the hosts of elvers move up into fresh water." And further: " From the data to hand, then, we may conclude that the American eel spawns earlier, that its larvae grow more rapidly (cf. Fig. 14), and that the full-grown larva is smaller than is the case with the European species."

Schmidt's Fig. 14 furthermore shows that a few tiny larvae of 7 mm may still be found in April, while in July the smallest is 25 mm. The position of Dana station 948, 22°14'N., 67°22'W., is also in good agreement with Schmidt's conclusion in reference to his Fig. 5: " From the position of the curves we can conclude that the breeding area of the American eel lies along the entire range north of the West Indian Islands. Its central portion lies west and south of the central breeding grounds of the European eel; the areas embraced by the two species, however, are apparently not separated, but seem to overlap." I would, however, emphasize that Dana station 948 lies well outside, towards the S.W., of the area where *A. anguilla* of any size was ever caught.

Tucker repeatedly (1959a, p. 495, p. 500) mentions the alleged finding of the eggs of the American eel by Fish (1927). These were taken near Bermuda Is. (32°02'N., 65°00'W.) by the " Arcturus " on 16 July 1925. Fish, herself, was very well aware of the possibility that she might be wrong about the identification. Happily her description is very careful, and it gives good reasons for Schmidt (1929, p. 16) and especially Tåning (1938, p. 315) to discard her identification. Bigelow and Schroeder (1953, p. 153) also doubt it. I would like to add that the " Arcturus " also caught *Anguilla* leptocephali from May to September at the same place as Fish's eggs. The sizes of these leptocephali fit very well with the picture given by Schmidt; using the figures given by Tåning (1938) it should be kept in mind that the " Arcturus " material was preserved in alcohol and therefore was more shrunken than

Schmidt's larvae, which were preserved in formalin. The " Arcturus " did not catch *A. rostrata* leptocephali until July, and then only two specimens, 39–43 mm, which is exactly what would be expected from a glance at the catch of Dana station 891 fairly near to Bermuda Is. (Schmidt, 1925, Fig. 14). That Tucker (1959a, p. 500) should consider a find of eggs so far north and lacking a concentrated oil-globule as explained by the assumption that they merely represented one of the many mistimed and misplaced spawnings, seems utterly improbable to me. The more so because the " Arcturus " also caught seven *A. anguilla* leptocephali in July, which also fitted into Schmidt's picture, but none was smaller than 18 mm, and this was a single specimen, while the rest were larger than 28 mm.

Incidentally I (Bruun, 1937, p. 9) have pointed out that Uchida (1935) also misidentified a leptocephalus close to *Leptocephalus similis* as the larva of *A. japonica*. Uchida overlooked the possibility that another genus of apodal fish might have the same number of myomeres as the *Anguilla*, as is the case with *Lept. similis* and *L. euryurus* in the North Atlantic; Uchida's larva may thus be a Pacific parallel to *A. japonica*, as are *L. similis* to *A. rostrata* and *L. euryurus* to *A. anguilla*.

VIII. Possible Temperature Effects on the Number of Vertebrae in *Anguilla*

Out of the sixteen species of the genus *Anguilla* examined by Ege (1939) *A. mossambica* has the lowest number of vertebrae, namely an average of 102·9, varying between 100 and 106. The highest number is found in *A. japonica*, with an average of 115·8 and a variation between 112 and 119. This makes a total variation of 100 to 119 within the genus.

From Table III it may be seen that *A. japonica* and *A. anguilla* represent the extreme high numbers, while *A. rostrata* in some way may be said to show a number rather close to the average number of the rest of the species.

Furthermore it may be noted that only in *A. bicolor* the subspecific difference may be about 2.

I do not want to discuss in detail whether one may be justified in expecting that the variation of the number of vertebrae should be directly proportional to the total number of vertebrae, when comparing species of higher taxons than a genus. Tucker (1959a, p. 498) supposes this when comparing *Salmo trutta* (order Isospondyli) with *Anguilla anguilla* and *A. rostrata* (order Apodes). I would just mention

TABLE III. Average numbers of vertebrae in the species of *Anguilla*. Fractions disregarded. (After Ege, 1939.)

Average no. of vertebrae	*Species or subspecies*
116	*japonica*
115	*anguilla*
114	
113	*australis australis, dieffenbachi*
112	*australis schmidti, megastoma*
111	*nebulosa labiata*
110	*bicolor bicolor*
109	*nebulosa nebulosa*
108	*reinhardti*
107	*rostrata, bicolor pacifica*
106	*borneensis, marmorata*
105	*interioris*
104	*obscura*
103	*mossambica, ancestralis, celebesensis*

that *Zoarces viviparus* (order Percomorphi) is an example showing that this is not the case. In Danish waters it has been shown (Schmidt, 1917; Ege, 1942) that *Zoarces viviparus* cannot be divided into well-defined geographical subspecies; there is a great variation even within the Danish waters, even so great that they represent the highest and lowest values found within the whole geographical range of this species, West and North European coasts. The lowest number found is 100 and the highest 125 (Ege, 1942, pp. 281–282). This means that the species *Zoarces viviparus* has a greater variation than all species together of the genus *Anguilla*.

If any conclusion may be drawn from this it would be that number of vertebrae in the species of the genus *Anguilla* are less affected by variations of the environment than in the single species of *Zoarces*.

A few examples of the variation in the number of vertebrae may show this quite clearly. *A. marmorata* (Quoy and Gaimard) has a geographical distribution right from S.E. Africa and Madagascar across the Indian Ocean to Indonesia and Taiwan, and farther in the Pacific to the Marquesas Is. Yet the total variation in the number of vertebrae in this huge area is only between 100 and 110, the average extremes being 104·6 (136 specimens, Celebes) and 106·4 (162 specimens, Tahiti). These figures are given by Ege (1939, p. 73). Other large samples from Réunion and New Guinea are in between, as also smaller samples from many places, except eight specimens from the

Marquesas having 106·9, but this is naturally not statistically significant.

These general observations may serve as a background for the following.

With Tucker (1959a, p. 498) we may assume that *Anguilla* shares the common susceptibility to factors, such as temperature, as has been shown to influence the number of vertebrae in other fishes, like *Zoarces* and *Salmo* (Schmidt, 1920, 1921; Tåning, 1952).

Schmidt (1927, 1928) was aware of this when he divided *Anguilla australis* Richardson into two geographical races, an eastern one from New Zealand, and a western from East Australia. After Schmidt's death, Ege (1939) worked this up in greater detail, showing that the eastern race, *Anguilla australis schmidti* Philipps, has on an average 111·7 vertebrae (1666 specimens) and the western race, *A. australis* Richardson has 112·6 (559 specimens). Similarly the Indian Ocean population of *A. bicolor bicolor* McClelland, distributed from East Africa, India, and Java to N.W. Australia, has 109·5 vertebrae (1251 specimens from nine localities in the whole range of distribution) and the Pacific population, *A. bicolor pacifica* Schmidt, distributed from Celebes along the north coast of New Guinea, has 107·1 vertebrae (324 specimens from four localities in the whole range of distribution). This is what would be expected in a species of fish with several breeding places, but it is certainly in sharp contrast to the conditions in the two North Atlantic species, *A. anguilla* having 114·7 vertebrae and *A. rostrata* 107·2 vertebrae. Even different year classes of *A. anguilla* show no variation as seen in Table IV.

TABLE IV. No. of vertebrae in elvers, caught at Epney, River Severn, England. (After Schmidt, 1913, p. 9.)

	1908	1909	1911
Average no. of vertebrae .	114·7	114·7	114·7
Total no. of specimens .	138	184	163

Now to assume that the differences between the American and the European eels are merely eco-phenotypical seems to me to be utterly improbable, even if only with the information above as a general background.

But even more so when we look into the details of how Tucker has combined results from experiments with *Salmo* with the observations above and the hydrography of the breeding places of the eel. When

Tucker (1959a, p. 498) writes: " Means of 56·86 and 60·06 vertebrae were obtained in batches of young from the same parents, a difference proportionally similar to that pertaining between whole populations of Atlantic *Anguilla*," he correctly refers to Tåning's (1952, p. 15) observation on temperature shock-effect, but omits to give the character of the shock and the temperatures before and after the shock at which the eggs were reared.

Tåning (1952, p. 15) gives the results of two experiments, one in which the extreme variation of average values is 58·69 and 60·12 vertebrae or a difference of 1·43, and another in which it is between 56·86 and 60·06 vertebrae; this latter is the one in the quotation from Tucker above and is the very extreme example of all Tåning's experiments.

Tåning had two control samples, one reared at 2·7°C averaging 58·38 vertebrae and one at 12°C averaging 59·36 vertebrae.

Now the great difference, cited by Tucker, of 3·20 vertebrae was only obtained in a very special way. The batch with 56·86 vertebrae was first reared at 2·4°C until the sensitive period, then exposed to a shock treatment of 20 day-degrees, or about 30 hr, at 16°C, and then again reared at 2·4°C. The other batch averaging 60·06 vertebrae was first reared at 12°C, then in the sensitive period exposed to 20 day-degrees, or about 177 hr, at 2·7°C. In short, the extreme result was only obtained if the eggs were reared at a certain low temperature, then in the sensitive period suddenly exposed to a quite different, very high temperature in a rather short time, after which the eggs were moved back to the original low temperature. These are conditions which cannot possibly be similar in any way to temperatures influencing the eel eggs during their development.

Here I would like to cite Schmidt (1929, p. 16): " The larvae recently emerged from the ova (praelarvae and quite young larvae) are extremely fragile, so much so that the majority undoubtedly perish in the nets even under the most favourable weather conditions, and our hauls therefore are not likely to present a true picture of the quantitative proportions between praelarvae and the somewhat larger larvae. Of the European eel, we have comparatively many praelarvae and quite young larvae, in which the oil globule of the yolk sac has not yet been resorbed. These are found somewhat deeper down than rather older larvae, but still in what may relatively be called surface strata, abt. 200–500 metres down."

This means that the number of myomeres in the larvae are so well developed that they can be counted and thus a distinction be made between *A. anguilla* and *A. rostrata* larvae; and furthermore that we

are at most allowed to consider temperature occurring between the oceanic thermocline, at about 10°C and 200–500 m below the surface; the hundreds of thousands of leptocephali of species of the order of eels, Apodes, have always been caught in the oceanic thermosphere, the upper layers of the ocean warmer than about 10°C (Bruun, 1947, pp. 164–165); even leptocephali with tubular eyes, like those belonging to the deep-sea eel *Synaphobranchus* live in the thermosphere (Bruun, 1937). But it is likely that the larvae of the genus *Anguilla* are hatched well above the oceanic thermocline, firstly because, as mentioned above, the newly hatched larvae were actually found between 200–500 m, and secondly because the temperature preference of *Anguilla* is probably at least 15°C. As may be seen from Schmidt (1929) and Jacobsen (1929) 15°C was found about 500 m below the surface all over the area where the Dana found the tiny larvae of both species of *Anguilla*. If we take the actual observations made in the area on the stations in the area from Schmidt (1929), we get Table V.

TABLE V. Temperature observations at the surface, 700 m, 500 m and 200 m (°C).

Station No.	*Date*	700 *m*	500 *m*	200 *m*	*Surface*
1239	11. ii.1922	10·9	14·70	20·76	23·42
1241	13. ii. 22	12·5	16·35	21·43	23·92
1261	9.iii. 22	9·5	13·32	19·83	24·83
1319	26.iv. 22	10·3	14·36	19·93	24·51
1321	28.iv. 22	10·8	13·88	18·57	23·37
1322	30.iv. 22	11·5	15·46	18·95	22·25
1333	6. v. 22	11·6	15·15	18·11	23·01
1335	8. v. 22	12·5	15·95	18·39	22·56

This agrees fairly well with the picture given by Tucker (1959a, Fig. 4), except that no newly hatched larvae have been taken north of 28°N.; his suggestion of spawning taking place right down to 700 m can only be founded on Fish's wrong identification of four eggs from an open net which had been down at 500 fathoms. But furthermore the temperatures below 500 m are probably too low, only about 9 to 12°C or well below the preference of *Anguilla*. But apart from this Tucker's conclusions are against the observed facts. He says (p. 498): " Assume a linear spawning area extending from 20–30°N. and at a depth (400–700 m) below the influence of surface currents. Eel eggs, rising through the lower layers, will encounter a substantially identical temperature

gradient until they strike the 18°C isotherm at about 300 m. From then on several conditions become differentiated simultaneously, roughly in relation to latitude. Eggs and larvae at the southern limit pass through the gradient 18–25°C during the last 250 m ascent; in particular, they encounter an abrupt 4° rise between 200 and 100 m which may well have the effect of ending segmentation and so fixing the number of somites/vertebrae in the range 103–111 recognized as typifying '*Anguilla rostrata* '.

" At the northern limit, however, the temperature gradient remains gradual right up to the surface, where a maximum temperature of barely 20°C is encountered. No temperature effect, certainly no shock effect, is likely, wherefore the addition of somites presumably continues to the genetically determined limit and results in the population with 110–119 somites/vertebrae which we recognize as '*A. anguilla* '."

As pointed out above all newly hatched larvae had the full number of myomeres, and they were caught between 200–500 m, never in nets fishing closer to the surface; I may add that even older larvae are never caught close to the surface, but always at about 25 m or deeper. Tucker's remark that closing nets were not used does not disqualify these statements because the newly hatched larvae were only caught when the nets had been down between 200 and 500 m, and older larvae were only caught quite rarely if the nets had not been down at 25 m or deeper. Finally I may add that there is no indication of any sort of a secondary thermocline anywhere which could possibly cause some shock effect even of the type mentioned by Tåning (1952, p. 15); here Tåning had two control samples, one kept at 4°C averaging 58·94 vertebrae, and one at 10°C averaging 59·60 vertebrae.

By transferring a sample, first reared at 4°C, in the sensitive period to 10° and keeping it there he obtained an average of 58·69, or only 0·25 vertebrae lower than the sample kept for the whole time at 4°C.

Apart from this slight lowering of the average number of vertebrae, far too small to satisfy Tucker's idea, it is impossible to imagine that there would be a sharp limitation between the conditions in the sea creating Tucker's imaginary shock and where they do not exist. The distance between 20°N. and 25°N. is 300 sea-miles, so the slope of the isotherms is in fact very gradual, and if Tucker were right we would have very many intermediate figures, making it impossible to distinguish between the two species of leptocephali.

Therefore I fail to see any support for Tucker's main assumption, that the difference between the American and the European eel is only eco-phenotypical. Field studies and experiments are both against it.

IX. Parallel Cases among North Atlantic Apodes

While studying the leptocephali of the two North Atlantic species of *Anguilla*, Schmidt at the same time collected probably at least 100 000 specimens of leptocephali of other species of Apodes. He published many studies on these; but here we may only discuss his findings as regards the two North Atlantic species, *Conger conger* and *C. oceanicus* Mitchell (Schmidt, 1931).

Schmidt had about 2500 larval *Conger* and gave the number of myomeres in 201 *C. conger* as varying between 154 and 163, average 158·2, while 288 larvae of *C. oceanicus* showed 140 to 149, average 144·6 myomeres. The distribution of the leptocephali of the two species is a striking parallel with that of the two species of *Anguilla*, except that *Conger conger*, as Schmidt points out, breeds along the whole extent of the area from the Sargasso Sea to the eastern part of the Mediterranean; throughout this extent he found tiny larvae, only 10 mm in length, always over great oceanic depths. As to *C. oceanicus*, Schmidt found quite tiny larvae in the West Indies, indicating a breeding place there.

From this it is obvious that *Conger* requires a much less special environment for its spawning than *Anguilla*. This is also borne out by the fact that Schmidt found leptocephali of a third species of *Conger* in the South Atlantic, off Argentine, where no *Anguilla* species occurs.

Tucker (1959a, p. 497) states: "In the Mediterranean, again, are several deeps which offer conditions apparently identical to those of the Sargasso, yet eels do not spawn in them nor anywhere in that Sea. In the open Atlantic the Cape Verde Basin, Monaco Deep and West Indian Basin, all on the obvious migration route, are likewise devoid of young larvae."

It is very easy to show that all these areas each have quite characteristic features of their own; it is in fact more easy to point at differences than at similarities in their hydrographic structures. For the time being we can only consider *Conger* and *Anguilla* as one example out of very many which discriminate in different ways in the choice of breeding places.

In 1937 I added two more cases similar to *Anguilla* and *Conger*, namely that of *Synaphobranchus kaupi* Johnson and *S. infernalis* Gill and of the two very closely related *Leptocephalus* species *L. euryurus* Lea and *L. similis* Lea.

The parent species of the two last mentioned species are not known with certainty; but as regards the adult *Synaphobranchus* I definitely know that they are of bathyal and abyssal distribution; so it is no wonder that the bottom-dwelling adolescent and adult stages have

partly overlapping distributions. Both species breed in the Sargasso Sea close to the West Indies; the parallelism to the two *Anguilla* species is found in the maximum size of the unmetamorphosed leptocephali, being about 90 mm in the western species, *S. infernalis*, and about 120 mm in the eastern species, *S. kaupi*. Furthermore the duration of the leptocephalus stage is about 8 months in *S. infernalis* and about 20 months in *S. kaupi*. The number of myomeres counted in 40 *S. infernalis* was 131–140 and in 262 *S. kaupi* 143–154.

Tucker (1959c, p. 1283) has commented on this as follows: "*Possible parallel cases.* Bruun (1937) has commented on the hitherto unexplained coincidence that, of four pairs of Atlantic apodal ' species ', having distributions roughly similar to those of the two types of *Anguilla* larvae and, moreover, larvae which can be taken ' at the same place and same depth within a certain area of the Sargasso Sea ', the American ' species ' of each pair has the lower number of vertebrae (Table 1). This situation may well be due to a common eco-phenotypy rather than to coincident genetic effects.

" TABLE 1. Numbers of Vertebrae or Myomeres in some North Atlantic Eels, mainly after Bruun (1937).

	East Atlantic	*West Atlantic*
Anguilla anguilla	110–119	—
Anguilla rostrata	—	103–111
Conger conger	154–163	—
Conger oceanicus	—	140–149
Synaphobranchus kaupi	143–154	—
Synaphobranchus infernalis	—	131–140
Leptocephalus euryurus	111–119	—
Leptocephalus similis	—	104–113 "

This table is identical with Table 10 of Bruun (1937), except that I had used the Figures given by Schmidt (1915, Table II) for two random samples of 266 specimens of each of the two *Anguilla* species; Tucker, more correctly, has given the full variation, probably from Schmidt (1913), thus adding the two very rare variants of 110 in *A. anguilla* and 103 in *A. rostrata*. But this does not alter the picture in any way. In *Synaphobranchus* and *Conger* there is no overlapping whatsoever in the numbers of myomeres or vertebrae, while there is a very slight one in the two other genera; in *Anguilla* and *Synaphobranchus* there is a certain horizontal overlapping of the breeding places, as also for

Conger. To what extent there is a vertical overlapping is not known, but Tucker's hypothesis, that each of the genera is represented by one species only, excludes the possibility that the eastern and western species might have different preferences as to temperature when spawning, hence spawning at different levels. It seems impossible to understand the case of the two *Conger* species without assuming the existence of two well established species. About *C. conger* we know that we have at least two well-defined breeding populations, one Mediterranean and one Atlantic (Schmidt, 1911). But nothing indicates that the Sargasso Sea spawners of *C. oceanicus* should be the parents of the leptocephali of *C. conger* occurring in this area. So here it seems quite impossible to agree with Tucker that this situation may well be due to an eco-phenotypy rather than to genetic effects. But if this is so, *Synaphobranchus* can be no different; never have any experiments shown shock effects of a magnitude such as the differences in the numbers of vertebrae in the two species of *Synaphobranchus*, not to speak of the *Conger* species.

So when *A. anguilla—A. rostrata* and *Leptocephalus euryurus—L. similis* are considered, it seems most logical to consider them as parallel cases in the sense that they also represent pairs of genetically different populations, and that they may not well be due to a common eco-phenotypy as Tucker suggests.

X. Other Species of Apodes Breeding in the Sargasso Sea

Out of the many thousands of leptocephali collected in the North Atlantic by Schmidt's efforts, only a few species more than hitherto mentioned have been examined.

One of them was treated by Schmidt himself in four papers (1912, 1930, 1931 ; Schmidt *et al.*, 1932); this was the leptocephalus of *Nessorhamphus ingolfianus*. " *Nessorhamphus ingolfianus* must be one of the commonest species of the North Atlantic. We have not yet counted up the total number of larvae of this species from all our cruises in the Northern Atlantic, but I may mention, that on the summer cruise of 1920 with M/S Dana I, no fewer than 4163 specimens were taken (against 5959 of *Anguilla vulgaris*).

" *Nessorhamphus ingolfianus* spawns in the Sargasso Sea at the same period as the Eel, i.e. in spring and early summer, somewhat later in the east than in the west, and the metamorphosis of the larva takes place especially in the months of August, September, and October." (Schmidt, 1930, p. 374). For this species Schmidt also identified the egg, and hatched the larva, and was thus able to make firm connection

with the larger leptocephalus, which he could follow through metamorphosis stages to at least adolescent specimens; the type specimen, caught mesopelagically, is 249 mm in length.

For our discussion the important point about this species is that, although breeding in the same area in the North Atlantic as the geminate species of *Anguilla*, *Conger*, *Synaphobranchus*, and *Leptocephalus similis—euryurus*, there is one and only one species in the North Atlantic; its number of myomeres being 150–160.

In fact, one could also speak about geminate species in *Nessorhamphus*, but here the breeding places are totally separated, the other species in the Atlantic *Nessorhamphus danae* Johs. Schmidt breeding around the Equator and having 135–145 myomeres. And then again a single leptocephalus found in the South Atlantic indicates a subtropical population of *N. ingolfianus* corresponding to the North Atlantic (Schmidt *et al.*, 1932, p. 252). Finally we may refer to the world-wide, but sporadic occurrence in all oceans; it is equally important to note the slight variation in number of myomeres from one population to another within the same species, and that the occurrences, except for the Equatorial and South Atlantic, coincide with areas where leptocephali of *Anguilla* species also occur.

The other apodal fish to be mentioned here is *Serrivomer beani* Gill and Ryder 1883, also of a meso- or bathypelagic occurrence, while its leptocephalus is epipelagic.

Schmidt (1930, p. 374) mentions its leptocephalus, *L. lanceolatus* Strömman, as one of several other Muraenoids spawning in the Sargasso Sea, but in this case spawning takes place in autumn and winter. Bauchot (1959) has given a very detailed account of the whole material, 5624 specimens, from which it is quite clear that there is only one breeding population; the number of myomeres is 156 to 163.

It is also possible, however, here to speak about geminate species, the other species being *Serrivomer brevidentatus* Roule and Bertin 1929, and its leptocephalus *L. lanceolatoides* Johs. Schmidt 1916 with the number of myomeres of 155 to 165. Thus the number of myomeres are essentially the same in *L. lanceolatus* and *L. lanceolatoides*, but several other characters make it easy to distinguish between the two (Schmidt, 1916; Bauchot, 1959), and the smallest leptocephali were caught between April and August. Bauchot studied a total of 1653 specimens of this species. Figures 42 and 43, in Bauchot (1959), show clearly that *L. lanceolatoides* spawns farther north than *L. lanceolatus*. But none of them show the slightest sign of splitting up into ecophenotypes.

This seems in good agreement with the fact that the adults live meso-

or bathypelagically in the huge North Atlantic eddy system centering in the Sargasso Sea.

As in the case of *Nessorhamphus*, similarly distributed, the biology of the adults does not induce a segregation into a western and an eastern population.

In contrast all the species of *Anguilla*, *Conger*, *Synaphobranchus*, and *Leptocephalus similis—euryurus* lead an adolescent life as bottom-dwellers, more or less close to the coasts or the continental slopes. This opens the possibility of having two populations and in time—as it is—pairs of closely related species.

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SOME ASPECTS OF PHOTORECEPTION AND VISION IN FISHES

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I. INTRODUCTION

The most important organ for photoreception in fishes is the eye, although other photosensitive sites are known. The eye, moreover, has especial significance because it is a visual organ, capable of image-formation. Like many other organs of fishes, the eye exhibits much structural and functional variation and specialization, the features of which have been related to environmental factors to which the fishes are normally exposed.

Descriptions and reviews of the piscine eye are now available in goodly number, the latest of which by Rochon-Duvigneaud (1943, 1958) and by Brett (1957) point the way to the earlier literature. The present review does not aim at being comprehensive. I have restricted myself to several aspects of photoreception in fishes, especially marine fishes; these aspects are ones in which I am most interested or in which there have been notable new advances. In particular, I have gathered together work dealing with photobehaviour and the functioning of the eye in marine environments. I have not attempted to deal with the gathering momentum of electrical studies on the retina, which could be reviewed more profitably in conjunction with similar studies on other animals.

II. Extra-Ocular Reception

Photoreception in many fishes may be mediated by structures other than the eyes. Skin, spinal cord, brain and pineal complex are involved in various degrees. Cyclostomes are light-sensitive but the receptor-regions are not identical in different forms. Hagfish and lampreys respond to light by general or increased locomotory activity after a rather lengthy reaction period (several seconds). The hag is practically eyeless, its photoreceptors are located in the skin and occur mostly at the anterior end of the head and in the cloacal region. Afferent impulses from the posterior photoreceptors travel through spinal nerves to the spinal cord. Thence they proceed anteriorly to the brain, but local reflexes can still be elicited after spinal section (Newth and Ross, 1955). The ammocoetes (larva of the lamprey) is virtually blind whereas adults have eyes. The caudal region is especially sensitive to light; photo-receptors occur in the skin and afferent pathways lie in the lateral line nerve. The middle region of the body shows some photosensitivity, due apparently to direct stimulation of the spinal cord by light, and there is a photosensitive region in the head in the region of the pineal complex. When the head of a lamprey is illuminated, its responses are less regular and reaction times are longer than those elicited by stimulation of the tail. It still responds to illumination of the head after removal of the pineal and parapineal bodies and the paired eyes; there are obviously other photoreceptors in the head, either in the skin or in the brain (Young, 1935a).

The experimental approach just described involves detecting sensitivity of photoreceptors and determining operative pathways. On a different plane are to be considered the kinds of responses evoked by different photoreceptors. In the ammocoetes, for example, illumination of the tail initiates swimming movements leading to burrowing; in the adult, simply swimming (negative photokinesis). When paired eyes of the adult lamprey (*Lampetra*) are illuminated, however, the consequences are uneasy movements of the animal and altered breathing rates. Moreover, lampreys undergo colour-changes, controlled by incident light. The colour-response disappears in the larva and is disturbed in the adult after destruction of the pineal complex, when the melanophores become expanded, and it is completely abolished in the adult by removal of the pineal complex and paired eyes. It seems, therefore, that dermal photoreceptors of the tail are primarily responsible for generalized swimming movements (leading to burrowing in larvae); the pineal organ controls colour-responses in the larvae and pineal plus paired eyes act synergetically in controlling colour-responses

of adults. No doubt the paired eyes play other roles in phototactic and directed activities (Young, 1935a, b).

Integumentary photoreceptors are present in blind cave fishes, but none was found in marine fishes examined by Parker (1909). However, there is evidence that the pineal body (Fig. 1) or the pineal complex (which term refers to the pineal body and adjoining brain tissue) is photosensitive in many teleosts. It has long been known that the melanophores of the minnow *Phoxinus* disperse when its pineal is stimulated by light, and the pineal also influences photokinesis. Since photosensitivity is not completely abolished by destruction of the

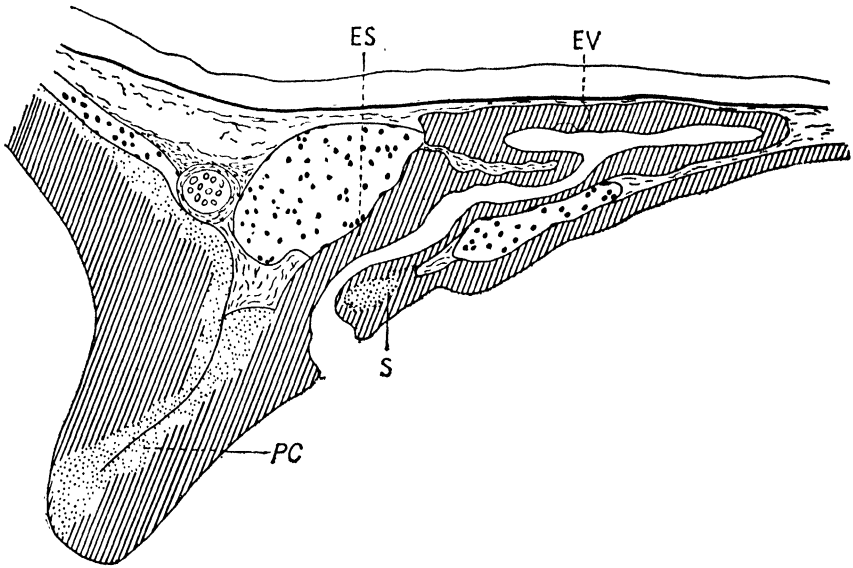


FIG. 1. Vertical section through the middle of the pineal region of the catfish (*Ameiurus*). Legend: ES, epiphyseal stalk; EV, epiphyseal vesicle; PC, posterior commissure; S, superior commissure. ×290. (From Terry, 1910.)

pineal, it has been postulated that there are additional photoreceptors in the wall of the diencephalon (von Frisch, 1911; Scharrer, 1928). Breder and Rasquin (1947) have shown that the pineal is concerned with photokinesis in blind characins (*Anoptichthys*) from caves and they (1950) have distinguished three groups of teleosts according to the character of the pineal covering. These are: (1) fishes with translucent tissue over the pineal (mostly light-positive); (2) fishes that have chromatophores on the surface of the head, which control light reaching the pineal (these fishes have changeable responses to light); (3) fishes with a permanently covered pineal area (light-negative); and some exceptions. In some fishes, which were blinded and which had the pineal area covered, light still exerted some effect, albeit to a reduced

degree. The results suggest that light was acting on some other photoreceptors, presumably in the skin.

The responses noted by Breder and Rasquin (1950) to stimulation of the pineal were photokinesis (apparently) and colour change, and responses of a like nature have been observed in sockeye salmon smolts (Hoar, 1955). The smolts showed avoiding reactions (when startled by an observer during the day, or by a light at night), negative phototaxis (or photokinesis), and colour-responses (pallor on a white background). Blinded fish showed no avoiding reaction by day, were startled by a light at night, were negatively phototactic (or photokinetic), and were darker than normal fish. Fish lacking pineal organs displayed avoiding reactions by day and by night; chromatophore-responses were variable. Fish blinded and lacking the pineal organ were very dark and were insensitive to light. The results demonstrate that stimulation of the pineal area in the salmon smolt influences the movement of pigment in melanophores and behavioural responses to light. The experiments involved variable degrees of injury to the pineal organ and to contiguous regions of the brain in some fish; a minor degree of photosensitivity not connected with the pineal organ and the paired eyes is not excluded by these experiments. Germane to this work are results obtained on frogs in which action potentials have been recorded from the pineal nerve after photostimulation (Dodt and Heerd, 1962). The responses show obvious parallels to those detected in the fish retina (p. 190), and an extension of this experimental approach to the fish pineal would be interesting.

III. Regulation of Light Reaching Sensory Surfaces

In fishes which inhabit regions where great diurnal changes of light-intensities take place, there are usually devices for controlling the amount of light reaching the photoreceptors, especially the eyes. We are concerned here with photomechanical changes; equally important, of course, are those changes in responsiveness of retinal neural elements and content of visual pigments, which come under the concept of dark-adaptation, in its more restricted meaning (Rushton, 1959).

A. *Pineal*

In many fishes the tissues in the roof of the skull over the pineal region (Fig. 1) are translucent, thus permitting light to reach the pineal organ and, perhaps, contiguous areas of the brain (see p. 173). Often there are chromatophores in the skin over the parietal foramen and, by their concentration and dispersion, they determine the amount of light reaching the pineal complex. Experiments involving removal of the

overlying chromatophores, or covering the pineal region, have produced changes in the responsiveness of *Gambusia* to light (Breder and Rasquin, 1950; Rasquin, 1958; Breder, 1959).

B. *Pupillary Movement*

Closure of the pupil in light occurs in many elasmobranchs and in a few teleosts (see Walls, 1942), and some degree of pupillary movement, albeit small, probably occurs in a great many bony fishes. Gilbert (1961) has confirmed that pupillary closure is not consensual in sharks; i.e. illumination of one eye causes closure of the pupil of that eye and not of its fellow. Young (1933a) was able to give a physiological explanation of this effect when he showed that the iris sphincter muscle of dogfish was not innervated, and it contracted in direct response to illumination. In rays (*Raia*) there is contralateral lowering of the opercular flap of an eye when the opposite eye is illuminated (Bateson, 1890b), and this presupposes the existence of a different kind of controlling system in these animals. Pupillary closure is very slight, variable and negligible in some species. e.g. *Squalus acanthias*.

Investigating two teleosts (*Uranoscopus* and *Lophius*) having extensive pupillary excursions, Young (1931a, b, 1933b) found that the responses are under the control of the autonomic nervous system. The sphincter is controlled by the sympathetic and the dilatator muscle by the oculomotor (parasympathetic nervous system). There are some species, however, notably the eel, in which there is a direct response to light, and the pupil of the isolated eye closes when it is illuminated. In these animals the pigmented smooth muscle fibres of the iris contract when stimulated by incident light. Studies of the isolated iris of the eel have shown that the action spectrum for contraction has a major peak at 500 mμ, and resembles the absorption spectrum for eel rhodopsin (Seliger, 1962).

C. *The Tapetum Lucidum of Chondrichthyes*

There is a mirror or tapetum lucidum (L. *tapete*, carpet) in the eye of chondrichthian fishes, which is responsible for the remarkable eye-shine that they exhibit. Eye-shine, of course, is most evident in those species whose pupils remain open when illuminated and in bathypelagic species with large pupils. The tapetum lucidum contains reflecting cells that lie in the inner layer of the chorioid, immediately underneath the choriocapillaris (Fig. 2). It is present in most elasmobranchs and it also occurs in holocephalans (Franz, 1905; Walls, 1942). It appears to be absent in the bathybenthic torpedo *Benthobatis* with rudimentary eyes; at least one is not mentioned by Brauer (1908). A tapetum is said to be lacking in *Laemargus* (=*Somniosus*, an abyssal shark), *Myliobatis*

(a pelagic ray) and *Selache* (a basking shark). Some of these statements stem from the early work of Brücke (1845). Nevertheless, a tapetum lucidum does exist in the Greenland shark, *Somniosus microcephalus*, and in another bathypelagic shark, *Spinax spinax* (*Etmopterus spinax*) (Franz, 1905; Berland, 1961).

According to Franz (1905, 1913), who made a comprehensive study of the eyes of cartilaginous fishes, the tapetum is occlusible, i.e. it becomes covered in light and exposed in darkness. Mobile melanophores, forming a layer underneath the reflecting cells, have pigmented

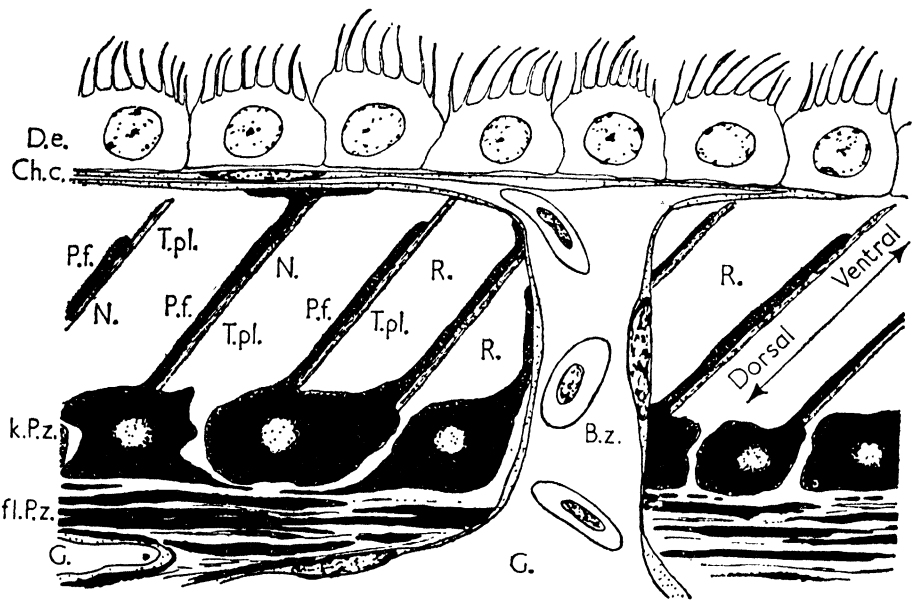


FIG. 2. Vertical section through the tapetum lucidum of *Mustelus laevis* in the partially occluded state. Middle of dorsal half of fundus. Legend: D.e., pigment epithelium; Ch.c., choriocapillaris; P.f., pigment-cell process; N, nucleus of tapetal plate; T.pl., tapetal plate; R., empty space; B.z., blood cell; G, chorioidal vessel; k.P.z., basal cell body of migratory chorioidal pigment cell; fl.P.z., usual flattened pigment cells of chorioidea. ×750 *ca.* (Reproduced with permission from Franz, 1931.)

processes which can extend over the tapetal plates, thereby concealing them. As Rochon-Duvigneaud (1943) has pointed out, Franz never subjected his ingenious hypothesis to experimental proof, and it is of some interest to examine the evidence on which it was based. Franz (*op. cit*) found that the dark-adapted eyes of *Squalus acanthias* and *Galeorhinus galeus*, when excised and exposed to light, initially had bright tapeta which quickly turned dark. He also examined eyes of *Mustelus*, *Scyliorhinus* and *Raia* with an ophthalmoscope and discovered that the tapetum turned dark in the latter two animals before the pupils became fully closed. Verrier (1930), however, who examined

chiefly *Squalus* and *Mustelus*, observed no difference in the disposition of chorioidal pigment of dark-adapted and light-adapted dogfish.

Obviously, there is some doubt about the occlusible properties of the elasmobranch tapetum, and its presence in some species still awaits confirmation. After long neglect, interest in this structure recently has been renewed. It has been found that in some benthic selachians from the neritic zone, the tapetum is fixed, i.e. non-occlusible; examples are *Scyliorhinus* and *Raia*. The eyes of these animals always exhibit a bright fundus, and a black ventral field below the optic stalk. In the latter region reflecting material is absent and there is a layer of black chorioidal pigment outside the retina. Pupillary movement is rapid and extensive. In some pelagic sharks, on the other hand, the whole interior of the dark-adapted eye shines brightly, but soon becomes very dark when exposed to light, owing to migration of black pigment which obscures the tapetum lucidum. Examples are *Mustelus* and *Squalus* (Nicol, 1961a, c). In these animals pupillary movement is slight or absent. Gilbert (1961) observed that the tapetum of the sharp-toothed shark *Negaprion* became occluded in less than an hour in bright light, but required 4 hr or more to become uncovered (when the shiny surface is exposed).

The chorioidal tapetum of selachians contains guanin, to which it owes its reflecting properties. Guanin was discovered in the chorioid of *Squalus*, *Mustelus* and *Scyliorhinus* by Kühne and Sewall (1880), who found that extracts gave a positive reaction to a purine test, involving the successive use of dilute nitric acid followed by sodium hydroxide. Extracts treated with sulphurous acid gave rise to crystals of gypsum, and it has been suggested that the guanin is compounded with calcium *in vivo*. The presence of guanin in the chorioid of *Squalus acanthias* was confirmed by Pirie and Simpson (1946), who recovered guanin hydrochloride from extracts. Also, a green fluorescent substance is present, which appears to be a pterin, xanthopterin.

Many intriguing problems, presented by the tapetum lucidum of elasmobranchs, still await clarification and resolution. Among them are the functional significance of the tapetum in terms of visual sensitivity and acuity; the mode of regulating the movement of chorioidal pigment to and fro over the reflecting plates; the significance of the orientation of the plates in diverse regions of the eye; and the efficiency of the system.

It is generally believed that elasmobranchs find food chiefly by smell, and it has been uncertain to what extent they make use of vision. Benthic species (*Scyliorhinus*, *Raia*, *Rhina*) hunt by scent, generally without making use of their eyes, but simple observation shows that

the common dogfish (*Scyliorhinus canicula*) sees an approaching net and is quite adept at avoiding capture (Bateson, 1890c). And recent work has shown that in clear water vision plays a predominant role in guiding sharks to prey at distances less than 50 ft (Gilbert, 1962).

D. *Retinomotor Changes in Teleosts*

In many teleosts movements take place in the retina which are collectively termed retinomotor movements. They involve migration of retinal pigment and displacement of rods and cones under the influence of light and other factors. The retinal pigment is contained in cells of the pigment epithelium, which bear processes that extend inwards between the receptor cells. In darkness, the retinal pigment moves outwards, towards the base of the pigment cell (withdrawal); in light, the pigment moves inwards (expansion). When movement of the rods and cones occurs, the rod myoids contract and the cone myoids lengthen in darkness; in light, the rod myoids lengthen and the cone myoids contract. Considered in conjunction, these several movements cause the outer segments of the rods to be exposed in darkness; in light, the outer segments of the cones are withdrawn towards the interior of the eye, whereas those of the rods are obscured. These changes, seemingly, are devoid of visual significance in total darkness; they are concerned with enhancing vision in bright and dim light.

Retinomotor changes are to be found in fishes inhabiting inshore waters and surface waters of the oceans. They do not occur in bathypelagic and bathybenthic species. In eels (*Anguilla anguilla*) the rods migrate whereas the cones do not; the eye of the conger (*Conger conger*) contains few or no cones, and it is uncertain whether the rods move (Garten, 1907). It is believed that only the pigment moves in flat-fishes (pleuronectids), and that rods and cones are stationary (Bayliss *et al.*, 1936). It has since been discovered that cones of flat-fish extend and retract in darkness and in light, and a report concerning soles (*Solea solea*) has been published (Nicol, 1961b).

The movement of pigment, cones and rods takes place rather slowly compared, for example, with the swift course of pupillary movement. Times given in the literature for maximal contraction or expansion range from 20 to 70 min for various species and conditions of observation. In *Ameiurus* and *Fundulus* the retinal pigment attains full expansion or retraction in 1 hr; cones shorten and rods lengthen (in light) in 45 min; reverse changes in cones and rods occupy 30 min or more. In *Abramis* the pigment requires 45 min to expand and 30 min to retract; cones shorten in 45 min and extend in 30 min (Arey, 1916). In *Leuciscus* pigment expands and retracts in 20 min to 1 hr; cones

elongate in 20 min in darkness (Pergens, 1896; Chiarini, 1904). The movement of pigment and cones in the common sole (*Solea solea*), exposed to light or darkness, occupies 30 min to 1 hr (Nicol, 1961b). Fuller data are available for young stages of salmon. Expansion of pigment in the Atlantic salmon (*Salmo salar*) exposed to light occupies 35 to 60 min; cones retract in 45 to 70 min. In darkness pigment and cones retract and elongate, respectively in 45 to 70 min (Fig. 3) (Ali *et al.*, 1961; Ali, 1962). Movements are faster in young stages of Pacific salmon (*Oncorhynchus* spp.). In the dark contraction of pigment occurs in 30 to 45 min; extension in 10 to 20 min. Cones shorten in 15 to 20 min and

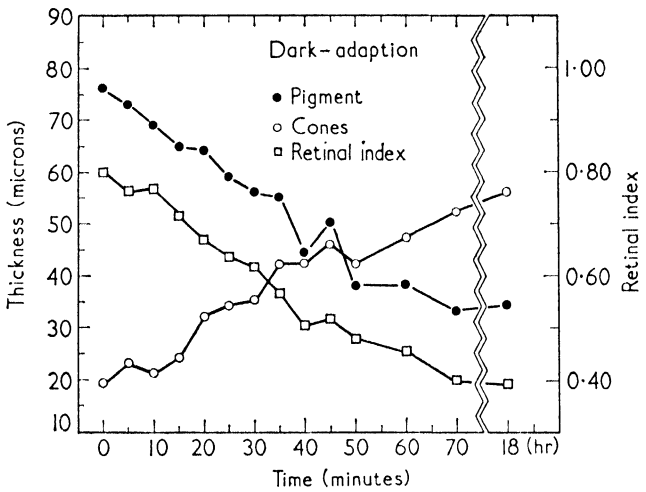


FIG. 3. Changes in thickness of retinal pigment and length of cones of young Atlantic salmon (*Salmo salar*) when transferred from light to darkness. Thickness of layer of pigment or cones (left) is plotted against time after transfer to darkness. Retinal index (right) = thickness of pigment-layer/thickness of pigment-layer + thickness of cone-layer. (Reproduced with permission from Ali *et al.*, 1961.)

elongate in 35 to 40 min (Ali, 1959). In some instances it has been shown that movements during exposure to light are completed sooner than the reverse movements occurring in darkness, e.g. in *Salmo salar* (Ali *et al.*, 1961). It will also be noticed that the movements of pigment and cones may take different times to reach completion.

The experiments from which the above information has been drawn were conducted under widely different conditions of illumination, and it is of importance to know the relationship between absolute light-intensities and retinomotor changes.

A photometric criterion used in early work was the level of illumination at which colours could just be distinguished (by the experimenter). At this level the retinal pigment of the bream (*Abramis*

brama) was partially retracted and cones were shortened. The threshold for movement of the cones was obviously below this level since they were still partially contracted in rather dimmer light (Garten, 1907). In *A. chrysoleucas* the pigment was fully retracted or partially expanded and cones showed signs of incipient movement at a light-level just permitting colours to be distinguished. When the light was bright enough to permit reading, the cones of *A. chrysoleucas* shortened greatly, but not to their minimal extent, and the rods of *Ameiurus nebulosus* began to elongate (Arey, 1919). The light-level at which colour vision begins lies between 0·01 and 0·001 ft c* (producing a brightness on a screen of about 0·0176 and 0·00176 millilambert,

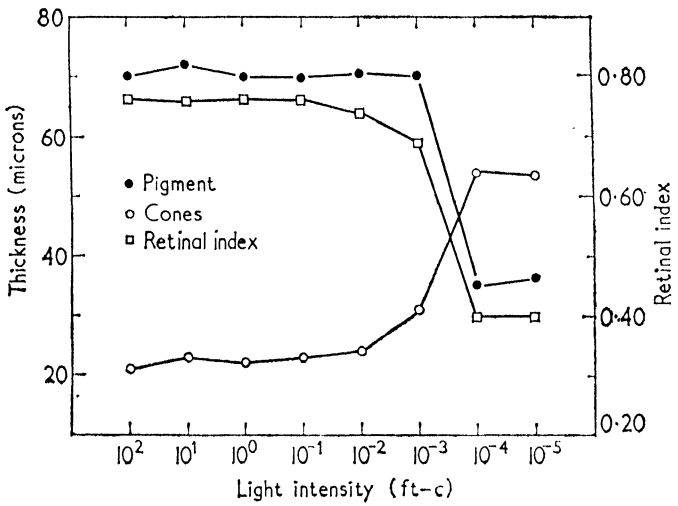


Fig. 4. Extent of retinomotor changes (retinal pigment and cones) produced by different light-intensities in the Atlantic salmon (*Salmo salar*). Cf. Fig. 3. (Reproduced with permission from Ali, 1961b.)

respectively). A paper sufficiently illuminated for reading has a brightness of 2 to 3 mL (produced by incident light of about 2 to 3 ft c).

The behaviour of retinal pigment and of cones over a wide range of illuminations has been determined in the Pacific and Atlantic salmons (*Oncorhynchus* spp. and *S. salar*, respectively) (Fig. 4). Absolute levels at which movement commences and at which steady state is reached vary in different species, and recourse should be had to the original papers for full data. In coho salmon (*Oncorhynchus kisutch*), for example, the retinal pigment commences contracting when the illumination falls below 1 ft c and is maximally contracted at 0·001 ft c. Cones start extending at levels below 0·1 ft c and are maximally

* 1 foot candle = 10·764 lux.

extended at 0·001 ft c (Ali, 1959, 1961a, b). The threshold for the retinomotor shift to the " dark " position drops during the night in *Lateolabrax* and *Cyprinus*: from 0·004 to 0·001 ft c before and after midnight in *Lateolabrax*, and from 0·00005 to 0·000006 ft c in *Cyprinus* (Tamura, 1957). There are obviously considerable differences in light-levels controlling the photomechanical changes of different fishes, and some degree of diurnal rhythmicity may exist (Welsh, 1938). In general it appears that pigment, cones and rods begin to adopt a position characteristic of darkness when the illumination falls below 1 ft c and positions of maximal retraction (pigment, rods) or extension (cones) are attained at levels below 0·01 ft c. This level of illumination is encountered during twilight, and in a landscape lit by the moon at phases between full and quarter. Full retreat of pigment, elongation of cones and shortening of rods are attained in dim light conditions that correspond to those associated with the switch to scotopic and rod vision in man.

Since these retinomotor changes in duplex retinae are almost certainly concerned with enhancing vision, it would be interesting to know at what light-intensity the change from phototopic to scotopic vision occurs in fish. The data for retinomotor changes could then be interpreted more adequately in terms of vision. Since retinomotor changes are so extensive in fishes, one wonders if the change from cone to rod vision and vice versa depends primarily on the ability of cones and rods themselves to respond; or if it depends rather on screening or exposure of the receptors.

Most observers have concerned themselves with only one level of illumination (and darkness), but Ali (1962) has considered the effect of different light-intensities on the extent and temporal course of retinomotor changes. He exposed yearlings of Atlantic salmon to two different intensities, viz. 900 and 0·1 ft c and determined the extent of movement of the retinal pigment and cones. In the stronger light the pigment became fully extended in 40 min and the cones fully retracted in 45 min. In the weaker light the pigment expanded, reaching a steady state in 35 min, and the cones shortened to a steady state in 55 min. The pigment was expanded to a greater degree and the cones more retracted in the stronger light. Placed in darkness, the pigment and cones took longer to return to the " dark " position after exposure to the strong light than after exposure to the weak light.

Possibly a fish does not often encounter abrupt changes from light to total darkness, and it is worthwhile discovering the speed at which movement of pigment and receptors proceeds under conditions of changing light-intensities encountered in nature, say at twilight below

1 ft c. There is an early experiment concerning *Abramis brama*, which were kept in failing daylight one afternoon until darkness, a period of 1½ hr; at the end of this time cones were found to be retracted (Exner and Januschke, 1905). Attempts have been made to relate the course of retinomotor changes in salmon with changes in environmental light-levels and fish behaviour. Ali (1959) has found that retinomotor changes of juvenile Pacific salmon (various spp.) lag behind the decrease of ambient light-levels occurring in nature (from 1 to 0·002 ft c in 20 min): this estimate was based upon the time required for dark-adaptation after exposure to light of 400 ft c. Under natural conditions of decreasing illumination during the evening, cones and pigment of pink salmon began shifting towards the " dark " conditions at levels below 1 ft c and movement was complete between 10^{-3} and 10^{-4} ft c. The natural illumination fell from 1 to 10^{-4} ft c in 45 min. In the laboratory retinae were in the " dark " condition after exposure for 90 min to 10^{-1} (cones) and 10^{-2} ft c (pigment). It is not clear from the descriptions what intensities the fish experienced before the experiment began (Ali and Hoar, 1959). In Atlantic salmon yearlings, exposed to 0·1 ft c, the retinal pigment retracted after 45 min and the cones became maximally elongated after 25 min. Retinomotor changes towards the dark condition commence in this species when the light falls to 0·1 ft c and are complete at an illumination of 0·0001 ft c. Environmental illumination falls to this extent in about 45 min (varying of course with cloud, etc.) and it might be expected from the data presented above that retinomotor changes would keep pace with this decrease (Brett and Ali, 1958; Ali, 1961a, b, 1962).

Photometric data for levels of illumination in the environment, and in experiments relating to retinomotor changes, have been presented as foot candles, and both sets of measurements are comparable. But other measurements relating to visual threshold, light-intensities in the sea, animal luminescence, etc., are given in energy units, ergs/sec, watts, or photons, and some day these various kinds of information will have to be collated and integrated. In view of the unspecified composition of the lights and illumination employed and measured in the first kinds of investigation mentioned above, this task may prove to be very difficult.

IV. Refraction, Accommodation and the Receptor Layer

It is generally believed that elasmobranchs are hypermetropic, and that they accommodate for near vision by moving the lens towards the cornea through contraction of a protractor lentis muscle. Teleosts, on the other hand, are believed to be myopic, and to accommodate for

distance. The teleost eye contains a retractor lentis muscle (campanula Halleri), contraction of which displaces the lens backwards along the axis of the fish's body and more or less inwards, according to the species. Hypermetropia in elasmobranchs, according to Franz, amounts to 10 to 15 dioptres, and they can accommodate from 15 to 20 dioptres. Verrier, moreover, found that hypermetropia was also characteristic of the eyes of teleosts, even when accommodated (references in Baylor and Shaw, 1962). Hypermetropia was detected in the eyes of a wide variety of fishes by Baylor and Shaw (1962). Some mean values for refractive error were 8 dioptres in alewife (*Alosa pseudoharengus*) and 14·6 to 15·8 in silversides (*Menidia menidia*). Dogfish and skate had a hypermetropia of 6 and 8 dioptres. Accommodation in some of the teleosts they examined amounted to 6 to 10 dioptres. In *Alosa* the refractive error in a line antero-posterior (main axis) was lower than in lateral view (3·6 *vs* 8·4 dioptres). The eye of the alewife is ellipsoidal, and is slightly longer (by 10%) in the antero-posterior axis than in the minor optic axis, from lens to centre of the fundus.

A most useful treatment of vision and lens functioning in the normal fish eye has been offered by Pumphrey (1961). The lens is spherical and its dioptric strength is high, ranging, for example, from several thousand dioptres in a juvenile fish a few inches long to several hundred in an adult 1 ft long. The focal length is short, and measurements of refraction have shown that there is a constant ratio of focal length to radius having limits of 2·5 to 2·6; this ratio is named after Matthiessen, its discoverer. It is obvious that a refractive error of, say, 10 dioptres in 1000 is quite small, and amounts to a displacement of focal length of only 100μ. Unfortunately, it is far from certain what reflecting surface is being examined in retinoscopy of the fish eye; Beer thought that retinoscopic reflexion occurred at the front of the retina; Baylor and Shaw (*op cit.*) from behind. The retinal pigment layer itself amounts to almost 100μ in eyes of salmon fry, the retina inside the external limiting membrane is 200μ thick, and rods, cones and pigment make considerable radial excursions. It still has to be demonstrated, convincingly, that the plane of focus in the eye at rest lies elsewhere than in the receptor layer; the so-called error may be one not of refraction, but rather of method.

The fish lens is virtually aplanatic and its focal length is remarkably short (2·5 $\times$ radius). It is argued that a lens having these characteristics and made of biological material whose refractive index cannot exceed 1·53, must have an index that decreases from a maximum of 1·53 at its centre to 1·33 at its periphery, where the index approximates that of the surrounding medium. This change of index is difficult to measure, but it is believed to be the only explanation that fits the facts.

The typical teleost eye is semi-ellipsoidal, about 3 to 10% longer in its antero-posterior axis than in the vertical or cornea-fundus axis and the lens is a concentric sphere. Let it be assumed that images of far objects are in focus on the anterior and central fundus when the lens is at rest, i.e. that these regions are emmetropic. The fish is then myopic for forward vision and when it accommodates by moving the lens backwards, it brings distant objects ahead into focus. Since the lens is displaced along an antero-posterior axis, emmetropia in lateral view is unaffected, but the range of clear vision behind the fish is simultaneously shortened. The extent to which the retractor lentis muscle is developed varies in different species; possibly the degree of accommodation is correlated with habits. The situation in elasmobranchs is still obscure because both the retina and lens are slightly ellipsoidal, and the lens is protracted.

Many nektonic teleost fishes possess adipose eyelids, which lie over part or all of the eye; when the eye is only partially covered the eyelids leave a vertical aperture over the pupil. Adipose eyelids are regarded as structures which enhance stream-lining (Walls, 1942). They are usually clear fleshy structures consisting of densely arranged parallel fibres which are oriented dorso-ventrally. Because of their structure they are strongly birefringent and act as an analyser for polarized light. The amount of light they absorb varies with the plane of polarization of the light, and some 40% less light is transmitted when the plane of polarization is parallel to the dorso-ventral axis than when it is parallel to the antero-posterior axis. The adipose eyelids thus provide a means by which fish can detect polarized light, at least in the peripheral field (Stewart, 1962). The possibility that this faculty may be utilized in the behaviour of fish has not escaped notice; depending upon refraction indices, the eyelids may also affect the focusing power of the eye.

A fovea is rare in fish, the outer segments of the rods and cones are fairly long and a considerable depth of focus is consequently to be expected. Cones in the fish eye tend to be large, well spread out and arranged in mosaic patterns; because of these factors the quality of an image, in focus, may be much inferior to that perceived by the human eye in air. In addition, the scattering properties of water reduce the ability to resolve images.

The structure and arrangement of cones in gadoid fishes have been described by Engström (1961), who has found an " accessory element " connected with the outer segment. Intraspecific differences have been reported in the retinae of *Sebastes marinus*, a benthic scorpion fish from deep water (Hanyu and Ali, 1962). In a specimen of *S.m. mentella* from 275 m, cones were longer than in a specimen from 549 m; rods were

larger in the fish from deeper water. Another subspecies, *S.m. marinus*, also from 275 m, had larger cones and smaller rods than *S.m. mentella* from the same depth. These results suggest the existence of intraspecific variation of retinal structure correlated with habitat differences; the sample as reported, however, is so small that confirmation is desirable; details concerning size of the fish and time of catches are not reported.

V. Visual Pigments and Spectral Sensitivity

Scotopic visual pigments in great variety have been identified in fishes: in general, they are of three main types. Rose-coloured pigments known as rhodopsins are the principal visual pigments in the rods of

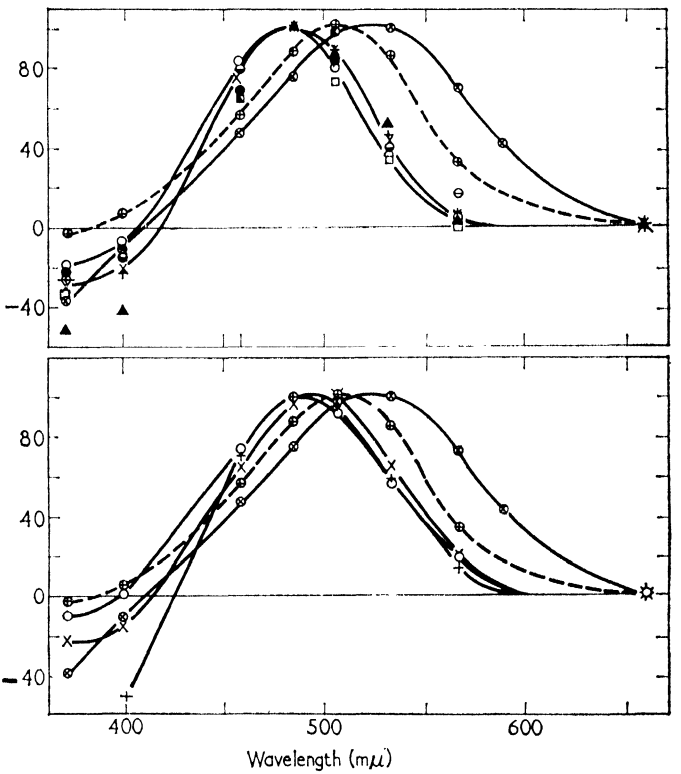


Fig. 5. Absorption-characteristics of scotopic visual pigments of deep-sea fishes, compared with those of coastal species. Curves show density-difference between unbleached and bleached retinae plotted against wavelength. The maximum fall in density for each pigment is made equal to 100%. Curves for the following species, above, O——O *Argyropelecus olfersii*, + *A. hemigymnus*, ×——× *Gonostoma elongatum*, ▲ *Chauliodus danae*, ● *Melamphaës unicornis*, ◒ *Searsia*, ■ *Synaphobranchus kaupi* (all deep pelagic), and ⊕——⊕ *Cottus bubalis*, ⊗——⊗ sea trout (coastal); below, O——O *Lampanyctus ater*, +——+ *Stomias boa*, ×——× *Diaphus rafinesquei*, *Cottus* and trout as before. (Reproduced with permission from Denton and Warren, 1957.)

coastal marine fish, e.g. spiny dogfish (*Squalus acanthias*), sea robin (*Prionotus carolinus*), black sea bass (*Centropristes striatus*), and surface oceanic species, e.g. the skipper (*Scomberesox saurus*). Purple-coloured pigments, known as porphyropsins, are the principal scotopic pigments of freshwater teleosts, e.g. tench (*Tinca vulgaris*) and bream (*Abramis brama*). Yellow or gold-coloured pigments known as chrysopsins,

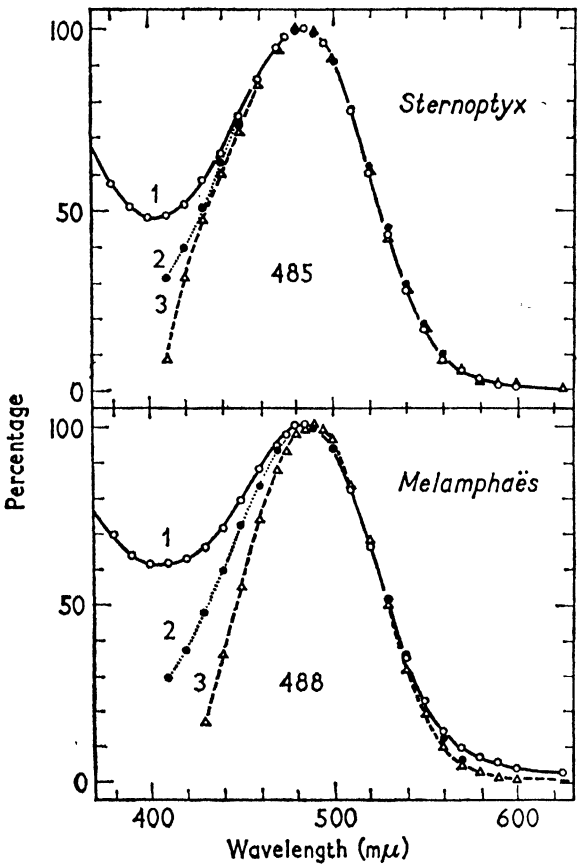


FIG. 6. Absorption spectra (curve 1) of extracts of retinae of two deep-sea fish (λ max. shown below each curve). (Curves 2 and 3 based on Dartnall's nomogram and difference spectra after exposure to yellow light, respectively; see original paper of Munz, 1958b, for details.)

visual golds or deep-sea rhodopsins, occur in the rods of deep-water oceanic fishes from the twilight (mesopelagic) zone, e.g. bathypelagic sharks (*Centrophorus squamosus*), chimaeroids (*Hydrolagus affinis*) and teleosts (*Gonostoma elongatum*, etc.). Rhodopsins contain retinene$_1$, derived from vitamin A$_1$, and exhibit maximal absorption around 500 mμ. Chrysopsins also contain retinine$_1$, and have maximal absorption in the blue, around 485 mμ (Figs. 5 and 6). Porphyropsins contain

retinene$_2$, derived from vitamin A_2, and have absorption curves shifted some 30 mμ towards longer wavelengths than do the rhodopsins. These distributions, although generally true, are not without exceptions; the striped mullet (*Mugil cephalus*), for example, is provided with a porphyropsin having maximal absorption at 520 mμ (Wald, 1939a, b, 1946; Dartnall, 1957; Denton and Warren, 1957; Munz, 1958a, b; Denton and Shaw, 1963).

Most workers have concerned themselves with extracting the visual pigments and then measuring their absorption characteristics. Denton and co-workers (*op. cit.*) have also measured the absorption of the intact retina; their results give relative spectral absorption and a direct estimate of density of visual pigment in the retina.

The terms rhodopsins and porphyropsins are regarded as generic designations for pigments based on retinene$_1$ and retinene$_2$ respectively, and within each group λ max exhibits a range of values. Maximal absorption of rhodopsins based on retinene$_1$, including visual golds and typical rose-coloured pigments, ranges all the way from 478 to 525 mμ. Dartnall and others have obtained various pigments from the eyes of pike and other freshwater fishes that have absorption maxima in the range 524 to 532 mμ (Dartnall, 1957; Rushton, 1959). The change from vitamin A_1 to vitamin A_2 brings about a major shift in absorption spectra towards the red; differences in absorption spectra within each system are determined, presumably, by the character of the protein moiety (i.e. the opsin) of the molecule. Some fishes possess two scotopic visual pigments, i.e. have a dual system. Wald (1946) has emphasized that an admixture of rhodopsin and porphyropsin is characteristic of certain euryhaline fishes, especially anadromous and katadromous fishes moving to and from fresh water. Eels (*Anguilla rostrata*) in the freshwater phase and killifish (*Fundulus heteroclitus*) have predominantly rhodopsin; salmonids, predominantly porphyropsin; and the anadromous white perch (*Morone americana*), exclusively porphyropsin. A marine puffer (*Sphoeroides annulatus*) has rhodopsin and porphyropsin in about equal proportions. Other dual systems found in marine teleosts involve admixtures of two rhodopsins or of two porphyropsins. In the deep-sea teleost *Bathylagus wesethi* there are two retinene$_1$ pigments having λ max at about 478 and 500 mμ and occurring in proportions 4 : 1 (Wald, 1939a, 1941, 1958, 1960; Crescitelli, 1958; Munz, 1958b).

Changes from one environment to another carried out by certain fish have prompted enquiries into the problem whether transformations of their visual pigments also occur at the same time. This does not appear to be so in salmon (*Salmo salar*) for Denton and Shaw (1963)

found that smolt (from sea water) and an adult salmon that was migrating upstream had purple-coloured retinae resembling those of freshwater fish, i.e. they retained the predominantly porphyropsin system also discovered in freshwater phases of salmonids. The eel (*Anguilla*) in its immature freshwater phase has a purple-coloured retina (chiefly rhodopsin, *vide supra*). But when the eel becomes silvery, preparatory to migrating, its retina becomes yellow and it acquires a visual pigment closely similar to that of deep-sea fish, with an absorption maximum shifted some 33 mμ towards shorter wavelengths (Fig. 7). This change involves the combination of retinene$_1$ with a new opsin. Conger eels pass part of their life in shallow coastal waters and return to deep water when sexually mature. The immature

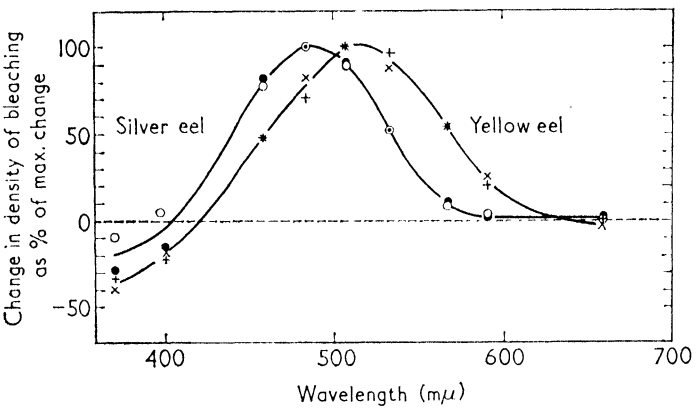


Fig. 7. Absorption characteristics of the retinae of immature (yellow) and mature (silver) eels. Spectral curves show difference in density between unbleached dark-adapted retinae and retinae bleached by strong white light. (Reproduced with permission from Carlisle and Denton, 1959.)

eels have a yellow visual pigment and they probably possess this form of pigment throughout their life (Wald, 1958; Carlisle and Denton, 1959). Evidence for lampreys is still incomplete. In the Pacific coast lamprey *Entosphenus tridentatus*, both up-stream and down-stream migrants contain rhodopsin. In the sea lamprey (*Petromyzon marinus*) up-stream migrants of the sea-run form contain porphyropsin, but down-stream migrants of the land-locked form contain rhodopsin. From this somewhat equivocal evidence it has been suggested that a change from rhodopsin to porphyropsin occurs in the sea lamprey as it approaches sexual maturity (Crescitelli, 1958; Wald, 1958, 1960).

It is impossible to do justice to the complexity of the subject and to the great amount of research which has been devoted to it in this brief summary; fortunately, detailed information may be obtained in the excellent reviews of Wald (1960), Dartnall (1957) and Crescitelli

(1958). One important idea which has come of this work and one which has been emphasized by some of the workers concerned, is that the visual pigments, of marine fishes at least, are adapted to the quality of light in their environment. There are considerable differences in the extent to which attenuation of different wavelengths occurs in natural waters. In coastal waters where there is much suspended matter and dissolved yellow substance, the water is green and maximal transparency lies in the region of the spectrum between 500 and 600 mμ, as does that of fresh waters. A set of normal transmission curves for

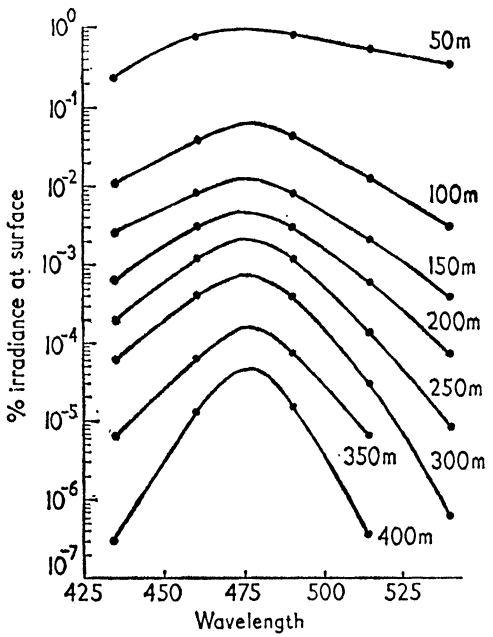


FIG. 8. Relative spectral curves of transmitted daylight at depths shown in the Bay of Biscay (46°29′N, 7°59′W, 10.30–11.30 h, 25 September). (Reproduced with permission from Boden *et al.*, 1960.)

different types of coastal waters, with rather flattened maxima between 500 and 570 mμ, is given by Jerlov (1951). To waters with these spectral qualities, the rhodopsins and porphyropsins of inshore, estuarine and anadromous species appear to be well suited, at least as regards their absorption characteristics at wavelengths between 500 and 535 mμ (Munz, 1958b). Clear oceanic waters are blue, and have maximal transparency in the region 400 to 500 mμ. With increasing depth, there is preferential absorption of short and long wavelengths below and above the blue-green region of the spectrum, and the residual light which reaches deeper water lies in the region around 475 to 480 mμ (Fig. 8) (Jerlov, 1951; Boden *et al.*, 1960). There is obvious biological

value in the shift of absorption maxima of rhodopsins, from values around λ max 500 mμ in surface species to λ max around 485 mμ in bathypelagic species (Denton and Warren, 1957; Munz, 1958a, b). Moreover, there is a great deal of bioluminescence in deep waters, and the light emitted is generally blue, with emission peaks around 480 mμ. It is a nice question whether one is to consider the colour of the luminescence adapted to the spectral sensitivity of the receptor, or vice versa.

Deep-sea fishes have pure rod retinae, whereas duplex retinae are encountered in coastal and freshwater fishes; colour vision is known to occur among the latter. For scotopic vision, at least, the relative sensitivity to different parts of the spectrum may be reasonably inferred from the absorption curves of the visual pigments, and this may be the only approach possible for bathypelagic species that are dead on recovery. However, when action spectra have been obtained, either from behavioural studies or electrophysiological recording, they have shown a very good fit with absorption spectra of scotopic pigments of the species in question (freshwater tench and sunfish, having porphyropsins) (Dartnall, 1957). The hagfish (*Myxine glutinosa*), as deduced from behavioural experiments, shows maximal spectral sensitivity between 500 and 520 mμ. It contains vitamin A_1 and its photosensitive pigment presumably is a rhodopsin containing retinene$_1$ (Steven, 1955).

Spectral sensitivity curves based on electrical activity of the retinae of several species of marine and freshwater fishes have been obtained. Potential changes (known as graded photopic responses) have been recorded from some units situated between the ganglion cells and the receptors. One type of response (the luminosity response, a hyperpolarization) is evoked by white light of any wavelength, with a peak response between 500 and 600 mμ (various shallow water teleosts). Other (chromatic) responses are paired positive and negative polarizations recorded from slightly deeper levels (from the receptor layer) than the luminosity responses. These potentials are usually evoked by light of long and short wavelengths, respectively, providing opposed red-green and yellow-blue colour mechanisms. On and off discharges corresponding to these potential changes have been recorded, and it has been found that the off process (generated by red light) inhibits the on process (generated by blue light). These electrical responses reflect indirectly the activity of receptors, presumably cones; photostimulation of single cones has yielded luminosity responses; however, it has not yet been possible to link the sensitivity curves with known visual pigments (MacNichol and Svaetichin, 1958; Svaetichin and

MacNichol, 1958; Wagner *et al.*, 1960; Mitarai, 1960; Svaetichin, *et al.*, 1960; MacNichol *et al.*, 1961).

VI. Transmission by the Lens

The lenses of fishes are singularly free from chromatic aberration (Pumphrey, 1961). If the lenses were pigmented and absorbed certain components of the incident light, they would alter the composition of light reaching the retina. It has been discovered that those of diurnal and of surface oceanic fishes, whose eyes are exposed to some near ultra-violet light, usually contain pigments absorbing short wavelengths (far blue and near ultra-violet, below 400 mμ). In nocturnal and deep-sea species the lenses are usually transparent to short wavelengths down to about 310 mμ. Among certain benthic species of the neritic zone (*Mustelus canis*, *Tautoga onitis*, etc.), the lenses show a gradual rise in density at wavelengths below 400 mμ to 320 mμ. Ultra-violet light is absorbed rapidly with increasing depth; values for absorption of light of 375 mμ range from 5%/m in clear oceanic water to 90%/m in turbid coastal water. The difference discovered in the transparencies of lenses are clearly related to the habits of the fishes and, furthermore, are adapted to the depths at which they live (Kennedy and Milkman, 1956; Denton, 1956; Motais, 1957; Armstrong and Boalch, 1961; Clarke and Denton, 1962).

VII. Photosensitivity and Visual Thresholds

The minimal light which fishes can perceive, the minimal light in which fishes can see objects, and the minimal light which regulates their various photoresponsive activities are factors which have received some attention.

Reliable values for minimal intensities of light which fishes can detect, and which govern their activities, are not easy to obtain, and recourse has sometimes been made to estimates based on human vision. The fully dark-adapted human eye can just detect a steady light from a large field having an intensity of about 3×10^{-8} μW/cm^2 on the cornea; this is light of λ 510 mμ, which is the wavelength of maximal efficiency for scotopic vision (Pirenne, 1956; Clarke and Denton, 1962). If the eye of a fish is as efficient as the human eye in absorbing blue-green light, it can just detect daylight having a flux at the pupil of 3×10^{-8} μW/cm^2. Unfortunately, there does not seem to be any measured value available for absolute threshold in fish. Since some other vertebrates and at least one invertebrate have absolute thresholds as low as, or lower than, that of man, it is highly probable that

many fishes are equally sensitive. Densities of retinal pigment in the human eye are only about 0·15 and some 30% of incident blue-green light is absorbed; densities in fish retinae are usually much greater than this, 0·6 in the skipper (*Scomberesox saurus*), and 0·58 in the conger eel (*Conger conger*). The retinae of these fish absorb about 75% of the light reaching their surfaces, a gain of over twice that of the human. Indeed, in deep-sea fish such as *Gonostoma* and *Xenodermichthys*, densities reach 1·0 or more, permitting absorptions of 90% or greater (Denton, 1959). It is known that the owl, nocturnal, has an absolute threshold one tenth lower than that of man, and fishes habitually living in dim light may have thresholds as low or lower (Pirenne, 1956). Denton and Warren (1957), following their investigation of visual pigments of deep-sea fish, have discussed this problem at length. The scotopic pigments or visual golds of such fish absorb maximally in the blue around 485 mμ, corresponding to the region of maximal transmission of clear oceanic water. After considering a number of advantages which the eyes of bathypelagic fish may possess—high pigment density, relatively large pupil, reduced " noise " level—they suggest that the gain in sensitivity of the eye of a deep-sea fish over that of the human may be as much as 100 times. This means that in very clear oceanic water, having an extinction coefficient of, say, 0·04, fish may be able to just detect daylight down to depths of 900 to 1000 m for a short time each day.

Recordings made with bathyphotometers in deep waters have shown that the flashes of luminous animals may be so frequent that they could conceivably provide background illumination having levels of 10^{-7} μW/cm^2 or more (see, for example, Clarke and Hubbard, 1959).

Light is heavily absorbed by water; transmission values range from around 65%/m for turbid coastal waters to 93%/m for clear oceanic waters. The eye is so sensitive, however, that in coastal waters, having absorption coefficients of around 0·13, a fish at 100 m can still perceive objects from sunrise to sunset on the darkest winter day (region of Plymouth). In much deeper waters, enhanced photosensitivity should increase the time each day when daylight is still perceptible to a fish.

In the human being visual acuity increases quickly as the light rises above absolute threshold. Similarly we may presume that a fish can begin to distinguish objects at some intensity only a few times brighter than absolute threshold (Clarke and Denton, 1962). In deep waters of the ocean this means that a fish can begin to perceive objects by filtered daylight at depths slightly less than those when it can just detect background light. In some experiments involving rheotactic responses of the sunfish (*Lepomis*) it was shown that it would just respond to

moving bars (subtending an angle of 11° at the eye) in a minimal illumination of 1×10^{-6} mL. It has been estimated that at this brightness the equivalent of about 1×10^{-6} μW/cm^2 would be falling upon the eye (Clarke, 1936). *Lepomis* is a shallow-water fish with a duplex retina; fishes living habitually in dimly-lit waters may be able to distinguish objects at much lower intensities. Thus, the mackerel continues to school at very weak light-intensities, which approach visual threshold for humans, and which are well below those at which aggregations of sunfish break up (Schlaifer, 1942).

Some observations on young salmon (*Oncorhynchus*) reveal that they cease feeding at light-intensities below 10^{-4} to 10^{-5} ft c (roughly 10^{-4} to 10^{-5} μW/cm^2) (Ali, 1959), and that they rise off the bottom and begin migrating at intensities below 0·01 ft c (approx. 10^{-2} μW/cm^2) (McDonald, 1960). The down-stream movement of young rainbow trout is influenced by much lower light-intensities (<0·0001 ft c) (Northcote, 1962). Both these responses involve visual discrimination (of food objects or objects on the bottom). Kinetic movements of trout and salmon larvae (*Salmo trutta*, *S. irideus* and *S. salar*) have a light threshold of 0·005 m c (=0·00047 ft c) (Woodhead, 1957). The results demonstrate the importance of ambient light-levels on behaviour patterns, but they do not necessarily reveal absolute threshold values. Activities at or near absolute thresholds may be important, however, only in some special environments.

There are enormous populations of luminescent animals in the oceans, hardly any in fresh waters (see, for example, Harvey, 1952). Since the light-organs of these animals are often tiny—indeed many of the light-producing animals themselves are quite small—it is practical to consider them as point-sources, and to estimate how far they can be perceived. The human eye can just perceive a small, steady light-source having a flux of $1{\cdot}6 \times 10^{-10}$ μW/cm^2 at the surface of the cornea (Pirenne, 1956; Nicol, 1958). Clarke (in Clarke and Denton, 1962) states that a small light could just be detected in clear oceanic water (transmission 97%/m) by a human observer at a depth of 56 m, when the intensity was $2{\cdot}8 \times 10^{-6}$ μW/cm^2 at the eye. Pirenne's value used by Nicol obtained as it was under ideal conditions by a co-operative human observer, is probably too high for natural conditions in the sea. Clarke's figure, on the other hand, is likely to be too low because of the difficult conditions under which it was obtained (foveal vision, partial dark-adaptation, etc.). As previously considered, many fish may have thresholds as low as or lower than that of man. Moreover, in deep oceanic waters, luminescent lights are usually blue and should have maximal efficiency for stimulating scotopic visual pigments of bathy-

pelagic fishes (visual golds). Measurements made of the lights of lantern fish show that the radiant flux ranges from $0{\cdot}1 \times 10^{-9}$ μJ (*ca.* 0·1 sec) to 52×10^{-9} $\mu W/cm_2$ at 1 m distance (Nicol, 1960; Clarke *et al.*, 1962). In clear oceanic water it has been estimated that another fish would see the light of a lantern fish at distances of 10 to 16 m. However, if a fish had a sensitivity 100 × that of man, it might detect luminescence at 50 m or more. Luminescent flashes are usually intermittent, and this feature may enhance their ability to be detected (Nicol, 1958).

Absolute thresholds for retinomotor changes to the " dark " condition in the eyes of various teleosts lie in the range 10^{-2} to 10^{-3} $\mu W/cm_2$ (p. 180). Since regulation of retinomotor responses has not been worked out satisfactorily, it is uncertain what receptors are involved.

Experiments on behaviour of the hagfish show that it responds by general activity to illumination down to 6 m c (perhaps lower); this is approximately equivalent to 0·5 $\mu W/cm^2$. Light levels of this order occur in coastal waters of 30 m or so where *Myxine* is found (Gustafson, 1935; Newth and Ross, 1955). The light is detected by generalized integumentary photoreceptors and a light level of 0·5 $\mu W/cm^2$ may be a representative value for absolute thresholds of such unspecialized receptors.

VIII. The Chorioidal Gland

The chorioidal gland found in the chorioidal layer of the eyes of most teleosts is a horseshoe-shaped structure containing a rete mirabile. Its blood supply comes from the pseudobranch via the ophthalmic or efferent pseudobranchial artery. The arterial capillaries entering the rete alternate regularly with the venous capillaries leaving it, and the venous outflow goes into the choriocapillaris. There is also a lentiform body in the chorioid near the falciform process. It is supplied by the retinal artery and its venous outflow also goes to the choriocapillaris. A common feature of both chorioidal gland and lentiform body is the regular alternation of arterial and venous capillaries within them, an arangement that permits maximal exchange of material on the counter-current principle (Barnett, 1951).

Parry and Holliday (1960) found that extirpation of the pseudobranch produced rapid darkening of the skin and, after some weeks, degeneration of the chorioid gland (in *Salmo*, *Clupea*, etc.). They suggested that the pseudobranch produced a hormone capable of causing expansion of chromatophores, and that the chorioidal gland regulated the entry of this substance into the general circulation. Retia associated with the swim-bladder are concerned with secretion of oxygen and it has been found that the chorioidal rete seems actively to secrete oxygen

into the fish eye. Direct measurements have demonstrated the existence of high oxygen tensions in the vitreous humour of many marine species; tensions ranged from 250 to 800 mm Hg (about 1·5 to 5 times that in the blood) in benthic and pelagic forms, all of which had well-developed chorioidal glands. In two fast-swimming pelagic fishes, bluefish and remoras, tensions up to 1320 mm Hg were measured. Fishes lacking or having but small retia had low tensions of oxygen in the vitreous humour. The chorioidal gland is well developed in active predatory teleosts; possibly its function of supplying oxygen to the retina is to be correlated with visual acuity, density of receptor elements and thickness of the retina (Wittenberg and Wittenberg, 1962). It is possible that the darkening associated with pseudobranch removal is the result of depressed retinal activity.

IX. Ecological and Behavioural Studies

Breder (1959) has presented an extensive review, containing much original information, of the responses of fishes to light. The following discussion is concerned especially with experiments and observations dealing with quantitative factors and the operation of photoreceptors.

Fishes living habitually in lighted environments make colour changes; the receptors for these responses are the pineal organ and paired eyes (see Section II). These responses can take place very quickly, for example in fishes living among coral reef (Longley and Hildebrand, 1941). Waring (1942) has presented an evolutionary scheme in which slow chromatic responses, mediated by hormones (in elasmobranchs), have been superseded by fast responses mediated by the nervous system (in teleosts). Eels were thought to occupy a transitional stage, with relatively slow responses; melanophores were innervated, but the nervous system played no part in the responses of intact animals. This is highly unlikely because Bateson (1890a) observed long ago that white spots in the conger eel come and go very suddenly.

A related visual reaction is shown by many fishes which will swim only over a matching (or contrasting) background. Breder (1959) has described how schools of clupeids, swimming over light sand, refused to pass over dark beds of weeds. Field observations indicate that this kind of reaction is correlated with the degree of pigmentation of the fish. Analogous behaviour is shown by various fishes that are more repelled by vertical nets reflecting light of long wavelengths than by those reflecting short waves, i.e. they pass in increasing numbers through nets coloured as follows: red, orange and yellow, green and blue. The responses are governed by visibility and contrast against back-

ground, and colour is more important than brightness; net colour becomes less important at twilight (Kanda and Koike, 1958a, b; Kanda *et al.*, 1958a, b; Breder, 1959). Fishermen have observed that pilchards avoid nets in " phosphorescent " waters at night; they call this phenomenon " brining ". The luminescence seemingly reveals the presence of the nets to the fish (Wilcocks, 1883).

Vision is the main factor governing the formation and maintenance of fish shoals. In general, as shown by numerous laboratory experiments and by observations in nature, shoals break up when the illumination falls below a certain level (Imamura, 1953; Breder, 1959). In aquaria, the schooling of mackerel ceases in darkness and after blinding (Schlaifer, 1942). The threshold level for schooling in the Pacific sardine (*Sardinops caerulea*) is well below 0·01 ft c (Loukashkin and Grant, 1959); in *Menidia*, *Hepsitia*, etc. schooling ceases at 0·05 ft c (Shaw, 1961). A check was kept on cod shoals in deep water (100 m) of the Barents Sea by means of echo sounder and it was observed that the shoals dispersed at sunset and reformed at sunrise (Ellis, 1956).

Much work has been done on the photo-responses of young salmon, especially in relation to their migratory movements. Juvenile salmon move downstream to salt water either as fry or smolts, and this movement is largely nocturnal. Various species of Pacific salmon exhibit considerable differences in their photo-responses, and Hoar (1958) has traced an evolutionary sequence among them on the basis of behaviour to light and other factors. Katadromous progress is associated with nocturnal activity: coho fry are active by day and by night, and their downstream progression at night is probably the result of more displacement with than against the current. Pink salmon, exemplifying the other extreme, become intensively active at night and rise to the surface; on losing visual contact with the bottom, they swim rapidly with the current, and their exit from the river takes place rapidly. Coho, on transformation to smolt, show increased nocturnal activity and strong concealing behaviour (Hoar, 1953; Hoar *et al.*, 1957; McDonald, 1960). Hoar (1958) has pointed out that the photo-reactions of young salmon depend both upon absolute intensities and on rates of intensity-change; the onset of nocturnal migration coincides with rapid decline of light-intensity. The movements of juvenile rainbow trout in and out of a freshwater lake, and of brook trout to and from salt water similarly are controlled by fall and rise of light-intensity (Smith and Saunders, 1958; McDonald, 1960; Northcote, 1962). Migration of silver eels downstream is also largely nocturnal (Deelder, 1954).

Correlating field-observation with retinomotor changes in juvenile

pink salmon, Ali and Hoar (1959) have found that crepuscular migration is initiated when the retina is only partially dark-adapted (by this they mean that elongation of cones and withdrawal of retinal pigment are only partially completed). The light-intensity in the evening falls rapidly (in 45 min) from 1 to 10^{-4} ft c while retinomotor changes and downstream movement are taking place. They have suggested that the young salmon rise toward the surface at twilight because they are only partially dark-adapted and can no longer see the bottom, i.e. the light-intensity is changing faster than the eye can adapt by retinomotor movements. Once visual contact with the bottom is lost, downstream transport follows. This interesting theory, based on a correlation, does not take into account the progress of dark-adaptation *sensu stricto*, and there is a notable dearth of information about the movement of the rods. Indeed, the radial movements of photoreceptors and retinal pigment obviously are adaptations to high and low levels of illumination, but their exact significance in terms of visual functioning has still to be established.

Some fish are affected more by an intermittent light than by a continuous light at night. Pacific sardine in a dark aquarium avoid a beam of intermittent light (illumination <1 ft c, flashing rate 60 times/min), and they display a typical fright reaction when such a light is used (Loukashkin and Grant, 1959). An intermittent light is used in California purse-seine fishing in order to keep the fish within the seine until the net has been closed (California Co-operative Oceanic Fisheries Investigation, 1958; von Brandt, 1959). Juvenile silver salmon (*Oncorhynchus kisutch*) give fright reactions when a light is quickly turned on and off the fish (Dunkan, 1956). And in some experiments involving migrating young spring salmon (*O. tsawytscha*), a beam of flashing light was found to be more effective in deflecting the course of the fish than a continuous light and a curtain of air bubbles (Brett and MacKinnon, 1953). On the other hand, yellow fish and little tunny, in aquaria, showed no differences in responses to continuous and interrupted lights (Tester, 1959). Special responses to flashing lights may be significant in connexion with luminous flashes of animals.

Many pelagic fishes diurnally make vertical migrations and these are probably regulated in large part by daily changes in light-intensity, as is known to be the case in planktonic invertebrates. Vertical movements from deep waters towards the surface at night, and descent at dawn, have been detected in pilchards or sardines (*Sardina pilchardus*), anchovies (*Engraulis encrasicholus*) and herring (*Clupea harengus*) (Dragesund, 1958; Cushing, 1959; Sara, 1962).

Of quite a different nature is the attractive influence which strong

artificial light exerts upon fish. This response, shown by many fishes, has been exploited by fishermen all over the world in various kinds of "light fishing", and a large literature has accumulated about the phenomenon (see Kristjonsson, 1959; von Brandt, 1959; Isa, 1961; Imamura, 1961; Sara, 1962). Herring, pilchards, sardine, cod and mackerel are some of the commercial fishes attracted by lamps at night. The behaviour is obviously peculiar and is not to be attributed to normal phototaxis. It is comparable to the attraction of moths to a lamp and involves some sort of visual disorientation connected with the darkness of the surrounding environment in contrast to the brightness of the lamp. Verheyen (1959a), analysing this behaviour, believes that it is an abnormal telotaxis in which the fish exchanges normal random movements for directed drift towards the light-source. Normal movements, in so far as they are affected by photic stimuli, are guided by differences in the light-intensities falling upon the two eyes and on different parts of the same retina. An artificial light is most effective in clear water at night when there is no reflexion from a background that would reduce contrast. Under these conditions the light is coming mostly from the source and usually affects only one eye at a time, producing grossly abnormal stimulation. In the absence of any other modifying stimuli, that from the lamp seizes control of the lower visual centres and directs muscular activity. When there is much scattering of the light, natural moonlight, or reflexion from the bottom, competitive photic stimulation of a more normal character intervenes and the effectiveness of the artificial light is reduced or nullified (Verheyen, 1956, 1958, 1959a, b).

There is accumulating evidence that behaviour is affected to some extent by wavelength as well as intensity. Pacific sardines (*Sardinops caerulea*) in an aquarium prefer blue or green light to white, and red light produces confusion and alarm in schools; in these experiments the fish were responding to the colour of the lights (Loukashkin and Grant, 1959). Tests made with coloured lights on various species of marine fish in tanks revealed that they were attracted by green and blue and were indifferent to red—*Spheroides*, *Monochantus*, *Fegu*, etc. *Anguilla* was exceptional in that it was indifferent to blue and green and was attracted by red light. These experiments took into account both relative radiant energy and radiant visual perceptibility (or spectral sensitivity) (Kawamoto, 1959; Sara, 1962). Mention has been made previously of how colour influences the effectiveness of nets. Most colours, of course, are soon eliminated by differential absorption with increasing depth, leaving monochromatic blue or green light (see Section V). The distinct retinal responses to lights of different wave-

lengths, mentioned in Section V, may have their counterparts in overt behavioural responses.

The sensory cues and factors which influence migrating fish when moving to and from their breeding and feeding areas have fascinated biologists, and evidence is now accumulating that fish can orientate on the sun and thereby follow a fixed compass direction. In one investigation some white bass (*Roccus chrysops*), a freshwater fish, were captured on their spawning grounds near shore, transported to the middle of the lake (a distance of 2·4 km) and there released. When this was done on clear days they subsequently made their way back to their particular spawning areas, but they failed to orientate and return on days that were overcast (Hasler *et al.*, 1958). The same investigators found that sunfish (*Lepomis*) could be trained to enter a box in a certain compass direction at any time of day. Both these fishes can certainly orient by the sun; in fact, they cannot orient themselves when it is not visible, and they must be able to compensate for movement of the sun during the course of the day. Moreover, it has been discovered by training experiments with *Lepomis* that they also adapt their diurnal sun-orientation rhythm to conform to seasonal changes in connexion with alterations in day length. This latter compensation, of course, is necessary to enable a fish to make use of sun-compass reactions throughout the year in the same latitude. Sun-compass reactions have been demonstrated in young silver salmon and other freshwater fishes (Hasler, 1960a; Schwassmann, 1960; Schwassmann and Braemer, 1961).

The experiments just mentioned deal with homing in local areas. Braemer (1960) simulated longitudinal displacement by conditioning freshwater fish to light-cycles that were delayed or advanced from those of the normal day. When they were tested subsequently out of doors, their sun-compass reaction now deviated by a certain angle from the previous direction, and this deviation was roughly equivalent to the amount of shift in time or longitude. If a fish is displaced in latitude, it encounters a change in length of the day and a change in the inclination of the sun's arc. Sunfish trained to orient to the sun in Wisconsin (43°N) were flown to Brazil (1°S). At the equator the sunfish oriented during the forenoon but became disoriented in the afternoon, apparently because of the high position of the sun. A sunfish flown to Montevideo (30°S) continued to compensate for the azimuth curve of the sun in the way that would have been correct in the northern hemisphere. Fishes living in the tropics must reverse the direction of the sun compensating mechanism during the course of the year, owing to the annual reversal of the position of the sun's azimuth. Cichlids (tropical and subtropical

fish) apparently can do this whereas sunfish (from the northern hemisphere) cannot (Hasler and Schwassmann, 1960).

Salmon, tuna and eels perform long sea migrations which occur at a relatively slow rate and during which they may be able to adjust gradually to changing photoperiod and sun-arc. Moreover, salmon in pelagic waters are known to carry out some of their migrations at night, when sun-compass reactions are not possible; other guiding factors must then be operative. On approaching parent streams or spawning grounds, other sensory cues must come into play (Hasler, 1960a, b).

X. Synopsis

Light-sensitive areas of cyclostomes are the skin, spinal cord, brain, pineal complex, and paired eyes when present. The hag is practically eyeless and has integumentary photoreceptors at the anterior end of the head and in the cloacal region. The caudal region of the ammocoetes is especially sensitive to light; photoreceptors additional to the pineal complex and the paired eyes occur in the head of the lamprey.

Integumentary photoreceptors occur in blind cave fishes and may be present in some marine fishes. The pineal region of many teleosts is sensitive to light and mediates some behavioural and colour responses.

Chromatophores over the pineal region control the amount of light reaching the pineal complex. Pupillary movement takes place in some benthic selachians and teleosts. An occlusible tapetum lucidum lies in the chorioidea of pelagic elasmobranchs and movement of pigment across the tapetum, in light or darkness, takes place slowly. Retinomotor changes—radial excursions of receptors and retinal pigment—in teleosts also occur slowly, in 30 to 60 min, and are related to changes in light-intensity. Threshold values of several species have been determined.

A slight degree of hypermetropia is postulated from retinoscopy of selachian and teleost eyes, the significance of which awaits explanation. The aplanatic condition and very short focal length of the teleost lens are thought to be the result of its having a changing refractive index from the centre to the periphery. When accommodating, the lens is displaced backwards along the antero-posterior axis and brings distant objects into focus on the posterior retina.

Rhodopsins, based on vitamin A_1 aldehyde, are characteristic of marine fishes. They have a great range of absorption maxima, ranging from maxima around 480 mμ (visual golds or chrysopsins of deep-sea species) to purple rhodopsins with maxima around 510 mμ in fishes of turbid coastal waters. The absorption characteristics of these various scotopic visual pigments seem to be related to the quality of light in the

environment—residual blue daylight or luminescence in clear oceanic waters, filtered blue-green or green light in inshore waters. The eel, when metamorphosing, changes purple rhodopsin for chrysopsin.

Lenses of diurnal and surface dwelling fishes, that encounter ultra-violet light, absorb short wavelengths, whereas those of nocturnal and of deep-water fishes are usually transparent to ultra-violet.

Despite great interest in photo-responses of fishes, estimates of visual thresholds are derived largely from observations on man and other animals. Fish may be able to just detect daylight having a flux of 10^{-8} $\mu W/cm^2$; for a small, steady light-source the threshold may be still lower. Various factors increasing the efficiency of the eye of fishes may improve these estimates by several degrees of magnitude.

Measurements of oxygen tensions in the vitreous humour indicate that the chorioidal gland of the teleost eye is a rete mirabile, concerned with supplying oxygen to the retina.

Recent ethological and ecological studies concerned with photic stimuli have dealt with colour changes, schooling, migratory movements of katadromous salmon and trout, diurnal vertical migrations, responses to intermittent light, coloured lights and strong steady lights, and the operation of sun-compass reactions in horizontal migrations.

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THE BIOLOGY OF CORAL REEFS

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I. INTRODUCTION

Early experience of coral reefs, for over a year on Low Isles and elsewhere on the Great Barrier Reef of Australia with a later summer at the former Carnegie Laboratory on the Dry Tortugas in the Gulf of Mexico, has left the writer with an enduring interest in these tropical marine communities. Although recent contacts with coral reefs have been largely from the air with some superficial study of the fringing reef at Zanzibar, advances in knowledge have been followed with great interest. This article, therefore, represents the general impressions of one who now views coral reef investigations from some distance but also with some realization of the gaps in knowledge which impede progress on the biological side. Many of these demand prolonged observation or experimentation and cannot be filled until some permanent centre for biological research, well staffed and well equipped, is established on a suitable coral formation, preferably a small atoll. There, work can be conducted not only throughout the seasons but also over a long period of years so that the broad pattern of reef changes may become known and major controversies settled.

In no branch of biology are we so close to the earth sciences as we are in the study of coral reefs. From the standpoint of a geologist, the

position has recently been admirably expressed by Ladd (1961) who states that " The building of reefs is primarily a biological process, but geological processes such as erosion and sedimentation enter as soon as the first reef organism is damaged by wave action. Thereafter, reef building is a combination of organic and inorganic growth. Ultimately the effects spread to many other scientific fields." It may be added that one effect of erosion and sedimentation is to produce new environments for life in which corals and other reef organisms have become adapted. There is no sphere in which the continual interplay between animal and environment is so well displayed or more worth while studying.

In what follows no attempt has been made to summarize all recent literature which has biological implications if only because the whole of the voluminous geological and geographical work on reefs, especially on the atolls of the Marshall Islands, has such implications. Attention has been restricted to what, in the author's personal opinion, appear to be the more significant aspects, or implications, of recent biological studies, these ranging from taxonomy to productivity. The occasion has also been taken to point out lines along which research might profitably be directed.

By corals we are here considering those coelenterates which are epifaunistic and form massive calcareous skeletons, namely members of the Hydrozoa (notably the Milleporina) and of the Anthozoa (the octocorallian *Heliopora* and *Tubipora* and the Scleractinia or Madreporaria). Attention is further restricted to the hermatypic (i.e. reef-building) species which live in shallow tropical waters. As living organisms these cannot be considered without relation to the highly complex marine communities or coral reefs of which they are the most characteristic, if not always the most numerous or even the most important, members. These reefs may be divided into fringing reefs, barrier reefs, atolls and also, as suggested by Wells (1957), patch reefs. The latter would apparently cover all but the first three categories, i.e. anything from a coral patch in an atoll lagoon to much more complex coral formations such as the low wooded islands in the lagoon channels within barrier reefs or the ring-shaped faros originally described in association with the atolls of the Maldives. While knowledge of the mode of growth of corals and of the effect on this of the forces of the physical and biological environment is essential to our understanding of coral reefs, the origin of the platforms on which reefs have grown up—and which constitutes the real "coral reef problem"—lies within the province of the geologist and the geographer and is not a matter with which a biologist is directly concerned. It will not receive more than incidental mention here.

Historically, the scientific study of coral reefs begins with the work of Darwin. In a centennial survey of his work this author was impressed by the paucity of Darwin's personal contacts with reefs. While on the *Beagle* he " had viewed atolls and barrier reefs from afar in the Pacific; he had examined one atoll with some care in the Indian Ocean where he had also viewed the fringing reef at Mauritius. He had seen living corals of many types and obtained some impression of their distribution in depth and also in relation to exposure on windward and leeward surfaces. And he had obtained some information, not all of it, as it eventually turned out, correct, about the submarine contours of coral reefs " (Yonge, 1958a). It was on the soundness of Darwin's observations on the distribution in depth and on the growth in exposure and shelter of living corals (coupled, of course, with his appreciation of the possibility of widespread subsidence) that the fundamental soundness of his conclusions rests. Hence a modern definition of a coral reef, such as that given by Wells (1957), represents essentially no more than an amplification of Darwin's original description.

In later nineteenth century and early twentieth century work on coral reefs, based largely on geographical surveys of reefs and subsequent museum description of coral skeletons, the living animal was largely overlooked. The geologist, T. Wayland Vaughan, in association with A. G. Mayor, was the first to study corals in relation to their environment and largely in the then recently established Tortugas Laboratory of the Carnegie Institution of Washington. His survey of this work in his " Corals and the Formation of Coral Reefs " (1919) may be regarded as the starting point in the modern study of living hermatypic corals. Undoubtedly, work had been hampered by lack of marine laboratories within coral reef areas. Between the First and Second World Wars this was partly made good by the establishment of a Dutch Laboratory at Batavia from which investigations were conducted on reefs throughout the East Indies, by the work of the Great Barrier Reef Expedition which, in 1928 to 1929, established a marine laboratory for 13 months at Low Isles, N. Queensland, and by the foundation by the Japanese in 1935 of the Palao Tropical Biological Station with a research programme based largely on the results of the Great Barrier Reef Expedition and so primarily biological. Meanwhile, the Tortugas Laboratory was opened for 3 summer months annually although work on corals diminished. Corals were little studied at the Bermuda Laboratory, admittedly at the northern limit of coral growth although, despite similar limitations, at Hawaii much valuable work came from the largely unaided efforts of C. H. Edmondson.

In this author's account of " The Biology of Coral Reefs " which

forms the final paper in Volume I of the Reports of the Great Barrier Reef Expedition (Yonge, 1940), the work of these laboratories was reviewed. Only the two last, and least important, survived the war. The Tortugas Laboratory was closed in 1940, the Dutch and Japanese lost not only their laboratories but the territories on which they were situated.

Since the war new activities have appeared. In the Atlantic the Lerner Laboratory at Bimini in the Bahamas and the Marine Laboratory of the University of Miami have replaced the Tortugas Laboratory, although no great attention has been paid to corals. The major activities in this field have come from the highly important work of Norman D. Newell and co-workers on the form and nature of West Indian and Bahamian reefs and that of T. F. Goreau of the University College of the West Indies, Jamaica, on the physiology and ecology of corals. His researches, with those coming from the Haskins Laboratory, New York, on zooxanthellae, undoubtedly represent the major recent contributions to our knowledge of living corals. And it should here be noted that a distinction must be drawn between the needs of an individual coral colony and those of the community (even if considered to be no more than the sum of all coral colonies) of which it forms a part.

Activities in the Pacific have been almost entirely American. They have been carried out by the United States government and been largely concentrated on the Marshall and Caroline Islands which became U.S. Trust Territory after the last war. There was immediate military need for information following a war fought in coral seas when too little was known about reefs and especially about atolls of which these islands largely consist. These investigations were intensified before and after the nuclear bomb tests at Bikini and adjacent atolls in the Marshall Islands. A massive series of reports, primarily geological and oceanographical but with many important biological data, have appeared, together with the *Atoll Research Bulletins* produced by the Pacific Science Board of the National Research Council and National Academy of Sciences. Papers in these Bulletins have covered every aspect of life on atolls, from anthropology to the ecology and systematics of the terrestrial and marine fauna and flora. Fortunately much of this work has recently been brought together in " Atoll Environment and Ecology " by Harold J. Wiens (1962).

Other major activities in the Pacific have included the important expedition to Raroia (Kon Tiki) Atoll in the Tuamotu Archipelago in the south-west Pacific, led by Norman D. Newell which, although primarily geological, provided most valuable information about reef

formations and ecology in the south Pacific and enabled first-hand comparisons to be made with Atlantic reefs. It is personally pleasant to note the continued activity of the Great Barrier Reef Committee at Brisbane which has established a small marine station at Heron Island in the Capricorn Group. Further observations have also been made at Low Isles, the most intensely studied coral formation in the world.

In addition, a variety of papers dealing with some aspect of the biology of corals and coral reefs have come from varied sources such as the Marine Biological Station at Ghardaqa (Red Sea), from various expeditions and above all from the notable series of systematic reports on coral collections mentioned later.

It is far from easy to deal adequately with the mass of information represented by these investigations in the major tropical oceans and pursued from such very varying standpoints. The two major themes are undoubtedly the intensive work on atolls in the Pacific, primarily geological and oceanographical but dealing with formations that owe their existence to the activities of living organisms, and the more intimate researches into the physiology of corals and their symbiotic zooxanthellae being carried out by T. F. Goreau at Jamaica. Some link between the two is provided by the attempts at evaluating productivity on Pacific reefs, notably by Odum and Odum (1955).

It would, however, appear best to deal with the general before the particular, i.e. to discuss reviews of coral reef problems and systematic work (including development) and then deal with the post-war work on Pacific atolls (including ecological findings). The comparative work of Newell gives a link with Atlantic reefs. On the other hand, the various estimates of productivity carried out on Pacific reefs are most suitably discussed after consideration of modern work on zooxanthellae coming from the Haskins Laboratory and of Goreau's investigations at Jamaica. These represent the present growing point in research on the individual coral on which, in the last resort, all else depends. It is gratifying to know that Dr. Goreau will himself be dealing with this in more authoritative detail in a forthcoming review.

II. Reviews

The great revival of interest in coral reefs is indicated by the number of review articles, all by geologists or palaeontologists writing from first-hand knowledge of reefs, which have appeared relatively recently. Ladd and Tracey (1949) give an authoritative sketch of post-Darwinian theories concerning coral reef formation with suggestions for the most promising lines of future work. Ladd (1950) gives a survey account of

recent reefs with a description of borings up to that on Bikini (the deeper one at Eniwetok which struck the basalt foundations was made in 1952 (Ladd *et al.*, 1953)) ending with the generalization that " the more that is discovered about the geological history of any reef or reef-encircled island, the more complicated its history appears." Very recently (1961) he has published an admirable general survey of coral reefs. But his only direct reference to living corals concerns growth with a mention of organic productivity. The more popular, but no less authoritative, paper by Newell (1959) again outlines the history of the coral reef controversy but contains an excellent comparison of Pacific and Atlantic reefs (to be discussed later) with a general account of the biology of coral reefs.

Umbgrove (1947), another geologist with exceptionally wide experience of coral reefs, this time in the East Indies, reviewed the results of 15 years of work before 1940 on reefs widely scattered through that region. Although he covered the work of other Dutch investigators, notably Kuenen, Verwey and Boschma (the last two being zoologists) the main biological implications of his review concern the environmental forces which influence coral growth.

There is finally the invaluable account of coral reefs by Wells (1957) in the first volume of the " Treatise on Marine Ecology and Paleoecology " and which, in relatively short space, gives the most comprehensive general account of coral reefs, in all their varied aspects, known to this author. He begins by noting that coral reefs " are scattered over an area of 190,000,000 square kilometres (68,000,000 square miles) wherever a suitable substratum lies within the lighted waters of the tropics beyond the influence of continental sediments, and away from the cool upwellings of the sea in the eastern parts of the oceans' basins." He refers later to " The coral-reef biotope " as " a facies of the marine tropical biochore ", with its " essential fauna and flora " as consisting " of corals and calcareous algae which dominate in numbers and volume and provide the ecological niches essential to the existence of all other reef-dwelling animals and plants." It follows from this that " The existence and potentialities of reefs are largely conditioned by the ecological requirements of hermatypic corals and calcareous algae." Here we have Darwin's original definition amplified and brought up to date.

III. Systematics and Distribution

Passing to works of systematic importance there come first the " Revision of the Suborders, Families, and Genera of the Scleractinia " by Vaughan and Wells (1943) and the comprehensive account of the

Scleractinia (Wells, 1956) in the "Treatise on Invertebrate Paleontology". These deal with structure (notably of the skeleton), physiology, ecology and distribution of corals. Both vertically and horizontally, starting from shallow mid-tropical waters, hermatypic corals diminish in numbers, giving place eventually to ahermatypic species. The probable course of evolution, in terms of skeletal elaboration, is outlined, but the difference in the sequence of development of organs and skeletal parts noted by Atoda (1953) may also be relevant here. It would also be illuminating if skeletal changes could be related to greater efficiency and wider powers of adaptation. Modern corals are highly adapted for life in the many different environments present on modern reefs and also for capturing zooplankton of all sizes. The form of the skeleton plays its part in these adaptations.

Knowledge of the coral fauna of the Eastern Pacific, from the Gulf of California, the Galapagos and other offshore islands, has been greatly extended by the work of Durham (1947, 1962), Durham and Barnard (1952), Hertlein and Emerson (1957), Squires (1959) and Durham and Allison (1960). Although apparently somewhat modified by later work, Durham and Barnard list a coral fauna of ninety-eight species representing thirty-nine genera. Although twenty-seven of these species are hermatypic, conditions, largely of temperature, prevent the formation of reefs. In a very full description of the recent (and also Pleistocene and Pliocene) coral fauna of the Gulf of California, Squires (1959) notes the gradual impoverishment going north. A southern fauna consisting of species of *Pavona*, *Pocillopora* and *Porites* loses first the species of *Pavona* and then of *Pocillopora* and finally those of *Porites*, which give place to kelp in the northernmost and coldest waters of the Gulf. Squires also notes that the coral fauna of the eastern Pacific has little affinity with that of the West Indian region, being essentially Indo-Pacific. The effect of Ekman's Eastern Pacific Barrier is negligible, at any rate for scleractinians, the more hardy of which are distributed over the entire width of the Pacific. The major recent contributions to coral systematics by Boschma, one of the most distinguished of modern workers on corals, are a series of papers (1948a, b, 1949, 1950, 1951) on the Hydrocorallia (not a systematic unit but a convenient term covering the very different Milleporina and Stylasterina formerly grouped together in the Hydrocorallinae). As discussed below, he has made a major contribution to the species problem in *Millepora*, deciding that instead of the one species suggested by Hickson, there are at least ten.

Major collections of corals from two of the richest areas in the world, the Great Barrier Reef of Australia and the Marshall Islands, have been

reported on by Crossland (1952) and Stephenson and Wells (1956) and by Wells (1954) respectively. These reports are the more valuable because of the wide field experience of the authors. Crossland spent much of his life studying first Indian Ocean and then Pacific corals and coral reefs. The collections of the Great Barrier Reef Expedition, which could cover only small sections of the 1250 miles of the Barrier series, consisted, Crossland found, of 174 species belonging to 54 genera and of these he states " 30 species are new, 2 of Barnard's have been given new names, and there are several curious varieties, 3 of which have been given names." Later, in the course of a survey of the coral fauna of Low Isles still affected by the cyclone of 1950, Stephenson and Wells (1956) estimated a possible 150 species. Wells (1955) has further shown how the number of coral species diminishes from north to south along the Barrier. No new species appear; hermatypic corals are always most abundant in the mid-tropics.

Regarding the Marshall Islands, Wells (1954) states that the coral fauna " includes 240 species and varieties (22 new) representing 52 genera (1 new) of hermatypic scleractinian corals, 15 species and varieties (3 new) representing 10 genera (1 new) of ahermatypic forms, and 11 species representing 6 genera of nonscleractinian corals." Wells had personal knowledge of the Marshall Islands and supplies important information, summarized later, about the distribution of corals on the seaward and lagoon reefs. He also discusses the wider question of the general distribution of Indo-Pacific corals.

Wells (1950) and Searle (1956) have described the coral fauna of Cocos-Keeling atoll and of Malaya and gradually the major task of describing the Indo-Pacific fauna is being accomplished. It is questionable whether there will again be papers equal in length to those of Crossland (1952) and Wells (1954) although major taxonomic problems remain. Knowledge about Atlantic corals is probably less complete; in a personal communication, Dr. T. F. Goreau states that publication of recent work in the West Indies is held up because of taxonomic difficulties.

The major difficulty persists of deciding the limits of variability within sessile animals forming large colonies, the growth form of which is inevitably—but also differentially— influenced by water movements. The tendency of the nineteenth century museum taxonomist studying coral skeletons was to multiply species. The later reaction of the field worker was to go to the other extreme and convert these museum species into growth forms. Thus *Millepora* was reduced by Hickson to the single species, *M. alcicornis* Linnaeus. More recently taxonomy has been largely in the hands of those who are also field workers and with

interesting results. Thus Wells (1954) reduced five species of *Porites* to one, *P. lichen*. On the other hand, Boschma (1948b, 1949, 1950) reversed Hickson's ruling by re-establishing, on the basis of the form of the skeleton and of the ampullae, eight formerly described species of *Millepora* and adding a new species, making ten in all. Crossland (1952) added yet another species.

Boschma's explanation (1948a) of the diversity of forms in *Millepora* —it may well serve for many other genera of hermatypic corals— involving both species and growth forms deserves to be quoted. " There are a number of species of *Millepora*, each of which is so strongly variable that under the influence of external conditions it may assume a form which is more or less typical for another species. If a *Millepora* larva happens to become fixed on a spot where the conditions of existence are ideal for the species, it grows out to a colony of the typical form. If it happens to become fixed on a spot where the conditions of existence for this particular species are unfavourable it may grow out to a colony with a growth form quite different from that of the typical form. If it happens to become fixed on a spot where the conditions of existence are altogether unsuitable for this particular species (although other species of *Millepora* may find here ideal conditions for a luxuriant development) the young colony dies. It is not to be denied that certain species which have a pronounced preference for distinct parts of the reefs in these parts only develop into colonies of the typical shape. A good example forms *M. platyphylla* that attains its most vigorous growth (the " honeycomb facies ") on the surf-swept edge of the reefs only, and changes into a leafy form when living in the quieter water of the lagoon."

As formerly stressed (Yonge, 1940), the great success of the Scleractinia may well be due to the presence of species highly adapted for a particular habitat along with others capable of modification to produce a variety of growth forms capable of life in a variety of environments. The relation between form and the two factors of light and water movement is shown in the work by Abel (1959) on the ahermatypic Mediterranean coral, *Cladocera cespitosa*. Similar observations could very suitably be made on tropical reef-builders.

IV. Settlement of Planulae

Final distinction between growth forms and species can only be achieved by observations in the field such as were carried out in the course of the Great Barrier Reef Expedition when marked corals were moved from one environment to another or colonies were split and the

two halves then exposed to different environments. A long-term programme of such experiments would be of great taxonomic value. Further possibilities are presented by the fusion of recently settled planulae which then give rise to colonies having the same form as those which arise from a single planula. Fusion of planulae has been observed in species of *Siderastrea*, *Pocillopora* and *Porites* and also in *Manicina areolata*. Identically shaped oval colonies of the last of these may consist of one, two or three " valley " systems indicating formation from one to three original planulae (Yonge, 1935a). There is here, it seems, a means of determining the effects of genetic constitution and of the environment. If planulae of known origin could be induced to settle together (and although in many planulation does occur at different phases of the moon there appears to be considerable overlap (see Atoda, 1947a, b, 1951 b, c)) successful fusion would indicate origin from different growth forms of the same species, failure to fuse origin from different species. It is, of course, possible that composite colonies might be produced, particularly if allied species with different breeding seasons could be induced to breed at the same time. This would be of no less interest, especially if the growth of the composite colony could be compared with that of each parental species.

Factors influencing the settlement of planulae have never been adequately analysed. Working on species of *Pocillopora*, *Seriatopora*, *Acrhelia* and *Euphyllia*, Kawaguti (1941b) found that within a certain range of light intensity, progressively lower in the order listed, all were positively phototactic, the reaction reversing in higher light intensities. All were negatively geotactic. Distribution of the adult colonies bore some relation to the reactions of their planulae. These in turn appeared to be correlated with the concentration of zooxanthellae. Edmondson (1946) tested the reaction of planulae of *Pocillopora damicornis*, *Cyphastrea ocellini* and the ahermatypic *Dendrophyllia manni*. His results indicate the greater abundance in surface waters of planulae during darkness or subdued light, i.e. a major effect of negative geotaxis. Like Kawaguti, he noted positive thigmotaxis. He observed reactions to temperature and salinity changes but more significantly noted that while the larvae of *Cyphastrea* and *Dendrophyllia* would both settle in total darkness, the young polyps of the latter (without zooxanthellae) survived for up to seven months, whereas those of the former soon died. Planulae of these two species, but not of *P. damicornis*, tended to settle in aggregations.

In a series of papers (1947a, b, 1951a, b, c, 1953), Atoda has described planulation, planulae, settlement and early development in *Pocillopora damicornis cespitosa*, *Stylophora pistillata*, *Acropora brüggemanni*,

Galaxea aspera and *Seriatopora hystrix* and also (1951d) asexual reproduction in the Seriatoporidae. Planulation occurs throughout the year and in all except *Acropora brüggemanni* in relation to some phase of the moon (a condition already known in some other corals). Although usually settling quickly, planulae can remain swimming for a considerable period. He confirmed and extended the observations of Edmondson that darkness delays settlement and found that it also retards subsequent development. With suitable facilities such studies could be greatly extended.

Factors governing settlement, including the nature of the substratum and aggregation, are of prime importance for sedentary animals. They have been extensively studied in temperate waters, notably in connexion with acorn barnacles, with *Spirorbis* and with species of *Ostrea* and *Crassostrea*. In corals there is the added problem of the effect of aggregation on the formation of compound colonies. There is also the later loss of attachment in certain genera and species, in the Indo-Pacific fungids and in the Atlantic maeandrine *Manicina areolata*, and in the ahermatypic Turbinoliinae which are adapted for life on an unstable substratum which, as noted by Vaughan and Wells (1943), gives little surface for settlement of the planulae.

V. Ecology of Atolls

The major contribution to the classic coral reef problem since World War II has come from the extensive United States investigations in the Marshall and Caroline Islands. Many atolls, notably Bikini and Eniwetok, have been examined in great oceanographical, geological and geographical detail. The major biological zones have been clearly defined. A comprehensive account of all aspects of this, extending of course to land flora and fauna and every aspect of human habitation, has recently been made by Wiens (1962) who has himself made notable contributions in the geographical field. These investigations may be said to have culminated in the final boring on Eniwetok where basalt was encountered at 4630 ft, the deepest coral being of late Eocene formation (Ladd *et al.*, 1953). The atoll is revealed as resting on a truncated volcano possibly similar in nature to the numerous sea mounts or guyots present in the north-west Pacific (Hamilton, 1956). Certainly to the east of the andesite line which represents the western limit of the Pacific basin, Darwin's views appear triumphantly justified. To the west of the line where there is extensive elevation, as at Tonga and Fiji, the course of reef formation must have been different.

The initial result of these surveys has been to confirm and extend

previous observations on the influence of trade winds on the configuration of reefs (see Yonge, 1951). The often striking differences between windward and leeward reefs were clearly demonstrated by the Dutch surveys in East Indian waters which have been summarized by Umbgrove (1947). In more intimate detail, at Low Isles and elsewhere, they are described in the reports of the Great Barrier Reef Expedition. The wide diversity of ecological niches on coral reefs has been revealed. This is even greater on atolls where in addition to exposed and sheltered outer shores (NE and SE and SW and NW respectively north and south of the equator) there is the enclosed lagoon with its exposed and sheltered shores (here SW and NW and NE and SE respectively). The consequent further increased environmental complexity influences the distribution of corals and other reef organisms. There can be no region of comparable size in the sea with such a diversity of ecological niches as an atoll.

The first stage in the analysis of such conditions must be descriptive. The geological background to Bikini and adjacent atolls has been provided by Tracey *et al.* (1948), Ladd *et al.* (1953) and Emery *et al.* (1954) while Munk and Sargent (1954) have described the interactions between the growth of the living reef surface and the force of the waves. The major biological survey is by Wells (1954) and can be only briefly summarized.

Viewed in section, as shown in Fig. 1, these Pacific atolls may be divided into the following regions (Tracey *et al.*, 1955) starting from the windward. (1) The outer seaward slope with a pronounced reduction in corals and coralline algae below about 10 fathoms. (2) A shallow " sublittoral " region with more gradual slope, rich coral population and often locally terraced. (3) The seaward reef margin with its algal ridge of *Porolithon* (= *Lithothamnion*) and characteristic surge channels (in region indicated by $\times$). (4, 5) An outer and an inner reef flat with characteristic zones of coral population described below. (6) The seaward beach of the island, usually buttressed with beach rock. (7) The more sheltered lagoon beach. (8) The shallow lagoon reef flat or lagoon shelf. (9) The lagoon reef margin. (10) The sheltered lagoon slope. (11) The lagoon floor. (12) Coral knolls or pinnacles (patch reefs) that rise in great numbers from the flat lagoon floor which is itself characteristically covered with the green calcareous weed *Halimeda*. Intense echo sounding has revealed the great abundance of these coral masses, over 2000 in the 24-mile-long lagoon at Eniwetok (Emery, 1948). (13) The more irregular and richer exposed lagoon slope leading to the lagoon reef margin (14). (15) The reef flat on the leeward side. (16) The seaward reef margin here without an algal ridge and surge

channels. (17) The reef slope with coral growth notably decreasing at about 10 fathoms but without the local terracing of the corresponding windward depths.

The further analysis of the more windward environments in terms of the coral species most characteristic of the different zones on Bikini is supplied by Wells (1954) and is illustrated in Fig. 2. With numbers indicating the same zones as in the preceding figure, the major areas are: A (=1), the seaward slope; B, the seaward reef; C, the island; D, the lagoon. Wells distinguished the following zones (indicated by the corresponding lettering in Fig. 2) in terms of their dominant corals. (a) *Sclerhelia-Dendrophyllia* zone of ahermatypic corals below 80 fathoms. (b) *Leptoseris* zone (between 50 and 80 fathoms) " marked by special species or a facies which differs from those of the surface reef forms but is not truly ahermatypic ". (c) *Echinophyllia* zone from 10 to 50 fathoms and the lowest to which " surface reef species extend and grow with any degree of strength". Then on the upper surface of the reef in regions of decreasing exposure come (d) the *Acropora cuneata* zone, (e) the *Acropora digitifera* zone, (f) the *Acropora palifera* zone, (g) a highly characteristic *Heliopora* zone with large colonies of this blue octocorallian, and (h) the *Porites lutea* zone. The three last occupy the greater part of the just-submerged reef flat (4–5), a region which Wells describes as that of microatolls (z). Their formation is the result of limited possibilities of upward growth causing the colonies, killed off at their summits, to enlarge peripherally around a dead and often partly excavated centre. The sheltered margins of the lagoon are characterized by (i) a *Porites andrewsi* zone and then (j) an *Acropora reticulata* zone found both on the lagoon reef flat (9) and at corresponding shallow depths near the summits of the coral patches. This overlaps with (k) an *Acropora formosa* zone which extends generally over the lagoon floor and terrace (l) an *Acropora rayneri* subzone entirely confined to the floor.

The highly significant environmental differences between the reef margins on the windward and leeward sides of reefs, already noted elsewhere, e.g. in East Indian reefs (Umbgrove, 1947) and at Low Isles and reefs of the Great Barrier series, have been described in great detail for these atolls, notably by Tracey *et al.* (1948), Munk and Sargent (1954) and Wells (1954, 1957). The windward margin, fully exposed to the oceanic surf, invariably possesses a massive algal ridge composed largely of *Porolithon* (= *Lithothamnion*) which extends seaward to a depth of up to 10 fathoms in the form of a series of buttresses or spurs with deep intervening grooves or surge channels (Fig. 3). Especially in regions of greatest exposure the upper end of these

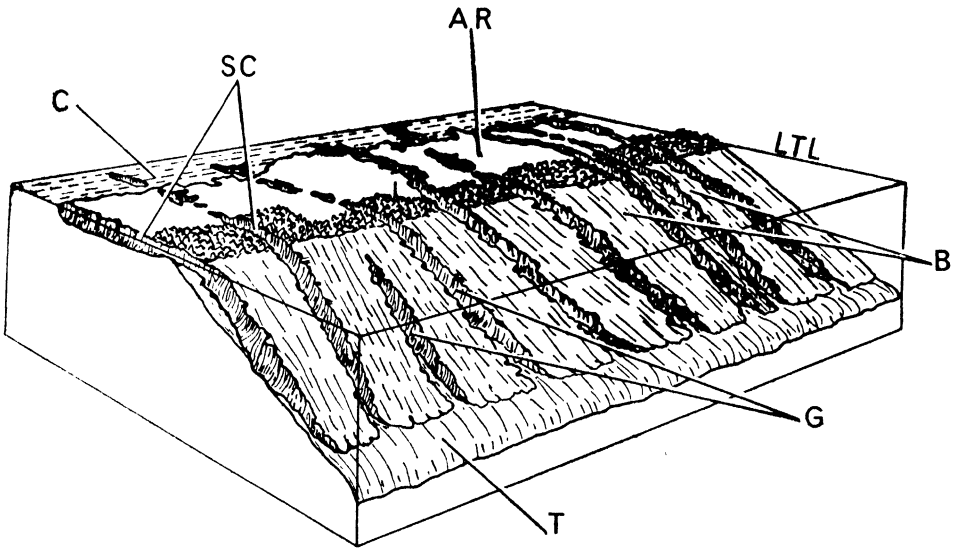


FIG. 3. Generalized sketch of seaward face and top of reef on windward side of Bikini Atoll. AR, algal ridge; B, buttresses or spurs; C, coral of reef flat; G, grooves; LTL, low tide level; SC, surge channels; T, terrace (about 10 fathoms). (After Munk and Sargent, 1954.)

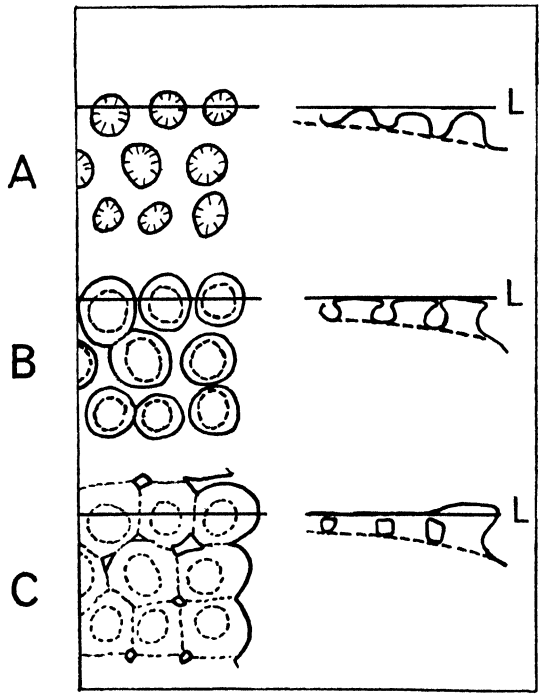


FIG. 4. Diagrams illustrating formation of room and pillar structures. Left, viewed from above; right, viewed in section. A, bosses of *Porolithon*; B, shelving and lateral growth in surf zone; C, development of new reef floor, with room and pillar structure below; L, low tide level. (After Tracey *et al.*, 1948.)

channels may become overarched by the upward growth of mushroom-topped masses of calcareous algae which then fuse with one another leaving channels below. Water entering along the surge channels is violently expelled through a series of blow holes on the reef surface. Details of these " room-and-pillar " structures are given in Fig. 4. As described in detail by Munk and Sargent (1954), the effect of the surge channels is to counter the force of entering seas. They are, as shown very clearly at Bikini, confined to the windward surfaces of the reef and play a clearly essential role in the maintenance of the reef mass against the full force of the oceanic surf.

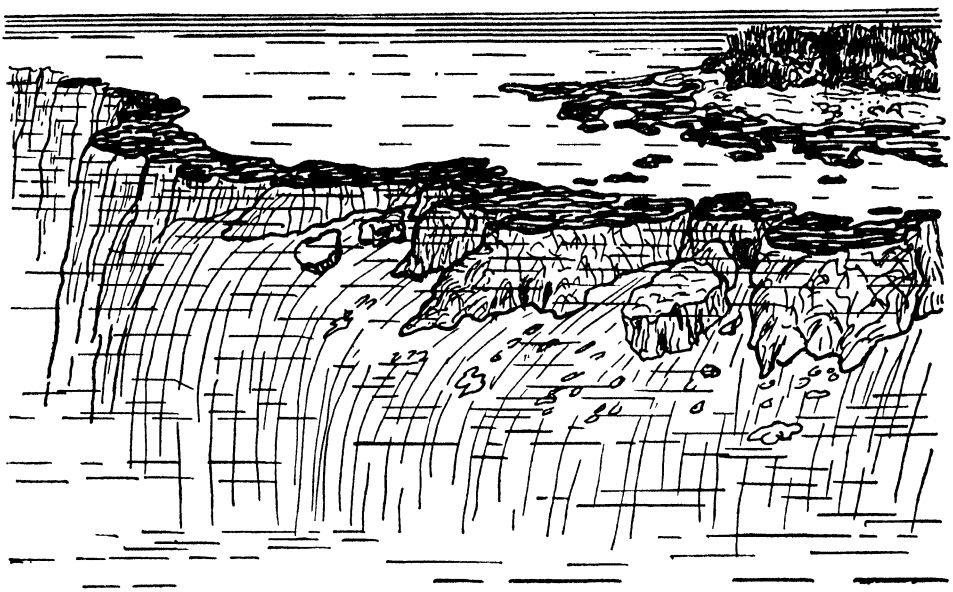


FIG. 5. Leeward reef edge at Rongelap Atoll showing large erosional re-entrants and almost vertical descent to depths of more than 30 fathoms. (After Tracey *et al.*, 1948.)

Marginal reefs on the leeward side, e.g. on the western side of Bikini, show evidence of some mechanical erosion due to summer change in winds. There is here a steeper seaward slope while embayments, often with contained boulders, are formed by collapse of portions of the reef margin (Fig. 5). This is essentially similar (on a far larger scale, admittedly) to conditions in the lee of Low Isles. Coral grows there with great profusion and usually under no constraint from the force of wind and weather. It is therefore in no condition to withstand the force of occasional summer storms of cyclonic force when great masses of coral are dislodged and thrown on to the surface of the reef flat. There it forms a conspicuous " boulder zone " but on the leeward, *not*

the windward, side of the reef flat. While conditions on the lee of an atoll, which cannot provide the same degree of shelter, are much more stable, this evidence of erosion does indicate the greater effect of storms on this usually more protected side of the reef.

There is general confirmation of these over-all findings in a variety of other surveys, e.g. in the Caroline Islands, by Tracey *et al.* (1961) working on Ifaluk Atoll, in the Tuamotu Archipelago of the South Pacific, following the important survey by Newell (1956) and co-workers* and, although here modified to a greater extent, in Caribbean reef formations off British Honduras (Stoddart, 1962a).

Detailed studies of particular areas, let alone work on the autecology of important species of corals—such as the study of *Goniastrea aspera* at Palao carried out by Motoda (1940b)—have hardly yet been attempted. Again, reference should be made to the relevant chapters in Wiens (1962) and in particular to the survey of Raroia (Newell, 1956) which involved descriptions of molluscan and other invertebrate populations (Morrison, 1954) with an account of the interrelationships of these organisms by Doty and Morrison (1954) and the plotting of the environmental niches of coral reef fishes by Harry (1953). However, it is impossible, at any rate on the basis of these Pacific studies which alone he quotes, to agree with Gerlach (1961) that " only recently has there been concern with detailed studies of the living habits of coral polyps, of their nutrition, and of their dependence on different environmental conditions ". It is precisely such work, at present only being conducted by Goreau at Jamaica (see below), which now needs to be *resumed* if we are to analyse the factors influencing the distribution of corals in the varied environments presented by a reef, and especially on an atoll. But we may accept the general conclusion of Gerlach that a reef does correspond, as Stephenson (1958) had already indicated, to the sublittoral Laminarian forests of colder seas—which does literally occur at the northern end of the Gulf of California (Squires, 1959). Above it, both a mid-littoral balanoid zone and a higher littorine zone may on occasions be identified.

VI. Atlantic Reefs

It has been generally accepted that Atlantic reefs are very much poorer than those of the Indo-Pacific with a more limited fauna of corals and associated animals and with a slower growth rate. In the light of recent information, these assumptions require some qualification. There is first the question of the coral fauna generally described by Smith (1948). According to Wells (1957) this includes " only 26

*Who report the presence of surge channels on the leeward side also at Raroia.

genera and some 35 species, compared with 80 genera and about 700 species in the Indo-Pacific ", adding that although *Acropora* and *Porites* are the most important genera in both regions, each is represented by only three species in the Atlantic compared with 150 and thirty species respectively in the Indo-Pacific. However, in 1961, Goreau extends the number of species, for the West Indies, to 46. He now considers (in correspondence noted earlier) that these numbers should be further increased.

Newell has made important comparisons between coral reefs in these two great faunistic areas, on the basis of personal experiences at Raroia (Newell, 1956) and in the Bahamas (Newell, 1955, 1958, 1959; Newell *et al.*, 1951; Newell and Imbrie, 1955). Unlike Pacific reefs, those of the West Indies are seldom on the margin of the submarine platforms from which they rise and which Newell thinks were probably formed by erosion during periods of low sea level in the Pleistocene. The reefs appear immature, seldom reaching the surface and being largely confined to more favourable, i.e. windward, areas. Owing to the long continued coolness of the West Atlantic during the Quaternary when conditions in the Indo-Pacific were tropical, the re-establishment of reefs was longer delayed and Newell does not think that West Indian reefs are more than between 3000 and 6000 years old. But they are situated on extensive platforms bounded by precipitous escarpments which very probably represent coral formations possibly originating as far back as the Jurassic and only finally killed off in the glacial periods of the Pleistocene.

Diagrams illustrating Newell's comparison between West Indian (A) and Pacific (B) reefs are shown in Fig. 6. The seaward slopes in the former are more gradual but in both he identifies a deeper " mushroom zone " (1) and a higher " elkhorn zone " (2) which reaches the always submerged reef crest in A. An algal ridge (3) which breaks the surface at low water of spring tides (the level shown in the figure) with its enclosed reef flat (4) is present only in B. What corresponds in A to the latter region but is continually submerged forms an extensive lagoon (5) much reduced in B. Recent corals form no more than a veneer over the older rocks (shown stippled) in A; this rock has been extensively increased by such coral in B (heavier stipple).

Goreau (1959b), in the first of a series of contributions which will greatly widen our knowledge, has given a detailed description of a fringing barrier formation (typical of many such) off the northern coast of Jamaica, i.e. on the weather side facing the NE trades. All is effectively submerged. By surface examination and by diving he divides the reef into the following series of zones (Fig. 7). (1) A *shore*

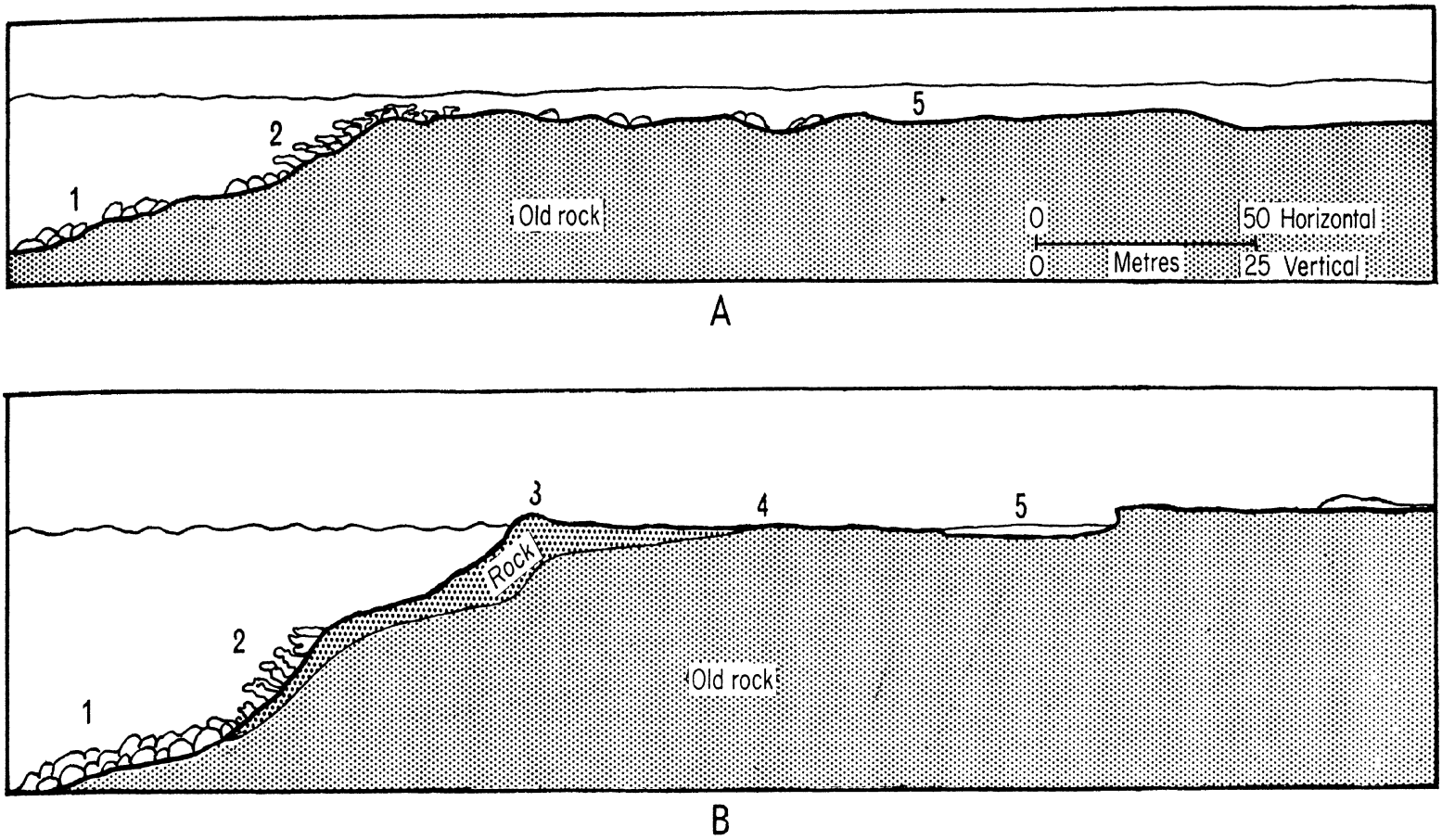


FIG. 6. Sections through windward reef margins. A, West Indian reef; B, Indo-Pacific reef. For explanation of lettering see text. (After Newell, 1959.)

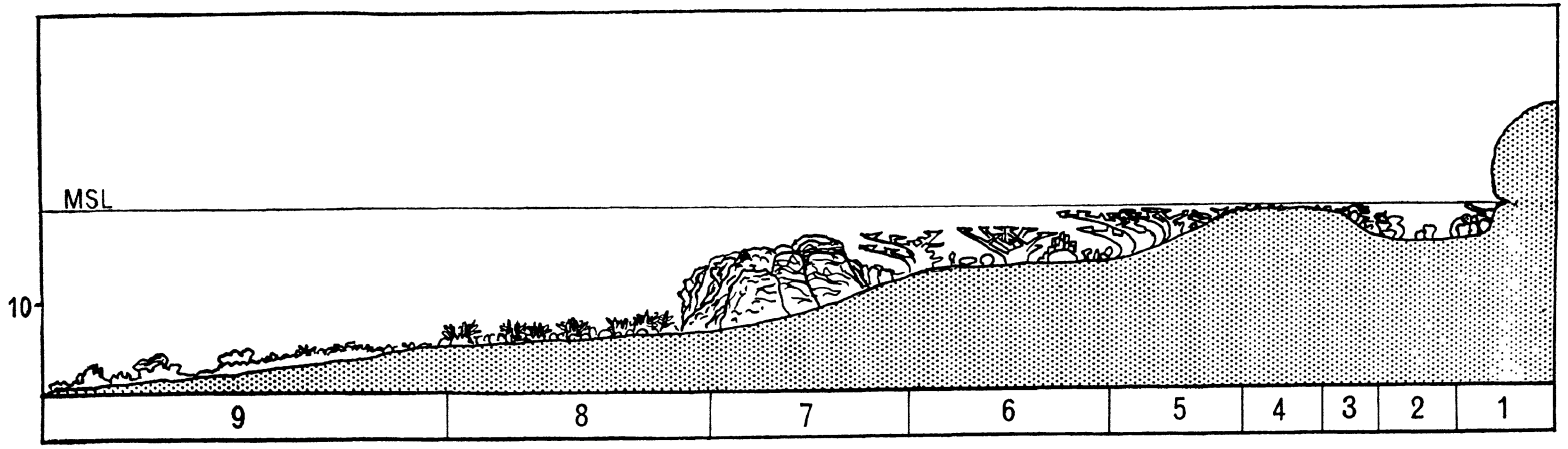


FIG. 7. Section through fringing barrier reef on north (windward) coast of Jamaica. MSL, mean sea level, depths in metres. For explanation of numbers see text. (After Goreau, 1959b.)

zone down to a depth of 3 m which has a mixed population of corals, including the most hardy species. (2) A *channel* or *lagoon zone* which is between 100 and 300 m wide and from 2 to 15 m deep. The bottom is sandy and, apart from the sand-dwelling *Manicina areolata*, commonest amongst eel grass, corals are sparse although gorgonids, molluscs and echinoderms are common. (3) A *rear zone* which represents the inner slope of the reef crest and over a depth of 2 to 3 m carries a rich population of corals including both solid and branching colonies, with the former the more numerous. (4) The *reef flat* or *Zoanthus zone*, most of which is covered by no more than half a metre of water and is about 40 m wide; it consists almost entirely of the unconsolidated skeletons of *Acropora palmata* on which there is a characteristic green growth of the zoanthid *Zoanthus sociatus* with a few corals largely confined to the shallow channel and pools. (5) The *palmata zone* which is the upper part

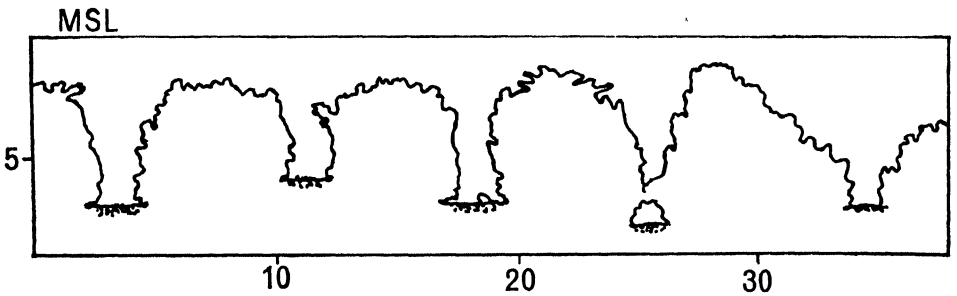


FIG. 8. Cross-sectional, i.e. east-west, transect through buttress zone (7 in Fig. 7). MSL, mean sea level. Depths and horizontal distances in metres. (After Goreau, 1959b.)

of the seaward slope descending to a maximum depth of 6 m and carrying a characteristic and almost exclusive population of "huge tree-like colonies of *Acropora palmata* which take the full force of the surf". The colonies are orientated in the direction of the prevailing seas forming " a great jagged comb with irregular teeth ". Its deeper areas (6) consist of a moat in which *A. palmata* is still dominant although more spaced out and with much dead coral below. There is also a greater wealth of other corals. (7) The *buttress zone*, which is described as " a region of spectacular underwater scenery ", consists of huge buttresses of living coral facing seaward and separated by narrow canyons up to 10 m deep, as shown in Fig. 8. More than 90% of the surface is covered with living coral colonies, the most important being the encrusting *Agaricia agaricites*, branching *Acropora palmata* and massive growths of *Montastrea annularis* which form the sides of the buttresses together with *Porites* spp. and *Millepora*. This is succeeded by (8) the *cervicornis*

zone which is from 30 to 100 m wide and from 8 to 15 m deep and is largely covered with immense beds of *Acropora cervicornis* although large colonies of *M. annularis* and *Porites* spp. also occur. (9) The *annularis zone*, which was the deepest surveyed, contains a wealth of massive coral colonies of which *M. annularis* is the most conspicuous with few *Acropora*. This reaches a depth of about 30 m.

In his account of reefs off British Honduras, Stoddart (1962a) agrees with Goreau in considering *M. annularis* as the principal reef builder with *A. palmata*, there attaining heights of 15 ft, as specialized for life in the shallower areas protected by these massive corals.

Examination of reefs off the southern coast of Jamaica also revealed zonation with increasing depth but with extensive hurricane damage. In general, therefore, there is the same pattern in these West Indian reefs as there is at Low Isles and other Australian reef formations (see Fairbridge, 1950) or at Bikini. There are elaborate windward reefs forming, to quote Goreau (1961b), " an organized coherent structure adapted for maximum attenuation of mechanical stresses set up by the constant battering of the seas " and possessing a vigour probably due to a combination of clear water and abundant planktonic food. The former, by its effect (to be described later) on the zooxanthellae, increases the rate of calcification, the latter provides for growth of the tissues and feeding surface. The major difference between fully exposed reefs in the Indo-Pacific (e.g. the Outer Barrier or NE of Bikini) and the Atlantic is the absence in the latter of a massive algal ridge breaking the surface at low water of spring tides. There is almost complete resemblance between the leeward reefs. All are less consolidated and grow in more turbid waters containing less zooplankton. They do not develop under such continuous mechanical restraint and for that reason are easily devastated by occasional cyclonic seas.

Unlike the Indo-Pacific, little of the West Indian coral fauna is ever exposed between tide marks. In his account of the ecology of the shores of Florida, Stephenson and Stephenson (1950) notes the presence of only eight, all notoriously hardy, species in this zone.

VII. Erosion

The growth processes of reef-building organisms, of which hermatypic corals are the most important, must be great enough to offset, probably normally more than offset, the effects of erosion. Destruction is the result of biological and non-biological factors, the relative importance of which is often difficult to determine. Newell and Imbrie (1955) note the conflict of views concerning the relative significance of

solution and of organic agencies in the formation of the characteristic intertidal " nick ".

We can here only concern ourselves with boring organisms, about which there is still very much to be learnt. Effectively nothing is known about the effect of the filamentous green algae invariably found as a green zone some distance within the surface of living coral colonies. Ranson (1955) notes the importance of the blue-green algae *Hyella* sp. and *Ostreobium* sp. which live on and just within the surface of coral rock while he also considers that *Porolithon* does not merely grow over but actually dissolves its way into underlying dead coral rock.

Thanks no doubt to the presence of nematocysts, corals are little affected by predators. In the West Indies, Marsden (1962) describes the activities of a coral-eating amphinomid polychaete, *Hermodice carunculata*, which crawls over *Porites porites* when it is expanded at night. It eats the polyps, fragments of which with nematocysts and zooxanthellae are found in the gut. The skeleton is presumably not affected and the tissues doubtless soon regenerate. A variety of parrot fishes (Scaridae) and file fishes (Monacanthidae) scrape or nibble living corals according to Motoda (1940b), Schultz (1948) and Bardach (1961). The latter estimated the amount, and discussed the probable importance, of the calcareous matter which passes through the gut of these omnivorous browsing fishes.

Although nematocysts protect living coral, the dead skeleton is penetrated by many organisms. Studies on Raroia by Doty and Morrison (1954) and Newell (1956) stress the significance there of blue-green algae which cover the intertidal rock surface and, possibly, of the deeper penetrating algal filaments. Together they consider these form the food of a series of gastropods which occupy very definite zones in the intertidal and supralittoral, in the order, from above downwards: *Melaraphe*—*Tectarius*—*Nerita*—*Thais*/*Morula*—*Turbo*. Of these, *Thais* and *Morula* are neogastropods and will be carnivorous, but the remainder, members of the Archaeogastropoda and Neritacea and so primarily herbivorous, doubtless scrape deeply with the radula into the rock which has previously been softened chemically by the algae. In the Atlantic, Newell and Imbrie (1955) found similar snails grazing in the intertidal " nick ".

A notable assemblage of animals bore deeply into the rock, including sipunculids (about which very little is known) and boring barnacles of the genus *Lithotrya*. Between them, Newell and Imbrie considered these worms and barnacles remove " as much as 50% of the rock substance in the intertidal nick " at Bimini. Umbgrove (1947) noted the importance of the urchin *Echinometra mathaei* in the same region in the

East Indies. Certainly in Pacific reefs, bivalve borers are no less important. Recent work on probably the most important genus, *Lithophaga*, has clearly demonstrated the initial chemical nature of the boring process and the nature of the modifications which have fitted members of the Mytilidae for boring (Yonge, 1955; Hodgkin, 1962).

Crossland (1952) associated the more vigorous coral growth characteristic of seaward reefs with " decreased activity of destructive organisms ". This is probably correct. The greatest surface of living coral occurs there and this we have seen to be largely immune from attack. Moreover, dead patches due to exposure or collections of sediment are not found on these exposed colonies. The results of an experiment involving local destruction of such seaward coral could be very informative.

Although consideration of the mechanical effects of the sea on the form of reefs lies outside the scope of this review, some of the effects of cyclones may be briefly mentioned. After its careful survey in 1928–29, Low Isles has suffered two cyclones, in 1934 and 1950. The effects of the first were almost immediately studied by Moorhouse (1936) who noted great destruction to branching corals such as *Acropora* and relatively greater survival by colonies of the more rounded *Favia*, *Porites* and the meandrines. He also observed peculiar effects in *Porites*, due apparently to stimulation of skeletal growth after lowering of the water level in the moats where these colonies live, which caused extensive damage. His paper contains a map showing the principal changes caused by the cyclone. A further, more detailed, survey was made in 1945 by Fairbridge and Teichert (1947, 1948) and Fairbridge (1950). They were particularly concerned with the formation of the shingle ramparts which move across the reef flat from the seaward side and of which four, the youngest probably originating after 1928, perhaps even after 1934, were then recognizable. They regarded them as in a state of " progressive evolution ". Damage by the cyclone had been largely repaired. A further map was produced.

The effects of the second and less severe cyclone in 1950 were studied 4 years later by Stephenson and Wells (1956) and Stephenson *et al.* (1958). Here again branching coral had suffered heavily but massive colonies had largely maintained themselves. The unstable fragments from the broken corals were still hampering recolonization on the seaward side. Further changes in the shingle ramparts were noted. These papers represent major additions to knowledge about this now well-known reef, changes in which have been so carefully studied since its original survey in 1928–29.

Turning to Atlantic reefs, Stoddart (1962a, b) has followed up an

account of reefs and cays off British Honduras with a preliminary account of a re-survey following the major hurricane of 1961. Over a stretch of some 5 miles north of the storm centre he found that 80% of the reef corals had disappeared while the summits of patch reefs were denuded of living coral. Even the groove-buttress system had been completely destroyed for 10 miles. The only surviving corals in the most devastated areas were massive forms, notably *Montastrea annularis*, already noted as the most important reef-builder amongst Atlantic corals (Goreau, 1959b).*

VIII. Physiology

Recent increase in knowledge about the physiology of corals has been largely confined to the notable work of Goreau on calcification and growth. The influence on this of the zooxanthellae demands prior description of the important recent work on these symbionts. There has been no further study of feeding, digestion, respiration or excretion since that carried out by the Great Barrier Reef Expedition (Yonge, 1930–31) and by the Palao Tropical Biological Station.

From that laboratory Kawaguti (1944b) has given an account of the pigments in various hermatypic corals. While the zooxanthellae (in the endoderm) provide a brown background, there is a wide range of pigments—green fluorescent, pink, purple, vermilion, yellow and white—in the ectoderm. The first probably serves as a protective light filter which could be the function of others. Pigments in the ahermatypic *Dendrophyllia* and *Balanophyllia* occur in both ectoderm and endoderm and are different.

Horridge (1957) studied co-ordination of protective retraction in various Scleractinia and Octocorallia. Responses to electrical stimulation in individual polyps, best seen in *Fungia*, resemble those in Actiniaria. In colonial genera, repeated stimulation may never, as in *Goniopora* and *Porites*, affect more than a local group of polyps or may eventually cause retraction of polyps throughout the entire colony.

IX. Zooxanthellae

A. *Nature*

Unicellular zooxanthellae are invariably present, usually, although not quite exclusively, confined to the endoderm, in all hermatypic corals. They lie within a type of wandering or carrier cell (see Goreau, 1961a, Fig. 8). They are normally present in the extruded planulae although, according to Atoda (1951a) not necessarily so in *Acropora*

*In the course of recent correspondence, the writer has been informed by Dr. Goreau that boring sponges are major agents of erosion on West Indian reefs.

brüggemanni. They are present in many other reef coelenterates—hydrozoans and scyphozoans as well as anthozoans—but not in ahermatypic corals. Knowledge about them has greatly increased within very recent years. They are now known to represent the vegetative stage of dinoflagellates. Hovasse (1937) had already, on morphological grounds, claimed their relationship with this group but direct proof came initially from Kawaguti (1944a) who cultivated zooxanthellae from *Acropora corymbosa* in Miquel-Allen's solution and found that some changed from spheres to motile organisms 8–12μ long and 5–8μ in diameter with the characteristic two flagella of the dinoflagellates (Fig. 9). He concluded that they were a species of *Gymnodinium*. It followed from his discovery that zooxanthella are not necessarily confined to the animal tissues and do not need to be conveyed from generation to generation by way of the egg.

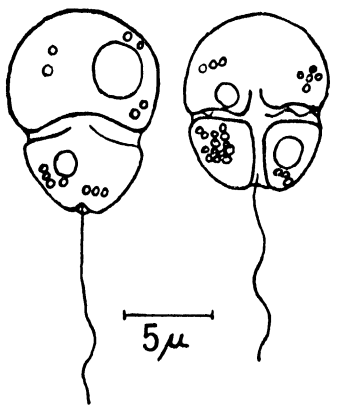


FIG. 9. *Gymnodinium* sp., dinoflagellate stage of zooxanthellae from *Acropora corymbosa*. Length of scale 5μ. (After Kawaguti, 1944a.)

Following support of this identification by Pringsheim (1955), Zahl and McLaughlin (1957) and McLaughlin and Zahl (1957), from the Haskins Laboratory, reported similar success at the Lerner Laboratory, Bimini, with the cultivation of zooxanthellae from the scyphozoan, *Cassiopeia* sp., and an anemone, *Condylactis* sp. Later (McLaughlin and Zahl, 1959) they added zooxanthellae from the Pacific anemone, *Anthopleura xanthogrammica*. They employed the most modern methods of isolation and cultivation, including the use of antibiotics, full details of which, together with a considerable bibliography, are given in the last paper. They found that, *in vitro*, (1) vegetative cells (i.e. zooxanthellae) may give rise to new vegetative cells; (2) such cells may give rise to motile cells which, in their possession of a transverse girdle, two flagella, one in the girdle and the other extending backwards, together with spiral movement, were undoubtedly dinoflagellate; (3) motile, i.e. dinoflagellate, cells were, for the first time, observed to change into

vegetative cells. They also confirmed previous impressions about the toughness of the outer membrane in the vegetative phase and gave much information about the maintenance and the nutritional requirements of these organisms. The most significant of these is the demonstrated ability " to utilize some normal animal metabolites, particularly waste products ". This, of course, lies at the base of their success as symbionts, enabling them to act as automatic agents of excretion for corals (Yonge, 1957).

The symbionts in *Cassiopeia* and *Condylactis* were identified as

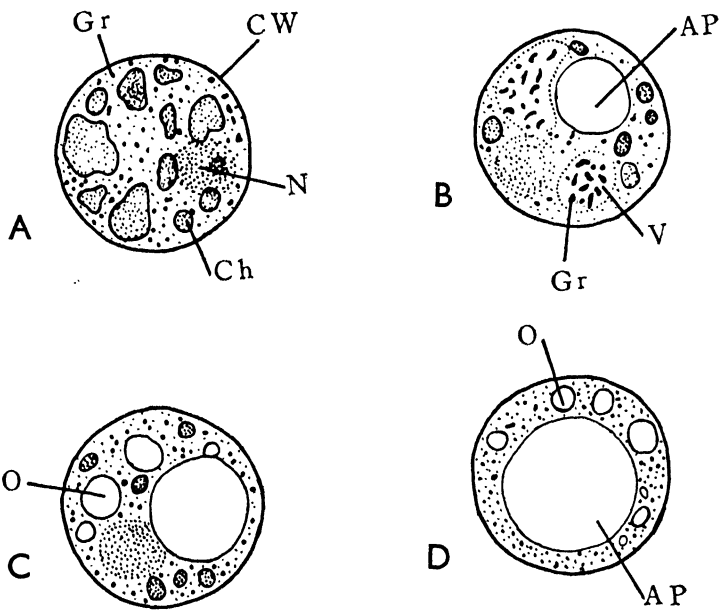


FIG. 10. *Symbiodinium microadriaticum*, vegetative cells. **A**, young vegetative cell containing numerous chloroplasts (Ch) and few products of metabolism; **B**, slightly older cell showing the characteristic brownish-orange "assimilation product" body (AP) and two vacuoles (V) containing rapidly moving granules (Gr); **C**, older cell showing a larger assimilation product and oil drops (O); **D**, very old cell containing greatly enlarged assimilation product, oil drops, numerous small granules, and no chloroplasts. CW, cell wall; N, nucleus. (After Freudenthal, 1962.)

Gymnodinium adriaticum but this has more recently been changed by Freudenthal (1962), working on those from *Cassiopeia*, to *Symbiodinium microadriaticum*. By observations of his cultures he has provided much the most complete account of the life history. Stages in the development of " the vegetative single thin-walled autotrophic cell, commonly recognized as the zooxanthella " are shown in Fig. 10A–D with details in the legend. Probably cells with a very large " assimilation product " (AP) have no further history. Others readily divide (Fig. 11B) with equal distribution of the cell inclusions apart from the " assimila-

tion product " which remains in the "parent" cell. Under certain conditions not yet fully understood, the cell wall thickens (C). These cysts may then develop into gymnodinioid zoospores (D–E) which in young cultures may form 80 to 90% of the population. Under other conditions

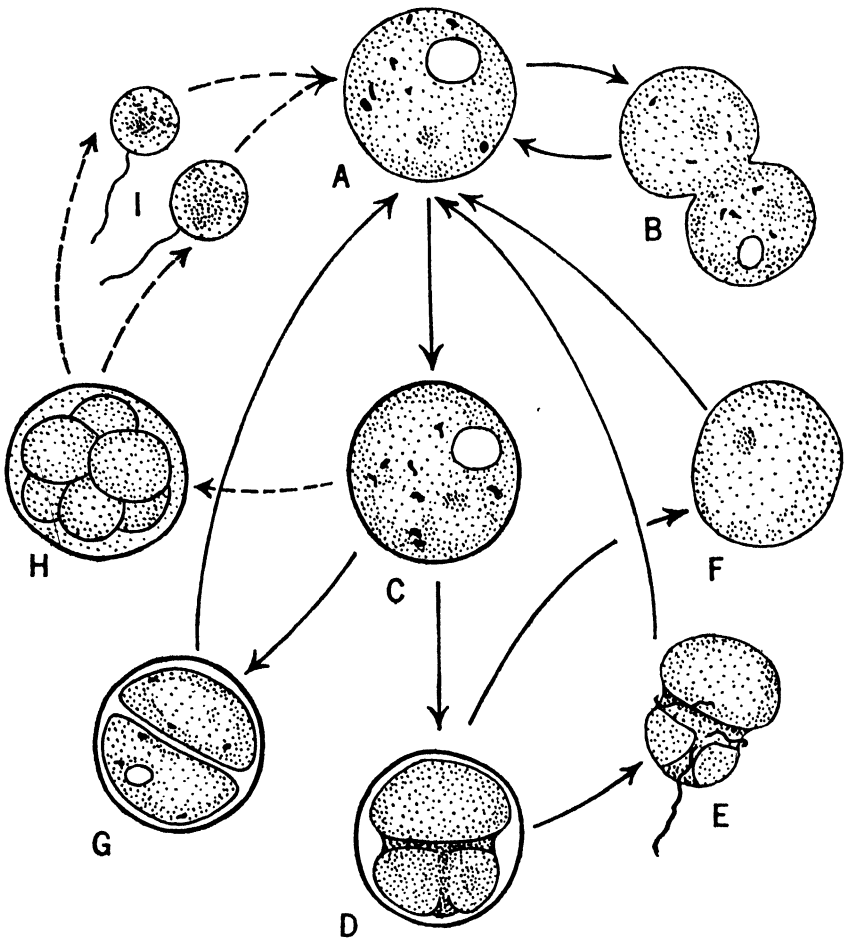


FIG. 11. Life cycle of *Symbiodinium microadriaticum*. **A,** vegetative cell; **B,** vegetative cell undergoing binary fission, producing two daughter vegetative cells; **C,** vegetative cyst, differing from the vegetative cell mainly in the thickness of the cell wall; **D,** mature zoosporangium, containing a gymnodinioid zoospore; **E,** gymnodinioid zoospore; **F,** aplanospore; **G,** cyst containing two autospores; **H,** cyst containing developing isogametes (?); **I,** liberated isogametes (?); internal detail not shown. (After Freudenthal, 1962.)

presumptive zoospores become aplanospores (D–F) which, like the zoospores, become converted into vegetative zooxanthellae (F–A; E–A). The cyst may also divide (usually into 2, sometimes into 4) forming autospores (G) which resemble the parent and on liberation

form zooxanthellae (G–A). Both in culture and also in the field, spherical bodies, each with a delicate flagellum, may appear and swarm (H, I). These, Freudenthal thinks, may be isogametes which on fusion may also give rise to zooxanthellae (this less certain sequence is indicated by the broken arrows C–H–I–A).

While all this work has been done on zooxanthellae from Scyphozoa and Actiniaria, the observations of Kawaguti (1944a) leave little doubt that the zooxanthellae in the hermatypic corals are either the same species or one with a similar life history. This assumption is here being made.

B. *Significance of the Association*

The advantage to the algal symbiont is clear. As " imprisoned phytoplankton " they gain protection. Immediate access to a source of CO_2 may be significant where algal concentrations rise to 30 000 per mm^3; this could otherwise produce severe local deficiency (Droop, 1963). Even more significant are supplies needed for protein synthesis. We now know much more than that nitrates and phosphates may be utilized. McLaughlin and Zahl (1959) have shown that as well as these inorganic sources, the zooxanthellae of *Symbiodinium* can utilize urea, uric acid, guanine, adenine or any of the twelve amino acids as a source of nitrogen, and also a wide range of phosphoric acids. Much, however, remains to be done on this subject in the experimental field. Zooxanthellae have been shown to intercept all phosphate that would normally be excreted by hermatypic corals (and is excreted by the ahermatypic *Dendrophyllia*). They will also remove all phosphate from 2·5 litres of water in which the corals were kept. When the content was raised from the normal figure of 3·41 mg/m^3 to the altogether abnormal one of 2036 mg of phosphate almost all of this was removed at the end of 5 days (Yonge and Nicholls, 1931a). The removal of ammonia from the surrounding water has also been demonstrated by Kawaguti (1953). On the other hand, lowered metabolism—resulting from starvation, exposure to sub-lethal temperatures or low oxygen tension—causes immediate ejection, via the " absorptive " zone just within the mesenterial filaments, of great numbers of algae. In other words, a major limiting factor in the concentration of zooxanthellae is the supply, from the animal in which they live, of suitable (and obviously widely ranging) sources of nitrogen and phosphorus. How much the content of zooxanthellae can be *increased* by external addition of such substances was not, but clearly could be, determined. This has bearings on the problem of calcification (see later).

For the animal the significance of the association has in the past been considered in relation to the possibility that the algae represent (1) a possible source of food, (2) a significant source of oxygen, (3) a significant contribution to excretion, (4) an aid to calcification.

It is no longer disputed that individual hermatypic coral colonies can live in darkness and so effectively without zooxanthellae (Goreau, 1959a). There is no sound evidence that hermatypic corals are not specialized carnivores (like possibly all coelenterates with the exception of the Xeniidae and related Octocorallia mentioned below). While there has been no recent work on the subject, it was shown (Yonge, 1940) that corals collect exclusively animal prey by means of (a) tentacles, (b) tentacles aided by temporary reversal of cilia, (c) orally directed cilia probably aided by extruded mesenterial filaments. There has been no further work on digestive enzymes but all that is known about those of coelenterates generally, notably sea anemones (Nicol, 1959), indicates action exclusively on animal matter.

(1) It is now known that in cultures algae excrete a wide range of organic substances, much of it mucilaginous but including peptides and glycolic acid possibly amounting in all to 50% of the carbon acquired in photosynthesis (Allen, 1956). The " juvenile " stages in the life history of the zooxanthellae (Fig. 11A) have a thin wall which would facilitate diffusion. They might even, it is suggested by Zahl and McLaughlin (1959), be actually digested by the animal. This seems improbable, the former the more likely although in this early stage little material may be extruded. It has, however, been demonstrated by Muscatine and Hand (1958), using the anemone *Anthopleura elegantissima*, that material can pass from the zooxanthellae into the animal tissues. They exposed the anemones to sea water labelled with $^{14}CO_2$ and by the use of autoradiographs showed the initial fixation of the labelled carbon in the zooxanthellae (confined to the endoderm) and its later presence widely dispersed throughout the body. Passage of material from the zooxanthellae is thus demonstrated but neither its nature nor its significance. Goreau and Goreau (1960a) have taken the matter further using the common Atlantic hermatypic corals *Manicina areolata* and *Montastrea annularis*. They ran experiments both in light and in darkness with corals containing zooxanthellae and with other corals which had lost their zooxanthellae following 3 months in complete darkness. After exposure for 50 hr to water containing $Na_2C^{14}O_3$, they found no significant uptake of radio-carbon in the dark or in the light where zooxanthellae were absent. Where these were present the tissue background activity was about five times higher than in corals kept in the dark. But they considered the level of the transfer

from the zooxanthellae to be " surprisingly low, especially if the possibility that the zooxanthellae supply the coral host with food materials is considered." Indeed, the level of radio-activity was much lower than that found by Muscatine and Hand, indicating that conditions in Actiniaria may not be a sound criterion for those in the Scleractinia. Goreau and Goreau conclude that at best the amount of transferred material could be of little significance as food. However, apart from their effect on calcium metabolism considered below, they reiterate an earlier conclusion (Goreau, 1959a), " that the zooxanthellae may have a general stimulating action on the coral host's metabolism, possibly mediated through vitamin or hormone-like trace factors which are secreted in small amounts by the algae but which by themselves do not contribute significantly to the nutrition of the coral ". Muscatine (1961) has shown that green *Chlorohydra viridissima* withstand starvation or reduced feeding better than do albino individuals. He considers that the zoochlorellae may represent a source of coenzymes or coenzyme precursors to the animal and that this may also be true of the zooxanthellae in hermatypic corals.

The obviously very different conditions existing in many of the tropical Alcyonacea, especially the Xeniidae, demand mention here. Species of the Xeniidae are common on Indo-Pacific reefs, being easily distinguishable owing to the soft velvety appearance of the large polyps. These show characteristic rhythmical pulsations recently studied by Horridge (1956). The presence of zooxanthellae and the reduction in the ventral (digestive) mesenterial filaments have long been known. Although they possess the typical eight pinnate tentacles, armed with nematocysts, Gohar (1940), working in the Red Sea, found no reaction to food of any kind. Later (1948) he found similar conditions in *Clavularia hamra* where also zooxanthellae are abundant and the mesenterial filaments poorly developed with no gland cells. " The endodermic lining of the coelenteric cavities ", he states, " is composed of small cells distended with zooxanthellae, and contain nothing else that may be considered as food."

In a series of experiments Gohar (1940) kept colonies of various species of the Xeniidae in circulating filtered and unfiltered sea water, similar sets in the light and in the dark. The unfiltered water contained zooplankton. All colonies kept in the dark gradually ceased to pulsate, showed symptoms of starvation and at the end of 2 weeks were beginning to disintegrate and were dying. When returned to the light, colonies already showing signs of starvation rapidly regained health and began to pulsate normally. Meanwhile, both sets of colonies, fed and starved, kept in the light, remained equally healthy.

This is in striking contrast to parallel experiments carried out over much longer periods on hermatypic corals at Low Isles (Yonge and Nicholls, 1931b). Colonies kept in the light and fed daily with plankton lived normally for up to 228 days (when the experiment terminated). Those starved in the light immediately began to extrude zooxanthellae. There were clear signs of starvation after only 9 days, the tissues obviously retreating. This was most clearly shown in *Fungia danai* where after 73 days the greater part of the upper surface of the skeleton was exposed, the " mouth " having about half the diameter of the disc. Colonies fed in the dark remained perfectly healthy for up to 228 days but grew paler with the continuous loss of zooxanthellae, starved for lack of light. Other colonies starved in the dark appeared much as those starved in the light except that more zooxanthellae were extruded and these were all obviously dead. More recently Goreau (1959a, 1961a) has made a regular practice of ridding hermatypic corals such as *Manicina areolata* of their zooxanthellae by keeping them for appropriate periods in darkness and without harm to the animals.

Thus in the hermatypic corals it is food, usually in the form of zooplankton, which ensures survival. Light is less relevant. In the Xeniidae, on the other hand, owing to needs of the contained zooxanthellae, light is essential but the presence or absence of zooplankton is immaterial.

In neither Scleractinia nor Alcyonacea, it may be noted, can the algae survive for long in the dark. They do not have the capacity possessed by the zoochlorellae in *Paramecium bursaria* and *Chlorohydra* of living chemotrophically at the expense of the host animal (see Yonge (1944) for references). Even when cultured, *Symbiodinium microadriaticum* shows no capacity for chemotrophy (McLaughlin and Zahl, 1959). Droop (1963) notes that " poor permeability—one of the factors responsible for obligate phototrophy—could be an advantage for life in a medium as rich in possibly toxic substrates as the interior of an animal cell."

The Alcyonacea (possibly also the Zoanthidea, according to Goreau and Goreau (1960b)), do appear to be more omnivorous than other coelenterates. In tropical, although not in temperate, species there is a range of feeding habit correlated in part with the presence of zooxanthellae. The temperate *Alcyonium digitatum* appears to be a typical coelenterate in its feeding reactions (Roushdy, 1962) although it possibly also accepts phytoplankton (Roushdy and Hansen, 1960). Nothing definite is known about the feeding habits of the numerous tropical species of *Alcyonium* but, since the work of Pratt (1905), it has been known that the ventral (i.e. digestive) mesenterial filaments of

genera containing zooxanthellae are reduced. The degree of reduction appears to be directly correlated with the abundance of zooxanthellae in the series *Lobophytum-Sarcophytum-Alcyonium* (tropical species)—*Sclerophytum* leading up to the Xeniidae in which these filaments are so reduced as to appear functionless. All of these genera demand light. Other tropical genera, such as *Acabaria* and other species of *Clavularia* (Gohar, 1940), apparently live as well in dim as in bright light.

As noted elsewhere (Yonge, 1957), the process of establishing an association between an animal and a unicellular plant must differ according to whether the animals be carnivorous (as in the Scleractinia) or herbivorous as these Alcyonacea appear to have become. In the former the animal must be initially specialized to take in and tolerate the plants, in the latter it is the plant which must be specialized to resist digestion within the animal. Certainly the end result in the two cases is very different although some source of energy additional to the zooxanthellae would appear necessary in the Xeniidae. The retention of the mouth, although narrow, is possibly significant.

Alcyonacea are often extremely abundant on Indo-Pacific (not West Indian) reefs. Thus on Low Isles they are a dominant part of the fauna, many of the colonies being large and in combined bulk covering wide areas especially in the sheltered anchorage zone as noted at the time of the Expedition and more recently by Stephenson *et al.* (1958) who noted their presence from M.L.W. to at least 20 ft below L.W.S. *Sarcophyton trocheliophorum, Lobophytum crassum* and *L. pauciflorum valdum* were conspicuous, *Simularia variabilis, S. flexibilis, S. polydactyla* and *Sphaerella echinata* were very common and *Sinularis conferta gracilis* and *Sphaerella echinata* were also present. Elsewhere *Nephthea mollis* is common, while species of *Xenia, Heteroxenia, Cespitularia, Clavularia, Pachyclavularia* and *Alcyonium* also occur. There seems little information about the abundance of these " soft corals " on the Pacific atolls.

A thorough and comparative study of feeding and digestion, in Alcyonacea showing all conditions from lack of zooxanthellae to their presence in greatest abundance, as in the Xeniidae, would be of the greatest value both for its own sake and for the light the results might show on conditions in the hermatypic corals.

(2) There have been many and extensive estimates of the oxygen produced by the zooxanthellae in the course of photosynthesis notably during the Great Barrier Reef Expedition (Yonge *et al.*, 1932). It was also found that respiration is unaffected by oxygen tension until this drops to between 40 and 50% saturation. There is certainly no recent evidence to support the view that the oxygen produced by the zooxan-

thellae is of significant value to the coral, the respiratory needs of which have been often greatly over-estimated by neglecting the effect of oxidation of the secreted mucus during the experimental period (Yonge, 1937).

(3) The presumable increase in metabolic efficiency of hermatypic corals owing to the presence of zooxanthellae which act as automatic agents of excretion (as already noted in their utilization of CO_2 and of sources of nitrogen and phosphorus) has been particularly stressed by this author (Yonge, 1940, 1944, 1957). Droop (1963) makes the added point that tropical animals frequently contain zooxanthellae whereas their relations in temperate and cold waters do not and associates this with the higher metabolic rate of the former and so their greater need for the complementary services of algae. It can be seen how natural selection would tend to preserve such an association in tropical waters.

It was felt that higher metabolism would involve faster growth which, although possibly of no particular value to the individual coral colony might " be an indispensable factor in the necessarily exceptional powers of skeletal formation possessed by the marine *communities* known as coral reefs " (Yonge, 1940). Proof of this clearly lay in experiments involving comparisons of growth rates in corals with and without contained zooxanthellae. It has recently been shown in the important work of Goreau and Goreau (see below) that hermatypic corals with zooxanthellae *do* grow faster than those deprived (by being kept in the dark) of algae. The major reason for this probably resides in the direct effect on skeletal formation, i.e. on calcium metabolism. This leads to consideration of the fourth possible effect of the association, at any rate in stony corals, namely as an aid to calcium metabolism.

(4) The possible influence of zooxanthellae on skeleton formation was experimentally studied by Kawaguti and Sakumoto (1948). Using four species of corals, they estimated the changes in calcium content in the relatively small volumes of water in which they had been kept. They claimed that uptake was greater in the light than in the dark. However, by using radioactive calcium–45 as a tracer, Goreau (1959a, 1961b) has developed an elegant and precise method enabling him to measure skeletal growth within a few hours of initial exposure. Methods have also been devised for the loading and setting out in natural sites on the reef of weighed and sealed glass jars containing corals with radioactive calcium–45 in the water, the corals later being sampled by means of a hollow steel core punch (Goreau and Goreau, 1959). Leaving for later discussion the growth data so obtained, our immediate concern is with the process of calcification and the possible role in this of the zooxanthellae.

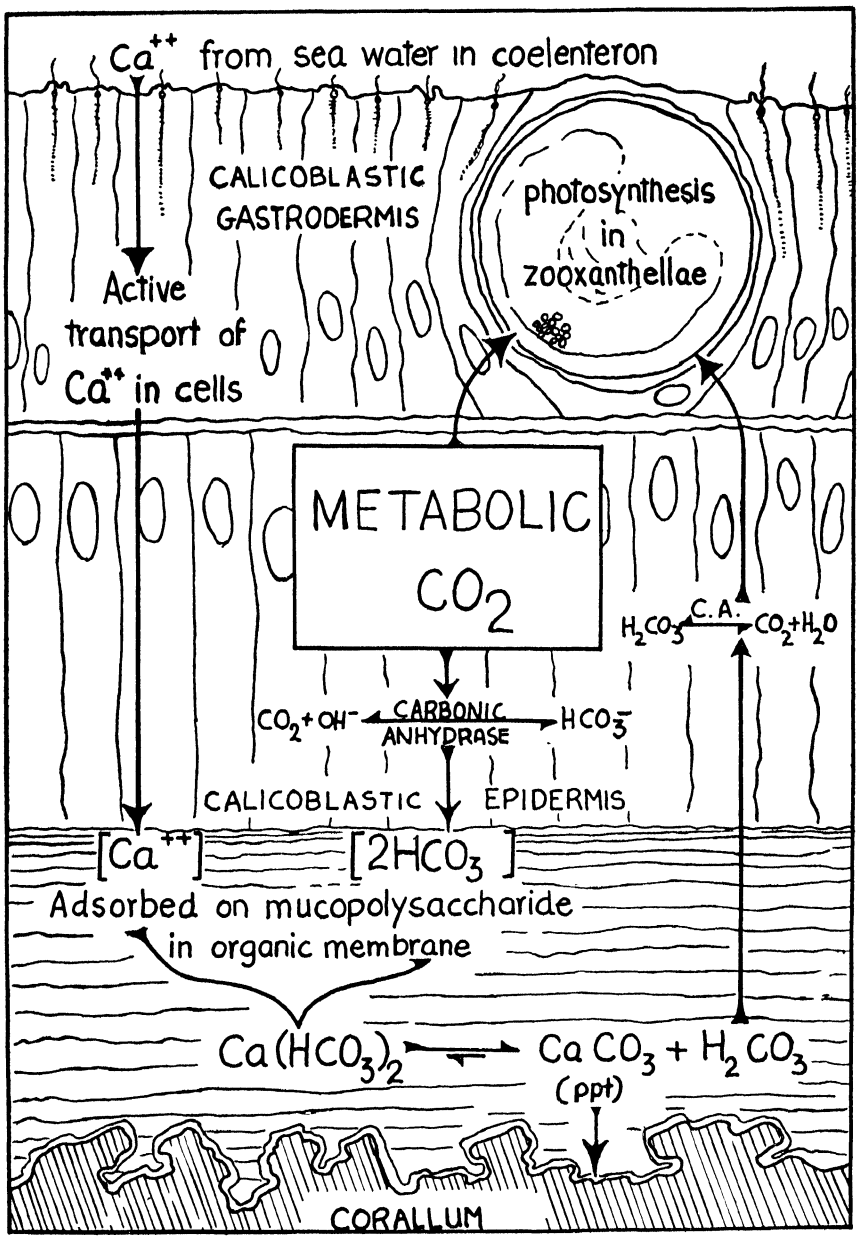


FIG. 12. Diagram (after Goreau, 1959a) showing possible pathways of calcium and carbonate during calcification in a reef-building coral. A diagrammatic cross-section of the calicoblastic body wall at the base of the polyp is shown but the parts are not drawn to scale. The coelenteron and the flagellated gastrodermis containing a zooxanthella are shown at the top of the figure, the calicoblastic epidermis is in the middle and the organic membrane with crystals of calcareous matter is at the bottom. The direction of growth is upward, i.e. calcium deposition is in a downward direction.

As shown diagrammatically in Fig. 12, calcium appears to be taken in directly from the water and not to be concentrated in the tissues prior to deposition in the skeleton. Indeed the living tissues effectively isolate the skeleton, preventing interchange or reaction with the sea water (Goreau and Goreau, 1960c). The skeleton, which consists exclusively of aragonite—the inability to secrete calcite has been suggested as a possible reason for the paucity of corals in cold waters—is, in the opinion of Goreau, formed *outside* the ectoderm cells. He postulates a passage, by as yet unknown means, of calcium through the tissues to be " adsorbed on a mucopolysaccharide-like material that forms part of the organic matrix and acts as the template upon which the initial stages of skeletal mineralization occur " (Goreau, 1961a).

He postulates that the calcium combines with bicarbonate, largely produced in metabolism, to form first calcium bicarbonate and then calcium carbonate but the efficiency of this depends on the effective removal of H_2CO_3 which depends on reactions catalysed by carbonic anhydrase. The various reactions are thus as follows:

$$Ca^{++} + 2\,HCO^-_3 \rightleftharpoons Ca(HCO_3)_2$$

$$Ca(HCO_3)_2 \rightleftharpoons CaCO_3 + H_2CO_3$$

$$H_2CO_3 \xrightleftharpoons{\text{carbonic anhydrase}} H^+ + HCO^-_3$$

$$H_2CO_3 \xrightleftharpoons{\text{carbonic anhydrase}} CO_2 + H_2O$$

The presence of carbonic anhydrase was demonstrated by treatment with the inhibitor, Diamox. Calcification was reduced by some 50% in light and 75% in darkness. The effect in light was to some extent reversed when zooxanthellae were present and photosynthesising. This is to be expected since both CO_2 and HCO_3 are fixed by these algae which would therefore assist calcification in hermatypic corals.

Indeed there can be no question about the advantage conferred by the presence of zooxanthellae. Goreau (1961b) states that growth in fourteen species is on the average ten times faster in sunlight than in darkness, calcification being actually reduced by 50% on a cloudy day. The results of experiments with *Manicina areolata* are shown in Fig. 13, the corals being deprived of zooxanthellae by a standard procedure of keeping them in darkness for 6 weeks.* By this means he has

* A much longer period was needed at Low Isles and one wonders why.

demonstrated that the much greater calcification in sunlight *is* due to the presence of zooxanthellae, the stimulatory effect of light on calcification disappearing in their absence. There was, moreover, greater calcification in darkness if zooxanthellae were present than there was in light if they were absent. This indicates that even when not photosynthesising, zooxanthellae may assist calcification by some general effect on metabolism. This could be by provision of some " growth factor " as already suggested by Goreau. But the effect of light on

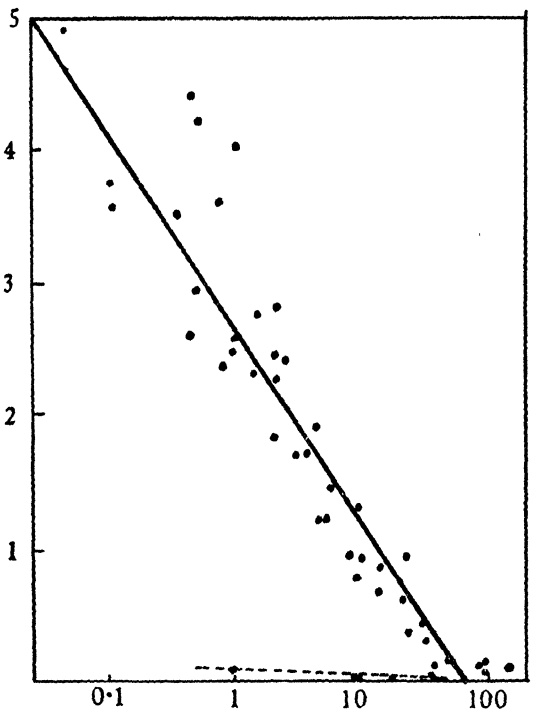


FIG. 13. *Manicina areolata*, calcification rate plotted against size. Ordinate, milligrams of calcium deposited per gram wet weight; abscissa, wet weight of colonies in grams. Solid line with zooxanthellae; dotted line *without* zooxanthellae. (After Goreau, 1961a.)

calcification (zooxanthellae being present) is so rapid that he feels some process other than one dependent on diffusion is involved. He has now (1961b) come to attribute at least some of the effect of the zooxanthellae to " speeding up the rate with which metabolic waste products are removed from the vicinity of the host's cells ", this including not only CO_2 used by the algae in photosynthesis but also available sources of nitrogen and phosphorus used in protein synthesis, i.e. much as suggested in more general terms by Yonge (1940). Since protein synthesis continues to some extent in the dark this could explain

the greater calcification in darkness when zooxanthellae are present. The " voracity " with which zooxanthellae will take in phosphorus (and presumably nitrogen) not merely from within the coral but also from the surrounding medium has already been mentioned (p. 241). It could be illuminating to discover to what extent the content of zooxanthellae in hermatypic corals could be actually *increased* by enriching the external medium with phosphates and ammonia. There is the final point that if, as suggested by Yonge and Nicholls (1931a), corals do obtain much of their energy by deaminization of protein, the beneficial effects of the zooxanthellae in removing the end products will be all the greater.

There is finally the fact, already noted on p. 218, that the presence of zooxanthellae appears to be essential for normal development in hermatypic corals. This in itself indicates a very intimate metabolic association between animal and plant.

X. Growth

A clear distinction must be made between growth of the tissues and that of the skeleton even though this is due to the secretory activities of the tissues. While both obviously increase in young corals there is a later slowing down in tissue increases which inevitably affects calcification; but if the tissues were finally to stop growing completely, calcification would presumably stop, otherwise the tissues would become increasingly attenuated owing to stretching over the ever-enlarging skeleton.

Early work on growth was entirely confined to the results of calcification, i.e. to measurements of length, diameter or weight of corals usually kept under natural conditions. These provided figures on which estimates of the possible rate of increase of coral reefs have been based. Information also covering tissue increase was later obtained by observing increase in the number of polyps, initially in developing colonies in the laboratory. Later Manton (1932) followed the growth of individual branches of *Pocillopora bulbosa* kept in the sea while Motoda (1940a) compared the number of polyps (or calyces) in the skeletal mass in varying sized colonies of *Goniastrea aspera*. The growth of single free individuals of *Fungia actiniformis* has been followed by Abe (1940) who demonstrated some relation between growth and environment although without analyzing the factors concerned.

It emerges from these observations that initial rapid growth rate of a colony, or of a single individual in the case of *Fungia*, is followed by a slowing down leading to almost complete cessation. In *Goniastrea*,

Motoda thinks this may be due to physiological senescence although admitting it could also be associated with decrease in the surface/volume ratio as the colony changed from the first flattened plate into the final massive hemispherical form. As shown by Kawaguti (1941a), during growth in these rounded colonies the volume increases in proportion to the cube of the radius whereas the surface area increases in proportion to the square of this. Thus in colonies with fifteen or less polyps he found the weight per polyp to be around 0·15 g, with about 40 polyps around 0·40 g and with between 468 and 486 polyps about 0·80 g. This means, of course, that the needs of calcification increase at a far higher rate than does the surface area of living tissue which

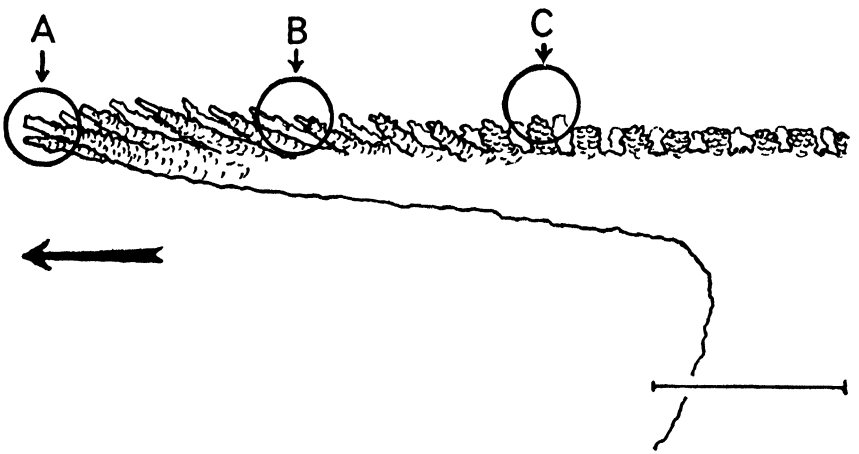


FIG. 14. Calcification rates in a branch of *Acropora conferta*. **A**, 8·2 ± 3·76 μg Ca mg N^{-1} hr^{-1}; **B**, 1·9 ± 0·92; **C**, 0·5 ± 0·10. Arrow shows direction of primary growth, scale represents 10 cm. (After Goreau, 1959a.)

represents the feeding surface. This could well explain the eventual cessation in growth.

Goreau's work has completely altered our understanding of both aspects of growth. He has estimated total nitrogen (as a measure of the living tissue) and the rate of calcification by the simultaneous use of ^{45}Ca and ^{14}C-carbonate (Goreau, 1961b). He had already (see Fig. 12) postulated distinct modes of entry and now finds that the labelled calcium is incorporated up to seventeen times as fast as the carbonate, indicating that greater quantities of carbon than of calcium are available in the tissues.

Apart from the effect of the zooxanthellae, the reasons for which do still remain somewhat uncertain, growth is influenced by " inherent species specific factors " (Goreau, 1961b). This is to be expected. All ahermatypic corals have their characteristic growth forms and associa-

tion with zooxanthellae in hermatypic corals would not be expected to modify pre-existing growth forms—except possibly in respect of light as discussed below. Thus in *Acropora conferta* (Fig. 14) the terminal polyps, which are large and pale, have a much higher calcification rate

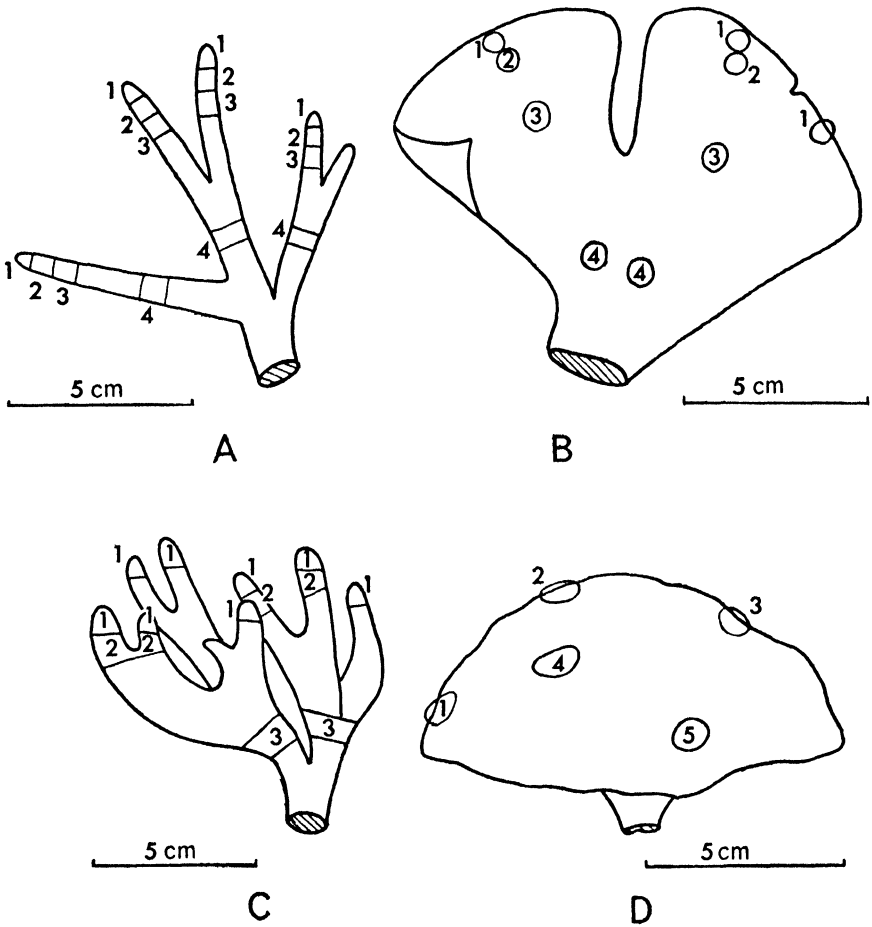


FIG. 15. Axial growth gradients measured in μg calcium per mg of tissue nitrogen per hour in **A,** *Acropora cervicornis* (1, 71·5; 2, 49·0; 3, 30·0; 4, 15·0): **B,** *A. palmata* (1, 50·0; 2, 30·0; 3, 15·0; 4, 8·0): **C,** *Porites furcata* (1, 20·0; 2, 4·0; 3, 2·0): **D,** *Colpophyllia natans* (1, 9·0; 2, 8·0; 3, 10·0; 4, 9·0; 5, 10·0). (After Goreau, 1961a.)

than the other polyps which although smaller have a much higher content of zooxanthellae.

Calcification rates control the eventual form of the colony. Thus in branching corals such as *Acropora cervicornis*, *A. palmata* and *Porites furcata* (Fig. 15, A, B, C) rates at the apical areas are up to ten times what they are in lateral or basal areas, whereas in massive colonies (D)

such as *Colpophyllia natans* (with which *Goniastrea aspera* could be compared) there is little difference from one area to another (Goreau, 1959a, 1961a). Nevertheless, the environment may exert a considerable constraining influence, for instance in the formation of flattened colonies of *Siderastrea radians* on intertidal beach rock compared with rounded colonies in still, deeper water (Yonge, 1935b).

These laboratory findings were confirmed by Goreau in the field. Further evidence was also obtained of discontinuous and irregular growth within a single symmetrical colony and also between individual colonies of the same species, conclusions already reached by earlier workers. The probability that calcification is not a continuous process is indicated by the lamellated nature of the skeleton. Field experiments on a wide range of corals revealed that there was no necessary correlation between rate of calcification and relative abundance of different species on the reefs. It appears that the race is not necessarily to the most quickly growing species.

Particular interest attaches to studies on *Manicina areolata* (Goreau and Goreau, 1960b). After a period of initial attachment, this interesting coral lives free on the surface of sand and so occupies the same habitat as the Indo-Pacific fungids (Yonge, 1935a). Here also the growth rate falls with increasing size (i.e. age). As shown in Fig. 13, the specific calcification rate in the smallest colonies was seventy-six times greater than in the largest. Senescence (perhaps by reduction in cell division) could account for this, as postulated by Motoda for *Goniastrea*. Goreau and Goreau do not think that zooxanthellae are in any way concerned. Unlike related massive corals, the ratio of surface area to volume (measured respectively by total nitrogen and weight) remains almost constant in this species. This is due to the increased folding of the surface with age which is rightly regarded as an adaptation for life in sand. As described and illustrated by Yonge (1935a), *M.* (= *Maeandra*) *areolata* can clear itself when covered with sand by a distension of the coenosarc with water. It can also, as observed by Goreau and Goreau, by similar means right itself after being turned over. These activities demand an extensive coenosarc capable of being raised well above the surface of the skeleton. The fungids are capable of similar movements.

XI. Effect of Light

The supreme influence of light on the growth of hermatypic corals has long been apparent. As stated by Umbgrove (1947), " the depth of the living reef is correlated with light penetration ". Earlier evidence

has already been reviewed (Yonge, 1940, 1958b) and positive phototropism strikingly revealed by the experiments of Kawaguti (1937) on regeneration of branches of *Acropora* suspended horizontally and upside down (Fig. 16).

This response to light is certainly associated with the presence of zooxanthellae. In both corals and other marine invertebrates containing algal symbionts, Kawaguti (1941b, 1944c) considers that the response to light varies in intensity with the concentration of algal cells. Gohar (1948) describes how both the expansion of the polyps and the growth of the stolon in the alcyonarian *Clavularia hamra*, already noted as containing zooxanthellae, are influenced by light. Zahl and

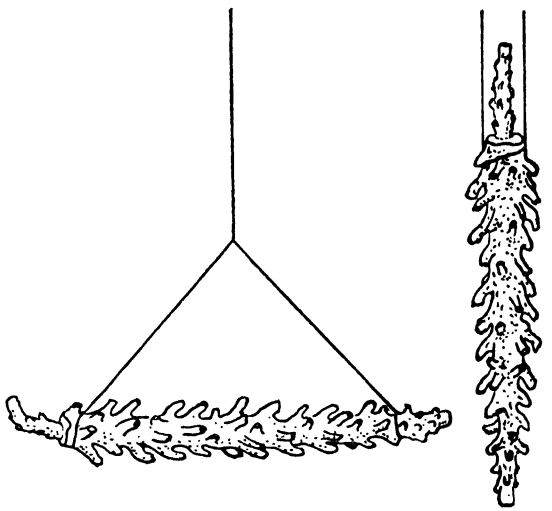


FIG. 16. *Acropora* sp., regeneration at broken end of branch when suspended in horizontal and reversed positions. (After Kawaguti, 1937.)

McLaughlin (1959), who give further references, state in summary " that every species of zooxanthellae-bearing marine animal has its own specific light needs and therefore shows characteristic positioning on the reef. This may be accomplished through any of the following means: (a) early selection of position, as with planulae or other freely motile larval forms; (b) gross body movements or posturing, as with anemones, medusae, and worms; (c) possession of light-filtering pigments, as with coloured corals and molluscs; (d) possession of light-concentrating devices, as with tridacnids; (e) possession of highly contractile and differentially light-absorbing tissues, as with most coelenterates and some molluscs."

There is the final question as to whether the positive reaction to light is the factor pre-conditioning establishment of the symbiosis or

whether it arose as a result of that association. In the sense that, as Goreau and Goreau (1959) have demonstrated, light intensity has a profound effect on coral growth owing to the presence of zooxanthellae, then the latter alternative appears the more probable. Droop (1963) makes the interesting suggestion that " irritability experiments with artificial associations could decide whether the reaction to an internal oxygen gradient is inherent or not."

XII. Productivity

Localized centres of high productivity in the open ocean, like oases in a desert, atolls are of compelling interest. Each lagoon, in the words of Von Arx (1954), " is essentially a ' lake in mid-ocean ', cupped in a shallow saucer-like basin supported by a solitary mountain peak ". It also represents an area of sea bottom raised from aphotic depths into the photic zone. Atolls lie across the trade wind belts, which fact accounts for an asymmetry due certainly to the greater force of seas on the windward side but possibly also to the greater quantity of zooplankton on that side. It has been claimed, as discussed later, that an atoll represents a completely closed system effectively neither taking material from nor releasing material into the surrounding ocean. But atolls have grown to their present size in the past and probably continue to grow and this must have involved, and still involves, some interception and utilization of organic and inorganic matter from the sea. The problem also arises with fringing and barrier reefs but there, particularly with the former, the factors are more difficult to analyse owing to the presence of complications such as the effect of land drainage and of greater sedimentation.

The extent to which lagoon waters are isolated from those of the surrounding ocean has been demonstrated by the work of Von Arx (1954) at Bikini and Rongelap. He notes they are influenced by four sources of energy, namely wind, waves, tides and the North Equatorial Current, with the trade winds much the most important. Apart from their effect on the seaward reefs, they cause a steady inflow of water through channels on the reef surface into the lagoon. There is no such major inflow on the lee where water movements are largely influenced by the tides. The wind also drives the surface waters in the lagoon, to a depth dependent on the force of the wind, in steady movement from seaward to leeward side. The greater part of this water cannot escape so is driven below to return upwind as a bottom current (Fig. 17). There is also a secondary circulation consisting of " two counter-rotating compartments, which move clockwise in the southern portions and

counter-clockwise in the northern portions." Measurements of water flow into and out of Bikini lagoon indicated that the total volume of water (approximately 28 $\times$ 10^9 m^3) is completely replaced every 39 days during the trade wind season and in about double this time during the summer. Thus there is retention with continuous replenishment.

The same picture emerges from the study of the plankton by Johnson (1954). Certain species are found in both open ocean and lagoon but four times more abundantly in the latter owing to retention of water within it. There are also endemic lagoon species able to pass the entire life history there. They live almost entirely in the deeper slowly moving levels which represent up to 90% of the water in the lagoons. Even upward migration at night may not take them out of

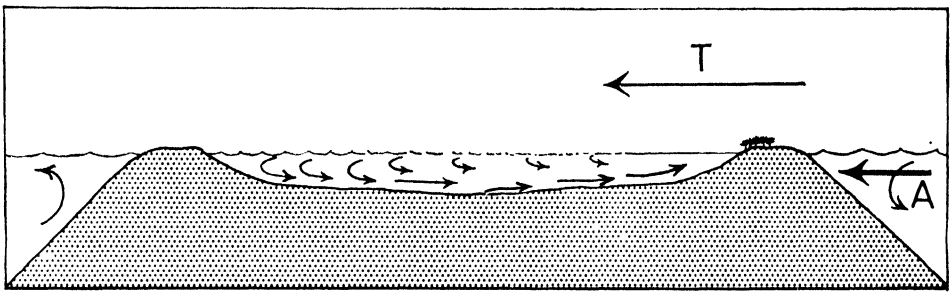


FIG. 17. Diagram (based on Von Arx, 1954) showing circulation in an atoll lagoon under the influence of trade wind (T). Surface current caused by this but the greater part of the water returns as a deep current which upwells on the sheltered side of the lagoon. While energy thus largely conserved within lagoon, maintenance and growth of the atoll depends on a constant supply of energy (zooplankton) from the open ocean (A).

this water which also contains the planktonic stages of the bottom-living invertebrates and fishes found in the lagoon. Little of this endemic and temporary plankton is lost into the ocean.

Various workers have attempted estimates of organic productivity on atolls and other reefs basing these on measurements of oxygen production, i.e. of carbon utilization, across the upper surfaces of windward reefs (Sargent and Austin (1949, 1954) on Rongelap Atoll; Odum and Odum (1955) on Eniwetok Atoll; Kohn and Helfrich (1957) on the fringing reef at Kapaa, Kauai, Hawaii). Their estimates indicate a high primary productivity of 1500–3500 g carbon fixed per square metre annually. This is up to 100 times higher than in the surrounding tropical ocean and four to eight times greater than in the most productive temperate seas.

But these upward-facing surfaces are inhabited by specialized plant communities largely of encrusting nullipores. In addition zooxanthellae

occur in the corals and almost all other coelenterates as well as in compound ascidians and bivalve Tridacnidae. There are also the blue-green and filamentous green algae on or in the coral skeletons and boulders. On the other hand the bulk of the fauna consists of the sessile animals which harbour these zooxanthellae. Corals are conspicuous but largely because of the great surface exposed. The biomass is small, there is no succession of overlapping surfaces and colonies as there is off the windward reef margin. All of these animals feed on zooplankton or phytoplankton and almost the only animals capable of feeding on the calcareous algae are parrot fishes (*Scarus*) which " move about the reef, grazing like a herd of sheep . . . Their tooth marks remaining on the rocks, are easily observed" (Schultz, 1948). These predominantly plant communities are not surprisingly autotrophic.

Unable to collect adequate supplies of zooplankton, Sargent and Austin and also Odum and Odum postulate that corals obtain nutriment from associated plants. The former indeed state that " under conditions of growth on the eastern reef of Rongelap Atoll, the association between corals and zooxanthellae seems to be essential to the individual colonies precisely because the corals must derive organic matter from the algae or die." They do not explain how this may be achieved. To meet the same postulated need, Odum and Odum, who estimated that the zooxanthellae comprised no more than 6% of the total plant mass, bring in the filamentous boring algae universally present in coral skeletons. They do not state how the animal could utilize products from plants separated from them by an appreciable depth of skeletal material. Moreover, Goreau and Goreau (1960b) found that in *Manicina areolata* the content of filamentous boring algae is very much less than that estimated by Odum and Odum.

This fundamental problem of coral nutrition has already been discussed in connexion with Goreau's work and his conclusion that the contribution of the zooxanthellae can be no more than some diffusable organic matter which may serve as a vitamin or hormone. Stephens (1960) has recently shown that *Fungia* can remove labelled glucose and also amino acids from solution. There remains the undoubted, well demonstrated, fact that corals are most highly adapted for the capture and extremely rapid digestion of exclusively animal prey and that, in relation to the bulk of the tissues, they have a literally enormous feeding surface in most species only exposed at night when zooplankton is abundant. Nevertheless in view of these contrary views the question posed by Hand (1956) as to whether corals are herbivorous must, following further investigation, be conclusively answered.

On the basis of their 6 weeks' survey of a reef on Eniwetok, Odum and

Odum attempted to draw up a balance sheet of gain and loss. While in the words of Hedgpeth (1957) " This *tour de force* will probably excite comment for some years ", it was surely somewhat premature. So little is yet known about food chains within a coral reef community; indeed the authors themselves are not too accurate about the trophic status of certain of the animals. Thus in their pyramids of biomass, apart from their assumption that coral are primary producers, they list the gastropods *Cypraea* and *Thais* and the Ophiuroidea all as herbivores whereas they are specialized carnivores, on the other hand crabs, indeed decapod Crustacea generally, are omnivores rather than carnivores. However it could be that the final estimate in dry biomass in grams per square metre of carnivores 11, herbivores 132, primary producers 703, may be a reasonable approximation.

But the prime criticism of this admittedly bold and very interesting attempt lies in the basic failure to distinguish between the outer seaward growing (or certainly maintaining) margin of the reef and the upper reef flat with the encircled lagoon. With little doubt the latter regions are in a more or less steady state with gain from and loss to the ocean roughly balanced. In the words of Odum and Odum, under present ocean levels the reef community may represent " a true ecological climax or open steady-state system ". Certainly the lagoon may be regarded as a localized area within which, over a long period of time (since late Eocene it would appear in the case of Eniwetok), productivity has been built up by a gradual accumulation of nutrients needed for protein synthesis. This has been achieved by intercepting nutrients in surface waters and, where zooxanthellae are present, retaining them in closed cycle within the " organism ". In consequence the lagoon and encircling surface reef is now an area of high productivity in oceanic waters of extremely low productivity. Some measure of the difference may be implied in the estimate of Emery *et al.* (1954) that sedimentation on the summit of an atoll is about 1000 times faster than in the surrounding depths. In the warm, well illuminated and well mixed lagoon waters there is a rapid turnover of the endemic planktonic and benthic population, although whether this amounts to an annual replacement by as much as 12·5 times the average standing crop, which is what Odum and Odum estimate, remains to be confirmed.

All this takes no account of the outer seaward surface. There, the hermatypic corals and associated animals can only be maintained from oceanic sources—and if they are not maintained the whole reef formation will be disrupted. There is no nutritional connexion with the reef flat and the lagoon. This exposed, seaward community is outside the closed system where essential nutrients are retained and

circulated. There is much evidence that the most actively growing corals are those some metres below the surface on the windward side. They have the major responsibility for maintaining the stability of the entire atoll against the constant battering of trade wind seas. This involves constant replacement of eroded or damaged surfaces. With the zooxanthellae of essential assistance in maintaining a high rate of calcification, there must also be a constant supply of food in the form of zooplankton if only to replace the organic matter continually being lost, carried around the atoll or dropped into profound depths. There can be no closed or autotrophic system in this environment. Although this is the most difficult of all coral reef environments to penetrate, every endeavour should be made to sample its waters and obtain some estimate of the amount of zooplankton, largely no doubt some distance below the surface, which is carried against these seaward reef surfaces. The position of the partly downward directed currents containing this essential zooplankton is indicated in Fig. 17, A.

We are thus brought logically to the supreme question which arises in any consideration of the biology of coral reefs, namely to what extent are the powers of growth capable of withstanding the full force of the sea; in other words, are modern reefs static, advancing or retreating? It has long been the opinion of the writer (Yonge, 1940) that seaward reefs do grow outwards against constant forces of wind and sea which mould their form. This is the opinion of Kuenen (1950), and also of Crossland (1952) who makes the point that " Permanent beds of living coral can exist only immediately along an outgrowing reef where their foundations are being continually extended." Emery *et al.* (1954) consider that the windward reefs at Bikini appear to be growing seaward. Newell (1956), on the other hand, considers that the seaward reefs at Raroia are getting narrower and that the surge channels are formed by erosion, i.e. in opposition to the more general view that it is the intervening algal ridges which are growing outwards.

By placing permanent marks on reef surfaces it should not be difficult to discover precisely what is happening. But certainly in the past the associated powers of growth and high calcification rate have permitted the formation of reefs exposed to the full force of oceanic seas. Munk and Sargent (1954) estimate that the waves beating against the windward reefs at Bikini dissipate a force of approximately half a million horsepower which the ridges and surge channels successfully withstand. It is indeed difficult to see how living reefs could successfully retreat before such forces. Once the powers of erosion gained the upper hand, the living reef surface would be breached and damage would be progressive and irrevocable. As suggested earlier, observation of the

results of a localized area of experimental destruction on an exposed reef surface, i.e. of breaching the surface of living tissue, could be most illuminating.

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THE BEHAVIOUR AND PHYSIOLOGY OF HERRING AND OTHER CLUPEIDS

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I. Introduction

A. *General*

Of all the clupeids the herring, *Clupea harengus*, has been most extensively studied. Perhaps it has been more the subject of research than *any* other fish species, partly due to its commercial importance and partly to the need for so much work before even the essentials of its complex biology could be exposed; thus the herring is bound to take up the main space in this review. Although most of the research has been concerned with the racial question and population studies, these aspects are only mentioned where experimental work has assisted such research. Therefore while natural mortality due to disease and predation, and fecundity in relation to reproductive biology, will be considered, fishing mortality and its estimation, and fecundity as a means of distinguishing races and for estimating stock size, will not.

For a general review of clupeid biology reference may be made to a recent bibliography (Scattergood, 1957), to a series of translations from Russian (Scattergood, 1959), to the monograph on the Clupeidae by Svetovidov (1952) and to general books such as those of Hodgson (1957) and Nikolsky (1957). Two recent special scientific meetings of the International Council for the Exploration of the Sea in Copenhagen (I.C.E.S.) in 1956 and 1961 covered much behaviour and physiological

work, some of which is described here. For a general review on fish physiology and behaviour, reference should be made to Bull (1952), who described techniques used for behaviour studies as well as giving estimates of the sensitivity of teleosts to environmental factors such as temperature, salinity and pH. He also (Bull, 1961) described the role of ethology in oceanographic research. Brown (1957) edited a valuable publication on the comparative behaviour and physiology of fish in general, much of which is applicable to clupeids.

The main species covered in this review are given below:

Clupea harengus L.—Atlantic herring (the Baltic herring is referred to by the Russians as *Clupea harengus membras* or salaka)

Clupea pallasii Val.—Pacific herring (considered by Russian workers to be a sub-species of *harengus*)

Sardina pilchardus (Walbaum)—European sardine or pilchard

Sprattus sprattus (L.)—Sprat

Sardinella aurita Val.—Gilt sardine

Sardinops caerulea (Girard)—Californian sardine (the taxonomic status of the Pacific sardines is discussed by Marr, 1957)

Sardinops melanosticta (Schlegel)—Japanese sardine

Brevoortia tyrannus (Latrobe)—Menhaden

Alosa spp.—Shads

Pomolobus pseudoharengus (Wilson)—Alewife

Caspialosa spp.—Caspian and Black Sea herrings

Clupeonella spp.—Caspian sprat or kilka

Some other species of clupeids and engraulids are also mentioned. In this review *Clupea harengus* will usually be referred to as " herring ", all other species being given their Latin names.

The behaviour and physiology of these fish have been studied, not only from experiments in aquaria, but also from more indirect observations at sea. Inferences have also been drawn from the extensive anatomical studies made on clupeids. Because of the commercial value of clupeids some importance has been given to their behaviour and physiology in relation to fishing gear.

The review is not arranged solely on the basis of organ systems; where possible it follows the life-history of the fish starting with fertilization, the egg and larval* stages and ending with maturation and spawning.

Due to the difficulty of covering the literature, particularly Russian and Japanese, it is regretted if any relevant papers have been omitted. However, the authors would like to acknowledge the help of the

* The word " larva " will be used to include stages from hatching to metamorphosis.

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B. *Characteristics of Clupeids*

The Clupeidae are to be found in all habitats from fresh water, e.g. some *Pomolobus* and *Harengula* species, to sea water. Many of them are anadromous such as *Alosa*, *Caspiolosa* and *Pomolobus*. The family contains species which lay demersal eggs offshore (herring), demersal eggs in shallow water (*Clupea pallasii*) and pelagic eggs (*Sardinops*).

Hatching takes place in a few days (the eggs being small) and there is little yolk available before the larva must find an external source of food. These larvae are usually very small and transparent, metamorphosing after some months to the adult form. The larvae and juveniles of marine species are often found on shallow inshore nursery grounds.

The fecundity is low compared with many teleosts, but the numbers of individuals are high. The adults of most species adopt a pelagic and shoaling habit and often make extensive migrations for feeding and spawning. They are mostly plankton and therefore seasonal feeders, laying down fat reserves which allow them to survive when food is scarce. Lacking much in the way of defence mechanisms, except protective colouration, speed and shoaling, and being present in such large numbers, most clupeids are heavily preyed upon by other fish, mammals and birds.

II. The Gametes

A. *Basic structure and composition*

1. *The sperm*

The morphology of herring sperm has been studied by Retzius (1905) and Ballowitz (1915) who described the successive stages in the transformation from spermatid to spermatozoon by the development of the tail piece. It is unlikely that the sperm of other clupeids differs significantly from that of the herring.

The head is composed almost entirely of nuclear material and is approximately 1μ in diameter; a short middle piece is followed by a

long (20μ) filamentous tail, with a pronounced axial filament running throughout its length and projecting as an " end piece " from the tip of the tail.

Some analyses of the ionic composition of the semen of herring have been made; these are given in Table I.

TABLE I

IONIC COMPOSITION OF HERRING SEMEN

	Milli-equivalents/litre Cl^-	Na^+	K^+	Freezing point depression (Δ°C)
Barnes (personal communication) . .	204	166	533	0·92
Holliday (unpublished).	215	172	549	0·92

Yamagawa and Nishimura (1927) listed the amino acids present in the semen of *Clupea pallasii* but did not comment on the functional significance of their findings.

2. *The egg*

Rass (1937) divided clupeids according to their eggs into three groups; these are given here in a modified form:

Demersal eggs, small perivitelline space, no oil globule—*Clupea harengus, Clupea pallasii, Pomolobus.*

Semi-pelagic eggs, large perivitelline space, no oil globule—*Sprattus sprattus, Alosa, Caspialosa.*

Pelagic eggs, large perivitelline space, with oil globule—*Sardina pilchardus, Brevoortia, Clupeonella, Sardinops, Sardinella.*

The eggs of the clupeids resemble each other fairly closely, all are globular in shape and in all of them the yolk is " compound ", i.e. with unfused droplets; in *Sprattus sprattus* the yolk is very clearly divided, giving it a segmental appearance. In all clupeids the nuclear area is large and yolk free. *Engraulis* has an oval egg.

When shed, the clupeid ovum has a thick outer chorion which, in the herring, is triple layered and porous (Bowers and Holliday, 1961). A similar structure is found in *Sardina pilchardus* (Andreu and dos Santos Pinto, 1957) and *Sardinops caerulea* (Andrews, 1931). A thin cytoplasmic membrane is closely applied to the chorion. Yamamoto, K.

(1955) described the position and structure of the micropyle, penetrating all three layers of the chorion in *Clupea pallasii*.

Few analyses have been made on the composition of the clupeid egg. The peripheral cytoplasm in the egg of *Clupea pallasii* contains a number of cortical alveoli with neutral muco-polysaccharide contents (Kanoh, 1953; Yamamoto, 1956); the same is true of the herring egg (Holliday, unpublished). The alveoli contain no lipids; the main yolk particles are separate from these, and give only a weak response to the P.A.S. test. Hempel (personal communication) found that the mean fat content of herring eggs was 1·32% of the wet weight and probably about 5·3% of the dry weight, in the southern North Sea in 1961. Lasker (1962) analysed the egg of *Sardinops caerulea* and found that over 70% of the dry weight was protein; lipids constituted 13% of the dry weight and the water content of the yolk averaged 91·2%.

B. *Tolerance to external conditions*

In the body of the parent herring the gametes are maintained in a relatively favourable environment. Herring eggs are slightly hypotonic to the body fluids of the female parent; Holliday (unpublished) obtained freezing point values of −0·75°C for ripe eggs in the gonads of female herring with blood freezing points of −0·92°C. Barnes (personal communication) and Holliday (unpublished) both obtained values of −0·92°C for the sperm of herring, i.e. the male gametes were isotonic with the blood of the parents.

On being released into the water the gametes often experience a vast change in concentration of the external medium. Strong osmotic forces are often exerted on them, and, with their large surface area/volume ratios, one might imagine them to be especially susceptible to osmotic death. On the contrary, they appear very tolerant (see Section III, C).

It is difficult to determine just what mechanisms are employed by the spermatozoa to survive these osmotic forces. They could survive by being impermeable or by being freely permeable, thereby changing drastically in composition but avoiding any osmotic gradient; alternatively there may be some non-electrolyte present which is capable of setting up a force opposing the osmotic forces of the environment.

Much more has recently been found out about regulation in the egg, and this is discussed in detail in a later section. When released into the water, whether fertilized or not, the herring egg rapidly approaches isotonicity with the medium. The osmotic forces are thus equalized passively. True regulation depends on the subsequent embryonic development (see Section III, C).

C. *Viability of the gametes and artificial storage*

Herring sperm remains fertile for at least 3 hr in sea water at 8°C (Blaxter, unpublished). Yanagimachi (1953) found that the sperm of *Clupea pallasii* remained fertile to a limited extent after 12 hr in sea water at 8–10°C. In Ringer solution or in lower salinities some fertility was retained after 24 hr. However, Stroganov (1938) showed that the sperm of *Caspialosa volgensis* lived for 1 min or less in fresh water and that sperm from mixed males survived less well than sperm from one male; of the eggs 60% could still be fertilized after about 30 hr.

Gamete storage has been developed mainly in salmonids as a piscicultural technique. In herring, short-term storage has been used (Blaxter, 1955) for transporting gametes from where the parents are caught to the laboratory for controlled rearing studies, and long-term storage for making cross fertilizations between herring races spawning at different seasons. For short-term storage, different diluents such as phosphate and borate buffers with and without chicken egg yolk were used, but the most satisfactory results were obtained by storing whole gonads dry at about 4°C. While fertilization of eggs may be obtained even after 6 to 7 days of dry storage, a high hatching rate is only to be expected after periods not exceeding 36 hr storage. Long-term storage has been achieved successfully with sperm, but not with eggs, by freezing in glycerol and diluted sea water to a temperature of −79°C. At least 6 months later the sperm were viable and crosses were made between spring and autumn spawning herring (Blaxter, 1957) and between different races of spring spawners (Blaxter and Hempel, 1961).

Storage of gametes within the dead parent's body does not seem to be successful and the fertilization rate was very low after 18 hr in herring. Stroganov (1938) found in *Caspialosa volgensis* that the sperm started to die 10–60 min after the death of the parent, if the testis was left *in situ*.

D. *Fertilization*

Fertilization in *Clupea pallasii* was described by Yamamoto (1958) as being normally monospermic. He showed that immediately following sperm entry the fertilization membrane, which was a protein structure, withdrew from the chorion thus forming a perivitelline space. Into this space are extruded the droplets of the cortical alveoli (Volodin, 1956). Yanagimachi and Kanoh (1953) found that the calcium ion concentration was critical for successful sperm entry. Yanagimachi (1957) described a factor bound to the egg membranes of *Clupea pallasii* that caused quiescent sperm to become active if brought near it. This

factor may be contained in the secretion of the oviduct (described in Section VI, X). Kryzhanovsky's observation (see Galkina, 1957) that the eggs of *Clupea pallasii* seemed to be fertilized by immobile sperm may have been due to the sperm in this instance not yet having been activated.

The present authors and Hempel showed that when released from the body of the female the egg of the herring had an osmotic concentration (Δ 0·75) equivalent to about 12‰ sea water. The process of fertilization tends to accelerate the change to isotonicity (discussed previously). Permeability is increased and it is probable that the mucopolysaccharide contents of the cortical alveoli are responsible for drawing the outside medium through the freely permeable chorion by some process of imbibition.

E. *Parthenogenesis*

Volodin (1956) described an instance of parthenogenesis in the herring. Nearly 60% of a number of unfertilized eggs, when placed in sea water, extruded droplets into the perivitelline space. A small proportion of these " activated " eggs stopped developing after bipolar differentiation had occurred, the remainder beginning cleavage. In 5% of the eggs this was abnormal, the cleavage furrows being in no definite order and blastomeres of different sizes being produced; these eggs died, usually before reaching gastrulation. The remaining eggs followed a pattern of apparently normal development, producing active embryos. Unfortunately observations were not made as far as hatching.

Just what the factor is that " activates " an unfertilized egg is not clear. It has been suggested that certain differences in osmotic pressure between the egg and the medium may stimulate division (Morgan, 1927). Unfortunately Volodin did not give the salinity of the water in which this development took place; apparently it could have been as low as 4·9‰.

Galkina (1957) described parthenogenesis in *Clupea pallasii* and found that it occurred to a greater extent in the lower salinities. Development proceeded as far as hatching but the larvae were abnormal.

III. The Developing Egg

A. *Embryology*

The embryonic development of the herring has been studied and described in some detail (Kupffer, 1878; Brook, 1885, 1886; Prince, 1907; Volodin, 1956; Toom, 1958) and also of *Clupea pallasii* (Hamana,

1936; McMynn and Hoar, 1953; Outram, 1955). The rate of development is closely linked with temperature (see Section III, B); for example at 14°C gastrulation begins 22 hr after fertilization, whereas at 11·5°C the eggs after 22 hr are still in the blastula stage. In the following account no references are made to either time or temperature scales.

Immediately after fertilization there is a rearrangement of the cytoplasm and yolk. The blastula resulting from cleavage forms a cap of small cells at the animal pole. Gastrulation then occurs. The cells of the blastula lift slightly from the surface of the yolk, retaining contact with it by a cellular " root " in the centre. Intucking occurs and first a dorsal and then a ventral lip of the blastopore is formed. The inwardly migrating cells from the lips meet to form a two-layered embryo, and growth of the peripheral cells over the surface of the yolk takes place. The blastopore closes when the migrating cells meet.

A head region is differentiated at the dorsal lip of the blastopore. Mesoderm cells migrate to form a layer between the ectoderm and endoderm, and segmentation then occurs. The embryo is about 2 mm long at this stage. As segmentation continues the nervous system is established and the rudiments of the sense organs (optic cups, olfactory capsules and otic vesicles) are developed. The head and trunk segments remain attached to the yolk, but the tail soon becomes free. The embryo shows occasional movements. The eyes are formed but lack pigment; two otoliths are present in the otic vesicles. The gut tube is formed and the heart commences beating (about 40 beats per min at 15°C). A dorsal aorta is present and a sub-intestinal vein; the only corpuscular elements visible in the blood are a form of leucocyte. The eyes then become pigmented and hatching glands appear on the head. The gut is open posteriorly, but although the stomodaeum is visible, the gut is still closed anteriorly.

According to McMynn and Hoar (1953) hatching of *Clupea pallasii* was nearly always head first through a softened part of the chorion.

The development of the herring is not necessarily typical for clupeids. Many of the species (*Alosa*, *Clupeonella*, *Caspialosa*) have a much shorter incubation time and Perceva (1939) and Lasker (1962) have found that *Caspialosa caspia* and *Sardinops caerulea* larvae respectively hatch with unpigmented eyes.

B. *Effect of temperature on rate of development*

Some of the published work is given in Table II.

From the equation of Hela and Laevastu for herring the biological zero (the theoretical temperature when incubation takes infinite time)

TABLE II

EFFECT OF TEMPERATURE ON RATE OF DEVELOPMENT AND TIME TO HATCHING

Author	Species	Temperature (T) °C	Time (D) Days	Equation	Remarks
Hela and Laevastu (1962) using Jean's (1956) and other data	Herring			$D = 4+44{\cdot}7e^{-0{\cdot}167T}$	
Blaxter (1956)	Herring			$D = -2{\cdot}0+\frac{165{\cdot}0}{T+1{\cdot}34}$	
Toom (1958)	Herring	12·8–19·0	7·7–4·2		Hatched in the sea
Ryder (1882)	*Alosa*	11–23 (normal range)	15–3		
Perceva (1939)	*Caspialosa caspia*	18·4–21·4	2·4–1·6		
Ahlstrom (1943)	*Sardinops caerulea*	13·5–16·0	3		Estimated from samples at sea
Miller (1952)	*Sardinops caerulea*	16·8	2·3		
Ahlstrom (1954)	*Sardinops caerulea*	12·6–18·0	4–2		
Murphy (1961)	*Sardinops caerulea*				Used Ahlstrom's results and graphed them
Ito (1958)	*Sardinops melanosticta*			$D=0{\cdot}5+28{\cdot}8e^{-0{\cdot}159T}$	Equation due to Hela and Laevastu (1962)
McMynn and Hoar (1953)	*Clupea pallasii*	8·5	10–11		
Outram (1955)	*Clupea pallasii*	4·4–10·7	40–11		
Motoda and Hirano (1961)	*Clupea pallasii*	3·1–7·8	22·9–16		Summary of Japanese work
Nikolsky (1957)	*Caspialosa*	19–22·7	*c.* 1·75		Summary of Russian work
	Clupeonella	17·9–19·8	*c.* 1·25		

is $-\infty$°C, but these authors give a time of 49 days at 0°C. Soleim (1942) found $-1{\cdot}2$°C for Atlanto-Scandian herring, Blaxter (1956) $-1{\cdot}34$°C for northern North Sea herring, and Blaxter and Hempel (1961) about 0°C for German coastal herring.

The product of temperature (using the biological zero) and time (" day degrees ") has been used as a means of comparing stages of development in larvae reared at different temperatures. This concept is unsatisfactory in some ways because of the difficulty in identifying equal stages of development from which to calculate the initial biological zero. Also as the temperature changes, so may the relative growth of different parts of the body. Even the time to hatching itself may vary as a result of environmental conditions other than temperature. Barlow (1961) has recently suggested that the time to reach a given developmental stage should be plotted against absolute temperature.

Ahlstrom (1943) found the Arrhenius relationship for hatching of *Sardinops caerulea* to be about 22,500. Blaxter (1956) found values ranging from 20,800 to 9,500 in herring, with Q_{10} values ranging from 6·5 to 2·0.

C. *Salinity tolerance and osmo-regulation of the developing egg*

1. *Salinity tolerance*

Ford (1929) found that herring eggs could be successfully fertilized and incubated in salinities down to 4·8‰. Kryzhanovsky (1956) reported normal fertilization of Baltic herring eggs in salinities as high as 25‰ (normally it is 4–5‰), although later development was abnormal. Brandhorst (1959) reported successful spawning in the Kiel Canal at a salinity of 5‰. Holliday and Blaxter (1961) measured the changes taking place in the embryonic tissues of herring reared in salinities from 5–55‰; they found a 100% fertilization in salinities from 25–55‰, becoming 70% in 12‰ and 5‰. Over 50% of the eggs hatched in salinities from 10–45‰. McMynn and Hoar (1953) showed that the eggs of *Clupea pallasii* would tolerate salinities at least as low as 6‰, and in a larger number of experiments found that the optimum salinity for development and hatching lay between 11·53 and 16·24‰. Galkina (1957) found in *Clupea pallasii* that percentage fertilization only fell off below salinities of 5‰.

2. *Osmotic regulation*

After fertilization the herring egg is almost isotonic with the water into which it has been shed, although it never reaches isotonicity with

very low (<5‰) salinities. The increased water content of eggs developing in these low salinities is reflected by the increase in size of the egg (Holliday and Blaxter, 1961). This is also found in *Clupea pallasii* (Galkina, 1957). Probably the mechanical pressure exerted by the chorion limits water inflow; this is certainly the case in the eggs of *Sardinops caerulea* (Lasker and Theilacker, 1962a). There is inflow of water into both the perivitelline space and the embryo. The chorion appears to be freely permeable, although there may be a binding of some ions by the colloid in the perivitelline space. Galkina (1957) found that the chorion in *Clupea pallasii* was strongest in salinities 10–28‰.

Unpublished work by the authors and Hempel showed that, during the early stages of development, the herring egg had little capacity to regulate the osmotic concentration of the yolk, although the individual cells of the blastula were apparently regulating. It was only after gastrulation was completed that the whole egg was regulated to an osmotic concentration equivalent to about one-third of the external medium in salinities above 12‰, and, in lower salinities to a value equivalent to 12‰ (Δ=0·72). At this stage the whole of the exposed surface of the yolk was enclosed within the endo- and ectodermal layers. It seems probable that the ability to regulate is a property of these cells. Lasker and Theilacker (1962a) showed that the degree of regulation maintained by embryos of *Sardinops caerulea* was similar to that in the herring (to about one-third of the external medium).

D. *Effect of temperature, pressure and CO_2 on eggs**

The effect of temperature on the incubation time for clupeid eggs is discussed in Section III, B. Meyer (1878b) found that normal development took place from 22° to 1°C, but death occurred at — 0·8°C. Toom (1958) found that eggs of Baltic herring would hatch at temperatures as high as 18·5°C and Blaxter (1956) that the optimum temperature varied in different races.

Ewart (1886) found that eggs lowered to a depth of about 200 m (21 atm) and left for some days hatched normally in the aquarium after being brought to the surface.

Kelley (1946) studied the effect of carbon dioxide tension on the eggs of *Clupea pallasii* and found that they could tolerate pH values ranging from 5·12–9·00 (the average ranging from 6·68–8·68), low pH values retarding development. The eggs would tolerate CO_2 values ranging from 0·00–67·76 ppm, the average values ranging from 0·088–27·06 ppm.

* Polikarpov and Ivanov (*Voprosy Ikhtiol.* 1, 583–9, 1961) found that exposure to radiation (2×10^{-8} curies/litre) from ^{90}Sr and ^{90}Y led to abnormalities in developing *Engraulis*.

E. *Egg mortality*

1. *Egg density*

Lea (1930) and Runnstrøm (1941b) showed that overcrowding of herring eggs on the sea bed off Norway resulted in a high mortality. Eggs in layers 0·5–2·5 cm thick showed mortalities of 43–80%. Cleaver and Franett (no date) found a similar occurrence in eggs of *Clupea pallasii* deposited in large clumps inshore. However, Parrish *et al.* (1959), who succeeded in taking egg samples by grab on the Scottish west coast, found no evidence of a differential mortality in eggs four to eight layers thick (i.e. 0·5–1·0 cm). McMynn and Hoar (1953) and Blaxter (1956, 1962) showed that the successful hatching of eggs of *Clupea pallasii* and Scottish herring respectively in aquaria depended to some extent on the density, crowding resulting in a low percentage hatch. In particular, the former authors found what appeared to be an intermediate optimum density for the best hatching; above and below this percentage hatch was reduced.

2. *Fungal and bacterial attack*

Toom (1958) found that eggs of Baltic herring were liable to attack by fungi when kept in the sea away from the spawning ground, although on the spawning ground they were not affected. In rearing experiments on herring fungal attack may reduce percentage hatching considerably, especially when the incubation period is long. Anon. (1952) reported on the high rate of infection by bacteria of some *Sardinops caerulea* eggs, and showed that this could be checked in aquaria by antibiotics.

3. *Predation*

Reports of fish with their stomachs gorged with herring eggs are to be found in the literature; indeed concentrations of haddock and coalfish were one of the first means of locating herring spawning grounds (e.g. Bowman, 1923). Even the stomachs of spawning herring sometimes contain eggs. Parrish *et al.* (1959) found on a herring spawning ground with a heavy population of ophiuroids that the ophiuroids were inversely distributed in relation to the eggs. The eggs of *Clupea pallasii* are deposited inshore (e.g. Rounsefell, 1930) and are liable to be eaten by birds at low tide (Cleaver and Franett, no date). Presumably the hazards facing demersal and pelagic eggs are somewhat different, the former being concentrated and available in large quantities, the latter being dispersed, at least some time after spawning, and yet liable to stranding.

IV. The Larva

A. *Development of organ systems*

The anatomy and development of the skeleton and organ systems after hatching is best known in herring. At hatching the larvae vary in length from 5–9 mm, the yolk being absorbed at 8–12 mm. The size of the larva and its yolk supply and the rate of absorption of yolk depend on the original egg size and race of the parents (Toom, 1958; Blaxter and Hempel, 1963). The larvae of *Sprattus sprattus*, *Sardina pilchardus* (Lebour, 1921) and *Sardinops caerulea* (Miller, 1952; Arthur, 1956), however, hatch at 3–4 mm and have used up their yolk at 5–6 mm.

In herring larvae only a primordial fin is present at hatching in addition to the pectorals; the eyes are large, the mouth is non-functional and the gut is straight. However, the jaw soon begins to grow forward. At first the lower jaw does not articulate, being suspended by an elastic ligament (Flüchter, 1963). Harder (1952) described the development of the alimentary system, showing that the pyloric caccae and caecum gradually started to develop at about 25 mm, the liver already being present. At this stage, too, the lateral musculature began to invest the gut. Harder (1960) also gave a comparative description of the development of the gut of many clupeids and related the gut proportions to the cross-sectional area of the body and body mass.

Bamford (1941) studied the lateral line in herring which was completely developed at 50 mm length. Sensory papillae are found in the head region (de Kock, unpublished) of newly hatched herring larvae, and over the body of *Sprattus sprattus* and *Sardina pilchardus* (Lebour, 1921). Holstvoogd (1957) described a well developed pronephros and archinephric duct in herring larvae 10 mm long; this is not present at hatching (Holliday and Blaxter, 1961). Maier and Scheuring (1923) quoted work on the development of the swim bladder and its connection with the labyrinth. At 7 mm the larvae had a much shortened swim bladder rudiment and at 14 mm the connection with the labyrinth had already been established. The gill arches are present at hatching but the gills are not functional until about 20 mm (Harder, 1954). The blood contains a form of leucocyte but no erythrocytes.

The general development of the fins and skeletal system of herring has been described by Lebour (1921), Schnakenbeck (1929), Bückmann (1950), Blaxter and Hempel (1961) and Blaxter (1962). Wells (1922) gave a description of the development of the chrondrocranium; in the newly hatched larva the ethmoid plate formed the roof of the buccal cavity and the upper jaw (palato-pterygo-quadrate) began to develop only at 13 mm. The detailed development of the vertebral column

was worked on by Ramanujam (1929) in herring and by Gwyn (1940) in *Clupea pallasii*. In herring the pectoral fins were present at hatching, but the dorsal, caudal and anal fins developed between 12 and 20 mm, the vertebrae starting to develop at about 25 mm. Harder (1953) has shown the relative changes in the proportions of the gut, skeleton and muscle at lengths from 6–245 mm. Lebour (1921) made a comparative study of the relationship between myotomes, vertebrae and fins in herring, *Sprattus sprattus* and *Sardina pilchardus*, as an aid to the identification of the larvae.

B. *Feeding of larvae*

1. *Yolk supply*

The early growth and survival of larvae depends partly on the yolk supply and, therefore, on the size of the egg. In herring this varies from race to race and from parent to parent*; spring and winter spawning herring produce larger eggs (up to four times the dry weight) than summer and autumn spawners (Rannak, 1958; Blaxter and Hempel, 1963). Larger eggs produce mainly larger larvae, but also larvae living longer on their yolk reserves. Both these factors could be of importance to brood survival where the food supply was minimal.

2. *Feeding behaviour*

On hatching, herring larvae show much vertical movement, but after some days more horizontal movement is observed. At the same time searching movements for food occur. Many authors have reported food taken by herring larvae still with yolk sacs. Food is taken by a darting movement following an S-shaped flexing of the body (Schach, 1939; Soleim, 1942; Bückmann *et al.*, 1953). The prominent eyes would appear to indicate the importance of vision to the larvae in seeking food. Similar feeding behaviour has been described by Breder and Krumholz (1943) in *Harengula pensacolae* and Maxfield (1953) found that the larvae of *Alosa sapidissima* took only zooplankton, suggesting a predatory type of feeding. No feeding was observed in darkness in rearing experiments on *Clupea pallasii* (Kurata, 1959) and Hentschel (1950) and Bhattacharyya (1957) showed a cycle of feeding activity in herring larvae caught at sea, suggesting no feeding activity by night. While this evidence supports the importance of vision and active selection of food to clupeid larvae, Lasker's (1962) observations, that the young larvae of *Sardinops caerulea* fed passively with gaping jaws, the eyes at this stage being non-functional, indicate a different mechanism. However, Arthur (1956) reported that older larvae of this

* Yolk sac size for larvae of a given length varied from year to year in *Clupea pallasii* (Iizuka *et al.*, *Bull. Hokkaido Reg. Fish. Res. Lab.* **25**, 1–10, 1962).

species seemed to feed only by day, indicating the importance of vision.

3. *Type and quantity of food taken*

Bowers and Williamson (1951) and Bhattacharyya (1957) have reviewed the large amount of work done on feeding of herring larvae caught at sea from the analysis of gut contents. While it is not intended to discuss the results in detail, it may be said that the size of food organisms taken seems to increase with the size of larvae and a limited selection (or rejection) takes place. For example, organisms such as the copepod *Acartia*, the diatom *Biddulphia* and dinoflagellate *Ceratium*, though present in the plankton, are not found in the gut. As larvae grow older they tend to take larger food organisms.* The apparently low percentage of larvae feeding reported by some authors, though not for the larger larvae examined by Bowers and Williamson, may be due to rapid digestion or defaecation on capture or fixation, or to night sampling. Arthur (1956) suggested that mainly sickly or starving *Sardinops caerulea* larvae might be caught, giving a biased estimate of percentage feeding. He also gave details of the feeding of these larvae and showed how the size of food increased from up to 80μ when 4 mm long to 200μ when 10 mm long. Cushing (1960) also described the increase in size of food taken by larvae of this species as it grew.

The importance of phytoplankton for clupeid larvae has been under discussion for many years. For example, Hardy (1924) found diatoms taken by herring larvae, but Bowers and Williamson (1951) did not. Arthur (1956) considered *Sardinops caerulea* larvae to be carnivores, less than 1% containing plant food, but *Brevoortia* larvae are supposed to utilize diatoms (Harder, 1960). Morris (1955) suggested that the ingestion of dissolved organic matter could be of importance to fish larvae (Pütter's Theory), but to date little evidence is available for or against this.

The quantity of food taken was found to vary with temperature and size in Baltic herring larvae (Waldmann, 1961). Meyer (1878a) reported herring larvae in his rearing experiments with as many as twenty organisms in the gut. In rearing experiments Blaxter (1962) found up to ten organisms at any one time in larvae 10–12 mm long and Kurata (1959) found up to nineteen organisms taken per day by *Clupea pallasii* larvae 15–40 days old.

4. *Digestion*

In herring larvae the food is passed almost immediately to the anal

* Iizuka *et al.* (*Bull. Hokkaido Reg. Fish. Res. Lab.* **25**, 1–10, 1962) reported an increase in mouth size with growth but no great change in size of food taken by larvae of *Clupea pallasii*.

end of the gut, where digestion takes place (criteria being transparency of gut contents) in 2–5 hr at 5–15°C in larvae 10–12 mm long (Blaxter, 1962). Blaxter and Hempel (1961) found digestion times of 4–6 hr at 10–12°C in slightly larger larvae, but Kurata (1959) gave times of 7–8 hr at about 9°C for *Clupea pallasii* larvae, clearance of the gut taking 12–20 hr, depending on the original quantity of food taken. Arthur (1956) calculated from feeding frequencies of *Sardinops caerulea* larvae caught at sea, that digestion took from 11 hr in the smallest larvae (? 4–5 mm) to 3 hr in those 25 mm long. This type of analysis from sea-caught larvae may not be reliable due to the difficulty of recognizing partly digested food, and the possibility of food being lost due to unusual stimulation.

5. *Starvation and the need for food* (*also see Section III, F*)

Very little is known about the time clupeid larvae can live without food, though clearly this is of great importance in relation to survival in areas of poor plankton. Blaxter (1962) found that herring larvae in rearing experiments could survive for 2 to 9 days without feeding. Lishev *et al.* (1961) reported a relationship between the abundance of herring (salaka) " fry " in the Bay of Riga and the number of food organisms from 1955–1961, and Nikitinskaya (1958a) that the larvae of *Clupea pallasii* required a food concentration in the sea of 20–50 mg/m^3. Dementeva (1958) considered that the mortality of Sea of Azov anchovy was not connected with food supply, due to the plasticity of feeding. Murphy (1961) estimated that the food organisms of *Sardinops caerulea* were spaced so that the larvae were on average not more than 3·5–5 cm away from a food organism.

6. *Adaptations in relation to food*

Nikolsky *et al.* (1961) compared the number of pyloric caecae and length of the alimentary tract in larval and young herring of different length from the Atlantic and parts of the Baltic. They showed in the oceanic form that the number of caecae was greater, but the variability less, while the alimentary tract was longer. They related this to the better feeding conditions in the Atlantic, in particular high variability being an adaptation to poor conditions (this has also been reported for egg size).

C. *Growth of larvae*

It is not proposed to discuss the growth of clupeid larvae estimated from material caught on larval surveys, though mention should be made of the work by Marshall *et al.* (1937) on the fat content and increase in

weight of Scottish (Clyde) herring larvae with length. Growth will vary as a result of biotic and abiotic factors as well as inherent ones such as yolk supply (Toom, 1958; Blaxter and Hempel, 1963). Few attempts have been made to correlate growth rates from year to year and place to place with such factors.

Growth rates have been studied in aquaria to a small extent. Meyer (1878a) and Schach (1939), using wild plankton as food, reared herring larvae whose growth rate was similar to that in the sea. They found the growth rate dropped when plankton was scarce. The best growth was found by Schach to be in the largest tanks. Blaxter and Hempel (1961) found an increased growth rate in reared herring larvae when coarser plankton was used as food. Blaxter (1962) found some evidence for better growth of herring larvae at higher temperatures and in larger tanks. Nikitinskaya (1958b), hatching larvae of *Clupea pallasii*, obtained less active and less well-developed larvae in temperatures outside the average of 3–6°C, and from the later hatchings at 3–6°C. Farris (1960) suggested that the overall growth of young *Sardinops caerulea* larvae was best approximated by two curves, an initial logarithmic and a subsequent exponential one. A common finding of many authors rearing fish larvae is the great size range of larvae of the same origin kept in the same tank, in conditions of apparently abundant food (discussed in Section VI, E). Another finding has been some abnormality of growth, mainly a foreshortening of the head region, as that described by Bückmann *et al.* (1953) for herring larvae. Nikolsky *et al.* (1961) analysed the variation in length of young herring from Norway and the Baltic (" salaka "). The Norwegian herring showed less variability, which they related to the greater stability of feeding conditions in the ocean.

D. *Rearing of larvae*

The successful rearing of herring and *Clupea pallasii* beyond the yolk sac stage has been achieved by a number of workers as summarized in Table III.

Morris (1956) gave a valuable review of marine fish rearing, particularly from the feeding point of view. From a study of this and published work in the table, the following facilities appear to be desirable for successful rearing: tanks with opaque walls, running sea water, even overhead illumination and a source of wild plankton (*Balanus* nauplii, obtained from the adults before spawning, also being satisfactory).

Little success seems to have been met with in rearing clupeids other than herring, though *Alosa* species have been reared in ponds in

TABLE III

DETAILS OF REARING EXPERIMENTS ON CLUPEIDS

Author	Species	Time kept	Size reached in mm	Food used	Type and size of tank used	Remarks
Meyer (1878a)	German coastal herring	5 months	65–70	Natural plankton	700 litres	
Schach (1939)	German coastal herring	2 months	40–60	Natural and cultured plankton	2500 litres tiled	7% of undamaged hatched larvae survived
Soleim (1942)	Norwegian herring	2 months	18	*Balanus* and *Artemia* nauplii	7–14 litres	
Dannevig (1948)	Norwegian herring	?	?25	*Ostrea*, *Balanus* and *Artemia* nauplii, natural plankton	56 litres earthenware pipe	105 out of 500 reared to size where vertebrae could be counted
Dannevig and Hansen (1952)	Norwegian herring	6+ months	30+	*Artemia* nauplii, natural plankton, minced *Mytilus* (later)	2450 litres cement	Presumably metamorphosed
Blaxter and Hempel (1961)	German coastal herring	4 months	20–39	Natural plankton, *Mytilus* larvae, *Artemia* nauplii	120 litres black painted glazed stoneware	Some metamorphosed
Blaxter (1962)	Scottish (Clyde) herring	3 months	25–33	*Balanus* nauplii, *Artemia* nauplii	50 litres black glass 2000 litres black fibre glass	None metamorphosed
McMynn and Hoar (1953)	*Clupea pallasii*	20+ days	10·2+	*Artemia* nauplii	600 ml beakers	56% still alive after 20 days
Kurata (1959) (pers. comm.)	*Clupea pallasii*	at least 40 days	14·5	*Artemia* nauplii	1200 ml jars	14·2% survival after 40 days when experiment discontinued

uncontrolled conditions (e.g. Pearson, 1952). The very small larvae of *Sardinops*, for example, make the successful rearing of these species a great challenge.

E. *Farming*

In some clupeids a form of fish farming has been attempted. For instance, Williamson (1909), using low temperatures, retarded the development of herring eggs so that they might be transported to New Zealand; this attempt failed. Japanese workers (see under Isasaki in Scattergood, 1957) tried to improve the fishery for *Clupea pallasii* at Akkeshi-machi in the early 1930's. Motoda and Hirano (1961) described experiments from 1939–1949 in which 2×10^{11} eggs of *Clupea pallasii* were transported on the west coast of Hokkaido in order to see whether the fishery could be improved, but without any apparently beneficial result. Bibov (1960), however, reported a successful project where 19 million herring eggs were transported from the Baltic to the Aral Sea between 1954–1956, resulting in the formation of a new stock there, the fish having established themselves to the extent of growing and spawning. The growth in length was up to one and a half times that in the Baltic and the growth in weight four times, and the fecundity five times, as great as the original parent stock. The importance of this type of project, which gives valuable ideas as to the plasticity of the characteristics of a species, cannot be overestimated.

In the shad *Alosa sapidissima*, pond culture has been successfully carried out on the eastern coast of the United States since the end of the last century. Recent publications on the subject are those of Pearson (1952) and Maxfield (1953).

Murphy (1960) and Hida and Thomson (1962) reported the establishment of *Harengula vittata* and *Dorosoma petemense* respectively in Hawaiian waters as bait fish for tuna.

F. *Mortality of larvae*

During the period from hatching to metamorphosis, it has been questioned whether clupeid larvae go through critical periods when high mortalities occur, for instance at the stage where the larvae change from their yolk to external food sources. High mortalities of herring larvae have been reported at sea by Soleim (1942). Bowers and Williamson (1951) commented on published work showing a low percentage of guts of herring larvae containing food. Low percentages may be due to extrusion of gut contents on capture and need not necessarily be a sign of poor feeding conditions or low survival rate of larvae. Hempel and Blaxter (1961b) measured the condition factor of

herring larvae caught at sea in different areas and found in some instances very low values indicating the larvae were near starvation. Lasker (1962) quoted reports of *Sardinops caerulea* starving in the sea.

The general subject of critical periods has been reviewed by Marr (1956), with new data on *Sardinops caerulea*, and he concluded that this concept should be treated cautiously. Farris (1960) took this study further and calculated the effect of different types of growth curves on estimates of larval survival. Taking data on the abundance of larvae of *Sardinops caerulea*, *Sardinops melanosticta* and *Engraulis japonica* caught at sea, he concluded that high mortality took place *before* the final absorption of the yolk, assuming that net selection, which might allow the escape of small larvae, was unimportant. This observation was supported by laboratory experiments on rearing *Sardinops caerulea* when a high mortality took place before absorption of the yolk. While such a mortality in the sea could be explained by predation, this was not so in tanks and Farris suggested that a high proportion of eggs might be imperfect, both in the sea and in tanks. This would be rather surprising on general biological grounds. Murphy (1961) discussed the critical period concept for *Sardinops caerulea*, suggesting how both poor food supply and low temperatures might retard development and prolong this period.

Bridger (1960, 1961) considered the fluctuations in the abundance of herring larvae in the southern North Sea and English Channel and concluded that the abundance depended on the number of eggs spawned by the *older* fish rather than on the total stock. This might be due to the older fish spawning later, at a time of better food supply for the larvae, or it might be due to intrinsic differences in the yolk supply, the older fish producing larger eggs with more yolk. A similar viewpoint has also been put forward by Marty (1959). Again on biological grounds it seems somewhat unlikely that large sections of a spawning population should be producing inviable larvae.

The importance of egg size on survival of larvae has been studied by Blaxter and Hempel (1963). They showed that within a race larger eggs tended to produce larger larvae on hatching as well as larvae that lived longer on their yolk. Whether larger larvae are more viable as a result of a larger mouth or greater activity remains to be tested. Certainly larger larvae take larger food organisms according to samples caught at sea (see Section IV, B). Between races the yolk supply had a very strong effect on survival, larvae living for from 12–25 days at 8°C, for instance, depending on their race. Nikitinskaya (1958b) found that the larvae of *Clupea pallasii* reared at temperatures above normal were smaller, less well-developed and less active, as

were the later hatching larvae at normal temperatures. She suggested that a wide variability in larval viability permitted the stronger larvae to survive when food was poor. Anokhina (1961), working on Baltic herring, found in a restricted sample that the variability of egg size was greater from parents with low fat content, suggesting that where fat was low, food was poor, and at least the larger eggs would have a chance of producing larvae which would survive. However, this result would bear further examination, particularly in relation to fat utilization and the different stages of maturation when yolk may be laid down. Ivlev (1955) measured the loss of weight in starving larvae of *Caspialosa volgensis*. After 20 days 54% survived, the average weight loss being 18·1% ; after 30 days when only 7% were left alive, the weight loss was 22·1%.

Laboratory studies of larval fish survival in general were referred to by Morris (1956) and Farris (1960). The occurrence of high mortalities in rearing experiments may not necessarily be paralleled in the sea. In rearing experiments on herring, the following causes of mortality have been reported—gas disease (bubbles of gas in the intestine) by Kotthaus (1939), Schach (1939), Soleim (1942), Dannevig (1948), Dannevig and Dannevig (1950), Dannevig and Hansen (1952) and Blaxter and Hempel (1961); attack by hypotrichous ciliates by Kotthaus (1939); becoming caught or cut by artificial glass-wool substrata by Schach (1939); attack by *Lentospora cerebralis* (?), and the use of unsuitable food by Dannevig and Hansen (1952); being sucked against the water outflow by Schach (1939); and capture by *Coryne* and blockage of the gut by Blaxter (1962).

Blaxter and Hempel (1961) found two phases of mortality in herring larvae during rearing experiments, the first after yolk sac absorption and the second at 18–20 mm. Both phases occurred despite an abundant, though not necessarily suitable, food supply. Many failures to rear clupeid larvae after absorption of the yolk must have been due to unsatisfactory food, but from cases where some larvae have survived, it would appear that the ability to survive varies widely from larva to larva, even from the same parents. The second phase of mortality mentioned above might have been due to the imperfect development of a particular organ system.

At present, proof of the existence of critical periods for survival of larvae in the sea must await the development of a sufficiently continuous and comprehensive sampling programme on a larval population. Clearly, however, the survival of a brood must depend on a number of factors, two of which are feeding, which has already been discussed, and predation.

G. *Predation on larvae*

While this may well be an important source of mortality (Marty, 1956), nothing is known of its extent in the sea, although some predatory species have been noted. Lebour (1923) described plankton investigations where herring larvae were observed in the guts of various species of medusae, in the ctenophore *Pleurobrachia* and in *Tomopteris*. Larvae were also taken with *Sagitta* attached to them. This was also observed in *Sardinops caerulea* by Arthur (1956). Marshall *et al.* (1937) reported an absence of herring larvae in the Firth of Clyde, possibly due to predation by medusae and ctenophores, while Stevenson (1947, 1962) cited ctenophores as preying heavily on the larvae of *Clupea pallasii*. Lebour (1924) and Arthur (1956) report cannibalism in herring and *Sardinops* respectively, adults eating the young. The latter also reviewed the work done on the possible effects of phytoplankton and metabolites on clupeid larvae.

H. *Salinity tolerance and osmo-regulation of larvae*

1. *Salinity tolerance*

This has been studied in newly hatched herring larvae by Holliday and Blaxter (1960) and Bishai (1961a), and in *Clupea pallasii* by Kurata (1959). Figure 1 shows the salinity tolerance of herring larvae. The most striking feature of the results is the very wide tolerance of the larvae, from 1·4–60‰ over 24 hr, and 2·5–52·5‰ over 168 hr. Bishai (1961a) found that herring larvae lived longer in salinities from 10–15‰ than in higher or lower salinities. The 24-hr values quoted for *Clupea pallasii* by Kurata were from 1·05–59·5‰. Kurata also gave figures for 10-day-old larvae (1·05–66·5‰) and 20-day-old larvae (2·45–40·25‰). No abnormalities of development were reported by these workers. However, Kryzhanovsky (1956) reported that if Baltic herring eggs, which normally develop in water of salinity 4–5‰, were transferred to salinities of 25‰ then abnormal development and death of the larvae occurred. Stevenson (1962) suggested that larvae of *Clupea pallasii* might die in the open sea due to its high salinity. It would appear that other clupeids have a wide salinity tolerance, for instance Perceva (1939) found that larval *Caspialosa caspia* would survive in fresh and " salt " water.

2. *Osmotic regulation*

Holliday and Blaxter (1960) showed that the tolerance of herring larvae was based on a process of active regulation. If the larvae were transferred from sea water to any salinity within their tolerance range

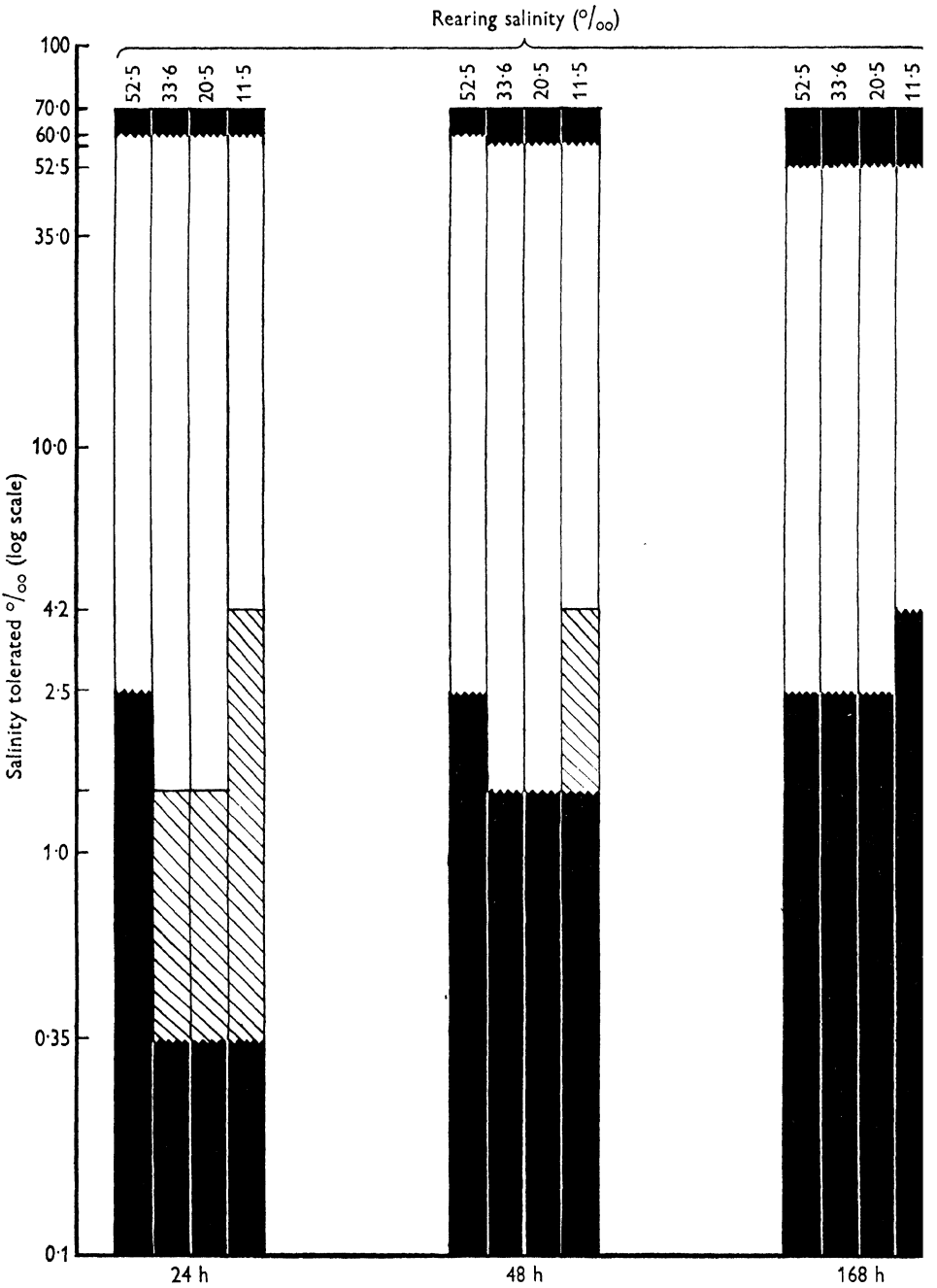


FIG. 1. The salinity tolerance of herring larvae reared in different salinities after varying periods in transfer salinities. (Reproduced with permission from Holliday and Blaxter, 1960.)

black—more than 50% dead; hatched—more than 50% alive, but larvae inactive; clear—more than 50% alive and active.

the body fluids first showed a rapid change in concentration. Regulation started within 6–12 hr and the body fluids were returned to close to their original value. In salinities above 12‰ (the isotonic point) the body fluids stabilized at a value roughly one-third of the external salinity. Below 12‰ the values were only slightly lower than the sea water values. The larvae showed changes in body weight corresponding

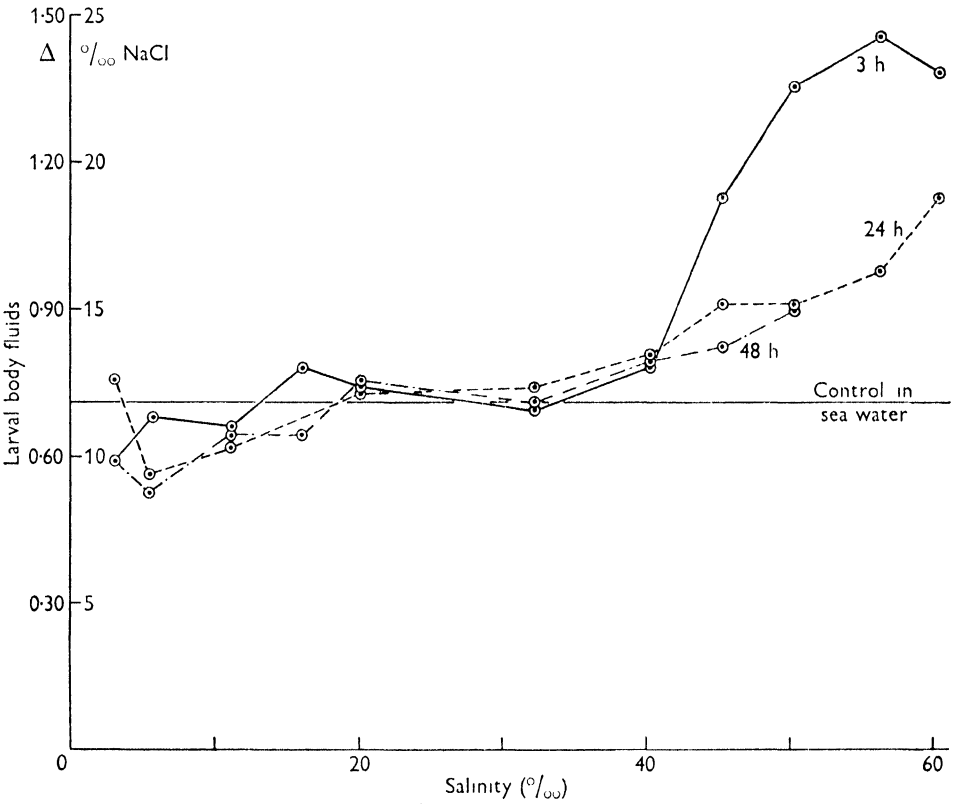


FIG. 2. Osmotic concentrations of larval body fluids, larvae transferred from sea water (32·3‰). (Reproduced with permission from Holliday and Blaxter, 1960.)

to a loss of water in the high salinities and a gain of water in the low salinities, the weight returning to near normal after successful regulation.

Within the salinity range 2·5–52·5‰ the larval tissues were regulated to equivalent salinities 9·8–15·0‰ (Δ = 0·59–0·90). Before regulation was complete, however, the larval tissues experienced and survived internal concentrations equivalent to 8·7–27·5‰ (Δ = 0·52–1·65); in normal sea water the value was equivalent to 12‰ (Δ = 0·72), see Fig. 2. Lasker and Theilacker (1962a) obtained results on *Sardinops caerulea* larvae showing that in sea water of 35‰ and 17‰ the

body fluids and yolk were regulated to a concentration equivalent to 15‰. They showed that whereas newly hatched larvae died in distilled water, larvae two days old survived for at least 24 hr, although the body fluids were reduced in concentration to about 9·7‰.

3. *Sites of regulation*

These have not been determined experimentally in fish larvae. Shelbourne (1957) suggested the epidermis, and this seems to be most likely.

4. *Effects on metabolism*

It might be expected that as the degree of regulation required depended on the difference between the environmental salinity and the tissue concentration, more metabolic effort would be required to survive in the extreme salinities. Lasker and Theilacker (1962a) found no difference in oxygen uptake in *Sardinops caerulea* larvae living in sea water or in sea water diluted until it was isotonic with the tissues. This work was extended by Lasker and the present authors, who found that there was no difference in oxygen consumption of herring larvae incubated and hatched in salinities ranging from 5–50‰. However, some variations occurred in the few hours immediately following abrupt transfer from one salinity to another, but as regulation was achieved the value returned to its previous level.

5. *Effects of starvation*

Ivlev (1955) showed that there was little difference in salinity tolerance between starved and normal *Caspialosa volgensis* larvae, although the range of salinities tested was small.

I. *Oxygen uptake*

Respiratory exchange in younger larvae almost certainly takes place over the body surface. Harder (1954) reported that the gills of herring were not functional until a length of about 20 mm. Volodin (1956) suggested that carotenoids in the yolk acted as respiratory pigments. A sensitive technique is required to measure the oxygen consumption of single larvae. As the activity of the larvae is dominant in determining the oxygen requirement, comparisons of metabolism in larvae of different age or in different environmental conditions are best made on individuals anaesthetized to the same level (determined by heart rate). Table IV gives values of oxygen uptake in some clupeid larvae.

TABLE IV

OXYGEN CONSUMPTION OF CLUPEID LARVAE

Author	Species	O_2 uptake μ litres/larva/hr	Remarks
Marshall *et al.* (1937)	Herring (Clyde, Scottish)	0·046	In the dark (8–12°C)
		0·037	In the light (8–12°C)
Lasker and present authors (unpub.)	Herring (German coastal)	0·07	Anaesthetized (8°C)
		0·70	Unanaesthetized (8°C)
Volodin (1956)	Herring (Baltic)	0·19	1 day post hatching (14°C)
		0·32	2 days post hatching (14°C)
		0·43	3 days post hatching (14°C)
Lasker and Theilacker (1962a)	*Sardinops caerulea*	0·08	Active (14°C)
		0·03	Inactive (14°C)

The effects of salinity on oxygen uptake were considered in Section IV, H.

J. *Dermal receptors*

Cunningham (1889, 1894) and Lebour (1921) described in larval *Sardina pilchardus* and *Sprattus sprattus* a number of small papillae placed alternately down the length of the body, about six on each side. de Kock (personal communication) found them also in the head region of herring larvae where they resembled small taste buds in structure, having a number of projecting sensory hairs (see Fig. 3). It is possible that they are chemoreceptors, or they may have some hydrodynamic function (they also resemble the lateral line organs of the adult, and the cupulae described by Verheijen (1956) on the adult *Sardina pilchardus*).

K. *Temperature, pH, oxygen, pressure and light as limiting factors*

Marshall *et al.* (1937) kept newly hatched herring larvae for a short time at 26°C without harm. Kurata (1959) found that *Clupea pallasii* larvae died after transfer from 6·6°C to 17–18°C. Blaxter (1960) showed that recently hatched herring larvae would tolerate 22–24°C and −0·75 to −1·8°C when acclimatized to temperatures between 7·5 and 15·5°C. The range of lethal temperatures tended to be narrowed by unfavourable salinities.

Bishai (1960b) found that " the activity " of herring larvae became restricted at pH values of 6·4 to 6·6, the lethal pH being lower. Raising the pH of the water from the rearing value of 8·1, to 8·5, caused death.

High oxygen tension was less important to newly hatched herring

(Bishai, 1960a), whose activity was " restricted " between 26·9–32·2% oxygen at 14°C; this occurred at 55–64% oxygen in larvae 3–4 days old. Larvae died in 6 hr at 11·6% saturation. The larvae would live at oxygen values up to 411·4%.

Bishai (1961b) showed that herring larvae could withstand pressures up to 4 atmospheres. No gas bubbles were found in the intestine when the pressure was released from 2 atm to 1 atm in 10 min.

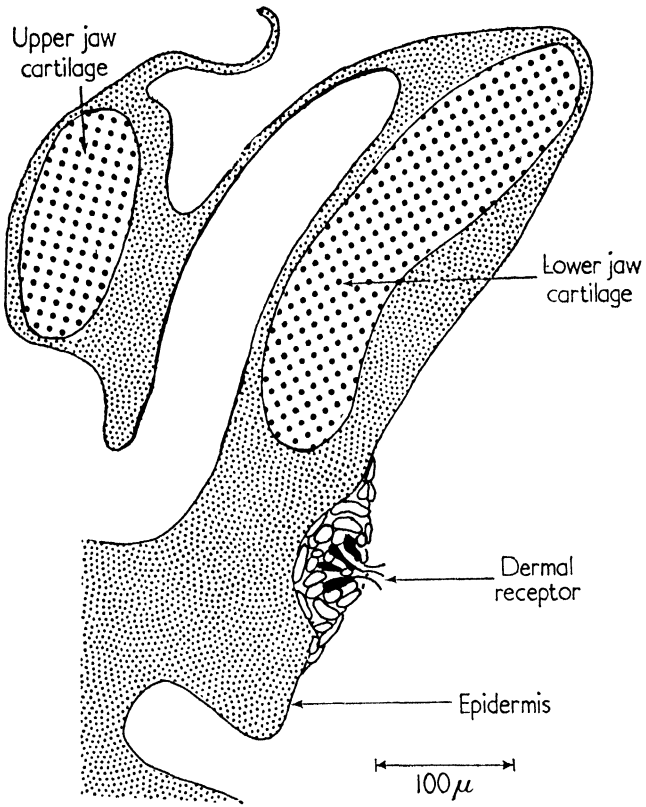


FIG. 3. Transverse section of the head of a herring larva showing a dermal receptor (de Kock—unpublished).

Ljubickaja (1957) reported that there were more *Sardinella* " spawn " and larvae dead near the surface in the Sea of Azov than near the bottom. She suggested this might be a mortality due to infra red light which was absorbed rapidly by sea water and would only affect organisms near the surface. Dementeva (1958) considered that sunlight would only be deleterious because it warmed up the surface layers.

Bishai (1960a) gave a good review of work on gas disease and its possible causes in rearing experiments on herring larvae. Six possible

causes were discussed—formation of gas by monads, swallowing of air bubbles, break-down of yolk material, lack of oxygen and therefore intake of air from above the surface, supersaturation of the water and swallowing of air for the swim bladder. Bishai concluded that supersaturation of the water, followed by involuntary swallowing by the larvae, was the most likely cause. Blaxter and Hempel (1961) also concluded in older larvae that active swallowing of air trapped on the surface, particularly in supersaturated water, was also a cause of gas disease and this might be eliminated by careful cleaning of the surface.

L. *Locomotory behaviour and rheotropic response*

On hatching, herring larvae tend to swim vertically to the surface and then sink head first to the bottom. At the end of the yolk sac stage this behaviour becomes replaced by horizontal searching movements for food. Breder and Krumholz (1943) reported that *Harengula pensacolae*, about 3 mm long, were unstable, the centre of buoyancy being lower than the centre of gravity and equilibrium being maintained by the pectoral fins. They moved by alternate sinking and swimming periods. Clupeid larvae with an oil globule swim upside down until this is absorbed.

Bückmann *et al.* (1953) found that herring larvae swam both with and against a current induced in a circular aquarium tank, while in an open air tank, and in harbour, they were always seen to swim anticlockwise. These authors mentioned the need for optical marks to get a rheotropic response. Blaxter and Dickson (1959) and Bishai (1960c) found that herring larvae about 8 mm long would orientate against a current passing through a tube. Bishai also found that the larvae did not show a pseudo-rheotropic response when striped paper was passed along the tube. Morris (1956) suggested that a current was of importance in rearing tanks as larvae would then tend to stem such a current instead of making frequent, probably disadvantageous, contacts with the walls of the tank.

M. *Vertical migration of larvae*

1. *General*

Reports of the distribution of clupeid larvae in the sea are difficult to compare and analyse due to sampling problems. In relation to diurnal vertical migration these are perhaps most serious. Johansen (1925) gave some evidence for a downward movement by day of herring larvae 10–18 mm long, while Russell (1926, 1928) had similar evidence for the larvae of *Sardina pilchardus* and *Sprattus sprattus* under 24 mm long. Silliman (1950) found that the larvae of *Sardinops caerulea*,

greater than 8 mm long, tended to move down in daytime, but not the smaller larvae, while Bridger (1958) found that older herring larvae (16–25 mm) around the English coast tended to go nearer the bottom than the younger ones by day, and Colton *et al.* (1961), in the Gulf of Maine, reported a diurnal migration of herring larvae, the extent of the migration increasing with size.

However, one of the most striking observations of Johansen, Russell and Silliman, and also of Stevenson (1947) on *Clupea pallasii*, was that greater numbers of larvae were caught by night, particularly large ones. For example, Johansen caught about four times as many 8–19 mm herring by night as by day, and no larvae longer than 20 mm at all by day. Russell caught ten to thirty times more *Sardina pilchardus* and *Sprattus sprattus* up to 24 mm long by night, Silliman about ten times more *Sardinops caerulea* over 8 mm long by night, while Stevenson (1947, 1962) caught five times the number of *Clupea pallasii* larvae up to 15 mm long by night, and none over 15 mm at all by day. Ahlstrom (1954) reported the undersampling of *Sardinops caerulea* in daylight, and Murphy (1961) showed in the same species how the ratio night hauls : day hauls increased with length of the larvae from 4·75–21·25 mm.

The first explanation given for this by Johansen (1925) and Russell (1926, 1928) was that vertical migration was taking place in daytime and the larvae were not being sampled, but both these authors thought that net avoidance by day might be significant, and Russell (1926) considered that swarm formation by day might account for lower catches, due to unevenness of the larval distribution. The vertical migration explanation was not supported by hauls made at greater depths (Russell, 1926, 1930), where no abundance of larvae was found by day. Stevenson (1947) and Silliman (1950) also found no concentrations of clupeid larvae at great depths. It seems that while restricted vertical migration and swarm formation might account for some of the difference found, avoidance of nets by day was the main factor, especially as the nets were moving slowly.

2. *Avoidance of nets and swimming speeds*

Net avoidance by sight was particularly emphasized by Silliman (1950), while Stevenson (1947) thought that phosphoresence at night in his area would make the net as visible by night as by day. New methods were clearly required to show the distribution of larvae. Bridger (1958), using a high-speed sampler, showed that herring larvae up to 25 mm long were caught in equal quantities by day and night, which clearly supported the view that net avoidance caused a serious sampling bias with tow nets used at low speeds. Tibbo *et al.* (1958) and

Colton *et al.* (1961) found that larger herring larvae in the Gulf of Maine were caught mainly at night by a metre net; the latter authors using a Hardy high-speed plankton recorder also found the ratio of larvae caught by this gear, compared with the metre net, increased with increasing size of the larvae. Silliman estimated that *Sardinops caerulea* larvae would have to swim at about 5 cm/sec to escape a net towed at 50 cm/sec.

Blaxter (1962), using herring larvae from 8–20 mm long in tanks, tested their reaction to visual stimuli such as moving obstacles, and vibrations up to 10 c/sec, and measured their swimming speeds. He found that they were remarkably unreactive to such stimuli under tank conditions. The maximum swimming speed varied from about 3 cm/sec for larvae 8 mm long to 30 cm/sec for larvae 20 mm long. There was a tendency for an increase in maximum swimming speed at the stage when the caudal fin developed at about 15 mm. Bishai (1960c) worked on sustained swimming speed of herring larvae 6–8 mm long and found that they could maintain 0·58–1·03 cm/sec for at least 1 hr.

From these data it seems likely that clupeid larvae have the swimming ability to escape nets towed at low speeds of, say, up to 2 knots (100 cm/sec); it is unlikely that they would escape from a high speed sampler towed at 5–6 knots (250–300 cm/sec). If the evidence put forward in this review of the importance of sight in clupeids is accepted, and sight is the most important means of detecting such nets, then even nets hauled slowly will catch larger larvae at night.

N. *Response of larvae to light*

Spooner (1933) studied the reaction of herring larvae to light using convergent and parallel beams to separate intensity and direction effects. Their photo-positive behaviour was in general more a reaction to direction, activity falling off at low light intensities. Woodhead and Woodhead (1955) also found a drop in activity of herring larvae kept in a dish with diffuse light from below—from 35% of the time active at 4,000 lux to 20% at 20 lux. This photo-orthokinesis was accompanied by a phototaxis, the larvae swimming towards directional light. In a tall vessel the larvae were active in complete darkness. Below 100 lux most movement was vertical; at higher light intensities more and more horizontal movement was observed as if there were a dorsal light reaction. It was suggested that this movement provided a mechanism for vertical migration. It is necessary to note also, however, that herring larvae gradually develop more horizontal movement during the yolk-sac stage as part of feeding behaviour. Soleim (1942) found herring larvae more often in lighted parts of an aquarium. Bückmann

et al. (1953) noted that herring larvae were more evenly distributed in black than in white vessels. Larger larvae in tanks with transparent walls developed deformities in the head and survived less well, presumably due to swimming against the walls.

V. Metamorphosis

Little is known about metamorphosis except in herring. This is partly due to the difficulty of rearing the young, but also to the lack of suitable fish samples from the sea, this particular size of fish demanding special techniques for its capture.

Metamorphosis is said to occur in herring between 25 and 45 mm,

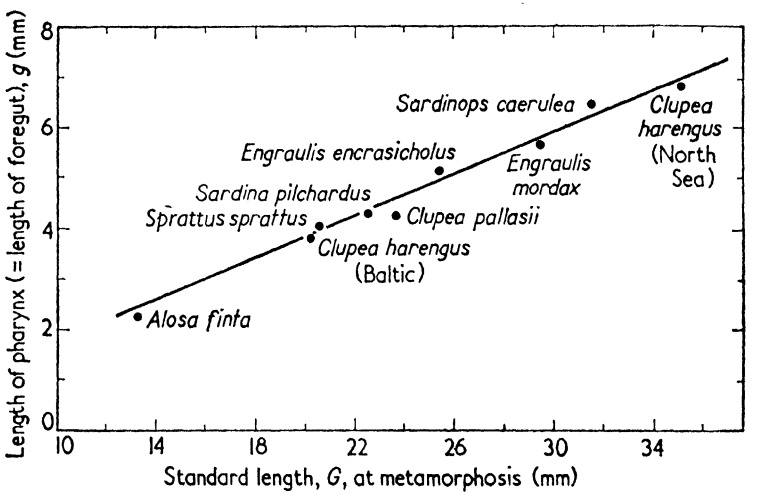


Fig. 4. Relationship between standard length at metamorphosis (G) and the length of the pharynx (= length of fore gut) of different clupeids. (Re-drawn with permission from Harder, 1960.)

depending on the race; in *Sprattus sprattus* it is 30–40 mm, in *Sardina pilchardus* 40–50 mm (Lebour, 1921) and in *Clupea pallasii* 25 mm (Stevenson, 1947). Harder (1960) related the length at metamorphosis in Baltic and North Sea herring, *Sprattus sprattus*, *Alosa finta* and *Engraulis encrasicholus* to the temperature of the water. He defined metamorphosis as the stage when the length of the pharynx and foregut were both 19·3% of the standard length (G), G being related to the temperature history during development (in month-degrees), such that clupeid species developing in colder water were smaller when they metamorphosed (see Figs. 4 and 5).

The main changes at metamorphosis are the development of the scales and of adult pigmentation in the form of melanophores and guanine. Ford (1930) gave a detailed description of the changes in the

vertebral column and position of the fins in herring at this stage. There was a forward movement of the dorsal fin and anus and a backward movement of the pelvic fins.

The speed of metamorphosis at sea is unknown but Blaxter and Hempel (1961) found it lasted about 10 days at 15°C in German coastal herring reared in tanks.

The heart, which prior to metamorphosis is composed of an outer myocardium with an endothelial lining, seems to be the source of erythrocyte formation (John, 1932). The endothelium thickens and megaloblasts bud off into the lumen of the atrium and ventricle, where they pass through an erythroblast stage to become erythrocytes. The spleen, which is the site of formation of erythrocytes in the adult, is not present at this stage.

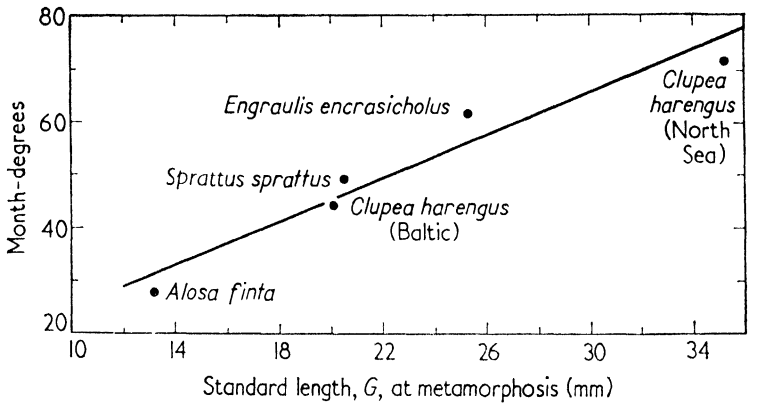


FIG. 5. Relationship between standard length at metamorphosis (G) and temperature history of larval clupeids in month–degrees. (Re-drawn with permission from Harder, 1960.)

Buchmann (1940) observed a large increase of thyroid activity at metamorphosis, the cell heights in the follicles increasing and colloid being formed and released. There was also a change in the pro-adenohypophysis which he believed was due to the production of thyrotropic hormone. According to Holliday (1960a), however, the application of a histochemical (P.A.S.) technique indicated that the site of thyrotropin production was the meso-adenohypophysis, and Buchmann may have been reporting the production of a growth hormone.

The formation of the gonads seems to take place at about this stage, at least in *Sardina pilchardus* where dos Santos Pinto and Andreu (1956) established the formation of the gonad at a length of 37 mm and sexual differentiation at 45 mm.

Little can be said about changes in the habits of clupeids after metamorphosis. Certainly herring at this stage start to shoal and are found inshore in large numbers. Whether there is a need to move into water of low salinity is not clear, though such a need has been correlated in other fish species with increase in thyroid activity. It may be that feeding conditions are more suitable, but there can be no doubt that young herring are particularly heavily preyed upon at this time.

VI. Post-Metamorphic Stages

A. *Establishment*

The general delicacy of clupeids was the reason given by such workers as Parr (1927), Spooner (1931), Loukashkin and Groody (1955) and Parrish *et al.* (1958) for the lack of experimental work on this important group of fish. Clupeids have not often been established in the aquarium. However, a number of attempts have been made not merely to keep the fish, but also to determine the reasons for the success or failure of the attempts and to perform experiments on them. These are summarized in Table V. Loukashkin and Groody (1955), Verheijen (1956), Farrin *et al.* (1957) and Parrish *et al.* (1958) reviewed the problems of establishing clupeids in aquaria, listing the factors that contributed to mortality at each of the stages of capture, transport, initial establishment and long-term maintenance and feeding. In general these authors concluded that epidermal damage was the principal cause of initial mortality. Parrish *et al.* suggested that osmotic dehydration followed the damage and these mortalities could be overcome by careful handling and keeping the fish in sea water of salinity roughly isotonic with the blood—about 16‰. It is interesting that, much earlier, Elmhirst (1908) accidentally discovered that herring survived best in an equal mixture of sea water and fresh water.

The size and structure of the aquarium, the rapidity with which the herring start to feed and the prevention of disease were the main factors controlling the long-term establishment of the herring (Parrish *et al.* 1958). Successful experimental handling was best carried out under anaesthesia with tricaine methane sulphonate. The herring always appeared very sensitive to disturbances, and showed no signs of becoming conditioned (or " tame ") in any way. They were influenced by the size of the tank, as feeding could not be initiated if the fish length : tank space ratio was too small.

Both Verheijen (1956) working on *Sardina pilchardus* and Parrish *et al.* (1958) on herring, found that feeding fish (in the case of herring also feeding *Gadus virens*) influenced non-feeding fish and caused them to begin feeding.

B. *Feeding*

1. *Behaviour*

In most clupeids this seems to be a direct, predatory snapping action. This was deduced by Hardy (1924) from the analysis of stomach contents of herring, and has been observed quite frequently in aquaria in a number of species, in herring for instance, by Battle *et al.* (1936), Bückmann *et al.* (1953) and by Verheijen (1953), in *Sardina pilchardus* by Mužinić (1960), in *Harengula pensacolae* by Breder and Krumholz (1943), in *Sardinops caerulea* by Loukashkin and Grant (1959), in *Pomolobus pseudoharengus* by Graham (1957) and in *Sardinella macropthalmia* and *Brevoortia tyrannus* by Breder (1959). Kirchhoff (1958), in a detailed study of the functional morphology of the herring, described a sucking action which would occur as food was being taken.

Kirchhoff (1958) also stated that herring had a suitable arrangement of gill rakers for filter feeding, and a study of gut contents in clupeids does suggest that some species are at least partly filter feeders. Radovich (1952) showed this for *Sardinops caerulea* and Komarovsky (1959) for *Sardinella aurita.* Gunter and Christmas (1960) reported findings of detritus and bacteria in the gut of *Brevoortia patronus*, and Harder (1960) cited *Brevoortia* and the engraulid *Cetengraulis* as diatom feeders. Lagler *et al.* (1962) stated that *Brevoortia tyrannus* swam with mouth agape through rich plankton, straining as much as 6·8 gallons of water a minute.

During feeding shoal formation tends to be disrupted. Hourston (1958) found this in *Clupea pallasii*, Graham (1957) in *Pomolobus pseudoharengus* and Breder (1959) for *Sardinella macropthalmia* and *Brevoortia tyrannus.* In fact, feeding could cause a considerable delay or change in any type of migration pattern (as discussed under Section VI, R). Jakobsson (1961) noticed how herring chasing and feeding on fish larvae changed their behaviour so markedly that they became very spread out and difficult to catch. Glover (1957) suggested that herring might be able to detect concentration gradients of their favourite food organisms. Thus feeding might cause an aggregation of dispersed fish, or a break up and possible dispersion of shoals which were already established.

2. *Selection of food*

Williamson (1917) observed herring in captivity. He found they could detect food from about 30–90 cm away depending on its size and that they rejected some food after taking it into the mouth. Blaxter and Holliday (1958) found that detection of food by herring kept in

aquaria was by eye; the fish attempted to take food regardless of shape, size or colour, once they were established. However, first texture, and then taste, were very important in selection within the mouth. Taste seemed to be dependent on water soluble, rather than fat soluble, substances. Anon. (1952) found in *Sardinops caerulea*, however, that the olfactory sense was of great importance in detection; this increased feeding activity after appropriate stimulation. The importance of smell was also mentioned by Cushing (1960).

Savage (1931) made a comprehensive study of the feeding habits of North Sea herring and reviewed earlier work by Hardy and others. He found, by also studying the plankton, that different food organisms were in the same proportion in the herring stomachs as in the plankton.

3. *Effect of light and temperature on feeding*

Clupeids not only appear usually to break shoal at night, they also stop feeding. This was reported in general terms by Zusser (1958a) for pelagic plankton-catching fish. Girsa (1961) reported also that visual feeders tend to disperse and stop feeding at about 0·1 lux. Girsa (see Section VI, U) developed the theme that light might be a signal for feeding and cause both attraction of fish and greater activity.

In aquaria Battle *et al.* (1936) found that captive herring did not feed in the dark but they, Johnson (1939a) and Blaxter and Holliday (1958), found feeding took place in moonlight (incident light intensity probably about 0·25 lux). Blaxter and Holliday found a threshold light intensity for feeding (using tungsten filament light) of about 3 lux; optimum feeding conditions appearing to be from 100 to 1,000 lux, feeding always being better when the daylight was not too bright. There appeared to be some evidence for a diurnal feeding rhythm, feeding activity being lowest from 0400–0800 hours. Williamson (1917) also reported that captive herring fed better in dim light. Loukashkin and Grant (1959) found that *Sardinops caerulea* would feed as well at 5 lux as at 200 lux, but did not try feeding the sardines in darkness. In view of their sensitivity to olfactory stimulation (Anon., 1952), this would make an interesting experiment.

At temperatures below 4°C, captive herring ceased to feed (Johnson, 1939a; Blaxter and Holliday, 1958), and Williamson (1917) also reported inactivity at low temperature. However, Battle *et al.* (1936) and Farrin *et al.* (1957) found feeding in captive herring at a temperature of 1°C and Kamshylov and Gerasimov (1960) even at −0·4°C. These findings may have been due to a longer acclimatization to the low temperatures, or to a difference in the physiological (or psychological) state of the fish.

4. *Effect of internal factors on feeding*

Williamson (1917) found that " hungry " herring were less easy to frighten and would feed better. It has often been said that spawning herring cease to feed, but sometimes they have been found with food in the gut—even herring eggs, which suggests feeding at some time during the mass spawning act, for herring do not appear to take food off the bottom.

The importance of psychological stimuli in feeding or initiating feeding is mentioned in Section VI, A, where it is seen that the presence of feeding fish, not necessarily of the same species, is a great incentive to feeding.

5. *Competition for food*

Variations in growth rate of clupeids kept in aquaria suggest the importance of dominant feeders, or of fish with more efficient utilization of food (see Section VI, E). But apart from intra-specific competition of this sort, about which practically nothing is known, there are indications of negative correlations between the abundance of related clupeid species in the same area. There have been changes in the dominant species recently, but whether these are reversible or not remains to be seen. Such correlations were discussed by MacGregor (1959) and Marr (1961) for *Sardinops caerulea* and *Engraulis mordax*, for *Clupea pallasii* and *Sardinops melanosticta* by Motoda and Hirano (1961), and for *Clupea harengus* and *Sardina pilchardus* by Cushing (1961). One possible explanation for these fluctuations could be competition for food, but the extent to which long-term changes in hydrographical conditions are responsible is not clear. It may be of significance that these changes occur near the extremes of the range of these species, where changes in hydrographical conditions might be expected to exert the maximum effect. Recently Southward (1963) has suggested that the increase of *Sardina pilchardus* and decrease of herring described by Cushing (1961) might be due to long-term temperature changes which put the herring at a disadvantage from the point of view of metabolism.

C. *The alimentary system*

1. *Morphology and anatomy*

Jacobshagen (1913) described the herring intestine as being short (one-half to three-quarters the body length) and associated this fact with the carnivorous diet of the fish. Harder (1960) compared gut morphology with body form, food and environment in forty-six

clupeid species and forty-two engraulids. He gave details of the different proportions of the gut at different stages of development in some of the species. There were population differences in gut length in herring, *Clupea pallasii*, *Sardina pilchardus*, *Sardinops caerulea* and some engraulid species. In particular he mentioned the very long guts of the diatom-eating clupeid *Brevoortia* and the engraulid *Cetengraulis*.

Stirling (1884) described the histology of parts of the gut of the herring. Both the oesophagus and stomach had thick muscular coats lined with glandular epithelium, the stomach having both simple and compound glands. All parts of the gut were innervated by the sympathetic system, the stomach being also supplied by the vagus nerve.

2. *Digestive enzymes*

The enzymes that have been found in the gut of the herring are set out in Table VI.

TABLE VI

DIGESTIVE ENZYMES IN THE HERRING

Region / Author	Stomach Regions			Pyloric caecae	Bile	Intestine	Liver
	Caecum	Cardiac	Pylorus				
Stirling (1884)	Strong pepsin	—	Pepsin	Trypsin and diastase	Diastase	—	—
Almy (1926)	Pepsin	Pepsin	Pepsin	Trypsin	—	—	—
Battle (1935)	—	Pepsin weak amylase and lipase	Pepsin weak amylase and lipase	Strong amylase and lipase	Slight amylase	Strong amylase and lipase	Slight amylase

Battle (1935) pointed out that the pyloric caecae take over the digestive activity normally attributed to the pancreas. This organ is present in the herring, but its contribution to digestion has not been studied. It may be that some of the gut enzymes do in fact originate in the pancreas. Almy (1926) concluded that gut enzymes were mainly responsible for the onset of decomposition of marketed herring.

3. *Effect of feeding*

Battle *et al.* (1936) investigated the changes in pH of the gut following a feeding experiment. The stomach contents were very acidic but

this acidity was neutralized by the bile in the intestine. More peptic activity was found in the full stomach than in the empty, or partly full one. The pH optimum for pepsin was between 2·5 and 2·85. Its activity increased with rise in temperature ($Q_{10} = 1{\cdot}5$). The level of trypsin in the pyloric caecae was highest in herring with full stomachs. Calcium salts present in the food increased the activity of trypsin. The pH optimum lay between 8·5 and 9·5, the Q_{10} being 1·5. The lipase of the pyloric caecae was rendered more active by the bile.

4. *Effect of enzymes on food*

Battle (1935) reported that live euphausiids, *Meganyctiphanes*, were killed in 3–4 min, and the copepods, *Calanus* and *Temora*, in 30 sec, by the action of the stomach secretions. Breakdown of the food started in the caecal and pyloric regions of the stomach, while in the pyloric caecae the food was in the form of an oily chyme, mixed with mucus. The bacteria in the gut might aid in digestion. Chitin from the food, and a large proportion of the oil, passed out with the faeces, often causing an oily film on the water in which herring were feeding.

5. *Time for digestion*

The length of time that the food stays in the gut depends on the temperature (Fig. 6) and on the feeding history of the fish. Blaxter and Holliday (1958) showed that food took longest to pass through the gut when fish were starved before and/or after the test feed. Battle *et al.* (1936) suggested that small herring retained food in the gut longer than large herring.

D. *Fat storage and metabolism*

1. *Cyclical changes*

The clupeids are seasonal feeders, building up large stores of fat to sustain them when food is in poor supply. The overall changes in body fat of the herring in relation to feeding, age, size, race and maturity stage have been extensively studied (for bibliography see Wood, 1958). Similar studies have been made on *Sardina pilchardus* (Hickling, 1945) and *Sprattus sprattus* (Lühmann, 1952). A good deal of individual variation exists, but it is the intensity of feeding that is the overriding factor in determining the fat reserves. The spring and autumn plankton peaks provide potentially rich feeding and whether the fish make use of this food depends to a large extent on the condition of the gonads, fish with well developed gonads feeding only to a very small extent. Thus the autumn-spawning herring feed and lay down fat reserves in

May and June and they stop feeding and lose fat in July and August. After spawning they feed and lay down fat once more and then, during the winter months, the fat reserves fall to their lowest point.

In winter-spring spawning herring the good feeding conditions in late spring and early summer (after spawning) build up the fat reserves. With the development of the gonads in late autumn feeding stops, and spawning in December-March means that the fish overwinter and spawn with fat reserves considerably lower than the autumn spawners.

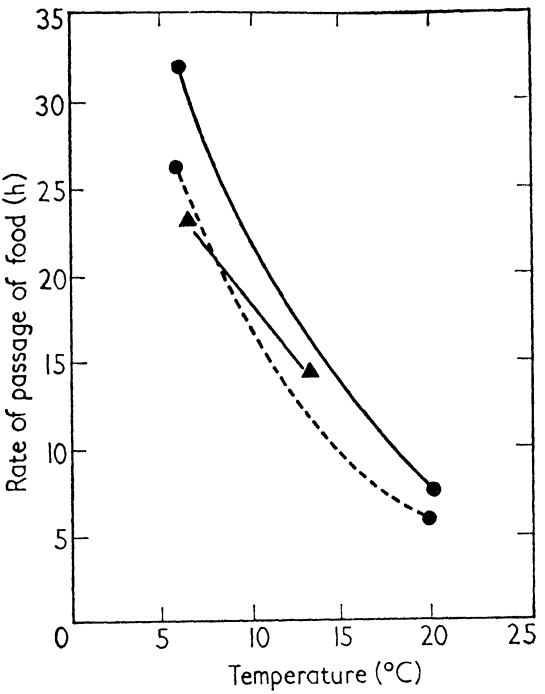


FIG. 6. Time taken for food to pass through the gut of herring.
●- - -● stomach: ●——● whole gut. Battle *et al.*, 1936)
▲——▲ whole gut. (Blaxter and Holliday, 1958)

The seasonal cycle in *Sardina pilchardus* is shown in Fig. 7. Hickling (1945) divided the pilchard's year into three parts. From April to July feeding was at a high level and the gonads ripened, taking priority over growth and fat reserves. From August to October, although feeding was poorest, the gonads made no demands and growth and fat deposition continued. Increased feeding in October meant that fat deposition reached its peak. There was no feeding from November to March and fat reserves fell sharply as they were called on for metabolism and gonad development. The decline in weight at this time was due almost entirely to this loss of fat.

2. *Fat deposits*

Fat is laid down in the connective tissue beneath the skin, in and between the myotomes, in the gut mesenteries and in the liver. Channon and Saby (1932) showed in the herring, that liver and mesenteric fat was more labile than muscle fat, being laid down and drawn on sooner. They estimated that 15% of the body fat was transferred to the gonads and 85% was metabolized during the spawning cycle.

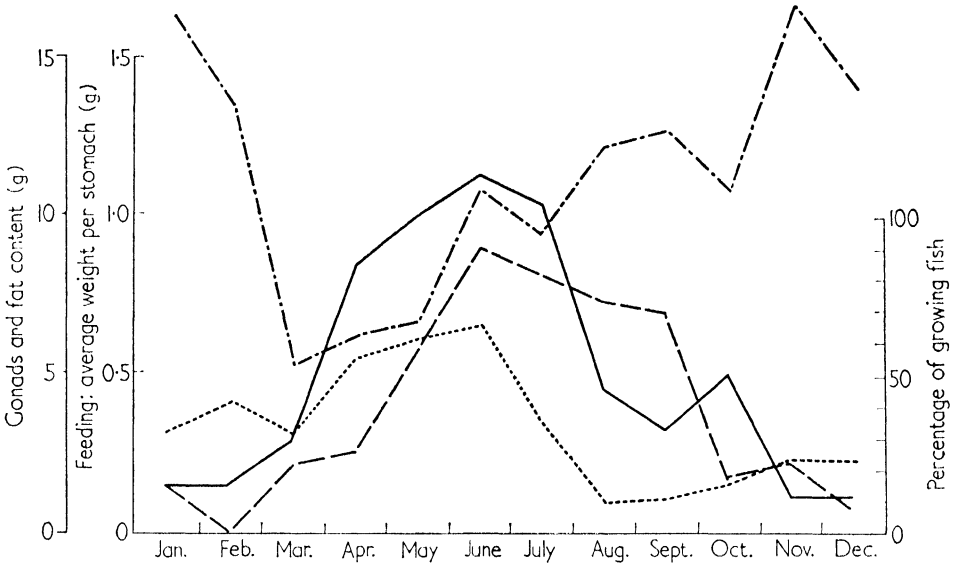


FIG. 7. The seasonal cycles of breeding, feeding, fat storage (scales on left) and percentage of fish growing, *Sardina pilchardus*. (Reproduced with permission from Hickling, 1945.)

——— feeding - - - - - growth
. . . . . breeding - · - · - fat storage

Brandes and Dietrich (1953a) showed that certain sites of the body musculature in the herring were richer in stored fat than others. The belly flaps had the highest concentration (47% fat), an area just in front of the dorsal fin was next (30% fat) and fat content diminished toward the head and tail. Lühmann (1953) pointed out that the activity of the tail muscle precluded the deposition of large amounts of fat in that region. (The effect of fat distribution on buoyancy is discussed in Section VI, N.)

3. *Characteristics of fat*

A good deal of work has been done on the characteristics of the fatty acids stored in clupeids. Lovern (1951) demonstrated that the fats stored in the herring were almost identical with the fats of the copepods in the diet of the fish. Lasker and Theilacker (1962b) showed

that the dietary fat of *Sardinops caerulea* (derived to a large extent from *Calanus*) was stored largely unaltered. They also showed that both the blood lipids and the lipids deposited in the gonad were practically identical, indicating that mobilization of fats from the intestine to the gonads was relatively direct. The lipids of the developing eggs caught at sea were almost identical with those from the eggs at different stages of maturation in the gonad. Changes were shown to occur in the fatty acid pattern of the lipids of the blood, gonad and mesenteries when the sardines were fed on an artificial diet. The herring does have the capacity to alter the fatty acid composition of the depot lipids, especially in regard to the degree of unsaturation of the fat, but the rapid ingestion of the highly unsaturated fats during the intense feeding periods causes a temporary swamping of the fishes' hydrogenation mechanisms (Lovern, 1938).

Cholesterol does not show the same kind of changes as the fatty acids. The level remains constant in the muscles, there being a slow transfer of cholesterol from the liver and mesenteries to the gonads, where cholesterol levels rise with the degree of maturation. The testis contains considerably more cholesterol than the ovary. Channon and Saby (1932) demonstrated that during the final stages of maturation more cholesterol was present in the gonad than could be accounted for in the depots, and they concluded that at this time the herring was synthesizing cholesterol.

4. *General*

The food available for metabolism, either from an external source or from the fat depots, obviously profoundly influences the timing and rate of many of the other physiological activities. It is not surprising then that at least loose correlations can be made between fatness and fecundity, maturation rate, age, growth etc. Most estimates of the " condition factor " of clupeids reflect to a large degree the state of the fat stores. A good deal of work still remains to be done on the correlations between fatness and gonad state, growth rate, etc., but at a more fundamental level than that of statistical correlation. A lot also remains to be done on the mechanisms involved in the metabolism of the oily diet of the clupeids, especially on the fate of the metabolic by-products.

E. *Growth*

1. *Methods of calculation*

Growth rates for the herring in the sea have been calculated by plotting the mean length or increment of length, against age, or by back

calculating the growth rate of older fish from the scales (l_1, l_2). The growth constants L∞ (the asymptotic length of the herring) and k (the growth constant) can then be obtained by fitting the growth equations of Bertalanffy (1938, 1949) to the back calculated lengths. Calculations of maintenance rations, conversion rates, etc., are best made on herring kept in the laboratory, where feeding rate, temperature and interval changes in size can be measured. Savage (1931), however, correlated the increase in length of North Sea herring with the amount of food taken.

2. *Maintenance, growth and feeding rates*

Experimental studies on the maintenance requirements of clupeids are summarized in Table VII.

TABLE VII

MAINTENANCE REQUIREMENTS OF SOME SPECIES

Author	Species	Maintenance ration wet weight	Remarks
Blaxter and Holliday (1958)	Herring	200 mg/g fish/week 140 mg/g fish/week	For 40 g fish at 12°C For 100 g fish at 12°C
Holliday (unpub.)	Herring	120 mg/g fish/week 64 mg/g fish/week	For 10–20 g fish at 11·4°C For 51 g fish at 11·4°C
Takahashi and Hatanaka (1960)	*Engraulis japonicus*	140–210 mg/g fish/week	For 1·4–5·6 g fish at 11–22°C

The figures obtained by Blaxter and Holliday (1958) are estimates and are almost certainly too high. The later experiments (Holliday, unpublished, and Takahashi and Hatanaka, 1960) are more accurate as they anaesthetized and accurately weighed the fish to obtain their information.

Ivlev (1960) calculated the energy expenditure of herring living in the Gulf of Finland and concluded that these fish needed to feed continuously for 15 hr a day to obtain sufficient food to meet their energy and growth demands, but presumably only at certain seasons of the year.

3. *Salinity and growth*

Canagaratnam (1959) quoted values obtained by Hodgson (1934) on adult herring from the Atlantic and Baltic to support his own experimental evidence (on salmonids) that there was a positive correlation

between the growth of a fish and the salinity of the water in which it lived (all other things being equal). Graham (1956) showed that marine *Pomolobus* had a more rapid rate of growth than the freshwater form of this fish, and Hoar (1952) thought that this was related to the high energy requirements of osmo-regulation in the freshwater environment (see Section VI, H).

4. *Growth of herring in the North Sea*

During and after 1950 a large increase in the growth rate of the herring of the North Sea and English Channel occurred (e.g. Ancellin, 1953; Gilis, 1954; Andersson, 1954; Cushing and Burd, 1957; Parrish and Craig, 1957). The increase in growth rate has been correlated with an increase in the abundance of *Calanus* in the North Sea (Cushing and Burd, 1956, 1957; Glover, 1958; Cushing, 1962). If this change in the growth rate is in fact a real one (and not an error in aging the fish, due to a change in the pattern of scale growth), it poses many physiological problems. For instance, was the herring " underfed " prior to 1950, retarded and living below its physiological limits? Has it now reached these limits or could it show an even higher growth rate? Was there any increased pituitary activity from 1950?

5. *Growth and maturation*

Burd (1956, 1958, 1962) studied the relationship between growth and the maturation cycle. He concluded that there was a minimal length, irrespective of age, that a herring must reach before maturation of the gonad commenced. Burd termed this the " Critical Length " (21·6 cm for herring of the southern North Sea). Obviously since the increased growth rate of 1950, herring have reached this length sooner than before 1950, and hence the age at first maturity has been advanced (by 1 year).

6. *Effect of age and sex*

Hickling (1940) showed that the male herring of the southern North Sea grew faster than the female. He found a disharmony of growth between the fish as a whole and the growth of the gonads, so that an increasing strain was put on older fish as they matured. Because of their better growth rate the strain was less on the males, but Hickling found no significant difference in mortality between male and female fish at any age. However, Wynne-Edwards (1929) showed that in the Manx herring growth of the body and the gonads was in harmony, and that spawning did not draw on the reserves of the fish more than could be replaced each year.

Westman and Nigrelli (1955) showed that in *Brevoortia tyrannus* the females grew faster than the males.

7. *Competition and growth*

The size hierarchy effect described by Brown (1957) in *Salmo trutta* was noticed by Holliday (unpublished) in herring. There was no sign of fierce competition between the fish and no " peck order ", but despite an abundant food supply the variability of size soon became obvious. An increase in size variability was also reported by Kamshylov and Gerasimov (1960) who kept young herring in aquaria, and MacGregor (1959) found an inverse correlation between the population density and the length and condition factor of *Sardinops caerulea* (although this may have been due to competition for a limited supply of food). An increase in size range would, of course, inevitably arise even with no difference in growth rate, assuming growth to be exponential in some young stages, if there was an initial size difference at the start of an exponential period. The size hierarchy phenomenon is another example of " social effects " existing between fish (another example is given in relation to the initiation of feeding in Section VI, A).

8. *Abnormalities of growth in the aquarium*

Farris (1956) obtained differences in the weight/length relationship in *Sardinops caerulea* fed on different diets. On a high protein diet their length increased at a higher rate than the weight, but an opposite effect was obtained on a high carbohydrate diet. Farris suggested that the differences were due to new cell formation on a protein diet, but increased weight of existing cells on the carbohydrate diet.

Other abnormalities of growth in the aquarium can usually be associated with the lack of space—tails become abraided, and the bones of the head distorted, by collisions with the walls of the tanks.

F. *Natural mortality*

1. *General*

Beverton and Holt (1959) reviewed the relationship between longevity, body size, natural mortality rate and growth rate in different clupeids and in many other fish species. They showed a tendency for the natural mortality rate (M), in so far as it was possible to measure this, and rate of growth (K) to be connected, faster-growing clupeids tending therefore to die off more quickly. They concluded that in a wide range of fish species the natural span of life was adjusted to the time needed to complete, or nearly complete, the growth pattern. In

clupeids, too, the maximum length attained seemed to be positively correlated with the life span and larger clupeids seemed to live to a greater age than fish of other species of comparable size.

Few attempts have been made to estimate the natural mortality rates of clupeids resulting from old age, internal " stress ", predation, disease and parasites. Presumably old age is of little importance in heavily fished stocks, though it is known, for instance, that the Atlanto-Scandian herring lives at least to an age of 20 years, from following the progress of the 1904 year class in the Norwegian fishery. The lifespan of other herring races and of other clupeid species seems to be considerably less, nearer 10–12 years, while in *Sprattus sprattus* it may be 5–6 years (see review by Beverton and Holt, 1959).

Estimates of natural mortality rate may be made by plotting the relationship between fishing intensity and total mortality and extrapolating back to zero fishing intensity. Independent estimates of natural mortality would be of value in confirming such extrapolations, but unfortunately this approach has been completely neglected in the past due to the extreme difficulty of making a census of predators and their food intake. However, in view of the fact that clupeids are so heavily preyed on, one might expect that relatively high estimates of natural mortality would be obtained.

2. *Predation*

In particular, Russian workers have stressed the need for more importance to be attached to studies on predation. Awerinzew (1935) described the mammals, birds and fish preying on the Barents Sea herring, and their effect on the migration pattern and capture by drift nets. Mitchell (1864, p. 37) reported the possible effect of the gannet, *Sula alba*, a diving bird, on herring stocks round the Scottish Coast. It was assumed that 200,000 of these birds near St. Kilda were feeding for 7 months of the year, taking five fish each per day on average. The total taken by this one colony of sea birds would thus have amounted to 214 million fish. Gunter and Christmas (1960) gave details of predation by sea birds, cetaceans and fish such as tuna on *Brevoortia patronus*. The accumulation of guano on the Galapagos Islands from sea birds feeding on *Sardinops sagax* off the Peruvian coast is a sign of the high level of predation there. This source of fertilizer has now been replaced by fish meal obtained by direct capture of the fish, but predation by the birds continues.

The behaviour of captive herring kept with cod (*Gadus callarias*) in a tank was described by Schäfer (1955). The fish usually reacted 80–90 cm away from the cod, the avoiding movement of the shoal

depending on its position in relation to the cod, and the angle of its approach. Loukashkin and Grant (1959) observed the effect of the kelp bass *Paralabrax clathratos* on *Sardinops caerulea* in aquaria and found little agitation among the sardines, none being taken by the predator. Apart from these aquarium studies, observations have been reported at sea on the effect of predators on shoals (see Section VI, Q).

3. *Disease and parasites*

It is not proposed to deal in any detail with this problem due to the difficulty of covering the literature. Diseases of herring due to fungi, bacteria and parasites have been described by Sindermann and other workers (see Scattergood, 1957). Reports of mass mortality of clupeids are uncommon, though Sindermann (1956) described a heavy mortality of herring in the Gulf of St. Lawrence due to *Ichthyosporidium* infection.

The distribution of parasites may vary geographically in herring populations, for instance, *Ichthyosporidium hofari*, *Kudoa clupeidae*, larval cestodes and nematodes, and the trematode *Brachyphallus crenatus*, in herring of the St. Lawrence and Gulf of Maine (Sindermann, 1957).

G. *Composition of the tissues*

1. *General*

The clupeids, and especially the herring, have been extensively analysed chemically, mainly to provide information on the quality of the fish as a marketable product. As Love's (1957) review points out, analytical figures vary enormously with age, sex, season and stock of fish. Unfortunately there are relatively few analyses aimed at elucidating the biological significance of the substances measured.

2. *Fat and water*

The most variable constituent is the body fat, dealt with in a previous section. The inverse linear relationship which exists between fat and water content (Brandes and Dietrich, 1953b) in the herring, and reported in other clupeids, is in fact an artificial relationship, apparent because most results have been expressed on a percentage (or other proportional) basis. An absolute fall in fat undoubtedly occurs, the *percentage* of other substances thus rises, although their *absolute* values do not. As Hickling (1945) pointed out for *Sardina pilchardus* the water and " ash " provided the stable framework of the fish body. The herring, *Sardina pilchardus* and *Sprattus sprattus* draw to a small extent on protein reserves during times of starvation and gonad maturation, but protein loss makes only a small contribution to any total weight loss. Changes in intracellular lipids would lead to biologically significant

changes in the proportions of intracellular water and proteins, but no measurements exist.

3. *Skin thickness and composition*

McBride *et al.* (1960) showed that sexually mature *Clupea pallasii* caught in January had 40% more collagen in the body than immature fish caught in June. The changes were found to be due almost entirely to seasonal changes in collagen content of the skin and scales. Hughes (personal communication) reported a similar finding in the herring, and it would appear that collagen content of the skin is highest when the subdermal fat content is lowest. Histological studies of the skin of these herring showed a much greater thickness of skin in the early spring than in the late summer.

4. *Changes in the blood*

Naumov (1956) found that the haemoglobin content of the herring's blood was highest (61–64%) during early maturation, but fell sharply (to 43%) at spawning and in the spent stages. Percentage haemoglobin increased with age and fatness. These changes may not represent actual changes in either circulating erythrocytes or their individual haemoglobin content, for any increase in the plasma volume would lower the percentage of haemoglobin per unit of blood. Estimations of blood volume and haematocrit values are clearly needed. Naumov also describes cyclical changes in the numbers and types of leucocytes with gonad maturation.

Sindermann and Mairs (1959a) studied pre- and post-spawning *Pomolobus pseudoharengus* (which is anadromous) and found no change in sedimentation rates, erythrocyte fragility, haemoglobin content or serum electrophoretic patterns between the two phases of the life of the fish. Sindermann (1958), Sindermann and Mairs (1958, 1959b, 1960) and Mairs and Sindermann (1960) studied the serology of Atlantic clupeids and compared them with *Oncorhyncus nerka* (the blue back). They found that *Pomolobus* and *Oncorhyncus* had a high degree of serological correspondence. *Alosa* was closer to the *Oncorhyncus* – *Pomolobus* complex than to either *Brevoortia* or the herring. The herring was furthest serologically from any of the other species studied. These authors were able to use the serological properties of the blood to differentiate between different stocks of the herring. Age appeared to alter the serological patterns in the herring, as did disease. Sprague and Vrooman (1962) studied the erythrocyte antigens in *Sardinops caerulea* and found two systems of blood groups (indicating two reproductively isolated groups).

5. *Nitrogenous extractives of tissues*

Shewan (1951) gave the proportion which nitrogenous extractives formed of the total muscle nitrogen. The clupeid fishes, with a value of 14 to 18%, lay between the flat fish – gadoid group (9 to 14%) and the elasmobranchs (34 to 38%). (Hunter and Dauphinée (1925) found that *Clupea pallasii* also occupied this position with respect to the arginase concentration of its tissues.)

Shewan (1955) found a close similarity in the composition of the basic amino acids between the herring and *Alosa finta*, and also that the herring (and other pelagic species) contained higher concentrations of histidine, and lower concentrations of carnosine and anserine than demersal species. It is paradoxical that the muscles of a pelagic, active fish should have low levels of carnosine and anserine; Yudaev (1949, quoted by Shewan, 1951) found that this condition was usually associated with lack of mobility and endurance. Yudaev (1950) also found that high histidine and low carnosine and anserine was characteristic of freshwater fishes. Hughes (1959a) suggested that there may be seasonal variations in the amounts of free amino acids, especially histidine, in the herring.

Data from various authors were compiled by Shewan (1951), who compared the trimethylamine oxide content of fish from fresh and salt water. *Pomolobus* had less (185 mg%) than the herring (250 mg%), but the difference between these clupeids was a good deal less than between other comparable fresh and sea water species. Seasonal variation of trimethylamine oxide content of *Clupea harengus* and *Sprattus sprattus* has been reported (Ronold and Jakobsen, 1947; Hughes, 1959b). However, the presentation of the data as a proportion (mg per 100 g fish) does not allow one to decide if this is a change in absolute values or another reflexion of the loss of fat.

6. *Effect of diet*

Farris (1958), working with *Sardinops caerulea*, found that if these fish were fed a high protein diet then the concentration of free aspartic acid in the tissues fell. It did not fall in fish fed a carbohydrate diet. Farris found that the proportion of fish having free aspartic acid and alanine in the tissues varied inversely with the condition of the fish, suggesting that during starvation amino acids were mobilized.

H. *Salinity tolerance and osmo-regulation*

1. *Tolerance*

The clupeids have freshwater, marine and anadromous representatives. Many of the marine forms come close inshore either when

juvenile, or to spawn (see Sections III, C; IV, H). The herring of the Baltic sea spend almost their entire life in brackish water. Massman (1954) recorded young *Brevoortia tyrannus* and *Anchova mitchilli* in completely fresh water.

The salinity tolerance of the herring was determined by Brawn (1960d) and Holliday and Blaxter (1961). The lower level lay between 5 and 6‰, the upper level between 40 and 45‰. Tagatz (1961) determined the tolerance of *Alosa* to abrupt changes of salinity. The juvenile form tolerated changes from sea water to fresh water, but not the reverse. The adult survived a transfer from fresh water to sea water, but not the reverse. This difference between juvenile and adult probably indicates differences in the physiological capabilities of regulation.

2. *Regulation*

Holliday and Blaxter (1961) gave the mean freezing point of herring blood as −0·95°C (equivalent to a salinity of 15·8‰). The value was slightly lower (−1·01°C) in the winter months. When the herring were transferred to salinities *within* the tolerance range the blood first showed changes in freezing point consistent with the osmotic loss of water in high salinities and gain of water in the lower salinities. These changes were reversed and regulation of the blood to a value close to its

TABLE VIII

IONIC COMPOSITION OF THE BLOOD OF HERRING TRANSFERRED TO DIFFERENT SALINITIES FROM SEA WATER (34°/$_{oo}$)

Transfer Salinity	Milli-equivalents/litre			
	Blood Na^+	Blood Cl^-	Muscle Na^+	Muscle Cl^-
34°/$_{oo}$	129	123	37	24
0°/$_{oo}$ 3 hr . . .	66	48	16	12
6°/$_{oo}$ 3 hr . . .	102	92	19	14
6°/$_{oo}$ 24 hr . . .	116	116	26	19
15°/$_{oo}$ 3 hr . . .	128	110	26	19
15°/$_{oo}$ 24 hr . . .	128	112	44	27
50°/$_{oo}$ 3 hr . . .	288	211	146	98

original took place within 24 hr. Total body weight changed in a similar way.

Unpublished data by Holliday on the ionic composition of the blood and muscle of the transferred fish (summarized in Table VIII) showed corresponding changes.

Outside the tolerance range the changes were more extreme and not reversible, the fish dying within 24 hr. It can be seen from Table VIII that muscle concentrations closely paralleled blood changes; it would appear that muscle concentration changes are largely the result of changes in intracellular water.

3. *Sites of regulation*

The problem facing the herring in low salinities is the excretion of excess water through the kidney. Holliday and Blaxter (1961) found that the kidney of the herring had a very high glomerular count, being obviously well adapted to dealing with this water (see Fig. 8). Nash (1931) also found that *Sardinella macrophthalmus* and *Sardinella anchovia* had high glomerular counts. The clupeids strongly resemble freshwater fishes in this respect. Unlike that in a freshwater fish the nephron of the herring contains no distal tubule. This segment is normally responsible for resorption of salts from the urine in freshwater fishes. It seems likely that the absence of this precludes salt conservation, and hence most herring cannot live in water below 5–6‰ although some do, e.g., in the eastern Baltic.

The regulation of ionic composition of the tissues is almost certainly carried out through the general gill epithelium. It now seems unlikely that the acidophil cells, described by Keys and Willmer (1932) as being chloride secreting, are concerned with this function (see Parry *et al.*, 1959). This would not affect the general conclusion of Graham (1956), on *Pomolobus*, that those fish having the greater relative head size (and hence gill area) would be more efficient at ionic regulation and hence survive better in certain environments.

4. *Effects of endocrines*

Hoar (1952) suggested that the high degree of osmotic regulation taking place in *Pomolobus* in fresh water made such a heavy demand on the hormones of the thyroid gland that growth was retarded; this situation did not exist in the marine forms of this fish, which had a higher growth rate (discussed in Section V, E).

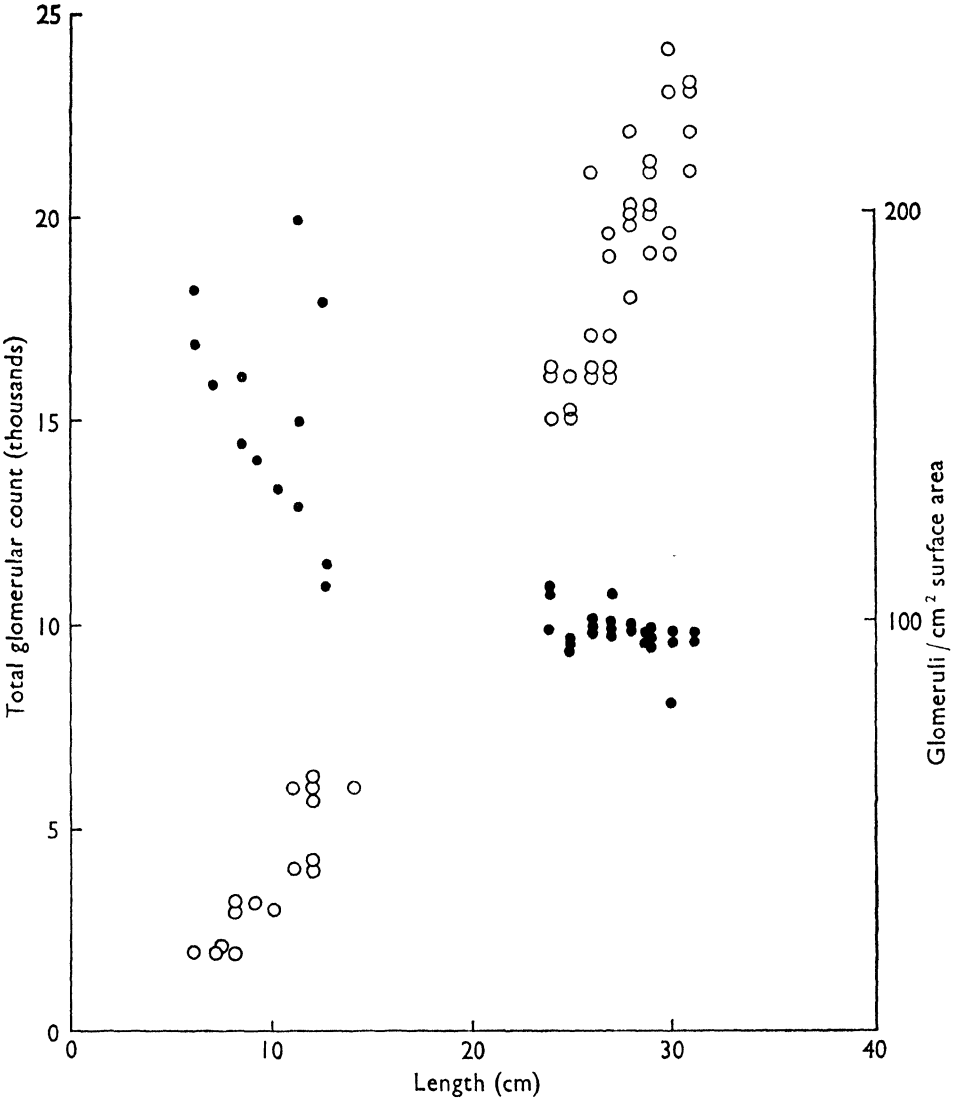


FIG. 8. The number of glomeruli in the kidney of herring of different length. (Reproduced with permission from Holliday and Blaxter, 1961.) o total count. ● count/unit area.

I. *Temperature, oxygen, CO_2 and H_2S as limiting factors*

(Reactions to gradients of these factors are considered in other sections)

1. *Temperature*

Kamshylov and Gerasimov (1960) found that Murman herring (? 10 cm long) died at −1·5°C. Brawn (1960c) mentioned the importance of determining lethal temperatures on newly caught clupeids, as the type of fat present in such fatty fish, which might be modified by an

aquarium diet, could affect the temperature tolerance. Using young Passamaquoddy herring she found that unacclimatized fish would withstand −1°C for a short time. There was a 50% mortality of unacclimatized herring 11·1—21·9 cm long at temperatures of 21·2–19·5°C in 48 hr, the smaller fish being more tolerant. As mentioned in the section on osmo-regulation, the freezing point of herring blood is about −0·95°C; temperatures below this would quickly freeze the blood unless super-cooling or depression of the freezing point took place.

Suehiro (1951), observing the factors causing mortality in bait fishes, found that unacclimatized *Sardinops melanosticta* 11·9–15·1 cm long had an approximate temperature range of 7–29°C; *Engraulis japonicus* 5·6–13·7 cm long had a range of 11–31°C. Phillips and Radovich (1952) thought that *Sardinops caerulea* had an upper level of tolerance of about 26°C. Graham (1956) acclimatized *Pomolobus pseudoharengus* to 5, 10, 15 and 20°C, and found the adults had an upper lethal limit (until 50% died on continual exposure) of 20–23°C (acclimatized at 10–20°C) and the yearlings of 15–23°C (acclimatized 5–9°C).

As reported in Section VI, B, low temperatures cause a reduction in both general and feeding activity, the temperature at which feeding ceases depending on the time of acclimatization.

2. *Oxygen*

Kamshylov and Gerasimov (1960) found that young Murman herring (? 10 cm) died at oxygen values below 2 ml/litre (30–33% saturation). Suehiro (1951) measured the oxygen requirements of clupeids. He reported that *Sardinops melanosticta* and *Engraulis japonicus* showed signs of difficulty at about 3 ml/litre, the rate of respiration increased and they put their noses above the water. The average lethal oxygen concentration for *Sardinops* was 2·02 ml/litre and for *Engraulis* 1·82 ml/litre.

3. *CO_2 and H_2S*

Shelford and Powers (1915) used young *Clupea pallasii* 6 cm long, and found that they died in 6 min when the H_2S concentration was 7·6 ml/litre and in 159 min when the CO_2 concentration was 20 ml/litre.

J. *The brain*

The physiology of the nervous system is virtually unknown in clupeids. Lissner (1925) and Blaxter and Holliday (1958) described the brain in relation to feeding (see Fig. 9), following the similar study of Evans (1952) on cyprinid fishes. The optic lobes in the herring dominate the fore-brain, indicating the importance of sight; the large

cerebellum, controlling movement and manoeuvrability, dominates the hind brain. The olfactory, facial and vagal lobes are small, indicating that chemoreception is not a dominant sense.

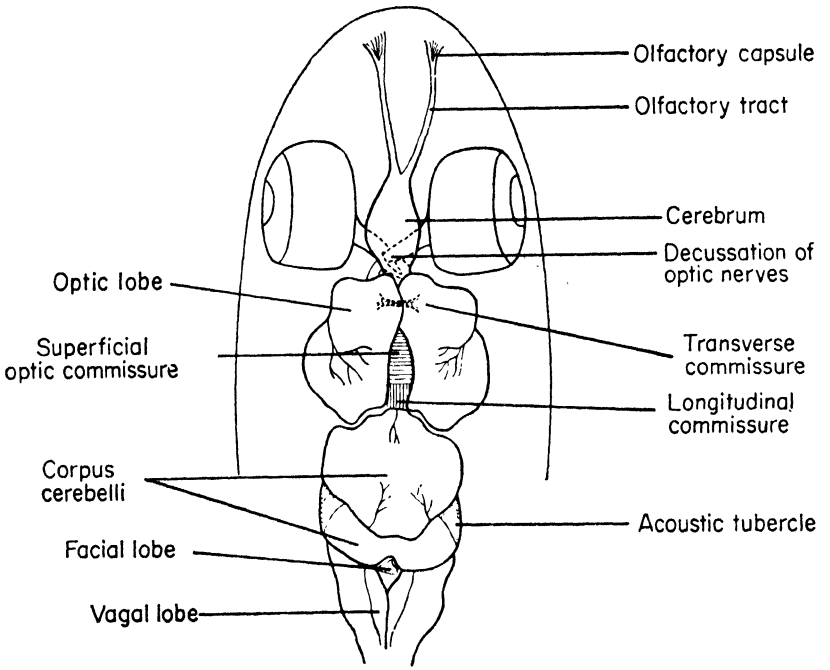


FIG. 9. Dorsal view of the brain of the herring. (Reproduced with permission from Blaxter and Holliday, 1958).

K. *Vision*

In this review, evidence has been compiled to show the importance of vision to clupeids. Shoaling, feeding and spawning, as well as avoidance of obstacles, seem to be behaviour patterns mainly controlled by sight.

1. *Structure of the eye*

The retina of *Sardina pilchardus* has been studied by Vilter (1950) who found a ventral foveal region where the cone: rod ratio was 8: 1. He related this to the visual acuity necessary for selective feeding on plankton. Baburina (1955), working on the " common pilchard " (? *Sardina pilchardus*), found that the cone: rod ratio varied from 22·4: 1 to 32·7: 1, the highest visual acuity being in the ventral posterior part of the retina, where the cones were most abundant of all. The eyes of the " sardine " and " sprat " were similar. Verheijen (1959a) found a

rotating action of the eyeball (nystagmus) in herring and an associated ventral foveal region where the cones were ten times as dense as elsewhere. No doubt the apparent high acuity of clupeids is an adaptation to feeding on small plankton organisms. As the light decreases, rod vision presumably becomes dominant and acuity drops; later, behaviour patterns associated with vision cease. Presumably the threshold light intensity at which such behaviour patterns cease will vary considerably; the continuation of feeding, for example, will depend to a great extent on the size of the food, but this has not been worked on.

2. *Vision at low light intensities*

The threshold light intensity at which various behaviour patterns cease are discussed under the particular behaviour pattern concerned, e.g. shoaling, feeding. Protasov *et al.* (1960), however, using a flicker fusion frequency technique, found that the transition from day to "night" vision occurred at 1·0–0·1 lux in *Engraulis encrasicholus*.

3. *Spectral sensitivity*

Some data are available on the spectral sensitivity of clupeids, though colour vision has not yet been demonstrated. Borisov and Protasov (1960) showed by electrophysiological techniques that the "anchovy" had a spectral sensitivity curve with a maximum at 500 mμ. There was a Purkinje shift, the maximum when light adapted being at 560 mμ. Blaxter (unpublished data), by finding the feeding threshold of young herring in different coloured light, and by other behaviour techniques, showed there was a maximum sensitivity in the blue-green, but the curve was plateau-like with a sharp fall off only in the red. A fairly high sensitivity in the violet suggests that experiments to test the reactions of clupeids to ultra-violet light would be worthwhile, though the existence of a positive reaction would depend on whether the lens would transmit short wavelength light. Fisher (personal communication) found that retinal pigment extracted from the eyes of dark-adapted herring had a maximum absorption at 500 mμ.

4. *Distance vision*

A little is known of the distance herring can see. For instance, Williamson (1917) found in aquaria that food could be seen 30–90 cm away depending on its size, and Schäfer (1955) that herring could see 1·0–1·5 m. Blaxter *et al.* (1960) found a reaction distance to nets of 1·5–2·0 m.

L. *Olfaction*

Burne (1909) described the olfactory pit of clupeids, showing it to be a simple pit similar to that of the salmon. Olfaction is of little importance in the detection or primary selection of food by herring (Blaxter and Holliday, 1958), this being done by sight. However, Anon. (1952) reported that olfaction was important in the initial approach to food made by *Sardinops caerulea*. Lagler *et al.* (1962) described a hydraulic system of lymphatic sinuses which filled and emptied the nasal sacs in response to pressure changes during respiratory movements.

Verheijen (1959b) could find no evidence of an alarm substance (" Schreckstoff ", reviewed by Schutz, 1956) in four clupeids*. It would be interesting to know whether species-specific odours exist which might help in any way to keep shoals together. Jones (1962) suggested that olfaction might be important for keeping herring together by night.

M. *The labyrinth, hearing, the effect of sound, and sound production*

1. *Labyrinth and hearing*

The recent review of Lowenstein (1957) gave the main function of the labyrinth in teleosts as:

Regulation of muscle tone
Reception of angular accelerations
Reception of gravitational stimuli
Reception of sound

In clupeids work has been restricted almost completely to anatomical descriptions. The equilibrium function of the labyrinth has already been mentioned. It seems that experimental work, such as removal of the otoliths at the point where the wall of the sacculus is separated from the buccal cavity by only a thin membrane, or the injection of anaesthetics, would be possible.

In the herring the labyrinth consists of a sacculus containing the sagitta, the largest otolith. The lagena, posteriorly, contains a smaller otolith, the asteriscus, while the dorsally placed utriculus contains the third otolith, the lapillus. Arising from the utriculus are the three semicircular canals. The otoliths are in contact with maculae receiving branches of the VIII nerve.

In relation to sound, the connection between the labyrinth and swim bladder seems to be of great importance. O'Connell (1955) described this in *Sardinops caerulea* and *Engraulis mordax*, at the same

* Pfeiffer (*Z. vergl. Physiol.* **43**, 578–64, 1960) also found no alarm substance in four clupeid species.

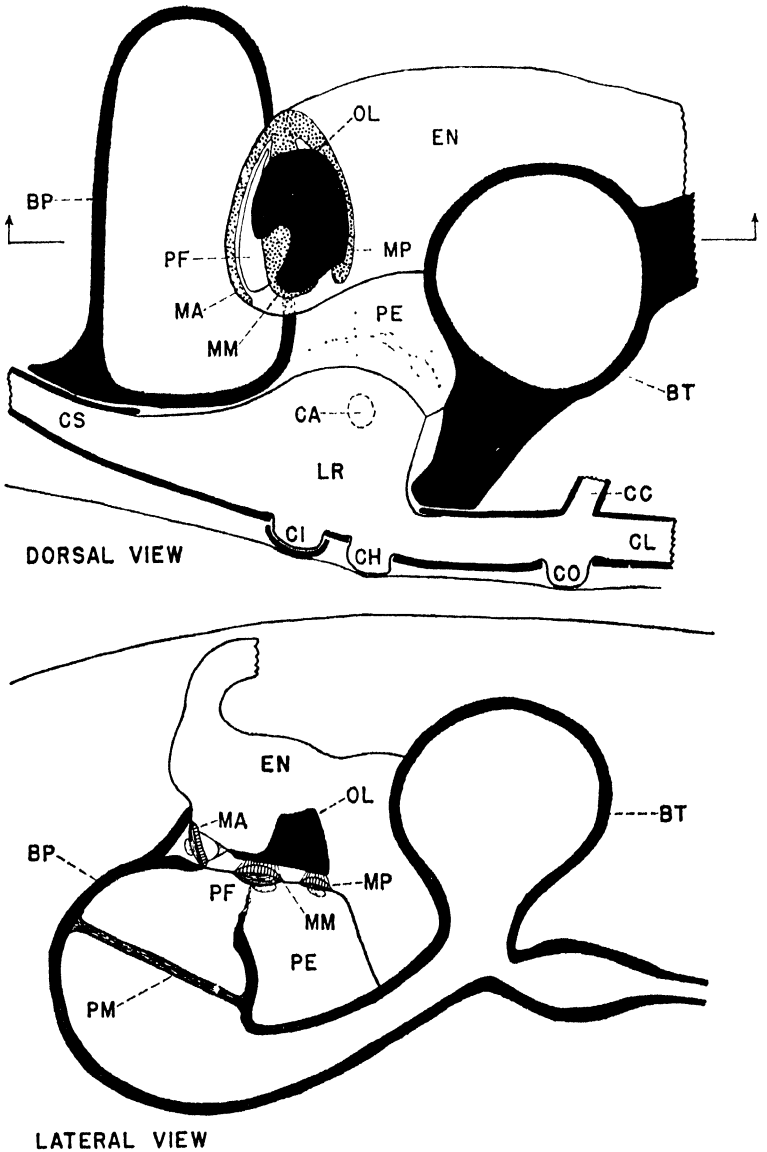


FIG. 10. Schematic drawing of relation between membranous labyrinth and gas vesicles on the left of the clupeid cranium. (Reproduced with permission from O'Connell, 1955.) The plane of the lateral view is marked on the dorsal view. The solid black areas represent bone. BP, prootic bulla; BT, pterotic bulla; CA, accessory temporal sensory canal; CC, occipital sensory canal; CH, preopercular sensory canal; CI, infraorbital sensory canal; CL, lateral sensory canal; CO, opercular sensory canal; CS, supraorbital sensory canal; EN, endolymphatic space; LR, lateral recess; MA, macula utriculus anterior; MM, macula utriculus media; MP, macula utriculus posterior; OL, otolith (lapillus); PE, perilymphatic space; PF, prootic fenestra; PM, prootic membrane.

time reviewing the earlier work of Maier and Scheuring (1923) on herring and Wohlfahrt (1936) on *Sardina pilchardus*. There seem to be few essential differences between the species (see Fig. 10). The anterior end of the swim bladder bifurcates into two tubes which widen out into vesicles within the pterotic and pro-otic bullae. The pro-otic vesicles are applied to perilymph cavities which have contact with the utricular part of the labyrinth through a pro-otic fenestra. The suggestion here is that the utriculus plays a part in hearing (Wohlfahrt, 1936; Verheijen, 1953), which is probably not true, for instance, of the Ostariophysi, where the swim bladder is associated with the sacculus-lagena part of the labyrinth (Lowenstein, 1957). Usually the utriculus has been considered to have an equilibrium function due to its connection with the semicircular canals as the pars superior of the labyrinth. According to Ridewood (1891) the utriculi in the herring are joined to one another by a canal which passes through the membranes of the brain just behind the pituitary fossa.

Wohlfahrt (1936) discussed in detail the possible auditory function of the utricular maculae. He considered that the lapillus also retained a residual equilibrium function. The pterotic and pro-otic bullae acted as resonators. O'Connell (1955), extending this hypothesis, saw the utriculus-swim bladder complex as widening the frequency range of the species, and perhaps their overall sensitivity, with at least a basic auditory response resting in the sacculus-lagena part of the labyrinth.

2. *Response to auditory and vibrating stimuli*

Little is known of this, though Verheijen (1953) considered that herring kept in aquaria could perceive up to 400 c/sec at medium intensity. Blaxter and Holliday (1958), using juvenile herring in aquaria, observed the effect of sounds of different frequency played through an underwater loudspeaker on feeding behaviour. At frequencies from 10–100 c/sec feeding temporarily stopped, the fish reacting strongly to the starting or stopping of the stimuli. From 500–5000 c/sec a " startle " reaction was observed but feeding was not interrupted.

It appears that commercial echo-sounders have no *observable* effects on herring. Dow (quoted by Moulton and Backhus, 1955) found no effect with a 50 kc/sec sounder, and Skoglund (1953) and Blaxter and Holliday (1958) none with a 30 kc/sec sounder. Bull (1961), however, has reported a response by some other teleosts to echo-sounders as shown by training techniques. If this is confirmed it points to the need to distinguish between sensitivity and response.

Rumyantsev (1960) reported serious lesions of the body wall and

ovaries of *Clupea pallasii*, which he thought were due to over exposure to high frequency transmissions from echo-sounders. It should be noted, however, that usual echo-sounding frequencies are well below the ultra-high frequencies used in sonic disintegrators, and that these observations have not been supported by experimental evidence.

3. *Sounds made by herring*

Recently Freytag (1961) recorded " piping " noises made apparently by herring and it was intended that these noises should be played back to the fish. Such reports are not new, and according to Freytag, the Russians are already using recorded noises to lure herring into places where they would be more easily caught. The connection between " piping " noises and the release of gas bubbles from the swim bladder is not clear.

4. *Lateral line*

Bamford (1941) demonstrated the complex lateral line system present on the head of herring (see Fig. 11). It was complete at 50 mm length and was the best developed of any teleost described to date. The canals opened to the exterior by pores and the lateral line organs were peculiar in being at the sides of the canals. Wohlfahrt (1937) found mainly a head system in *Sardina pilchardus*, the anterior part being innervated by the trigeminus-facialis nerve and the posterior part by the vagus. Although no canals were present on the surface of the body, except in a limited way in the scapular region, the body surface was innervated by the ramus lateralis and ramus dorsalis of the vagus. This is probably true of other clupeids. There were also free lateral line organs on the head but these were not seen on the trunk. Verheijen (1956), however, by very careful handling and anaesthesia of *Sardina pilchardus* kept in aquaria, photographed trunk cupulae.

Both herring and *Sardina pilchardus* have enormous supra-orbital dilatations of the lateral line system which Bamford thought might be pressure receptors, because they overlay the temporal fossa and were in contact with the brain. This seems unlikely unless the brain were enclosed in a non-compressible bony case, the only contact with the exterior being through the temporal fossa.

The lateral line is considered to be responsible for localization of objects or disturbances at a distance—or " distant touch " perception (Lowenstein, 1957). It would respond both to disturbances created by other organisms as well as perhaps reflections of disturbances made by its own swimming movements. Clupeids kept in the dark in aquaria do not seem to swim into the walls, which may be due to the lateral

line. It may be that a complex head lateral line is found in other shoaling species and plays some part in maintaining the shoaling, though sight seems to be the more dominant sense. It has also been put forward that the lateral line could play a part in proprioception, particularly in relation to swimming.

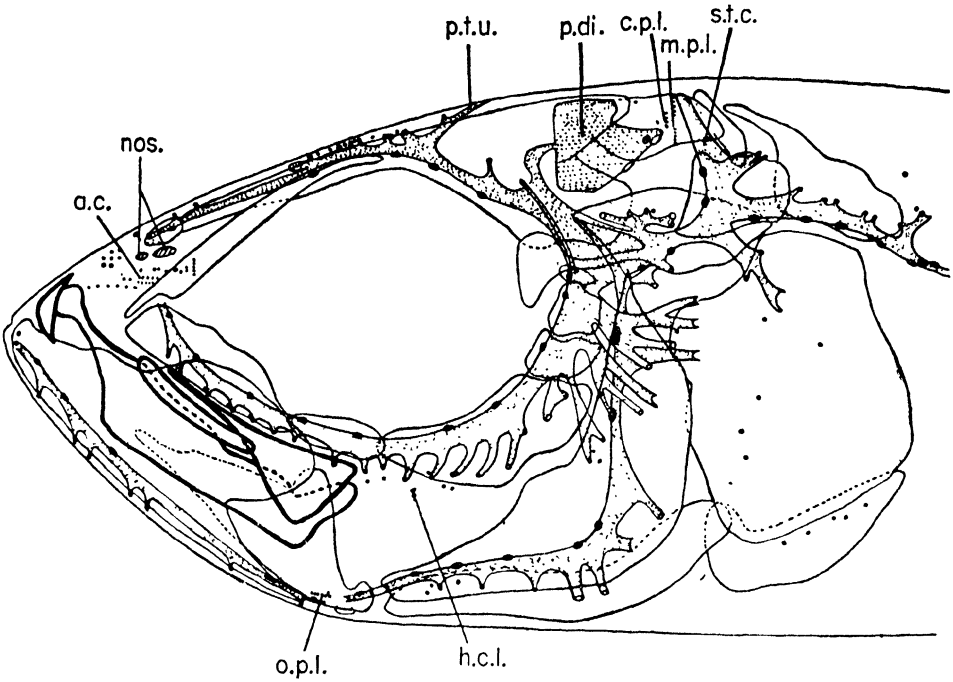


FIG. 11. The lateral line system on the head of a herring 50 mm long, upper jaw in dark outline. (Reproduced with permission from Bamford, 1941.)

ac = anterior commissure
hcl = horizontal cheek line
pdi = posterior dilatation
mpl = middle pit line
nos = nostril
ptu = posterior tubule
cpl = central pit line
stc = supra temporal canal
opl = oval pit line

N. *Buoyancy and equilibrium*

1. *Buoyancy*

The seasonal variation in fat content of clupeids means also a seasonal variation in tissue density (Jones and Marshall, 1953). The distribution of fat in herring is such that the fish will remain on an even keel, the " centre of gravity " of fat distribution being just anterior to the dorsal fin (Brandes and Dietrich, 1953a; Love, 1957). It seems likely that there is an abrupt change of density of body tissue at

spawning, for the ovary, at any rate, is mainly composed of proteinaceous yolk.

Immediate changes in density such as those required during vertical migration, or during movement into water of a different temperature or salinity, may be controlled by the swim bladder or perhaps by fin movements. The function of the swim bladder may be deduced from its structure. This has been described by many earlier workers, but especially in herring and *Sprattus sprattus* by Maier and Scheuring (1923) and in *Sardinops caerulea* and *Engraulis mordax* by O'Connell (1955). The clupeids are physostomes with an open pneumatic duct between the swim bladder and the gut. In clupeids there is also an anal duct leading to the exterior, but this is not present in *Engraulis*.

The presence of smooth muscle in the wall of the swim bladder suggests that the volume may be controlled, but the anal duct does not seem to be equipped with a sphincter muscle while the pneumatic duct seems to be designed for peristalsis. There is no well-developed gas gland. An increase of pressure in the swim bladder, required to compensate for a reduction in volume at greater depths, might be brought about by secretion of gas from the epithelial lining, or perhaps by swallowing air at the surface and keeping it under pressure by means of the muscular wall until a relaxation of the muscles would be neutralized by the increase of hydrostatic pressure at greater depths. O'Connell suggested that the pneumatic duct might pump in air (from outside or perhaps from decomposition products in the gut), while excluding food particles and parasites by peristaltic action. The anal duct might collapse if internal pressure was too low and act as a safety valve if too high. The release of gas from fish rising to the surface is a well known phenomenon observed by fishermen. Verheijen (1953) found that a specimen of *Sprattus sprattus* released gas bubbles from the anal opening after 70 sec when the pressure was reduced at a rate of 40 mm Hg/min. Release of gas also occurs through the pneumatic ducts where an anal duct is present (Brawn, 1962), but whether gas might diffuse through the swim bladder wall is not known.

Jones and Marshall (1953) discussed the high sinking factor $\left(\frac{\text{Density of fish} \times 100}{\text{Density of water}}\right)$ of herring (reported by Magnan to be 1034 compared with the range 980–1013 for most other fish) and considered that the value should be redetermined. This high sinking factor will, presumably, vary greatly with the fat content and an average value would be hard to arrive at. If it is usually as high as this, the fish would require to make considerable compensation to maintain a level in the water. Brawn (1962) found a mean sinking factor of 1003 for herring

and thought that the value obtained by Magnan was high due to loss of gas from the swim bladder. Brawn (1960a) watched by television the behaviour of herring lowered and raised in an underwater cage, and found that descent seemed to be mainly by sinking. Presumably to do this they would have to be dense to start with, this density and the speed of descent increasing as the swim bladder became compressed, unless there was some compensation by the swim bladder.

2. *Equilibrium**

Fat deposits are such (Foster, quoted by Love, 1957) that there is no difference in buoyancy of the head and tail regions which might give equilibrium difficulties. Maintenance of equilibrium is presumably by means of the labyrinth, but a dorsal light reaction may also be present. Clupeids kept in aquaria often start to swim vertically when the light is reduced to a low level, this being later compensated for; Loukashkin and Grant (1959) reported this in *Sardinops caerulea*, and Radakov and Solovyev (1959) and Zaitsev and Radakov (1960) observed herring by night from a submarine to be sometimes vertical.

O. *Swimming*

1. *Rheotaxis and swimming ability*

The ability of clupeids to stem currents is well known, but it seems that this depends on the presence of visual or tactile reference points (Brawn, 1960a). She showed that herring 15–30 cm long, kept in an underwater cage and watched by television, ceased to swim against the current at low light intensities. Jones (1962) also questioned the ability of herring shoals in mid-water to stem currents, although it might be possible in a deep shoal for the fish near the bottom to act as markers for other fish above them. His observations on the movements of herring in relation to tide were not conclusive enough to show whether the stemming was maintained in darkness after the fish left the bottom.

The maximum and cruising speeds of some clupeids have been measured. Blaxter and Dickson (1959) found that captive herring ranging from 1–26 cm swam at speeds (for distances at least ten times their body length) of 2–200 cm/sec (temperature 5–18°C). Herring 20–25 cm long could swim at near their maximum speed for 1000 lengths. Brawn (1960a) (as part of the recent Passamaquoddy herring investigations) used freshly caught fish in the underwater cage, which was towed by a research vessel, and found that herring 15–27 cm long at 11–12°C had maximum speeds of 90–143 cm/sec (maintained by 50%

* See also Section VI, Q.

of fish for 1 min). Boyar (1961) (also as part of these investigations) found that captive herring, 6·0–21·9 cm long, in an annular rotating trough, maintained a maximum speed for 30 sec of 69–132 cm/sec at temperatures ranging from 1·4–5·6°C and 9·5–11·2°C. Boyar also measured the endurance of fish of different lengths in different water velocities. These results are shown in Fig. 12.

Schärfe (1960), from echo-sounding records, found that shoals of herring seemed to be keeping ahead of a trawl moving at 3 knots (170 cm/sec), and that the best catches were obtained at trawling speeds of 3·5–4·5 knots (200–250 cm/sec).

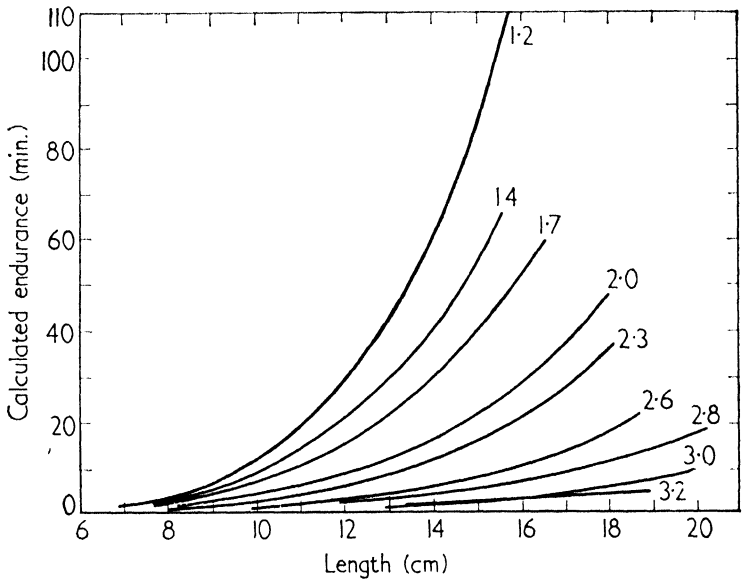


FIG. 12. Calculated endurance of herring of different length in different water velocities (re-drawn with permission from Boyar, 1961).

In contrast Stringham (1924) observed *Pomolobus pseudoharengus* of unknown length making headway against a current of 300 cm/sec, but not against one of 405 cm/sec. Dow (1962) measured the speed of the same species, 27·1–31·2 cm long, swimming against a very rapid flow of water in an artificial sluice. In current velocities of 350–400 cm/sec the maximum speeds ranged from 415–485 cm/sec, for periods of 3–4 sec. These and the results for captive herring are plotted in Fig. 13. The results are a little difficult to compare as Dow's fish were not captive and were in fact the best performers of many others involved in the experiments, and the extent to which the high current speed may have influenced them is not known. Clearly the question is raised of how far the swimming performance of captive fish may be underestimated, and

also the possibility of fish used to strong currents having a very well-developed means of finding routes where the velocity of the current is minimal. This might perhaps be a function of the lateral line system.

The mechanism of clupeid locomotion has not been worked on. It is presumably little different from other groups. Recent work by Rosen (1961) has shown that fish may progress by means of their reaction to vortices created by the head. The whole body would then be

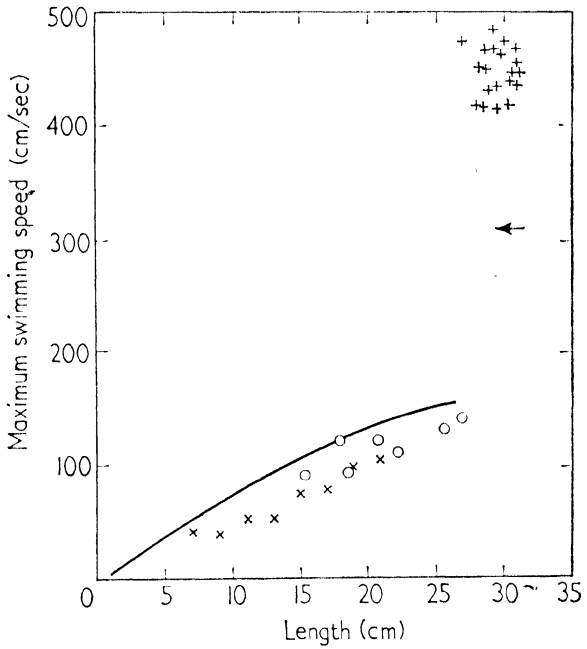


FIG. 13. Maximum swimming speeds of clupeids (see text for further details).
—— herring (Blaxter and Dickson, 1959)
o herring (Brawn, 1960a)
x herring (Boyar, 1961)
+ *Pomolobus* (Dow, 1962)
← *Pomolobus* of unspecified length (Stringham, 1924)

involved in locomotion rather than the tail alone, the reaction being similar to the movement of fish on a peg board as described by Gray (see in Rosen).

2. *The skeleton and swimming*

Harder (1953) reported on the change in proportions of the cross-sectional area of herring occupied by gut, skeleton and muscle. The proportions of the gut remained constant, the skeleton showing a negative allometry and the muscle a positive allometry, as the fish became adult. Blaxter (1962) showed how the swimming speed of

herring larvae suddenly increased when the caudal fin developed. Symmons (personal communication) has drawn attention to the presence of a strong elastic longitudinal ligament ventral to, and in close association with, the vertebral column of almost all clupeiform species. Its skeletal importance has never been suggested before, but Symmons believes it might be associated with fish having good powers of swimming and leaping. The ligament is probably capable of producing a spring effect, making rapid movements of the tail more effective by a side-to-side snapping action. She suggests that this is a source of potential energy which may account, in part, for the endurance of these fish.

P. *Activity*

The study of the levels of activity of clupeid fishes is becoming increasingly important to the fishery biologist. It influences both fish location and fish capture.

1. *Diurnal variations in activity*

The intriguing problem of whether the herring ever " sleeps " was apparently solved by Radakov and Solovyev (1959) and Zaitsev and Radakov (1960), who observed herring from a submarine. As night fell the herring became motionless in the surface waters, remaining at various angles to the horizontal " as if drowsy ". The fish became increasingly active just before dawn, and in the early morning all migrated down several hundred metres. If a searchlight was played on the motionless herring, they became active and moved away from the beam.

Blaxter *et al.* (1960) found that at night herring were not herded by towed ropes, or even underwater lights (though young herring may be attracted by artificial lights). It would appear that the physiological state of the herring is different by day and night.

2. *Control of activity*

Parry and Holliday (1960) and Holliday and Parry (1962) suggested that the pseudobranch in fishes controlled their activity by governing in some way the availability of oxygen to the fish and its utilization at the tissues. Removal of the pseudobranchs resulted in a reduction in metabolism coupled with an ability to survive in conditions of oxygen lack, fatal to normal fish. The pseudobranch was linked by its blood system to the choroid gland of the eye, where it could be controlled by the amount of light falling on the retina. This system might explain diurnal variations in the activity of fish.

Buchmann (1940) described an increase in thyroid activity in the herring at spawning, when there was a high level of activity.

Studies on *Brevoortia tyrannus* (Gray, 1954) showed that it had a very high gill surface area per unit of body weight (ten times greater than in *Opsanus*). Also Gray and Hall (1930) found the blood sugar level was higher—75 mg/100 ml blood, compared with 15 mg/100 ml in *Opsanus*, and so was the iron content (41 mg/100 ml, compared with 13·5 mg/100 ml in *Opsanus*). Dawson (1933) reported a high level of erythrocyte precursors in the blood of *Brevoortia*, presumably maintaining a high proportion of functional red blood cells. Vernberg and Gray (1953) and Vernberg (1954) showed that the oxygen uptake of the intact *Brevoortia* was very high, as it was also in its excised brain tissue (twice that of similar tissue from *Opsanus*). The oxygen uptake of isolated muscle tissue was no higher in *Brevoortia* than in any other fish. It was concluded that the nervous system imposed a higher level of activity on the muscle by direct stimulation.

Q. *Shoaling*

1. *General*

A shoal or school is here defined as a group of fish which are polarized or orientated in the same direction as a reaction to one another, rather than a common reaction to an external stimulus. The fish tend to have a regular spacing and move at about the same speed.

The general concept of shoaling was discussed by Breder (1959) who referred to clupeids and quoted work on rather unusual social groupings in *Pomolobus* and *Alosa*. He pointed out that the shoaling habits of clupeids might be to some extent correlated with the immobility of their pectoral fins; fish with mobile and flexible pectorals, being able to " back up ", had a form of locomotion less suited to a shoaling habit. The importance of the silvery skin of clupeids was also discussed. In some conditions this might cause flashing and help to keep the shoal together in poor light; on other occasions the mirror effect might reflect the colour of the surroundings and so act as a camouflage. Manteufel and Radakov (1960) discussed the adaptive importance of shoaling in relation to defence, feeding, migration and spawning, and mentioned clupeids. The high incidence of shoaling in these fish may be connected with their susceptibility to predation. It is well known that they either form shoal or shoal more tightly as a result of stimuli which may be harmful, but the survival value of shoaling is by no means certain.

2. *Survival value of shoaling*

Ulrich (1951) made underwater observations on herring in the Baltic and found that they formed up into shoals in response to stimulation from himself or the presence of fish. Schäfer (1955) also observed the disturbing effect of predators on herring in aquaria. The pattern of movement was related to the position of cod on approach of the shoal, an indentation being caused in that part of the shoal nearest the cod. Manteufel and Radakov (1960) found that only straggling herring were taken by predators in an aquarium, tight shoals causing " confusion " of the predators. Blaxter and Parrish (1958) reported an extreme tightening of shoaling in *Sprattus sprattus* preyed on by *Caranx*, but few of the sprats survived as a result. Allen (1920) observed a " ball " of *Sardinops caerulea*, 2 m in diameter, under attack from diving birds. The birds caused indentation of the ball but apparently were unable to extract fish from it. Phillips and Radovich (1952) found that shoals of *Sardinops* and *Engraulis* were not overexcited by attacks from carangids and sphyraenids and only stragglers were taken. If the shoals became disorganized, they were then more prone to attack. Breder (1959) reported seeing shoals of *Sardinella* attacked by *Caranx*, without affecting the behaviour of the shoals. While most evidence has been interpreted as shoaling preventing predators picking out their prey, there is the possibility that large shoals might cause a concentration of predators in a particular area, so that the overall survival value of shoaling must remain somewhat uncertain. Shoals might, of course, act as a frightening stimulus to predators, large, tightly-packed shoals appearing as a single organism.

Shoaling may aid the fish in escape from moving nets, but certain types of fishing practice, for instance purse seining, depend on the presence of shoals of reasonable size. Manteufel and Radakov (1960) reported that it was more difficult to catch tightly packed shoals of herring in the Baltic, though Galkov (1958) was of the opinion that the mobility of the herring determined their susceptibility to capture, shoaling perhaps playing a subsidiary role. (See Section VI, V for further discussion.)

Breder (1959) and Manteufel and Radakov (1960) also pointed out the importance of transmission of stimuli by shoals. The passage of a stimulus seemed to depend on the transmission of visual movements, rather than of noise through a shoal, noises probably being absorbed in many cases. While solitary fish might well react to noise, visual stimuli would be more quickly passed through a shoal and would also be more quickly received than a sound one, as long as the water was clear. It seems rather unlikely that any clupeids produce an " alarm

substance " (see Section VI, L) but this would be more effective in a shoaling species. Just how well chemical stimulation would pass through a shoal is not clear, but it would almost certainly be slower than a visual one.

Another possible advantage of shoaling might be in the detection of gradients of hydrographical conditions, or of food, such that the part of a shoal in favourable conditions might linger, the other side moving faster and so wheeling round towards the more favourable conditions (see Section VI, R).

Shaw (1962) has recently suggested that shoaling may be the most efficient way to move through the water, turbulence being used in a reciprocal way to reduce drag in neighbouring fish.

The disadvantages of shoaling seem to be twofold. One is the possibility of attracting predators to large concentrations of their prey, the other is the limiting effect on food supply. MacGregor (1959), for instance, found an inverse correlation between adult population size and average length and condition factor of *Sardinops caerulea*, suggesting that there was less food available and poorer growth where the population density was high.

3. *Structure of shoals*

This is not well known in clupeids though Schäfer (1955) observed that small herring were near the top in herring shoals of mixed size. This type of size delimitation is discussed by Breder (1959). Phillips and Radovich (1952) found mixed shoals of *Sardinops caerulea* and *Engraulis mordax*, and in European waters it is common to find mixed shoals of small herring and *Sprattus sprattus*. It seems that clupeid shoals may be mixed both in age and species.

An interesting observation was that of Wood *et al.* (1955) who found no change in the shoaling behaviour of tagged herring, or of their untagged neighbours, in aquaria.

4. *Size and shape of shoals*

The size of herring shoals is discussed by Balls (1951). Off the Norwegian coast they might be miles wide, though the more usual size in the North Sea was probably " that of a house ". Jakobsson (1961) found that some fishable shoals of herring in Icelandic waters contained 50–200 tons of fish. Tibbo and Brawn (1960) estimated the density of a shoal off the East American coast as about 2 kg/m^3, and that one shoal contained 22,000 metric tons. From a submarine, Radakov and Solovyev (1959) estimated the length of some herring shoals in the northern Atlantic to be 1500 m long. While shoals are probably in many cases amorphous, Bolster (1958) found from echo surveys in the

southern North Sea that herring shoals in strong tidal streams were cigar-shaped with their long axes parallel with the tidal streams. Whether this shape is brought about by the pattern of tidal currents or whether it in some way reflects the swimming ability of the fish, a few being faster, a few slower, the majority being average, is not known. Runnstrøm (1941b) also found herring shoals off the Norwegian coast in the form of a long narrow streak, and shoals of *Sardina pilchardus* may also be cigar-shaped (Cushing, 1960).

Glover (1957) called for a study of the factors causing dispersion or aggregation in herring. Jakobsson (1961) has given an account of the factors which might determine shoal size off Iceland. The formation of large shoals seemed to be positively correlated with the numbers of some zooplankton organisms such as *Calanus*, with the mixed water in the border areas between warm and cold water masses, and with shallow and irregular bottom configurations. There seemed to be a negative correlation between large shoals and fast-swimming food organisms such as fish larvae, and with deep and uniformly cold water. These gross factors which may control shoal size must be accompanied by other more intimate stimuli between individual fish.

5. *Maintenance of shoals*

It has been extensively reported that shoals tend to break up to feed (see Section VI, B) and that shoaling behaviour ceases in darkness. Loukashkin and Grant (1959) cited many authors who had reported this.

The effect of low light intensities on clupeids is shown in Table IX.

Apart from some sea observations and in *Anchoviella*, an engraulid, there seems to be dispersion of shoals at low light intensities, suggesting the extreme importance of vision in keeping shoals together. The observation of Zusser (1958a), Radakov and Solovyev (1959) and Radakov (1960) of some " schools " existing in darkness needs to be further examined, in particular as to whether the fish were in true schools or unpolarized groups, and what effect the means of observation had on behaviour. It is always possible that phosphorescence in the water may help fish to keep together at night (Cushing, 1960).

Jones (1962) has also suggested that the breaking up of clupeid shoals, as observed especially in aquaria, might not necessarily be invariable. He watched the movements of herring shoals in the southern North Sea by echo-sounder. Both dense traces and " fleck " traces were probably attributable to herring; the " fleck " traces (small groups of fish) disappeared at night, while the dense traces (large groups) became more diffuse. He suggested that while the

TABLE IX

EFFECT OF LOW LIGHT INTENSITY ON SHOALING

Author	Species	Size (cm)	Observation
Verheijen (1953)	Herring	2–12	Stopped shoaling in aquarium as light intensity dropped
Schäfer (1955)	Herring	—	Ditto
Newman, Puchkov quoted by Loukashkin and Grant (1959)	Herring	— —	Stopped shoaling in darkness
Blaxter and Parrish (1959)	Herring	*c.*25	Stopped shoaling in 8 m^3 aquarium at 0·01 to 0·001 photopic lux
Dragesund (1958)	Herring *Sprattus sprattus*	—	Echo traces in Norwegian waters more diffuse at night, but could be concentrated by artificial lights
Radakov and Solovyev (1959)	Herring	—	Observed from research submarine "Severyanka" to remain "widely spread out, in small or even large schools at night"
Blaxter *et al.* (1960)	Herring	*c.*25	Stopped shoaling in 225 m^3 aquarium at 1·0 to 0·1 photopic lux, depending on number of fish and their maturity
Radakov (1960)	Herring	—	Observed from research submarine "Severyanka" to be passive and usually scattered at night but also in "small groups and shoals". Activity increased at dawn
Jones (1962)	Herring	—	Echo traces in southern North Sea more diffuse at night, but herring still appear to keep together
Parrish (personal communication)	Herring	—	Echo traces in northern North Sea sometimes dense at night
Owatiri *et al.* (1953)	Sardine *?Sardinops melanosticta*	—	Echo traces in Japanese waters more diffuse at night
Zusser (1958a)	Caspian sprat *?Sprattus sprattus phalericus*	—	Activity decreased at night, but remained in "motionless shoals"
Loukashkin and Grant (1959)	*Sardinops caerulea*	—	Stopped shoaling in darkness (0·1 lux) in aquarium
Moulton (1960)	*Anchoviella*	—	Shoals remain intact at night, blinded fish still shoal
Girsa (1961)	Anchovy (?species)	—	Disperse at low light intensities below 0·1 lux

small groups disappeared at night, the larger ones were kept together by a chemical sense reacting to a substance produced by the herring themselves, only large groups producing enough to keep the individuals together. This might explain why clupeids at sea could keep together in the dark, whereas they could not in aquarium tanks, where the smell would be pervasive. It seems, however, basically unlikely that the fish could polarize by smell, and unorientated aggregations at night would be perhaps more likely. The importance of the lateral line in shoaling is completely unknown, but it might play some part in keeping fish together in darkness.

Galkov (1958) reported that small dense schools of herring, sometimes as deep as 500 m, have been seen to migrate actively across the Norwegian current by day and night. Craig and Priestley (1961) also photographed herring by flash on a spawning ground off the west coast of Scotland and found that the fish were orientated sometimes by day *and* night, the light on the bottom being below threshold. These fish were near the bottom and could all have been reacting to an external stimulus, such as tide, in the same way and not to each other. Indeed Valdez and Cushing (1959) reported that layer traces in the southern North Sea, which were probably herring, formed up in general at the first slack water after dusk and remained as a layer until the first slack water after dawn. It seemed as if the herring shoals could not break up until slack water and once dispersed in the tidal stream, could not reform into shoals until the next slack water with good light conditions.

No evidence is available that sound might be important for clupeids keeping together, but recently Freytag (1961) has reported that herring may make sounds, and Moulton (1960) has suggested that *Anchoviella* shoals may keep together by sound.

At the present time it may be said that vision appears to be of great importance to the maintenance of the shoal but the extent to which clupeid shoals may keep together, or remain polarized, as a result of interaction between the individuals due to other stimuli must remain an open question.

The more important question for the fisheries biologist is the control of shoal size, for while herring may be present in fairly high density, it is the size of shoal which may decide whether certain fisheries are to be successful or not. Some factors such as spawning, predation and feeding on slow-moving organisms, as well as gradients in hydrographical conditions or certain bottom configurations may keep shoals together, or even catalyse the formation of larger shoals by the fusion of smaller ones. Other factors such as feeding on fast-moving organisms, darkness and uniform hydrographic conditions may either tend barely

to maintain the *status quo*, or even cause rapid dispersion. The relative importance of shoal size and shoal numbers depends on the type of fishery and the searching power available to detect the presence of fish. Large shoals are usually more valuable to fisheries using encircling gear, while more numerous but smaller shoals, but not too small, are more valuable to trawl and drift net fisheries.

R. *Migrations*

1. *General*

The migrations of clupeids have been studied by plotting distribution of the fish, and by internal and external tagging. Such work started on *Clupea pallasii* about 1930, on *Sardinops caerulea* a little later and on *Clupea harengus* just after the Second World War. How the migrations are controlled is not well known. Cycles of hormone activity (see Sections VI, P; VI, X) suggest that there is a cycle of internal endocrine secretion, which may well give the fish an urge to migrate; the question of whether this cycle is an endogenous one, or one brought about by environmental conditions, such as temperature or day length, is also discussed in these sections. The problem to be discussed here is how the urge to migrate is directed along certain fairly well-defined routes. Is this essentially an undirected process, as a result of kineses (random movements where the speed of movement or turning frequency depends on environmental conditions), or is it an active, orientated movement (taxis) on the part of the fish, or is it a mixture of the two?

An undirected process could come about as follows. The fish might overwinter and remain relatively inactive in conditions of low temperature and poor food. The end of this period would appear as the fish became more active in response to rising temperature or inanition. Their movements would then be limited by unfavourable water masses (of low temperature or salinity and with poor food) as well as by the depth of water or by land masses. The fish would tend to aggregate where food was good, but as the season went by it would be necessary to postulate some factor which would direct them to the spawning ground. Assuming that a feeding phase were followed by a further spawning migration, this might be triggered off by the fat content reaching a certain value. The direction of the spawning migration might be partly controlled by non-optimal water masses and by aggregation, in the case of herring, in areas of suitable depth and substrate for depositing eggs. After spawning, the urge to migrate would subside and the fish would tend to drift off with the prevailing currents.

The active process would postulate such factors as sun orientation

and contranatant migrations, as those described by Russell (1937), and the reaction in a directed way to gradients of biotic and abiotic factors.

2. *Aggregations*

What evidence is available for clupeids aggregating in certain areas? Most work to date has been on Atlanto-Scandian and North Sea herring. The effect of hydrographic conditions, particularly temperature, on the North Sea herring has been partly reviewed by Hela and Laevastu (1962). The work of Dietrich *et al.* (1959) showed that the herring of the North Sea collected in the core of cold bottom water (6–7°C) on the Fladen ground in summer and autumn. An example of their distribution in August 1955 is given in Fig. 14. The time during which they remained in this area depended on the temperature, and the extent of their vertical migration depended on the position and steepness of the thermocline. Rogalla and Sahrhage (1960) found a somewhat different picture in early summer 1959 where the herring seemed to avoid the colder bottom temperatures as they did the cold, low-salinity outflow from the Skagerak. Schubert (personal communication) found later that herring particularly concentrated where there were hydrographical discontinuities in the North Sea. Biryukov (1958) found a partial tendency for herring to collect in cool water in the North Sea (for instance in 7·5–8·5°C in June) but also for them to collect where there were the sharpest temperature gradients (see Fig. 15). Craig (1960) showed an association between rapid warming of the surface water and northerly winds with reduced catches of older herring in the Scottish summer fishery in the north-western North Sea. Steele (1961) observed that herring leaving their overwintering area in the Skagerak tended to collect along the outside of the Baltic outflow in the late spring, and that they would follow the movements and breaking down of this barrier to some extent. Devold (1961) and Polonskij (1961), for example, showed the now well-known relationship between the Norwegian herring and hydrographic conditions, the fish collecting along the " Polar Front ".

Clearly the hydrographic and plankton conditions are connected and plankton, being so varied in species, is often the best indicator of the origin of water masses. This is discussed by Glover (1957) and Pavshtiks (1956).

Pavshtiks reviewed much of the evidence supporting the correlation between herring and plankton as shown by Russian workers and by British workers such as Fraser, Hardy, Henderson, Lucas, Savage and Wimpenny; to this evidence should be added Cushing's (1955) report and the work of Jakobsson (1961). There appear to be well

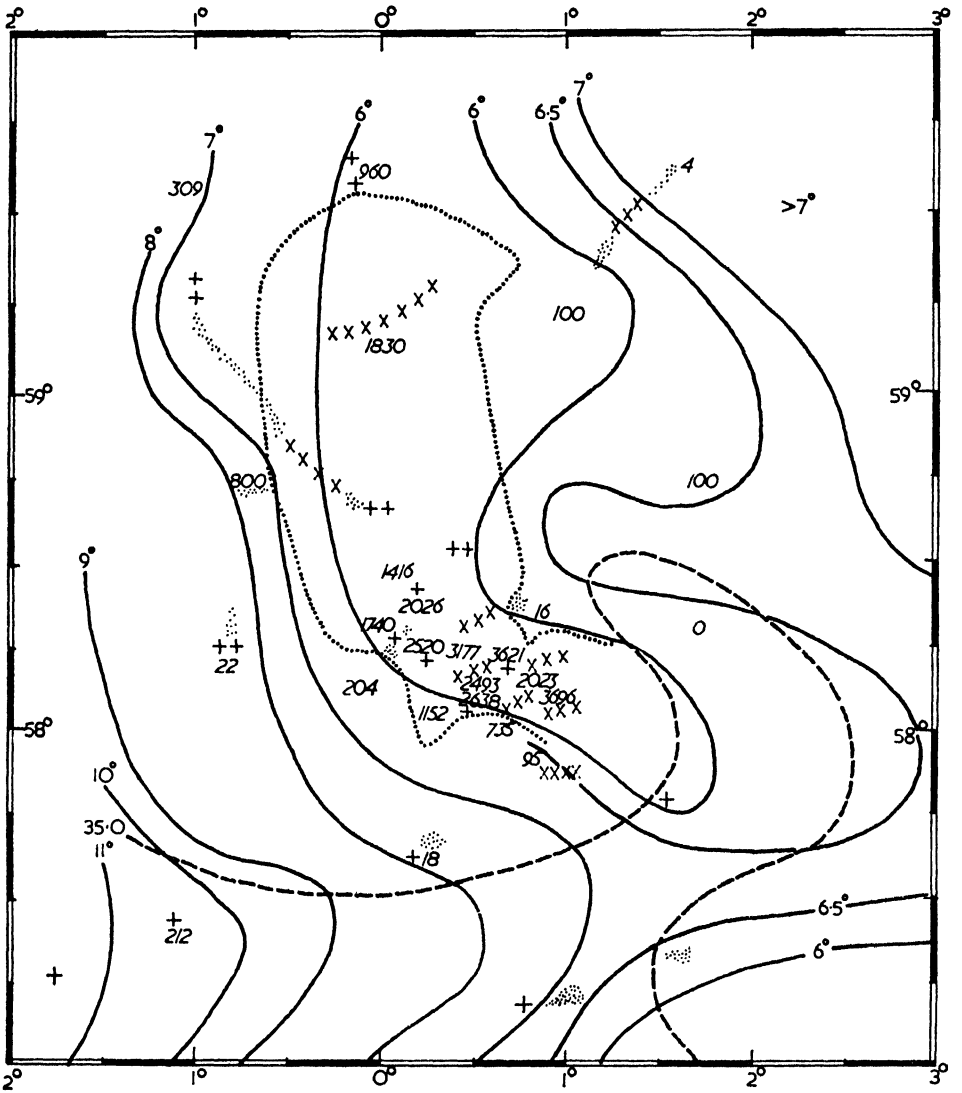


FIG. 14. Distribution of herring in Fladen ground area related to temperature. (Re-drawn with permission from Dietrich *et al.*, 1959.)

——isotherms
– – – – isohalines
. . . . isoplath for 1000 herring per half-hour trawl
xxx frequent
+ + + moderate } concentrations of herring from echo-sounding record
: : : : : rare

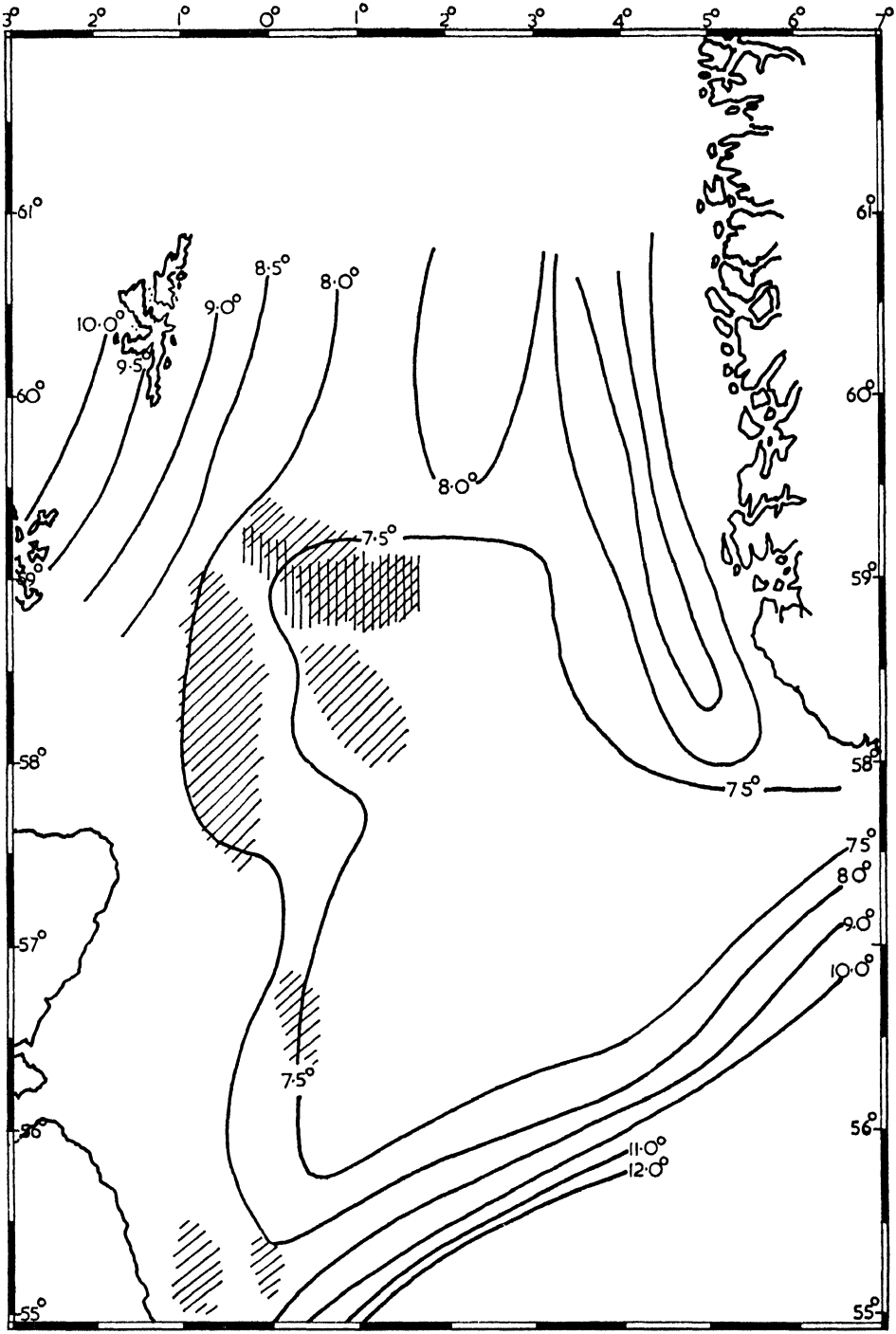


FIG. 15. Distribution of herring concentrations from 21/6/57 to 3/7/57 related to temperature near the bottom. (Re-drawn with permission from Biryukov, 1958.)

established connections between zooplankton, particularly *Calanus*, and herring, both in the North Sea and north-east Atlantic. Sometimes, however, the correlation fails and it is clear that the physiological state of the fish as well as the size and type of plankton need to be taken into consideration. Blooms of *Phaeocystis* seem often to be avoided, perhaps partly or wholly due to the absence of large zooplanktons in such blooms. However, the possibility of the phytoplankton being unpalatable or of gills becoming clogged by such blooms cannot be disregarded and could be tested by experiment. Pavshtiks also discussed how annual fluctuations in plankton abundance could shift the feeding grounds of herring. It is difficult to do justice to the enormous amount of work done in correlating zooplankton and herring. Glover (1957) described the possible effect of oceanic influence and its concomitant plankton changes on the Scottish East Coast and Shetland fisheries, suggesting broadly that an increased oceanic (Atlantic) influence in the northern North Sea might cause a shift of fish southwards. Williamson (1961), by means of statistical analysis, suggested some relationship between " northerliness " of the stock, oceanic influence and the abundance of certain zooplankton groups. The suggestion here is that oceanic conditions are avoided by North Sea herring. Fraser (1961) has put forward the hypothesis that pure oceanic water is not conducive to good growth of plankton and this, and possibly an element of " distastefulness ", might cause the avoidance. On the other hand, mixed water appeared to give good conditions for zooplankton production, which might partly account for herring being found along hydrographical fronts. These fronts might also delimit areas of unfavourable water, thus acting as migratory blocks. Steele (1961) showed that euphausiids were to be found along the Baltic water front off the Norwegian coast in the spring, possibly partly causing the collection of herring there. Devold (1961), too, reported on the feeding of Norwegian herring along the " Polar Front ". Jakobsson (1961) showed very interesting correlations between the abundance of zooplankton and the concentration of herring off the north coast of Iceland (see Fig. 16); he suggested that some zooplankton would tend to cause the formation of larger shoals where it was abundant.

FIG. 16. *a*. 4–11/7/1957. *b*. 7–19/7/1958. The relationship between herring shoals off Iceland and the concentration of zooplankton. (Re-drawn with permission from Jakobsson, 1961.)

continuous line—path of research vessel
transverse line—concentration of herring traces
● —zooplankton concentrations
× —phytoplankton concentrations

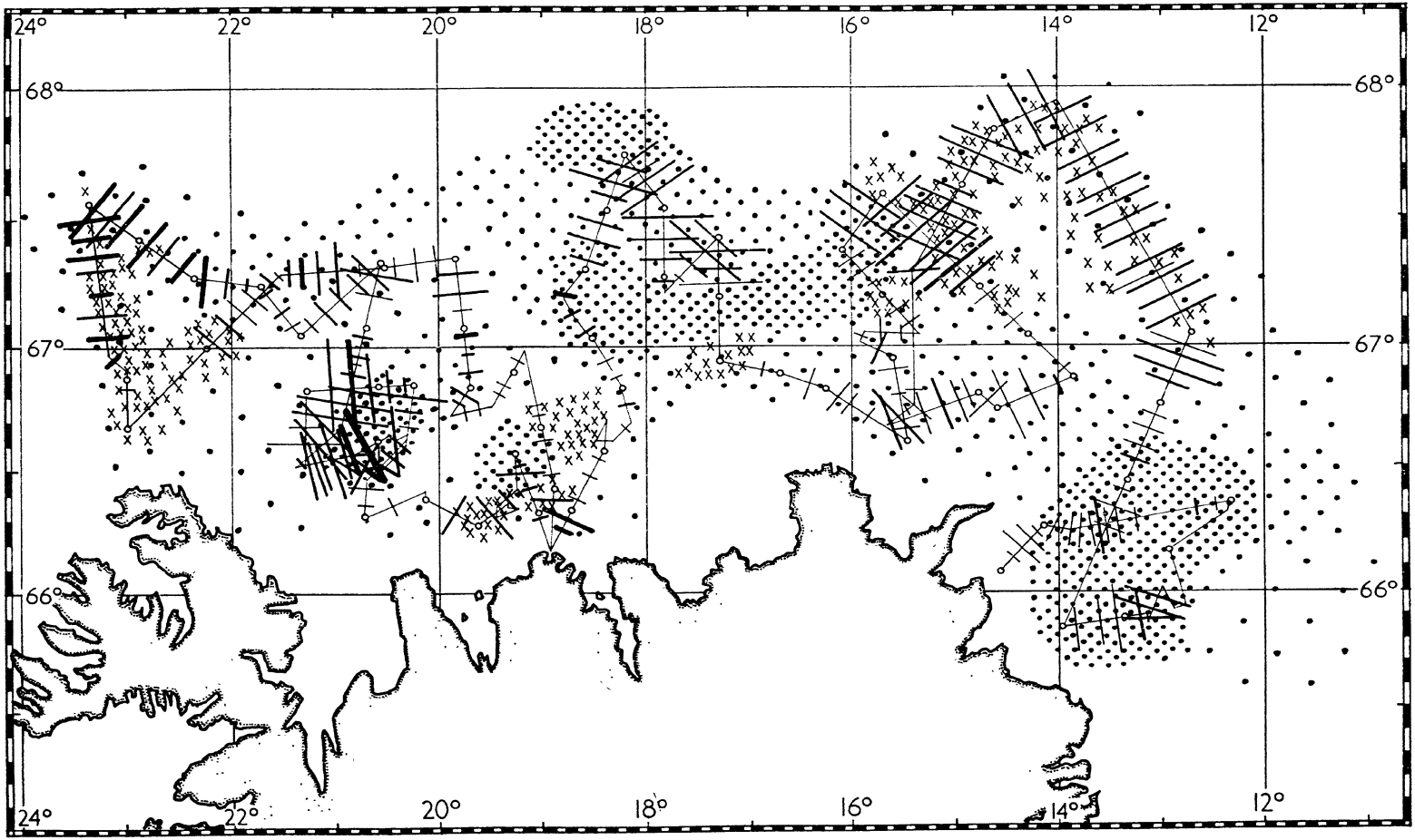


FIG. 16*a*. 4–11/7/1957. (See legend foot of facing page.)

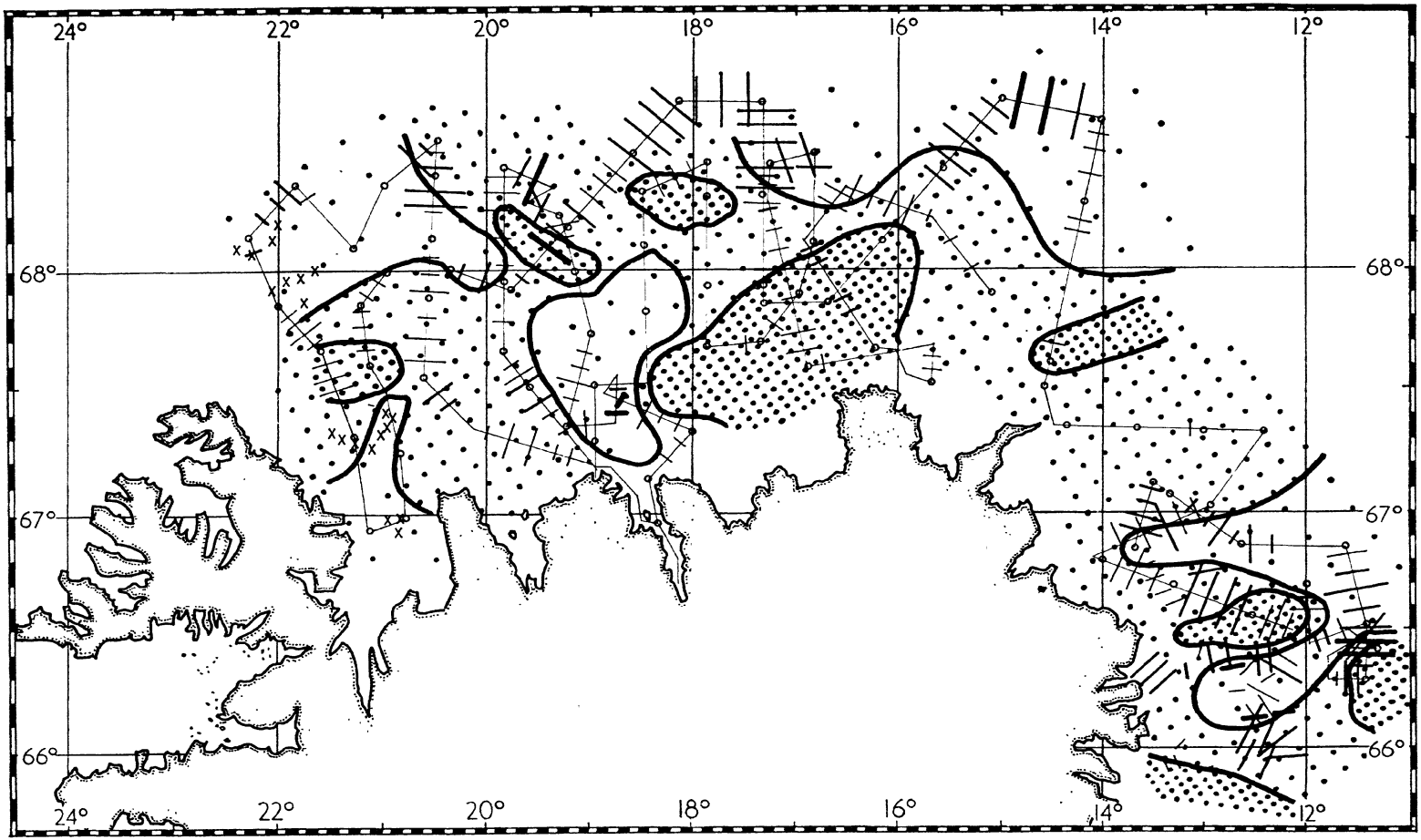


FIG. 16*b*. 7–19/7/1958. (See legend foot of p. 336.)

In species other than herring correlations have been found, particularly between temperature and fish concentrations. Hela and Laevastu (1962) reported Russian work in the Baltic showing how *Sprattus sprattus* was mainly caught in summer in water of 10–15°C, and Japanese workers showed that the best catches of *Sardinops melanosticta* on southern grounds were made where the surface temperature ranged from 12–16°C. Pavshtiks (1956) quoted Russian work where this species was found to delay its spawning migration if food was abundant. Phillips and Radovich (1952) also reported that the distribution of *Sardinops caerulea* was correlated with temperature. Hourston (1953) collected data showing that *Clupea pallasii* was found in less saline water off the British Columbia coast.

It seems possible, too, that long-term hydrographical changes may affect the distribution of fish on a more permanent basis. Devold (1961), for example, has shown that the annual migration to the Norwegian coast of the Norwegian herring is becoming progressively later each year. He suggested that this might ultimately bring the fish into such different environmental conditions for a given stage in the life cycle that the spawning time might be radically altered (this is also discussed under Section VI, X). Motoda and Hirano (1961) reported on long-term temperature changes (and reviewed similar reports from the eastern Pacific) affecting the distribution of the spawning of *Clupea pallasii*. Such hydrographical changes also seem to have affected the distribution and spawning of *Sardinops caerulea* (Murphy, 1961). It is clear that temperature changes on a long-term basis may not only affect distribution of fish by putting certain, formerly colonized areas " out of bounds ", but may also affect growth, maturation and time of first maturity (see Section VI, X).

The mechanism of aggregation in areas of favourable conditions might be explained on the theory of the kinesis, the fish tending to move less in favoured areas, and more rapidly in areas which are unfavourable. In the case of feeding the shoals would, in any case, tend to break and slow down to allow the fish to feed. It is not clear whether such mechanisms could account for the total migration pattern observed in the life cycle. Could, for instance, the movement of northern North Sea herring from the edge of the Norwegian deeps to the feeding grounds, the westward and then southward movement to the spawning grounds, and the eastward drift after spawning, be only the result of a series of kineses? It is possible that the herring might be prevented from leaving the North Sea by unfavourable Atlantic water and from further westward movement by the land mass of Scotland. With an urge to move, they would then turn south or east to a favourable substratum

for spawning and then drift with the current back to the Skagerak to overwinter. But this approach may be too simple, particularly in relation to the further southward movement of the southern North Sea spawners, some of which pass through Scottish waters, and in relation to the migration of Norwegian herring from Icelandic waters.

Another factor in migration is the sudden movement of fish from productive fishing grounds often without any apparent cause. Sometimes these movements may be correlated with unfavourable weather and they may also be due to lack of food or the arrival of predators.

There is a wide field open for the experimental study of phenomena relating to kineses in fish and how their speed of movement may be controlled by the environment. For instance, Loukashkin and Grant (1959) found that *Sardinops caerulea* swam more rapidly in unfavourable red light.

3. *Directed orientation*

Much more difficult is the explanation of directed orientation which may well be of great importance. Can clupeids detect, and react to, gradients of hydrographical conditions or of food or of some unspecified chemical and thus actively seek an optimal environment? Glover (1957) suggested that herring might be able to detect concentration gradients of food organisms, though it is not clear what the mechanism would be. Presumably the fish would move slower and slower as food became more abundant, which would be more of a kinetic response. It seems unlikely that gradients of temperature or salinity would ever be abrupt enough, except perhaps vertically, for single fish to detect them along the length of their bodies. Shelford and Powers (1915) reported that *Clupea pallasii* in tanks could detect a temperature change of 0·6°C, but their temperature preference experiments were inconclusive. Anon. (1956) reported that *Sardinops caerulea* acclimated to 17–19°C usually occupied a region of temperature 18–22°C in a tall tank with a gradient from 4°C at the bottom to 34°C at the top. *Engraulis mordax* acclimated to 12°C remained in 12–14°C, acclimated to 17°C in 15–18°C and acclimated to 20°C in 18–20°C. It is conceivable that a very large shoal could occupy an area where a gradient existed such that one side of the shoal experienced more favourable conditions than the other. In this event, the fish in the favourable conditions might start to move more slowly, introducing a " wheeling " effect and a turn of the shoal towards the more favourable area (Steele, 1961).

Contranatant migration seems unlikely in a pelagic fish out of contact with stationary reference points (see Section VI, O) but a denatant drift, which would essentially be passive, seems quite probable.

For instance, at certain times of year spent herring are to be found on the Fladen ground and off the Belgian coast where the prevailing currents might have taken them after spawning.

Nothing is known of the ability of marine fish to orientate to the sun, though this ability is present in *Lepomis* (Hasler *et al.*, 1958). It is also known that sunlight may have a directional component to considerable depths (e.g. to 90 m, Sasaki *et al.*, 1958). This would provide a mechanism for the southerly migration of maturing herring in the North Sea, but probably not for the migration of Norwegian herring during the winter darkness, where the herring are at the surface at night and 300–500 m deep by day and moving 6–7 miles in 24 hr (Devold, personal communication). Devold has shown that the initial migration of the Norwegian herring towards the spawning grounds might be merely the following of a hydrographical front at speeds of 6–7 miles per day but, in the later stages near the coast, they broke through the barrier into the Atlantic water towards the coast, as if by some directional urge, attaining sometimes speeds of 20–40 miles per day. Galkov (1958) reported that small schools of herring migrated across the Norwegian current by day and night at depths down to 500 m.

One inevitably turns to the question of learning in this respect. Wynne-Edwards (1962) suggested that tradition played an important part in the movements of fish migrating in a regular manner. If this were so, a highly deleterious effect would be produced if stocks were reduced to too low a limit, for a breakdown in the migration pattern would result. It is well known that in herring the older fish usually mature and enter the spawning fishery first, as if they might have been leading the recruit spawners; but how is one to explain even a learned ability to orientate?

4. *Summary*

It may be said, by way of summary, that there is good evidence for the aggregation of clupeids into defined areas, partly as controlled by land masses and partly as the result of kineses. These favourable areas may themselves be moving, giving yearly variations of the migration pattern. This, and a possible drift with the residual current after spawning to overwintering or feeding areas (depending on the spawning time), may partly explain migration. A more directed movement, particularly to the spawning grounds, needs also to be postulated, but it has yet to be explained, either as a result of a contranatant migration, or as a reaction to gradients of temperature or chemical factors by means of a taxis, or as a result of an orientation to the sun or other

celestial bodies. No evidence either is forthcoming, so far, of a learning factor in migration.

S. *Vertical migration*

1. *Occurrence and extent of vertical migration*

Since the advent of the echo-sounder it has been possible to follow the variations and extent of vertical migration in clupeids, a study which would have little meaning in the aquarium. Runnstrøm (1941b) was one of the pioneers of research work with the echo-sounder. He traced some of the characteristic movements of Atlanto-Scandian herring, showing that the shoals rose at dusk and sank in daylight, being found then at depths of 150 m or more. This has also been well demonstrated and photographed by Solovyev and Degtyarev (1957). Devold (1953) and Ryzhenko (1961) found such shoals down to 400 m in the daytime, rising to 50 m or less by night. Dragesund (1958) watched the diurnal movement of herring shoals when a ship lay over them for long periods. Later Devold (1961) reported that Atlanto-Scandian herring were being found during their migrations down to 500 m by day, tending to keep below 100 m even at night, particularly in later years.

In the North Sea the diurnal movements, though similar, are greatly restricted by the depth of water. Balls (1951) has described the movements in relation to depth, particularly in the southern North Sea. Biryukov (1958) reported a migration from 140–160 m up to 10–40 m in the northern North Sea. Okonski and Konkol (1957) showed how herring rose towards the surface at night in the Skagerak. Brawn (1960b) studied the seasonal and vertical distribution of immature herring in Passamaquoddy Bay. The extent of the upward migration by night in this shallow water varied from 5–20 m depending on the season, the fish being deeper in the months January to April. Tester (1943) showed diurnal vertical movements of *Clupea pallasii* in British Columbia waters and Nomura (1958) in *Sardinops melanosticta* in Japanese waters.

The general pattern of vertical migration seems to be an upward movement at night followed by a spreading out of the fish. At dawn the fish come together and descend. Balls (1951) called the upward movement in the shallow southern North Sea (20–60 m) a " wine glass " effect, the herring being spread over the bottom by day, rising together at dusk and spreading out again in darkness. Cases have been reported (see Section VI, Q) of herring shoals or aggregations retaining their entity at night, but this seems less common and it is not certain what the nature is of these groups of fish. It is also clear (Lucas, 1936;

Krefft and Schüler, 1951; and Richardson, 1960) that herring are also caught by night on the bottom with trawls, though the catches are usually smaller and their composition different. The extent to which this is caused by behaviour in relation to the net by different fish in different light intensities is not quite clear, but this is a problem of interpretation in comparative fishing experiments.

2. *Light*

The following of a preferred light intensity would explain the movements, though presumably the light intensity at night would be much lower than the preferred intensity by day. In Polar conditions, vertical migration of herring was not found according to Zusser (1958a).

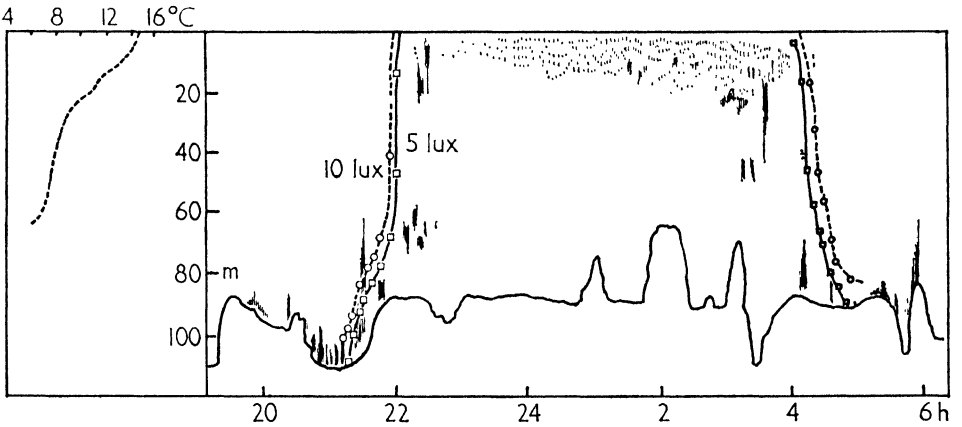


FIG. 17. Vertical movements of herring shoals in relation to light intensity at different times of the day (July 1955, 55°35′N, 01°21′W) with bathythermograph temperature profile on the left. (Re-drawn with permission from Postuma, 1957.)

Johnson (1939b) first showed the importance of light in determining the depth of young herring shoals off New Brunswick. Balls (1951) ascribed the lack of echo traces in the shallow southern North Sea to the herring hugging the bottom in a high light intensity. He also observed herring leaving the bottom earlier in the evening when the sky was overcast. Richardson (1952) related the downward movement of shoals in the North Sea to light intensity as measured in arbitrary units by a light meter. Here it was apparent that the night intensity was much lower than the preferred day intensity. Postuma (1957) showed that in general herring in the North Sea preferred light intensities below 1 lux (see Fig. 17) and Chestnoy (1961) showed that the depth of herring shoals could be correlated with isolux lines and gave data showing that the depth drift nets should be shot at different times

of day and night. Brawn (1960b), in Passamaquoddy Bay, found no relationship between mean solar radiation and the depth of shoals of immature herring. Nomura (1958) reported *Sardinops melanosticta* sinking to a depth by day where the illumination was 10–1000 lux.

3. *Temperature*

Schubert (1950) reported that northern North Sea herring would not migrate upwards through thermoclines of 6 deg. C in 3 m, but would through 2 deg. C in 3 m. In shallower depths herring were found to

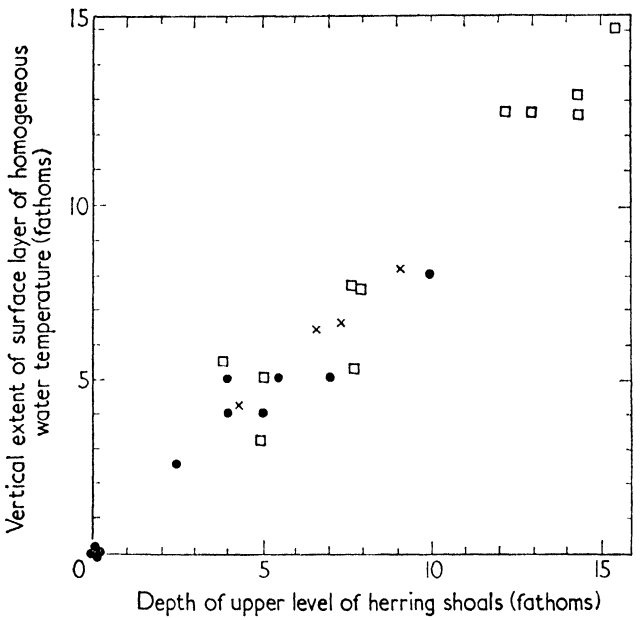


FIG. 18. The depth of herring shoals at different vertical extents of the surface layer of homogeneous water temperature. (Re-drawn with permission from Postuma, 1957.)

□ 1954 ● 1955 x 1957

remain below a thermocline of 2 deg. C in 5 m. Richardson (1952) found that herring passed upwards through a thermocline of 2·45 deg. C in 5 m. Postuma (1957) showed that North Sea herring would not migrate upwards beyond the point where the gradually rising temperature ceased to rise (see Fig. 18). Thus where there was a deep layer of water at the surface where the temperature was homogeneous, the herring remained deep. Solovyev and Degtyarev (1957) found that herring in the Viking Bank area would not move up into cold, less saline water of Baltic origin, and Devold (personal communication) found that spawning Atlanto-Scandian herring would not move up into low salinity

water of 5°C or less at the surface. Temperature may also affect movement downwards. Biryukov (1958), also in the North Sea, found that herring would not move downwards by day through thermoclines which were too steep (for instance, 3 deg. C in about 10 m). They then remained by day at the depth of the thermocline, moving upwards to the surface at night. Solovyev (1959) found in the East Iceland Current that herring would not move down into colder water, and Devold observed that these herring would not move into cold water when feeding in the summer. Brawn (1960b) found a complex relationship between the daytime depth of immature herring shoals in Passamaquoddy Bay and the water temperature (measured at 30 m). At temperatures below about 7°C there was an inverse relation between the median depth of the shoals and temperature, the herring tending to go deeper when the water was colder. Above about 7°C the herring did not stay higher by day. This could not be explained by a simple temperature-activity hypothesis, the herring sinking lower in cold water due to inactivity, because at night they rose to the surface layers, regardless of the temperature. Zusser (1958a) reported that Atlantic and Baltic herring and the Caspian sprat *Clupeonella* did not swim below water of a certain temperature, and Lovetskaya (1956) that *Clupeonella* showed greater vertical movements at higher temperatures.

Aquarium observations (Kamshylov and Gerasimov, 1960) showed that young Murman herring would not swim from water at 4·2°C to water of 1·8°C in a tank, while Shelford and Powers (1915), using *Clupea pallasii*, found they reacted to temperature differences of 0·6°C.

4. *Feeding*

Girsa (1961) related the vertical migration of marine organisms in general to the change in availability of their food. Richardson (1952) and Ryzhenko (1961) reported vertical migration in herring which were not feeding. However, Ryzhenko also described herring which may have been following luminescent patches of plankton. It seems unlikely from both sea and aquarium observations (see Section VI, B) that clupeids feed by night and it is probable that feeding is at its peak at dusk and dawn. Why less feeding seems to be found by day is not certain.

5. *Other factors*

Aquarium observations on herring one year old (Bückmann *et al.*, 1953) suggested that they might be prevented from vertical migration by sharp salinity gradients, and Kamshylov and Gerasimov (1960) reported that young Murman herring in aquaria would not swim

through a sharp salinity barrier, except temporarily, to get food. It is also clear that vertical migration might also be modified by such factors as tide; Valdez and Cushing (1959) showed that the breaking and re-forming of what was thought to be herring shoals depended on the state of tide and the amount of light. Catches of herring vary with moon phase and the depth of shoals may be lower where there is a moon (see Section VI, T).

It seems likely that the control of vertical migration is extremely complex, depending on a number of external factors, the effect of which will be modified by internal factors such as the age and physiological state of the fish and the size of shoals. Any prediction of the depth to which shoals will rise at night or sink by day needs to be based on data from a given area at a given time.

6. *Adaptive value of vertical migration*

Zusser (1958a) described the advantage to the fish of changing their environment twice per day, giving them a greater choice of food and the possibility of better distribution by currents. Wynne-Edwards (1962) developed the idea that the numerical density of animals was regulated at certain specified times, in the case of plankton, when they migrated to the surface at night. This hypothesis could also be extended in a modified way to vertical migration of clupeids.

7. *Speed of vertical migration and pressure changes* (see also Section VI, N)

Runnstrøm (1941b) reported an upward movement of 100 m in 1 hr in Atlanto-Scandian herring and Dragesund (1958) an upward movement of sprats (?) of 15 m in 45 min. Krefft and Schüler (1951) gave speeds of 75 m/hr up and 200 m/hr down in North Sea herring. On a more experimental basis, Blaxter and Parrish (1958) measured the speed of clupeids following the vertical movements of artificial lights. Herring 15–25 cm long moved up at speeds up to 13·5 m/min and down at speeds up to 36 m/min; sprats, 5–15 cm long, swam up at speeds up to 30 m/min. The pressure changes involved ranged from increases of 16–180% and decrease of pressure from 18 to 73% for herring, and increases of 22 to 225% and decreases of 11 to 67% for sprats. Brawn (1962) put immature herring from Passamaquoddy Bay into cages which she raised and lowered. They withstood being lowered from the surface to about 50 m (change of pressure 0 to 4·7 kg/cm^2) at a rate of 0·06 kg/cm^2/sec, and being raised to the surface again at a speed of 0·07–0·08 kg/cm^2/sec. The herring were also subjected to greater stresses in a sterilizer. After a pressure increase of 1·4 kg/cm^2 they

were decompressed at a rate of 0·9 kg/cm²/sec without harm. Rates greater than 1·8 kg/cm²/sec were probably injurious.

There is no reason to suppose that clupeids, which are physostomatous, should suffer from inflated swim bladders on decompression, but it is possible that decompression might cause embolisms, which could account partly for mortality of herring caught by trawl at considerable depths.

It appeared from Brawn's (1960a) work that herring in cages sank swimming horizontally and rose swimming vertically. The data on swimming speeds show that upward movement tends to be slower. This might be partly a gravitational effect and partly a need to compensate for decreasing pressure, which might be a more serious problem than increasing pressure.

8. *The "swim"*

This has been discussed in Section VI, V, but it is a phenomenon particularly associated with vertical migration in the shallow waters of the North Sea (Graham, 1931; Balls, 1951).

T. *Effect of the moon*

Probably the first scientific enquiry into the lunar influence on clupeid catches was that of Fulton (1906), who found the total herring catch in the Inveraray district of Scotland from 1860–1900 to be 293,035 crans over the new-moon period, and over the full-moon period 215,152 crans. He thought the difference might be due to fishermen fishing less at full moon as they thought the fish would see the nets. The analysis of the pre-war southern North Sea herring catches by Savage and Hodgson (1934) showed the striking dependence of the catch on the moon phase. Around full moon the catch might be double that at other times, but the course of the season's fishing was influenced by the date of the full moon. If it was in the 2nd week of October good fishing could be expected for about 5 weeks. If the full moon was near the end of October, there tended to be only one peak of good catches, which made the fishing more dependent on bad weather. Hickling (1947), however, found little evidence of the moon phase on the trawl fishery for herring from Milford Haven (South Wales) from 1933–1940. It seemed that if the moon was full in the last part of September the trawl fishery suffered, but there was no effect comparable with southern North Sea.

Since the war only Jens (1954) has published further analyses of herring catch statistics based on moon phase. He used the German lugger drift net catches in the North Sea in 1953, and found a peak

about 4 days after full moon and a second lower peak one day after new moon.

Tester (1938b) analysed the catches of *Clupea pallasii* off Vancouver Island from 1933–1937 and found the lowest catches at new and full moon, which he thought was due to a reduction in the influx of herring into the channel during the spring tides. Clark (1956) reported that Californian sardine fishermen tied up during the full-moon period because they caught so few fish. Normally the fish were found by the phosphorescence they created and this was best observed before moonrise or after it set.

It is clear that a lunar influence on catch may reflect the behaviour of fish, or that of the fishermen. The following might be the causes of a lunar influence on fish behaviour, with a resultant effect on the catch:

(*a*) The light of the moon might cause a change in the activity level of fish, particularly in shallow water, for instance in the southern North Sea. It might change the extent of vertical migration (particularly in deep water) or horizontal migration. These effects might vary with the physiological state of the fish, e.g. whether they were near spawning or not.

(*b*) The light of the moon (probably 0·5 lux or less) might raise the level of illumination near the surface sufficiently to allow the fish to see the nets (see Section VI, V), or to change the pattern of shoaling.

(*c*) The tidal effect associated with the moon's phases might also have a variable influence on the excitability of the fish, or on their horizontal or vertical migration, or on their shoaling behaviour.

(*d*) The light or tidal effect of the moon might affect predator-prey relationships.

These different factors, combined with the possible effect of weather and of moon phase on fishing practice, make a causal analysis of this type of data very difficult. Possibly lunar effects may have been smoothed out since the war by changes in the length of buoy ropes used on the nets, by the use of echo-sounders, or by changes in fishing grounds.

U. *Attraction to artificial lights*

1. *Occurrence*

Published accounts of the attraction or repulsion of clupeids to artificial lights are shown in Table X.

TABLE X

ATTRACTION OF CLUPEIDS BY ARTIFICIAL LIGHTS

Author	Species	Area	Observation
Krefft and Schubert (1950)	Young herring	North Sea	Attracted to surface by 100 W searchlight
Day (personal communication)	Young herring *c.* 10 cm	East Coast of America	Attracted to surface by lights of 5–1000 W
Borisov (1955)	Young herring	Murmansk (Atlantic)	Attracted by lights
Blaxter and Parrish (1958)	Young herring 5–25 cm	Scottish inshore waters	Attracted by underwater lights from 15–1500 W
Schüler and Krefft (1951)	Adult herring	North Sea	Repelled by 40 W underwater light and 500 W searchlight
Richardson (1952)	Adult herring	North Sea	Shoals descend 7–10 m due to 60 W searchlight
Dragesund (1958)	Adult herring	Norway	Sometimes attracted, sometimes repelled by 1500 W searchlight
Tikhinov (1960)	Adult herring	Atlantic	Repelled by lights
Ryzhenko (1961)	?Adult herring	Atlantic	"Attacked" lights of research submarine "Severyanka"
Richardson (1952)	*Sardina pilchardus*	Southern North Sea	Attracted by lights
Radovich and Gibbs (1954)	Young *Sardinops caerulea*	Eastern Pacific	Attracted by 750 W lights above the surface
Borisov (1955)	*Alosa, Caspialosa, Clupeonella*	Caspian	Attracted by lights
Borisov (1955)	*Clupea pallasii*	Pacific	Attracted by lights
Verheijen (1956)	*Sardina pilchardus*	Mediterranean	Attracted by lights
Blaxter and Parrish (1958)	*Sprattus sprattus*	Inshore Scottish waters	Attracted by lights
Dragesund (1958)	*Sprattus sprattus*	Norway	Attracted by lights
Nikonorov (1958)	*Clupeonella*	Caspian	Detailed description of reaction to lights

These observations were all made at sea, mainly in an attempt to develop light fisheries. Loukashkin and Grant (1959) made a detailed aquarium study of the effect of coloured and white light on *Sardinops caerulea*; this species preferred blue and green light and disliked red light, exhibiting a fright reaction both to this and flashing white light.

2. *Variability of the reaction*

While attraction to artificial lights has been frequently observed, especially in young clupeids, such reactions will vary widely depending on the environment and the physiological state and age of the fish, as well as on the type of stimulus itself. Lovetskaya (1956) found seasonal differences in the Caspian sprat (? *Clupeonella*) and Shubnikov (1960) found that more ripe *Clupeonella* males were attracted than females. This could have been associated with the higher feeding activity of the males. Belyaeva and Nikonorov (1960) found that the behaviour to lights changed in relation to the condition of the fish, ecological factors, amount of moonlight, temperature, turbidity, current and the nature of the light source. Schüler and Krefft (1951) found that herring (?) would not pass through a thermocline of 4·63 deg. C in 5 m under the attraction of a lamp.

The intensity of the light source was found to be important by Borisov (1955); higher intensities attracted *Clupeonella* more effectively. Of different colours used, yellow was most effective, but probably because it was the brightest light. Nikonorov and Patejev (1959) gave details of the best light condition for *Clupeonella*. Blaxter and Parrish (1958) found, too, that higher light intensities collected more organisms, presumably due to their greater penetration.

3. *Explanation for light attraction*

This has been reviewed by Belyaeva and Nikonorov (1960), who suggested that " curiosity ", feeding, positive phototaxis, hypnosis, following of optimum light intensity, disorientation or conditioned reflex might be responsible. They favoured the idea of a " testing reflex ", referring particularly to *Clupeonella*. Zusser (1958b) and Borisov and Protasov (1960) considered that phototaxis was no explanation, but that attraction was due to a conditioned response; the fish normally associated feeding with light, to the extent that attraction to light had become a conditioned response associated with feeding, the unconditioned response. This requires to be proved experimentally. Verheijen (1958) developed the idea that attraction was due to a mass disorientation, such as that caused by lighthouses to migrating birds and insects. The mechanism of this disorientation would be as follows:

The lamp would appear to the fish as a point source, stimulating only one eye at a time. This would give the effect of unilateral blinding, causing the fish to swim in a deviating path to the light. While this might occur in clear water and might be the explanation for those fish seen swimming in a disorientated and disturbed manner near lights (e.g. Ryzhenko, 1961), it does not so easily explain the orientated swimming in the vicinity of lamps reported by some authors, nor attraction in very turbid water. It seems not unlikely that different explanations may apply to different species.

4. *Light fisheries*

Schärfe (1953) has given a comprehensive review of the use of lights by fishermen. Dragesund (1958) gave some details of this in the Norwegian fishery for Atlanto-Scandian herring, while Radovich and Gibbs (1954) described the blanket net used in Japanese fisheries for sardines. The use of lights has been developed most by Russian fishermen (Borisov, 1955) and by the Japanese. The most recent development is the use of light to attract clupeids initially into a region where they become influenced by an electric current. This leads them to the inlet of a pump, from whence they are pumped on deck. This was described by Smith (1955) on an experimental basis for young *Clupea pallasii*, and engraulids in Puget Sound. This method of fishing is now in extensive use, for instance in the Caspian, as a means of catching *Clupeonella* (e.g. Nikonorov, 1958). A theoretical discussion of the various factors involved in determining the optimum conditions for establishing a light fishery is given by Hela and Laevastu (1962).

V. *Reaction to nets and other obstacles*

A review of the reaction of fish, in many instances clupeids, to nets was given by Mohr (1960), who discussed the senses involved and the importance of ecological and physiological factors and of learning in captive fish.

1. *Reaction to stationary nets*

Experiments at sea all point to the importance of sight in avoiding such nets. Tokarew and Aslanova, quoted by Mohr (1960), reported the desirability of nets being as invisible as possible in the North Sea herring and in the Black Sea sardine fisheries. Aslanova gave reaction distances to nets of 4 m to a few cm, depending on turbidity and light intensity. v. Brandt (1954) showed the better catching power of Perlon nets in the Baltic herring fishery. Andreev (1955) discussed also the advantage of having nets of low visibility.

Mohr (1960, 1961) developed the idea of a relationship between quantity of fish present (and therefore shoal size) and net avoidance, small shoals avoiding nets better than large shoals, where the " shoaling pressure " was greater and the fish less able to perceive danger in their surroundings. The concept of the " swim ", a sudden panic reaction of herring, usually associated with slack tide in shallow depths of water, was discussed by Graham (1931) and Balls (1951). At the time of the swim the fish show a panic reaction due, perhaps, to the state of tide, crowding and sexual or migrating impulses, and they swim into the nets.

Aquarium observations on captive herring were made by Verheijen (1953), who mentioned the importance of sight for perceiving obstacles. Blaxter and Parrish (1959) also found that sight seemed to be the dominant sense in avoiding nets placed across a tank. The more contrast the net had (by reason of mesh size, twine thickness, or colour) in relation to the background, the more it was avoided. The herring failed to perceive monofilament nylon nets or sheets of transparent plastic, suggesting an inability to react to any form of reflected sound or pressure waves from obstacles. Fish " blinded " by means of opaque plastic over the eyes, failed to respond to the nets. The reaction distance of normal fish was of the order of 1 m in a small tank in high light intensities. Nets which were avoided in daylight were swum through at night, and it was possible to measure a threshold light intensity when the herring started to pass through the nets. This was between 0·001 and 0·0001 photopic lux in small tanks (4 m × 2 m) and 0·01 to 0·001 lux in much larger tanks (16 m × 13 m). Mohr (1961) did similar experiments with nets, but did not measure such threshold values. He found that the monofilament nylon nets were not perceived when the twine was less than 0·2 mm in diameter. The same author (1962) showed that transparent Perlon netting of 0·3 mm and mesh size 4 cm was avoided by 50% of individual fish, the reaction distance being 1–10 cm. Small shoals of 40–100 fish almost never swam into the net while larger shoals frequently did, showing the effect of shoal " pressure ".

2. *Reaction to moving nets*

This has been studied at sea by echo-sounder and by indirect methods such as analysis of catch from nets towed at different speeds. Schärfe (1955) followed the reaction of herring shoals to trawls by echo-sounder in a small boat and observed no general scaring effect. Springer (1957) followed the reactions of *Sardinella anchovia* to a trawl by underwater television. The fish showed no strong fright reaction but

they increased their swimming speed slightly to avoid the different parts of the gear. Schärfe (1960), in a review paper, reported the tendency of herring to swim downwards when frightened by a pelagic trawl, reacting 2–4 m from the headline or ground rope. At 3 knots (170 cm/sec) the herring appeared to swim ahead of the net, but at 3·5+ knots (200+ cm/sec) they were overtaken. Okonski and Konkol (1957), however, reported an upward movement by herring in the Skagerak when scared by a pelagic trawl. Clearly the direction of movement depends on the position of the shoal in relation to the net as well as on other possible factors. Galkov (1958) stressed that the capture of Atlanto-Scandian herring by pelagic trawl depended very much on their mobility, catches being best in November and December when mobility was low. Mohr (1962) compared the echo traces obtained from a transmitter on board ship with those from a transmitter on the headline of a herring trawl. The reaction of the herring differed, depending on their concentration. Small groups of fish kept about 5 m away from the headline and ground rope; large groups appeared not to react at all, due to greater shoaling " pressure ". Mohr pointed out the variability of behaviour of herring to nets with such factors as maturity stage, shoal sizes and time of day. Manteufel and Radakov (1960) reported that tightly packed shoals of herring were more difficult to catch by trawl in the Baltic, suggesting that shoaling assists the fish in reacting to the net and avoiding it. Manteufel *et al.* (1958) showed that herring shoals in the Baltic were frightened by the boards, warps and net of a trawl, and also by the fishing vessel itself 30 m above. The shoals soon returned to their previous position after the net had passed. In contrast, Radakov (1962) observed shoals of *Clupeonella delicatula* and *Engraulis encrasicholus* swimming, apparently without agitation, within a trawl towed at 1·5 knots.

Lucas (1936), Krefft and Schüler (1951) and Richardson (1960) showed that trawl catches of North Sea herring were better by day, there being size and maturity differences in the catches. While vertical migration may play the principal part here, it is also possible that herring catches are poorer at night because the fish are more spread out (if they are not shoaling), or because they are not herded by the extremities of the net, the net having, therefore, a lower effective width.

In relation to this, the aquarium observations of Blaxter *et al.* (1960) showed the importance of sight to herring in avoiding moving obstacles. They tested the herding ability of ground ropes, floats, panels of netting, underwater lights and air bubbles. The more conspicuous the obstacle and the greater its effective height, the better the herding, the

fish reacting at distances usually of about 2 m and swimming on average at distances of about 2 m in front of all types of obstacle in good light conditions. At speeds of 150 cm/sec (2·7 knots) or above, they were soon overtaken by the gear. At night, shoaling and all herding ceased, herring not responding even to strings of underwater lights. The threshold light intensity for loss of the herding response was between 0·5 and 0·05 photopic lux.

The importance of sound and vibrating and pressure stimuli to clupeids in avoiding nets is difficult to assess due to the difficulties of avoiding echoes in tanks and the difficulty of producing suitable sound sources of low frequency to simulate the sounds made by warps and boards. However, Schärfe (1960) suggested that light netting was desirable for the manufacture of the pelagic Engels trawl in order to prevent too great a pressure wave in front of it. Although the main object of this would be to reduce drag, it might also reduce the stow in front of the net to which fish could respond.

3. *Reaction to air bubbles*

The work on the Maine coast of the U.S.A. on the reaction of young herrings to " curtains " of air bubbles has been summarized by Smith (1961). The shoals of fish might be led into anchored nets or kept within the confines of an estuary or bay ; now this seems to be developing into a commercial technique. According to Smith (personal communication), the curtain was sometimes effective at night. Due to moonlight or phosphorescence, however, the air bubbles were usually visible at night, and it was possible that the method was ineffective on very dark nights. This would agree with the observations of Blaxter and Parrish (1959) and Blaxter *et al.* (1960), that captive herring do not react to air bubble barriers in darkness. Nikonorov (1958) found that *Clupeonella* in aquaria would pass through air bubble curtains in daylight.

4. *Learning in net avoidance*

Our lack of knowledge of this has been discussed by Mohr (1960), who quoted Aslanova's observation of sardine avoiding an area where they had been frightened. Mohr (1961) reported some signs of learning in captive herring, which were being subjected to the presence of nets in their aquarium. Devold (personal communication) pointed to the gradual increase of the depth of migration of the Norwegian herring as it approached the coast in late winter. The main component of this stock is the 1950 year class and various explanations may be offered to

account for this behaviour. Devold has put forward learning as a possibility—the fish learning to keep lower in order to avoid the nets after frequent migrations to the coast during their lifetime. Another possibility is that the fish with a tendency to swim higher in the water might have been fished out, or there may be a hydrographical explanation. Polonskij (1961) found an increased warming of surface layers during this time.

5. *Effect of electricity*

Groody *et al.* (1952) and Loukashkin and Grant (1954) studied the effect of electrical fields on *Sardinops caerulea*. The fish orientated to face the anode and were forced to it, when subjected to pulsating direct current and rectified 60-cycle alternating current of different wave forms. The current density required to produce galvanotropism was critical and varied inversely with the size of fish. Densities below the optimum produced little response; those above the optimum might cause temporary paralysis or death.

W. *Learning*

Clupeids in aquaria do not seem to become tame as do many other marine species. This may be a characteristic of shoaling species which are the prey of many other types of animals. There are apparently no reports of conditioned responses being set up in clupeids, though this would clearly be of great value in fish behaviour studies, particularly in relation to the sensitivity of clupeids to stimuli of different intensity and quality (e.g. Bull, 1952). Unfortunately the locomotory behaviour and general manoeuvrability of clupeids, and their lack of marked behaviour patterns except shoaling, would make the work more difficult. However some Russian workers (see Section VI, U) considered that attraction to artificial light was the result of a conditioned response set up by the association between light and feeding.

Clearly learning and memory could be of the greatest importance in capture and avoidance of fishing gear. Both Devold and Mohr (see Section VI, V) have stressed this point, but it is doubtful whether its importance can ever be assessed, except indirectly by fishing trials on a population of known size in an enclosed area, where fish that had been caught could be marked and released.

The role of learning and memory in migration has been discussed by Wynne-Edwards (see Section VI, R). Possibly the only way of assessing this would be in plotting the migration patterns of a stock being reduced to a very low level and consisting of recruit fish.

X. *Maturation of the gonads*

1. *Maturity scales*

The assessment of sexual maturity has been for some time part of the routine sampling of herring populations by fisheries workers. Gonads are classified into arbitrary maturity stages (I, II, III, etc.), by estimation of such criteria as the shape and colour of the gonad, its size in relation to that of the body cavity, size of eggs, etc. The classification of Hjort (1910) was (with slight modifications) recommended for general adoption by the International Council for the Exploration of the Sea (Ehrenbaum, 1930). Jensen (1950) discussed the relative merits of the international scale, and that proposed by Johansen (1919) which was used for a while by Danish fishery biologists. Naumov (1956) discussed another scale in relation to fecundity and ovarian development. More recently Heincke's (1898) scale (modified by Aasen, 1952) has been suggested as being preferable to the Hjort scale, in that it allows closer distinctions to be made between stages.

2. *Morphology*

The general gonad morphology and gross micro-anatomy was described in the herring by Cunningham (1896), Hjort (1910), Bullough (1940) and Williamson (1945).

3. *Histological changes during maturation*

Naumov (1956), Polder (1961) and Bowers and Holliday (1961) independently published detailed accounts of the herring gonad. Andrews (unpublished) gave a similar account for *Sardinops caerulea* and Andreu and dos Santos Pinto (1957) and dos Santos Pinto (1957) for *Sardina pilchardus*. The herring has a total spawning, i.e. all the developing eggs mature as one batch and are spawned together. In *Sardinops caerulea* and *Sardina pilchardus* the eggs are produced and released in successive crops throughout the season. The general development is, however, apparently the same for all clupeids.

(*a*) *The testis.* The germ cells develop in a system of connective tissue tubules (see Fig. 19), these tubules being lined with connective tissue cells which may function as Sertoli cells. Figure 20 summarizes the changes in the relative occurrence of the germ cells at each stage of development in the herring. The increase in size of the testes is brought about by the rapid increase in total number of germ cells in the gonad. Spermatozoa first appear at Stage II (Fig. 21). Just prior to spawning (Stage VI) the tubules are packed with sperm; after spawning the tubules shrink as the connective tissue contracts. Relict sperm are

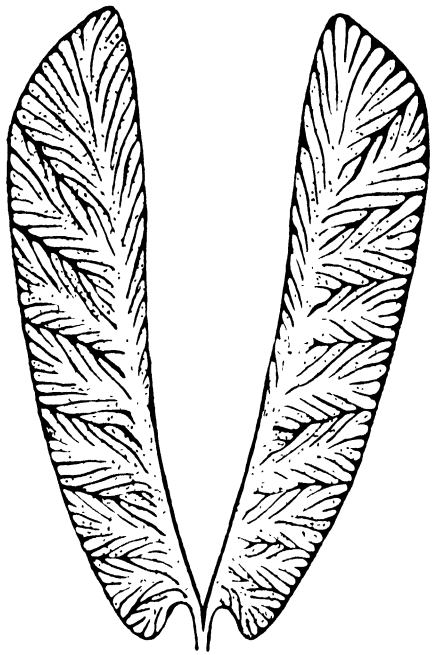


FIG. 19. Diagram of the herring testis (from Cunningham, 1896).

ingested by phagocytes. Recovery of the testis is preceded by consolidation of the connective tissue tubules and their relining with connective tissue cells.

None of the authors working on the herring found cells that could be undisputedly called Leydig cells (or lobule boundary cells) as described by Marshall and Lofts (1956) in *Sprattus sprattus*.

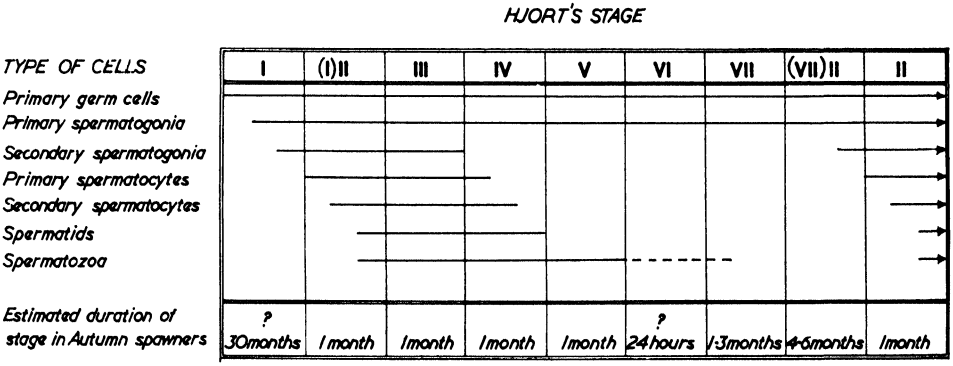


FIG. 20. Changes in the relative occurrence of the germ cells in herring. (Reproduced with permission from Bowers and Holliday, 1961.)

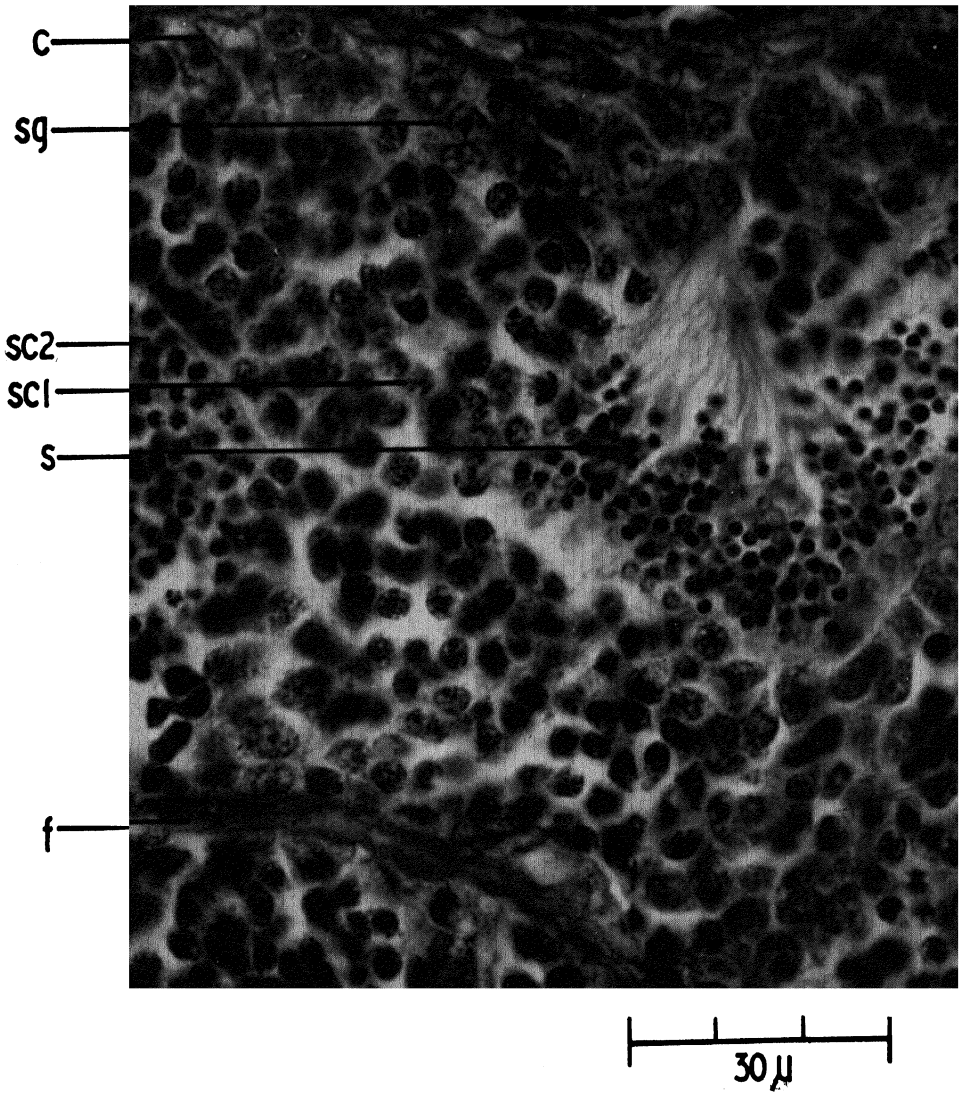


FIG. 21. Section of herring testis. (Reproduced with permission from Bowers and Holliday, 1961.)

c—connective tissue cells
sg—spermatogonia
sc 2—secondary spermatocyte
sc 1—primary spermatocyte
s—spermatozoa
f—fibrous connective tissue

(*b*) *The ovary.* The basic structure of the herring ovary is shown in Fig. 22. The oocytes develop within the septa, and those that mature in any one year become surrounded by a follicle composed of an outer connective tissue theca externa and an inner granulosa layer of

specialized connective tissue cells. A large proportion of the oocytes remain in a resting phase each year and have no fully formed follicle, each oocyte apparently spending one year as a resting cell and maturing the following year. The development of the chorion and the laying down of yolk in the egg is dependent on the presence of the granulosa cells of the follicle. The increase in size of the ovary in the herring is

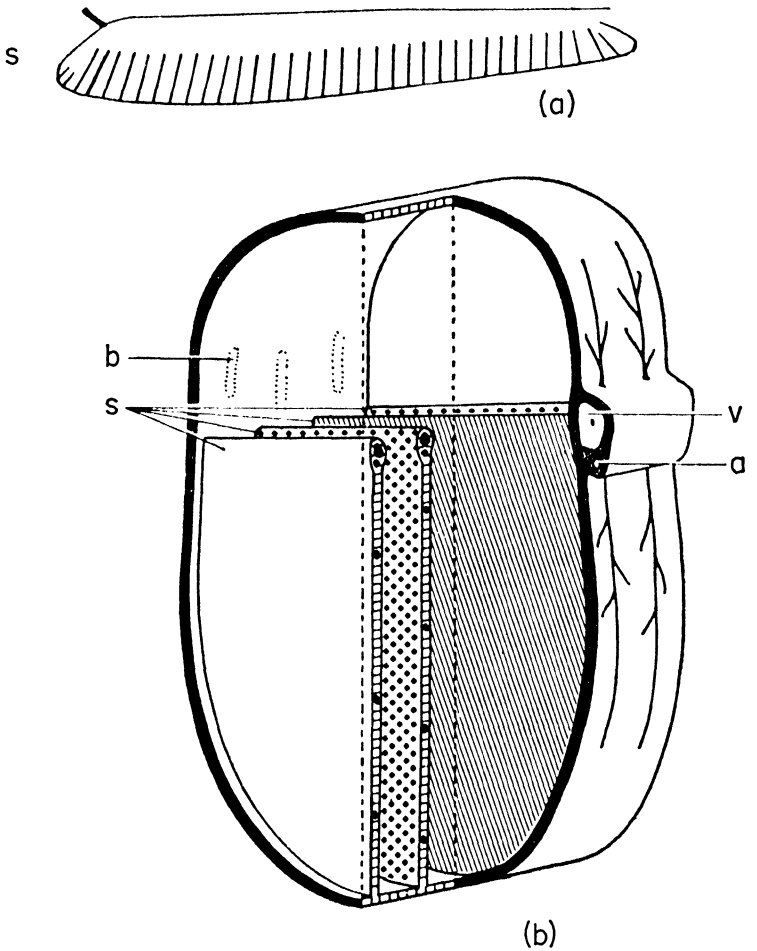


FIG. 22. (*a*) Longitudinal diagrammatic section of the herring ovary. (*b*) Simplified model of herring ovary. (Reproduced with permission from Polder, 1961.) a—artery, v—vein, s—septa, b—place of attachment of additional septa.

the result of the growth of the individual eggs, and not by any increase in the number maturing. Thus there is an increasing difference in size between the resting and the maturing oocytes (Fig. 23), but the fecundity is apparent at Stage II.

(*c*) *Ovulation.* All the eggs appear to ovulate together (see Section VI,

X, 8). The glandular lining of the oviduct produces a secretion which bathes the ovulated eggs. Following ovulation the granulosa cells are cast off the follicles and pass to the exterior.

(*d*) *Recovery.* As in the male there is a contraction and thickening of the connective tissue. A further crop of oocytes is formed to augment the resting oocytes of the previous year.

(*e*) *Degeneration of eggs.* Pre- and post-ovulatory degeneration of eggs occurs in all clupeids that have been studied, but nothing resembling a glandular " corpus luteum " is formed as a result of this degeneration. There is so far no evidence of any endocrine activity in the herring

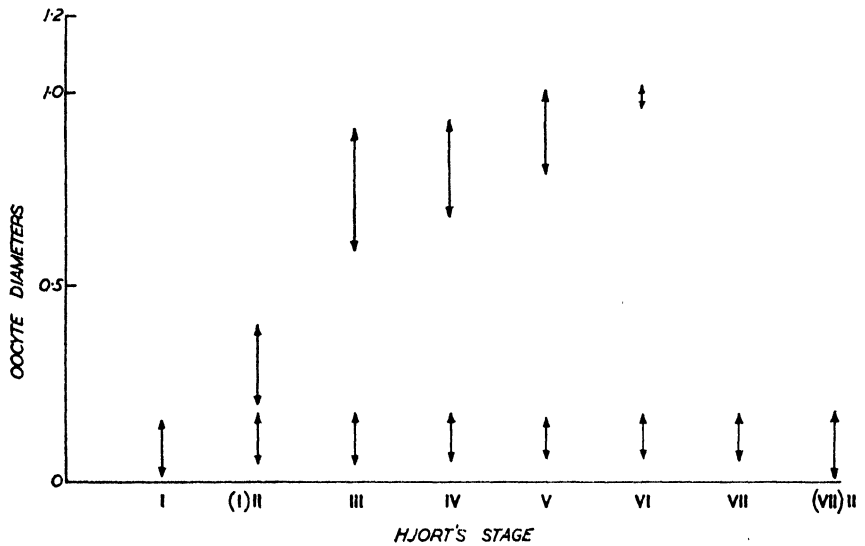


FIG. 23. Change in diameter of oocytes (mm) with maturation stage. (Reproduced with permission from Bowers and Holliday, 1961.)

ovary. Weisman *et al.* (1936) assayed extracts on immature mice but obtained no response.

4. *Fecundity*

This has been studied in considerable detail recently as a character with which to distinguish one stock of herring from another, e.g. Baxter (1959). Marty (1956) gave an excellent summary of fecundity in relation to race, age and length (see Fig. 24). Nagasaki (1958) studied fecundity in *Clupea pallasii* and MacGregor (1959) correlated fecundity with length, age and weight in *Sardinops caerulea.*

There is probably a maximum fecundity for a given fish that is genetically determined, and attained under perfectly suitable environmental conditions. It is likely that available food supply, age,

water temperature, etc., can all in some degree modify fecundity. Bibov (1960) found that the offspring of the Baltic herring did not have the same fecundity as their parents when they were reared in a different environment. Anokhina (1959, 1960, 1961) reviewed fecundity as an adaptive character that might vary as environmental factors varied. She studied the relationships between fecundity and size of ova, the

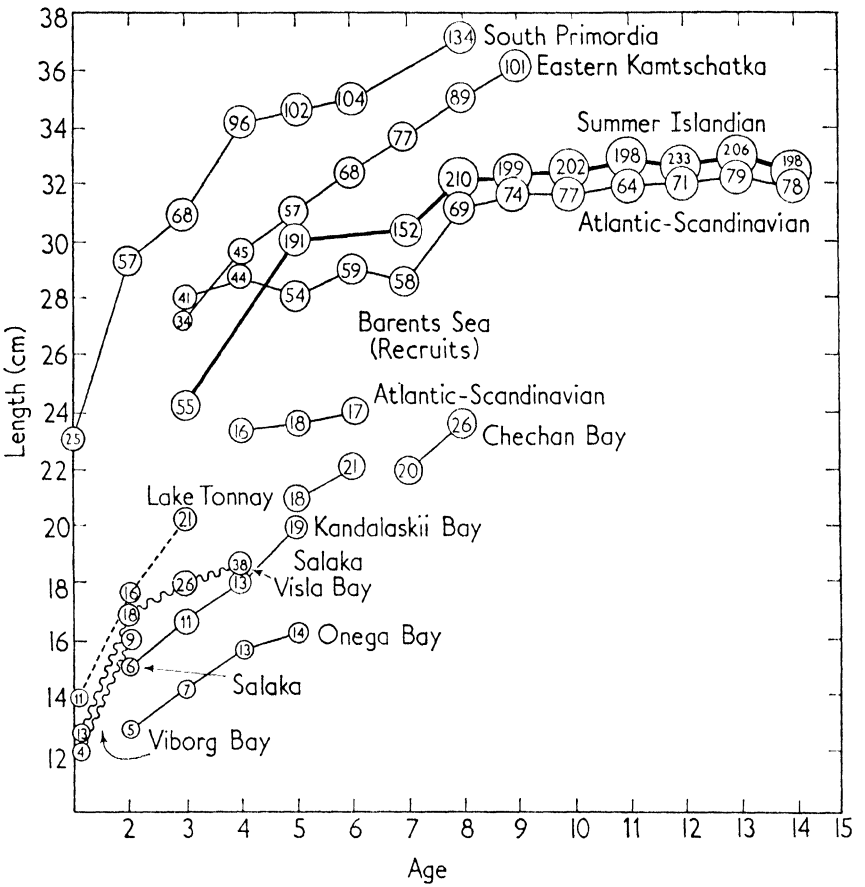


FIG. 24. Fecundity of sea herring by age and size. (Reproduced with permission from Marty, 1956.)

fatness of the fish and the feeding conditions. There were some individual variations, but in general there was a positive correlation between fecundity, fatness and feeding. In poor conditions there was a larger range in the size of the eggs produced; presumably it is more advantageous to produce a small number of larvae from large eggs than a large number of larvae from smaller eggs.

Naumov (1956) found that the *total* fecundity of *Caspialosa* species

in which the eggs were matured and spawned in batches, was higher than in the Murmansk herring which had a total spawning. Naumov attributed this to the need to spawn enough eggs at any one time to ensure a successful spawning. Andreu and dos Santos Pinto (1957) found in *Sardina pilchardus* that the general stock of oocytes from which the annual fecundity takes a proportion increased by the fourth power of the body length.

5. *The pituitary*

This was studied histologically by Buchmann (1940) and Holliday (1960a). Both described changes in vascularity and cellular activity which appeared at certain stages in the maturation cycle. Gonadotrophic activity is apparently localized in the meso-adenohypophysis. From about gonad Stage III onwards this region becomes increasingly vascular and the cells more abundant and larger in size. After spawning this area appears relatively inactive. Assay of the whole pituitary confirmed that the gonadotrophic activity was highest in Stages IV–VI. Holliday (1960a) studied the maturation of herring in the aquarium. The ovaries developed to about Stage III–IV only after a high level of feeding had been maintained; they then regressed. The testis developed normally but in miniature. Histological examination of the pituitaries showed that they were still in the immature, inactive state, suggesting that development beyond Stages III–IV depended on a higher level of pituitary activity.

6. *Timing of maturation in the sea*

Naumov (1956) attempted to correlate the state of maturity in the herring with temperature, feeding, salinity of the water and amount of solar radiation. Although each stage was found under fairly well defined and differing degrees of these environmental variables, it was difficult to ascribe to any of them the actual control of maturation.

Sahrhage (1954) found that southern North Sea herring were not ripe in early December 1952 when sea temperatures were 2 deg. C below normal, whereas in early December 1953, when temperatures were 2–3 deg. C above normal, more than 50% of the herring were ripe. Devold (1961) suggested that the Norwegian herring, whose spawning was gradually becoming later each year, might eventually change their spawning time and grounds completely; from being spring spawners off the Norwegian coast, they would spawn in early winter in the Skagerak.

Different " races " of herring mature and spawn at different times of the year, even though they sometimes share the same environment, for example, Iles (1962) suggested that autumn and winter spawning

herring were both to be found at Stage V in September on the East Anglian grounds, the winter spawners spending a further 2 to 3 months in this stage before spawning in the English Channel. One can only conclude that these fish are giving different responses to the same environmental stimuli, implying a genetical difference (Blaxter, 1958).

The control of the process of maturation may well be due to a number of essential factors interacting. An adequate food supply and a certain temperature history prior to spawning seem to be important, while the influence of day length is possible from studies on other fish, though uncertain in herring.

The age of first spawning may well depend on a " critical length " being reached before maturation commences, certain phases of maturation requiring a given level of fat before they proceed further. This critical length may be a product of the genotype and vary between different races (for instance, Atlanto-Scandian herring first spawn at a much greater length than many other races, and also have a greater maximum length). Superimposed on this, a certain temperature history might advance or retard maturation a little. Stimulation of the gonads by the pituitary, at least in the later stages, would be timed by these two factors as well as being possibly more basically timed by day length.

Two apparently contradictory observations are relevant here. One was the observation of herring workers at Lowestoft in the 1950's (e.g. Cushing and Burd, 1957) that the southern North Sea herring seemed to have changed its age at first spawning from predominantly 4 years old to predominantly 3 years old, the significant points being increased growth rate and a decrease in age of first spawners of *exactly one year*. The implication here is firstly of a genetical control of spawning time and of an inflexible reaction to the environment, such as might be expected from day length as a critical controlling factor, otherwise increased growth rate and maturation might have led to spawning weeks or months earlier rather than one year. Set against this must be the Norwegian observations by Devold (1961) that the spawning time of the Atlanto-Scandian herring is becoming *progressively later* each year off the Norwegian coast, the hypothesis of Parrish (personal communication) that southern North Sea herring may sometimes tend to spawn progressively earlier each year as they get older, and the general observation that recruit spawners spawn later than older fish.

7. *Duration of maturity stages*

Naumov (1956) recorded the number of months in the year when the Murmansk herring could be found at any particular maturity stage.

His figures do not allow the calculation of the mean duration of each stage for individual fish. Iles (personal communication) concluded that there was no simple relationship between the time of maturation and the time of spawning. The herring could remain for a variable length of time in a maturity stage, depending on the suitability of the environment for further maturation.

8. *Ovulation*

The timing of ovulation in the clupeids is closely linked to the time of spawning. Holliday (1960b) described ovulation in anaesthetized herring. A split appeared in the follicle and the egg was extruded through this (becoming distorted as it did so)—the process taking about 15 min. The ovulated eggs could be retained for at least 7 days before spawning, probably maintained at this time by the secretions of the oviduct. This fluid was apparently taken up by the eggs after ovulation. Holliday (1960b) showed that hypophysectomy prevented ovulation (and sperm release) in the herring. Injection of pituitary extracts restored these processes.

9. *Control of shedding*

The elasticity and muscles of the gonad wall, together with the muscles of the cloaca, exert a close control on the release of the gametes; shedding stops if the conditions become unfavourable.

10. *Hermaphroditism*

This has been described in *Sardina pilchardus* by dos Santos Pinto (1953, 1954) and reviewed in the herring by Holliday (1962). It was clear that in the herring the male portions of the gonad were maturing at a faster rate than the female portions—suggesting a higher degree of responsiveness to the pituitary hormones by the spermatogonia and spermatocytes than by the oocytes. However, spawning apparently did not take place until both portions of the gonad were fully mature. It is interesting to note that Iles (personal communication) has found that in the sea the male herring normally mature, stage for stage, faster than the females and the male herring could be in spawning condition before the female. Bowers and Holliday (1961) described the presence of ripe sperm in the testes of male herring as early as Stage II.

Y. *Spawning*

1. *Spawning grounds*

The general properties of herring spawning grounds have been described, for example, by Bolster and Bridger (1957) and by Parrish

et al. (1959). Hydrographic surveys of these grounds before and after spawning have led to many correlations between such factors as temperature, salinity and coastal influence and the onset of spawning.

2. *Factors controlling spawning*

Runnstrøm (1941b) suggested that Norwegian herring responded to a particular type of oceanic water. Hela and Laevastu (1962) reviewed the effect of temperature on spawning. They found that in the spring, herring would spawn in water from 0–12°C, and in the autumn from 8–15°C. Apparently different stocks responded to different temperature conditions. Although in general the herring spawns in relatively shallow, coastal water, Devold (personal communication) and Solovyev and Degtyarev (1957) reported herring spawning to 200–240 m. *Clupea pallasii* spawns on weeds in the littoral zone (Rounsefell, 1930), the eggs being often exposed at low tide. Ahlstrom (1954) described the spawning places, times and temperatures of *Sardinops caerulea.* Spawning was found from March to September but mainly in the spring in temperatures from about 13–20°C. Cushing (1960) gave values of 8–17°C for the spawning limits of *Sardina pilchardus.* Most authors (e.g. Delsman, 1930; Devold, personal communication; Schaeffer, 1937) agree that clupeids do not spawn in total darkness. Vision presumably plays a part in the selection of the spawning bed, and the exclusion of light stopped the spawning of herring in aquaria (Holliday, 1960b).

Dragesund (1960) kept a number of herring in a netted cove and found that spawning was delayed for 3 months and was then induced by a rise in temperature. Outram (1951) found that *Clupea pallasii* were stimulated to spawn by a sudden influx of fresh water into the tank. Holliday (1960b) could not find any direct stimulation of the spawning of herring by either temperature or salinity fluctuations. Herring selected a spawning bed on the basis of its general pattern—which was most effective when it presented the fine broken appearance of the gravel on which they normally spawned.

3. *Spawning behaviour*

Ewart (1884) and Holliday (1958) described the spawning behaviour of the herring. The female pressed close to the bottom, depositing a ribbon of eggs on to the substrate, while the male fish swimming above the females released ribbons of milt into the water. There was no pairing or courtship behaviour; it was an indiscriminate, mass spawning. At the end of the spawning the fish appeared exhausted and showed signs of distress. Rounsefell (1930) and Schaeffer (1937) described the

spawning of *Clupea pallasii*. The eggs were deposited in much the same way as in *Clupea harengus*, but the males deposited the sperm directly on top of the eggs. No pairing of the fish was observed and again it appeared a mass spawning. The anadromous shads (*Alosa* sp.) spawn in rivers, on fine gravel. There appears to be a form of nuptial behaviour in these freshwater spawners (Medcof, 1957).

Less is known of the spawning of the clupeids that lay pelagic eggs. Ahlstrom (1943) deduced that *Sardinops caerulea* spawned in mid-water between 2000 and 2400 hr. This was confirmed by Cushing (1960) in *Sardina pilchardus*.

4. *Homing*

Although the spawning grounds of herring, at least, remain much the same from year to year, the extent to which herring spawn year after year in the same place is not well known, and even less is known about whether individual herring return to the grounds on which they were spawned.

A study of meristic and other characters on different spawning grounds in the southern North Sea led Zijlstra (1961) to the view that homing might take place in herring, but only tagging of spawning fish, to date largely unsuccessful, would confirm this. However, Krefft (personal communication) who tagged spawning herring in the Elbe Estuary in April 1957, had a fish returned almost exactly 2 years later from the Skagerak. There are also cases of sudden outbursts of spawning in new places, e.g. of herring in the Texel area of the southern North Sea in 1961.

The ability of recruit spawners to return to the grounds where they themselves were spawned would demand a remarkable feat of larval or racial " memory ", greatly exceeding that of salmonids. At this stage one might assume that if no change in spawning time took place between parents and offspring, the recruits would return, by reason of the spatial and temporal dimension of their migration pattern, and possibly by following older spawners, roughly to the area where they were spawned. Once having achieved this, memory might play some part so that the recruits themselves the following year helped to lead younger fish to the spawning grounds. At present it is not clear how different spawning grounds might appear to fish due to their topography, type of bottom, fauna, chemical or hydrodynamic nature, so that one spawning ground could be distinguished from another. Without more evidence it would seem likely that any return would be to the approximate area of previous spawnings.

Instances have been recorded, however, of spawning times and

habits changing. Devold (1961) pointed to the gradual northward movements and latening of the spawning herring off Norway in the spring, and he suggested that this latening might eventually result in the spawning grounds changing from the Norwegian coast to the Skagerak, giving a " Swedish herring period ". Parrish (personal communication) has suggested that as the southern North Sea (Downs) herring become older they may sometimes spawn farther and farther to the north.

Z. *Racial characters, the genotype and the environment*

The nature of the racial complex in herring, *Clupea pallasii* and *Sardinops caerulea* has not been considered to any great extent by trained geneticists or systematists. Genetical work hardly exists, due to the difficulty of rearing clupeids. The so-called racial characters are used in the separation of stocks for the purpose of assessing migration and the effects of fishing. A great expenditure has been made on research into scale and otolith types, body proportions and meristic characters. Reviews of racial investigations are given by Ahlstrom (1957) in *Clupea pallasii* and by Marr (1957) in *Sardinops caerulea.*

Only the meristic characters and their plasticity will be discussed further, the influence of the environment on them being shown in Table XI.

TABLE XI

EFFECT OF THE ENVIRONMENT ON MERISTIC CHARACTERS

Author	Species	Place	Correlation
Runnstrøm (1933)	Herring	Norwegian coast	Negative correlation between mean vertebral counts (m.v.c.) of O-group fish in 1931 and March temperatures in different latitudes
Le Gall (1935)	Herring	N.E. Atlantic	Correlation between keeled scales and temperature, m.v.c. and salinity
Runnstrøm (1941a)	Herring	N.E. Atlantic	Negative correlation between m.v.c. of adults and temperature during spawning at different latitudes

TABLE XI—*continued*

Author	Species	Place	Correlation
Bückmann (1950)	Herring	S.E. North Sea	Negative correlation between m.v.c. and sea surface temperature in winter for sea-caught winter-spawned larvae
Hempel (1953)	Herring	German coast	Negative correlation between mean myotome count (m.m.c.) and temperature for reared larvae
Blaxter (1957)	Herring	Scottish coast; cross Scottish W.♂ x Scottish E. coast♀	Negative correlation between m.m.c. and temperature for reared larvae; no difference in spring and autumn spawned larvae reared at the same temperature; no influence of ♂ on "hybrid" larvae
Bückmann and Hempel (1957)	Herring	German coast	Negative correlation between m.v.c. of sea-caught herring larvae and surface temperature about spawning time
Day (1957)	Herring	E. Canadian coast	Negative correlation between m.v.c. of adults and temperature at spawning
Hempel and Blaxter (1961a)	Herring	German coast; cross Scottish coast♂ x German coast ♀; Scottish west coast	Negative correlation between m.m.c. and m.v.c. and temperature; positive correlation between m.m.c. and salinity. Influence of ♂ (Scottish) on m.m.c. of Scottish x German "hybrid". All work on reared larvae
Hubbs (1925)	*Clupea pallasii*	N. American coast	Increase in m.v.c. northwards
Rounsefell (1930)	*Clupea pallasii*	N. American coast	Increase in m.v.c. northwards
Rounsefell and Dahlgren (1932)	*Clupea pallasii*	Prince William Sound	Negative correlation between m.v.c. and air temperature during spawning season

TABLE XI—*continued*

Author	Species	Place	Correlation
Tester (1937)	*Clupea pallasii*	Jap Inlet British Columbia	Negative correlation between m.v.c. and air temperature at spawning season; gradation in vertebral count with latitude
Tester (1938a)	*Clupea pallasii*	Barkley Sound British Columbia	Negative correlation between m.v.c. and water temperature during spawning season
McHugh (1942)	*Clupea pallasii*	British Columbia	Negative correlation between m.v.c. of sea-caught larvae and temperature at spawning
McHugh (quoted by Marr, 1957)	*Sardinops caerulea*	American west coast	Latitudinal differences in m.v.c.

From this table it may be seen that both temperature and salinity may modify meristic characters. Gabriel (1944) has developed the idea that temperature affects the relationship between the processes controlling growth and differentiation, so that low temperatures, giving high meristic counts, would retard differentiation relative to growth. The use of meristic characters in racial investigations need not be invalidated if this plasticity is appreciated, and if the environment does not fluctuate too greatly. It seems likely that the modifications take place only during early development, especially before hatching; Hempel and Blaxter (1961a) found a sensitive period 6 to 7 days after fertilization at 10°C.

The importance of the genotype is difficult to judge. It seems likely that it provides a general basis for the number of meristic units, the actual number being controlled by environmental factors. Larvae of widely different origin reared under similar conditions retained the difference in mean vertebral count of the parents (Hempel and Blaxter, 1961a). Egg size might provide an inherited effect, herring races with larger eggs tending to have higher mean vertebral counts, but this does not always hold (e.g. within the North Sea). It is certainly true that larger individuals have higher vertebral counts (Tester, 1937; McHugh, 1942). Mean vertebral counts may also change with age and time; e.g. Bückmann and Hempel (1957) found them gradually increasing in larvae off the German coast sampled in successive months. These

authors suggested that larvae with low counts were selected out, while Barlow (1961) suggested that selection may take place for factors connected with high or low vertebral counts, such as sensitivity to temperature changes giving different metabolic rates or Q_{10}'s in different larvae.

Apart from meristic characters, which appear to have at least some genotypic basis, Blaxter (1958) has put forward the following as genotypically based characters—egg size, length at first spawning, spawning season, maximum length attained—to which might be added fecundity differences. These are discussed in different sections in this review, but little is known about their control, and so their value in racial and fisheries investigations remains questionable—do herring change their spawning season, can egg size and fecundity change out of all relationship to the normal increases which may occur with increasing age, why do Atlanto-Scandian herring spawn when older than other races? Some answers may be obtained from Russian experiments on transplanting herring from the Baltic to Aral Seas (Bibov, 1960), but the question remains whether they could occur in the normal environment. Graham (1962) suggested from studies on otolith characters that herring do not necessarily spawn at the same season as that in which they were hatched.

Interfertility of spring- and autumn-spawning herring (Scottish West and East Coasts) and of different spring-spawning races (Scottish West Coast and Baltic) has been shown by storage of sperm (Blaxter, 1957; Hempel and Blaxter, 1961a).

On the basis of a study of the characteristics of herring races, Blaxter (1958) concluded that spring- and autumn-spawning herring should in general be referred to different species. At the other extreme, Russian workers consider *Clupea pallasii* to be a subspecies of *harengus*. Differences in opinion as to the systematic status of different clupeids, which are also found in *Sardinops*, may seem academic, but they have more far-reaching connotations for the behaviourist and physiologist. For instance, what significance should be attached to the very different types of spawning grounds frequented by *pallasii* and *harengus*.

VII. Conclusions

From the point of view of distribution and numbers the clupeids are obviously a very successful group of fishes. One reason for this is their unspecialized nature so that they are able to deal with a wide variety of environmental conditions. For example, the primitive kidney with its high glomerular count enables them to exploit a wide range of

salinities, and the tolerant eggs and larvae can survive in marine, littoral, estuarine and in some cases freshwater conditions. They are, however, well adapted to a pelagic, shoaling mode of life—mechanically, hydrodynamically, as well as in the biochemical composition and potential activity level of their tissues. Although they depend on a fluctuating food supply, the ability to store fat enables them to survive at all seasons. Presumably this adaptability has led to the formation of the complex racial system.

Clupeids are found in large numbers despite the level of predation to which they are subjected. Presumably the advantages of shoaling far outweigh the disadvantages. Relatively low fecundity does not seem to have been a handicap and this is true where the egg is demersal, as well as where it is pelagic. Nor does a small egg, with little yolk and a small larva dependent on external food soon after hatching, appear to be a disadvantage. The size of a spawning stock seems to have little effect on the subsequent year class strength, so that egg potential does not appear to be in any way limiting. What determines the year class strength, in herring at least, remains a mystery, and yet the fluctuations can be large.

Unfortunately, many other aspects of the herring basic biology remain a mystery—in particular its means of migration, the control of its reproductive processes and the interrelationship between different races and the extent to which flow may take place between them. Other problems which have scarcely been touched on are the role of olfactory and auditory stimuli and the function of the complex lateral line in the life of clupeids, and the advantage of the soft body and deciduous scales to their survival.

One aspect of specialization is the apparent dominance of vision among the other senses. It seems to be the sense used before all others in feeding, shoaling, spawning and escape.

It is interesting to speculate upon the evolutionary position of the clupeids. Even the accepted marine species, such as the herring, have some associations with a freshwater way of life. This is shown in serological, biochemical and anatomical correspondences with freshwater fishes, as well as in certain aspects of behaviour, such as demersal spawning. It seems most likely that the teleosts originated in fresh water and that the clupeids have retained stronger links with their origins than have other teleosts; perhaps this is due to a much more recent colonization of the sea.

It has become clearer in the past few years that fisheries problems cannot be solved without a better knowledge of behaviour and physiology. This has been emphasized by Hardy (1949) and Bull (1961).

and that this is now generally appreciated is shown by the increase in such work in fisheries laboratories. Much of the work described in this review has been done with equipment only available at such laboratories, i.e. research boats and marine aquaria, and it remains a cause for regret that marine fish of commercial importance are still to a large extent neglected by many universities due to lack of facilities.

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