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°/₀₀ to 18°/₀₀, and the mesohaline, from 18°/₀₀ to 5°/₀₀ (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°/₀₀ to 36°/₀₀ (Galtsoff and Merrill, 1962). In the subtidal regions of the coastal waters this species is found in salinities of 20°/₀₀ to 25°/₀₀.

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°/oo to 12°/oo) to the high salinity water of Sinepuxent Bay (32°/oo to 33°/oo) 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 °/oo 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°/oo to 30°/oo. 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°/oo 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 opti-

mum 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

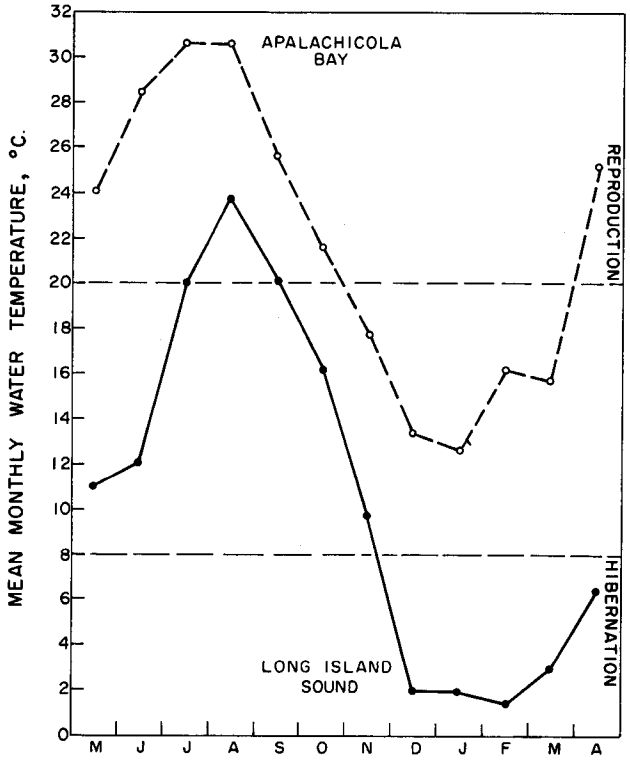

FIGURE 368.—Mean monthly temperature in °C. of water in Apalachicola Bay (upper curve) and Long Island Sound (lower curve).

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 6½ 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.

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.

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

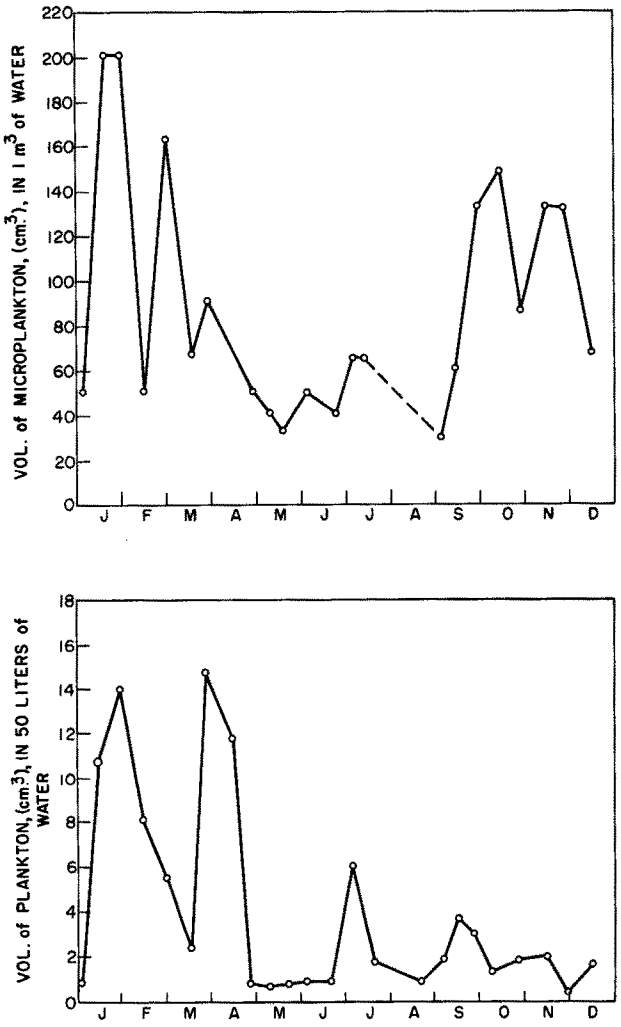

FIGURE 369.—Seasonal changes in the volume of plankton (upper curve) in cm.³ per 50 l. and microplankton (nannoplankton) in cu. cm. per 1 m.³ (lower curve) in Long Island Sound in 1932 and 1933.

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_o 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

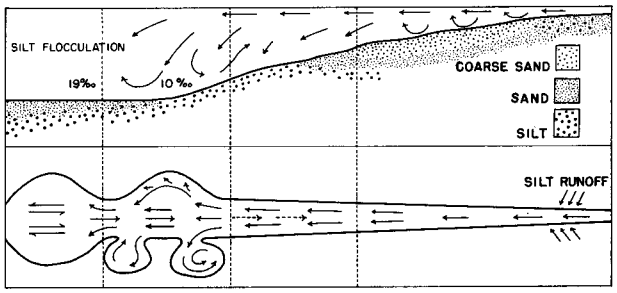

FIGURE 370.—Diagrammatic representation of the sorting out and deposition of coarse sand, fine sand, and silt in an estuary. The lower part of the diagram indicates the complex system of current and counter current. From Rochford, 1951.

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.

[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,

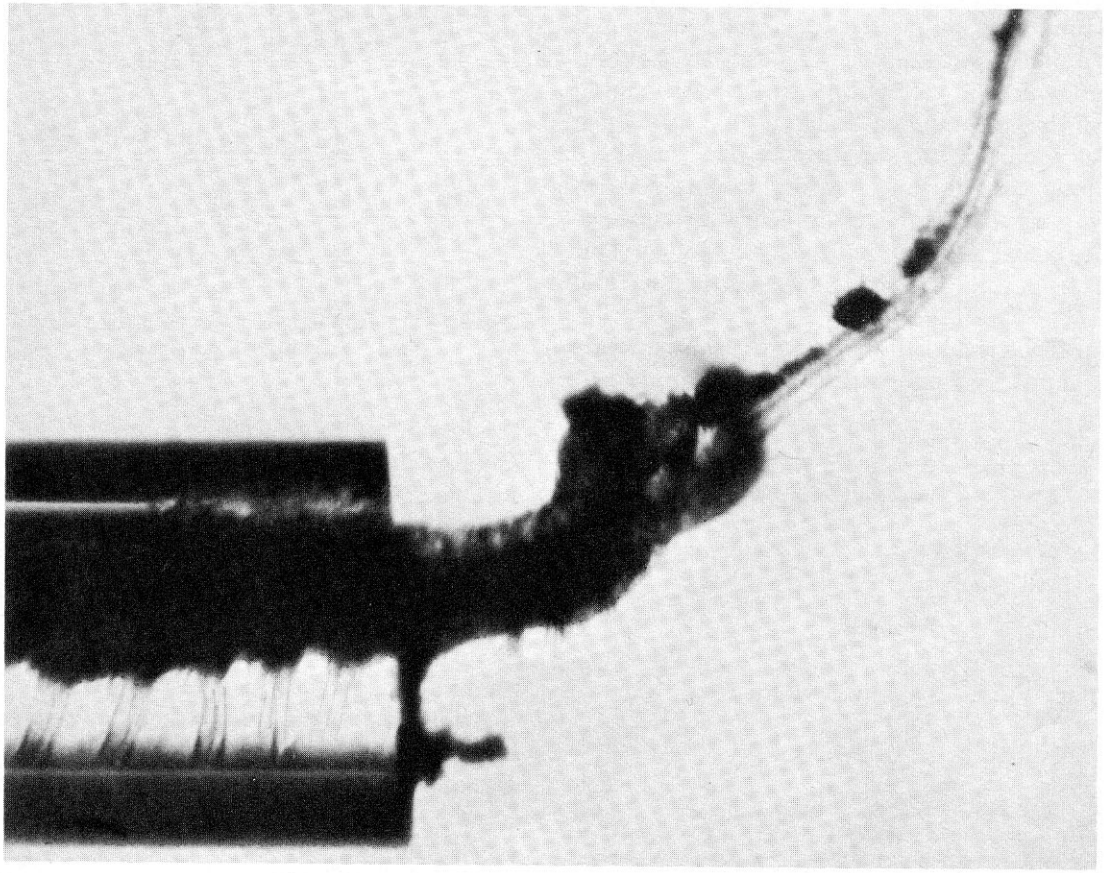

FIGURE 371.—Photograph of live *P. ligni* collecting mud. The worm is contained in a glass tube placed in sea water containing silt in suspension. Mud particles along the grooved antennae are transported toward the mouth and have begun to accumulate at the edge of the glass tubing.

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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

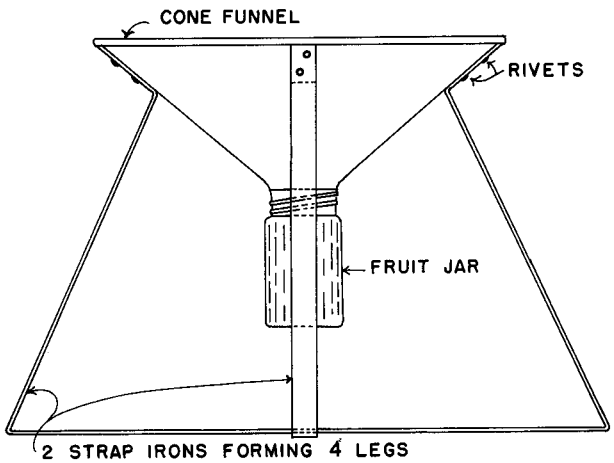

FIGURE 372.—Mud trap for collecting sediments settling from water.

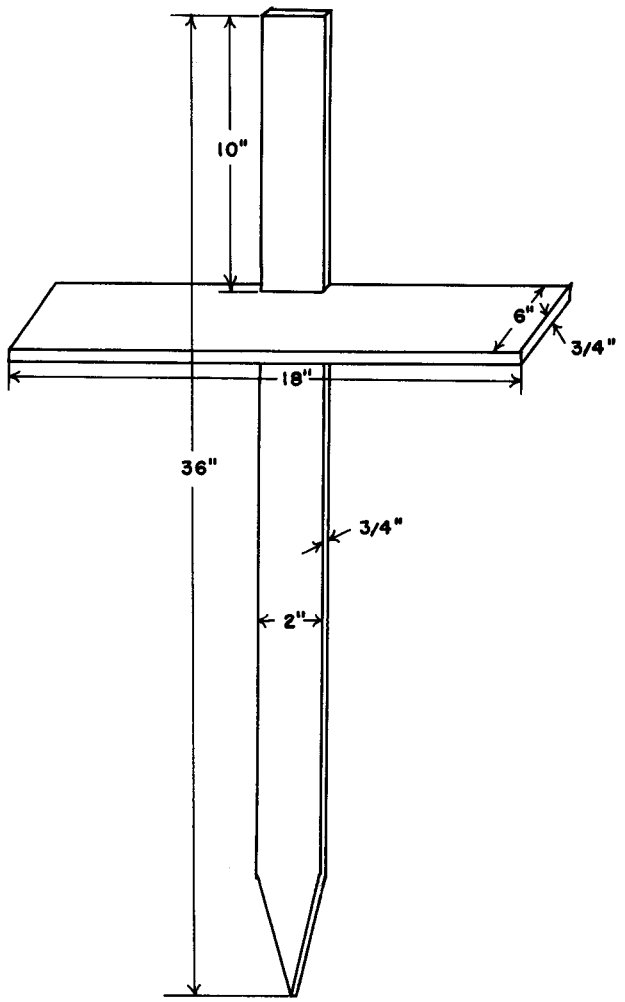

FIGURE 373.—Mud board for measuring the accumulation of sediment on tidal flats.

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.

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 tur-

bidimeter 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 subse-

quently 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.

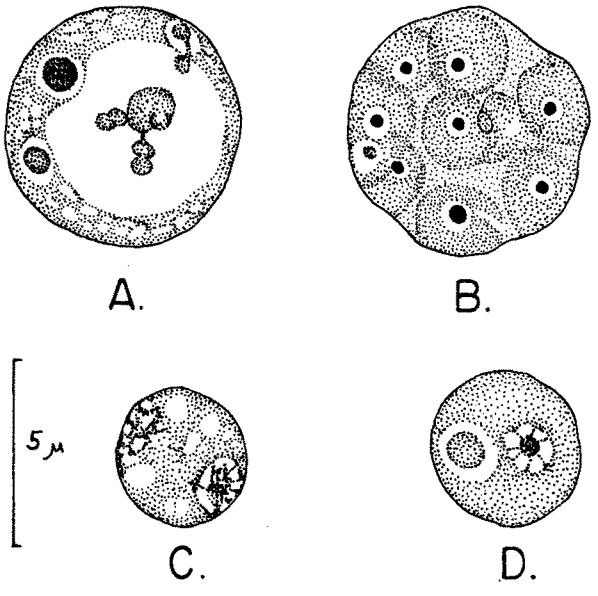

FIGURE 374.—Drawings of *Dermocystidium marinum* stained with Heidenhain's iron hematoxylin and eosin. A—A mature spore with markedly irregular vacuoplast, cytoplasmic inclusions, and very large vacuole. B—Multiple fission resulting in several daughter cells. C—A binucleate stage with chromatin in diffuse 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