CHAPTER XVIII

ENVIRONMENTAL FACTORS AFFECTING OYSTER POPULATIONS

The various species of the family Ostreidae inhabit the coastal waters within the broad belt of the sea, limited by the latitudes 64° N. and 44° S. Some large aggregations cover many square miles of bottom of littoral and intertidal zones; they also thrive above the bottom attached to rocks and underwater structures, branches and trunks of fallen trees, and miscellaneous objects. These aggregations of live oysters and empty shells are called oyster bottoms, oyster beds, oyster banks, or oyster reefs. The expressions are not well defined either biologically or in the legal sense and are used interchangeably. Only those species of oysters which form large and dense populations are important to man as a source of food. Those living singly and widely dispersed are of no commercial value.

Descriptions of oyster bottoms found in the world literature combined with personal observations over the course of years in the United States, France, Italy, the West Indies, Cuba, Venezuela, Panama, Hawaii, and some of the South Pacific islands have convinced me that, regardless of the species of oysters present, certain major factors are common to all oyster bottoms.

It is a matter of historical interest that more than 80 years ago Möbius (1883) established the concept of a biocenosis or a social community using an oyster bank as an example. According to his definition every oyster bed is to a certain degree—

> . . . a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. The total number of mature individuals of all the species living together in any region is the sum of the survivors of all the germs which have been produced at all past breeding or brood periods; and this sum of matured germs represents a certain quantum of life which enters into a certain number of individuals, and which, as does all life, gains permanence by means of transmission.

Möbius further commented that a change in one factor of a biocenosis affects other factors of the environment and eventually changes the community character. Relative abundance of various species constituting a bottom community is affected by changes in estuarine environment and by man's activities which alter the environment. Patterns of currents, salinity gradients, and turbidity of water may be changed by dredging operations, construction of inshore installations, and other harbor and waterway improvements. Commercial dredging removes substantial portions of natural oyster grounds; planting of seed oysters for growing increases artificially the population densities. Inadvertent introduction of foreign species, competitors, and predators disturbs the established biological balance. Finally, excessive discharge of domestic sewage and trade wastes causes irreparable damage to productive oyster bottoms.

The productivity of a sea bottom may be measured by determining the sum of weights of all animals and plants in a unit of area. The value, called community biomass, is of considerable theoretical interest to the marine ecologist engaged in the study of oceanic productivity. It has, however, no practical application in determinations of the productive capabilities of a community dominated by a single species such as oyster, clam, or scallop. The species productivity of any bottom may be materially reduced by competitors, predators, and other conditions that may suppress the reproduction and growth of commercially utilizable organisms while not affecting or even sometimes encouraging the growth of noncommercial forms.

Descriptions of oyster bottoms usually provide information regarding their location, type of bottom, depth and salinity of water, the principal species associated with oysters, and the abundance or absence of predators. This type of description is found in the papers of Dean (1892) on South Carolina grounds; Moore on the condition and extent of oyster grounds in Texas (1907), Louisiana (1899), Mississippi Sound (1913), James River, Virginia (1910), Delaware Bay (1911); Pearse and Wharton (1938) on oysters of Apalachicola Bay; Frey (1946) on oyster bars in the Potomac River; Hagmeier and Kändler (1927) on oyster banks in North Freisland shoals, Germany; Joubin on the coast of France (1906, 1908), and many others.

Because of the great diversity in the kind and number of species forming an oyster community only a few generalizations can be drawn from descriptive data: 1) in common with other bottom communities, oyster grounds of the warm southern waters support a greater variety of species than do the colder waters of the northern latitudes, and 2) the variety of plant and animal species is less in waters of low salinity than in adjacent areas of higher salt concentrations.

The inferences are in accord with observations made by European ecologists and summarized by Hedgpeth (1953). In the Elbe estuary the weight of all invertebrates per square meter of bottom decreases from 6,068 g. in the area of full oceanic salinity to only 37 g. in brackish water. A similar decrease in the weight of community biomass is found along the northern coast of Germany, although the difference is much smaller ranging from 304 g. per square meter of sea bottom to 16 g. in the inshore areas. The decrease in the biomass cannot be attributed to a single factor of the environment since other conditions such as rate of water movements, sedimentation, and food content are associated with the salinity changes.

There are many well-documented cases of destruction of productive oyster bottoms by human activities. Möbius (1883) cites formerly rich oyster beds of Cancale, Rochefort, Marennes, and Oléron on the West Coast of Europe in which the oyster populations were replaced by cockles and mussels. The newcomers were present in small numbers while the oysters flourished but greatly increased in abundance when the removal of oysters left more space for them to settle.

Many well-documented examples may be cited of the destruction of oyster bottoms by sand and mud stirred up by dredging operations in nearby areas. One incidence of this nature occurred in 1935 to 1938 near the Buzzards Bay entrance to the Cape Cod canal, Mass., where valuable oyster grounds were buried under 8 to 12 inches of material that was disturbed by dredging and then settled on the oyster grounds. Three to four years later the area was repopulated by quahogs and continues to remain highly productive, although the species composition has been completely changed.

Discounting minor local variations, the basic requirements of the oyster are identical regardless of the location of the oyster bottoms. The suitability of a bottom area for the development of a productive oyster community can, therefore, be evaluated if the effects of different environmental factors are estimated.

Principal factors favorable for the propagation, growth, and general welfare of an oyster community are character of bottom, water movements, salinity of water, temperature, and food. The unfavorable or destructive factors that tend to inhibit the growth and productivity of a community are sedimentation, pollution, competition, disease, and predation. The interaction of these five positive and five negative factors acting simultaneously on a community determines its utilizable productivity.

POSITIVE FACTORS OF ENVIRONMENT

CHARACTER OF BOTTOM

Oysters may grow equally well on a hard, rocky bottom or on semihard mud firm enough to support their weight. Shifting sand and soft mud are the only types of bottoms which are totally unsuitable for oyster communities. With the exception of these extreme conditions oysters adapt themselves to a great variety of bottoms. They thrive well on shore rocks and underwater structures which are left exposed at low tide. The controlling factor in this situation is the climate, since no oyster can survive several hours exposure to below freezing temperature, and, therefore, none are found growing near the surface in the latitudes where in winter they may be killed at low tide, or frozen in the ice and carried away by tidal currents. The degree of softness and instability of the bottom can be quantitatively measured by penetrometers, and by determining the amount of bottom material transported by currents of different velocities. The depth of sinking into a mud layer of a probe of known dimensions under constant weight can be used as a measure of the relative softness of sediment. The determination must be made in situ because the removal of a sample and handling in the laboratory changes the consistency of mud. A penetrometer to evaluate certain physical properties of marine sediments in situ has been designed by Miller (1961). The instrument is a conical probe which is driven at low, constant speed into the bottom; resistance to penetration as the probe sinks into the bottom is recorded graphically. An instrument answering these specifications and constructed at the University of Rhode Island has been used in research at the Narragansett Marine Laboratory at Kingston, R.I., and has proved reliable in providing information about compactness, degree of plasticity, allowable bearing loads, and other properties of sediments. No reliable method has yet been developed for measuring the resistance of sediment to water current in the sea.

A soft muddy bottom may be artificially improved by planting oyster or clam shells to attain the desired firmness. Other materials, such as gravel and slag from blast iron furnaces, have been tried experimentally but are less satisfactory, primarily because of the greater weight and higher cost. At present the reinforcement of oyster bottoms by shells remains the principal practical method used on a large scale for the improvement of oyster bottoms or for the establishment of new ones.

Soft muddy bottoms may be gradually converted by the oysters themselves into oyster banks or reefs because of an innate ability of larvae to choose a substratum upon which to settle. This ability is probably common to most species of bottom invertebrates having free-swimming larvae (Verwey, 1949). The process begins with the attachment of several larvae to a single shell or other hard object lying on the surface of the mud. Other larvae attach to those that have already settled, and soon a cluster of oysters is formed on the surface of the mud (fig. 365).

Dead oyster shells dropping from clusters provide additional surfaces, and the reef begins to grow horizontally and vertically. The process is typical for the tidal flats of South Carolina and Georgia where successive phases can be easily observed. Oysters grown on mud have long, slender shells.

The suitability of bottom to an oyster community may be expressed by an arbitrary scale from 0 to 10, according to the relative softness and stability. Bottom conditions fully unsuitable for the formation of any oyster community may be designated as zero. The zero value of any positive factor denotes conditions under which the community cannot exist, regardless of the values of all other factors of the environment. The zero value of bottom factor refers either to extremely soft mud not capable of supporting the weight of an empty shell or to shifting sand; both conditions are unsuitable for oysters. Marginal conditions are indicated by 1, and optimum conditions by 10. The highest value of bottom factor may be assigned to firm and stable bottoms such as rocks and hard or sticky mud. The value of 1 is assigned to the soft muddy bottoms of the South Atlantic States and Texas.

FIGURE 365.—Initial stage in the formation of an oyster bank on very soft mud of a tidal flat. Photographed at low tide near Brunswick, Ga.

WATER MOVEMENTS

Free exchange of water is essential for the growth, fattening, and reproduction of oysters. An ideal condition is represented by a steady, nonturbulent flow of water over an oyster bed, strong enough to carry away the liquid and gaseous metabolites and feces and to provide oxygen and food. Furthermore, an oyster bed can expand only if the larvae are carried by the currents and at the time of setting are brought in contact with clean, hard surfaces. Estuaries seem particularly suitable for the expansion of oyster communities and for the annual rehabilitation of oyster populations reduced by harvesting because some larvae, carried back and forth by the oscillating movements of tidal waters, eventually settle beyond the place of their origin.

In large embayments, such as Long Island Sound, the difference between the surface and bottom salinities is small, about 1°/₀₀ or 2°/₀₀. In tidal rivers and true estuaries the differences between the salinities of the lower strata and those at the surface are considerable. Salinity stratification, as will be shown later, complicates the pattern of circulation.

The great variety of conditions found in the bodies of water within the tidal zone makes it difficult to define the term "estuary" in a few precise words. A Latin dictionary (Andrews, 1907) defines the word "Aestuarium" or "Aestus" as a part of the seacoast overflowed at flood tide but at ebb tide left covered with mud and slime. Some authors extend the concept of an estuary to include such large bodies of water as the Mediterranean Sea and the Gulf of Mexico, while others restrict the use of the term to relatively small coastal indentures in which the hydrographic regime is influenced by the river discharge at the head and the intrusion of sea water at the mouth. Cameron and Pritchard (1963) define an estuary as "a semienclosed coastal body of water having free connection with the open sea and within which the sea water is measurably diluted with fresh water deriving from land drainage." The essential features of a true estuary are the inflow of river water at the head and the periodical intrusion of sea water at its mouth. Stommel (1951) classifies estuaries by the predominant causes of movement and mixing of water, which may be due either to tide, wind, or river flow. Rochford (1951) points out the significant differences between brackish water and estuarine environment. According to his ideas, brackish water refers to a dynamically stable environment of lakes, lagoons, etc., in which sea water, diluted by fresh water, is not necessarily influenced by tidal movements. On the other hand, the estuarine environment, influenced by tidal rise and fall, is dynamically unstable.

The persisting factors of a typical estuarine environment are seasonal salinity variations and circulation exchange between the river and sea water. The intruding salt water forms a wedge or prism with its base at the mouth and the tip at the upper part of the estuary. The position of the wedge along the bottom and its dimensions depend to a great extent on the flow of the river water.

Circulation and mixing of water is a highly complex problem adequately discussed in the papers of Rochford (1951), Ketchum (1951a, 1951b), Pritchard (1951, 1952a, 1952b), and in the textbook, The Sea, vol. II, edited by Hill (1963).

It is important for a biologist to understand that the type of circulation that prevails in a specific estuary depends on physical structure, i.e., size, depth, bottom configuration, etc., river flow, and vertical salinity gradients along the entire length from head to mouth. Circulation pattern and mixing have important biological implications in the study of the distribution and transport of sediments, pollutants, and plankton, including free-swimming larvae of sedentary invertebrates.

The volume of fresh water entering at the head of an estuary occupies the upper layer and exceeds the volume of the up-estuary flow in the lower and more saline layer by an amount sufficient to move the fresh water toward the sea (Pritchard, 1951). As one moves seaward, the volume of saline water contributed by the ocean increases while the river water, entered at the head of the estuary is being removed. The process of removal of river water, called flushing, continues throughout the estuary from its mouth to the so-called "inner end" which is defined by Ketchum (1951b) as "the section (of an estuary) above which the volume required to raise the level of the water from low to high water mark is equal to the volume contributed by the river during a tidal cycle." Consequently, there will be no net exchange of water through this section during a flood tide and the water above the section should be completely fresh.

The salinity at any location below the inner end varies with tide but returns to substantially the same level on successive tidal stages. Assuming that a net seaward transport of fresh water during any tidal cycle is equal to the volume introduced by the river in the same period of time, and that there is no net exchange of salt water through the cross section during the same tidal cycle, Ketchum (1951b, 1954) advanced a simplified theory which permits an easy calculation of the proportion of water removed by the ebb tide. This theory is based on the assumption that in each of the volume segments, limited by the average excursion of water on the flood tide, the water is completely mixed at high tide. Accepting this assumption, which is obviously a simplification of the actual conditions, the rate of exchange in a given segment (r_n) has the value $r_n=\frac{Pn}{Pn+Vn}$ in which Pn is the intertidal volume and Vn the low tide volume of the segment n. The average length of time required for the river water with a particle suspended in it to move through a segment of an estuary is called flushing time, which is defined as a ratio obtained by dividing the volume of river water, calculated from the salinity data, by river flow. The ratio is expressed in number of tides. In Raritan Bay, N.J., a survey made by the Woods Hole Oceanographic Institution indicates the flushing time for the entire estuary was 60 tides.

If a stable pollutant is discharged at a constant rate at the head of an estuary and is uniformly mixed as it is transported downstream, its proportion in the water can be calculated by using the formula of Hotelling which was applied in determining the concentration of pollutant over Olympia oyster beds (Hopkins, Galtsoff, and McMillin, 1931). According to this formula the proportion p of a contaminant in a basin is:

$$p=\frac{a}{a+b}\left[\frac{1-(1-a+b)^t}{V}\right]$$

where a is the rate of discharge of contaminant in acre-feet per day, b the rate of influx of water into the basin in acre-feet per day, V the total volume of the basin in acre feet, and t time in days since the pollution started.

In this formula it is assumed that the influx and efflux occur discontinuously once a day. By assuming that the influx of contaminated water and the efflux are continuous, Tuckerman (see: Galtsoff, Chipman, Engle, and Calderwood, 1947, p. 100) arrives at the following formula:

$$p=p_\infty[1-(1-K)^t]$$

where p_∞ is the limit which the proportion of contaminated water approaches after a long time and $K=\frac{a+b}{V}$. Computations made by using the two formulas indicate the same value for the $p_\infty=\frac{a}{a+b}$, but differ in the rate at which this limit is approached. For the small values of $K=\frac{a+b}{V}$ which are usually encountered in estuaries, the two rates are practically identical and the simpler Hotteling formula may be applicable.

In many estuaries the water is stratified. With relation to stratification and circulation patterns Pritchard (1955) distinguishes four types of estuaries—highly stratified (type A), moderately stratified (type B), and virtually homogeneous (types C or D). The reader interested in the dynamics and flushing in different types of estuaries should consult the original contributions of Pritchard (1952a, 1952b, 1955) and Pritchard and Kent (1953) in which the complex hydrodynamical problem is analyzed. It is sufficient for a student of oyster ecology to realize that vertical and horizontal distributions of oyster larvae will be different in each of the four principal types of estuaries.

A free-swimming organism such as bivalve larva cannot be considered in the same manner as a material dissolved in water or as an inanimate body passively transported by water movements. Larvae of bivalves, barnacles, and other invertebrates may have a tendency to swarm and, therefore, their distribution may not be uniform even in a homogeneous environment. Oyster larvae react to changes in the environment by periodically closing their valves and dropping to the bottom or by swimming actively upward or in a horizontal plane. Consequently, they may be carried upstream or downstream according to their position in the water column. Field observations in the estuaries of New Jersey and Chesapeake Bay (Carriker, 1951; Manning and Whaley, 1955; Nelson, 1952) in which the salinity of water increases from surface to bottom indicate that vertical distribution of larvae is not uniform. The late umbo larvae of *C. virginica* have a tendency to remain within the lower and more saline strata, and are probably stimulated to swim by the change in salinity at flood tide. A brood of larvae swimming within a given salinity layer will be passively moved in the direction of the current. Nelson observed that in Barnegat Bay, N.J., the brood of larvae of setting size was carried about 3 miles up the bay in a single evening spring tide. In Yaquina River, a small tidal stream along the ocean shore of Oregon, swimming larvae were transferred by tidal currents and set several miles above the natural beds (Fasten, 1931; Dimick, Egland, and Long, 1941). There are many other places where setting grounds are far above the spawning grounds. Since the seaward discharge of water in an estuary usually exceeds the landward movement, it was difficult to visualize a mechanism by which the larvae can be transported up an estuary and left there. The existence of such a mechanism became apparent, however, from the hydrographic studies by Pritchard (1951). He found that estuaries may be considered as being composed of two distinct layers: an upper layer in which the net movement is toward the mouth (positive movement), and the lower layer in which the net movement is toward the head of the estuary (negative movement). There is a boundary between the two layers which may be called "the level of no net motion" (fig. 366). Since the net movement seaward does not result in a net displacement of the lines of constant salinity in the upper layer, there must be a progressive transfer of the deeper, higher salinity water of the lower layer upward, across the boundary level, to be included in the seaward transfer. The role of the strongest tidal currents is primarily that of providing energy for the mixing processes. Computations made by Pritchard show that superimposed on tidal oscillation there is a residual or nontidal seaward drift on the surface and a net landward drift along the bottom. He applied his theory to a study of the seed oyster area of the James River, Va., and found that below a depth of about 10 feet there is a net (or residual) upstream movement of water at an average speed of slightly more than one-tenth of a knot. This is the type of estuary

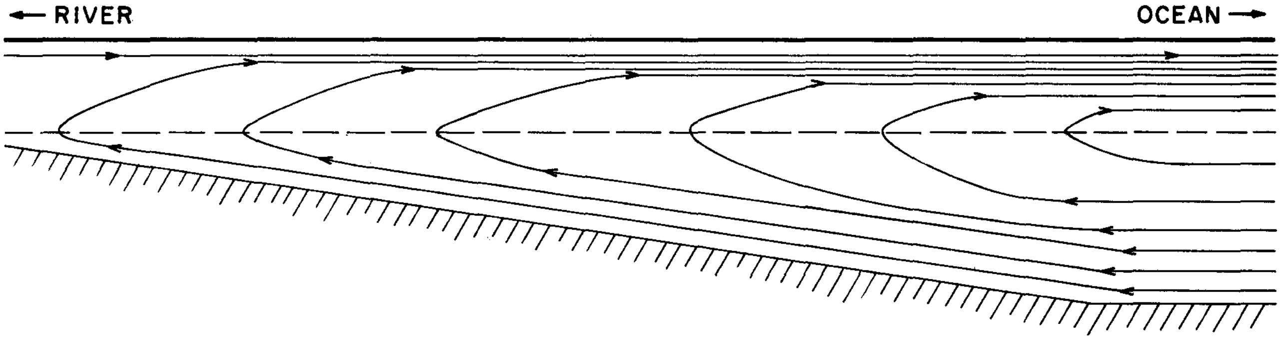

FIGURE 366.—Estuarine structure and net (i.e., nontidal or residual motion of water). Dotted line marks the boundary between the upper and lower net movement; the boundary is the level of "no net motion." From Pritchard, 1951, fig. 3.

in which larvae move from the spawning grounds at the mouth of the river up into the seed oyster bed area. Bousfield (1955) applied Pritchard's ideas to an analysis of distribution of barnacle larvae in the Miramichi estuary, New Brunswick, Canada. The retention of larval populations in this estuary was found to be due to a combination of two factors: changes in the average vertical distribution of successive larval stages, and the strength and direction of transport by residual drift at different depths. This theory of larval retention and the mechanism of transport is not applicable to bodies of water in which there is no salinity stratification or where the residual upriver drift is insignificant.

Least favorable in the life of an oyster community are occasional turbulent currents of high velocities which may dislodge and carry away young and even adult oysters not attached to the bottom. Oysters attached to rocks and other structures are not destroyed by strong currents, but their valves are injured by small pebbles and sand acting as an abrasive material. Live oysters with shells damaged by abrasion can be found in the Sheepscot and other tidal rivers along the coast of Maine.

Continuous renewal of sea water running over a bottom in a nonturbulent flow is the most desirable condition for a flourishing oyster community. On the basis of experimental studies discussed in chapter IX, p. 195, it may be assumed that under optimal conditions of temperature and salinity an average adult *C. virginica* transports water at the rate of 15 l. per hour. With 250 large oysters to a bushel and 1,000 bushels per acre, an oyster bed of that size would require 3.75 million liters of water per hour. My observations show that under the best of conditions oysters can take in water only from a distance not exceeding 2 inches from the shell. It is, therefore, necessary to know the rate of water exchange within the narrow layer adjacent to the oyster bottom. The situation may be different in the case of vertical mixing of water due to turbulent flow.

The amount of water available to an oyster population can be calculated if the number of individuals on the bottom and the rate of water movements are known. In the case of a turbulent flow, vertical mixing of water depends on the degree of turbulency. If the mixing extends to the height of 1 foot above the mud line, the total volume of water in which the oyster population lives in our example is 1 acre-foot or 325,851 gallons (1.25 million l.). It follows that the current velocity must be strong enough to renew the volume of the layer above three times (3.75÷1.25) every hour or 72 times in 24 hours. In cases of greater population density the current requirements are proportionally higher. Due allowance should be made, of course, for the presence of other water-filtering animals which compete with the oyster for food. It is clear, therefore, that great concentrations of water-filtering organisms are possible only where there is sufficient renewal of water. The oyster reef in the Altamaha Sound, Ga., (fig. 367) is a good example of this condition. Such concentrations of live oysters crowded over a limited space cannot exist in sluggish water and are found only in rapid tidal streams.

The water movement factor can be evaluated by determining whether the rate of renewal of water over the bottom is sufficient for the needs of the population and whether the pattern of circulation is such that a certain percentage of

FIGURE 367.—Oyster reef in Altamaha Sound, Ga., at low tide, March 1925. The highest point was about 6 feet above the bottom; water at the foot of the reef was 8 inches deep. The reef consists of live oysters growing on the side and upper surfaces and attached to empty shells.

oyster larvae will be retained in the estuary by the end of the larval period. It is obvious that the requirements of water movements for the growing of oysters are different from those necessary for the settlement of larvae.

SALINITY

The general rule that the composition of sea water is constant and varies only in the degree of dilution by fresh water is applicable to the estuaries and other basins which have direct communication with the sea. Only in exceptional cases is the circulation in an estuary so impeded that stagnation and oxygen deficiency develop and render the area unsuitable for oyster growth and reproduction.

Oysters like many other euryhaline organisms are able to live in sea water of very wide range of salinity. According to the so-called Venice system of classification of saline waters adopted at the symposium organized by the International Association of Limnology and the International Union of Biological Sciences at Venice, Italy, in April 1958, the range of salinity favorable for *C. virginica* falls within two zones, the polyhaline, from 30°/oo to 18°/oo, and the mesohaline, from 18°/oo to 5°/oo (Symposium for the Classification of Brackish Waters, 1958). Populations of oysters found beyond the upper or lower limits of the range exist under marginal conditions. Their growth and gonad formation are inhibited, and they are often decimated either by floods, in the lower zone of the range, or by predators which usually remain in more saline waters. The noncommercial oyster of the Atlantic and Gulf coasts, *O. equestris*, prefers more saline waters and has been found on buoys as far as 20 miles offshore where surface salinities ranged from 33°/oo to 36°/oo (Galtsoff and Merrill, 1962). In the subtidal regions of the coastal waters this species is found in salinities of 20°/oo to 25°/oo.

An unstable salinity regime is an important ecological factor in the tidal rivers and streams inhabited by *C. virginica;* diurnal, seasonal, and annual fluctuations are the normal features of such an environment. Their effect on *C. virginica* depends on the range of fluctuations and the suddenness of the changes. For instance, oysters that were replanted in September from a low salinity area of the upper Chesapeake Bay (10‰ to 12‰) to the high salinity water of Sinepuxent Bay (32‰ to 33‰) all perished within 3 to 4 weeks after planting. Examination of the new grounds disclosed that the sudden change in salinity during hot weather was the primary cause of mortality. On the other hand, a similar transfer made by the same grower succeeded in October and November when the air and water temperatures were much lower.

The mean values of diurnal, seasonal, and annual salinities are of little significance for evaluating their effect on an oyster population. The oyster can isolate itself from the outside environment by closing its valves tightly and survive adverse conditions, provided they do not last indefinitely (see: ch. VIII). Since changes in salinity are commonly associated with temperature changes, an attempt was made by Hedgpeth (1953) to combine the two factors to express what he calls "hydrographic climate." He plotted ranges of means and extremes or monthly means of salinity against temperature and obtained polygons which provide a graphic representation of the conditions existing in a given area for the indicated period. The method appears to be useful and may be profitably applied to oyster research.

Oysters inhabiting the parts of estuaries in which salinity is below 10 ‰ are seriously affected by fresh water and could be destroyed by floods lasting for several weeks. Mobile Bay, Ala., investigated in 1929, may be cited as an example of this condition. Oysters in Mobile Bay grew on reefs which extended from the upper to the lower parts of the bay. The river discharge into the bay normally resulted in a salinity gradient from 5‰ to 30‰. However, in the 36 years from 1893 to 1929 the two tributaries, the Tombigbee and Selma Rivers, rose 27 times to flood stage with the flood conditions lasting from 4 to 31 days. The height of the rivers at flood stage in February and April 1929 was 65.4 and 56.2 feet, respectively, and lasted for 32 days (Galtsoff, 1930) with the result that fresh water prevailed over almost the entire bay and the mortality at different parts of the bay varied from 100 percent in the upper parts to 85 and 54 percent at the passes to Mississippi Sound.

Oysters in Mississippi Sound often suffer from long-continued low salinities. Mortality of oysters in the Sound occurs when the local precipitation in the Sound area, in the Pearl River basin, or at some more distant point in the Mississippi River basin occurs more or less simultaneously and lowers the salinity to a harmful level (Butler, 1949b, 1952).

Freshets sometimes kill oysters in the James River, Va. During a 6-week period from May 1 to June 15, 1958, many of the native oysters died, and as many as 90 percent perished on some grounds where salinity did not become suitable until July 1 (Andrews, Haven, and Quayle, 1959). In a test made at the Virginia Fisheries Laboratory at Gloucester Point, oysters held in trays in low salinity areas were "conditioned" to a low physiological state (absence of heart beat and ciliary motion and loss of mantle sensitivity). The investigation lead to the conclusion that oysters conditioned slowly at low temperatures and low salinities can endure a prolonged situation of unsuitable environment. Andrews, Haven, and Quayle infer that "the mechanism of conditioning appears to be a type of narcotization," an interesting idea which, however, needs verification.

The first symptoms displayed by an oyster affected by water of lowered salinity are partial or complete contraction of the adductor muscle and slowing or cessation of water current through the gills. With the drop counting technique described in chapter IX it can be shown that the ciliary activity of the gill epithelium immediately decreases when it comes in contact with water of lowered salinity. The effect may be brief or prolonged, depending on the degree of change from the salinity level to which the oyster had been adapted. When the salinity change is about 10‰ and continues for several hours, both the rate of water transport and the time the oyster remains open are decreased, and under extreme conditions the feeding and respiration cease. Experimental studies on the adaptation of oysters to salinity changes were first made by Hopkins (1936) on *C. gigas* of the Pacific coast. He recorded the changes in the opening and closing of the valves, and registered the deflection of a small plate placed in front of the cloacal current. As indicated in chapter IX this method is not reliable for a quantitative determination of the volume of water transported through the gills but is adequate for determining the relative strength of the cloacal current. The results show that the adaptation to new conditions depends upon the degree of change. Recovery was more rapid when the salinity was increased than when the same degree of change was made in the opposite direction. At a salinity of about 13°/oo very little water was transported even after several days were allowed for adaptation, but recovery to normal activity followed rapidly after the return of the oyster to a normal environment in water of 26°/oo to 29°/oo. Increased salinity, from 25°/oo to 39°/oo, produced no significant changes in the water transport by *C. gigas*. An unfavorable effect was recorded at 56°/oo, which is considerably above the normal range of the oyster's habitat.

In experiments at the Bureau of Commercial Fisheries Biological Laboratory, Milford, Conn. (Loosanoff, 1952), *C. virginica* from Long Island Sound accustomed to water of a stable salinity of about 27 °/oo were placed directly in water of 20, 15, 10, and 5 °/oo made by the addition of a corresponding amount of fresh water. The loss of food caused by the addition of plankton-free water was compensated by providing measured amounts of phytoplankton culture. The decrease in the rate of water transport was proportionate to the degree of change and varied from 24 to 99.6 percent of the normal rate. Six hours of exposure to the lowest salinities tested resulted in no permanent injuries, and within a few hours after transfer to the salinity of their natural habitat the oysters fed, reformed the crystalline styles, and discharged true feces and pseudo feces. Other experiments at Milford at the same time demonstrated that oysters conditioned to live in low salinities can tolerate lower concentrations of salts than oysters living in more saline waters. Although the oysters were observed to feed in water of 5 °/oo salinity their shell movement and water transport were abnormal and growth was inhibited.

The reproductive capability of oysters is inhibited by low salinity. Butler (1949a) showed that this is due primarily to the failure of gonad development in oysters of the marginal area of upper Chesapeake Bay; his findings were confirmed by experiments with Long Island Sound oysters (Loosanoff, 1952). These experiments have not demonstrated whether the failure of gonad development is the direct result of lowered salinity or is due to inadequate feeding.

Long-continued exposure to salinities above the 32°/oo level also has an unfavorable effect on oyster populations. This can be seen from the conditions of Texas oyster beds. During the 6-year drought from 1948 to 1953, the salinity in the bays of the central Texas coast generally rose well over 36°/oo and at times reached the 40°/oo level without an appreciable decrease in the winter (Parker, 1955). Previous records, from 1922 until 1948, show that during most of the year salinity in this area ranged from 5°/oo to 25°/oo with somewhat higher salinities in the summer. With the increase in salinity there was a gradual replacement of *C. virginica* populations by *O. equestris*. In 1952 over half of the young oysters (spat) were *O. equestris*, whereas in years of low salinity the reefs were comprised primarily of *C. virginica*. It is not known whether the observed change was due to the inhibition of gonad formation or to the failure of oyster larvae to reach setting stage. From an ecological point of view it is, however, significant that the replacement of one species by another took place at the time of the increase in salinity of water. The surviving *C. virginica* were observed to develop different shell characteristics: the valves became crenulated, thin, sharp, and highly pigmented.

Under certain circumstances the influx of fresh water into estuaries may be beneficial. Some of the carnivorous gastropods, flatworms, and starfishes, which are highly destructive to oysters, are killed by brackish water that constitutes a barrier through which they cannot penetrate. Decrease in the salinity of water protects the populations of oysters at the heads of the bays. Periodical flushing wipes out the predators and restores the productivity of beds. The population of oysters in areas highly infested by their enemies, as in the Apalachicola Bay, the upper half of the Delaware Bay, and many others, cannot exist if the access of fresh water to oyster bottoms is diminished and the salinity increases above the 15°/oo level.

The evaluation of the salinity factor can be estimated by determining the total percentage of time the brackish water of less than 10°/oo or water of salinity exceeding 34°/oo remains on an oyster bottom. The zero value is assigned to conditions unsuitable for the oyster's existence; marginal conditions are indicated by 1, and optimum conditions by 10. The values between are based on the percentage of time the oyster population is affected by unfavorable salinities.

TEMPERATURE

A great difference in climatic conditions exists within the range of distribution of *C. virginica.* The water temperature under which the species lives varies from a minimum of about 1° C. during the winter in northern states to a maximum of about 36° C., which occasionally has been observed in Texas, Florida, and Louisiana. The temperature of oysters exposed to the sun at low tide on the flat registers 46° to 49° C. measured by inserting a small thermometer between the slightly opened valves. Normally oysters of the tidal zone remain exposed for 2 to 3 hours at the maximum. Occasionally strong offshore winds drive the waters away and oysters beds in shallow places remain out of water for several days. Such instances occur along the coast of Texas where as a rule the low stage of water is caused by strong northern winds. The exposed population may perish either from excessive warming or from freezing temperatures brought from the north by cold fronts.

The temperature regime affects the life of the oyster by controlling the rate of water transport, feeding, respiration, gonad formation, and spawning. *C. virginica* ceases feeding at a temperature of 6° to 7° C. The maximum rate of ciliary activity responsible for the transport of water is at about 25° to 26° C.; above 32° C. ciliary movement rapidly declines. Nearly all functions of the body cease or are reduced to a minimum at about 42° C. Using the seasonal fluctuations of temperature, it is easy to determine the percentage of time during which oysters in any given locality continue to feed and reproduce. Similar observations may be made on the growth of shells and calcification. Two curves in figure 368 show the seasonal changes in mean monthly temperatures in two localities separated by about 11.5 degrees of latitude. The northern location of oyster grounds of Long Island Sound is at about lat. 41° 30′ N.; the southern location is that of Apalachicola Bay, Fla., at about lat. 30° N. The two curves, upper for Apalachicola and lower for Long Island Sound, parallel each other but are at two distinct levels. The difference is greatest during the winter and early spring and is smallest during the fall. The two temperature levels indicated by broken lines mark the periods of successful mass spawning and setting of oysters at temperatures of 20° C. and above and the inhibition of feeding and growth of the oysters below 8° C., often called hibernation. Apalachicola oysters continue to feed and grow throughout the year, and their reproductive season may last for 7 months or 58 percent of the year, whereas the period of feeding and growth of the northern oysters is limited to about 6¾ months, or 56 percent of the time and the reproductive season is restricted to 2 summer months, or about 16 percent of the time. The use of monthly means based on several years of observations gives a picture of a general condition not unduly influenced by short-term fluctuations which may differ from year to year.

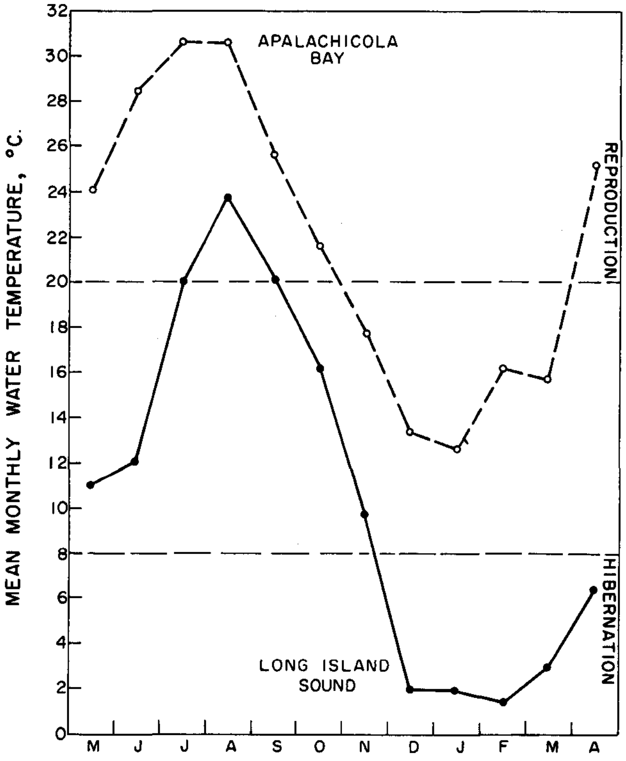

FIGURE 368.—Mean monthly temperature in °C. of water in Apalachicola Bay (upper curve) and Long Island Sound (lower curve).

Little is known about the prolonged effect of temperatures above 32° to 34° C. on oyster populations. From a few physiological observations it may be inferred that long continued exposure to high temperature is unfavorable and impedes the normal rate of water transport by the gills.

The percentage of time available to an oyster population for growth and "fattening", or for reproduction, can be used in evaluating the effect of the temperature factor on the productivity of an oyster bottom. A distinction should be made between the reproductive capability of the population and its growth and "fattening". In the practice of oyster culture the areas of bottom most suitable for setting are not considered desirable for the rapid growth and conditioning of oysters for market and vice versa.

FOOD

The quantities of food available to water-filtering animals may be determined by taking plankton and nannoplankton samples and by noting the food requirements of a given species. It has been shown by Jørgensen (1952) and Jørgensen and Goldberg (1953) that the oyster (*C. virginica*) and the ascidians (*Ciona intestinalis* and *Molgula manhattensis*) filter about 10 to 20 l. of water for each ml. of oxygen consumed, and that about two-thirds of the energy absorbed by them can be used for growth. The actual food requirements of the animals studied by Jørgensen probably do not exceed 0.15 mg. of utilizable organic matter per liter of water used. Determinations of phytoplankton in American coastal waters made by Riley (1941), Riley, Stommel, and Bumpus (1949), and Riley and Gorgy (1948), show that the organic matter of the phytoplankton in their samples ranged from 0.17 to 2.8 mg. per liter. These waters contain enough material to supply the energy requirements of *C. virginica* which, according to my determinations, differ from those made by Jørgensen (see p. 210 in ch. IX); under normal conditions at 24° to 25° C. *C. virginica* uses from 3 to 4 mg. of oxygen per hour.

Quantitative samples of plankton and microplankton taken throughout the year from the water over a thriving oyster population can be compared with samples collected in the plankton-poor waters of the tropics. The water should be pumped from the bottom zone, with care being taken not to stir the sediment. Vertical hauls are useless since the water a few inches above the oysters does not come in contact with them except in the case of strong vertical mixing.

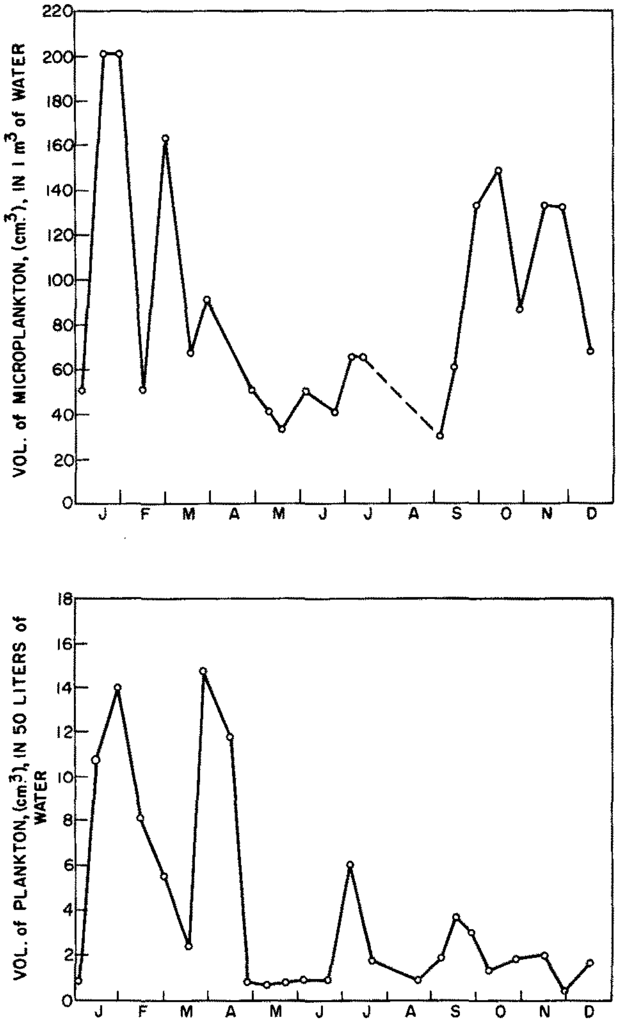

FIGURE 369.—Seasonal changes in the volume of plankton (upper curve) in cm.^{3} per 50 l. and microplankton (nannoplankton) in cu. cm. per 1 m.^{3} (lower curve) in Long Island Sound in 1932 and 1933.

Seasonal changes in the volume of plankton and microplankton of water over a commercially productive oyster bed in Long Island Sound are shown in figure 369. Both types of samples were collected at the same time. For the plankton study 50 l. of water were filtered through No. 20 bolting silk. The collected material was preserved in 2 percent formalin and transferred into tall glass cylinders, and its volume read 24 hours later after the material had settled at the bottom; the results are expressed in cm.^{3}. For microplankton determination a 1 liter sample was taken from the bottom and the water passed through a high-speed Foerst-Juday type centrifuge rotating at 20,000 r.p.m. The centrifugate was transferred to a 15 mm. diameter tube and centrifuged for 5 minutes in a clinical centrifuge at 14,000 r.p.m. and its volume measured. Since the waters of Long Island Sound are relatively free of silt, the amounts of detritus in the samples were insignificant. Seasonal fluctuations of plankton and nannoplankton follow a typical pattern of maximum development from about the middle of January to the end of April, followed by a decrease during May to September and a second maximum, smaller than the first, in September to November. The latter period is of greater significance for the northern oysters because they do not feed during the winter months of January and February.

Another method of determining plankton productivity of water over an oyster bottom was used in a study of the York River, Va. (Galtsoff, Chipman, Engle, and Calderwood, 1947). In this case the water sample was obtained by means of a Birge-Juday plankton trap. Two liters of the sample were passed through the Foerst-Juday centrifuge, and the centrifugate extracted for 15 minutes in 10 ml. of 80 percent acetone. A comparison of the color was then made with standards of nickel sulfate and potassium dichromate (Harvey, 1934), and the results expressed in pigment units per liter of original sample. Each unit was found to be equivalent to approximately 10,000 diatoms and dinoflagellates present in York River water. So far as seasonal changes in plankton are concerned, the results were similar to those observed in Long Island Sound. Although the total energy requirements of certain filter-feeders are known, no information is available about the specific food that is needed for their growth and reproduction. Certain types of phytoplankton, such as *Chlorella*, have antibiotic properties and are harmful to some bivalves. Too little is known about the specific food requirements of various organisms. The total bulk of phytoplankton may be made of the materials of low nutritive value or may consist of such organisms as *Rhizosolenia*, *Chaetoceras*, and others which cannot be ingested by the oyster because of their size and shape.

In evaluating the food factor the abundance of plankton should be compared in different areas during the period when the oyster is actively feeding and accumulating glycogen. This period usually occurs shortly after spawning (ch. XVII). The amount of phytoplankton per unit of volume of water on oyster bottoms of highest commercial yield and consisting primarily of algae that can be utilized by the oyster represents the optimum value of food factor (score 10); while the phytoplankton content of water from the marginal areas is assigned the score 1.

Another and more accurate method may be used. It is based on the determination of metabolic rate of oysters during the period of feeding. The nutritive value (food energy) of the sample of phytoplankton can be determined by using a bomb calorimeter and measuring the heat of combustion in calories. Knowing the rate of water transport by the oyster at a given temperature and salinity, it is easy to calculate whether the food supply on oyster grounds is adequate. Unfortunately, the method widely used in nutritional studies has not yet been applied in oyster research.

The high concentrations of phytoplankton which occur during blooms are not desirable features and can be harmful. Experimental work has clearly shown that at a certain high concentration of several forms (*Nitzschia closterium*, *Prorocentrum triangulatum*, *Euglena viridis*, and *Chlorella* sp.) the rate of water transport of oysters is reduced and feeding ceases (Loosanoff and Engle, 1947). The deleterious effect is caused by the cells themselves and by their metabolites. These laboratory findings are in accord with field observations in Great South Bay, N.Y., where a mass development of a *Chlorella* like organism adversely affected valuable oyster beds. Another example of a danger of excessive development of a single microorganism is the so-called red tide (Galtsoff, 1948, 1949) along the western coast of Florida. Sudden development of the dinoflagellate, *Gymnodinium breve*, causes extensive mortality of fishes and kills many oysters growing along the shores of the affected area.

Conditions are ideal for the feeding of oysters when water free of pollution and containing a low concentration of small diatoms and dinoflagellates runs over a bottom in a nonturbulent flow.

NEGATIVE FACTORS OF ENVIRONMENT

The environment itself may interfere with the welfare of oyster populations. Negative factors decrease or inhibit reproductive capabilities; destroy the population by causing extreme adverse conditions; increase the incidence of disease; inhibit the fattening and the growth of oyster body, thus decreasing the productiveness of an oyster bed; and interfere with the formation of shell and so deprive the oysters of their principal means of protection against adverse situations and attacks of enemies. All negative factors are evaluated by determining the degree of their harmfulness and assigning them scores from 1, for 10 percent effectiveness, to 9, for 90 percent. The score 10, indicating 100 percent destructiveness, is omitted because no oyster population can exist under such a condition. Zero score means complete absence of a negative factor.

SEDIMENTATION

Rapid settling of suspended material may be highly destructive to an oyster community. All coastal waters contain a certain amount of solids in suspension of either organic or inorganic origin. The particles settle on the bottom, depending on their weight and shape, chemical composition, temperature, viscosity of water, and character of water movements. The velocity of the fall of a particle through a liquid is a function of the radius of the particle governed by Stoke's law:

$$v=\frac{2(P_0-P)gr^2}{gn}$$

where v is the velocity of sinking, P_0 and P are the densities of the particle and of the liquid respectively, r the radius of the particle, n the absolute viscosity of the liquid, and g the acceleration of gravity. It is assumed in the equation that the particles are spherical, that they are small enough so that the viscosity of the water is the only resistance to their fall, and that their sinking is not impeded by adjacent particles. The equation is applicable to spheres varying in size from 0.2 to 200μ and suspended in quiet water. Obviously such conditions represent the "ideal" situation which cannot be found in an estuarine environment. Here the water is in almost constant motion with rapid changes in the direction and velocity, and carries sediments consisting of particles of differing sizes, shapes, and densities. The discussion of the physical aspects of sedimentation problems is beyond the scope of this book. The reader interested in these problems is referred to comprehensive textbooks on the subject (Twenhofel, 1961; Linsley, Kohler, and Paulhus, 1949). For an understanding of the ecological effects of sedimentation it is enough to describe in general terms the conditions under which silt particles are transported and deposited on estuarine bottoms.

Observations made on waterflow in a tube show that at low velocities the particles of a liquid move in parallel lines and the resistance to their motion is due to viscosity. This condition is called streamline or laminar flow. High velocity of the water and roughness in the walls of the tube make the stream break into a turbulent flow characterized by irregular, eddying, and rolling movements. The formation of the eddies counteracts the gravitational settling of particles, and more material is moved upward than sinks toward the bottom. When the amount of sediment picked up by a turbulent flow exceeds the amount deposited, the bottom is eroded. If the gravitational force predominates, more material is being deposited than carried away and the bottom is rapidly covered by the sediment. In an estuary both processes alternate following the rhythmic changes in the direction and velocity of tidal currents. In many instances an equilibrium is established and continues for a long period of time unless the balance between the two forces is upset by violent water movements from severe storms or floods. Depending on the configuration of the bottom, certain areas of an estuary are scoured, while vast quantities of sediments are deposited on others. This is typical on oyster grounds in many tidal streams.

The material suspended in coastal water is a very complex mixture of particles of differing size, shape, specific gravity, and mineralogical composition. The particles are sorted out as they are moved by the water. According to Trask (1950, p. 10), slowly moving water seems to make for poorer sorting than a fast moving current. To a sedimentation geologist the resulting pattern of

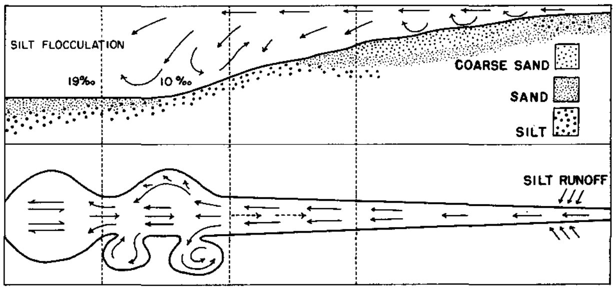

FIGURE 370.—Diagrammatic representation of the sorting out and deposition of coarse sand, fine sand, and silt in an estuary. The lower part of the diagram indicates the complex system of current and counter current. From Rochford, 1951.

the size distribution of sediment may serve as an indication of the mode of its deposition. A schematic representation of sorting of the material suspended in water and its deposition in the four zones of an estuarine system according to the distance from the mouth of the river is shown in figure 370, redrawn from Rochford (1951). At the head of an estuary silt is transported by tidal streams further than sand and because of flocculation, caused by the influx of saltier water, smothers the beds near the mouth (middle and left parts of fig. 370). The complexity of the horizontal pattern of currents is shown on the lower part of the diagram.

Particles immediately above the bottom move by rolling, sliding, and jumping. Outside of this narrow "bed layer" (Einstein, 1950) the particles in water constitute the suspended load; their weight is continuously supported by the fluid until they reach the lower part of the estuary where they are deposited over the bottom and on tidal flats.

The problem of transport and settling of sediments in the sea is not well understood (Trask, 1950, p. 9) and is being intensively studied by many oceanographic institutions of the world. In tidal waters where oyster beds are located the problem becomes more complex because the rate of transport and settling is greatly influenced by periodic changes in current velocities, turbulence, salinity, temperature, density and viscosity of water, and size, shape, roughness, and specific gravity of transportable particles. In the tidal regime where salty oceanic water mixes with fresh water another important factor called flocculation enters into this already complex picture. Small dispersed particles of clay and of organic detritus have a tendency to aggregate in small lumps. In the purification of drinking water flocculation is produced artificially by adding a coagulant such as aluminum sulphate ($Al_2(SO_4)_3 \cdot 18\ H_2O$). In estuaries where sea and fresh water mix the flocculation is caused by the change in the electric charges of the particles which occur with the change in the hydrogen ion concentrations.

Laboratory experiments with kaolin suspension show that flocculation of particles about 4μ in diameter may occur at constant pH (8.5) by increased concentrations of Na^+ at constant SO_4^{--} concentrations (Whitehouse, 951, 11952).[9] The results indicate the tendency of positive ions to cause the flocculations of the negatively charged particles.

Flocculation in coastal waters may be observed from the deck of a ship at the time of freshets along the coastline of the Carolinas and Georgia. Large patches of aggregated silt particles show clearly in the salty offshore water while the brownish color of less saline water at the mouth of a river remains uniform.

Rochford (1951) states that flocculation of silt takes place in the salinity zone of less than 19°/oo and higher than 10°/oo (fig. 370). Since flocculation depends on several factors including temperature, pH, and the type of sediments in suspension, one may expect a great variation in the rates of settling in the various estuaries of the Atlantic and Gulf coasts.

The gross effect of sedimentation may be measured by determining the depth of deposition of silt over an oyster bottom per unit of time and area. Less noticeable, but highly significant, is the deposition of a thin layer of sediment over the hard surfaces to which many organisms, including oyster larvae, attach. A deposit of loose sediment only 1 or 2 mm. thick is enough to make the surface of shells and rocks unsuitable for the attachment of larvae and to cause failure of setting. I have observed such conditions many times in certain sections of Oyster River, Chatham, Mass.; in the Wiweantic River of the Cape Cod area; in the small rivers and creeks emptying into Delaware Bay; and in the Rappahannock and York rivers, Va. Undoubtedly similar conditions may be found in many other places where silt is transported by estuarine currents. Light sedimentation is not harmful to populations of adult oysters, but may be heavy enough to interfere with their reproduction.

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[9] WHITEHOUSE, U. GRANT.

1951. A study of chemical sedimentation and of physical oceanography sponsored at Texas A. and M. College by the American Petroleum Institute through the Scripps Institution of Oceanography of the University of California (A.P.I. Project 51). Progress report for the quarter ending December 31, 1951. The Texas A. and M. Research Foundation, Project 34, The Agricultural and Mechanical College of Texas, Department of Oceanography, College Station, Texas, 9 pp. (Preliminary report).

1952. A study of the chemistry of oceanic sedimentation sponsored at Texas A. and M. College through the Scripps Institution of Oceanography of the University of California (A.P.I. Project 51). Progress report for quarter ending December 31, 1952. The Texas A. and M. Research Foundation, Project 34. The Agricultural and Mechanical College of Texas, Department of Oceanography, College Station, Texas, 11 pp. (Preliminary report).

Many formerly productive oyster bottoms along the Atlantic Coast of the United States have been destroyed by a high rate of sedimentation. Dead oyster reefs buried below a surface of mud in the waters of Louisiana and Texas are good examples of this process. The silting of estuaries may be studied by the simple method of comparing the depth of water shown in navigation charts of 25 or 50 years ago with present soundings. From these differences the total amount of deposit accumulated over the given period of time can be computed. The reduction of volume of water in a basin due to sedimentation can be determined from these data and from the computations of the capacities of reservoirs (Dobson, 1936). Brown, Seavy, and Rittenhouse (1939) successfully used this method in determining the rate of silting over a distance of 19.4 miles of the York River, Va. In 1857 the water volume of this sector of the river, estimated at mean low tide, was 227,780 acre-feet. By 1911 it was reduced to 222,189 acre-feet, and in 1938 was only 206,896 acre-feet. The cumulative volume of sediment deposited during the period 1857–1911 was 5,591 acre-feet, and from 1911 to 1938 reached 20,884 acre-feet. The annual deposition for the first period of 55 years was 104 acre-feet, which represented 0.05 percent loss of water volume; during the second period of 27 years (1911 to 1938) the annual deposition increased to 566 acre-feet, which corresponded to an annual 0.25 percent loss of water. The increased rate of silting during the later period was explained by an increased erosion of soil over the watershed resulting from faulty agricultural practice, deforestation, and an increase in population.

The filling of bays and estuaries with sediments is a general phenomenon along the Texas coast, and is particularly pronounced in Laguna Madre and near the mouth of the Colorado River in Matagorda Bay where some of the buried oyster reefs are found under 14 feet of mud (Norris, 1953). During the last 36 years silting has destroyed 6,000 to 7,000 acres of productive oyster reefs near Matagorda. These beds were described in detail by Moore (1907) and resurveyed in 1926 by Galtsoff (1931a). In 1926 the principal reefs opposite the mouth of the Colorado River were surrounded by very soft mud but were still productive. Now the mud of the Colorado River has completely buried these reefs and pushed the head of fresh water seaward. For the Neuces River, a small stream emptying into Corpus Christi Bay, the accumulation of silt recorded by comparing the depths given on 1880 charts with those issued in 1937 varied from 4 feet near the ship channel to less than 1 foot at the south shore (Price and Gunter, 1943). The average annual accumulation of sediment near the ship channel was about 0.8 inches, only slightly less than the annual increase of oyster shell in height. Under such conditions an individual oyster, even if it grew in the vertical position that oysters usually assume in soft mud, in 6 to 7 years would have sunk in mud for about three-quarters of its height and perished.

The soft, muddy tidal flats typical for the inshore waters of the South Carolina and Georgia coast are usually devoid of oysters. U.S. Bureau of Fisheries experiments on oyster farming in 1939 and 1940 in the vicinity of Beaufort, S.C., demonstrated the complete unsuitability of these areas for oyster culture. Reinforcement of these flats by shells planted in a layer about 1-foot thick and strong enough to support a man's weight was a complete failure. The shells acted as baffles, with the result that in a short time mud filled all the crevices between them and in about 6 weeks completely covered everything with a smooth layer of silt (Smith, 1949). Similar results were obtained with brush and other materials placed on the surface of the mud; in a few months not a trace of them could be seen on the surface. On the other hand, oysters grew well along the opposite side of the river where a swift current kept the bottom scoured.

Accumulation of silt over an oyster bottom is sometimes caused by the activity of various mud-gathering and mud-feeding invertebrates. Chief among them are several species of the mud worm, *Polydora*. The two long antennae of these worms protrude from the tube in which the animal lives and sweep the surrounding water. Mud particles suspended in the water are caught by the epithelium of the antennae and by ciliary motion are transported toward the head to accumulate around the worm's body and thus making the tube. Some of the mud is ingested and passes through the intestime. *P. websteri* invades the shell cavity of the oyster, settles on the inner surface at a right angle to the edge, and builds a U-shaped mud tube with both orifices external. The structure is soon covered by a layer of conchiolin deposited by oyster and becomes a semitransparent blister.

As the worm grows the cavity it occupies is enlarged by boring to provide for its increased size. Several shell layers are deposited by the oyster over the blister. The mechanism of boring is not well understood; probably erosion of the shell is accomplished by a combined chemical and mechanical action. *P. ligni* is found living in mud tubes on tidal flats or attached to shells and rocks. On several occasions the reproduction of *P. ligni* on the oyster bottoms of Delaware Bay was so rapid that nearly every live oyster of the affected area was killed by a deposit of mud several inches thick consisting of numberless live worms and their tubes. The process of gathering mud by *Polydora* is shown in a photograph (fig. 371) taken of a live worm, which was placed in a glass tubing for observation in the laboratory.

Oysters themselves accumulate large quantities of organic sediment, which is discarded with the feces. During feeding the oyster discharges fecal ribbons at the rate of several centimeters per hour. In a sluggish current large quantities of fecal masses settle in the crevices between the oysters and contaminate the bottom. The situation may become serious enough to cause a decline in the productivity of oyster beds, as has been demonstrated by Japanese biologists (Ito and Imai, 1955).

Organic material constitutes a major portion of marine muds. The physical properties of a sediment may be of lesser importance to oyster ecology than the complex biochemical changes associated with the bacterial decomposition of its organic components that result in the formation of carbon dioxide, ammonia, phosphates, sulfates, and various organic acids. In the case of anaerobic oxidation, methane and hydrogen sulfide are formed (Waksman, 1942; Waksman and Hotchkiss, 1937). The effect of these products of decomposition on bottom populations probably is the main reason for the slower rate of growth for oysters on the bottom than for those which are kept above the bottom on trays or are suspended from rafts and floats (Shaw,

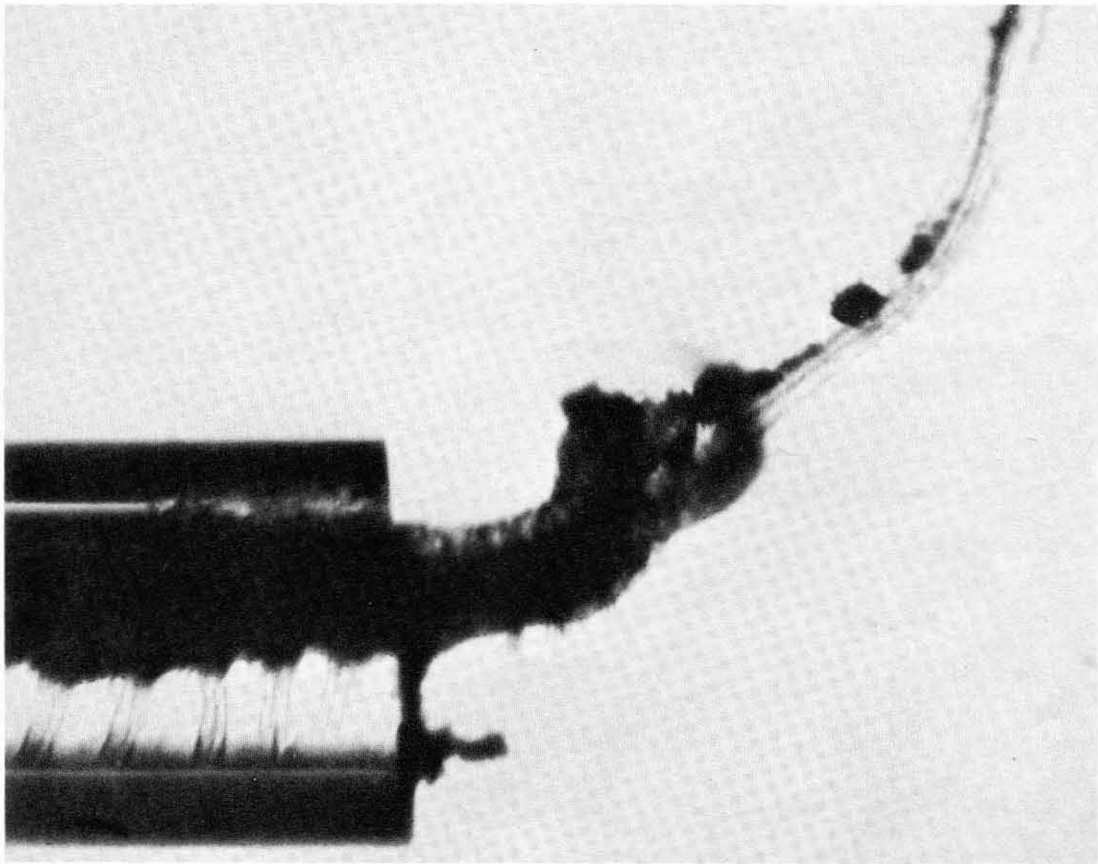

FIGURE 371.—Photograph of live *P. ligni* collecting mud. The worm is contained in a glass tube placed in sea water containing silt in suspension. Mud particles along the grooved antennae are transported toward the mouth and have begun to accumulate at the edge of the glass tubing.

1962). It appears paradoxical but true that the conditions of a natural environment do not add up to the ideal situation for the life of a bottom inhabiting mollusk such as the oyster. Location on rocks and underwater structures above the mud line appears to offer a more favorable environment.

Determination of the amount of silt settling on the bottom can be made with a mud trap of the type shown in fig. 372. The trap consists of a metal funnel riveted to a metal frame and a quart size container (fruit jar) screwed to the funnel. The trap is set on the bottom for the desired length of time, then carefully lifted, and the amount of sediment settled over the area of the funnel and inside the jar is measured.

Data obtained with a mud trap of the type shown above measure the rate of settling of sediments on the bottom. One should bear in mind, however, that a certain portion of the sediment deposited during slack tide may be washed away as the current velocity increases with tidal changes. Furthermore, mud already settled on the bottom may be stirred by wave action and resettle on an adjacent area. The actual accumulation of sediment can be measured with a mud board of the type shown in fig. 373. A wooden stake 36 inches high supports a flat board 18 inches long and 6 inches wide, mounted horizontally, and the stake is forced into mud so that the board is level with the bottom. This type of trap can be used conveniently on tidal flats.

A trap to be used below low water can be made of a flat board ½ square yard in area. To prevent the loss of sediment the board has slanted borders about 4 inches wide, projected above its upper surface. The trap is set on four short legs; its surface is ruled in squares to facilitate the measurements of the area covered with sediment. The thickness of the sediment is measured with a ruler. Since the board cannot be lifted without disturbing and losing the accumulated sediment, observations must be made by a diver.

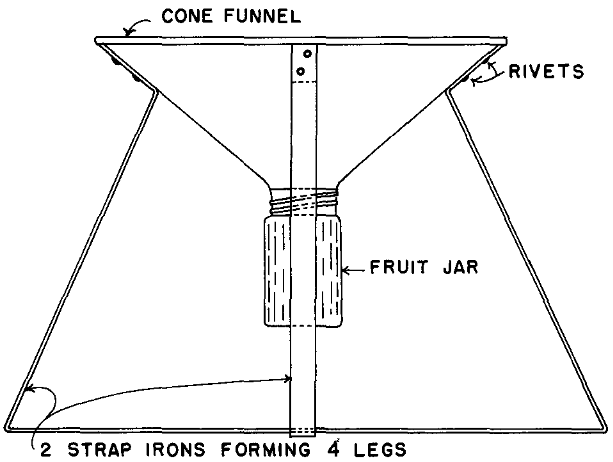

Figure 372.—Mud trap for collecting sediments settling from water.

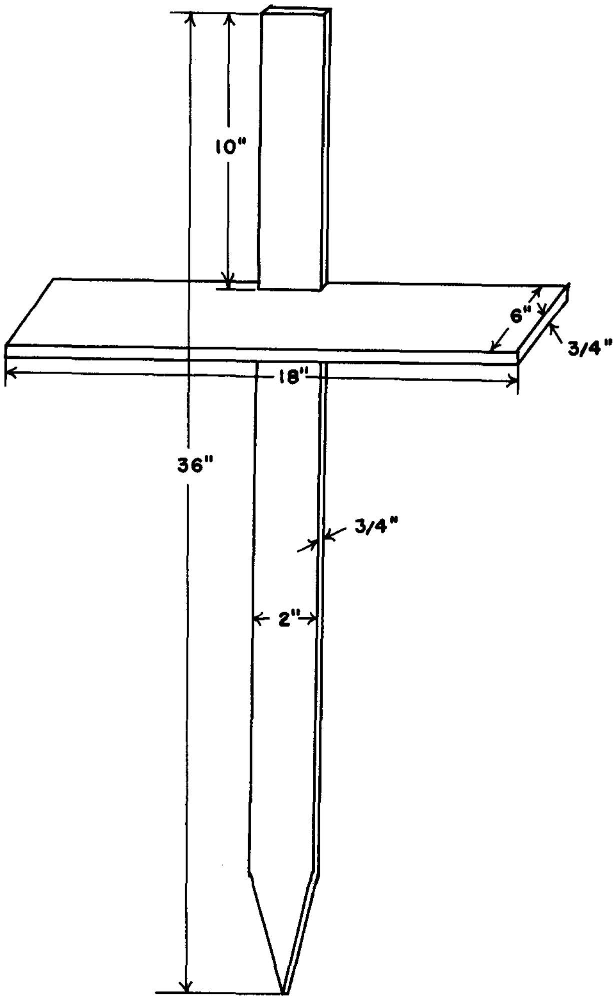

Figure 373.—Mud board for measuring the accumulation of sediment on tidal flats.

An indirect estimate of the amount of material in suspension can be made by using a Secchi disc and recording the depth of extinction of white color. The results are affected by the visual acuity of the observer, illumination, and the condition of the sea surface.

The amount of suspended material in a sample of water can be determined with a simple turbidimeter of the type used primarily in fresh-water studies; more accurate results are obtained with an electrophotometer and spectrophotometer. The turbidity of the collected samples is compared with standards made of known dilutions of a suspension of 1 g. of kaolin (or silica clay) in 1 l. of water.

Evaluation of the effect of sedimentation on oyster bottoms can be made by considering the location of oyster bottom in the estuary; the amount and character of sediment in suspension; the type of estuarine circulation; and the rate of accumulation of sediment on oysters. A score of zero is assigned to the ideal conditions under which no deposits settle on live oysters. The opposite extreme, valued at 10, is found in the areas of heavy sedimentation, not suitable to oysters. All intermediate conditions scored from 1 to 9 can be evaluated on the basis of field observations.

DISEASE

Oysters suffer from both noncontagious and infectious diseases. The first category is associated with the malfunction of physiological systems of organs and deficiencies in the environment, such as lack of food, unsuitable salinity and water temperature, and pollution by domestic sewage and various trade wastes. The second category, infectious diseases, is caused by pathogens and parasites. Clear distinction between the two types of pathological conditions is not always possible because resistance to infection is lowered by an unfavorable environment, and an oyster weakened by adverse conditions more easily succumbs to infection.

With few exceptions the outward symptoms of a disease are nonspecific. The more common symptoms are slow growth, failure to fatten and develop gonads, recession of the mantle, and valves that remain slightly agape. There is often a corresponding abnormal deposition of shell material that in a chronic condition causes the formation of short and thick shells ("huître boudeuse" of French biologists). The valves do not close tightly because the adductor muscle is weakened. The body of a sick oyster is watery, often discolored (dirty green and brown), and bloody with blood cells accumulating on the mantle and on the surface of the gills.

The etiology of oyster diseases is not well known. A few microorganisms infecting the oyster have been definitely identified as pathogens; the taxonomic position of others is not known, and some are called by code numbers. Oyster populations throughout the world suffer from periodic widespread mortalities which may be associated with infections, but since the life cycles of some of the pathogens have not been described, the evidence remains circumstantial.

The widespread mortality of oysters rarely can be attributed to a single factor of the environment; in most cases it occurs as a result of the combination of several adverse conditions including infection.

Malpeque Bay disease

One of the most persistent and mysterious ailments of oysters is the Malpeque Bay disease, which in 1915 and 1916 struck the populations of *C. virginica* in the bays of Prince Edward Island, Canada, causing the death of 90 percent of the oysters, and in later years appeared along the Canadian mainland. The most distinctive symptom associated with the disease was the occurrence of yellow-green pustules, up to 0.5 cm. in diameter, on the surface of the visceral mass, along the edges of the mantle, and on the adductor muscle and the heart. Despite lengthy field and experimental studies conducted from the epidemic year to the present, the causative agent has not been found, although there is no doubt that the mortality of Malpeque Bay oysters was due to an infection (Needler and Logie, 1947). With the expectation that the survived oysters were of disease resistant stock, the Department of Fisheries of Canada and the Fisheries Research Board organized in 1957 a rehabilitation project and transferred oysters from Prince Edward Island to devastated mainland areas. Unfortunately the hopes did not materialize fully since a high proportion of the spat that settled on the rehabilitated area did not show the expected level of resistance. It is hoped, however, that a resistant stock will develop from a small number of survivors over a period of several years (Drinnan and Medcof, 1961).

Dermocystidium marinum

Dermocystidium marinum Mackin, Owen, and Collier, a fungus of uncertain taxonomic position infecting *C. virginica*, is probably the most dangerous pathogen associated with periodic mortalities of oysters in the waters of southern States. The microorganism infects oyster tissues producing single, spherical, vacuolate cells which reproduce by endogenous free cell formation and subsequently liberate uninucleate sporelike bodies. The following detailed description of the species is reproduced verbatim from Johnson and Sparrow (1961, p. 539):

> Mature thallus a hyaline, spherical, spore-like body, 2–30μ, averaging about 10μ in diameter; each cell containing a large, slightly eccentric vacuole in which a polymorphic, refractive vacuoplast usually occurs; nucleus oval, eccentric; cleaving internally to form a short hypha terminated by an apical, conidium-like swelling.

Dermocystidium can be identified on cross-sections of an oyster stained with hematoxylin, Giemsa or other histological stains, or in teased preparations stained with Lugol solution (fig. 374).

Identification of *Dermocystidium* by microscopic examination of tissues is time consuming and difficult. The diagnostic technique developed by Ray, Mackin, and Boswell (1953) facilitates the examination of large numbers of samples. Small pieces of tissues are removed from the gaping oysters and placed in Carrel tissue culture flasks containing a small amount of sterile water to which streptomycin and penicillin have been added to prevent bacterial growth. Prior to excision the tissues are washed in sterile sea water, then placed for 10 minutes in a 10 percent solution of sodium merthiolate (1:10,000), washed again in sea water, and allowed to remain for several hours in sterile sea water fortified with 1,000 units each of streptomycin and penicillin. Tissues parasitized with *Dermocystidium* disintegrate completely in about a week, while in the controls they remain intact. The debris of disintegrated tissues consists mainly of minute spheres of *Dermocystidium* cells. Unfortunately the contamination of samples with molds, yeast, and ciliate protozoans could not be entirely prevented and failures were "much more frequent than were successes, and most of the experiments were discarded." The data presented by Ray, Mackin, and Boswell show that the major effect of *Dermocystidium* infection is marked loss of weight, averaging 33 percent.

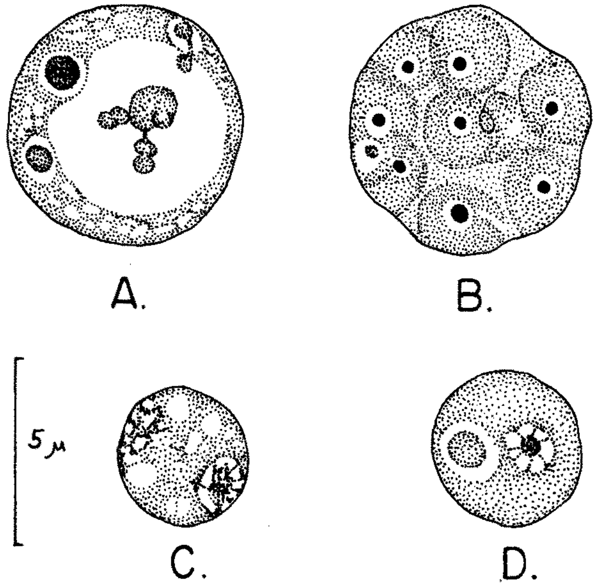

FIGURE 374.—Drawings of *Dermocystidium marinum* stained with Heidenhain's iron hematoxylin and eosin. A—A mature spore with markedly irregular vacuoplast, cytoplasmic inclusions, and very large vacuole. B—Multiple fission resulting in several daughter cells. C—A binucleate stage with chromatin in diffuse condition, and showing beginning vacuolation of the cytoplasm. D—An immature spore with small vacuole and vesicular nucleus. Figure 1 from Mackin, Owen, and Collier, Science, vol. 111, No. 2883, 1950, p. 329.

The infection may combine with other factors to produce a mortality of oysters which, according to Mackin (1961a), can virtually destroy seed oysters planted in Louisiana in a single summer. *Dermocystidium* studies in southern waters established the significant fact that the effect of the parasite "is not only a matter of disease but of season, summer losses accruing from disease being significantly greater than those of early spring months" (Ray, Mackin, and Boswell, 1953). The importance of environmental factors (temperature and salinity) is clearly demonstrated by these findings.

According to Mackin (1961b), the disease caused by *Dermocystidium* affects the oysters from Delaware Bay to Mexico but in the more northerly part of the range is not apparent in winter. It is not clear, however, if *Dermocystidium* remains in a dormant stage or if it disappears from oysters. In the Gulf States winter temperatures are probably not low enough to eliminate the parasite, and consequently considerable mortality may occur in mild winters.

Dermocystidium marinum and possibly other species of the genus have been reported from *O. frons*, *O. equestris*, *O. lurida*, *Mya arenaria*, *Mulina lateralis*, *Macoma baltica*, *Mercenaria* (*Venus*) *mercenaria*, *Anadare transversa*, *Anomia simplex*, *Ensis minor*, *Laevicardium mortoni*, and *Lyonsia hyalina* (Johnson and Sparrow, 1961, p. 540).

Many phases of the life history and biology of *Dermocystidium* require elucidation, particularly the transport of spores by water and their penetration into the tissues, the details of reproductive cycles, the relationship between environmental conditions and degree of infection.

Disease associated with *Haplosporidium*

Excessive mortality of oysters in Delaware Bay in a 6-week period of April and May 1957 wiped out from 35 to 85 percent of planted oysters and almost completely ruined the oyster industry of the State. A microorganism consistently found in tissues of infected oysters was designated by the code name MSX and later on was tentatively identified by Mackin as one of the Haplosporidia. The organism invades the connective tissue surrounding the intestine and digestive diverticula. Early plasmodial stages and ensuing stages of development are shown in two illustrations (figs. 375 and 376) made in the laboratory from a preparation kindly supplied by Haskin.

Mortality of oysters on the eastern shore of Virginia near Seaside was investigated from 1959 to 1961 by the Virginia Institute of Marine Science. The microorganism causing the disease and first designated as SSO was described by Wood and Andrews (1962) as a sporozoan, *Haplosporidium costale*, n. sp., infecting connective tissues of oysters and producing a truncate spore encased in an operculum with a lid. An early plasmodium with 6 to 12 nuclei is from 6 to 8μ in size (fig. 377). *Haplosporidium* has been found in live oysters as early as February, and in mid-May to June the infection may cause high mortality. How the parasite infects the oysters is not known, and its life history is not fully understood (Andrews, Wood, and Hoese, 1962).

Shell disease

This disease, which is probably associated with an unidentified fungal infection of oyster shell, is not particularly serious in *C. virginica*, but has been reported to cause catastrophic mortalities in the population of *O. edulis* in Oosterschelde, Holland. The disease can be recognized by bottle-green or orange-brown rubberlike warts and spots

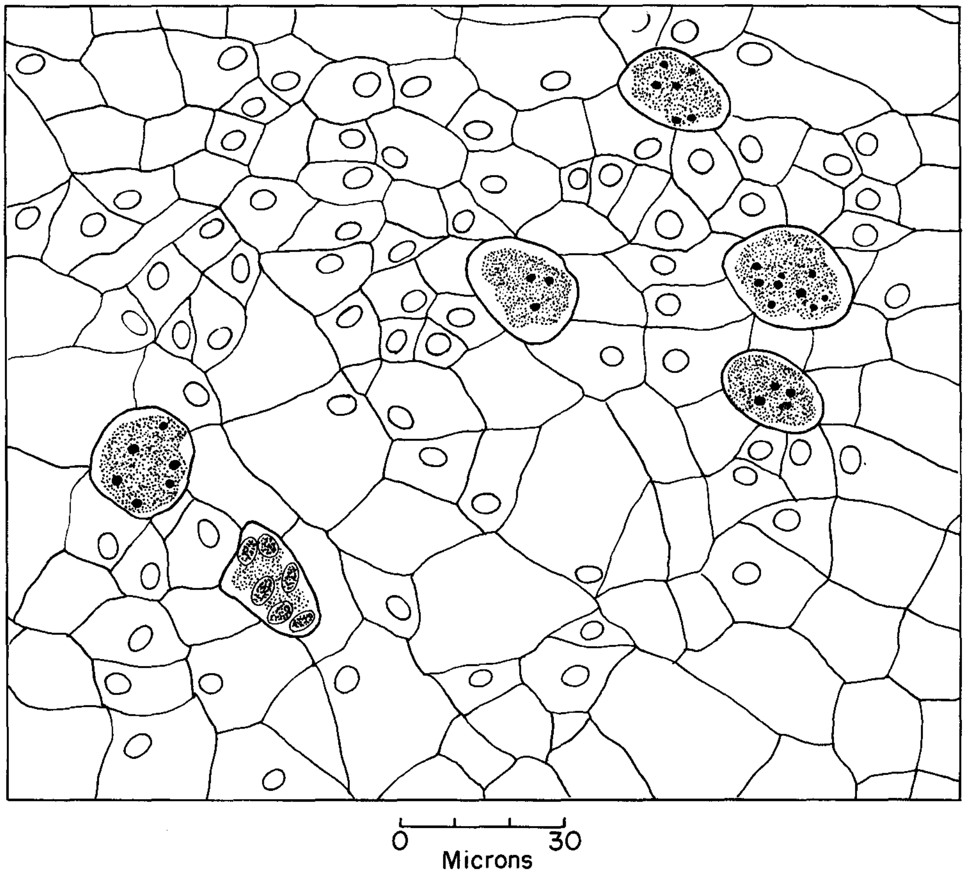

FIGURE 375.—Plasmodial stage of MSX in the connective tissue of heavily infected *C. virginica* from Delaware Bay. Bouin, hematoxylin-eosin.

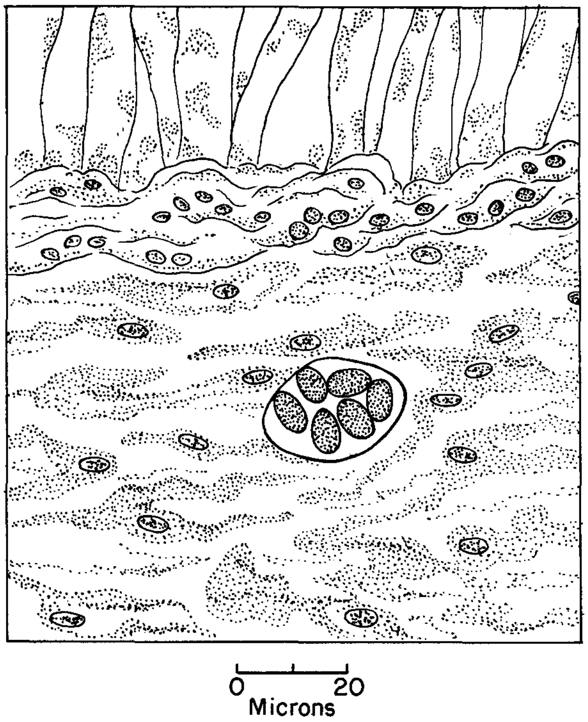

FIGURE 376.—Later stage of development of MSX in the connective tissue of heavily infected *C. virginica* from Delaware Bay. Formalin 10 percent, iron hematoxylin.

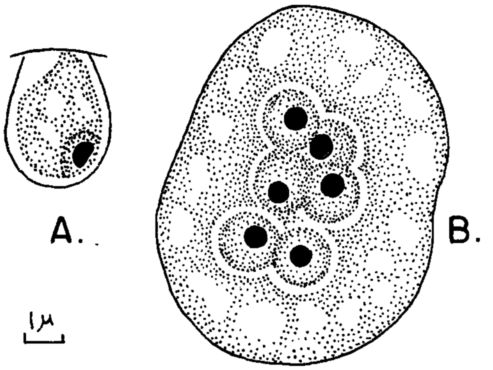

FIGURE 377.—*Haplosporidium costale.* A—mature spore; B—early plasmodium. From Wood and Andrews, fig. 1, Science, vol. 136, 1962, p. 711.

on the inner surfaces of the shell and, in more advanced cases, by deformation of the shell edges and hinge. Examination of thin slides of shell show abundantly branching fungus. The shell disease in Oosterschelde was studied by Korringa (1951a), who discovered that it spreads at water temperatures above 19° C. and that the higher the temperature the more vigorous the attack. The fungus was not isolated from Dutch oysters and remains unidentified. Korringa believes that it survives in the old green cockle shells scattered as cultch over the bottom and that its spores are probably carried by the water currents. Wholesale cleaning, removal of old shells, and disinfecting of young infected oysters with a solution of "an organic salt of mercury" (not fully specified by Korringa) are recommended as control measures.

Shell disease in Dutch oysters has been known since 1902, but at that time occurred only in a limited percentage of oysters. Its rapid spread in the years following 1930 was probably due to the enormous quantities of old cockle shells, about 40,000 to 50,000 $m.^3$, scattered annually as spat collectors. This gave the fungus a chance to proliferate more rapidly and infect the oysters. Voisin (1931) describes the disease in oysters imported from Zeeland, Holland, for planting in the Marennes area on the west coast of France. He states that more than 40 percent of these oysters had shells infected by a fungus, probably belonging to the genus *Monilia.* The identification is merely a guess and cannot be verified.

Foot disease

Foot disease or "maladie du pied" of French oyster growers occurs in *O. edulis* and *C. angulata* in the waters of the western and southern coasts of Europe. Korringa suggests that it is probably identical with the shell disease. The name is an obvious misnomer because the foot is lacking in all adult oysters.

"Foot disease" has existed in the Arcachon region since 1877. Giard (1894) described its parasitic nature and attributed it to a schizomycete fungus *Myotomus ostrearum* Giard, a genus not listed in Johnson and Sparrow's treatise on fungi (1961).

The disease affects the area of the attachment of the adductor muscle, primarily on the lower, concave (left) valve, and in certain cases the upper, flat valve. The surface of the shell under the muscle is covered with small, rough dark green spots. In advanced cases the muscle becomes detached from the valve and forms irregular cysts of horny and slightly elastic material. Later on when the cyst extends beyond the area of the muscle attachment, the cyst walls become covered with calcareous shell deposit. According to Giard (1894) and Dollfus (1922), the parasitic fungus grows by utilizing the conchiolin of the shell and stimulates its secretion by the mantle.

The progress of the disease is slow. During the advanced stage shell movements are affected and the oyster has difficulty in closing its valves, thus becoming an easy prey for its enemies.

Foot disease is found in *C. virginica,* particularly in oysters inhabiting muddy waters of the southern States, but in my experience it never reaches epizootic proportions. The cysts of an affected oyster (fig. 378) contain a suspension of blood cells, debris, and numerous bacteria which probably represent secondary infection. The disease does not present a serious menace to the oyster fishery of the coastal states.

Hexamita

The flagellate *Hexamita inflata* was first found in the intestinal tract of *O. edulis* (Certes, 1882). It is present in *C. virginica* of Prince Edward Island, Canada, and southern Louisiana, and in *O. edulis* in Dutch waters (Mackin, Korringa, and Hopkins, 1952). Heavy infection with *Hexamita* causes breakdown of connective tissue cells, general inflammation, the appearance of many trophozoites in blood vessels, and necrosis of adjacent tissues. The early stages of the disease appear to be intracellular, and are usually found in the leucocytes of the blood vessels. The trophozoite is oblong and narrow at the anterior, with six anterior and two posterior flagella. Cysts found in advanced stages of the disease are small, about 5 μ in diameter; they contain two or four small nuclei and have no flagellar structure. The complete life cycle of the parasite has not been described. The method of infection appears to be by cysts liberated after the disintegration of an infected oyster body. Experimental studies by Stein, Denison, and Mackin (1961), who used diseased *O. lurida,* give no evidence that *Hexamita* is a highly pathogenic parasite because there was no significant difference in the mortality between the experimental and control specimens.

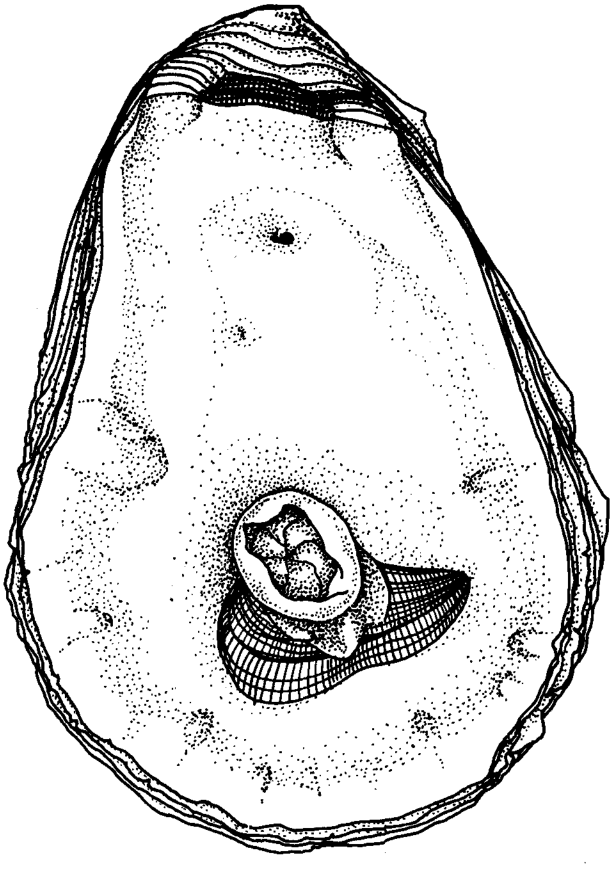

FIGURE 378.—Large cyst filled with blood cells, bacteria, and debris of muscle tissue in *C. virginica.*

Nematopsis

Cysts of the gregarine *Nematopsis* are frequently found in the tissues of several European bivalves including *O. edulis, Mytilus, Cardium, Donax, Tellina, Mactra, Solen,* and others (Dollfus, 1922). Observations by Louis Léger (quoted from Dollfus) showed that vegetative stages of the gregarine are often found in the kidneys and that the spores with sporozoites are usually located in the gills. Léger also showed that the intermediary hosts are the crabs *Carcinus moneas* and *Portunus depurator. Nematopsis* develops in the intestinal canal of the crab and forms cysts which are rejected into water and are transmitted with water currents. There was no evidence that *Nematopsis* is pathogenic.

The species *N. ostrearum* from *C. virginica* has been described by Prytherch (1940), who found the parasite in the oysters of Virginia, North Carolina, and Louisiana. He expressed the belief that mortality of oysters in Virginia and Louisiana was directly caused by this gregarine. *Nematopsis* is widely distributed throughout the waters from the Chesapeake Bay states to Louisiana. Its distribution indicates no correlation with oyster mortalities in that area (Landau and Galtsoff, 1951).

Trematodes and parasitic copepods

The trematode, *Bucephalus haimeanus* Lac. Duth., is occasionally found in *O. edulis* and *C. virginica.* According to Tennent (1906), who studied its life history, the worm thrives in oysters of brackish water and is inhibited by an increased salinity. In cases of heavy infestation, the gonads and digestive diverticula are almost completely replaced by cercariae and by the long germ tubes of the sporocysts, which after their liberation infest *Menidia*, other small fishes, and *Tylosurus marinus*. Destruction of the gonad is the most obvious pathological effect caused by *Bucephalus*. So far this trematode has not been suspected of causing mortalities in oyster populations.

The parasitic copepod *Mytilicola intestinalis* is common among mussels of the Mediterranean. Another species, *M. orientalis*, infests *C. gigas* and *Mytilus crassitesta* of the Inland Sea of Japan. The parasitic copepod is found in the intestinal tract of bivalves and is easily recognized by its red color and relatively large size which makes it visible to the naked eye. In the United States *Mytilicola orientalis* is widespread in lower Puget Sound, occurring in *O. lurida* and *C. gigas, Mytilus edulis, Paphia staminea*, and *Crepidula fornicata*. Infection is heaviest in the common mussels, often reaching 100 percent in some areas (Odlaug, 1946). A single specimen of *Mytilicola intestinalis* was found by Pearse and Wharton (1938) in *C. virginica* on the Gulf coast of Florida. The presence of *M. orientalis* in *O. lurida* in the lower Puget Sound area interferes with their fatness, but apparently inflicts no serious injuries to oyster stocks. In *C. gigas* the copepod produces metaplastic changes in the gut, completely destroys the ciliated epithelium, and penetrates the underlying connective tissue (Sparks, 1962).

The presence of parasites in adult oysters makes them unmarketable for esthetic reasons and, therefore, detracts from the commercial productivity of oyster bottoms.

Any disease factor, regardless of the identity of the pathogen, can be evaluated by determining the percentage of the infected oysters, the intensity of infection, the loss caused by the mortalities, and the decrease in yield of marketable oysters.

COMMENSALS AND COMPETITORS

The shell and body of the oyster are the natural abodes for many plants and sedentary animals which attach themselves to the shell surface or bore through it to make for themselves a well-protected residence; some settle on the soft body without penetrating its tissues while others invade the inner organs. The difference between the commensals, i.e., organisms which share the food gathered by the host, and the parasites, which live at the expense of their hosts and sometimes inflict serious injuries, is not very sharp. Some commensals may cause injury to the host and become parasites.

Competitors are those organisms which live in close proximity to each other and struggle for the space and food available in the habitat. Some appear to be innocuous while others by virtue of their habits and high reproductive capabilities are harmful.

Boring Sponges

Small round holes on the surface of mollusk shells indicate the presence of the most common animal associated with the oyster, the boring sponge. There are seven species of the genus *Cliona* along the Atlantic Coast of the United States. In a case of heavy infestation the shell becomes brittle, breaks under slight pressure, and reveals conspicuous tunnels and cavities filled with yellow sponge tissue. Microscopic examination shows a typical sponge structure with numerous siliceous spicules from 150 to 250 μ long, of the type called tylostyles, and small skeletal elements of different shapes and sizes known as microscleres. Species identification is based on the type of cavities or galleries made by the sponge and the shape and sizes of the spicules (Old, 1941). Small fragments of shell material at the holes by *Cliona* may suggest mechanical action of the sponge. Warburton (1958) found experimentally that sponge cells in contact with a surface of calcite form a reticulum of fine pseudopodia and filaments. A corresponding pattern of lines is etched into the mineral, and the marked areas are of the same size and shape as the fragments discharged by the sponge. Apparently the cytoplasmic filaments penetrate the calcite by secretion of minute amounts of acid and undercut fragments which are carried out by excurrent canals of the sponge.

It is not known whether boring sponges use the organic component (conchiolin) of the shell, but it is obvious that they do not draw their nutrients from the body of the oyster. The sponge touches the surface of the body only in cases of old, heavy infestation. In such instances the holes made by the sponge are rapidly covered by a deposition of conchiolin. The holes made by the sponge are clearly visible on the inner surface of the valve under a newly deposited layer of conchiolin (fig. 379). The race between the sponge and the oyster

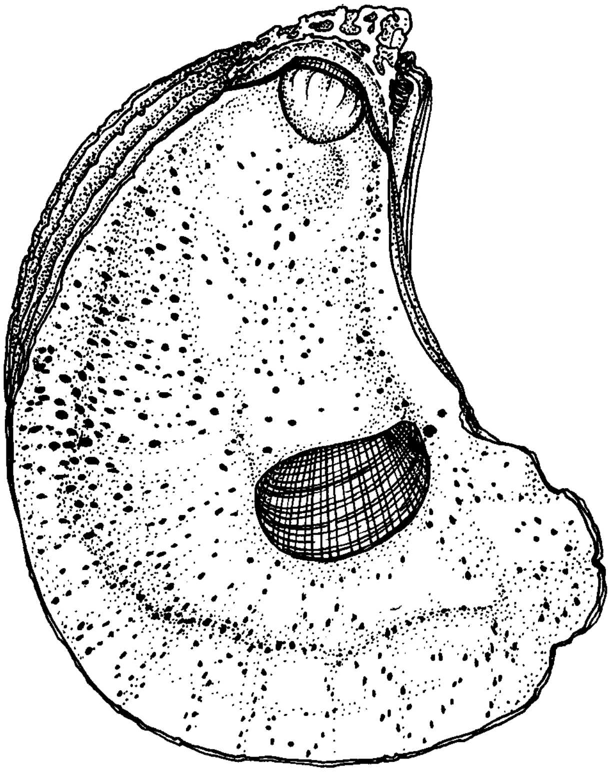

FIGURE 379.—Left valve of adult *Crassostrea virginica* heavily infested by boring sponge, *Cliona celata*. Woods Hole.

continues, and in most cases the oyster's protective measures prevent direct contact between the sponge and the mantle. However, should the deposition of shell material be delayed by adverse conditions, the sponge makes direct contact with the mantle and produces lysis of the epithelium and underlying connective tissue. Dark pigmented pustules form exactly opposite the holes in the shell. This extreme case observed in oysters kept for several months in the laboratory is shown in fig. 380. The tissue of these oysters is flabby, and the mantle is easily detached from the shell surface.

All oyster bottoms are, to a certain degree, infested by boring sponges which are found in both live oysters and empty shells. There are certain areas, however, where the infestation is particularly heavy and the growth of the sponge is very rapid. After the death of an oyster the sponge continues to grow on the shell, forming large, irregular masses 2 or more feet wide and several inches thick. About 30 years ago such large specimens were common in the bays and harbors of southern Cape Cod, but now they are found only in deep offshore waters. The effect of the boring sponge can be estimated by determining the percentage of oysters with heavily infested and brittle shells and by comparing their solid and glycogen contents with those of uninfested oysters.

Boring clam

Oyster shells in the south Atlantic are often infested with a boring clam, *Diplothyra smithii* Tryon of the family Pholadidae. Many papers on oyster biology refer to this clam as *Martesia* sp., but the taxonomy of the family revised by Turner (1955) corrects the nomenclature and restricts the name *Martesia* to wood-boring clams.

The boring clam *D. smithii* is about one-half inch long. It is usually found inside the shell material in a cavity which increases in size with the growth of the clam. The range of distribution extends from northern Cape Cod (Provincetown, Mass.) south to the east and west coasts of Florida, Louisiana, and Texas. I have found no live clams in oyster shells during my long-continued studies in New England waters, and only a few live specimens have been recovered from dead oyster shells around Tangier Sound in the Chesapeake Bay. In southern waters the boring clam is very common, particularly on some reefs on the Texas coast. In 1926 oysters from Matagorda Bay, Tex., were found to be so heavily infested by *Diplothyra* that over 200 clams of various sizes were found in a single adult (fig. 381). In order to make this count the shell was dissolved in hydrochloric acid and the bodies of the clams were collected.

As the cavity bored by the clam increases and approaches the inner shell surface, the oyster protects itself by depositing layers of conchiolin over the nearly perforated areas. Very rarely does one find an oyster in which there is a direct contact between the clam and oyster mantle. On the outer surface of the shell the presence of clams is indicated by small holes. The weakening of the shell structure is the main effect of the boring clam on the oyster.

Mud worms

Of the several species of Polydora found in the intertidal zone of the Atlantic and Pacific coasts of the United States, only two, *P. websteri* Hartman and *P. ligni* Webster, are important to oyster ecology. *P. websteri* is found in oyster shells and on the inner surfaces near the valve

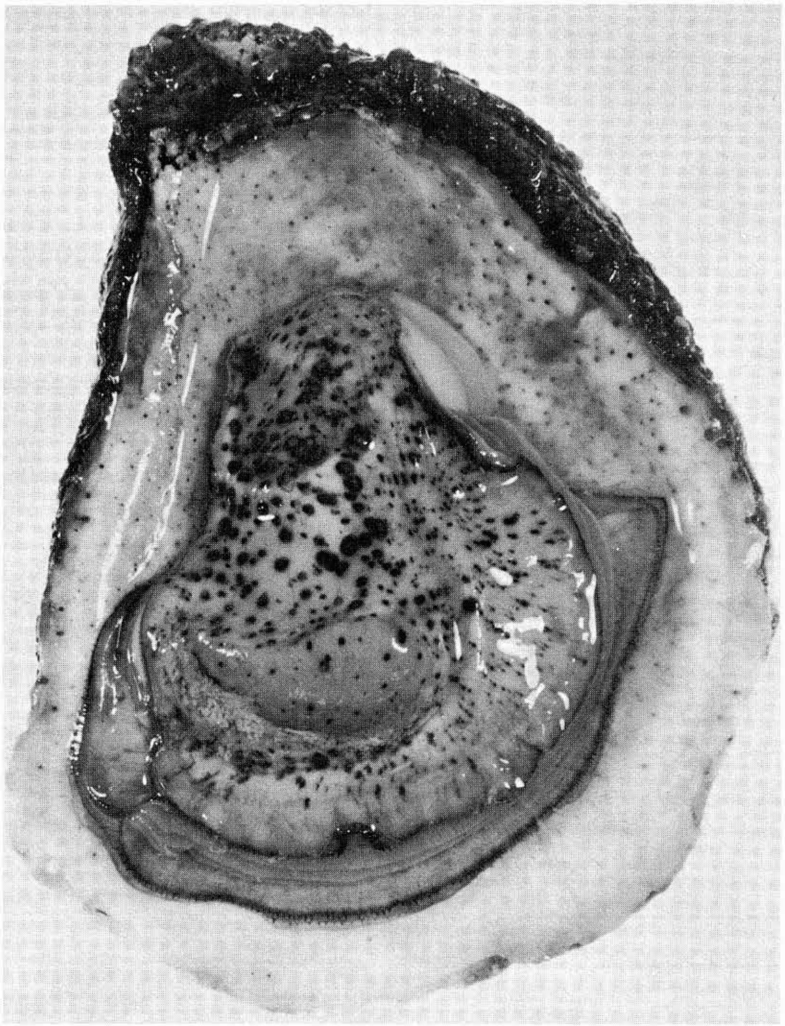

FIGURE 380.—Black pustules on the surface of the visceral mass and mantle of *C. virginica* caused by contact with boring sponge, *Cliona celata*. Photograph of an oyster kept in the laboratory tanks at Woods Hole.

edges. The worm accumulates mud and builds a U-shaped tube which is covered by semitransparent shell material secreted by the oyster. The formation is usually called a blister. *P. ligni* is abundant on tidal flats where it can be found living in small mud tubes or in crevices of waterlogged wood structures and other submerged objects. The mud worm may be indirectly destructive to oysters, for when many worms settle on shells they can smother an entire oyster population with their tubes. *P. ciliata* (Johnston) has been accused of extensive mortalities of oysters in New South Wales, Australia (Roughly, 1925). Frequent reports of finding this species on the coast of eastern America are based on erroneous identifications and probably should be referred to as *P. websteri* (Hartman, 1945). Korringa (1951b) finds no serious injuries by *P. ciliata* to oysters (*O. edulis*) in Dutch waters and thinks that in many areas the damages were caused by *P. websteri* and *P. hoplura*.

Knowledge of the life histories of *P. websteri* and *P. ligni* is incomplete. Both species lay eggs in capsules attached to the inner walls of the tube in which the animal lives. The egg-laying was noticed in the Woods Hole laboratory when *P. ligni* were placed in small glass tubing of appropriate length and diameter (fig. 382). The process of egg laying has never been observed in spite of frequent examination of several tubes during both day and night (Mortensen and Galtsoff, 1944). However, egg capsules were found attached to the walls of the tubes shortly after *Polydora* were left undisturbed in darkness.

The eggs develop within the capsule until the larvae have acquired three pairs of setiferous segments; then they leave the tube. At a temperature of 21° to 23° C. the development of *P. ligni* under laboratory conditions varied from 4 to 8 days. Larvae of *P. websteri* (fig. 383) also have three setiferous segments. According to Hopkins (1958), planktonic larvae, presumably *P. websteri*, occur in Louisiana waters throughout the year; eggs were found in the tubes when water temperature ranged between 12° and 18° C.

The duration of the pelagic life of either species of *Polydora* is not known. The planktonic larvae grow and develop additional segments before they settle on the substratum. Since the largest *P. websteri* worm found in plankton had 17 segments and the smallest found on oysters also had 17 segments, it is probable that this species settles at that age. The appearance of young *P. ligni* at an early bottom stage is shown in fig. 384.

The larvae of *P. websteri* settle on the rough exterior surface of young oysters and make shoe-shaped burrows near the extreme edge of the valves. As the worm grows it enlarges its burrow. The process of excavation is probably chemical, apparently similar to that described by Wilson (1928) for *P. hoplura* and by Hannerz (1956) for *P. ciliata*.

The tubes of *P. ligni* are made of mud particles held together by mucus secreted by the antennae and the body surface. Ciliary motion along the tentacle grooves serves as an efficient mud-gathering device. Experimental evidence shows that if the lumps of mud are too large or if particles consist of the finest sand or foreign materials such as corn starch or powdered glass, the ciliary motion is reversed and the material is rejected. These laboratory observations prove that the worm is capable of selecting the substances needed for the building of a soft tube.

The tube inhabited by the worm, whether U-shaped or straight, is lengthened by the worm at both ends. To accomplish this *P. ligni* reverses its position in the tube by folding itself halfway and sliding over its own ventral side. The process, frequently observed in the Woods Hole laboratory, is accomplished with great speed and remarkable ease.

The amount of mud which *P. ligni* can accumulate in the formation of their tubes is astonishing. A sample collected on June 8, 1944 from the tidal flats of Delaware Bay contained about 430 closely packed worm tubes per square inch of mud area. They all lay nearly perpendicular to the surface. A cubic inch of the washed and dried sample weighed 20 g., of which 12.8 g. consisted of mud with the balance made up of sand, empty shells, and organic matter. On this basis it is estimated that the worms gathered 4.9 pounds of dry mud

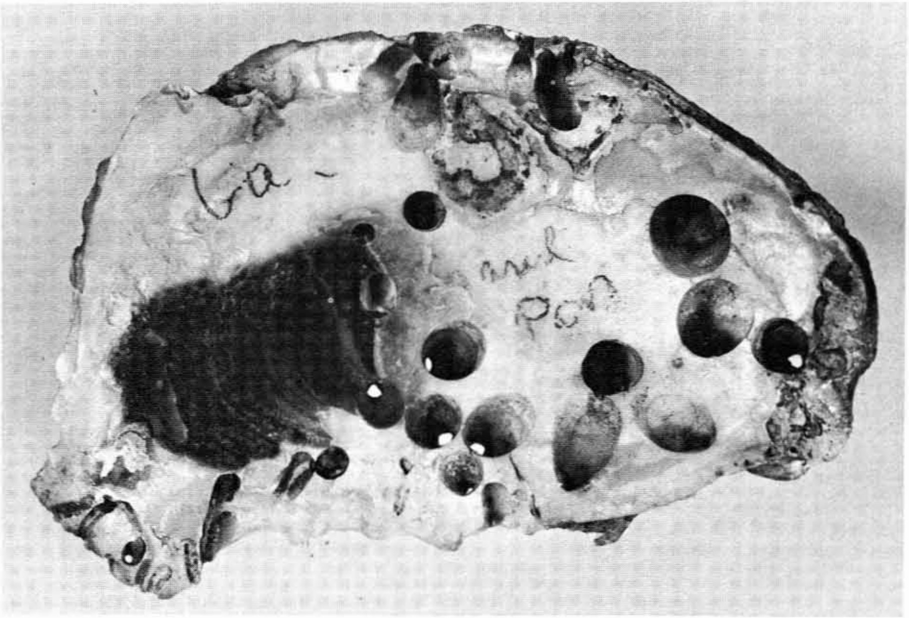

FIGURE 381.—Photograph of an adult *C. virginica* from Matagorda Bay, Tex., heavily infested with *D. smithii*. The outer layer of the shell was chiseled off to expose the cavities.

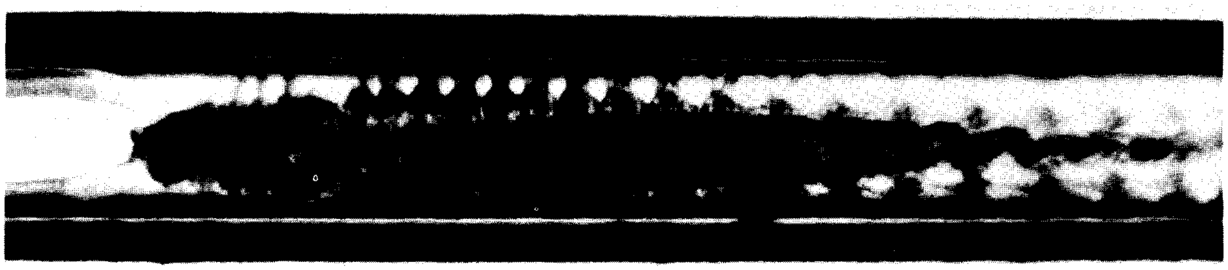

FIGURE 382.—Photograph of live *P. ligni* lying quiescent inside a glass tube. Dorsal view.

per layer of surface 1 square foot in area and 1 inch deep.

Since *P. websteri* is confined in oysters to mud blisters and does not come in direct contact with oyster tissues, it causes no visible injuries. This view is corroborated by the observations of Loosanoff and Engle (1943), who found that oysters heavily infested with *P. websteri* and grown in trays above the bottom were in excellent condition.

However, personal observations made in Seaside, Va. and in Texas bays convinced me that oysters heavily infested by mud worms (fig. 385) are usually in poor condition. This opinion is shared by Lunz (1940, 1941), who calls the mud worm a pest in South Carolina oysters. According to his observations, 20.9 percent of the oysters growing on the hard surface of tidal flats are infected, and the percentage increases to 51.9 on soft, muddy bottoms above low-water mark. There is no

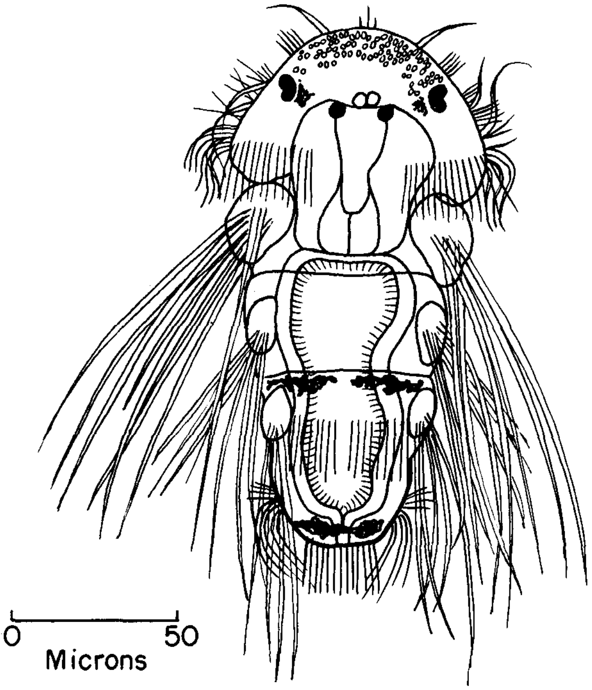

FIGURE 383.—Drawing of newly emerged larva of *P. websteri* viewed alive from the dorsal side. From Hopkins, 1958.

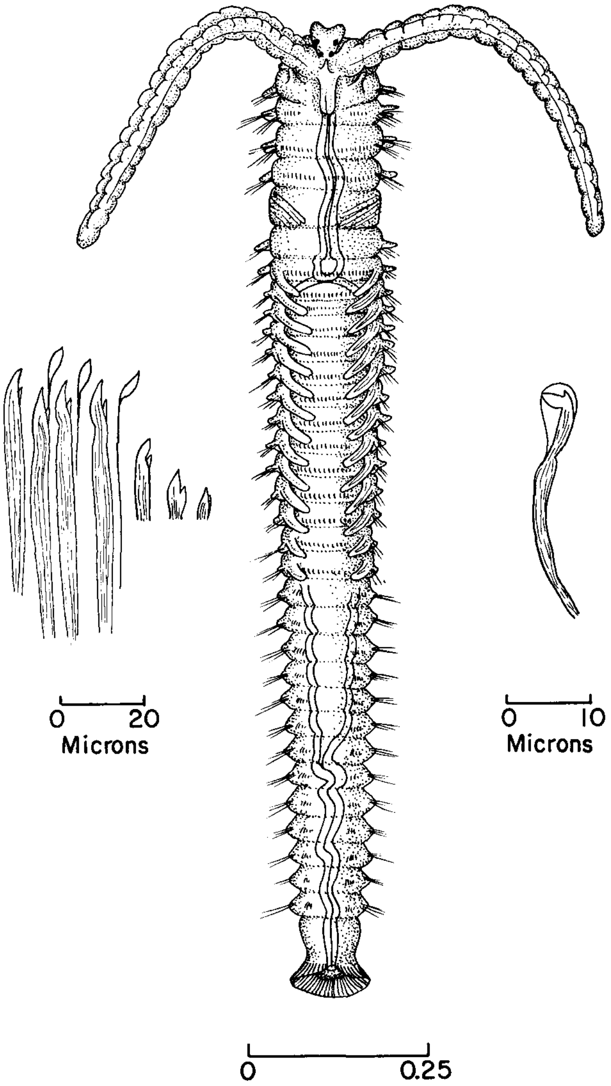

FIGURE 384.—Young "bottom stage" of *P. ligni* Webster. Modified bristles from fifth segment at left, and ventral hooded crochet at right. From Fauvel, 1927.

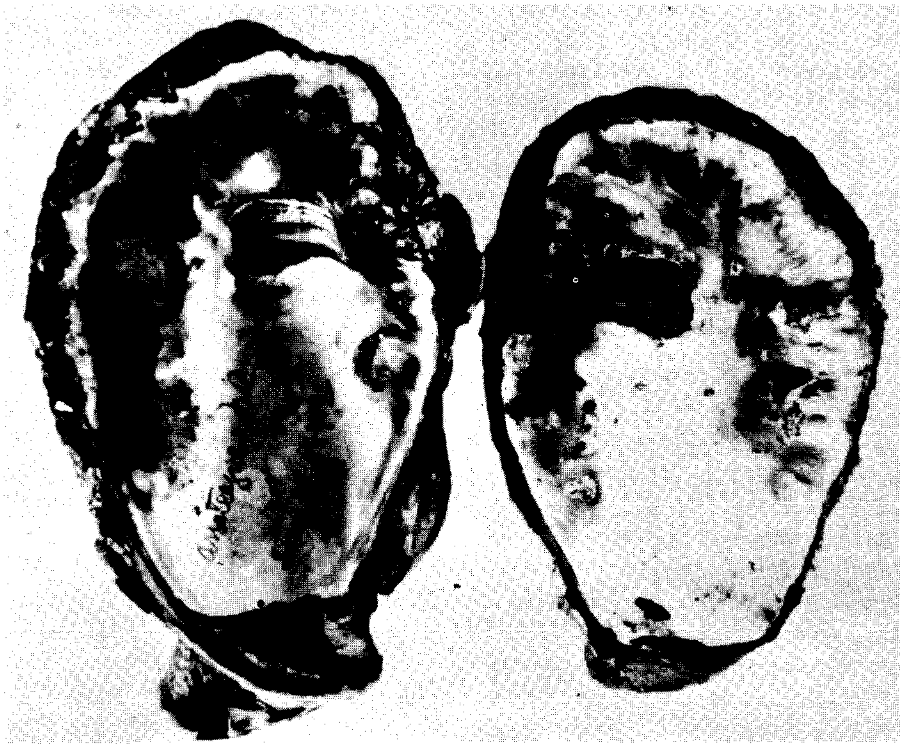

FIGURE 385.—Oyster shells with mud blisters made by *P. websteri* from the grounds at Assateague Island, Va.

evidence, however, that infestation by the mud worm constitutes a serious menace to the oyster population.

Oyster Crab

Several species of the large family Pinnotheridae, commonly called oyster or pea crabs, are associated with oysters, mussels, and other bivalves. The adult females have been known since ancient times and were first described by Aristotle. The males of the American species, *Pinnotheres ostreum* Say, are much smaller than the females and are rarely seen. Usually one or two adult crabs per oyster can be found, and the percentage of infestation varies from zero in some New England waters to about 77 percent in New Jersey. The latter figure, quoted from Christensen and McDermott (1958), refers to the "invasion" of the oyster crab on certain grounds of Delaware Bay. The oyster crab is also abundant in Virginia waters, where its life history has been studied by Sandoz and Hopkins (1947). Some oysters contain a surprisingly large number of these crabs; the maximum reported in a seed oyster was 262 (Stauber, 1945).

Larvae of the oyster crab are pelagic until late summer. At this time larval development is completed, the first crab stage is reached, and the small crabs invade the mantle cavities of oysters. At this time the carapace width of the young crabs ranges from 0.59 to 0.73 mm.

The female crab may be found in various parts of the water-conducting system of the oyster, but settles chiefly on the surface of the gills, in the promyal and suprabranchial chambers, and grows with the growth of the host. The males are not permanently attached to their host and may leave to enter other oysters for copulation.

For many years the oyster crab has been considered an innocuous commensal; however, the female crabs which have settled on the oyster erode its gills and impair their function. More serious lesions may develop and cause leakage of water from the tubes, which further reduces the efficiency of the food collecting apparatus and of the gills. Rapid regeneration of the damaged gills probably saves many oysters from death, but interference with the normal gill functions causes a relatively poor condition in many infested oysters.

Spirochaetes

Tissues of oysters are often infected by spirochaetes which may be found in the stomach, crystalline style sac and in the gonads after spawning. Dimitroff (1926) identified 10 species and found that 91 percent of the oysters sold in Baltimore, Md. were infected. He reported the following species: *Saprospira grandis* Gross; *S. lepta, S. puncta; Cristispira balbiani* (Certes); *C. anodontae* Keysselitz; *C. spiculifera* Schellack; *C. modiola* Schellack; *C. mina; C. tena;* and *Spirillum ostrae* Noguchi. The species are harmless to oysters and man.

Perforating algae

The empty shells of oysters and other mollusks found on tidal flats and on the bottom are frequently perforated by various algae. Bornet and Flahault (1889) gave a detailed description and illustrations of several species, some of them also found in the carapaces of crabs. Live mollusks do not escape the attacks of perforating algae. *O. edulis* of various ages living in the channel of Saline de Cagliari, Italy, were found to be infested by three species: *Hyella caespitosa* Bornet and Flahault; *Mastigocoleus testarum* Lagerheim; and *Gomontia polyrrhiza* (Lagerheim) (Agostini, 1929). The algae penetrate the periostracum, then spread across the prismatic layer, and form branching threads in the inner layer of shell. Apparently the growing tips of the filaments dissolve the calcium carbonate of the shell and make possible the expansion of algae which, in severe cases of infestation, spread through the entire valve and become noticeable by the greenish color of the valve's inner surface. The color cannot be rubbed off the surface since the alga is separated from the oyster and does not come in direct contact with its body. The algal filaments can be studied on fragments of shell or after decalcification in acid.

Gomontia polyrrhiza, continuously distributed along the Atlantic coast, has been reported from North Carolina and Connecticut, to New Brunswick, Canada, growing in empty shells along the shores and occasionally found in live *Spirorbis* and barnacles (Taylor, 1937).

Live oysters infested with perforating algae are occasionally found in shallow bays and estuaries of Cape Cod. The inner surfaces of the valves are bluish-green. At Woods Hole I saw under a microscope a network of perforating algae resembling *Gomontia* and probably mixed with other species. The plants have not been positively identified.

Perforating algae do not appear to be harmful to oysters. Continuous growth in empty shells accelerates the disintegration of the shells and the return of calcium salts to the sea.

Fouling organisms

Many sedentary marine organisms use oyster shells as a convenient place to attach, either permanently or temporarily. They do not penetrate the shell nor do they inflict any direct injury on the oyster, but they do compete with it for food and space and sometimes smother the oyster by their accumulated mass. The most conspicuous among them is the American species of slipper shell, *Crepidula fornicata* (L.), which received international notoriety because of the havoc it caused for oyster growers in Europe.

Various species of *Crepidula* are very common gastropods found attached to hard objects near or below low water. *C. fornicata* does not present a problem to oyster growers in the United States, although sometimes in certain estuaries, as in Cotuit Bay, Mass., it becomes a nuisance because of its extraordinary abundance. Slipper shells settle on oyster shells and tend to form a spirally curved chain of individuals, the sexes of which change from female to male (fig. 386).

The lowest and, therefore, the oldest members of the chain are always females. The uppermost are males, and those between the two extremes are hermaphrodites, which undergo changes from female to male. To the biologist the species is of interest because the alteration of sex which takes place in this mollusk offers an excellent opportunity for experimentation. Grounds heavily infested with *Crepidula* are, therefore, of great value as a source of material for marine biological laboratories. Oyster growers do not share this enthusiasm because the presence of large numbers of unwanted slipper shells requires additional work in cleaning the oysters before delivery to market.

On many occasions *C. fornicata* has been introduced to Europe with the shipment of live oysters from the United States. It has established itself in Essex, Northumberland, Falmouth, England, and in South Wales. In 1929 the first specimens of *C. fornicata* were noticed in the Oosterschelde, Netherlands, and in 1932 to 1933, according to Korringa (1950), the situation became alarming. The mollusk spread to the German and Dutch

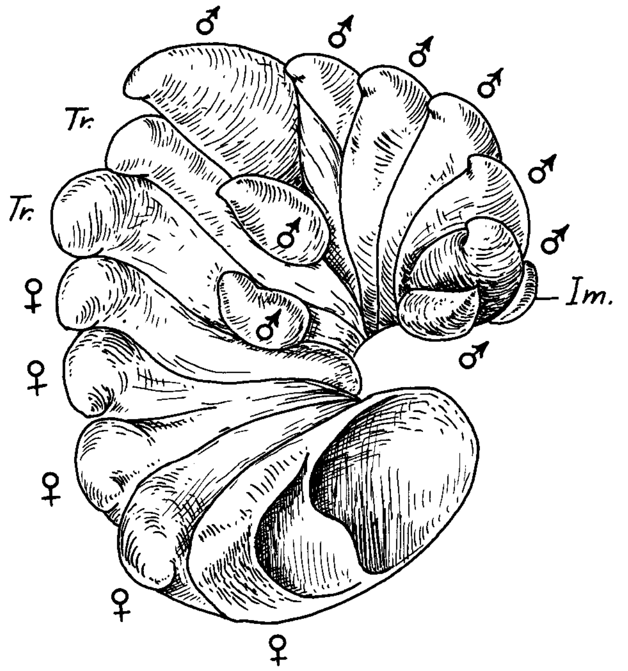

FIGURE 386.—Chain of *C. fornicata*. Female mollusks, the oldest of the group, are at the bottom; the males occupy the uppermost position with the hermaphrodites (tr.) between the two groups. From Coe, 1936.

Wadden Zee and the Limfjord in Denmark, where it successfully competed for space and settled on scattered shells, making it impossible for the larvae of *O. edulis* to set on them. Furthermore, a large amount of silt and soft mud was deposited by *Crepidula* and rendered the bottom unsuitable for oyster planting.

The story of *C. fornicata* is an excellent illustration of the possible danger of introducing a foreign species, which under new conditions, and in the absence of natural enemies and diseases, may reproduce and survive at a rate which upsets the natural balance of nature.

Other fouling organisms may be of a seasonal nature. Some of the oyster bottoms along the Atlantic coast of the United States are often covered with millions of tunicates of the species *Molgula manhattensis* (De Kay). This ascidian can be so abundant in a dredged sample that the oysters are hidden under the gray mass of tunicates. I observed this condition in the mouth of Chester River, Md.; undoubtedly it occurs in other places along the coast. The fouling by *Molgula* is seasonal; the organism dies and the remnants are sloughed off in the fall. Among the 29 species of invertebrates collected from oysters suspended from a raft in the water of Oyster River, Mass., four species constituted the largest portion of the biomass: *Molgula manhattensis*, *Botryllus schlosseri*, *Amphitrite ornata*, and *Balanus balanoides*. The worm *Amphitrite* was found in typical tubes of mud about one-quarter-inch or more in diameter.

At the height of the fouling season in August, the weight of the animals and plants and of sediment accumulated by them comprised 44 percent of the total weight of a string of oysters. The death of *Molgula* in October and the sloughing off of its cases reduced the weight to 11 percent. Later on in November the weight increased to about 17 percent because of the growth of the remaining organisms.

The shells of living oysters are frequently covered with encrusting Bryozoa. In New England waters and in Chesapeake Bay the appearance of Bryozoa usually precedes the time of setting of oyster larvae. When the oysters complete their development, the shell surfaces may be covered with Bryozoa colonies and unsuitable to receive the set of spat. There is a possibility, not fully substantiated, that a great many oyster larvae are eaten by Bryozoa, and Osburn (1932) thinks they are detrimental to the oyster beds in Chesapeake Bay. Marie Lambert made a faunistic study of the Bryozoa collected during the summer on live oysters in the Oyster River near Chatham, Mass. She recorded two species of Endoprocta and five species of Ectoprocta. The most common on oyster shells were *Bowerbankia imbricata* and *Schizoporella unicornis*. The latter is an encrusting bryozoan (fig. 387) commonly found on oyster grounds of Connecticut, part of Long Island Sound (Hutchins, 1945), and Chesapeake Bay.

Dense setting of barnacles on oyster shells is very common throughout the range of distribution of *C. virginica*. In many instances, the space that would have otherwise been available to oyster larvae is already occupied by barnacles, or the spat becomes covered with barnacles and fails to grow. Barnacles have no adverse effect on adult oysters.

The assemblage of invertebrate species found living in close association with the oyster reflects the fauna of the region and naturally differs from place to place. In some areas oysters may be almost entirely free of fouling organisms, while in others their shells are hidden under a heavy mass of siliceous sponges, hydroids, compound ascidians (*Botryllus*), and Bryozoa.

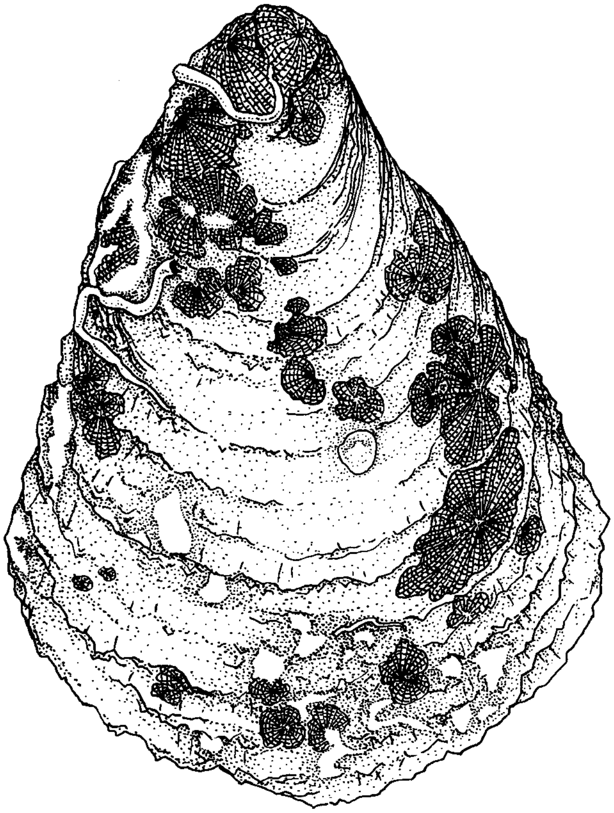

FIGURE 387.—Oyster from Oyster River, Chatham, Mass., covered in part by the colonies of the bryozoan *Schizoporella unicornis* and the compound ascidian (white spots) *Amaroucium constellatum.* Fouling is beginning; within a few days the surface of the shell may be completely covered with these two animals.

The fouling is always seasonal, and with the onset of cold weather many animals and plants die and slough off. Possibly because of the periodicity of fouling, the oysters survive and with few exceptions are not affected by the organisms growing on their shells. An exception is the invasion of oyster beds by mussels (*Mytilus edulis* L.), which in several situations may completely cover an oyster bed with a thick layer of mud mixed with excreta.

A number of annelids are commonly associated with oyster communities, living between clusters of oysters or in the shells. Sometimes a surprisingly large number of worms crawl out of the shell crevices when Epsom salt is added to the water in which oysters were kept. Hartman (1945) lists seven species of annelids inhabiting the spaces between clusters of living oysters. Korringa (1951b) describes more than 30 species of annelids which in Dutch waters live on or in the shell of *O. edulis.* Except for the boring Spionidae, the worms apparently cause no direct harm to oysters, but some of the mud-gathering species of Nereidae materially increase the deposition of sediment over an oyster bed. No evidence has been found of any other adverse effects of annelids on oyster communities.

Various siliceous sponges are very common members of the epifauna of oyster bottoms. With the exception of the boring sponges, they do not affect oyster populations. The red sponge, *Microciona prolifica,* is often found on highly productive oyster bottoms.

Of the protozoa that live on oyster shells, the stentorlike infusorian, *Folliculina* sp., commonly inhabits brackish water beds. This relatively large protozoan, measuring from 200 to 800 μ, lives in bottle-shaped cases attached to the leaves of *Elodea,* and *Potamogeton* found in the mouths of rivers and on shells of other mollusks. During the warm season it rapidly multiplies and appears swimming with other plankton. Mass occurrences of folliculinids in the Chesapeake Bay were recorded by Andrews (1915) and in Oosterschelde, Netherlands, by Korringa (1951a). Different species are widely distributed in the coastal waters of the United States (Andrews, 1944). The number of this infusoria found attached to a single oyster shell has varied from one to several hundred.

In many localities along the eastern shore of the United States, oyster beds are frequently overgrown by various algae. *Gracillaria confervoides* (Linnaeus) Greville is one of the species which sometimes completely covers an oyster bottom with its thick growth. Huge masses of the plant wash away from the home grounds and pile on beaches. Of the many other algae found growing on oyster shells, several are in some regions as abundant as *Gracillaria: Enteromorpha, Ulva, Griffitsia, Ceramium, Chondria, Champia,* and *Scytosiphon.* During experiments on raft culture in Oyster River near Chatham, Mass. in 1956 to 1959 (Shaw, 1962), the shells of young oysters suspended in water became covered with a very dense growth of *G. confervoides.* Since there was no noticeable ill effect on the oysters, an examination was made of the periphyton, the organisms living loosely attached to the plant's branches. The prevailing form was found to be a diatom *Lycosoma* sp., which was not present in the river plankton outside the immediate area occupied by *Gracillaria.* The stomach content of the oysters consisted of many *Lycosoma*, some half-digested, and of *Skeletonema*, which was also abundant among the branches. It is apparent that some constituents of the periphyton may be ingested and that the microscopic flora of the environment provides a substantial amount of food not available in true phytoplankton.

Some of the seaweeds cause unexpected damage to commercial oyster grounds. *Colpomenia sinuosa* (Toth) Derbes and Solier, a common seaweed in many parts of the word, is one of them. It grows along the Pacific Coast of North America from Alaska to southern California, along the eastern coast of Australia and in France. The thallus of *Colpomenia* is of a papery texture and hollow; it can grow attached to oyster shells to the size of a hen's egg or tennis ball. On sunny days at low tide in shallow water photosynthesis may be so intense that gas bubbles fill up the thallus, and on the return of the tide the inflated balloon floats out to sea carrying with it the young oysters. In 1906 *Colpomenia* became such a nuisance on the western coast of France at Vannes that the oystermen called it "oyster thief." The floating oysters carried out by the ebb current were not returned to shore with flood tide, and the losses were severe enough for local oystermen to organize the recapture of oysters with nets and to tear off the inflated algal ballons by dragging faggots over the bottom (Church, 1919).

In 1961 the seaweed, *Codium fragile* subsp. *tomentosoides* (Goor) Silva, was introduced to Cape Cod waters with oysters brought from Peconic Bay, Long Island, N.Y. This Pacific Ocean species, not indigenous to Massachusetts, occurs in abundance along the western coast of Europe. It is not known how the alga was introduced to Long Island where in January 1957 it was found at East Marion attached to dead *Crepidula* shells (Bouck and Morgan, 1957). In Oyster River, near Chatham, Mass., where the Long Island oysters were planted the shells were covered with a luxuriant growth and had to be thoroughly scrubbed before being shipped to market. The following year the plants were so large (fig. 388) that on sunny days they acted as "oyster thieves" by lifting the oysters from the bottom with gas-filled branches and floating them off with the tide.

Eel grass, *Zostera marina*, frequently covers the

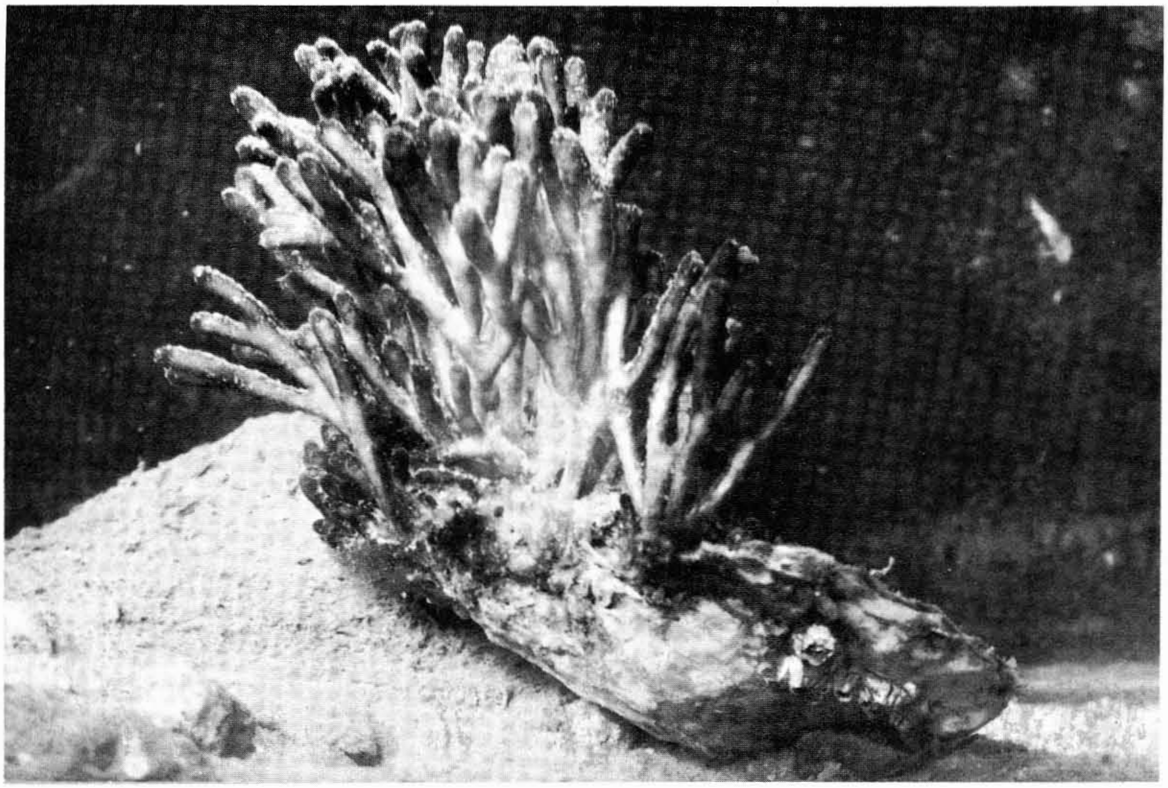

FIGURE 388.—*C. fragile* introduced into Oyster River, Chatham, Mass., with oysters from Long Island. Two-year-old plant.

entire oyster bottom but apparently exerts no ill effect on oyster populations. This is not the case, however, with another aquatic plant, the Eurasian watermilfoil, *Myriophyllum spicatum*, which by 1933 was established on the Virginia and Maryland sides of the Potomac River; since 1959 it has increased rapidly in the Chesapeake Bay area, including the Potomac River, and is found also in the fresh and nontidal waters above Washington D.C. In recent years the growth of the plant has become spectacular and is a threat to brackish water oyster grounds, which may become covered with a heavy layer of decomposing leaves and stems of the milfoil (Beaven, 1960; Springer, Beaven, and Stotts, 1961).

The effect of commensals and competitors on the productivity of an oyster bottom can be evaluated for each species if the intimate relationship to the host is clearly understood and the relative abundance of a species is determined. A single species which appears to be innocuous under normal conditions may become destructive and dangerous because of its mass development. All these conditions should be evaluated in order to express their effect in numerical terms. Commensals such as bryozoans, barnacles, and tunicates so completely cover the shell surface that the settlement of young oysters upon it is prevented. Thus the negative effect of fouling may be considered in relation to the productivity of setting grounds. On the other hand, in southern waters where setting continues for the greater part of the year and oysters become overcrowded with successive generations of young, the reduction and prevention of settlement of spat may be beneficial because it reduces overcrowding and permits better growth and fattening of oyster stock. The struggle for space is an essential factor in the life of an oyster community.

PREDATORS

The list of many enemies that prey on oysters includes flatworms, mollusks, echinoderms, crustaceans, fishes, birds, and mammals. Not all of them are equally destructive to oyster populations. The most dangerous are those which prefer oyster meat to other types of food, and in search of it invade the oyster grounds.

Carnivorous gastropods

The deadliest enemies of oysters are various gastropods inhabiting coastal waters. The most widely distributed species is the common oyster drill, *Urosalpinx cinerea* (Say), which is found along the entire Atlantic Coast from Canada to Florida. With a shipment of *C. virginica* the common oyster drill was introduced to the Pacific Coast of the United States (1870 and the following decades), and to Great Britain (1920 and probably earlier) where the American oysters were planted at Brightlingsea and West Mersea. In a short time the drill became very abundant along the coast of Essex and across the Thames estuary. At present *Urosalpinx* is the most dangerous and the most widely distributed of all the predators of oysters in Europe.

Oyster planting by shellfish growers is the major factor in the wide dispersal of *Urosalpinx* in this country and its introduction into areas which formerly were free of the pest. The migration of drills is rather limited. When hungry, they may move at an average rate of 15 to 24 feet per day in the direction of food. To a certain extent the drills are dispersed by floating objects to which they may cling and by hermit and horseshoe crabs which have been seen bearing as many as 140 drills per animal (Carriker, 1955).

The drill is particularly destructive to young oysters. In Cape Cod coastal waters, which are infested by these snails, the oyster spat has very little chance of surviving the first year; often small seed oysters are wiped out before the end of the second year. Adult oysters with thick shells suffer less, and the losses sustained during 1 year by the 4 and 5 year classes are insignificant. There are many localities in Long Island Sound, on the eastern shore of Virginia between Chincoteague and Cape Charles, and in other regions where drills commonly kill 60 to 70 percent of the seed oysters and sometimes annihilate the entire crop.

Fortunately, brackish water effectively bars the drills from the upper parts of estuaries and tidal rivers. Survival of drills in water of low salinity depends on temperature and on the concentration of salts to which they were adjusted. It may be accepted as a general approximation that minimum survival salinities at summer temperatures vary from 12°/₀₀ to 17°/₀₀ in different regions.

Extensive literature on the biology and control of oyster drills has been critically reviewed by Carriker (1955), who has also made a detailed study of the structure and function of the proboscis and drilling apparatus of the drills (Carriker, 1943).

The maximum height of adult drills varies in different localities between 25 and 29 mm.; a giant form reaching 51.5 mm. in height is found in the area of Chincoteague Island, Va., and is considered a subspecies *U. cinerea follyensis* (fig. 389). As the common name indicates, the *Urosalpinx* attacks oysters and other mollusks by drilling a round hole in the shell. The hole, usually made in the upper (right) valve of the oyster, tapers toward the inner surface; the shape of the hole identifies the attacker, and the presence of drilled empty shells on oyster grounds is reliable evidence of the inroads made by the snail on an oyster population.

For a long time boring was considered an entirely mechanical process. Observations made by Carriker (1961a) showed that both chemical and mechanical actions are involved. Secretion from the accessory boring organ, called ABO for short, softens the shell, probably by an enzyme acting on the conchiolin, and the softened material of the shell is removed by abrasive action of the radula. Active drilling continues for a few minutes and is followed by a long period lasting up to an hour of chemical action during which the ABO gland remains in contact with the shell.

The oyster is not the only victim of drills. They show preference, in fact, to barnacles, and usually stop drilling oysters if a rock covered with live barnacles is placed near by. A well-developed chemical sense permits the drills to distinguish between young and adult oysters. If both kinds are offered to hungry snails kept in a large tank with running sea water, the majority of active drills will choose the young oysters. The drills are positively rheotactic and in running water orient themselves against the current. The orientation is not, however, precise and the path of a moving drill is a meandering line only generally directed against the current.

Light has an effect on the orientation of drills. They move away from a strong source of light, but move toward it at lower intensities (Carriker, 1955). In dim light, the phototactic response is lost. In laboratory tests at Woods Hole, I noticed no orientation of drills toward the window side of the tank; the drills distributed themselves at random. They have a tendency to climb away from the bottom (negative geotaxis) and congregate on rocks, pilings, and on the wall

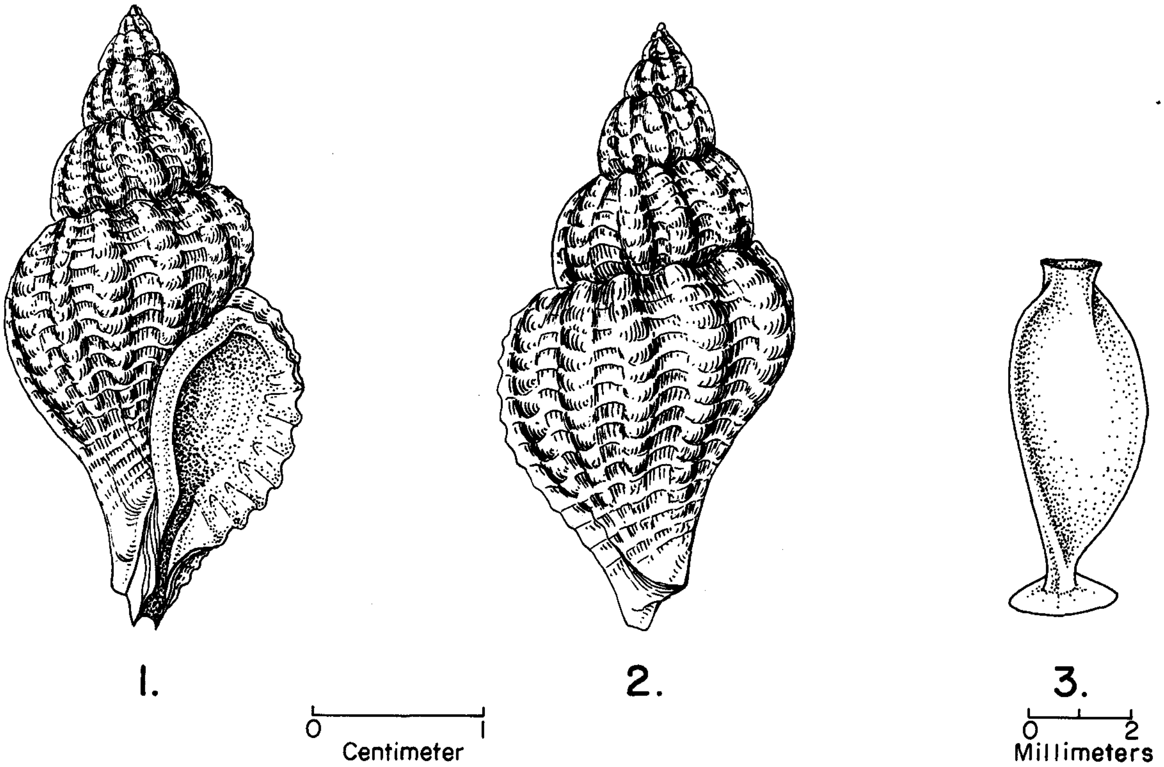

FIGURE 389.—*U. cinerea follyensis* from Chincoteague Island region, Va. 1—apertural view; 2—abapertural view; 3—egg cases.

of tanks. Drills put in the bottom of a vertical glass tube about 1 inch in diameter and 6 to 8 feet tall, filled with sea water, will climb to the top of the tube and remain there. Negative geotaxis is pronounced, particularly during the reproductive period. At this time drills climb on any objects above the bottom level and ascend rocks and various underwater structures to lay their eggs, which are deposited in tough, leathery capsules (fig. 389, 3). The egg-laying period depends on geographical location and local conditions. Summarizing the data from various sources, Carriker (1955) estimates that the number of egg cases deposited by one drill per season ranges from 0 (in an immature female) to 96 for older females. In Woods Hole harbor, the breeding season lasts from the end of June to the middle of August. The number of egg cases deposited by a single female kept in laboratory tanks varied from five to nine; the average number of eggs in each case was nine. The number of eggs per egg case varied in different localities from eastern Canada to Chesapeake Bay from 0 to 22 and from 1 to 29 in British oyster beds. (Cole, 1942).

A second species of drill, *Eupleura caudata* (Say), (fig. 390), is found in the same waters as *Urosalpinx* but is usually less abundant. Various observers estimate that in different locations it comprises from 2 to 29 percent of the total drill population (Carriker, 1955). The behavior of *Eupleura* is similar to that of *Urosalpinx.* Its food habits have not been studied, but occasional observations in the laboratory indicate they are probably not different from those of *Urosalpinx.*

In the York River, Va., where the growth and reproduction of *Eupleura* were studied by MacKenzie (1961), the snail becomes active as the temperature rises over 10° C. Spawning begins late in May at 18° to 20° C., reaches a peak in June and early July at 21° to 26° C., and ends in early August. Mature females (kept in cages) deposit an average of 55 cases, each containing an average of 14 eggs. In the absence of mortality, each female *Eupleura* may produce over 700 young drills each season. The leathery egg capsules are vase-shaped with two distal projections (fig. 390, 3) and are easy to distinguish from the egg cases of *Urosalpinx* (fig. 389, 3).

Conchs of the genus *Thais* occur on both the Atlantic and the Pacific coasts. The snails have strong polymorphic tendencies and form local races which greatly complicate the taxonomy of the species. A review of the speciation problem of *T. lamellosa* Gmelin made by Kincaid (1957)

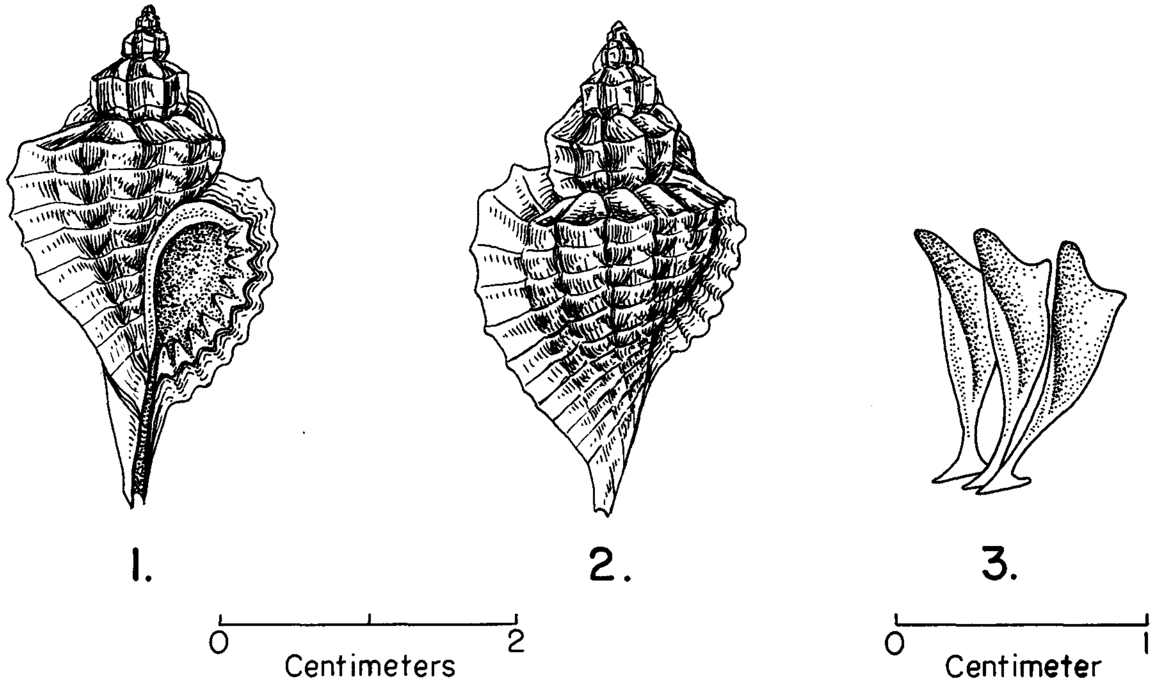

FIGURE 390.—*Eupleura caudata* (Say) from 1—apertural side; 2—from abapertural side, 3—egg cases.

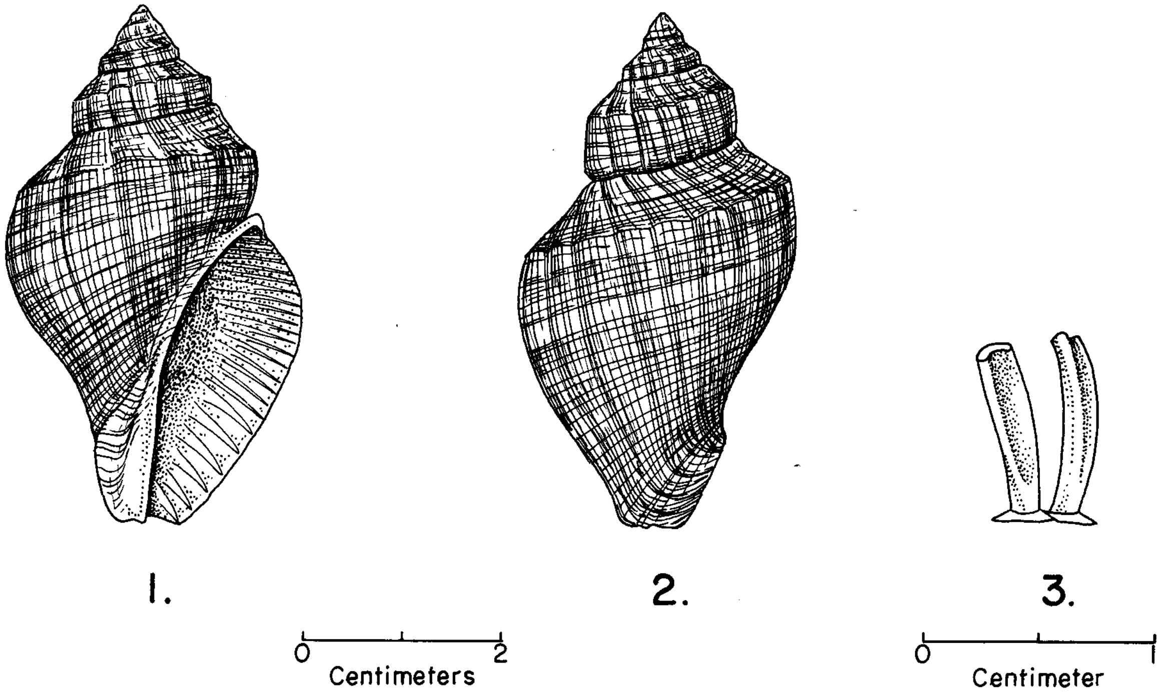

FIGURE 391.—*T. haemastoma floridana* Conrad from the shores of Pensacola Bay, Fla. 1—apertural view; 2—abapertural view; 3—egg cases.

contains interesting material regarding this and other species of the genus.

T. haemastoma is a common oyster predator in the waters of the South Atlantic and Gulf states. There are two subspecies, *T. haemastoma floridana* Conrad, which occurs from North Carolina to Florida and the Caribbean (fig. 391), and *T. haemastoma haysae* Clench (fig. 392), common on oyster grounds of northwest Florida, Louisiana, and Texas (Clench, 1947). *T. haemastoma floridana* is a medium-size gastropod with a relatively smooth shell and a single row of low spines. *T. haemastoma haysae* is a large, rugged snail, sometimes measuring 4½ inches in height. It can be distinguished from the other subspecies by double rows of prominent spines around the whorls and spire.

The behavior of the two varieties apparently is similar. The conchs feed on oysters and other mollusks, penetrating their shells from the edge by using the ABO gland or by drilling holes in the shell (Burkenroad, 1931; Carriker, 1961a). The entrance at the edge of the valves is often inconspicuous and may be easily overlooked.

Conchs multiply very rapidly because of their great fecundity and high survival rate of larvae. *Thais haemastoma* lays eggs in groups of about 800 to 975 enclosed in each egg case, with each female depositing more than 100 cases. These figures refer to my laboratory observations on conchs kept in captivity. The eggs are deposited in horny and transparent egg cases of a creamy color, which becomes brownish and finally turns reddish-purple. The breeding season in Louisiana waters begins by the end of March and reaches its peak in April and May. There is usually a rapid decline of egg laying in June and a complete cessation of reproduction in July. At the beginning of the breeding period the conchs become very active and develop a strong tendency to climb on structures and rocks to attach their egg cases above the bottom. Because of this behavior they can be trapped during the breeding season on stakes which the oyster growers erect on the grounds. Gregariousness is very pronounced, and many conchs can be trapped in this way in a relatively short time. The number of egg cases attached to a single stake may be enormous. One stake which I obtained as a sample was covered with a solid mass of egg capsules over a 5-foot length; the estimated number of cases was about 8,000. The incubation period is not known definitely, but judging from the growth of hydroids and other fouling animals on the conch cases, I believe it is not less than 2 weeks.

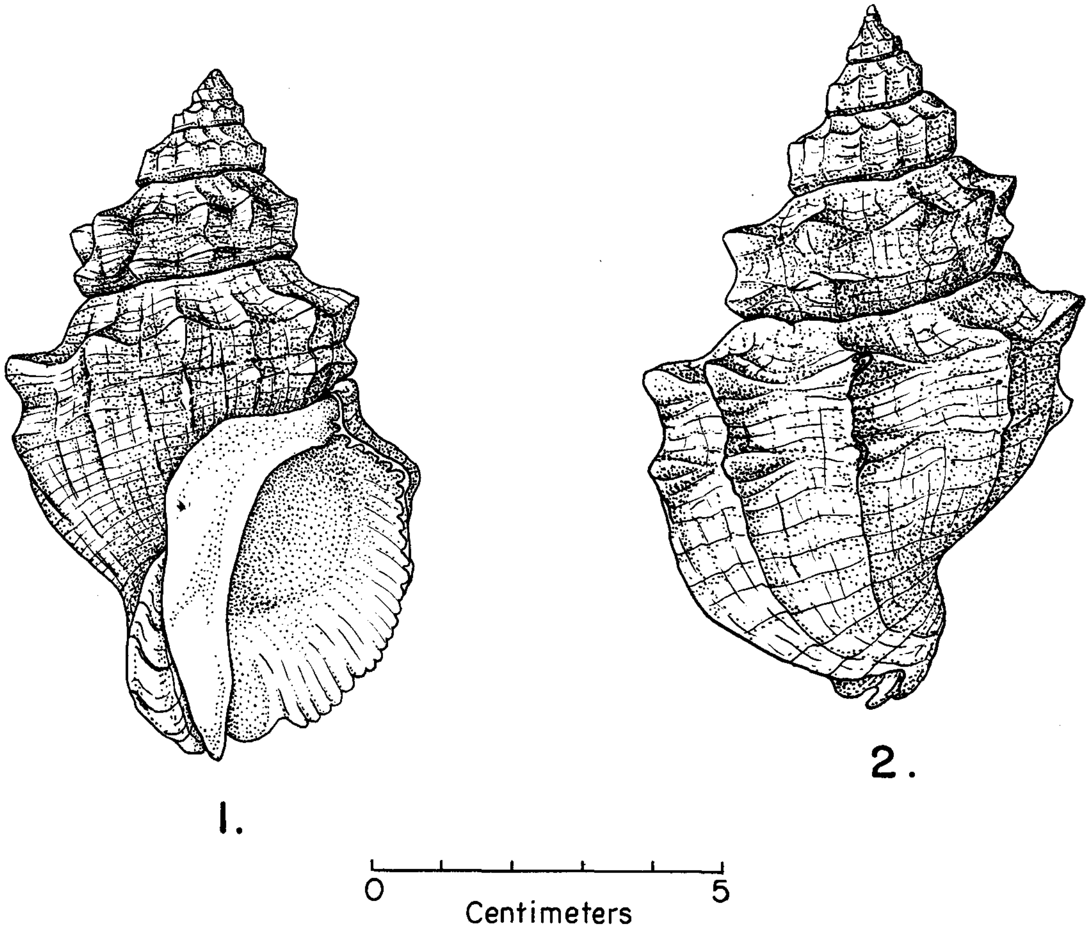

FIGURE 392.—*T. haemastoma haysae* Clench from Bastian Bay in the lower part of the Mississippi River delta. 1—apertural view; 2—abapertural view. Natural size.

The larvae that escape from the egg capsules are veligers, which pass through a free-swimming period of unknown duration, and are widely dispersed by tidal currents before they settle on the bottom and begin attacking small oysters and other bivalves.

The distribution of *Thais* is checked by fresh water. The conch is immobilized by a salinity of 10°/oo, and a 1- or 2-week exposure to a salinity of 7°/oo kills them (Schechter, 1943).

The effect of sudden changes in water salinity on the rate of crawling of *Thais* was corroborated by my observations at the Bureau of Commercial Fisheries Biological Laboratory at Gulf Breeze in northwestern Florida. The crawling of these snails in the tanks was automatically recorded on a kymograph. The movements stopped immediately when the salinity of the water was artificially reduced from 15°/oo or 17°/oo to 8°/oo or 9°/oo. The snails became active again when the salinity returned to the former level.

Two species of conchs found on oyster grounds of the Pacific coast are *Thais lamellosa* Gmelin (fig. 393), a native snail, and *Ocenebra* (*Tritonalia*) *Japonica* Dunker (fig. 394), introduced from Japan. *T. lamellosa* has been considered by some fishery biologists as a predator on *O. lurida*, but Kincaid (1957) discards this view as not substantiated by his 50 years of familiarity with the marine fauna of the region. He states that since *T. lamellosa* feeds mainly upon barnacles and mussels, the snail should be classified as "the only invertebrate friend" of the oyster, presumably because it destroys its competitors. Chapman and Banner (1949) found that under experimental conditions *T. lamellosa* drilled some *O. lurida*, but that in a natural environment it showed a preference for mussels (*Mytilus edulis*).

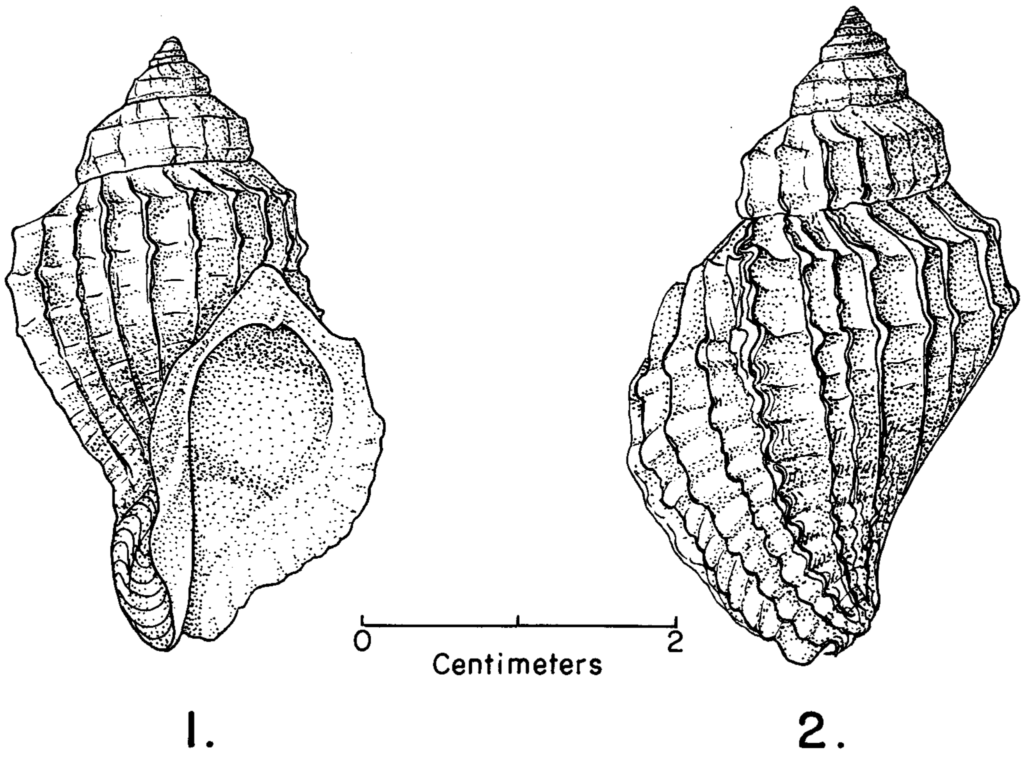

FIGURE 393.—*T. lamellosa* Gmelin, a native species of the Pacific coast of the United States. 1—apertural view; 2—abapertural view.

The Japanese species, *Ocenebra japonica*, is far more dangerous than the native snail. Mortalities due to devastation by this snail are estimated at 15.4 to 22.6 percent. The first specimens of *O. japonica* were introduced into the waters of Puget Sound with the planting of Japanese seed oysters, a practice which began in 1902 and 1903 and which reached considerable proportions by 1922 when from 1,500 to 4,000 boxes, each containing about 5,000 seed, were planted annually. In October 1928 while examining the oyster beds in Samish Bay, Wash., I found a number of *O. japonica* Dunker (Galtsoff, 1929, 1932), and warned oystermen and state officials of the possible damages that could result if the practice of bringing infested seed oysters from Japan was continued. The warning received no attention. In the late 1940's *Ocenebra* was well established in the waters of Puget Sound and became a serious menace to the native oysters. When given a choice of food, *Ocenebra* prefers *O. lurida* and Manila clams, *Venerupis japonica*, to *C. gigas* (Chew, 1960). It drills holes in the shell by combined chemical and mechanical action (Carriker, 1961a). The fertility of the species is high, the female laying an average of 25 egg cases, each containing about 1,500 eggs. The egg cases are often found in the inaccessible crevices of the concrete walls of dikes surrounding the Olympia oyster beds. Salinity of 18°/oo adversely affects *Ocenebra*, and brackish water of less than 12°/oo salinity is lethal.

Large conchs or whelks, *Busycon carica* Gmelin and *B. canaliculatum* Linné, are common in the shallow water of the Atlantic coast and occasionally attack oysters and open them by inserting the edge of the shell between the valves and forcing them apart (Colton, 1908). Carriker (1951) reinvestigated the problem and found that penetration of shells of oysters and clams is a purely mechanical process which consists of chipping by the edge of the conch's shell combined with rasping of the radula. The shell edge of an oyster destroyed by these conchs bears the marks of the attack (fig. 395). In the northern part of Cape Cod, *Busycon* seems to attack the oyster in preference to other mollusks, annelids, or dead fish, which they are known to consume. Local depredations on oysters observed in the Cape Cod area (Shaw, 1960, 1962) may be severe enough to warrant trapping of conchs during their reproductive

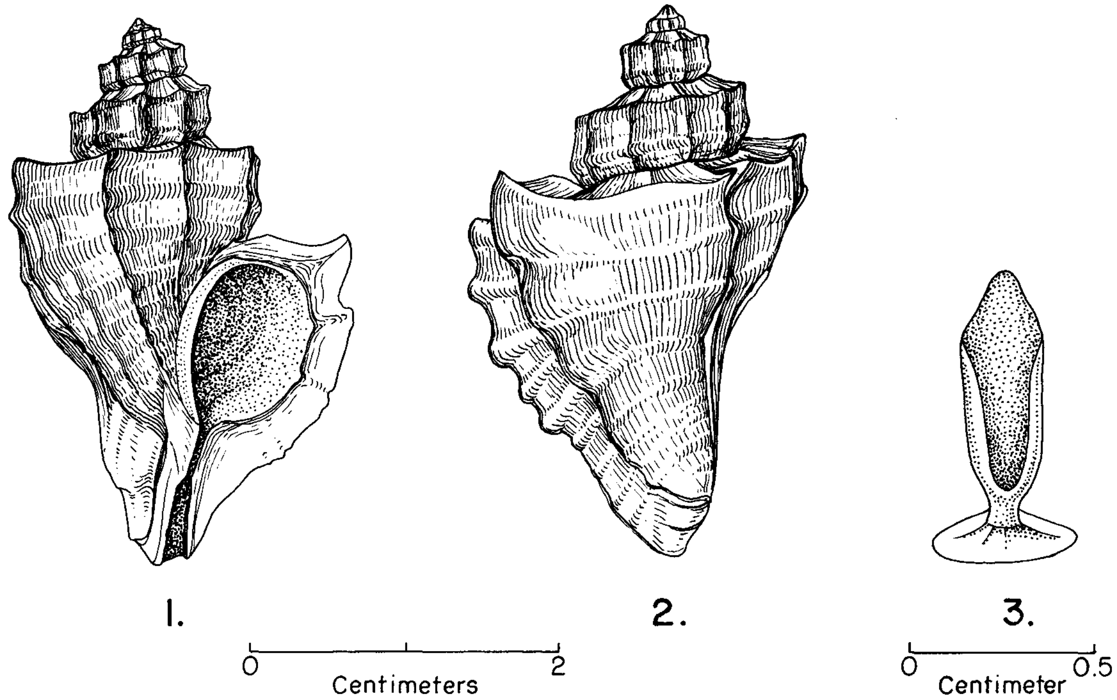

FIGURE 394.—*O.* (*Tritonalia*) *japonica* Dunker, Japanese species from oyster bottom of Puget Sound, Wash. 1—apertural view; 2—abapertural view; 3—egg case.

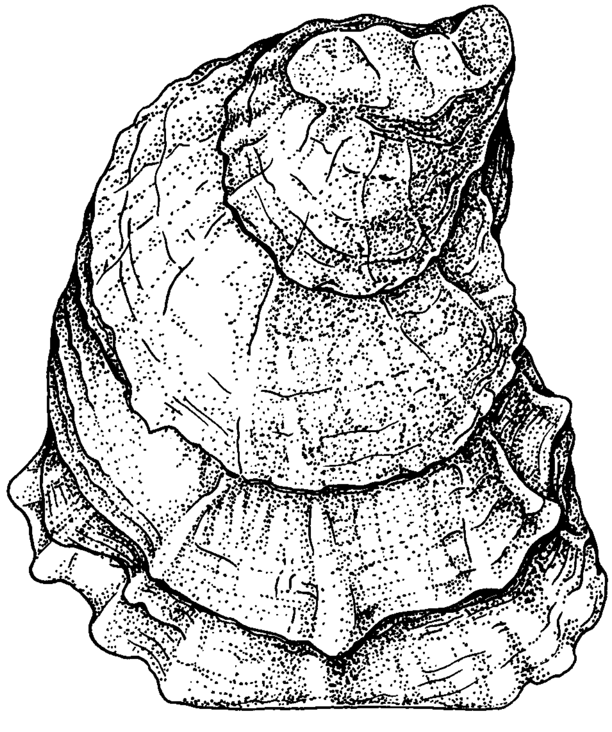

FIGURE 395.—Edge of the shell of an oyster killed by *Busycon* in Oyster River, Chatham, Mass. Straight line at the lower edge of the shell indicates the place of rasping by the conch's radula after the valves were chipped.

cycles. In Cape Cod estuaries, egg cases of conchs are a familiar sight on tidal flats at low water (fig. 396). Under experimental conditions the conchs were found to consume in summer about three adult oysters per week (Carriker, 1951).

Small parasitizing pyramilid snails of the genus *Odostomia* (*Menestho*) congregate in large numbers at the very edge of oyster shells. When the valves are open, the snails extend their pro-

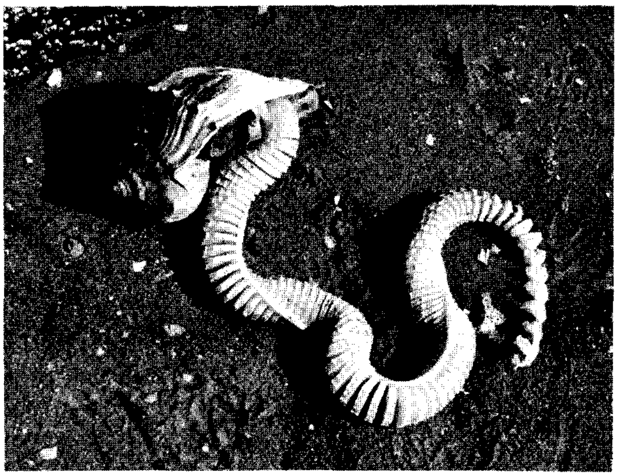

FIGURE 396.—*B. carica* depositing egg capsules at low Tide. Woods Hole.

boscides to the edge of the oyster's mantle and feed on the mucous and tissues. These ectoparasites are probably a great nuisance to the oyster, but there is no evidence that they can be regarded as important enemies. Two species have been found associated with *C. virginica: O.* (*Menestho*) *bisuturalis* Say which has a range from New England to Delaware Bay, and *O.* (*Menestho*) *impressa* Say which is found from Massachusetts to the Gulf of Mexico.

Starfish

The starfish of the Atlantic Coast is also a highly destructive predator on oysters. The common species, *Asterias forbesi* (Desor), is the most familiar animal in tidal pools, on rocks, and beaches of the Eastern Coast of the United States, often found exposed by the receding tide. Accurate statistics of the destruction caused by this species are not available, but a few selected examples emphasize its deadly efficiency. In 1887 the State of Connecticut estimated the loss caused by starfish at $463,000; the sum represented the destruction of over 634,246 bushels of oysters or nearly half of the total harvest for the year (1,376,000 bushels). The numerical strength of a starfish population over a relatively small area can be visualized from the record of only one company which in 1929 removed over 10 million adult starfish from 11,000 acres of oyster grounds in Narragansett Bay.

As a rule the starfish populations on various parts of the coast fluctuate within wide limits with years of great abundance usually followed by relative scarcity. These fluctuations cause many oystermen to believe that starfishes invade their grounds periodically. Studies of the problem conducted simultaneously in Buzzards Bay, Narragansett Bay, and Long Island Sound (Galtsoff and Loosanoff, 1939) demonstrated that sudden increases in the abundance of *A. forbesi* are due primarily to the high percentage of survival of its free-swimming larvae and their successful setting (fig. 397).

The reproductive season of *A. forbesi* in New England waters slightly precedes that of *C. virginica.* When oyster larvae reach setting stage, the space available for their attachment is already occupied by young starfishes only several mm. in diameter, hungry, and ready to attack the spat. The new set of oysters may be completely wiped out by young starfish.

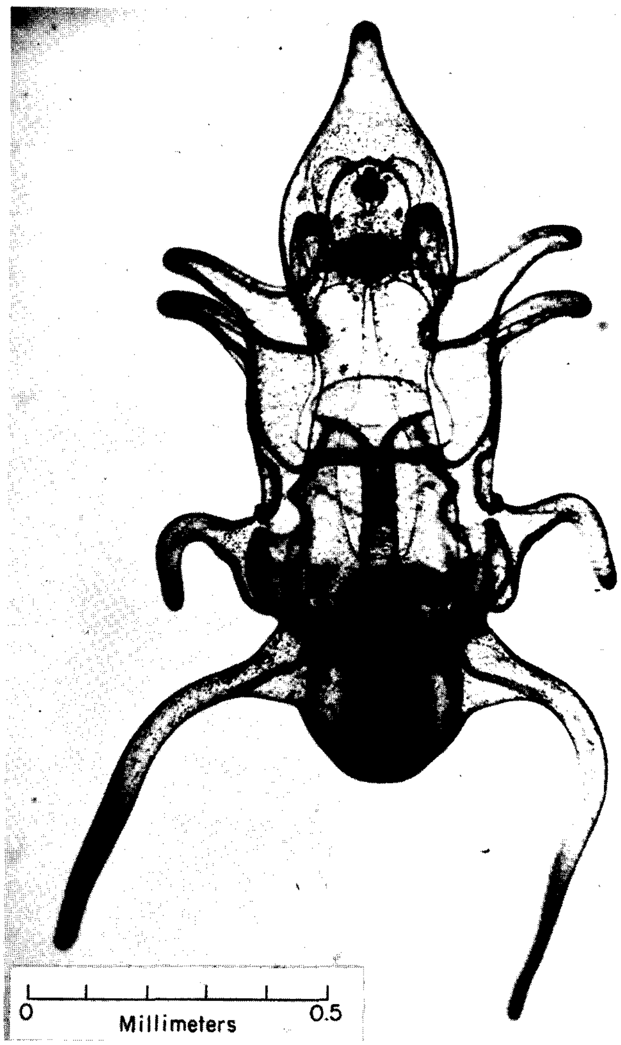

FIGURE 397.—Photomicrograph of live larva, brachiolaria, of *A. forbesi* from a plankton tow in Buzzards Bay.

The movements of *A. forbesi* in concrete tanks are slow, random, and apparently not directed by tactic reactions. Initially it was difficult to reconcile this fact with the experience of oyster growers in Long Island Sound who reported that oyster bottoms thoroughly cleaned by mopping or dredging were invaded within the next 24 hours by swarms of starfish. Underwater observations were made in Long Island Sound by members of the Bureau of Commercial Fisheries Biological Laboratory in Woods Hole who used an underwater television camera. The underwater photographs showed clearly that starfishes are passively transported by the tidal currents which in Long Island Sound are fairly rapid. The animal curls up the tips of the rays, releases its hold on the substratum, and floats just above the bottom.

Many thousands of starfish are transported in this way from place to place and settle on new grounds when tidal currents slacken.

The starfish leaves no identifying marks on its victim, and only empty shells remain as evidence of a destructive attack. The recent death of oysters is indicated by the cleanliness of the valves, which contain no foreign growth and are still attached to each other. The method by which the starfish succeeds in forcing oysters or clams to relax their muscles and open the valves has puzzled biologists for a long time. It seemed doubtful that the starfish could exhaust its victim and open it by main force, and suggestions were made, not well corroborated by observations, that the prey was killed by suffocation or that a substance secreted by the stomach of the starfish produced relaxation of the adductor muscle of the oyster. Sawano and Mitsugi (1932) reported that an extract of starfish stomachs poured over the heart of living molluscs produced tetanus and often inhibited the heart beat; this seemed to give some support to the "anesthetic" hypothesis. Critical experiments made in Woods Hole by Lavoie (1956) show, however, that the effects of extracts prepared from digestive organs of starfish and introduced into the adductor muscle or poured over the heart of *Mytilus* were generally identical with those produced by plain water. On the other hand, the force exerted by the tube feet of starfish in opening shellfish was measured manometrically and was found to exceed 3,000 g. The measurement was made using mussels in which the adductor muscles were severed and replaced by steel springs or plastic cylinders.

Lavoie noticed that a tiny opening of about 0.1 mm. between the valves of the mollusks was sufficient to permit the insertion of starfish stomach. The pulling of valves apart is probably repeated at intervals while the stomach remains partially compressed. The observations of Feder (1955) on *Pisaster ochraceus* show that this starfish can open its prey by force alone. Another Pacific Coast species, *Evasterias troschelii*, was found to exert a force in excess of 5,000 g. during an attack on artificial clams baited with *Mytilus* meat (Christensen, 1957). The fact that starfishes are able to open mollusks by force alone does not eliminate the possibility of an additional narcotizing effect produced by starfish secretion. The problem of how the starfish opens its prey has not yet been finally solved, although present evidence favors the mechanical hypothesis.

Not all starfishes feed by everting their stomachs and digesting the body of the victim without ingesting it. Many of them are scavengers feeding on dead animals found on bottoms while others are capable of catching and consuming live fishes. Many interesting cases of starfish attacks on various marine animals including fishes are described by Gudger (1933).

Starfish are usually found in water of high salinity and do not invade the oyster grounds in brackish waters. The salinity level between 16°/oo and 18°/oo below which *A. forbesi* cannot exist is a natural barrier to the distribution of this species. This conclusion is based on field observations along the Atlantic coast and on experiments at the Bureau of Commercial Fisheries Biological Laboratory, Milford, Conn. (Loosanoff, 1945). In New England waters, starfish are controlled by mopping or dredging to remove them, and by dispersing calcium oxide and other chemicals to kill them or to make a protective chemical barrier around an oyster bed.

Flatworms

Turbellarians of the genus *Stylochus* and *Pseudostylochus*, commonly known as oyster leeches, are predators which attack adult and young mollusks and frequently inflict serious damage to oyster populations. In 1916 and 1917 attacks of *Stylochus* on oysters in Cedar Keys on the west coast of Florida killed about 30 percent and in one or two localities 90 percent of the adult oysters. The mortality of oysters in Apalachicola Bay, Fla., allegedly caused by the "leech," was investigated for the U.S. Bureau of Fisheries by Pearse and Wharton (1938), who could not state definitely that the distruction was due to *S. inimicus* Palombi[10] and suggested that the oysters were first weakened by some unknown cause and that *Stylochus* invaded those which were unable to protect themselves. *S. frontalis* tolerates water of low salinity (6°/oo), but according to Pearse and Wharton does not lay eggs in salinities less than 15°/oo.

S. ellipticus (Girard), found in Atlantic coastal waters and also reported from the Gulf (Hyman, 1939, 1954), lives among oysters, shells, barnacles, and rocks. The turbellarian was reported to destroy young oysters on the flats at Milford,

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[10] The identification was corrected by Hyman (1939) who found that the Florida leech belongs to the species *S. frontalis* Verrill.

Conn. (Loosanoff, 1956). Apparently it has no difficulty in entering oyster spat through the slightly opened valves. On the Pacific coast, the flatworm *Pseudostylochus ostreophagus* Hyman (Hyman, 1955) was reported to cause mortalities of from 6 to 42 percent among the imported Japanese seed oysters on various grounds. The worm bores keyhole perforations in the shells of young oysters (Woelke, 1957).

Crabs

Ryder (1884) was the first to include the blue crab, *Callinectes sapidus* Rathbun, and the common rock crab, *Cancer irroratus* Say, in the list of oyster enemies. He quoted complaints of oystermen working in Great South Bay, Long Island, N.Y., who stated that the crabs eat small oysters up to the size of a 25-cent coin and invade the the oyster planting grounds.

For many years crabs were not mentioned in oyster literature as potential enemies, but in the 1930's and 1940's there were reports from the U.S. Bureau of Fisheries Biological Laboratories at Milford, Conn., and at Pensacola (Gulf Breeze), Fla., that under certain conditions the blue crab, the rock crab, and the green crab, *Carcinides moenas* (Linneaus) destroyed oysters kept in outdoor tanks or placed in baskets with the crabs. Lunz (1947) reported that at Wadmalaw Island, S.C., the blue crab was probably the most serious pest in 1946 and destroyed more than 80 percent of the young oysters set on collectors. The crab's diet includes a great variety of food, including oysters. There is no evidence that they are attracted specifically by oysters, but it is apparent that they may destroy many small oysters in clusters by cracking their shells.

Mud prawns and fish

Brief mention should be made of the family Calianassidae (genera Upogebia and Callianassa), popularly known as "mud prawns" or "burrowing shrimps", which excavate deep burrows under oyster bed dikes. This activity drains water from the grounds, exposes the beds of *O. lurida*, and smothers the young oysters with material thrown up in burrowing (Stevens, 1928).

In the southern waters of the Atlantic coast, oyster beds are often invaded by schools of black drum, *Pogonias cromis* (Linnaeus), which feed on mollusks and occasionally cause extensive destruction of oysters, leaving behind piles of crushed shells. The fish uses its powerful pharyngeal teeth to crush the shells (fig. 398).

The diamond stingray of the Pacific coast, *Dasyatis dipterurus* (Jordan and Gilbert), also devours oysters, crushing them with powerful teeth. To ward off attacks by this fish, oyster grounds in California are surrounded by high fences, a practice used for the same purpose by French oystermen.

Birds

Various species of ducks are enemies of small *O. lurida* of the Puget Sound area. The extent of damage to oyster grounds near Olympia, Wash., was estimated in the fall of 1928 by the United States Biological Survey. McAtee, who conducted the field studies, reported (quoted from Galtsoff, 1929) that at that time 87 percent of the bluebills (*Nyroca marilla* and *N. affinis*) fed principally on oysters, which comprised 80.5 percent of the bulk of the food found in their stomachs. In 38 percent of white-winged scoters

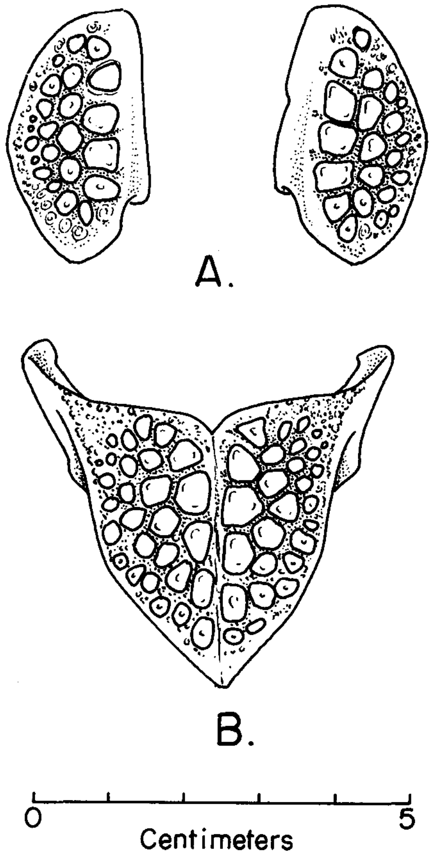

FIGURE 398.—Pharyngeal teeth of small size black drum *P. cromis*, used for crushing oyster shell. A—upper teeth; B—lower teeth.

(*Melamita deglandi*), about 70 percent of their stomach contents consisted of oysters. The number of birds in the Olympia Bay of Puget Sound during the 2-week period of daily observations (November 16–29, 1928) averaged 2,000. Together the three species of ducks were destroying about 8,000 oysters per day and causing material damage to the small oyster industry of the area.

The effect of predators on an oyster population can be evaluated by determining the percentage of oysters killed.

Man

Among the highly destructive predators of oysters, man occupies the most prominent position. Long before our era the stone age dwellers of the coast of Europe subsisted primarily on shellfish which they gathered from shallow water by wading and hand picking. The American Indians used oysters and clams for food, and dried and smoked shellfish meat for the food supplies which they took on their travels. On both continents numerous shell heaps or so-called kitchen middens dot the coastline and indicate the locations of primitive habitations or camp sites. A famous shell heap on the banks of the Damariscotta River, Maine, and many others are evidence of the former productivity of the oyster beds of past centuries. With the development of oyster fishing gear, man became able to gather oysters much more efficiently and extended his efforts to deeper water. Oyster dredges of various designs and dimensions remained for a long time the principal and very effective gear, until the appearance in the last quarter of a century of various mechanical suction pumps and other harvesters of much greater efficiency.

With the improvement of fishing methods, the oyster bottoms of the northern States became overfished and many were depleted. This was the fate of many oyster grounds along the shores of the Gulf of Maine, in New Hampshire, Massachusetts, and Rhode Island. In colonial times the earliest white settlers of New England feared the disappearance of their favored seafood and saw the necessity of protecting their shellfish resources by such legislative measures as restricting the size of catch and prohibiting the selling of oysters out of town. The results were ineffective, and many oyster bottoms, particularly in the northern part of New England, were destroyed.

The world's richest oyster bottoms in the Chesapeake Bay suffered a similar fate, but the depletion was more gradual and not as complete as in more northern waters. Regulations prohibited power dredging and set aside certain areas for the use of tongers only, but they were not sufficient to maintain the productivity of the oyster bottoms. The production of oysters continued to decline because of a general disregard of the basic conservation principle that the sustained yield of any renewable natural resource can be maintained only if the quantity removed does not exceed the quantity restored annually by reproduction and growth. Throughout the world the shellfish resources are depleted when more are taken than nature is able to replace.

Man must be regarded, therefore, as the most dangerous predator. On the other hand, through his action the productivity of an oyster bottom can be brought to the highest level. Since ancient times it has been known that oysters can be propagated and cultivated. The development of oyster culture in this country was particularly successful in the waters of Long Island Sound where the depleted shellfish resources were not only restored by oyster farming, but many thousands of acres of previously barren bottom were converted into productive farms under water. Thus, man as an ecological factor appears in a dual capacity—as a primitive destructor and as a progressive cultivator. Unfortunately, at present Long Island Sound is no longer a highly productive oyster farming area. The decline may be attributed to poor setting, low survival rate of young oysters, devastation caused by several hurricanes, and the high cost of farming operations.

At present the knowledge of oyster biology has advanced to such a level that effective methods can be employed both for sound management of natural, wild populations of oysters, and for development of highly productive farms for breeding selected strains of oysters. The continuous decline of oyster beds is due not to a lack of knowledge but to failure to apply it.

Aquatic resources of the tidal areas along the Atlantic and Gulf coasts of the United States are threatened by human activities other than overfishing. Many formerly productive areas of the coast have been damaged beyond reconstruction by the filling of marsh lands for industrial sites, by the construction of thruways, marinas, real estate developments, and trash and garbage disposal areas, by ever-increasing discharge of domestic sewage and trade wastes, and by numerous contaminants which reach natural waters as a result of widespread and nonselective use of insecticides and pesticides. Danger from the discharge of radioactive materials from nuclear plants and the disposal of low level radioactive wastes in the sea not far from shore presents a new and serious threat to the usefulness of the renewable aquatic resources of coastal areas.

Some of the changes produced by man such as improvement of coastal waters for navigation, construction of hurricane barriers, use of tidal land for building of industrial plants are consistent with rapid population growth and industrialization. Other changes, such as pollution, destruction of natural oyster beds by failure to return shells and other materials needed for the attachment of young oysters, and overfishing are unnecessary and should be avoided.

A balance between the needs associated with industrial progress and population pressure on one side, and effective conservation of natural aquatic resources on the other can and must be found.

POLLUTION

The pollution problem is complex. It has many facets that should be studied from social, economic, and biological points of view. An investigation of the biological aspects of pollution, discussed in this section, deals with the complex ecological relationship between the life in the tidal areas and the environment affected by the addition of a number of organic and inorganic contaminants.

One of the major difficulties encountered in studies of the biological effects of pollution is the lack of a generally accepted definition of the term. Pollution means different things to different people: to a Public Health officer pollution implies a potential health hazard caused by the discharge of domestic sewage and industrial waste; an engineer of a manufacturing plant is primarily concerned with the quality of water needed for the industry; the conservationist has in mind danger to wildlife and means for its protection; sport and commercial fishermen fear that foreign substances discharged into coastal waters will affect the availability of fish; a marine ecologist tries to find out how the animal and plant life is affected by changes in the environment; and the layman, considering that pollution is synonymous with filthy conditions on beaches and in coastal waters, raises his voice in protest against unsanitary and esthetically objectionable situations.

In court litigations involving damages allegedly caused by pollution, a biologist appearing as an expert for either side is handicapped in his testimony either by lack of a legal definition of pollution or by the generalities used to describe it. No definition of the term pollution is given in the Oil Pollution Acts of 1924 and 1961. The Water Pollution Control Acts of 1948 and 1961 (United States Congress, 1948, 1961) make frequent references to the "abatement of stream pollution" and declare in the 1948 act that pollution is a public nuisance "which endangers the health or welfare of persons in a State other than that in which the discharge originates." The inclusion of the word "welfare" puts emphasis on the economic aspects of pollution and, therefore, increases the scope of the definition.

After conducting a comprehensive study of all available State, Federal, and international pollution laws, the U.S. Public Health Service (1950) prepared the following broad definition of pollution:

> "Pollution" means such contamination, or other alteration of the physical, chemical or biological properties, of any waters of the State, or such discharge of any liquid, gaseous or solid substance into any waters of the State as will or is likely to create a nuisance or render such waters harmful or detrimental or injurious to public health, safety or welfare, or to domestic, commercial, industrial, agricultural, recreational, or other legitimate beneficial uses, or to livestock, wild animals, birds, fish or other aquatic life.

Although this definition is broad and useful, it has not been incorporated in existing Federal statutes and, therefore, lacks legal weight.

The amount of waste discharged into coastal waters of the United States from municipalities and industrial plants in the last decade has reached astronomical proportions and is being augmented by runoff water which carries the numerous organic phosphorus and hydrocarbon insecticides used in both control and eradication of agricultural crop-damaging pests. Under present conditions it is probably impossible to find water along our coast which has not been contaminated.

Some pollutants contain highly toxic substances and cause mortalities among marine populations. Others are less toxic and have no lethal effect on adult organisms but decrease the rate of survival of their larvae; decrease the rate of growth of juvenile forms and affect the reproductive capability of an organism. Sublethal concentrations of such poisons can also destroy one or several links of the food chain in the sea, and so affect the food supply for the population of animals or plants important for human welfare. The normal ecological environment may be so changed that some planktonic organisms, most useful to shellfish as food, disappear and are replaced by a luxurious growth of microorganisms not only useless but even harmful to water-filtering mollusks. Although great advances have been made in the technique of bioassays, the results of short-term tests lasting no longer than 72 hours are of little use in determining the effects of prolonged exposures of fish or shellfish to low concentrations of poison. Furthermore, since the criteria for the welfare of marine populations are not known, it is impossible to set requirements for purification of pollutants before they are permitted to be discharged into the sea. The Federal Water Pollution Control Act of 1961 authorizes the Secretary of Health, Education, and Welfare to organize comprehensive programs of investigation which in the course of years will solve many of the existing pollution problems.

Detailed descriptions of all types of pollution that may affect the productivity of oyster bottoms and methods of their detection and control are beyond the scope of the present chapter, which is limited to a discussion of the general principles applicable to the majority of situations and to a description of the most important types of pollutants encountered on oyster bottoms. Bibliographical references listed at the end of the chapter are limited to the more pertinent papers. Discussions of more specialized pollution problems are listed in a bibliography prepared by Ingram (1957) and also appear in papers published in Tarzwell (1957, 1960).

The production of oysters in the United States is declining at a rapid rate (Galtsoff, 1956). As a sedentary animal devoid of any means of locomotion after setting, the oyster is vulnerable to environmental changes which weaken it and make it less resistant to infection. Under natural conditions unspoiled by human activities, the oyster is in an equilibrium with its environment; this adjustment, which may be called a steady state, is the result of thousands of years of adaptation and natural selection. It may be upset by the sudden presence of materials not normally found in sea water or by excesses or deficiencies of its normal components.

Two types of pollution are commonly found on oyster grounds: domestic sewage and trade wastes. In natural waters both types of pollutants undergo gradual changes which lead to a degree of purification, but at the same time deposit sediments that cover oyster beds and change the character of the bottom. Natural purification is not effective, however, in the case of detergents and radioactive waste, which constitute a growing menace to the safety and purity of our coastal waters.

Domestic sewage

Contamination of water by domestic sewage is the oldest type of pollution; it probably began during prehistoric times when man settled on the shores of the rivers and bays and used natural waters as the easiest and most convenient way of disposing of the excrements and unwanted waste. The problem has reached enormous proportions with the population growth and the necessity of disposing of quantities of domestic sewage in an organized manner.

The discharge of untreated domestic waste has a threefold effect. It covers the bottom with a sludge which smothers the oyster bed, affects the normal functions of mollusks by reducing the oxygen content of the water, and at the same time greatly increases the bacterial content of the water. Oysters, in common with other water-filtering mollusks, retain and accumulate these bacteria in their bodies. The degree of pollution is determined by the abundance of *Escherichia coli* found in the water. The bacterium itself is not pathogenic, but is used as an index of pollution. Procedures for determining the abundance of *E. coli*, the so-called MPN (most probable number), are described in great detail in Jensen (1959). They are strictly followed by State and Federal Public Health Officers and other officials responsible for certifying grounds from which shellfish may be harvested for human consumption. Areas in which the MPN of *E. coli* exceed the permissible maximum of 70 per 100 ml. are condemned and cannot be used for harvesting, but under certain specified conditions the polluted oysters and clams can be taken for planting to an unpolluted area. The presence of *E. coli* above the prescribed MPN eliminates the utilization of grounds for commercial fishery, but does not affect the survival and growth of the oyster population.

Industrial waste

The most common industrial pollutants entering oyster-producing areas stem primarily from the following industries: oil; paper; steel; chemicals; paints; plastics; leather; and food. The character of industrial waste varies with the product.

Because of the increase in the number of oil burning ships and the necessity of transporting crude oil in huge tankers that occasionally break and spill their cargo, oil pollution of the open sea has become a difficult international problem. Although federal and state laws forbid the discharge of oil into coastal waters, many of the bays and harbors of the United States are heavily polluted by oil. Through surface tension oil spilled on the surface of water spreads rapidly into a thin film or oil slick. In muddy waters suspended particles of clay and sand absorb oil, coalesce, and gradually sink to the bottom. In shallow waters oil laden sediment is disturbed by waves, and an oil slick reappears on the surface, sometimes considerable distances from the source of pollution. The absence of an oil slick is not, therefore, a reliable sign that water is not polluted. Crude oil absorbed by sediments retains its toxicity to oysters and other organisms for a considerable time (Chipman and Galtsoff, 1949).

With the expansion of the pulp and paper industry along the Atlantic and Pacific Coasts, pollution of coastal waters by red and black liquors, the waste products of this industry, became serious. Both types of waste contain toxic substances which adversely affect oyster physiology. As in other types of pollution, the discarded material is usually oxidizable and has high oxygen demand. It is, however, only in extreme instances of gross pollution that the oxygen content of the water is lowered to the point that it suppresses the principal physiological functions. Poisons, present in trade waste, are more dangerous than the high oxygen demand because they directly affect the function of the various organs. In spite of great variety in the composition of trade wastes their toxic effect can be demonstrated by constructing a toxicity curve which shows how the pollutant depresses the function that was selected for testing. An oyster heart preparation (see ch. XI, p. 247) can be used conveniently because of the great sensitivity of the heart muscle to many poisons and drugs. Another measurable function is the transport of water by the gills for feeding, respiration, and discharge of excreta. This function ceases when the valves are closed. The presence of pulp mill pollutants reduces the number of hours the valves are open in proportion to the concentration of toxic substances in the water. Under normal conditions and at temperatures of 60° to 70° F. oysters remain open on an average of 20 to 22 hours a day. If the logarithm of concentration of black liquor or crude oil extract is plotted against the number of hours closed, the relationship can be expressed by a straight line as shown in fig. 399. Toxic substances of pulp mill effluents and the extracts of crude oil affect the frequency of ciliary beat and so interfere with the coordination of ciliary motion with the result that the pumping capacity of the gills is reduced. The reduction is proportional to the concentration of physiologically active materials (fig. 400). This type of relationship was found in studies on the pollution of oysters by red and black liquor and by water soluble components of crude oil (Galtsoff, 1931b; Galtsoff, Chipman, Engle, and Calderwood, 1947; Chipman and Galtsoff, 1949). The observations on crude oil are in agreement with data reported

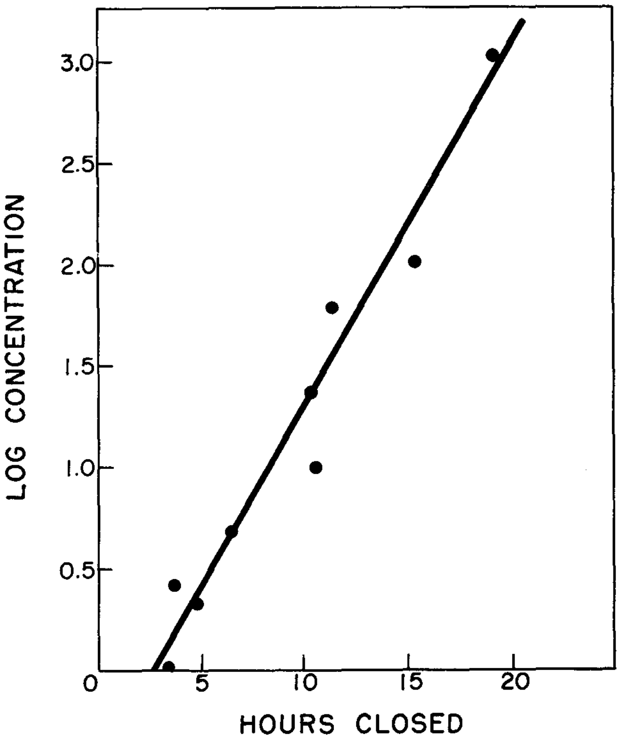

FIGURE 399.—Effect of concentration of pulp mill effluent discharged into the York River on the number of hours oysters are closed during every 24-hour period. From Galtsoff, Chipman, Engle, and Calderwood, 1947.

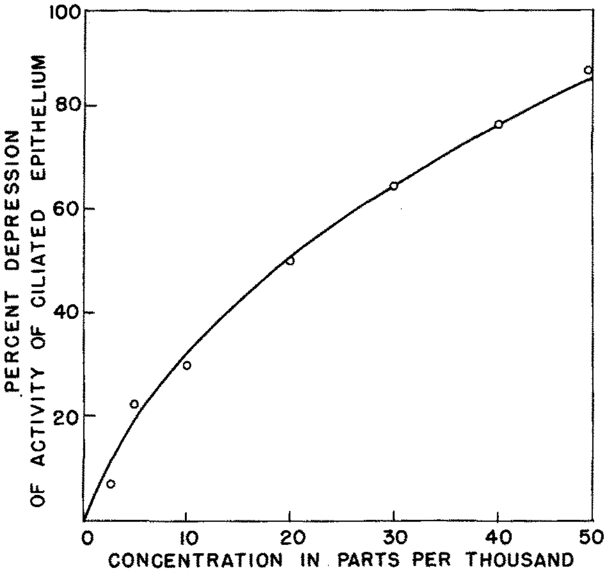

FIGURE 400.—Depression of the activity of ciliated epithelium of oyster gill by increased concentration of pulp mill effluent (black liquor) of specific gravity 1.0028. From Galtsoff, Chipman, Engle, and Calderwood, 1947.

by other investigators (Seydel, 1913; Veselov, 1948) on the toxicity of crude oil to fishes.

Determination of the toxicity of some pollutants is difficult because they may be present in such low concentrations that they are near or below the threshold of sensitivity to chemical methods. Their presence in even minimal quantities should be considered potentially dangerous to sedentary animals unable to avoid them. Another detection problem is that in many industrial plants the discharge of effluents is not continuous but is frequently interrupted or made during the night and early hours of the morning. Pollution studies must include taking composite samples of water with automatic samplers over a period of several hours. Some contaminants are unstable; after being discharged into sea water they are gradually oxidized, precipitated, neutralized, and become less harmful. The rate of this self-purification of water depends on many conditions, temperature, salinity gradient, sedimentation, and currents. To avoid inconsistencies in results, toxicity tests with such materials should be carried out only with stabilized samples (Odlaug, 1949).

Bioassays made within a few days indicate the presence or absence in water of a physiologically active substance but do not determine whether the pollution is lethal to the animal. Long-term field and laboratory observations are needed to determine the lethal effects of a low concentration of pollutants.

Ecological studies in polluted waters show that under certain conditions the normal environment may be modified by the contaminant and become unsuitable for growth and reproduction of oysters. Pollution of Shelton Bay, Puget Sound, Wash., with red liquor discharged by a local pulp mill boosted the production of the diatom *Melosira* sp. to such an extent that the beds of *O. lurida* in the bay became covered with a thick layer of this fouling plant. A similar effect occurred in laboratory tests with red liquor made by Odlaug (1949). Oysters affected by red liquor were useless because of their poor quality and poor taste; their reproduction stopped completely. Normal conditions were restored after discharge of the pollutant was discontinued (McKernan, Tartar, and Tollefson, 1949).

The biologist who studies pollution of natural water should remember that there is no harmless pollution. All types of pollution are harmful to marine populations; only the degree of their effects differs. Frequently it is claimed that the enrichment of sea water by phosphates, nitrates, carbohydrates, and other organic matter is beneficial and will tend to increase productivity. In the case of water pollution by duck farms in Moriches Bay, Long Island, N.Y., indiscriminate pollution by duck manure caused an imbalance of nutrient salts and boosted the outbreak of microorganisms which had an adverse effect on shellfish (Redfield, 1952). Useful enrichment of sea water can be achieved only by controlled and balanced fertilization.

Oxidation is important in reducing or destroying the toxicity of certain contaminants of sea water (Galtsoff, Chipman, Engle, and Calderwood, 1947). The efficiency of oxidation is influenced by temperature and by the manner in which the pollutant is added to the water. Preliminary storage in tanks is helpful in removing objectionable solids, and cascading the effluent from storage tanks to the place of discharge will expedite its oxidation. The U.S. Public Health Service found that 10,400 factory outlets in 1950 were pouring their waste into natural waters of the United States; only 657 of them had waste treatment plants of adequate capacities. In about 30 percent of the plants, the method of treatment was unsatisfactory. The number of plants which at present discharge their waste into coastal waters and the amount of waste are not known.

Radioactive waste

The disposal of radioactive waste in the sea presents a new threat to shellfish resources; the concentration of radioactive materials in the bodies of water-filtering mollusks may render them unsafe for human consumption. Chipman (1960) showed that many of the radionuclides added to sea water become associated with both living and nonliving particles suspended in water. Experiments at the Radiobiological Laboratory of the Bureau of Commercial Fisheries at Beaufort, N.C. (Chipman, Rice, and Price, 1958; Rice and Willis, 1959), indicated that nearly all fission product radionuclides, and also those of the trace metals, that are added to algal cultures associate with marine plankton used by shellfish. If continuously available, radioactive particles may accumulate in filtering organs, on the body surface, and in the digestive tract of oysters and other shellfish.

The accumulation of radioactive pollutants in coastal waters is likely to become higher than it is at present if the current practice of dumping radioactive wastes from nuclear plants and many research institutions close to shore or in the lower parts of a river (Columbia River) continues indefinitely. This unwelcome possibility must be watched carefully, and a great deal of research remains to be done before a clear picture emerges of the potential dangers associated with the disposal of low level radioactive waste and the contamination of our fisheries resources.

To evaluate the effect of pollution on the productivity of oyster bottoms the following data are needed: the type and extent of pollution in relation to the total volume and movements of water in an estuary; the stability of the pollutant; its physiological action; the effect of long-continued exposure of oysters to low concentrations; and the determination of the lethal concentration of a pollutant killing 50 percent of a population, the so-called LD 50.

COMBINED EFFECT OF ENVIRONMENTAL FACTORS

Known effects of any single factor of the environment do not give a true picture of the situation found in nature. Factors of the environment always act jointly. One serious weakness of many ecological studies of marine populations is the tendency to correlate the results of biological observations with one or possibly two selected factors of the environment, such as temperature, salinity, or hydrography, and to disregard the effect of others. In reality, any factor can exert its effect only in conjunction with others. It is impossible to separate the effect of chemical changes caused by a pollutant from the movements of water and from the effects of the pollutant on the food chain. Changes in the character of a bottom brought about by sedimentation cannot be separated from changes in sea water chemistry, or the food chain. An increase in the salinity of water encourages the invasion of grounds by some competitors and predators, while lowered salinity forms a barrier to inroads by starfishes and drills.

The combined action of several factors produces a far greater effect than that caused by any single factor. Findings of what effects combined factors have on agricultural plants (Rübel, 1935) are fully applicable to conditions affecting aquatic animals. So far, however, no adequate studies have been made on the problem of measuring the joint effect of several factors of aquatic environment. The relationship of all factors probably can be expressed by a very complex formula of the type developed by Riley (1947) for seasonal fluctuations of phytoplankton populations in New England coastal waters. The very complexity of a formula of this type precludes its usefulness for the practical purpose of evaluating conditions on oyster bottoms. The oyster biologist is often confronted with the necessity of expressing his opinion on the quality of the oyster beds. His impression is given in general, nonspecific terms as adequate, good, very good, marginal, etc., which do not disclose the reasons for a particular evaluation.

My proposed method of scoring eliminates the uncertainty of personal impressions and assigns to each factor a value which indicates the degree of its effectiveness on a given population of oysters. The method has been applied successfully in the evaluation of oyster bottoms in New England, the south Atlantic coast, and in some Gulf States (Galtsoff, 1959). It has been already stated above (p. 399) that the optimal condition of existence with reference to a single positive factor can be assigned the numerical value of 10. Degrees of inadequacies are given numerical values in descending numbers from nine to one. Negative factors are treated in much the same way. Complete absence of a negative factor refers to optimal conditions, and therefore, is designated zero, while the degrees by which the factor adversely affects an oyster population are assigned the numbers diminishing from nine, for 90 percent of negative influence, to one, which denotes 10 percent or less of harmful effect. The zero value of a positive and 10 value of a negative factor are omitted because under the proposed system such values denote complete unsuitability of environment for the existence of an oyster population.

A combination of environmental conditions which determine the productivity of an oyster bottom is summarized in simple tabular form by listing in two separate columns all positive (+) and all negative (−) factors and assigning to them their rank. As an example of the method, the data for one of the highly productive areas in the northern Cape Cod area, where observations were made for several years, are presented in table 46. In this area, which approaches ideal conditions, the presence of predators is the only serious problem.

The overall evaluation is made by summing up all positive factors, Σf^+ and all negative factors, Σf^- and by deducting the sum of the negative factors from the sum of the positive. Under this system the highest score of 50 refers to a theoretical situation where all positive factors are optimal and negative factors are absent. The low score of 10 and less refers to marginal conditions. Tabulation of factors is of great practical advantage because it shows at a glance the causes of low productivity and how it can be improved. The following tabulation shows the scores that in my opinion apply to various degrees of productiveness of oyster bottoms:

Excellent	41–50
Good	31–40
Average	21–30
Poor	11–20
Marginal	10 and less.

TABLE 46.—*Evaluation of the productiveness of an oyster ground in the northern part of Cape Cod*

Positive factors (+)	Score	Negative factors (−)	Score
Bottom	10	Sedimentation	----
Water movement	10	Disease	----
Temperature	5	Competition	2
Water quality	10	Predation	5
Food	10	Pollution	----
Total	45	Total	7

Note.—Overall score 45−7=38; ---- in negative score indicates absence of a factor.

In its present form, the method obviously oversimplifies the problem because it considers all the factors as equally significant, which may not be true. The present lack of understanding of the interaction within a complex ecological system bars expression of this interrelation in a more precise form. Growing interest in studies of the sea and its resources, however, gives promise of rapid progress in determining the intricate relationships among the principal factors that govern the prosperity of marine populations. The resulting knowledge will provide the basic data for designing effective methods of utilization and conservation of the renewable resources of the sea.

BIBLIOGRAPHY

ABBOTT, R. TUCKER.
1954. American seashells. D. Van Nostrand Co., Inc., New York, 541 pp.

AGOSTINI, ANGELA.
1929. Sulle alghe perforanti la conchiglia di *Ostrea edulis* L. del Canale delle Saline di Cagliari. Reale Comitato Talassografico Italiano, Memoria 159, Venezia, Premiate Officine Grafiche Carlo Ferrari, pp. 1–14.

ANDREWS, ETHAN A. (editor).
1907. A new Latin dictionary, founded on the translation of Freund's Latin-German lexicon. Revised, enlarged, and in great part rewritten by Charlton T. Lewis and Charles Short. American Book Company, New York, 2019 pp.

ANDREWS, E. A.
1915. Distribution of *Folliculina* in 1914. Biological Bulletin, vol. 29, No. 6, pp. 373–380.
1944. Folliculinids on oyster shells. Journal of Marine Research, vol. 5, No. 3, pp. 169–177.

ANDREWS, JAY D., DEXTER HAVEN, and D. B. QUAYLE.
1959. Fresh-water kill of oysters (*Crassostrea virginica*) in James River, Virginia, 1958. Proceedings of the National Shellfisheries Association, vol. 49, August, 1958, pp. 29–49.

ANDREWS, JAY D., JOHN L. WOOD, and H. DICKSON HOESE.
1962. Oyster mortality studies in Virginia: III. Epizootiology of a disease caused by *Haplosporidium costale* Wood and Andrews. Journal of Insect Pathology, vol. 4, No. 3, pp. 327–343.

BARNES, H.
1957. Processes of restoration and synchronization in marine ecology. The spring diatom increase and the "spawning" of the common barnacle, *Balanus balanoides*. Colloque International de Biologie Marine Station Biologique de Roscoff (27 Juin–4 Juillet 1956), l'Année Biologique, Année 61, serié 3, tome 33, pp. 67–85.

BEAVEN, G. FRANCIS.

1955. Water chestnut threatens disaster to Maryland water areas. Maryland Tidewater News, vol. 12, No. 1, suppl. No. 5, pp. 1–2.

1960. Water milfoil invasion of tidewater areas. Maryland Department of Research and Education, Chesapeake Biological Laboratory, Solomons, Md. Reference No. 60–28, 4 pp. [Mimeographed.]

BONNOT, PAUL.

1937. Setting and survival of spat of the Olympia oyster, *Ostrea lurida*, on upper and lower horizontal surfaces. California Fish and Game, vol. 23, No. 3, pp. 224–228.

BORNET, ED., et CH. FLAHAULT.

1889. Sur quelques plantes vivant dans le test calcaire des mollusques. Bulletin de la Société Botanique de France (Congrès de Botanique tenu à Paris du 20 au 25 Aout 1889), tome 36, pp. cxlvii–clxxvii.

BOROUGHS, HOWARD, WALTER A. CHIPMAN, and THEODORE R. RICE.

1957. Laboratory experiments on the uptake, accumulation, and loss of radionuclides by marine organisms. National Academy of Sciences—National Research Council, Publication No. 551, ch. 8, pp. 80–87.

BOUCK, G. B., and E. MORGAN.

1957. The occurrence of *Codium* in Long Island waters. Bulletin of the Torrey Botanical Club, vol. 84, No. 5, pp. 384–387.

BOUSFIELD, E. L.

1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. National Museum of Canada, Bulletin No. 137, Department of Northern Affairs and National Resources, National Parks Branch, Biological Series No. 46, Ottawa, 69 pp.

BROWN, CARL B., LOUIS M. SEAVY, and GORDON RITTENHOUSE.

1939. Advance report on an investigation of silting in the York River, Virginia, October 25–November 5, 1938. Sedimentation Studies, Division of Research, SCS–SS–32, U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C., 12 pp.

BRUNE, GUNNAR M.

1958. Sediment is your problem, wasted soil and water. AIB 174, Soil Conservation Service, U.S. Department of Agriculture, 16 pp.

BRUST, HARRY F., and CURTIS L. NEWCOMBE.

1940. Observations on the alkalinity of estuarine waters of the Chesapeake Bay near Solomons Island, Maryland. Journal of Marine Research, vol. 3, No. 2, pp. 105–111.

BURKENROAD, MARTIN D.

1931. Notes on the Louisiana conch, *Thais haemastoma* Linn., in its relation to the oyster, *Ostrea virginica*. Ecology, vol. 12, No. 4, pp. 656–664.

BUTKEWITSCH, W. S.

1928. Die Bildung der Eisenmangan-Ablagerungen am Meeresboden und die daran beteiligten Mikroorganismen. Berichte des wissenschaftlichen Meeresinstituts, Band 3, lief 3, pp. 63–81. [In Russian with German abstract.]

BUTLER, PHILIP A.

1949a. Gametogenesis in the oyster under conditions of depressed salinity. Biological Bulletin, vol. 96, No. 3, pp. 263–269.

1949b. An investigation of oyster producing areas in Louisiana and Mississippi damaged by flood waters in 1945. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 8, 36 pp.

1952. Effect of floodwaters on oysters in Mississippi Sound in 1950. [U.S.] Fish and Wildlife Service, Research Report 31, 20 pp.

CAMERON, W. M., and D. W. PRITCHARD.

1963. Estuaries. *In* M. N. Hill (editor), The sea: ideas and observations on progress in the study of the seas. Vol. 2, Composition of sea-water—comparative and descriptive oceanography, sec. III, Currents, ch. 15, pp. 306–324. Interscience Publishers, John Wiley and Sons, New York.

CARRIKER, MELBOURNE ROMAINE.

1943. On the structure and function of the proboscis in the common oyster drill, *Urosalpinx cinerea* Say. Journal of Morphology, vol. 73, No. 3, pp. 441–506.

1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. Ecology, vol. 32, No. 1, pp. 73–83.

1955. Critical review of biology and control of oyster drills, *Urosalpinx* and *Eupleura*. [U.S.] Fish and Wildlife Service, Special Scientific Report—Fisheries No. 148, 150 pp.

1961a. Comparative functional morphology of boring mechanisms in gastropods. American Zoologist, vol. 1, No. 2, pp. 263–266.

1961b. Interrelation of functional morphology, behavior, and autoecology in early stages of the bivalve *Mercenaria mercenaria*. Journal of the Elisha Mitchell Scientific Society, vol. 77, No. 2, pp. 168–241.

CASPERS, HUBERT.

1949. Ökologische Untersuchungen über die Wattentierwelt im Elbe-Ästaur. Verhandlungen der deutschen Zoologen vom 24 bis 28 August 1948 in Kiel, pp. 350–359.

1950. Die Lebensgemeinschaft der Helgoländer Austernbank. Helgoländer wissenschaftliche Meeresuntersuchungen herausgegeben von der Biologischen Anstalt Helgoland, Band 3, pp. 119–169.

1951. Quantitative Untersuchungen über die Bodentierwelt des Schwarzen Meeres im bulgarischen Küstenbereich. Archiv für Hydrobiologie, Band 45, pp. 1–192.

CERTES, A.

1882. Note sur les parasites et les commensaux de l'huitre. Bulletin de la Société Zoologique de France, vol. 7, pp. 347–353.

CHAPMAN, WILBERT MCLEOD, and ALBERT HENRY BANNER.

1949. Contributions to the life history of the Japanese oyster drill, *Tritonalia japonica*, with notes on other enemies of the Olympia oyster, *Ostrea lurida*. State of Washington, Department of Fisheries, Biological Report No. 49 A, pp. 167–200.

Chew, Kenneth K.

1960. Study of food preference and rate of feeding of Japanese oyster drill, *Ocinebra japonica* (Dunker). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 365, 27 pp.

Chipman, Walter A.

1960. Accumulation of radioactive pollutants by marine organisms and its relation to fisheries. Biological Problems in Water Pollution. *In* Transactions of the 1959 Seminar, pp. 8–14. U.S. Department of Health, Education, and Welfare, Public Health Service, Robert A. Taft Sanitary Engineering Center, Technical Report W 60–3.

Chipman, Walter A., and Paul S. Galtsoff.

1949. Effects of oil mixed with carbonized sand on aquatic animals. [U.S.] Fish and Wildlife Service, Special Scientific Report—Fisheries No. 1, 52 pp.

Chipman, Walter A., Theodore R. Rice, and Thomas J. Price.

1958. Uptake and accumulation of radioactive zinc by marine plankton, fish, and shellfish. U.S. Fish and Wildlife Service, Fishery Bulletin 135, vol. 58, pp. 279–292.

Christensen, Aage Møller.

1957. The feeding behavior of the seastar *Evasterias troschelii* Stimpson. Limnology and Oceanography, vol. 2, No. 3, pp. 180–197.

Christensen, Aage Møller, and John J. McDermott.

1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* Say. Biological Bulletin, vol. 114, No. 2, pp. 146–179.

Church, A. H.

1919. Weighing moorings. Journal of Botany, vol. 57, No. 673, pp. 35–37.

Clench, William J.

1947. The genera *Purpura* and *Thais* in the western Atlantic. Johnsonia, vol. 2, No. 23, pp. 61–92.

Coe, Wesley R.

1936. Sexual phases in *Crepidula*. Journal of Experimental Zoölogy, vol. 72, No. 3, pp. 455–477.

Cole, H. A.

1942. The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. Journal of the Marine Biological Association of the United Kingdom, vol 25, No. 3, pp. 477–508.

Collier, Albert, and Joel W. Hedgpeth.

1950. An introduction to the hydrography of tidal waters of Texas. Publications of the Institute of Marine Science, University of Texas, vol. 1, No. 2, pp. 121–194.

Colton, Harold Sellers.

1908. How *Fulgur* and *Sycotypus* eat oysters, mussels and clams. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 60, pp. 3–10.

Crowell, Sears.

1957. *Eugymnanthea*, a commensal hydroid living in pelecypods. Pubblicazioni della Stazione Zoologica di Napoli, vol. 30, pp. 162–167.

Danglade, Ernest.

1919. The flatworm as an enemy of Florida oysters. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1918, appendix 5 (Document 869), pp. 1–8.

Dawson, C. E.

1955. A contribution to the hydrography of Apalachicola Bay, Florida. Publications of the Institute of Marine Science, University of Texas, vol. 4, No. 1, pp. 13–35.

Dean, Bashford.

1892. The physical and biological characteristics of the natural oyster-grounds of South Carolina. Bulletin of the U.S. Fish Commission, vol. 10, for 1890, pp. 335–361.

Dimick, R. E., George Egland, and J. B. Long.

1941. Native oyster investigations of Yaquina Bay, Oregon. Progress Report II covering the period July 4, 1939 to September 30, 1941. Oregon Agricultural Experiment Station, Corvallis, Oreg. Cooperating with the Fish Commission of the State of Oregon and the Lincoln County Court, 153 pp.

Dimitroff, Vladimir T.

1926. Spirochaetes in Baltimore market oysters. Journal of Bacteriology, vol. 12, No. 2, pp. 135–177.

Dobson, G. C.

1936. A formula for capacities of reservoirs. Soil Conservation, vol. 1, No. 7, pp. 7–9.

Dollfus, Robert P.

1922. Résumé de nos principales connaissances pratiques sur les maladies et les ennemis de l'Huître. Notes et Mémoires No. 7, 2d ed., Office Scientifique et Technique des Pêches Maritimes, Paris, 58 pp.

Drinnan, R. E., and J. C. Medcof.

1961. Progress in rehabilitating disease affected oyster stocks. Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B., General Series Circular No. 34, October 1961, 3 pp.

Dunbar, M. J.

1957. The determinants of production in northern seas: A study of the biology of *Themisto libellula* Mandt. "Calanus" series No. 14, Canadian Journal of Zoology, vol. 35, No. 6, pp. 797–819.

1960. The evolution of stability in marine environments natural selection at the level of the ecosystem. American Naturalist, vol. 94, No. 875, pp. 129–136.

Eberzin, A. G.

1951. Ob izmenenii sostava chernomorskoi konkhiliofauny v sviazi s invasiei *Rapana* i o znachenii etogo iavleniia dlia palentologii. (Change in composition of the molluscan fauna of the Black Sea following the invasion of *Rapana*, and its significance for paleontology.) Doklady Akademii Nauk S.S.S.R., tom 79, No. 5, pp. 871–873.

Einstein, Hans Albert.

1950. The bed-load function for sediment transportation in open channel flows. U.S. Department of Agriculture, Soil Conservation Service, Technical Bulletin No. 1026, 71 pp.

Einstein, H. A., and J. W. Johnson.

1950. The laws of sediment transportation. *In* Parker D. Trask (editor), Applied sedimentation, ch. 3, pp. 62–71. John Wiley and Sons, New York.

Ekman, Sven.

1947. Über die Festigkeit der marinen Sedimente als Faktor der Tierverbreitung. Zoologiska Bidrag från Uppsala, Band 25, pp. 1–20.

Ellis, M. M., B. A. Westfall, and Marion D. Ellis.

1946. Determination of water quality. [U.S.] Fish and Wildlife Service, Research Report 9, 122 pp.

Emery, K. O., and R. E. Stevenson.

1957a. Estuaries and lagoons. I. Physical and chemical characteristics. *In* J. W. Hedgpeth (editor), Treatise on marine ecology and paleoecology, vol. 1, Ecology, ch. 23, pp. 673–693. The Geological Society of America, Memoir 67, Waverley Press, Baltimore, Md.

1957b. Estuaries and lagoons. III. Sedimentation in estuaries, tidal flats, and marshes. *In* J. W. Hedgpeth (editor), Treatise on marine ecology and paleoecology, vol. 1, Ecology, ch. 23, pp. 729–749. The Geological Society of America, Memoir 67, Waverley Press, Baltimore, Md.

Fasten, Nathan.

1931. The Yaquina oyster beds of Oregon. American Naturalist, vol. 65, No. 700, pp. 434–468.

Fauvel, Pierre.

1927. Polychètes sédentaires. Faune de France, vol. 16, pp. 1–494.

Feder, Howard M.

1955. On the methods used by the starfish *Pisaster ochraceus* in opening three types of bivalve molluscs. Ecology, vol. 36, No. 4, pp. 764–767.

Fretter, Vera, and Alastair Graham.

1962. British prosobranch molluscs. Their functional anatomy and ecology. The Ray Society, London, 755 pp.

Frey, David G.

1946. Oyster bars of the Potomac River. [U.S.] Fish and Wildlife Service, Special Scientific Report No. 32, 93 pp.

Fritsch, F. E.

1959. The structure and reproduction of the algae, Vol. 2, Foreword, Phaeophyceae, Rhodophyceae. Myxophyceae. Cambridge University Press, Cambridge, 939 pp.

Fujita, Tsunenobu.

1925. Etudes sur les parasites de l'huître comestible du Japon *Ostrea gigas* Thunberg. Traduction accompagnée de notes, de diagnoses et d'une Bibliographie par Robert-Ph. Dollfus. Annales de Parasitologie, Humaine et Comparée, tome 3, No. 1, pp. 37–59.

Galtsoff, Paul S.

1929. Oyster industry of the Pacific Coast of the United States. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1929, appendix 8 (Document 1066), pp. 367–400.

1930. Destruction of oyster bottoms in Mobile Bay by the flood of 1929. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1929, appendix 11 (Document 1069), pp. 741–758.

1931a. Survey of oyster bottoms in Texas. [U.S.] Bureau of Fisheries, Investigational Report No. 6, vol. 1 (1936), 30 pp.

1931b. II. The effect of sulphite waste liquor on the rate of feeding of *Ostrea lurida* and *Ostrea gigas*. *In* A. E. Hopkins, Paul S. Galtsoff, and H. C. McMillin, Effects of pulp mill pollution on oysters, pp. 162–167. [U.S.] Bureau of Fisheries, Bulletin No. 6, vol. 47.

1932. Introduction of Japanese oysters into the United States. [U.S.] Bureau of Fisheries, Fishery Circular No. 12, 16 pp.

Galtsoff, Paul S.

1948. Red tide. Progress report on the investigations of the cause of the mortality of fish along the west coast of Florida conducted by the U.S. Fish and Wildlife Service and cooperating organizations. [U.S.] Fish and Wildlife Service, Special Scientific Report No. 46, 44 pp.

1949. The mystery of the red tide. Scientific Monthly, vol. 68, No. 2, pp. 108–117.

1956. Ecological changes affecting the productivity of oyster grounds. Transactions of the Twenty-first North American Wildlife Conference, pp. 408–419.

1959. Ecological evaluation of the usable productivity of bottom communities. International Oceanographic Congress (1959), Preprints, pp. 233–234. American Association for the Advancement of Science, Washington, D.C. [Summary in English; Abstract in Russian.]

1960. Environmental requirements of oysters in relation to pollution. *In* C. M. Tarzwell (compiler), Biological problems in water pollution, pp. 128–134. Transactions of the 1959 Seminar. U.S. Department of Health, Education, and Welfare, Public Health Service, Robert A. Taft Sanitary Engineering Center, Technical Report W 60–3.

Galtsoff, Paul S., Walter A. Chipman, Jr., James B. Engle, and Howard N. Calderwood.

1947. Ecological and physiological studies of the effect of sulfate pulp mill wastes on oysters in the York River, Virginia. [U.S.] Fish and Wildlife Service, Fishery Bulletin 43, vol. 51, pp. 59–186.

Galtsoff, Paul S., and Victor L. Loosanoff.

1939. Natural history and method of controlling the starfish (*Asterias forbesi*, Desor). [U.S.] Bureau of Fisheries, Fishery Bulletin No. 31, vol. 49, pp. 75–132.

Galtsoff, Paul S., and Arthur S. Merrill.

1962. Notes on shell morphology, growth, and distribution of *Ostrea equestris* Say. Bulletin of Marine Science of the Gulf and Caribbean, vol. 12, No. 2, pp. 234–244.

Galtsoff, Paul S., Herbert F. Prytherch, and James B. Engle.

1937. Natural history and methods of controlling the common oyster drills (*Urosalpinx cinerea* Say and *Eupleura caudata* Say). [U.S.] Bureau of Fisheries, Fishery Circular No. 25, 24 pp.

Giard, Alfred.

1894. Sur une affection parasitaire de l'huitre (*Ostrea edulis* L.) connue sous le nom de maladie du pied. Comptes Rendus Hebdomadaires des Séances et Mémoires de la Société de Biologie, série 10, tome 1 (vol. 46), pp. 401–403.

Grice, George D., Jr.
1951. Observations on *Polydora* (mudworm) in South Carolina oysters. Contributions from Bears Bluff Laboratories, No. 11, 8 pp. Bears Bluff Laboratories, Wadmalaw Island, S.C.

Gudger, E. W.
1933. Echinoderm enemies of fishes. How starfishes and sea urchins catch and eat fishes. New York Zoological Society, Bulletin, vol. 36, No. 3, pp. 71–77.

Gunter, Gordon.
1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas Coast, including the commercial shrimp. Publications of the Institute of Marine Science, University of Texas, vol. 1, No. 2, pp. 7–51.
1961. Some relations of estuarine organisms to salinity. Limnology and Oceanography, vol. 6, No. 2, pp. 182–190.

Hagmeier, A., und R. Kändler.
1927. Neue Untersuchungen im nordfriesischen Wattenmeer und auf den fiskalischen Austernbänken. Wissenschaftliche Meeresuntersuchungen herausgegeben von der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel und der Biologischen Ansalt auf Helgoland, Neue Folge, Band 16, Abteilung Helgoland, Heft 2, Abhandlung Nr. 6, pp. 1–90.

Hamaker, J. I.
1930. The composition of beach sand with special reference to its organic component. Bulletin of Randolph-Macon Women's College, vol. 16, No. 4, pp. 1–15.

Hannerz, Lennart.
1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Polcilochaetidae N. fam. in the Gullmar fjord (Sweden). Zoologiska Bidrag från Uppsala, Band 31, pp. 1–204.

Hargis, William J., Jr., and Clyde L. MacKenzie, Jr.
1961. Sexual behavior of the oyster drills: *Eupleura caudata* and *Urosalpinx cinerea*. Nautilus, vol. 75, No. 1, pp. 7–16.

Hartman, Olga.
1945. The marine annelids of North Carolina. Duke University Marine Station, Bulletin No. 2, pp. 1–151.

Harvey, H. W.
1934. Measurement of phytoplankton population. Journal of the Marine Biological Association of the United Kingdom, vol. 19, No. 2, pp. 761–773.

Hathaway, Ralph R., and K. D. Woodburn.
1961. Studies on the crown conch *Melongena corona* Gmelin. Bulletin of Marine Science of the Gulf and Caribbean, vol. 11, No. 1, pp. 45–65.

Hedgpeth, Joel W.
1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publications of the Institute of Marine Science, University of Texas, vol. 3, No. 1, pp. 107–224.
1957. Estuaries and lagoons. II. Biological aspects. *In* Joel W. Hedgpeth (editor), Treatise on marine ecology and paleoecology, vol. 1, Ecology, ch. 23, pp. 693–729. The Geological Society of America, Memoir 67, Waverly Press, Baltimore, Md.

Hewatt, Willis G., and Jay D. Andrews.
1954. Oyster mortality studies in Virginia. I. Mortalities of oysters in trays at Gloucester Point, York River. Texas Journal of Science, vol. 6, No. 2, pp. 121–133.

Hill, M. N. (editor).
1963. The sea: ideas and observations on progress in the study of the seas. Vol. 2, Composition of sea-water—comparative and descriptive oceanography. Interscience Publishers, John Wiley and Sons, New York, 554 pp.

Hopkins, A. E.
1936. Adaptation of the feeding mechanism of the oyster (*Ostrea gigas*) to changes in salinity. [U.S.] Bureau of Fisheries, Bulletin No. 21, vol. 48, pp. 345–364.

Hopkins, A. E., Paul S. Galtsoff, and H. C. McMillin.
1931. Effects of pulp mill pollution on oysters. [U.S.] Bureau of Fisheries, Bulletin No. 6, vol. 47, pp. 125–186.

Hopkins, Sewell H.
1958. The planktonic larvae of *Polydora websteri* Hartman (Annelida, Polychaeta) and their settling on oysters. Bulletin of Marine Science of the Gulf and Caribbean, vol. 8, No. 3, pp. 268–277.

Hornell, James.
1917. The edible molluscs of the Madras Presidency. Madras Fisheries Bulletin, vol. 11, Report No. 1 (1917), pp. 1–51.
1922. The common moluscs of South India. Madras Fisheries Investigations, 1921 (second series), Bulletin, vol. 14, Report No. 6 (1921), pp. 97–215.

Hoyt, W. D.
1920. Marine algae of Beaufort, N.C., and adjacent regions. Bulletin of the U.S. Bureau of Fisheries, vol. 36, for 1917–1918, pp. 367–556. (Document 886.)

Hutchins, Louis W.
1945. An annotated check-list of the salt-water bryozoa of Long Island Sound. Transactions of the Connecticut Academy of Arts and Sciences, vol. 36, pp. 533–551.

Hutchinson, G. Evelyn.
1948. Circular causal systems in ecology. Annals of the New York Academy of Science, vol. 50, art. 4, pp. 221–246.

Hyman, Libbie H.
1939. Some polyclads of the New England Coast, especially of the Woods Hole region. Biological Bulletin, vol. 76, No. 2, pp. 127–152.
1954. Free-living flatworms (Turbellaria) of the Gulf of Mexico. *In* Paul S. Galtsoff (coordinator), Gulf of Mexico—its origin, waters, and marine life, pp. 301–302. [U.S.] Fish and Wildlife Service, Fishery Bulletin 89, vol. 55.

1955. The polyclad flatworms of the Pacific Coast of North America: additions and corrections. American Museum Novitates, No. 1704, 11 pp.

INGERSOLL, ERNEST.

1881. The oyster-industry. *In* The history and present condition of the fishery industries, 251 pp. Tenth Census of the United States, Department of the Interior, Washington, D.C.

INGRAM, WILLIAM MARCUS.

1957. Handbook of selected biological references on water pollution control, sewage treatment, water treatment. [U.S.] Public Health Service, Publication No. 214, 95 pp. (Public Health Bibliography Series, No. 8).

ITO, SUSUMU, and TAKEO IMAI.

1955. Ecology of oyster bed. I. On the decline of productivity due to repeated cultures. Tohôku Journal of Agricultural Research, vol. 5, No. 4, pp. 251–268.

JENSEN, EUGENE T. (editor).

1959. Manual of recommended practice for sanitary control of the shellfish industry. Part 1: Sanitation of shellfish growing areas. U.S. Department of Health, Education, and Welfare, Public Health Service, Publication No. 33, 1959 revision, 36 pp.

JOHNSON, T. W., JR., and F. K. Sparrow, Jr.

1961. Fungi in oceans and estuaries. J. Cramer, Weinheim, Germany; Hafner Publishing Company, New York, 668 pp.

JØRGENSEN, C. BARKER.

1952. On the relation between water transport and food requirements in some marine filter feeding invertebrates. Biological Bulletin, vol. 103, No. 3, pp. 356–363.

JØRGENSEN, C. BARKER, and EDWARD D. GOLDBERG.

1953. Particle filtration in some ascidians and lamellibranchs. Biological Bulletin, vol. 105, No. 3, pp. 477–489.

JOUBIN, L.

1906. Notes préliminaires sur les gisements des mollusques comestibles des côtes de France. Les côtes de la Loire à la Vilaine. Bulletin du Musée Océanographique de Monaco, No. 59, pp. 1–26.

1908. Etudes sur les gisements de mollusques comestibles des côtes de France. Bulletin de l'Institute Océanographique No. 115, pp. 1–20.

KETCHUM, BOSTWICK H.

1951a. The flushing of tidal estuaries. Sewage and Industrial Wastes, vol. 23, No. 2, pp. 198–209.

1951b. The exchanges of fresh and salt waters in tidal estuaries. Journal of Marine Research, vol. 10, No. 1, pp. 18–38.

1954. Relation between circulation and planktonic populations in estuaries. Ecology, vol. 35, No. 2, pp. 191–200.

KINCAID, TREVOR.

1957. Local races and clines in the marine gastropod *Thais lamellosa* Gmelin. A population study. The Calliostoma Company, Seattle, Wash., 75 pp.

KORRINGA, P.

1950. A review of the papers on molluscs presented at the Special Scientific Meeting on Shellfish of the International Council for the Exploration of the Sea, Edinburgh, October 10, 1949. Journal du Conseil, vol. 17, No. 1, pp. 44–59.

1951a. Investigations on shell-disease in the oyster, *Ostrea edulis* L. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 128, Contributions to Special Scientific Meetings 1949, Part 2: Shellfish Investigations, pp. 50–54.

1951b. The shell of *Ostrea edulis* as a habitat. Archives Néerlandaises de Zoologie, tome 10, pp. 32–152.

1951c. *Crepidula fornicata* as an oyster-pest. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 128, Contributions to Special Scientific Meetings 1949, Part 2: Shellfish Investigations, pp. 55–59.

LACKEY, JAMES B., GEORGE VANDER BORGH, JR., and JOSEPH B. GLANCY.

1952. General character of plankton organisms in waters overlying shellfish-producing-grounds. National Shellfisheries Association, 1952 Convention Addresses, pp. 152–156.

LANDAU, HELEN, and PAUL S. GALTSOFF.

1951. Distribution of *Nematopsis* infection on the oyster grounds of the Chesapeake Bay and in other waters of the Atlantic and Gulf states. Texas Journal of Science, vol. 3, No. 1, pp. 115–130.

LAVOIE, MARCEL E.

1956. How sea stars open bivalves. Biological Bulletin, vol. 111, No. 1, pp. 114–122.

LINSLEY, RAY K., JR., MAX A. KOHLER, and JOSEPH L. H. PAULHUS.

1949. Applied hydrology. 1st ed. McGraw-Hill Company, New York, 689 pp.

LOOSANOFF, VICTOR L.

1945. Effects of sea water of reduced salinities upon starfish, *A. forbesi,* of Long Island Sound. Transactions of the Connecticut Academy of Arts and Sciences, vol. 36, pp. 813–835.

1952. Behavior of oysters in water of low salinities. National Shellfisheries Association, 1952 Convention Addresses, pp. 135–151.

1956. Two obscure oyster enemies in New England waters. Science, vol. 123, No. 3208, pp. 1119–1120.

LOOSANOFF, VICTOR L., and JAMES B. ENGLE.

1943. *Polydora* in oysters suspended in the water. Biological Bulletin, vol. 85, No. 1, pp. 69–78.

1947. Effect of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). [U.S.] Fish and Wildlife Service, Fishery Bulletin 42, vol. 51, pp. 31–57.

LUNDBECK, JOHANNES.

1926. Die Bodentierwelt norddeutscher Seen. Archiv für Hydrobiologie Supplement—Band 7, 473 pp.

LUNZ, G. ROBERT, JR.
1940. The annelid worm, *Polydora*, as an oyster pest. Science, vol. 92, No. 2388, p. 310.
1941. *Polydora*, a pest in South Carolina oysters. Journal of the Elisha Mitchell Scientific Society, vol. 57, No. 2, pp. 273–283.
1947. *Callinectes* versus *Ostrea*. Journal of the Elisha Mitchell Scientific Society, vol. 63, No. 1, p. 81.

MACARTHUR, ROBERT.
1955. Fluctuations of animal populations, and a measure of community stability. Ecology, vol. 36, No. 3, pp. 533–536.

MACKENZIE, CLYDE L., JR.
1961. Growth and reproduction of the oyster drill *Eupleura caudata* in the York River, Virginia. Ecology, vol. 42, No. 2, pp. 317–338.

MACKIN, J. G.
1951. Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. Bulletin of Marine Science of the Gulf and Caribbean, vol. 1, No. 1, pp. 72–87.
1961a. Mortalities of oysters. Proceedings of the National Shellfisheries Association, vol. 50, for the year 1959, pp. 21–40.
1961b. Status of researches on oyster diseases in North America. Proceedings of the Gulf and Caribbean Fisheries Institute, Thirteenth Annual Session, November 1960, pp. 98–109.

MACKIN, J. G., P. KORRINGA, and S. H. HOPKINS.
1952. Hexamitiasis of *Ostrea edulis* L. and *Crassostrea virginica* (Gmelin). Bulletin of Marine Science of the Gulf and Caribbean, vol. 1, No. 4, pp. 266–277.

MACKIN, J. G., H. MALCOLM OWEN, and ALBERT COLLIER.
1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n. sp. in *Crassostrea virginica* (Gmelin). Science, vol. 111, No. 2883, pp. 328–329.

MANNING, JOSEPH H., and H. H. WHALEY.
1955. Distribution of oyster larvae and spat in relation to some environmental factors in a tidal estuary. Proceedings of the National Shellfisheries Association, vol. 45, August 1954, pp. 56–65.

MCKERNAN, DONALD L., VANCE TARTAR, and ROGER TOLLEFSON.
1949. An investigation of the decline of the native oyster industry of the State of Washington, with special reference to the effects of sulfite pulp mill waste on the Olympia oyster (*Ostrea lurida*). State of Washington, Department of Fisheries, Biological Report No. 49 A, Seattle, Wash., pp. 115–165.

MCMASTER, ROBERT L.
1962. Seasonal variability of compactness in marine sediments: a laboratory study. Geological Society of America Bulletin, vol. 73, No. 5, pp. 643–646.

MEDCOF, J. C., and A. W. H. NEEDLER.
1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). Journal of the Fisheries Research Board of Canada, vol. 5, No. 3, pp. 253–257.

MENZEL, R. WINSTON, and SEWELL H. HOPKINS.
1955. The growth of oysters parasitized by the fungus *Dermocystidium marinum* and by the trematode *Bucephalus cuculus*. Journal of Parasitology, vol. 41, No. 4, pp. 333–342.

MILLER, CLARENCE E.
1961. A penetrometer for in situ measurements in marine sediments. *In* D. S. Gorsline (editor), Proceedings of the First National Coastal and Shallow Water Research Conference, October 1961, Baltimore, Md., Los Angeles, Calif., and Tallahassee, Fla., p. 116. Sponsored by the National Science Foundation and the Office of Naval Research, Tallahassee, Fla.

MÖBIUS, KARL.
1883. XXVII. The oyster and oyster-culture. Translated by H. J. Rice by permission of the author from the book published in 1877, Die Auster und die Austernwirthschaft, Verlag von Wiegandt, Hempel und Parey, Berlin, 126 pp. U.S. Commission of Fish and Fisheries, Part 8. Report of the Commissioner for 1880, appendix H, pp. 683–751.

MOORE, H. F.
1899. Report on the oyster-beds of Louisiana. U.S. Commission of Fish and Fisheries, Part 24. Report of the Commissioner for the year ending June 30, 1898, pp. 45–100.
1907. Survey of oyster bottoms in Matagorda Bay, Texas. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1905 and special papers (Document 610), pp. 1–86.
1910. Condition and extent of the oyster beds of James River, Virginia. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1909 and special papers (Document 729), pp. 1–83.
1911. Condition and extent of the natural oyster beds of Delaware. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1910 and special papers (Document 745), pp. 1–30.
1913. Condition and extent of the natural oyster beds and barren bottoms of Mississippi east of Biloxi. [U.S.] Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1911 and special papers (Document 774), pp. 1–42.

MORTENSEN, EDITH, and PAUL S. GALTSOFF.
1944. Behavior and tube building habits of *Polydora ligni*. [Abstract.] Biological Bulletin, vol. 87, No. 2, pp. 164–165.

NEEDLER, A. W. H., and R. R. LOGIE.
1947. Serious mortalities in Prince Edward Island oysters caused by a contagious disease. Transactions of the Royal Society of Canada, series 3-vol. 41, sec. 5, pp. 73–89.

NELSON, THURLOW C.
1952. Some observations on the migrations and setting of oyster larvae. National Shellfisheries Association, 1952 Convention Addresses, pp. 99–104.

Newcombe, Curtis L., and William A. Horne.

1938. Oxygen-poor waters of the Chesapeake Bay. Science, vol. 88, No. 2273, pp. 80–81.

Newcombe, Curtis L., William A. Horne, and Boland B. Shepherd.

1939. Studies on the physics and chemistry of estuarine waters in Chesapeake Bay. Journal of Marine Research, vol. 2, No. 2, pp. 87–116.

Norris, Robert M.

1953. Buried oyster reefs in some Texas bays. Journal of Paleontology, vol. 27, No. 4, pp. 569–576.

Odlaug, Theron O.

1946. The effect of the copepod, *Mytilicola orientalis* upon the Olympia oyster, *Ostrea lurida*. Transactions of the American Microscopical Society, vol. 65, No. 4, pp. 311–317.

1949. Effects of stabilized and unstabilized waste sulphite liquor on the Olympia oyster, *Ostrea lurida*. Transactions of the American Microscopical Society, vol. 68, No. 2, pp. 163–182.

Old, Marcus C.

1941. The taxonomy and distribution of the boring sponges (*Clionidae*) along the Atlantic Coast of North America. Chesapeake Biological Laboratory, State of Maryland, Department of Research and Education, Solomons Island, Md., Publication No. 44, 30 pp.

Osburn, R. C.

1932. Bryozoa from Chesapeake Bay. Ohio Journal of Science, vol. 32, No. 5, pp. 441–446.

Owen, H. Malcolm.

1957. Etiological studies on oyster mortality. II. *Polydora websteri* Hartmann—(Polychaeta: Spionidae). Bulletin of Marine Science of the Gulf and Caribbean, vol. 7, No. 1, pp. 35–46.

Parker, Robert H.

1955. Changes in the invertebrate fauna, apparently attributable to salinity changes, in the bays of central Texas. Journal of Paleontology, vol. 29, No. 2, pp. 193–211.

Pearse, A. S., and G. W. Wharton.

1938. The oyster "leech" *Stylochus inimicus* Palombi, associated with oysters on the coasts of Florida. Ecological Monographs, vol. 8, No. 4, pp. 605–655.

Price, W. Armstrong, and Gordon Gunter.

1943. Certain recent geological and biological changes in south Texas, with consideration of probable causes. Proceedings and Transactions of the Texas Academy of Science, vol. 26 (1942), pp. 138–156.

Pritchard, Donald W.

1951. The physical hydrography of estuaries and some applications to biological problems. Transactions of the Sixteenth North American Wildlife Conference, pp. 368–376.

1952a. A review of our present knowledge of the dynamics and flushing of estuaries. Chesapeake Bay Institute of the Johns Hopkins University, Technical Report 4, Reference 52–7, 45 pp.

1952b. Salinity distribution and circulation in the Chesapeake Bay estuarine system. Journal of Marine Research, vol. 11, No. 2, pp. 106–123.

1953. Distribution of oyster larvae in relation to hydrographic conditions. Proceedings of the Gulf and Caribbean Fisheries Institute, Fifth Annual Session, November 1952, pp. 123–132.

1955. Estuarine circulation patterns. Proceedings, American Society of Civil Engineers, vol. 81, separate No. 717, pp. 717-1—717-11.

Pritchard, D. W., and Richard E. Kent.

1953. The reduction and analysis of data from the James River operation oyster spat. Chesapeake Bay Institute of the Johns Hopkins University, Technical Report 6, Reference 53–12, 92 pp.

Prytherch, Herbert F.

1940. The life cycle and morphology of *Nematopsis ostrearum*, sp. nov., a gregarine parasite of the mud crab and oyster. Journal of Morphology, vol. 66, No. 1, pp. 39–65.

Puffer, Elton L., and William K. Emerson.

1953. The molluscan community of the oyster-reef biotope on the central Texas coast. Journal of Paleontology, vol. 27, No. 4, pp. 537–544.

Rasmussen, Erik.

1951. Faunistic and biological notes on marine invertebrates. II. The eggs and larvae of some Danish marine gastropods. (Report from the Isefjord Laboratory No. 2). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København, bind 113, pp. 201–249.

Ray, Sammy M.

1952. A culture technique for the diagnosis of infections with *Dermocystidium marinum* Mackin, Owen, and Collier in oysters. Science, vol. 116, No. 3014, pp. 360–361.

1954. Biological studies of *Dermocystidium marinum*. The Rice Institute Pamphlet, Special Issue, November 1954, Monograph in Biology, Houston, Texas, 114 pp.

Ray, S. M., and A. C. Chandler.

1955. Parasitological reviews, *Dermocystidium marinum*, a parasite of oysters. Experimental Parasitology, vol. 4, No. 2, pp. 172–200.

Ray, Sammy, J. G. Mackin, and James L. Boswell.

1953. Quantitative measurement of the effect on oysters of disease caused by *Dermocystidium marinum*. Bulletin of Marine Science of the Gulf and Caribbean, vol. 3, No. 1, pp. 6–33.

Redfield, Alfred C.

1952. Report to the towns of Brookhaven and Islip, N.Y., on the hydrography of Great South Bay and Moriches Bay. Woods Hole Oceanographic Institution, Reference No. 52–26, April 1952, 80 pp.

Reid, George K.

1956. Ecological investigations in a disturbed Texas coastal estuary. Texas Journal of Science, vol. 8, No. 3, pp. 296–327.

1957. Biologic and hydrographic adjustment in a disturbed Gulf Coast estuary. Limnology and Oceanography, vol. 2, No. 3, pp. 198–212.

Renn, Charles E.

1940. Effects of marine mud upon the aerobic decomposition of plankton materials. Biological Bulletin, vol. 78, No. 3, pp. 454–462.

Rice, T. R., and Virginia M. Willis.

1959. Uptake, accumulation and loss of radioactive cerium-144 by marine planktonic algae. Limnology and Oceanography, vol. 4, No. 3, pp. 277–290.

Riley, Gordon A.

1941. Plankton studies. III. Long Island Sound. Bulletin of the Bingham Oceanographic Collection, Peabody Museum of Natural History, Yale University, vol. 7, art. 3, pp. 1–93.

1947. Seasonal fluctuations of the phytoplankton population in New England coastal waters. Journal of Marine Research, vol. 6, No. 2, pp. 114–125.

1953. Theory of growth and competition in natural populations. Journal of the Fisheries Research Board of Canada, vol. 10, No. 5, pp. 211–223.

Riley, Gordon A., and Samy Gorgy.

1948. Quantitative studies of summer plankton populations of the western North Atlantic. Journal of Marine Research, vol. 7, No. 2, pp. 100–121.

Riley, Gordon A., Henry Stommel, and Dean F. Bumpus.

1949. Quantitative ecology of the plankton of the western North Atlantic. Bulletin of the Bingham Oceanographic Collection, Peabody Museum of Natural History, Yale University, vol. 12, art. 3, pp. 1–169.

Rochford, D. J.

1951. Studies in Australian estuarine hydrology. I. Introductory and comparative features. Australian Journal of Marine and Freshwater Research, vol. 2, No. 1, pp. 1–116.

Roughley, T. C.

1925. The story of the oyster. Australian Museum Magazine, vol. 2, No. 5, pp. 163–168.

Rübel, Eduard.

1935. The replaceability of ecological factors and the law of the minimum. Ecology, vol. 16, No. 3, pp. 336–341.

Ryder, John A.

1884. A contribution to the life-history of the oyster. (*Ostrea virginica*, Gmelin, and *O. edulis*, Linn.). *In* George Brown Goode, The fisheries and fishery industries of the United States. Section I, Natural history of useful aquatic animals, pp. 711–758.

1888. A tumor in an oyster. Proceedings of the Academy of Natural Sciences of Philadelphia, 1887, vol. 39, pp. 25–27.

Sandoz, Mildred, and Sewell H. Hopkins.

1947. Early life history of the oyster crab, *Pinnotheres ostreum* (Say). Biological Bulletin, vol. 93, No. 3, pp. 250–258.

Sawano, Eishirô, and Kinji Mitsugi.

1932. Toxic action of the stomach extracts of the starfishes on the heart of the oyster. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 7, No. 1, pp. 79–88.

Schechter, Victor.

1943. Tolerance of the snail *Thais floridana* to waters of low salinity and the effect of size. Ecology, vol. 24, No. 4, pp. 493–499.

Seydel, Emil.

1913. Ueber die Wirkung von Mineralölen auf Fischwasser. Mitteilungen des Fischerei-Vereins für die Provinz Brandenburg, Band 5, Heft 3, pp. 26–28.

Shaw, William N.

1960. Observations on habits and a method of trapping channeled welks near Chatham, Massachusetts. U.S. Fish and Wildlife Service. Special Scientific Report—Fisheries No. 325, 6 pp.

1962. Raft culture of oysters in Massachusetts. U.S. Fish and Wildlife Service, Fishery Bulletin 197, vol. 61, pp. 481–495.

Sieling, Fred W.

1960. Mass mortality of the starfish, *Asterias forbesi*, on the Atlantic Coast of Maryland. Chesapeake Science, vol. 1, No. 1, pp. 73–74.

Smith, G. M.

1934. A mensenchymal tumor in an oyster (*Ostrea virginica*). American Journal of Cancer, vol. 22, No. 4, pp. 838–841.

Smith, R. O.

1949. Summary of oyster farming experiments in South Carolina 1939–1940. [U.S.] Fish and Wildlife Service, Special Scientific Report No. 63, 20 pp.

Söderström, Adolf.

1923. Über das Bohren der *Polydora ciliata*. Zoologiska Bidrag från Uppsala, band 8, pp. 319–326.

Sparks, Albert K.

1962. Metaplasia of the gut of the oyster *Crassostrea gigas* (Thunberg) caused by infection with the copepod *Mytilicola orientalis* Mori. Journal of Insect Pathology, vol. 4, No. 1, pp. 57–62.

Springer, Paul F., G. Francis Beaven, and Vernon D. Stotts.

1961. Eurasian watermilfoil—a rapidly spreading pest plant in eastern waters. Presented at the Northeast Wildlife Conference, Halifax, Nova Scotia, June 11–14, 1961, 6 pp. [Mimeographed.]

State of California.

1962. Water pollution control act. Division 7, California Water Code (Including 1956 (1st Ex. Sess.), 1957, 1959, and 1961 Legislative Amendments). The Resources Agency of California, Water Pollution Control Boards, Sacramento, Calif., 17 pp.

Stauber, Leslie A.

1943. Graphic representation of salinity in a tidal estuary. Journal of Marine Research, vol. 5, No. 2, pp. 165–167.

1945. *Pinnotheres ostreum*, parasitic on the American oyster, *Ostrea* (*Gryphaea*) *virginica*. Biological Bulletin, vol. 88, No. 3, pp. 269–291.

Steemann, Nielsen E.

1957. The balance between phytoplankton and zooplankton in the sea. Journal du Conseil, vol. 23, No. 2, pp. 178–188.

Stein, J. E., J. G. Denison, and J. G. Mackin.

1961. *Hexamita* sp. and an infectious disease in the commercial oyster *Ostrea lurida*. Proceedings of the National Shellfisheries Association, vol. 50, August 1959, pp. 67–81.

STEVENS, BELLE A.

1928. Callianassidae from the west coast of North America. Publications of the Puget Sound Biological Station, vol. 6, pp. 315–369.

STOMMEL, HENRY.

1951. Recent developments in the study of tidal estuaries. Woods Hole Oceanographic Institution, Reference No. 51–33, May 1951, 15 pp.

SUPREME COURT of LOUISIANA.

1944. Doucet v. Texas Co., et al., No. 37036, Supreme Court of Louisiana, February 7, 1944. Southern Reporter, Second Series, 17 SO. 2d, No. 4, pp. 340–349. West Publishing Company, St. Paul, Minn.

SYMPOSIUM for the CLASSIFICATION of BRACKISH WATERS.

1958. The Venice system for the classification of marine waters according to salinity. Limnology and Oceanography, vol. 3, No. 3, pp. 346–347.

TARZWELL, CLARENCE M. (compiler and editor).

1957. Biological problems in water pollution. Transactions of the 1956 seminar, 272 pp. U.S. Department of Health, Education, and Welfare, Public Health Service.

TARZWELL, CLARENCE M. (compiler).

1960. Biological problems in water pollution. Transactions of the 1959 Seminar, 285 pp. U.S. Department of Health, Education, and Welfare, Public Health Service, Robert A. Taft SanitaryEngineering Center, Technical Report W 60–3.

TAYLOR, WILLIAM RANDOLPH.

1937. Marine algae of the northeastern coast of North America. University of Michigan Press, Ann Arbor, Mich., 427 pp.

TENNENT, DAVID HILT.

1906. A study of the life-history of *Bucephalus haimeanus;* a parasite of the oyster. Quarterly Journal of Microscopical Science, vol. 49, No. 196, pp. 635–690.

THORSON, GUNNAR.

1957. Bottom communities (Sublittoral or shallow shelf). *In* Joel W. Hedgpeth (editor), Treatise on Marine Ecology and Paleoecology, vol. 1, Ecology, ch. 17, pp. 461–534. The Geological Society of America, Memoir 67. Waverley Press, Baltimore, Md.

TRASK, PARKER D. (editor).

1950. Applied sedimentation. John Wiley and Sons, Inc., New York, 707 pp.

TWENHOFEL, WILLIAM H.

1961. Treatise on sedimentation. 2d ed., completely revised. In two volumes. Dover Publications, Inc., New York, 926 pp.

TURNER, RUTH D.

1955. The family Pholadidae in the western Atlantic and the eastern Pacific. Part II. Martensiinae, Jouannetiinae and Xylophaginae. Johnsonia, vol. 3, No. 34, pp. 65–160.

U.S. PUBLIC HEALTH SERVICE.

1950. Suggested state water pollution control act and explanatory statement. Federal Security Agency, Division of Water Pollution Control, Public Health Service Publication No. 49, 23 pp.

1951. Water pollution in the United States. Federal Security Agency, Public Health Service, Water Pollution Series No. 1, Public Health Service Publication No. 64, Washington, D.C., 44 pp.

UNITED STATES 80th CONGRESS.

1948. An act to provide for water pollution control activities in the Public Health Service of the Federal Security Agency and in the Federal Works Agency, and for other purposes. Public Law 845, 80th Congress, 2nd Session, Approved June 30, 1948, Chapter 758, pp. 1155–1161.

UNITED STATES 84th CONGRESS.

1956. Federal Water Pollution Control Act. Public Law 660, 84th Congress, Approved July 9, 1956, 18 pp.

UNITED STATES 87th CONGRESS.

1961. An act to implement the provisions of the Internal Convention for the Prevention of the Pollution of the Sea by Oil, 1954. Public Law 87–167, 87th Congress, S. 2187, August 30, 1961, 6 pp.

VERWEY, J.

1942. Die Periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. Archives Néerlandaises de Zoologie, tome 6, livraison 4, pp. 363–468.

1949. Habitat selection in marine animals. Folia Biotheoretica, No. 4, pp. 1–22.

1952. On the ecology of distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply, with a short review of the feeding behaviour of bivalve mollusks. Archives Néerlandaises de Zoologie, tome 10, livraison 2, pp. 171–239.

VESELOV, E. A.

1948. Vliyanie na ryb zagryazneniya vody neftyu. (Effect of crude oil pollution on fishes.) Rybnoe Khoziaistvo (Fish Husbandry), vol. 24, No. 12, pp. 21–22.

VOISIN, P.

1931. Biologie ostréicole. La maladie des huitres de Zélande. Revue des Travaux de l'Office des Pêches Maritimes, tome 4, fascicule 2, pp. 221–222.

VOLTERRA, VITO.

1928. Variations and fluctuations of the number of individuals in animal species living together. Journal du Conseil, vol. 3, No. 1, pp. 1–51.

WAKSMAN, SELMAN A.

1933. On the distribution of organic matter in the sea bottom and the chemical nature and origin of marine humus. Soil Science, vol. 36, No. 2, pp. 125–147.

1942. The peats of New Jersey and their utilization. Bulletin 55, Geologic Series, Department of Conservation and Development, State of New Jersey, Trenton, N.J., 155 pp.

WAKSMAN, SELMAN A., and MARGARET HOTCHKISS.

1937. On the oxidation of organic matter in marine sediments by bacteria. Journal of Marine Research, vol. 1, No. 2, pp. 101–118.

WARBURTON, FREDERICK E.

1958. The manner in which the sponge *Cliona* bores in calcareous objects. Canadian Journal of Zoology, vol. 36, No. 4, pp. 555–562.

WELLS, HARRY W.
1959. Notes on *Odostomia impressa* (Say). Nautilus, vol. 72, No. 4, pp. 140–144.

WELLS, HARRY W., and MARY JANE WELLS.
1961. Three species of *Odostomia* from North Carolina, with description of new species. Nautilus, vol. 74, No. 4, pp. 149–157.

WILSON, DOUGLAS P.
1928. The larvae of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède. Journal of the Marine Biological Association of the United Kingdom, vol. 15, No. 2, pp. 567–603.

WOELKE, CHARLES E.
1957. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. Proceedings of the National Shellfisheries Association, vol. 47, August 1956, pp. 62–67.

1961. Pacific oyster *Crassostrea gigas* mortalities with notes on common oyster predators in Washington waters. Proceedings of the National Shellfisheries Association, vol. 50, August 1959, pp. 53–66.

WOOD, JOHN L., and JAY D. ANDREWS.
1962. *Haplosporidium costale* (Sporozoa) associated with a disease of Virginia oysters. Science, vol. 136, No. 3517, pp. 710–711.

YONGE, C. M.
1955. Adaptation to rock boring in *Botula* and *Lithophaga* (Lamellibranchia, Mytilidae) with a discussion on the evolution of this habit. Quarterly Journal of Microscopical Science, vol. 96, part 3, pp. 383–410.