U. S. DEPARTMENT OF COMMERCE
Daniel C. Roper, Secretary
BUREAU OF FISHERIES
Frank T. Bell, Commissioner

EXPERIMENTAL OBSERVATIONS ON SPAWNING, LARVAL DEVELOPMENT, AND SETTING IN THE OLYMPIA OYSTER *OSTREA LURIDA*

By A. E. Hopkins

From BULLETIN OF THE BUREAU OF FISHERIES
Volume XLVIII

Bulletin No. 23

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1937

For sale by the Superintendent of Documents, Washington, D. C. - - - - - - - - - - - - - Price 25 cents

National Oceanic and Atmospheric Administration

ERRATA NOTICE

One or more conditions of the original document may affect the quality of the image, such as:

Discolored pages
Faded or light ink
Binding intrudes into the text

This has been a co-operative project between the NOAA Central Library and the Climate Database Modernization Program, National Climate Data Center (NCDC). To view the original document, please contact the NOAA Central Library in Silver Spring, MD at (301) 713-2607 x124 or www.reference@nodc.noaa.gov.

LASON
Imaging Contractor
12200 Kiln Court
Beltsville, MD 20704-1387
March 21, 2005

EXPERIMENTAL OBSERVATIONS ON SPAWNING, LARVAL DEVELOPMENT, AND SETTING IN THE OLYMPIA OYSTER, *OSTREA LURIDA*[1]

By A. E. HOPKINS, *Aquatic Biologist, United States Bureau of Fisheries*

CONTENTS

INTRODUCTION

The native oyster of the Pacific coast has never been produced in great enough abundance to reach markets all over the country. Toward the end of the nineteenth century extensive commercial use was made of the crops growing naturally on tide lands of Puget Sound and Willapa (Shoalwater) Bay, in the State of Washington, resulting in almost complete depletion in most of the favorable localities. In 1902, according to Galtsoff (1929), 154,000 bushels of oysters were produced; in 1904, 170,000 bushels reached the market; while in 1926 only about 58,000 bushels were grown. Since this time production has been at an even lower level. The native Willapa Bay oyster has been almost completely destroyed so that it is now difficult to find in the local markets. The native oyster is unique in the United States in that it never attains a shell length much greater than about 5 centimeters (2 inches), and for this reason is used primarily for special dishes such as cocktails and pan roasts. It is too small to serve on the half shell.

Oyster growers commonly market them in 2-bushel sacks, containing about 5,000 oysters, or about 2,500 to the bushel. Most of the native oysters now grown on the

[1] Bulletin No. 23. Approved for publication Oct. 14, 1936.

Pacific coast are produced in the southern portion of Puget Sound in the vicinity of Olympia, Wash. They are sold on the market as Olympia oysters, and a distinction is made between them and the same species grown in other localities.

According to Stafford (1914) the species was described by Carpenter, who gave the name, as follows: "*Ostrea lurida*, n. s. Shape of *edulis:* texture dull, lurid, olivaceous, with purple stains." The species is known to occur in bays and estuaries from British Columbia to southern California. However, in some respects the oysters are quite different both in appearance and marketability with respect to their place of origin. Townsend (1893) hardly considered the native oyster of San Francisco Bay of commercial significance, although present in large numbers. The same species, farther north, at that time was bringing good prices in the markets. This was due in part to the difference in climate in the two localities, and in part to the fact that growers were beginning to cultivate their grounds and care for their crops systematically, instead of merely harvesting the natural supply.

Because of their susceptibility to the hot sunshine of summer and the freezing winds of winter, native oysters in Washington thrived only where they were relatively protected. Natural beds were found where the oysters were covered with water at low tide because of the slope of the tide land, or where seepage from underground would keep them moist in summer and relatively warm in winter. Pot holes would contain oysters while the intermediate ground, which becomes completely exposed at low tide, would be bare.

At the end of the last century, a few years after the appearance of Dean's work (1890) describing the method of oyster culture employed in France, the oystermen began to build dikes or structures on the tide lands which would keep the beds covered at low tide. The dikes are, in principle, closely similar to those described and pictured by Dean as the "oyster parks" used in France. Whether or not the French system furnished the original inspiration for the mode of oyster culture that was developed in Puget Sound within a few years is not known, but owners of natural ground began to build dikes around the beds so that the oysters would remain covered with water at low tide.

After a few years of experimentation, during which it was demonstrated that dikes make it possible to grow oysters on ground previously unused as well as to reduce mortality due to freezing, the entire industry in Puget Sound undertook systematically to dike the natural beds and expand to other grounds. Until very recent years most of the dikes were built of concrete, set well down into the bottom. The thickness of these dikes varies from about 6 inches to nearly 12 inches, depending upon the location. Now dikes are usually built of creosoted lumber, which lasts a long time and is more readily handled (figs. 1, 2, 3). Also, breaks due to settling are less frequent and more simply repaired. Dikes have been constructed on relatively level mud flats and on sloping banks. In the latter case the dikes are arranged in terraces, involving a great amount of hand labor for leveling. In all cases, when new ground is made, the rather soft natural bottom has to be surfaced with gravel to make it hard and firm as well as to maintain a relatively constant level in spite of the swift tides.

In southern Puget Sound, according to the tide tables of the U. S. Coast and Geodetic Survey, the maximum range of tide is 20 feet, from -3.8 to $+16.2$ feet. Most of the oyster grounds are between the -1-foot and the $+3$-foot tide levels, though some dikes require a tide as high as $+8$ feet to cover them. A few natural beds are in sloughs or shallow channels where they are never exposed. On the other hand, the natural beds of the same species in Yaquina Bay, Oreg., are covered by from 10 to 20 feet of water at low tide. In Puget Sound oyster growers have found

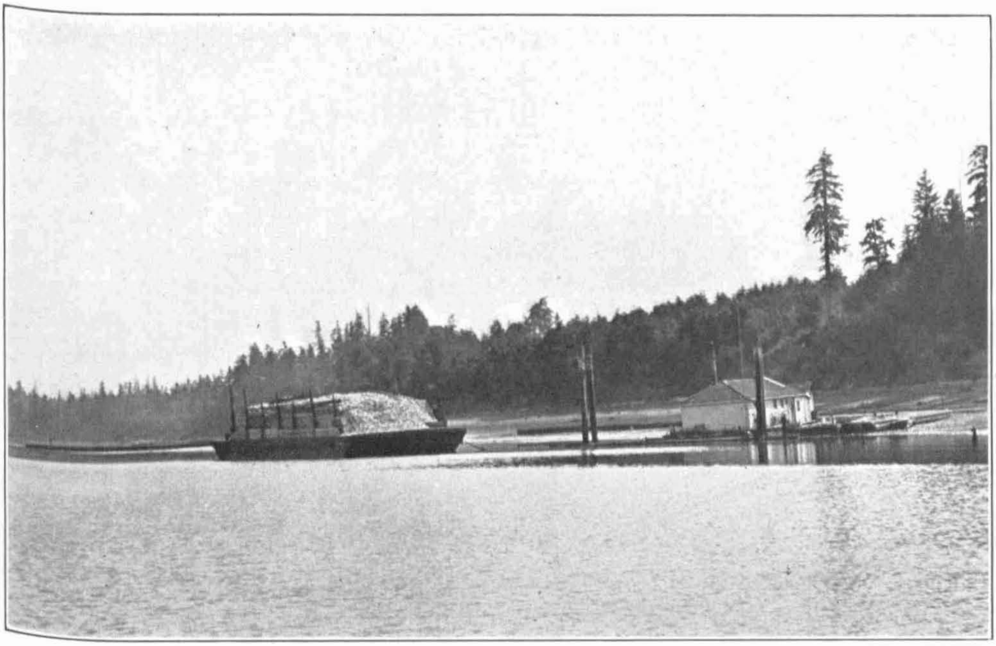

FIGURE 1.—Scowload of Japanese oyster shells near a culling house ready to be planted on the diked ground.

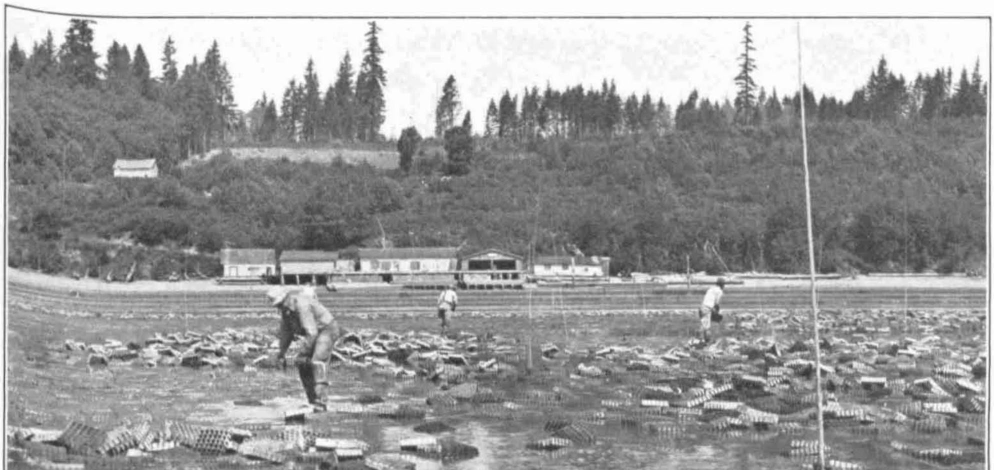

FIGURE 2.—Egg-crate fillers as spread from scows at high tide on diked ground being placed so that they will be completely covered at low tide.

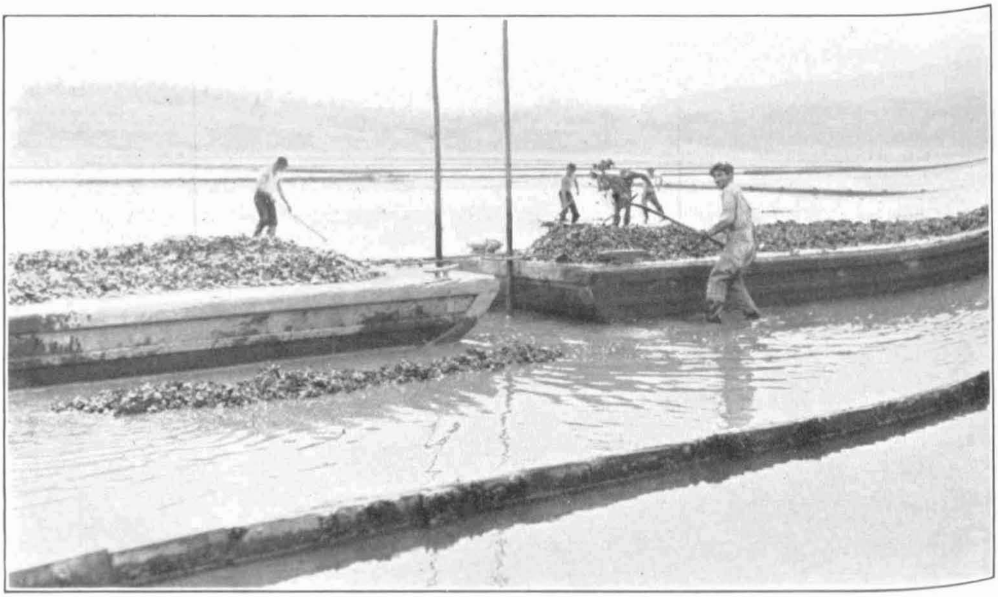

FIGURE 3.—Crew of men taking up seeds for transplantation to market grounds.

that the higher dikes are best for catching seeds while the lower grounds produce a superior product for market.

METHOD OF CULTIVATION

Although Galtsoff (1929) gave a description of the Olympia oyster industry and the methods of cultivation in use, it is necessary to review these matters briefly because of their bearing upon the experimental work which is described below. After spawning is well under way in June the oyster growers plant cultch, either shells or manufactured collectors, on the seed grounds. Until about 1930 the only cultch available was the native shells from the opening houses, but with the recent plantings of Japanese oysters a great quantity of these large shells is obtainable (see fig. 1). The development of the concrete-coated egg crate filler has also made larger plantings of cultch possible (see fig. 2). The spat which are caught are generally left on the seed ground for about 3 years before they are transplanted to growing grounds. Seeds are usually moved in April and May, permitting planting of new cultch on the same ground a short while later. Generally the seeds moved in spring are culled the following winter, though only the largest oysters reach market.

All oysters are taken up by hand since the grounds are exposed when the tide is low (see fig. 3). At low tide on one day a place to set a scow is cleared by forking the oysters to either side. The scow is staked in position at high tide and, when the ground is again exposed, the oysters forked onto it. As soon as depth of water permits, the scow is towed to the culling house and the oysters unloaded into a "sink float", made of two logs and a bottom, so that the oysters are washed free of mud as well as protected from weather conditions. They are taken up in wheel barrows from the sink float and loaded onto the large table in the culling house, where by tedious hand labor the marketable oysters are separated from the mass of shells and smaller seeds which are returned to the ground. The workers also separate the "slipper shells", or "cups", *Crepidula fornicata*, and the whelk or native snail, *Thais lamellosa*, and spread them high upon the beach to die and dry so they may be used as cultch. Cullers are paid extra for the snails and "cups" which they remove.

The culled oysters are spread in another sink float where they are frequently forked over until the water washes them thoroughly clean. As required for market they are packed in 2-bushel sacks and shipped to the opening houses. The cullers take up the oysters, return the seeds to the beds, and prepare the oysters for market and are paid on the basis of the number of sacks shipped. Japanese do almost all of this work as well as the shucking in the opening houses.

The small size of the Olympia oysters, in proportion to that of the Eastern and Pacific (Japanese) species, renders them much more expensive to handle. The average age of the marketable oyster is about 4 years, and about 5,000 of them are required to fill a 2-bushel sack. Ordinarily about 3 gallons of meats are obtained to the sack, so that a gallon contains about 1,600 oysters, as compared with 150 to 250 Easterns and about 50 to 200 Pacifics.

ENEMIES OF THE OYSTER

Although during the last few years there has been no apparent large mortality due to parasites, there are various organisms taking a constant toll of the crops. Ducks have given more trouble near Olympia than any other enemy (Galtsoff, 1929) and several species of these find the small size, single, native oysters an ideal, readily accessible food supply. Combating these is most difficult; and although some years ago a strenuous campaign was waged against them, the growers now appear to accept the damage passively.

For some years the great problem of oyster growers has been the "cup", *Crepidula fornicata,* which was presumably introduced into these waters with Eastern seed oysters. Although not a parasite, the species multiplied until many of the diked beds contained far more "cups" than oysters. Since the growers first became uneasy about them, they have paid the cullers extra for separating them out, and in this way have considerably reduced their numbers. However, even now it is not unusual for equal numbers of sacks of oysters and "cups" to be culled from a bed. The species appears to thrive much better in the diked beds than on the natural seepage grounds.

Several kinds of predatory snails are found on the grounds. The native whelk, *Thais lamellosa,* occurs in great abundance; and the writer has found that these drill some adult oysters and, in places, a great many spat. They appear to attack mussels primarily. They were previously unrecognized as an active enemy but are now culled out along with the "cups." Also, their habit, during the breeding season in late winter and early spring, is to come together in large clusters around a shell or rock where the egg cases are deposited. During this time they may be taken up in sacks and placed on the beach to die. The moon snail, *Polynices cewisii,* is frequently seen on oyster grounds but is primarily a clam borer and probably seldom attacks oysters.

The Eastern oyster drill, *Urosalpinx cinerea,* introduced with seed oysters from the Atlantic coast, may be found in some places, though only in Samish Bay where Japanese oysters are now grown is it relatively abundant. Of greater potential importance is the Japanese oyster drill, *Tritonalia japonica,* which has been introduced with seeds from the Orient. Few Japanese seeds have been planted near the important Olympia oyster grounds and no damage to native oysters has yet been noted. However, in Samish Bay, this drill has propagated rapidly and for the last few years has been causing tremendous mortality among the Japanese oysters. After a visit to Samish Bay in 1928, Galtsoff (1929) wrote:

> Although at present there is no evidence that *Tritonalia japonica* is destructive to oysters, yet as a matter of precaution it is desirable to restrict the planting of Japanese species to the waters in the northern part of Puget Sound and not to extend them to the areas where high-priced Olympia oyster bottoms are located.

When the writer first visited this ground 4 years later a great many drilled shells were found. In 1935 there was evidence of still greater mortality.

The rapid propagation of the species to dangerous proportions indicates the problem which Olympia oyster growers may soon face, especially since the thin-shelled, slow-growing native oysters would probably be more easily attacked than the relatively heavy-shelled Japanese oyster. Unfortunately, Galtsoff's suggestion was not followed, and it is known that the drills have been introduced near some of the native beds. On one ground in Oyster Bay a number of drills have been found, introduced presumably with Japanese oyster shells from Samish Bay. At the time of writing nothing is being done to prevent rapid spread of the pest to other grounds.

At times starfishes become abundant enough to destroy many oysters, but these are readily removed from the cultivated beds. One of the greatest problems of growers is to maintain their dikes against the "crawfish" or mud-shrimp, *Upogebia pugettensis,* (MacGinitie, 1930) which has a habit of burrowing under the dikes and opening passages which are rapidly enlarged by flow of water.

AIMS OF INVESTIGATION

A great many comprehensive experimental studies have been made on the biology of the oyster of the Atlantic coast, *Ostrea virginica*, but the only significant investigation on the practical phases of the biology of *O. lurida* was that of Stafford (1914, 1915, 1916, 1917, and 1918). He made his observations in British Columbia, in the northern part of Puget Sound, where the system of oyster culture had not been developed to an extent comparable to that in use near Olympia. Townsend's (1893) early paper gave the first general description of the industry on the Pacific coast. Recently Coe (1931a, 1931b, 1932a, and 1932b), Hori (1933), and Hopkins (1935, 1936) have furnished more specific information about the species.

The primary purpose of this investigation, which was undertaken in the spring of 1931 and continued through 1935, was to make an analysis of spawning activities and setting habits of larvae with reference to environmental conditions. By developing such information, it was hoped that oyster growers might be assisted in the catching of sufficient seed oysters to restore and expand the industry. In the following pages the more important of the results are described.[2]

HYDROGRAPHICAL OBSERVATIONS

The usual methods were employed for the taking and testing of water samples at different depths and under different tidal conditions. Specific gravity was measured with hydrometers certified and corrected by the National Bureau of Standards. A Hellige hydrogen-ion comparator was used with phenol red to determine the pH. Temperature of water samples was tested with standard thermometers, and in addition, continuous records of water temperature on the oyster grounds, at the level of the oysters, were made with a frequently checked thermograph.

GENERAL DESCRIPTION OF REGION

Puget Sound is an extremely irregular, deep body of water extending roughly 200 miles north and south in British Columbia and the State of Washington. It is continuous with the Pacific Ocean through the Straits of Juan de Fuca. The Sound is broken up into numerous bays and inlets which are generally quite deep except at their upper ends. Natural beds of native oysters were originally found in many of the small bays but were soon exhausted in all except a few localities where conditions necessary for successful propagation were especially favorable.

The several bays near Olympia, Wash., have continued to produce oysters, while beds in other places disappeared, largely because of favorable environmental factors and because of the development of the system of diking the grounds and planting cultch employed by the growers. These bays are separated from the ocean by more than 150 miles of water, yet changes in salinity are relatively slight, due to the great depth throughout the Sound.

[2] I wish to express my thanks to Charles R. Maybury, director of the Department of Fisheries and Game of the State of Washington and to Charles R. Pollock, supervisor of fisheries, for their cooperation in maintaining the laboratory and supplying an assistant and boats. Since the division of commercial fisheries became an independent department in December 1932, the director, B. M. Brennan, has continued to support this work under trying financial conditions and he deserves much credit for what has been accomplished.

It is a pleasure to express my thanks to the growers of Olympia oysters, all of whom have willingly given every possible assistance. I am particularly indebted to J. J. Brenner, E. G. Brenner, and D. I. Ginder, of the J. J. Brenner Oyster Co.; Ole Hanson and J. S. Waldrip, of the Olympia Oyster Co.; G. W. Ingham, Olympia Oyster Investment Co.; E. N. Steele; Charles Brenner; W. J. Waldrip; J. B. Bowman; J. H. Post; and the late Mrs. Minnie Blass.

A large part of the credit for this work is due to H. H. Adams, who served during 5 years as a most capable and efficient field assistant.

In figure 4 a portion of a chart (from U. S. Coast and Geodetic Survey, chart no. 6460) is reproduced to show the general contours of the most important bays in which Olympia oysters are cultivated. All of the observations here described were made in the area illustrated. The most extensive and successful grounds are in Totten Inlet, commonly called Oyster Bay. Mud Bay (Eld Inlet) is next in importance. Oakland Bay and Little Skookum (Skookum Inlet) also contain important grounds, but during the last few years, since a pulp mill began operation in the vicinity, they have been almost entirely out of production. (See Hopkins, Galtsoff, and McMillin, 1931; Hopkins, 1931a). The location of cultivated grounds is indicated on the chart. These are on the mud flats in the upper ends of the bays and on the relatively narrow beaches along the shores adjoining deep water. Altogether there are only something like 400 to 500 acres of producing grounds. Budd Inlet, on which Olympia is located, originally contained widespread beds of natural oysters, but has been condemned on account of sewage pollution.

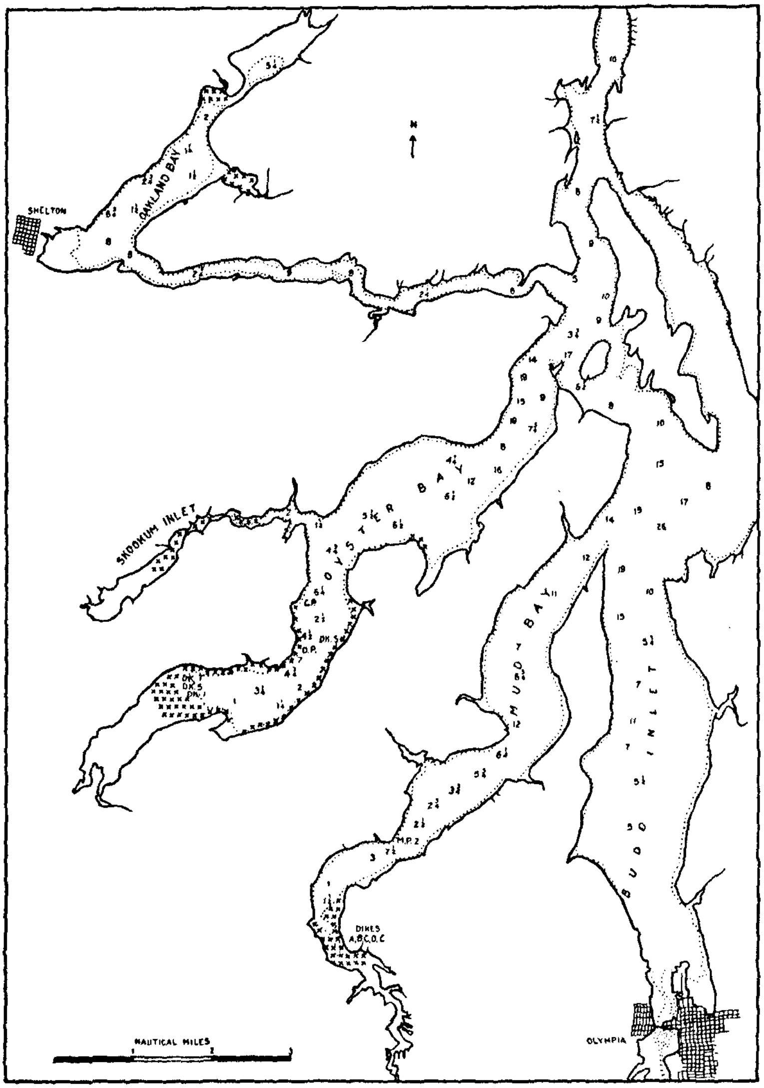

FIGURE 4.—General contours of oyster-producing bays near Olympia, Wash. Numbers refer to depth in fathoms. Location of diked beds is shown by x's. Dikes in which most observations were made are indicated. Depth samples were taken in channels off Corters Point (C. P.), Maple Point (M. P.), and Deepwater Point (D. P.).

TEMPERATURE

A Bristol recording thermometer was installed on a frame well above the high tide level but with the bulb fixed at the level of the oysters in the dike below. Protected though they are by a few inches of water at low tide, the oysters are nevertheless subjected to considerable variations in temperature as affected by both tides and seasons. The thermograph records were analyzed by averaging the readings on each hour of the day. This is necessarily not strictly accurate, but undoubtedly the error involved is within that inherent in the instrument itself.

A graph (fig. 5) is reproduced to illustrate the daily maximum, minimum, and average temperatures during winter (December 1932, January and February 1933) and summer (June through August 1933). This well represents the extremes, for during summer, at low tide, the water frequently reached 25° to 30° C., and during winter dropped to almost −2° C., or close to the freezing point of seawater. In the latter instance a great many oysters which were not well covered with water of high salinity were frozen and killed. The minimum temperature during summer and the maximum during winter show only slight fluctuations, since in summer the extreme low tides are during the day and in winter at night, the local temperature of the air not greatly affecting that of the water around the oysters at high tide. The difference between winter maximum and summer minimum is about 10° C.

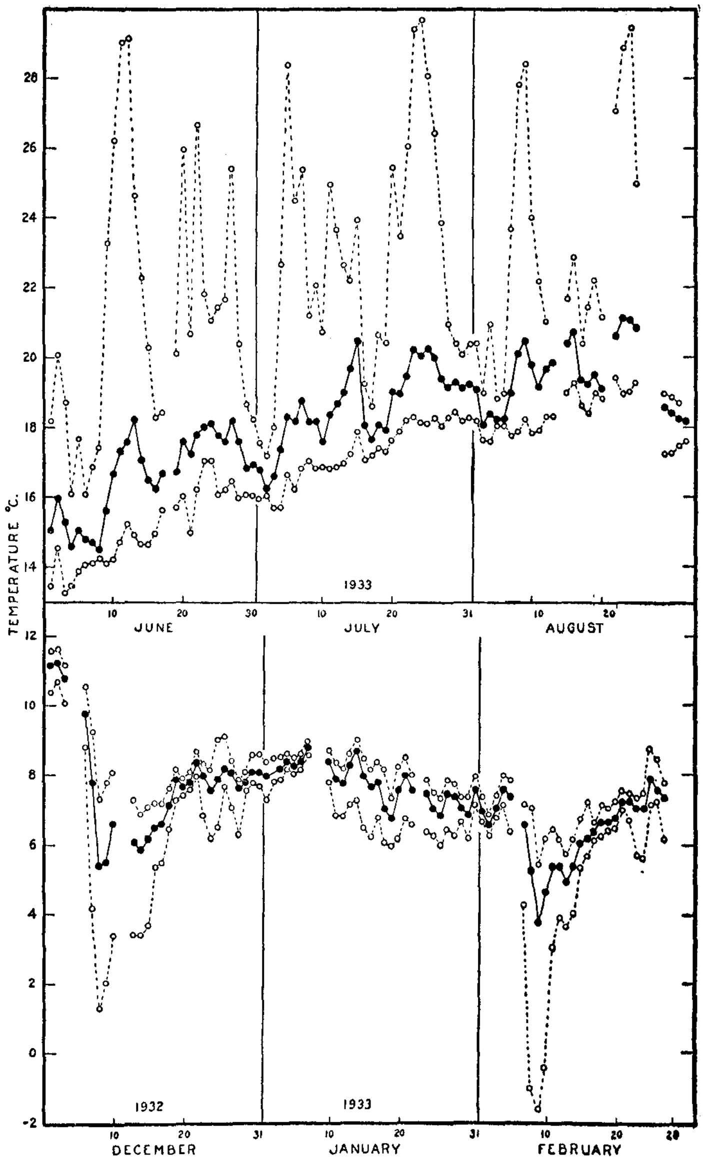

FIGURE 5.—Daily average, maximum, and minimum temperature on an oyster bed in Oyster Bay during winter and summer, as shown by thermograph records.

In order to show in detail the changes in water temperature in the dikes during a 24-hour period, as influenced by the range of tide, a graph (fig. 6) is given on which the continuous temperature records during 4 days are reproduced. Neap tide and spring tide temperature records are shown for typical days during both winter and summer. In the record for August 2 it will be noted that during the several hours that the dike was exposed by a −1.7-foot tide the temperature rose gradually from about 19° to about 30° C., and that when the flood tide poured over the dike the temperature dropped about 5° almost instantly. The other summer record was taken a few days later when low tide occurred at about 5 o'clock of a cool morning, and although the dike was not quite exposed there was a marked drop in temperature. The picture for temperature variations during winter is almost the reverse, the low tide occurring at night when the air is coolest. In all cases the variation is slight except at low tide when the water is shallow and readily reacts to sunshine and atmospheric conditions. That is, it is the surface water which responds readily to weather conditions; and the oysters may be under 16 feet of water at high tide and 3 or 4 inches a few hours later.

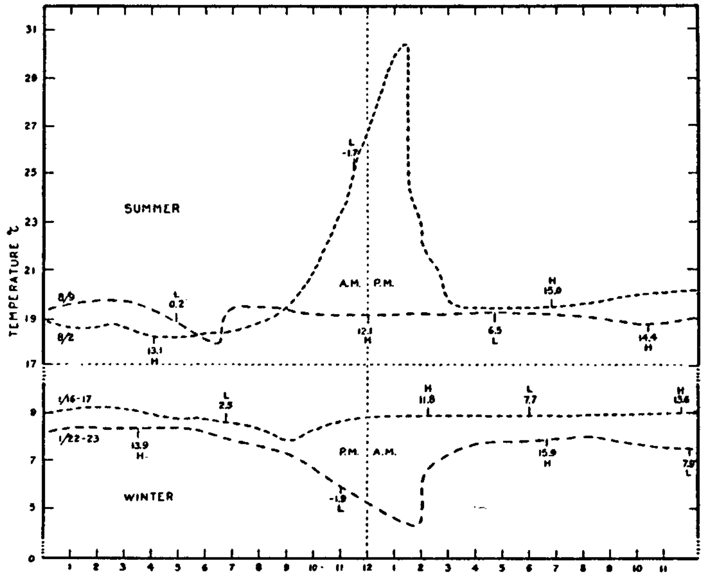

FIGURE 6.—Reproductions of portions of thermograph records showing variations in water temperature on oyster ground during four 24-hour periods, two in summer and two in winter. The most variable records refer to spring tides, the others to neap tides. Time and height (in feet) of high (H) and low (L) tides are indicated.

Seasonal variations in water temperature from year to year are relatively uniform, but the differences between successive seasons are sufficient to have a considerable bearing upon the spawning of oysters. In table 1 the monthly averages for 4½ years are given, as calculated from thermograph records obtained in Oyster Bay. The highest average water temperature is usually in August, the lowest in January or February. The annual variation is represented graphically in figure 7 for the 2 years (1933, 1934) when the temperature values were most widely different from one another. The spring rise in the curve for 1934 occurred about a month earlier than in 1933, accounting for a comparable difference in the time of spawning. Included on the graph are monthly averages of daily readings of maximum and minimum air temperature at Olympia. These records were supplied through the kindness of Charles F. Norrie, official weather observer. Water temperature is clearly correlated with air temperature.

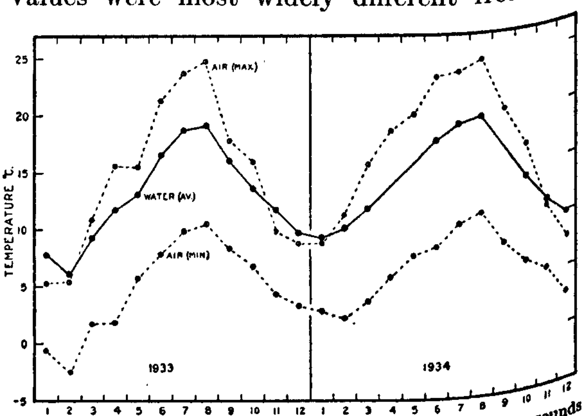

FIGURE 7.—Average monthly temperature of water on oyster grounds during 2 years as related to monthly averages of maximum and minimum daily air temperature at Olympia.

Other aspects of the temperature conditions are considered in later sections referring to the comparison of Oyster and Mud Bays in salinity, pH, and temperature.

TABLE 1.—*Average monthly water temperature in dike in Oyster Bay, calculated from thermograph records*

[Temperature °C.]

Month	1932	1933	1934	1935	Month	1931	1932	1933	1934	1935
January	7.28	7.70	9.38	7.66	July	18.2	18.10	18.71	19.27	19.48
February	6.36	6.07	10.07	8.88	August	18.45	18.61	19.12	19.79	19.45
March	8.56	9.30	11.83	9.22	September	17.04	17.09	16.07	------	18.60
April	10.61	11.76	------	12.03	October	13.15	14.61	13.69	13.90	15.41
May	14.02	13.06	------	15.46	November	9.92	11.70	11.78	11.41	8.95
June	17.00	16.64	17.67	17.93	December	7.88	7.89	9.61	9.78	9.38

TABLE 2.—*Comparison of dikes 5 and S in salinity, temperature, and pH*

Date	Dike 5				Dike S			
	Tide and depth	Temperature	Salinity	pH	Tide and depth	Temperature	Salinity	pH
1932		° C.				° C.		
Jan. 5	F—6 ft	7.4	27.72	8.0				
12	E—10 ft	7.3	27.17	8.0				
19	F—10 ft	7.3	27.36	8.0				
27	E—10 ft	6.2	25.48	8.0				
Feb. 4	E—7 ft	5.0	26.34	8.0				
11	E—8 ft	6.3	27.35	8.0				
24	E—4 ft	7.4	24.27	8.0				
Mar. 2	E—7 ft	7.1	25.24	8.0				
8	E—4 ft	8.0	21.98	8.0				
15	E—8 ft	8.0	25.93	8.0				
22	Exp	8.2	24.60	8.2				
29	E—8 ft	8.3	24.61	8.2				
Apr. 12	Ebb	10.1	24.13					
19	Exp	12.1	21.14	8.4				
26	Exp	15.0	22.75	8.0				
May 3	Exp	18.9	24.94	8.0				
10	Exp	15.6	26.24	7.8				
17	Exp	23.3	26.33	8.4				
19	Exp	13.9	25.87	7.8				
21	Exp	14.4	26.82	8.0				
24	Ebb	14.4	26.76	8.0				
31	Exp	19.4	26.24					
June 2	Exp	19.4	26.17	7.8				
4	Exp	15.0	27.32	8.2	Exp	16.1	27.32	8.0
6	Ebb	17.8	26.63	8.0	Exp	17.5	27.49	8.4
8					Exp	20.3	27.11	8.2
13					Exp	18.9	27.23	7.8
15	Ebb	13.9	28.04	8.0	Ebb	13.6	26.64	8.0
17	Exp	29.4	27.74	7.8	Exp	14.4	27.65	8.0
20	Exp	20.0	27.12	7.8	Exp	12.2	27.47	8.2
22	Exp	18.9	27.31	8.0	Ebb	21.7	26.30	7.9
24	Exp	19.4	27.81	7.9	Exp	20.6	27.85	8.0
27	Exp	18.3	27.64	7.7	Exp	16.4	28.03	
29					Exp	15.5	28.07	
July 1	Exp	24.4	27.18	8.0	Exp	21.9	27.07	8.0
4	Exp	18.3	27.69	8.0	Exp	17.8	27.86	8.0
6	Exp	28.9	29.42	7.4	Exp			
8	Exp	20.0	28.15	8.0	Ebb	22.8	28.12	7.8
11	Exp	16.1	27.16		Exp	15.3	27.97	
13	Exp	16.7	27.60		Exp	15.5	28.03	
15	Exp	16.4	27.63		Exp	15.5	27.98	
18	Exp	25.0	27.94	7.8	Exp	18.6	27.99	7.9
20	Exp	20.5	28.21	7.8	Exp	18.6	28.21	7.9
22	Exp	21.1	28.21	7.8	Exp	21.4	28.57	7.8
25	Exp	16.1	28.33		Exp	16.1	28.59	
27	Exp	16.1	28.13		Exp	15.8	28.59	
29	Exp	17.2	26.80	8.0	Exp	16.1	27.69	8.0
Aug. 1	Exp	17.2	28.01	7.8	Exp	17.8	27.69	7.8
3	Exp	20.0	28.16	7.8	Exp	18.3	28.35	7.8
5	Exp	22.2	28.24		Exp	25.0	28.30	7.8
8	Exp	16.1	28.40		Exp	16.1	28.60	
12	Exp	15.3	27.61		Exp	15.5	28.01	
15	Exp	16.7	27.89		Exp	16.4	28.03	
19	Exp	18.9	28.17	7.8	Exp	18.9	28.31	7.9
22	Exp	16.1	26.88		Exp	16.1	27.27	
26	Exp	18.9	28.17	7.4	Exp	16.4	27.54	7.6
29	Exp	18.0	28.69		Exp	16.9	28.82	
31	Exp	17.8	28.28	7.9	Exp	16.1	27.97	7.9
Sept. 2	Exp	16.1	28.30		Exp	16.7	28.55	
5	E—Surf	16.7	28.69		E—Surf	16.7	28.53	
9	Exp	13.0	29.08		Exp	13.3	26.97	
12	Exp	17.2	28.56		Exp	17.8	28.71	
16	Ebb	15.5	29.00		Ebb	16.1	28.36	
19	Ebb	14.4	28.94		Ebb	14.4	29.04	
23					Ebb	16.1	28.78	8.0
26	Exp	13.3	28.21	7.8	Exp	13.3	28.65	7.8
30	Exp	17.3	28.59	7.8	Exp	17.1	28.87	7.6
Oct. 4					E—Surf	15.4	29.28	
7	F—Surf	14.4	28.99		F—Surf	13.6	29.22	
11	1 ft	12.8	28.26	7.4	Exp	17.8	27.47	7.8
14	E—18 in	15.0	28.04	7.8	Exp	15.0	28.64	7.8
17	E—4 ft	14.2	28.33	7.9	E—Surf	13.4	28.48	7.9
21	E—7 ft	13.3	28.64	8.0	E—5 ft	13.3	28.98	8.0
24	F—3 ft	12.3	29.13	8.0	F—4 ft	12.4	23.57	8.0
28	F—Surf	12.1	28.73	8.0	F—Surf	12.2	28.84	8.0
31	E—6 ft	11.4	28.08	8.0	E—4 ft		29.02	8.0
Nov. 4	E—8 ft	10.1	28.93	8.0	E—Surf	10.1	28.04	7.9
7	F—6 ft	11.0	28.48	7.9	F—4 ft	11.1	28.66	7.9
14	E—6 ft	10.3	27.21	7.9	E—5 ft	10.2	26.62	7.9
21	F—8 ft	10.4	26.92	7.8	E—6 ft	10.4	26.33	7.8
28	E—Surf	10.2	25.61	7.8	E—6 ft	10.1	26.22	7.9
Dec. 5	E—8 ft	9.2	26.53	7.8	F—8 ft	9.4	25.21	7.8
19	E—8 ft	6.4	26.25	7.9	E—8 ft	6.4	26.65	7.9

NOTE.—F=flood; E=ebb; Exp.=exposed.

SALINITY AND pH

Because of the predominant deep water in Puget Sound and the relatively small streams flowing into the southern portion the variations in salinity are not often great, save on the surface. Samples were taken during summer in the exposed dikes, while throughout the rest of the year, when low tides occurred at night, samples were taken at surface and bottom at the same places. Description of conditions is here limited chiefly to Oyster Bay and Mud Bay, in which most of the experimental work was done. Since the two bays offer marked hydrographical and biological differences, it is necessary to go into some detail in describing the relative values of salinity and pH as a preliminary to the presentation of biological work.

On the chart (fig. 4) it will be seen that the two bays are not markedly different in size, though Oyster Bay is somewhat longer. In both, most of the oyster beds are located at the upper ends where there are relatively level, or gently sloping, bottoms exposed at low tide. More fresh water enters Mud Bay through creeks and seepage than goes into Oyster Bay, but no large stream enters either. Low salinity probably never accounts for any mortality in these bays, though in periods of very heavy rain the creeks sometimes wash quantities of silt over some of the beds.

Table 3.—*Comparison of temperature, salinity, and pH, at low tide in 4 dikes in Mud Bay*

(Dike A adjoins shore; others in order to edge of channel)

Date	Dike A			Dike B			Dike C			Dike D		
	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
1931	°*C*			°*C*			°*C*			°*C*		
June 1	19.4	27.25	------	21.7	27.31	------	20.5	27.18	------	20.5	27.12	------
June 5	20.0	27.07	------	20.8	27.07	------	21.1	26.88	------	21.1	26.88	------
June 13	15.7	25.90	------	------	------	------	16.0	25.78	------	15.8	26.05	------
June 17	17.8	26.27	------	17.9	25.91	------	18.3	26.31	------	18.3	26.30	------
June 22	16.7	26.58	------	17.0	26.31	------	17.2	26.45	------	16.7	25.28	------
June 25	13.5	24.60	------	13.6	26.27	------	13.5	25.75	------	13.9	24.43	------
June 29	18.0	24.99	------	17.8	25.84	8.0	18.3	24.58	7.8	17.8	25.17	7.8
July 1	18.3	25.95	------	18.9	25.62	------	19.4	25.84	------	19.7	25.95	------
July 3	17.2	26.65	------	20.0	26.08	------	20.8	26.18	------	21.4	26.18	------
July 9	19.4	26.26	8.0	19.7	26.02	7.8	19.4	25.90	7.8	19.4	25.87	7.8
July 13	16.3	27.06	7.8	16.7	26.94	7.8	16.4	26.82	7.8	16.7	26.82	7.8
July 17	21.1	27.81	8.0	21.7	27.75	8.0	21.7	27.60	8.0	23.6	27.57	8.0
July 20	22.2	27.93	8.0	22.2	27.48	8.0	21.7	27.75	8.0	22.2	28.07	8.2
July 23	17.2	27.83	8.0	17.2	27.83	8.0	17.2	27.83	8.0	17.2	27.83	8.0
July 25	19.4	27.75	8.0	19.4	27.06	8.0	20.0	27.50	7.8	20.0	27.48	7.8
July 29	25.8	28.42	8.0	26.1	28.40	7.8	25.8	28.27	7.8	26.9	28.01	7.8
Aug. 3	26.3	28.12	8.0	26.4	27.79	8.0	25.5	27.75	------	26.4	27.69	8.0
Aug. 7	14.7	28.13	7.8	15.0	27.95	7.8	15.3	27.98	7.8	15.3	27.98	7.8
Aug. 12	21.4	28.65	8.0	21.1	28.51	8.0	20.5	28.36	8.0	21.1	28.10	7.8
Aug. 21	15.0	28.59	7.8	15.0	28.41	7.8	15.0	28.60	7.8	15.0	28.30	7.8
Aug. 24	17.5	29.72	------	17.5	28.51	------	17.5	28.31	------	17.5	28.19	------
Aug. 26	18.9	28.82	------	18.9	28.31	7.8	18.6	28.15	7.8	19.3	28.24	7.8
Sept. 5	17.8	25.52	7.4	18.5	27.84	7.4	18.3	27.63	7.4	18.6	26.58	7.4
Sept. 10	15.5	28.65	------	15.5	28.35	7.8	15.5	28.06	------	15.5	27.92	------
Sept. 26	16.7	28.51	------	16.1	28.19	------	15.8	28.26	------	15.0	27.78	------
Oct. 8	11.7	28.44	7.8	11.1	27.88	7.6	10.5	27.64	7.6	11.1	27.65	7.7

In order to indicate the general results of tests on oyster grounds throughout the year, and the close comparison in salinity and pH of the water on various grounds, the values are given in table 2 for samples taken in two dikes in Oyster Bay, 1932. During the summer season samples were taken at low tide when the dikes were exposed and the water quite warm, while at other times of year bottom samples were taken. The day-to-day variation in salinity is not great, and although dike 5 is well up the bay and dike *S* about 2 miles away (see chart, fig. 4) there is little difference to be noted.

TABLE 4.—*Comparison of average monthly values of salinity and pH in a dike in Oyster Bay and one in Mud Bay during 2 years*

Date	Oyster Bay, dike 5			Mud Bay, dike B			Date	Oyster Bay, dike 5			Mud Bay, dike B		
	Number of samples	Average salinity	Average pH	Number of samples	Average salinity	Average pH		Number of samples	Average salinity	Average pH	Number of samples	Average salinity	Average pH
1932							1933						
January	4	26.93	8.00	3	27.75	8.00	January	4	24.02	7.87	4	26.49	7.90
February	3	25.99	8.00	4	25.76	7.98	February	3	25.68	8.10	4	25.25	8.10
March	5	24.47	8.08	4	25.37	8.00	March	3	24.70	8.17	2	26.84	8.10
April	3	22.67	8.20	3	27.52	8.30	April	5	25.86	8.30	4	24.92	8.26
May	7	26.17	8.00	4	24.05	8.10	May	11	26.39	8.20	7	24.91	8.12
June	9	27.31	7.91	9	25.84	7.88	June	12	27.36	7.97	12	25.65	8.05
July	13	27.88	7.85	12	25.93	7.90	July	12	28.11	7.92	13	26.68	7.88
August	11	28.05	7.74	10	26.53	7.84	August	11	28.21	7.96	13	26.97	7.94
September	8	28.67	7.80	10	28.00	8.00	September	6	28.29	7.93	7	26.99	7.96
October	7	28.49	7.85	4	28.64	7.87	October	4	27.49	7.90	4	23.59	7.90
November	4	27.88	7.90	5	27.39	7.92	November	4	24.45	7.80	4	27.42	7.75
December	2	26.39	7.85	2	27.48	7.80	December	3	24.64	7.80	1	26.36	7.80

In Mud Bay, however, into which more fresh water flows, there is a distinct gradient (table 3) in the salinity of the water at low tide in a series of 4 dikes from the shore (dike *A*) to the edge of the channel (dike *D*). The first three dikes are on the same level but the last (*D*) is about 1 foot lower. The lower level does not account for the salinity difference. The main body of fresh water from creeks at the head of the bay follows the channel, while the contours of the bay tend to carry the more saline water at flood tide to the west side of the bay.

The variation in salinity between individual samples taken at any time is relatively slight and the values over a period of a year may be best indicated by monthly averages. In table 4 the average monthly salinity and pH are given for 2 full years, 1932 and 1933, in two typical dikes, dike 5 in Oyster Bay and dike B in Mud Bay. The summer samples refer to conditions at low tide when the dikes were exposed. During the rest of the year the values refer only to bottom samples taken at relatively high tide. The more clearly to represent seasonal variations, the data are plotted in figures 8 and 9. The lowest salinity occurs generally during late winter and early spring, depending upon the time of greatest precipitation, and the annual variation, expressed in this manner, is usually between about 24 and about 29 p.p.mille.

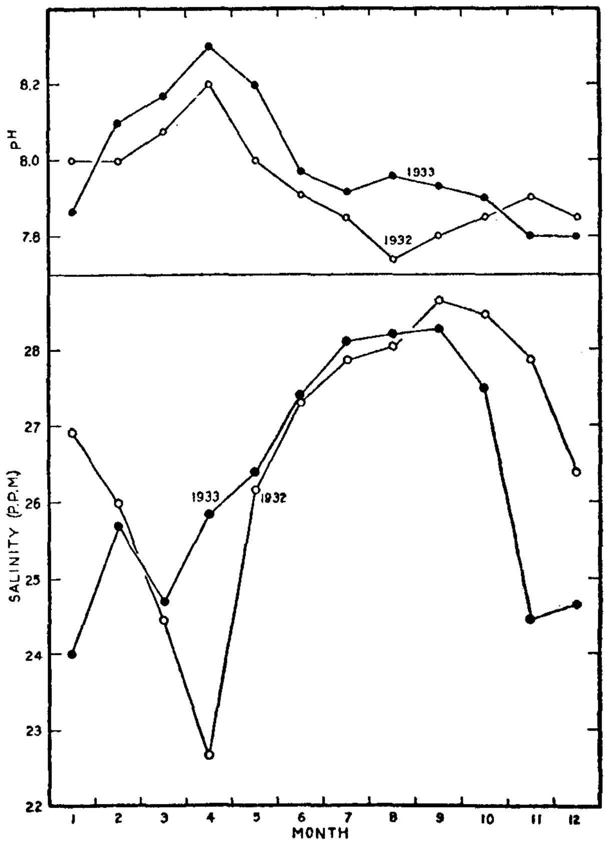

FIGURE 8.—Average values of salinity and pH of water on oyster ground (dike 5) in Oyster Bay during 2 years. Most summer samples were taken at low tide while during the remainder of year bottom samples were taken. Compare with Mud Bay, figure 9.

The salinity on the oyster grounds in Mud Bay is more variable than in Oyster Bay, as may be seen by comparing the figures, and heavy rains affect the water more quickly in the former. The hydrogen-ion concentration varies in a more orderly manner during the year and the two bays are similar in this respect. During late winter the pH rises rapidly from a low of about 7.8, reaching the maximum of about 8.3 in April. It then drops rapidly until midsummer, after which it is relatively stable. This is discussed further below.

The mode of sampling on the oyster grounds involves some lack of constancy throughout the year because all samples were taken during the day, so that for a large part of the year the tide was relatively high while in summer the dikes were exposed. A better picture of the high-tide salinity and pH was obtained by making studies in the deeper channels a short distance below the oyster grounds, off Corters Point in Oyster Bay and Maple Point in Mud Bay. That the results may be used to indicate conditions obtaining on the oyster grounds is shown in table 5, in which the surface temperature, salinity, and pH are compared for three places in Oyster Bay during summer. The salinity off Corters Point and Deepwater Point is almost identical with that in the exposed dikes, although in the last the temperature and pH are decidedly different because of exposure to sunshine and warm air and the respiratory activity of oysters and other organisms.

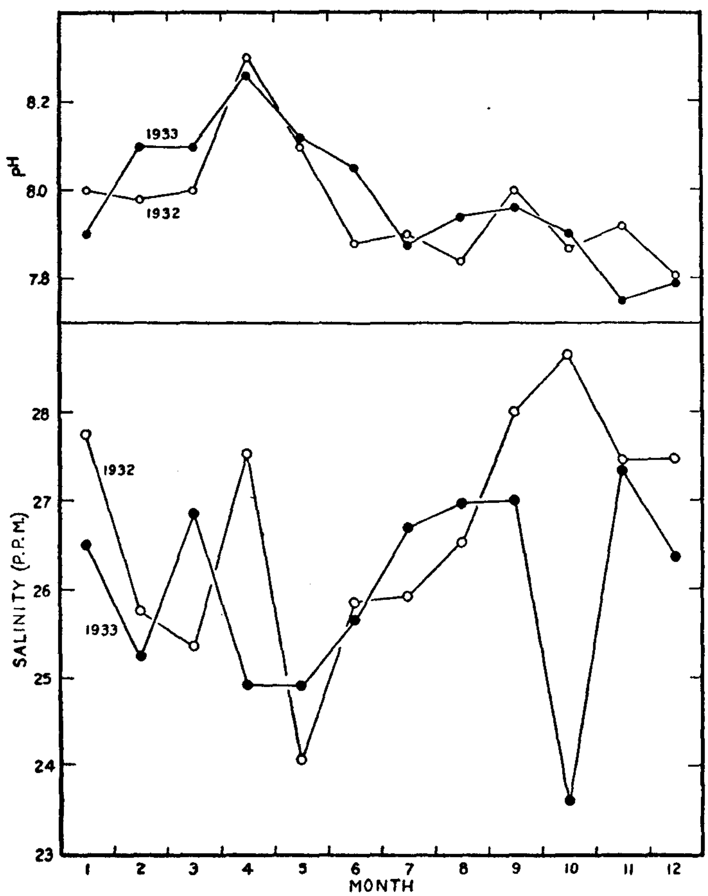

FIGURE 9.—Average values of salinity and pH of water on oyster ground (dike *B*) in Mud Bay during 2 years. Summer samples were taken at low tide while during the remainder of the year bottom samples were taken. Compare with Oyster Bay, figure 8.

To show briefly the annual variation in the waters of the two bays the average monthly values of salinity and pH at surface and bottom for Corters Point (Oyster Bay) and Maple Point (Mud Bay) are given in table 6 for 2 consecutive years. The surface salinity in Oyster Bay throughout the year is generally higher than in Mud Bay, though at the bottom the relationship is reversed and higher salinity prevails in Mud Bay. A similar difference was noted above with respect to the water over the oyster grounds of the two bays at low and high tide. The same average values are reproduced graphically in figures 10 and 11. The lowest salinity is to be found in late winter, near the end of the rainy season, and early in spring the gradual rise in bottom salinity begins. The bottom salinity in Oyster Bay varies during the year from about 26 to 29 parts per mille, in Mud Bay from about 27 to 29.5 parts per mille. The difference between bottom and surface is much greater in the latter bay, indicating the extent of adaptation required of the oysters during the tidal cycles. Shown in the figures also is the monthly precipitation as recorded at Olympia by C. F. Norrie. Rain is markedly seasonal at this place, with almost no rainfall during summer. The low salinity in winter is directly correlated with precipitation, though there is considerable lag in the salinity at the bottom.

TABLE 5.—*Salinity, temperature, and pH in Oyster Bay at 3 different points during summer (see chart, fig. 3)*

Date	Tide	Corters Point			Deepwater Point			Dike 1		
		Surface			Surface			Low tide		
		Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
		° C.			° C.			° C.		
June 27	F	16.0	27.57	------	15.0	27.94	------	22.2	27.66	------
June 30	F	17.7	26.64	------	14.4	28.28	------	18.9	27.36	------
July 10	------	15.3	28.40	8.4	15.0	28.37	8.2	16.7	28.40	8.2
July 15	F	18.0	28.60	8.4	------	28.60	8.4	27.2	28.75	8.0
July 18	E	19.1	28.98	8.4	20.5	28.35	8.2	26.1	28.63	8.2
July 24	F	19.6	28.64	8.4	18.3	28.69	8.4	19.4	28.56	7.8
July 27	F	17.2	29.29	8.4	18.0	29.13	8.4	27.2	29.09	7.8
July 30	F	18.9	29.02	8.4	18.3	28.86	8.4	27.8	28.98	7.8
Aug. 1	E	19.4	29.20	8.4	20.5	28.86	8.4	25.3	29.09	8.0
Aug. 3	E	18.0	29.33	8.4	18.3	29.17	8.4	23.5	28.99	8.0
Aug. 8	F	17.5	27.74	8.2	17.5	29.56	8.2	17.5	28.53	7.8
Aug. 11	F	17.5	29.29	8.2	17.8	29.11	8.2	23.3	29.37	7.8
Aug. 13	E	19.0	29.54	8.2	19.7	28.11	8.2	27.2	28.41	7.8
Aug. 15	E	18.2	29.61	8.2	18.9	29.78	8.2	24.4	29.65	7.8
Aug. 22	F	18.4	29.13	8.2	17.2	28.98	8.2	17.5	29.13	7.8
Aug. 27	F	18.7	29.99	8.2	17.2	29.76	8.2	23.3	29.56	7.8
Aug. 29	F	18.3	29.90	8.1	18.9	29.81	7.7	25.0	29.58	7.8
Sept. 8	F	16.7	29.52	8.0	16.7	29.20	8.0	16.7	28.86	7.6
Averages	------	17.97	28.91	8.28	17.72	28.92	8.23	23.28	28.81	7.91

NOTE.—F=flood; E=ebb.

TABLE 6.—*Average monthly values of salinity and pH at surface and bottom off Corters Point (Oyster Bay) and Maple Point (Mud Bay) during 2 years*

Date	Corters Point					Maple Point				
	Surface			50 feet		Surface			30 feet	
	Number samples	Average salinity	Average pH	Average salinity	Average pH	Number samples	Average salinity	Average pH	Average salinity	Average pH
1932										
January	4	25.45	7.92	27.68	8.05	4	25.06	8.0	28.91	8.0
February	3	26.68	8.0	27.97	8.0	4	23.88	7.97	28.59	8.0
March	5	24.27	8.02	25.78	8.04	4	23.45	8.0	27.16	8.0
April	3	24.34	8.3	26.86	8.3	4	25.37	8.33	27.89	8.4
May	6	26.94	8.4	27.69	8.4	4	26.94	8.4	28.15	8.4
June	3	27.92	8.4	28.10	8.4	4	27.42	8.2	28.31	8.3
July	3	28.34	8.27	28.38	8.37	2	27.43	8.15	28.28	8.2
August	4	28.32	8.23	28.53	8.3	5	28.31	8.14	28.84	8.36
September	4	28.94	8.3	28.67	8.15	2	29.11	8.15	29.43	8.2
October	7	29.01	8.01	29.20	8.0	5	29.29	7.98	29.58	8.05
November	5	27.26	7.86	28.18	7.93	5	25.45	7.87	28.95	7.92
December	3	25.79	7.73	26.78	7.8	2	26.74	7.8	28.14	7.85
1933										
January	4	23.79	7.87	26.38	7.87	4	26.27	7.83	27.20	7.9
February	4	25.59	8.1	26.21	8.1	4	24.61	8.0	27.47	8.1
March	4	24.10	8.13	26.26	8.15	4	23.56	8.1	27.00	8.1
April	5	26.05	8.28	26.78	8.34	4	24.76	8.27	27.46	8.3
May	12	27.11	8.24	27.66	8.28	8	26.81	8.23	27.92	8.31
June	11	27.75	8.13	28.00	8.18	12	26.29	8.17	28.41	8.23
July	11	28.30	8.15	28.46	8.18	11	27.50	8.05	28.70	8.12
August	11	28.43	8.12	28.57	8.12	12	27.84	8.03	28.51	8.04
September	6	28.67	8.07	28.95	8.13	7	28.32	8.0	28.59	7.99
October	4	27.79	8.1	28.23	8.1	4	27.48	8.02	28.86	8.02
November	4	26.13	7.8	26.96	7.8	4	26.40	7.8	27.30	7.8
December	3	20.53	7.8	25.32	7.8	1	18.58	7.8	27.17	7.8

In these two figures the annual variations of hydrogen-ion concentration are very striking. The lowest pH value is generally in December, when it averages about 7.8. In late winter it rises rapidly, reaching a maximum of about 8.4 usually in April and May, from which it gradually drops during the rest of the year. The time of highest pH is somewhat later than the time of lowest salinity and is probably due to the prolific development of diatoms and other algae in the water which contains large amounts of fertilizing materials such as nitrates, brought in by the inflowing drainage water which is becoming warmer during early spring. The warming water and the brighter light, associated with the presence of necessary chemical substances, permit the active multiplication of plant life, and photosynthesis rapidly removes carbonic acid, raising the pH. Later, however, as available fertilizing materials become fixed by the algae and as the water becomes warmer the respiratory activity of marine animals, including oysters, crustaceans, and others, restores a high percentage of carbonic acid to the water, lowering the pH.

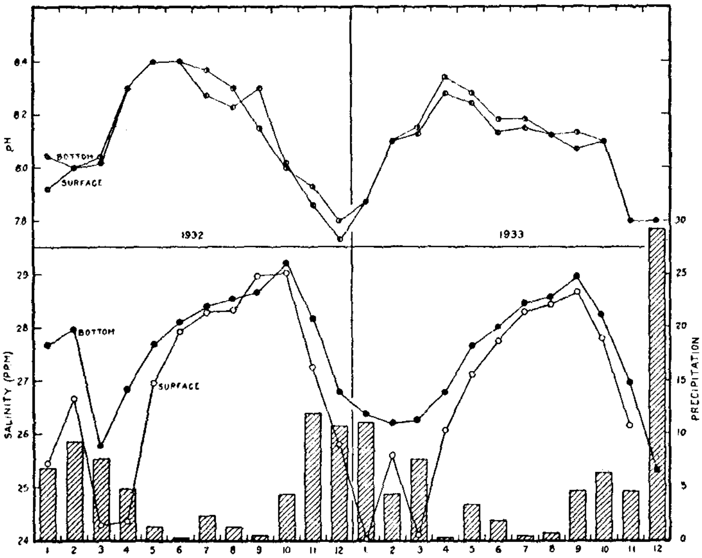

FIGURE 10.—Average monthly values of salinity and pH at surface and bottom (50 feet) off Corters Point (Oyster Bay) during 2 years. Total monthly precipitation (Olympia) is also shown. Compare with Mud Bay, figure 11.

In this regard it is of interest to call attention to changes in the pH and salinity of the water in a dike during a complete tidal cycle. In figure 12 the depth of water in a dike is shown throughout a 24-hour period in summer as related to the salinity and pH of the water. During ebb tide the water level became lower than the dike, leaving it exposed at about 1:15 p. m. At about 4:45 p. m. the flood tide came up to the dike level. During the time the dike was exposed the pH dropped from 8.0 to 7.9, because of carbonic acid excreted by oysters and other organisms, and the salinity rose slightly, due partly to evaporation and partly to stratification of the water permitting the less

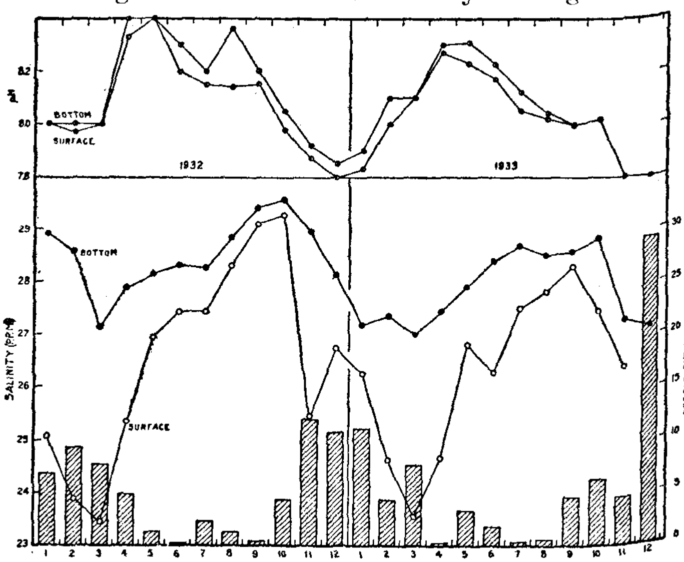

FIGURE 11.—Average monthly values of salinity and pH at surface and bottom (30 feet) off Maple Point (Mud Bay) during 2 years. Total monthly precipitation (Olympia) is also shown. Compare with Oyster Bay, figure 10.

saline to remain at the surface. During the flood tide both salinity and pH rose. Variations during the rest of the period are relatively slight, though in accord with this interpretation.

TABLE 7.—*Comparison of values of salinity, temperature, and pH off Corters Point during 1932 at different depths*

Date	Tide	Surface			6 feet			15 feet			30 feet			50 feet		
		Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
1932		°C.			°C.			°C.			°C.			°C.		
Jan. 5	E	7.3	26.74	8.0	7.4	27.25	8.0	7.4	27.66	8.0	7.4	28.35	8.0	7.4	28.39	8.0
12	E	6.0	23.96	7.8	6.4	24.89	8.0	7.4	27.86	8.0	7.4	27.86	8.0	8.0	27.39	8.0
19	F	7.0	24.60	7.9	7.1	24.78	8.0	7.2	26.65	8.0	7.2	27.72	8.0	7.2	27.86	8.2
27	E	6.2	26.51	8.0	6.3	26.09	8.0	6.4	26.19	8.0	7.0	27.01	8.0	7.0	27.16	8.0
Feb. 4	E	4.3	26.03	8.0	5.1	27.41	8.0	5.2	27.79	8.0	5.3	27.99	8.0	5.3	27.99	8.0
11	E	5.4	27.98	8.0	5.4	27.66	8.0	6.1	27.68	8.0	6.1	27.68	8.0	6.0	27.77	8.0
24	E	6.4	26.04	8.0	7.2	27.63	8.1	7.0	28.10	8.0	7.0	28.10	8.0	7.0	28.16	8.0
Mar. 2	E	6.3	23.59	8.0	6.4	23.53	8.0	7.2	24.99	8.0	7.3	25.97	8.0	7.3	26.19	8.0
8	E	7.1	23.75	8.0	7.3	23.59	8.0	7.3	23.68	8.0	7.3	25.62	8.0	7.3	24.85	8.0
15	F	7.3	25.53	8.0	7.4	25.32	8.0	7.4	26.53	8.0	7.4	27.11	8.0	7.4	26.39	8.0
22	E	8.1	24.79	8.0	8.1	25.79	8.0	8.1	25.87	8.0	8.1	25.91	8.0	8.1	25.81	8.0
29	E	8.3	23.69	8.1	8.4	23.48	8.2	8.4	24.65	8.2	8.2	24.66	8.2	8.2	25.64	8.2
Apr. 12	E	10.3	23.50	------	10.2	24.02	------	9.1	25.81	------	9.0	26.09	------	9.0	26.17	------
19	E	9.4	25.91	8.2	10.1	27.89	8.2	9.4	25.90	8.2	9.3	27.75	8.2	9.3	27.83	8.2
26	E	15.1	23.41	8.4	13.1	26.00	8.4	10.4	28.16	8.4	10.2	28.03	8.4	10.2	26.58	8.4
May 3	E	12.2	25.91	8.4	11.4	26.18	8.4	11.0	26.58	8.4	--------	-------	------	10.3	26.63	8.4
10	E	12.3	26.80	8.4	12.1	27.30	8.4	12.1	28.53	8.4	11.3	27.20	8.4	11.2	28.84	8.4
17	F	15.0	26.67	8.4	14.3	27.27	8.4	13.1	27.39	8.4	13.0	27.40	8.4	13.0	27.32	8.4
21	E	13.2	27.32	8.4	13.1	27.31	8.4	13.7	26.97	8.4	13.0	27.43	8.4	13.0	27.46	8.4
24	E	13.2	27.41	8.4	13.2	27.74	8.4	13.0	27.66	8.4	13.0	27.69	8.4	13.0	28.30	8.4
31	E	13.4	27.52	8.4	14.0	27.45	8.4	13.2	27.41	8.4	12.4	26.26	8.4	12.4	27.63	8.4
June 6	E	13.4	27.78	8.3	14.0	28.03	8.4	14.0	27.79	8.4	13.3	27.90	8.4	13.3	28.06	8.4
15	E	15.0	27.94	8.4	15.0	28.01	8.4	15.0	27.95	8.4	14.4	28.01	8.4	14.4	28.12	8.4
22	E	16.0	28.03	8.4	16.0	27.99	8.4	15.4	27.84	8.4	15.4	27.95	8.4	15.4	28.12	------
July 8	E	17.2	29.83	8.4	17.0	28.26	8.4	17.1	28.21	8.4	16.3	28.39	8.4	16.2	28.41	8.4
18	E	15.4	28.39	8.2	16.3	28.42	8.2	16.1	28.30	8.2	16.0	28.31	8.2	16.0	27.00	8.2
20	E	17.2	28.51	8.2	17.0	28.59	8.2	17.0	28.30	8.2	16.4	28.30	8.2	16.3	28.48	8.2
29	F	16.2	26.67	8.2	16.0	28.59	8.4	16.0	28.24	8.4	15.4	28.24	8.4	15.4	28.24	8.5
Aug. 3	F	16.3	28.35	8.3	16.3	28.42	8.3	16.3	28.30	8.4	16.4	28.35	8.4	16.4	28.48	8.4
10	F	17.4	28.21	8.2	17.3	28.21	8.2	17.1	28.57	8.3	17.0	28.35	8.2	16.4	28.68	8.2
17	F	18.0	28.30	8.2	17.4	28.41	8.4	17.1	28.31	------	17.0	28.31	8.4	17.0	28.37	8.4
24	F	17.2	28.44	8.2	17.0	28.45	8.2	16.3	28.59	8.2	16.3	28.66	8.2	16.3	28.59	8.2
Sept. 23	F	15.3	28.74	8.4	15.2	29.05	8.4	15.1	28.59	8.0	14.4	29.07	8.0	14.4	28.98	8.0
28	F	16.4	28.91	8.2	15.4	29.07	8.2	15.3	29.00	------	15.1	28.91	8.2	15.1	28.98	8.2
30	E	15.2	28.94	8.2	15.1	29.04	8.2	15.1	29.00	8.2	15.1	29.07	8.3	15.1	29.07	8.2
Oct. 11	F	14.1	28.94	8.2	14.1	29.20	8.1	14.1	29.13	8.1	14.0	29.65	8.1	13.4	29.22	8.1
14	F	14.2	29.11	8.0	14.2	29.11	8.0	14.2	29.00	8.0	15.0	29.28	8.0	14.1	29.23	8.0
17	F	14.0	28.87	7.9	14.0	28.85	7.9	14.0	28.69	7.9	14.2	28.71	7.9	14.2	29.23	7.9
21	F	13.2	29.08	8.0	13.3	28.95	8.0	13.3	29.16	8.0	13.3	20.47	8.0	13.3	29.18	8.0
24	F	12.4	29.11	8.0	12.5	29.16	------	13.0	29.32	8.0	13.0	29.22	8.0	13.0	29.22	8.0
28	F	12.4	29.09	8.0	12.4	29.28	8.0	12.3	28.98	8.0	12.3	29.14	8.0	12.3	29.28	8.0
31	F	--------	28.88	8.0	--------	29.05	8.0	--------	29.36	8.0	--------	29.05	8.0	--------	29.02	8.0
Nov. 4	F	11.0	29.11	7.9	11.0	28.98	8.0	--------	29.29	8.0	11.0	29.32	8.0	11.0	29.43	8.0
7	F	10.3	26.92	7.9	11.1	28.53	7.9	11.1	29.09	7.9	11.1	28.95	7.9	11.1	29.29	7.9
14	E	10.2	27.17	7.9	10.4	27.52	7.9	10.4	27.79	7.9	10.4	28.06	7.9	10.4	27.79	------
21	E	10.4	26.62	7.8	10.4	27.00	7.8	10.4	26.42	7.9	11.0	27.39	7.9	11.0	27.21	7.9
28	E	10.0	26.58	7.8	10.1	26.85	7.9	10.1	26.85	7.9	10.2	27.39	------	10.2	27.20	7.9
Dec. 5	F	9.2	25.39	7.7	9.4	26.59	7.8	9.4	25.96	7.8	9.4	25.95	7.8	9.4	27.11	7.8
19	E	6.4	26.73	7.8	6.4	27.16	7.9	7.1	27.20	7.9	7.2	27.38	7.9	7.2	27.39	------

NOTE.—E=ebb.; F=flood.

TABLE 8.—*Temperature, salinity, and pH of water at different depths off Maple Point (Mud Bay) during 1 year*

Date	Tide	Surface			3 feet			10 feet			20 feet			30 feet		
		Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
1932		°C.			°C.			°C.			°C.			°C.		
Jan. 5	F	4.3	21.49	8.0	5.4	26.11	8.0	7.2	28.66	8.0	7.4	28.91	8.0	7.4	29.16	8.0
3	E	7.3	27.64	8.0	7.4	27.89	8.0	8.0	29.66	8.0	8.1	28.73	8.0	8.1	28.87	8.0
22	E	4.2	24.33	8.0	7.0	26.82	8.0	7.2	28.30	8.0	7.3	28.75	8.0	7.3	28.95	8.0
30	E	3.4	26.78	8.0	5.3	27.79	8.0	6.4	28.15	8.0	7.0	28.95	8.0	7.0	28.65	8.0
Feb. 6	E	5.3	28.04	8.0	5.3	27.78	8.0	5.3	27.88	8.0	6.0	28.56	8.0	6.0	28.48	8.0
13	E	4.0	21.46	8.0	5.1	27.75	8.0	6.2	28.55	8.0	6.3	28.77	8.0	6.3	28.73	8.0
19	F	6.1	26.13	8.0	6.3	26.13	8.0	6.4	27.61	8.0	6.4	27.84	8.0	6.4	28.57	8.0
26	E	8.3	19.89	7.9	8.3	29.82	8.0	8.0	29.49	8.0	8.0	28.12	8.0	8.0	28.61	8.0
Mar. 3	F	6.1	22.95	8.0	6.4	28.27	------	7.1	27.61	8.0	7.2	27.27	8.0	7.2	27.36	8.0
10	E	7.2	21.28	8.0	8.0	24.00	8.0	8.0	27.43	8.0	8.0	27.88	8.0	8.0	28.17	8.0
17	E	8.3	25.62	8.0	9.0	25.77	8.0	8.3	25.44	8.0	8.1	27.59	8.0	-------	27.73	8.0
26	E	8.0	23.95	8.0	7.4	28.94	8.0	8.0	25.01	8.0	8.1	25.09	8.0	8.1	25.37	8.0
Apr. 1	F	8.4	25.72	8.4	9.0	25.95	------	8.3	27.48	------	8.3	27.90	------	8.3	27.83	------
15	F	10.0	26.96	8.4	10.1	26.60	8.4	10.0	27.56	8.4	9.0	27.31	8.4	9.0	28.01	8.4
21	E	10.3	22.92	8.2	10.3	23.01	8.2	10.3	26.09	8.3	10.2	28.59	8.4	10.1	28.19	8.4
29	F	11.3	25.88	8.4	11.4	26.85	8.4	11.0	26.04	8.4	10.1	27.83	8.4	-------	27.54	------

TABLE 8.—*Temperature, salinity, and pH of water at different depths off Maple Point (Mud Bay) during 1 year*—Continued

Date	Tide	Surface			3 feet			10 feet			20 feet			30 feet		
		Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
1932		° *C.*			° *C.*			° *C.*			° *C.*			° *C.*		
May 6	E	11.4	26.00	8.4	11.3	26.45	8.4	11.3	26.97	8.4	11.1	27.41	8.4	11.1	27.52	8.4
13	E	12.4	27.64	8.4	12.3	27.88	8.4	12.3	27.93	8.4	11.2	28.30	8.4	11.2	28.48	8.4
20	E	12.3	27.03	8.4	12.3	27.17	8.4	12.2	27.32	8.4	12.1	28.13	8.4	12.1	28.56	8.4
27	F	14.3	27.11	8.4	14.0	27.20	------	13.3	27.54	8.4	12.3	28.01	8.4	12.2	28.03	8.4
June 3	F	14.0	26.74	8.2	14.0	27.30	8.2	13.2	27.66	8.2	13.0	28.19	8.2	12.4	27.98	8.2
10	E	19.2	27.14	8.2	18.0	27.03	8.4	15.4	28.15	8.4	14.0	28.19	8.4	13.4	28.16	8.4
16	E	15.1	27.60	8.2	15.2	27.81	8.4	14.4	28.39	8.4	14.2	28.21	8.4	14.0	28.65	8.4
23	E	15.1	28.21	8.2	15.2	28.12	------	15.2	28.39	8.2	14.4	28.51	8.2	14.0	28.46	8.2
July 16	F	16.2	26.58	8.1	16.2	27.65	8.2	16.0	27.65	8.2	15.3	27.92	8.2	15.2	28.03	8.2
21	E	16.2	28.28	8.2	16.1	28.45	------	16.0	28.12	------	15.2	28.43	------	15.1	28.53	------
Aug. 2	F	17.2	28.06	8.2	16.4	28.37	8.4	16.4	28.37	8.4	16.2	28.64	8.4	16.2	28.89	8.4
4	F	20.0	28.33	8.2	18.0	28.66	8.2	17.3	28.99	8.4	17.4	28.82	8.4	17.4	28.91	8.4
11	F	15.3	28.19	8.1	15.3	28.19	8.2	15.3	28.35	8.2	15.2	28.87	8.2	15.1	28.60	8.2
18	F	17.4	28.06	8.0	17.4	28.48	8.2	17.0	28.08	8.4	16.4	28.87	8.4	16.4	28.74	8.4
25	F	16.4	28.93	8.2	16.0	28.82	8.4	15.4	29.08	8.4	15.0	29.22	8.4	15.0	29.08	8.4
Sept. 22	F	15.2	29.63	8.4	15.0	29.22	8.4	15.0	29.34	8.4	14.2	29.47	8.4	14.2	29.69	8.4
29	F	15.2	28.59	7.9	15.2	28.80	8.0	15.1	28.80	8.0	14.4	28.99	8.0	14.4	29.17	8.0
Oct. 5	F	14.3	29.08	8.0	14.3	28.95	8.0	14.2	29.18	8.2	14.2	29.47	8.2	14.2	29.75	------
11	F	13.1	29.63	8.2	13.1	29.70	8.2	13.0	29.87	8.2	13.1	29.87	8.2	13.1	29.85	8.2
15	E	13.4	28.95	7.9	13.4	29.27	7.9	13.2	29.13	7.9	13.2	29.33	7.9	13.2	29.84	7.9
18	E	12.4	29.20	7.8	12.4	29.22	7.8	12.4	29.13	8.0	13.0	29.38	8.0	13.0	29.16	8.0
25	F	12.4	29.58	8.0	13.0	29.31	8.0	13.0	------	8.0	13.0	29.23	8.0	13.0	29.28	8.0
Nov. 1	E	10.4	26.96	7.9	11.2	27.11	7.9	11.2	29.70	8.0	11.2	29.23	8.0	------	29.36	8.0
8	F	11.0	23.53	7.9	11.0	24.71	7.9	11.0	26.40	7.9	11.2	29.72	7.9	11.2	29.42	7.9
17	E	11.4	27.12	7.9	11.4	27.17	7.9	11.4	28.82	7.9	11.3	28.93	7.9	11.3	29.22	7.9
22	F	8.2	22.92	7.8	10.2	28.69	7.9	10.2	28.50	7.9	10.2	28.69	7.9	10.2	28.79	7.9
29	E	10.2	26.73	------	10.2	27.18	7.8	10.2	28.08	7.9	10.2	28.17	------	10.2	27.95	7.9
Dec. 6	F	8.3	26.17	7.8	9.0	26.65	7.8	9.0	27.84	7.8	9.1	27.85	7.8	9.1	28.06	7.8
20	F	7.1	27.31	7.8	7.0	27.16	7.9	7.0	28.30	7.9	6.4	28.22	7.9	6.4	28.22	7.9

NOTE.—E=ebb; F=flood.

To indicate in detail the changes in temperature, salinity, and pH at different depths, tables 7 and 8 are reproduced, showing the observations made over a period of 1 year in Oyster Bay and Mud Bay, at the points previously described. In Oyster Bay samples were taken at surface, 6, 15, 30, and 50 feet; in Mud Bay at surface, 3, 10, 20, and 30 feet. These tables give in detail both the seasonal variation in the water and the effect of depth. The surface water is, in some cases, quite different from that below.

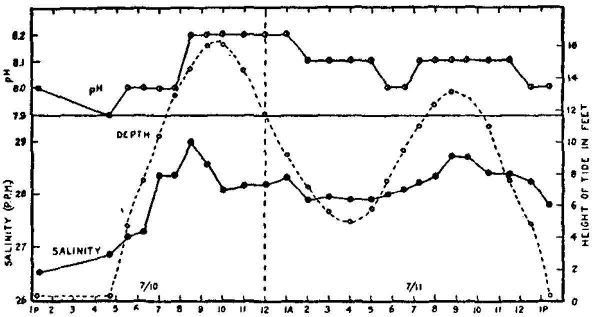

FIGURE 12.—Variation in salinity and pH in a dike in Oyster Bay during a complete tidal cycle. See also figures 34 to 37.

TABLE 9.—*Comparison of temperature, salinity, and pH of water at different depths during winter and summer off Corters Point, Oyster Bay; and Maple Point, Mud Bay*

Depth	Winter [1]			Summer [2]			Depth	Winter [1]			Summer [2]		
	Temperature	Salinity	pH	Temperature	Salinity	pH		Temperature	Salinity	pH	Temperature	Salinity	pH
Maple Point:	° *C.*			° *C.*			Corters Point:	° *C.*			° *C.*		
Surface	5.8	24.75	8.0	16.5	27.82	8.16	Surface	6.4	26.06	7.9	16.3	28.21	8.28
3 feet	6.7	26.37	8.0	16.1	28.16	8.27	6 feet	6.7	27.05	8.0	16.3	28.29	8.31
10 feet	7.2	28.61	8.0	15.6	28.29	8.32	15 feet	7.0	27.62	8.0	16.1	28.21	8.3
20 feet	7.4	28.61	8.0	15.1	28.53	8.32	30 feet	7.1	27.91	8.0	15.8	28.25	8.32
30 feet	8.0	28.99	8.0	14.9	28.57	8.32	50 feet	7.1	27.93	8.0	15.7	28.36	8.3

[1] December 1931, January and February 1932.
[2] June, July, and August 1932.

Some of these data are given as averages for winter (December, January, and February) and summer (June, July, and August) in table 9 to indicate stratification of the water, for it has been shown by Nelson and Perkins (1931) that the behavior of oyster larvae may be determined by the salinity at different depths. The values for Maple Point (Mud Bay) are plotted graphically in figure 13. In winter the salinity at surface and 3 feet is much lower than at greater depths but in summer the difference between surface and bottom is not so great. However, the pH in summer becomes lower toward the surface, probably because of planktonic animals, while in winter it is uniform from surface to bottom. In Oyster Bay (fig. 14) the salinity, temperature, and pH are almost identical from surface to bottom though during the winter the surface water is less saline and of slightly lower pH. The presence of the deep waters adjacent to the oyster grounds accounts for the high degree of stability indicated by these figures.

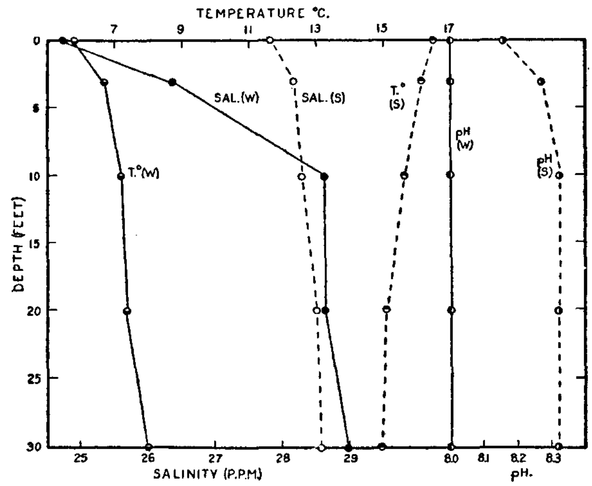

FIGURE 13.—Vertical distribution of salinity, temperature, and pH off Maple Point (Mud Bay) summer (S) and winter (W). Compare Oyster Bay, figure 14.

TABLE 10.—*Comparison of water near mouths of Mud Bay and Oyster Bay at ebb (E) and flood (F) tides during summer*

Date	Tide	Mouth of Oyster Bay						Mouth of Mud Bay					
		6 feet			30 feet			6 feet			30 feet		
		Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH	Temperature	Salinity	pH
		°C			°C			°C			°C		
May 24	E	11.1	28.39	8.2	11.2	28.53	8.2	10.1	28.69	8.3	10.2	28.39	8.3
	F	12.0	27.86	8.0	12.2	27.98	8.2	11.4	28.30	8.2	12.0	28.44	8.2
May 26	E	11.1	28.39	8.2	11.2	28.53	8.2	10.4	28.13	8.4	11.1	28.27	8.4
	F	11.3	27.79	8.3	11.4	28.06	8.2	11.1	27.85	8.4	11.1	28.37	8.4
May 29	E	12.1	27.98	8.2	12.2	27.85	8.2	11.2	28.41	8.2	11.4	28.35	8.2
	F	12.4	27.55	8.2	12.4	27.66	8.2	12.4	27.85	8.2	12.2	27.75	8.2
May 31	E	12.1	28.08	8.2	12.1	28.08	8.2	11.0	28.16	8.2	10.3	28.56	8.2
	F	12.2	27.83	8.4	12.2	27.79	8.3	12.0	28.04	8.2	12.0	28.69	8.2
June 2	E	13.0	28.24	8.2	12.3	28.06	8.2	11.3	28.60	8.2	11.3	28.66	8.2
	F	13.2	27.90	8.2	12.3	28.06	8.2	11.1	28.40	8.2	11.0	28.71	8.2
June 9	E	11.4	27.66	8.2	11.3	27.77	8.2	10.4	28.12	8.2	10.2	28.50	8.2
	F	12.4	27.77	8.2	12.4	27.95	8.2	12.4	28.16	8.2	12.3	28.37	8.2
June 14	E	14.0	27.99	8.4	13.4	28.30	8.4	12.3	28.31	8.4	12.2	28.64	8.4
	F	14.0	27.64	8.4	13.3	27.88	8.4	12.2	28.35	8.4	11.4	28.68	8.4
June 28	E	15.0	28.21	8.2	14.3	27.88	8.2	13.2	28.51	8.2	12.4	28.60	8.2
	F	15.1	28.04	8.0	15.1	28.04	8.0	15.1	28.45	8.4	14.0	28.04	8.4
July 5	E	15.1	28.48	8.2	15.0	28.40	8.2	13.3	28.85	8.2	13.2	28.59	8.2
	F	14.4	28.48	8.2	14.3	28.74	8.2	13.2	28.74	8.2	13.0	28.69	8.2
Average	E	12.8	28.10	8.22	12.7	28.17	8.23	11.5	28.42	8.24	11.4	28.50	8.25
Average	F	13.0	27.87	8.20	12.8	28.02	8.21	12.3	28.24	8.26	12.1	28.41	8.26

NOTE.—E=ebb; F=flood.

Further comparison of the two bays is shown by samples taken during summer at points near their mouths at depths of 6 and 30 feet at ebb and flood tides. (See table 10.) The water entering Oyster Bay is of a lower salinity than that going into Mud Bay, while at the upper end of the latter more fresh water flows in. As a result, in Mud Bay the oysters are subjected to frequent changes in salinity at different stages of the tide while in Oyster Bay the changes are relatively slight. These differences are considered below in the comparison of the spawning and setting activities of oysters in the two places. It may be noted on the chart (fig. 4) that the mouths of Oyster and Oakland Bays are close together but that the latter bay is entered through a long, narrow channel. It is of interest to compare the salinity in the dikes of the two bays at low tide. In table 11 salinities are given for dike 5 in Oyster Bay, a typical dike in Skookum Inlet, and one in Oakland Bay. Larger streams flow into Oakland Bay and elimination is less readily accomplished, so that even during dry summer weather the salinity is lower than in Oyster Bay. Water entering the latter at flood tide is of lower salinity than that which goes into Mud Bay, probably because of outflow from Oakland Bay and neighboring waters. Complete exchange of water with tides is accomplished much more slowly than in Mud Bay, the water in which is therefore higher in salinity as well as colder and not as favorable for the propagation of oysters.

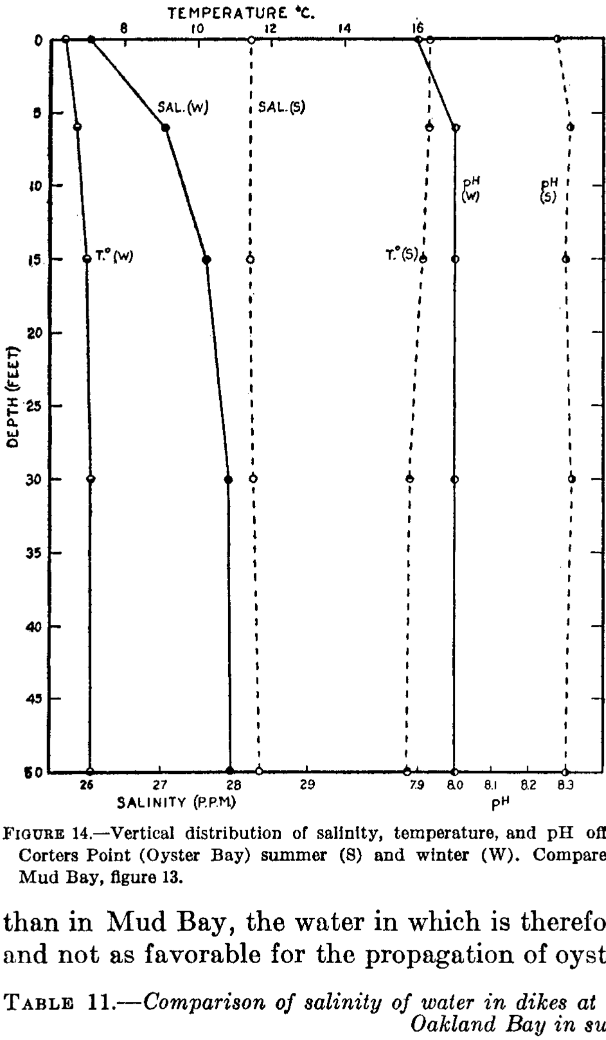

FIGURE 14.—Vertical distribution of salinity, temperature, and pH off Corters Point (Oyster Bay) summer (S) and winter (W). Compare Mud Bay, figure 13.

TABLE 11.—*Comparison of salinity of water in dikes at low tide in Oyster Bay, Little Skookum, and Oakland Bay in summer*

Date	Oyster Bay	Little Skookum	Oakland Bay	Date	Oyster Bay	Little Skookum	Oakland Bay
1933	*Salinity*	*Salinity*	*Salinity*	1933—Continued	*Salinity*	*Salinity*	*Salinity*
May 22	27.17	25.68	23.30	June 21	27.49	----------	25.43
May 24	27.05	----------	24.03	June 23	27.43	27.01	25.10
May 26	26.91	23.86	23.69	June 26	27.16	26.06	25.52
May 29	26.88	25.09	23.66	June 28	28.07	----------	24.65
May 31	27.35	----------	24.22	June 30	27.92	----------	24.94
June 2	27.17	----------	24.71	July 3	27.69	25.25	24.90
June 5	27.50	25.91	24.09	July 5	27.77	----------	25.46
June 7	27.59	----------	24.23	July 7	27.11	----------	25.99
June 9	27.27	25.47	24.37	July 14	27.83	26.97	26.15
June 12	26.77	25.61	25.39	July 17	28.01	26.68	26.05
June 14	27.54	----------	25.76	July 19	28.12	----------	25.91
June 16	27.21	26.10	24.83	July 21	28.21	27.16	24.25
June 19	27.92	25.97	25.10	July 24	28.13	28.22	26.44

SPAWNING

The native oyster of the Pacific coast, *Ostrea lurida*, is biologically similar to the European oyster, *O. edulis*, in that it is hermaphroditic and viviparous. In his original studies of the native oyster, Stafford (1913, 1914) described the hermaphroditism, pointing out that in the gonad, or ovotestis, eggs and sperms may be seen close together. Until the recent work of Coe (1931a, 1931b, 1932a) no further exact information on the mode of reproduction in this species was published. Coe studied in detail the spermatogenesis and life history of this oyster near La Jolla, Calif., and found it to be protandric. He stated that germ cells mature in the 1-year-old oyster and that at first the individual is male. During the rest of its life it is alternately female and male, although at any one time germ cells of both sexes may be found in the gonad because seldom are all of the sexual products discharged before the next phase begins.

Stafford (1915) stated that spawning involves the discharge of eggs or sperm balls from the gonad into the suprabranchial or cloacal chamber from which they reach the mantle chamber. He described this activity as follows:

> Eggs and sperms are liberated from the gonaducts into the suprabranchial chamber, and make their way through the water-tubes and gill-slits to the branchial chamber, which also serves as a brood chamber. In doing this they are assisted by the pressure of their mass * * *. Sections of oysters at the spawning season show eggs in the cavities of the gills. They do not pass readily through the gill-slits on account of the narrowness of the latter, but with the increasing mass and pressure the gills become stretched and the slits enlarged, and besides the gills appear in places to suffer disintegration.

This explanation is obviously inadequate, for one has difficulty in understanding how the small increase in pressure due to eggs would force them through the gill apertures. Also, it is clear that considerable coordination would be required to keep the cloacal chamber completely closed and prevent direct escape of the eggs. Galtsoff (unpublished manuscript) studied spawning in *Ostrea virginica* and reached the more probable conclusion that suction, created by opening of the valves during spawning, draws the eggs through the small openings in the gills. Elsey (1935) found that the openings, or ostia, in the gills of *O. lurida* and *O. gigas* have a diameter proportional to that of the eggs. The eggs of the former are about twice as great in diameter as those of the latter, and the ostia are about one-third larger.

As has been described by Nelson (1922), Galtsoff (1930b, 1932) and others, eggs are finally discharged from the mantle chamber in *Ostrea virginica* but sperms are washed out through the cloaca with the water pumped by the gills. Stafford considered that in the native oyster the sperms also pass through the gills as do the eggs. While Stafford may have actually observed the discharge of sperms in this manner, the writer has frequently seen them issuing from the cloaca as in other species. At the time of spawning the sperms of *O. lurida* are in clusters, or balls, made up of from 250 to 2,000 or more sperms, according to the estimate of Coe (1931b), who stated further that in contact with sea water the matrix in which the sperms are imbedded disintegrates, permitting them to swim free. Both Stafford and Coe considered that eggs are fertilized by sperms brought into the branchial chamber where the eggs are held, with the water pumped by the gills. Stafford thought self-fertilization might occur, though according to Coe's interpretation this is unlikely. It is uncertain whether the sperms from one individual will stimulate spawning in functionally female specimens, as described by Galtsoff (1930b, 1932) for other species, though such is probable.

The eggs are held in the anterior end of the mantle or branchial chamber adjacent to the gills and labial palps. Here they develop for a considerable period. It is remarkable that they are not swept out along the "waste canals" in the walls of the mantle which normally function to eliminate particles of silt and other rejected material. Stafford (1914) estimated that in British Columbia the period of development within the maternal "brood chamber" is about 16½ days, while Coe (1931a) suggested "a period of approximately 10 to 12 days, perhaps" in southern California. Stafford's work on this species is published in a series of six papers (1913, 1914, 1915, 1916, 1917, 1918) some of which are frequently referred to below.

SIZE OF BROODS

Oysters have always aroused interest because of the very large numbers of eggs which they discharge. Various means of estimating the number of eggs spawned by an individual have been employed with highly divergent results. Galtsoff (1930a) gave a brief review of the literature on the subject and indicated that previous estimates for the average-size female of *O. virginica* vary from about 9 millions to about 60 millions. He made what is apparently the most thorough and accurate study by causing oysters to spawn and then making statistical counts of the eggs. He found that a female of *O. virginica* discharged from 15 millions to about 114 millions in a single spawning period, and that after spawning had occurred the meat still contained a large quantity of eggs. During three periods of spawning one specimen of *O. gigas* discharged a total of about 92 million eggs. The number of eggs spawned by a single individual throughout an entire season would be considerably greater than these counts.

These species are of the oviparous type while the Olympia oyster is viviparous. In the waters of the United States are two viviparous species of oysters, *O. lurida*, on the Pacific coast, and *O. equestris*, described by Gutsell (1926) on the South Atlantic coast. The latter is too small to be of commercial use. *O. edulis*, the European oyster, is also of this type and although the largest of the three it is much smaller than the common American oyster. Because of their small size the viviparous oysters cannot be expected to discharge the large quantities of eggs described above, but they have a considerable biological advantage in that every specimen is presumably capable of functioning each season as a female, while in *O. virginica* only about half of the individuals are female. In the latter sex-change occurs, as recently studied by Coe (1932c, d), but not with the frequency found in the native oyster. The fact that the larvae are carried in the limited space of the branchial chamber in viviparous species would also appear to set a limit to the size of the broods.

Moebius (1883) estimated, by an apparently satisfactory method, that the average brood of *O. edulis* consists of about one million larvae. Stafford (1918) stated that the much smaller native oyster bears broods of about the same size, although his method of estimating the number is not clear. In order to establish with reasonable accuracy the number of larvae produced, counts were made of a number of broods.

A gravid individual was carefully opened and the larvae rinsed from the gills and mantle. After killing them with formalin they were shaken in a measured quantity of water and exactly determined samples placed in a flat-bottom dish and counts made by means of a counting plate. Specimens of various sizes were used, though most of them were of market size. Counts were made of the separate broods of 13 oysters, and on the mixed broods of 2 groups of 6 oysters. Table 12 gives the results and includes measurements of the shells of the maternal parents and the stage of development of the larvae in those broods which were separately counted.

The average of all 25 broods is 214,642 larvae per oyster, although single broods varied from about 70,000 for the smallest specimen to 355,000 for one of the larger ones. These specimens were in general considerably smaller than those used in the two series of mixed broods, which represent more fairly the number of larvae produced by the standard market-size oyster. The average of the Oyster Bay series is 283,273 and of the Mud Bay series, consisting of somewhat smaller specimens, 247,199. The number of larvae produced obviously depends upon the size of the maternal individual and upon the degree of "fatness", or amount of stored nourishment, which is required for the maturation of the eggs. The data here described indicate that the ordinary marketable native oyster produces a brood of from 250,000 to 300,000 larvae.

TABLE 12.—*Number and stage of development of larvae in broods of 13 oysters, and number of larvae in 2 groups of 6 broods each*

Oyster specimen no.	Length	Width	Number of larvae	Stage
	mm	*mm*		
121	32.7	23.5	130,628	Morulae.
125	30.3	24.0	113,142	Straight-hinge 160μ–170μ.
126	28.0	23.5	95,667	Do.
127	29.5	27.5	150,600	Morulae.
128	29.0	23.0	156,875	Do.
129	29.7	21.2	184,114	Late morulae.
130	31.0	25.8	355,500	Morulae.
131	23.5	19.2	69,490	Straight-hinge 160μ–170μ.
132	28.2	24.4	126,174	Do.
139	36.2	26.2	293,473	Early gastrulae.
140	29.2	27.0	213,781	Gastrulae.
141	28.5	23.3	136,666	Do.
142	36.8	26.2	171,818	Do.
Oyster Bay				
1	38.1	33.0		
2	40.6	30.5		
3	45.7	30.5		
4	38.1	30.5		
5	40.6	33.0		
6	45.7	35.5		
Average			283,273	
Mud Bay				
1	38.1	30.5		
2	38.1	30.5		
3	38.1	33.0		
4	38.1	25.4		
5	43.2	25.4		
6	35.5	27.9		
Average			247,199	

It has been observed that most specimens carrying larvae appear to have discharged almost all of the eggs from the gonad, for the meats are generally transparent and watery. This is in contrast to Galtsoff's (1930a) observation on *Ostrea virginica* that at a single spawning only a relatively small proportion of the eggs are discharged. The difference may be related to the fact that the native spawns alternately as male and female (Coe, 1931a, b).

Stafford (1914) stated that the presence both in the parent and in the bay of all swimming stages shows "that the young do not all swarm out from the brood chamber of the mother at the same time, age, or size, but filter out gradually, perhaps during the gaping condition of the shell while respiration is going on in the parent." In table 12 the stage of development of the larvae of 13 broods is given. In proportion to the size of the parent there does not appear to be a significant difference in the number of larvae per brood with respect to stage of development, although it is true that the largest broods consist of embryos. While this evidence neither confirms nor refutes Stafford's idea of the gradual release of the larvae, it is probable that many of the free-swimming larvae of small size found in plankton samples may be the result of abortions. Disturbing the parent oysters appears to cause them to discharge broods of "white larvae" or those which have not developed valves. In many cases oysters have been taken up from the beds and placed in dishes of clean running seawater in the laboratory, and those specimens bearing young larvae observed to discharge them by opening and closing the valves. That such abortions occur in nature is shown by statistical sampling of the oysters on certain beds.

RELATION OF TEMPERATURE TO SPAWNING

The development and discharge of germ cells are well known to be functions of the water temperature. As was shown in table 1 and figure 7 the average temperature of the water in southern Puget Sound begins to rise in early spring from the winter minimum of about 6° to 9° C., reaching a level of 18° to 20° C. in August. During the early months of spring the gonads begin active development and the stored nourishment of the bodies is used in the maturation of the eggs and sperms. The extensive researches of Stafford (1913), Churchill (1920), Gutsell (1924), Nelson (1928a, b, c), Prytherch (1929), Galtsoff (1930b, 1932), and others have demonstrated that there is a certain minimum, or critical temperature below which little or no spawning occurs. In *Ostrea virginica* this minimum is 20° C. for spawning by the female, although the male is able to spawn at a lower temperature. Galtsoff's observations are particularly significant, for he was able to show by laboratory experimentation that at a temperature of 20° C. or above, the sexually mature female may be induced to spawn by adding either sperms or sperm extract to the water. Below 20° C. sperms would not stimulate spawning. It is of importance to note that Galtsoff's work confirmed the conclusion of previous investigators based upon ecological observations. In the same manner he was able to induce spawning in the Japanese oyster, *O. gigas*, by addition of sperms when the temperature was 25° C. or higher, although more recently Elsey (1933) wrote that spawning could be stimulated at 22° C.

Orton (1920) stated that the European oyster, *Ostrea edulis*, spawns when the water temperature reaches about 60° F. (15° to 16° C.). In *O. lurida* Coe (1931a) found specimens bearing larvae whenever the water temperature was as high as 16° C., while Hori (1933) set the minimum at 14° and the maximum at 20° C. The exactness of such observations is not always clear, however, for it is questionable whether the temperatures given are actually averages or merely approximations, and maxima and minima are not stated.

Prytherch (1929), in his thorough study of various phases of the spawning and setting behavior of *Ostrea virginica* near Milford, Conn., concluded that spawning begins when the temperature at high tide reaches 20° C. He considered that the lower pH (7.2) of the water at low tide, when the temperature was much higher, was the factor preventing spawning. At high tide, on the other hand, when the water reached about 20° C. and the pH was about 8.2 the oysters spawned. It is obvious that some factor in addition to temperature is necessary to stimulate spawning, and the suggestion that a high pH is required appears, from his results, to be well founded. Judging from these investigations, it is to be concluded that it is not the maximum temperature on any particular day which must be up to the critical level, but the minimum, or high-tide temperature.

It is clear, also, that the gonads must be at the required state of maturity before spawning will take place, regardless of temperature, for it was noted (Hopkins, 1931b) near Galveston, Tex., that the oysters were not ready to spawn during spring until the water temperature, after a rapid rise, reached about 25° C. At the same time, it has been well demonstrated that, with other factors favorable, spawning in *O. virginica* begins when the high-tide temperature reaches the critical minimum of 20° C. It is important to know what conditions of temperature influence *O. lurida* in this respect. (Hopkins, 1936.)

A thermograph was placed on a frame in Oyster Bay so that the sensitive bulb was at the level of the oysters in the dike below. The records, therefore, represent with a high degree of accuracy the conditions of temperature of the water surrounding the oysters. The variation in water temperature on the oyster grounds during winter and summer and at different stages of tide has been described in table 1 and figures 5 and 6.

Although he appeared to be uncertain of the specific factor involved in stimulating the beginning of spawning, Orton (1926) concluded that spawning of *O. edulis* takes place primarily during the full-moon tidal period. Prytherch's (1929) work indicated that the rise in water temperature, due to warming of the tide lands during the extreme low tides, was responsible for stimulating reproductive activity. He stated that in Milford Harbor, Conn., "the majority of the oysters spawned at the end of the July full-moon tidal period, when the water was brought to a favorable spawning temperature." Nelson (1928 a, b) concluded that there is a definite relationship between the rapidity of the rise in temperature after the high-tide temperature reaches 20° C. and the time required for the initiation of spawning in *O. virginica*. He found during several seasons that spawning started from 52 to 94 hours after the temperature of 20° was reached, depending upon the rapidity of the subsequent rise. His observation is in accord with Galtsoff's (1930b, 1932) experimental finding that a sharp rise in temperature will induce discharge of germ cells.

In the case of Olympia oysters, however, the grounds are diked and are all between low- and high-tide levels. The variation in salinity and pH at different stages of the tide is usually not very great (fig. 12) but the temperature is subject to wide fluctuations. When the tide is low the oysters are covered by only a few inches of water which quickly responds to weather conditions. During the day low tides in March, when the weather is favorable, the temperature may rise to 20° or 25° C., probably causing the maturation of eggs and sperms. Actual spawning does not usually begin until late in April or some time thereafter.

During each season oysters were opened systematically on representative grounds in both Oyster Bay and Mud Bay to determine when spawning started and the number of adults bearing larvae throughout the season. Sampling was begun well in advance of the spawning period and consisted in the opening of 100 oysters on each of the test beds, 2 or 3 times a week. When a gravid individual was found the larvae were placed in a vial and preserved with formalin for examination in the laboratory. The method is described in greater detail with reference to the rate of larval development, and it is necessary here only to state that graphs of the results were made showing the percentage of oysters bearing larvae throughout each season. From these results and the thermograph records it is possible to correlate spawning activity and water temperature.

Four graphs (figs. 15–18) are reproduced showing the percentage of gravid oysters on different days and the daily average and minimum temperature. Three of the figures refer to Oyster Bay, one to Mud Bay, but all agree with respect to the influence of temperature upon spawning. In 1932 (fig. 15) no specimens bearing larvae were found until May 17, when 12 out of 100 bore very young embryos. The temperature record shows a sudden rise at this time. For some days the average temperature had varied from 13° to 15° C., but the minimum, or high-tide temperature had been relatively stable. On the 16th the minimum temperature rose from about 12° to over 13° C., and was followed by the sudden onset of spawning. For several weeks afterward, while both minimum and average temperature steadily increased, spawning was quite prolific. On the same graph the daily range of tide is plotted to indicate possible correlation with tidal periods, as described by Orton (1926). This is discussed below.

149604—37——4

In Oyster Bay in 1933 (fig. 16) the graph has a somewhat different appearance because spawning was relatively light. On May 18, 2 percent of the oysters bore newly spawned eggs, though the minimum water temperature was only about 12° C. On the 24th or 25th, however, spawning started at a considerable rate and continued thereafter. At this time the minimum temperature was about 13° C. and the average about 14° C. It is remarkable that the few oysters which spawned early did not retain the larvae, for it may be noted on the graph that the first conchiferous larvae, of about 5 days development, were not found until the 31st. It is probable that a few oysters were able to discharge eggs but subsequent low temperature caused abortions. Though this record is not as clear as could be desired, it indicates definitely that the first successful spawning took place when the minimum temperature reached approximately 13° C.

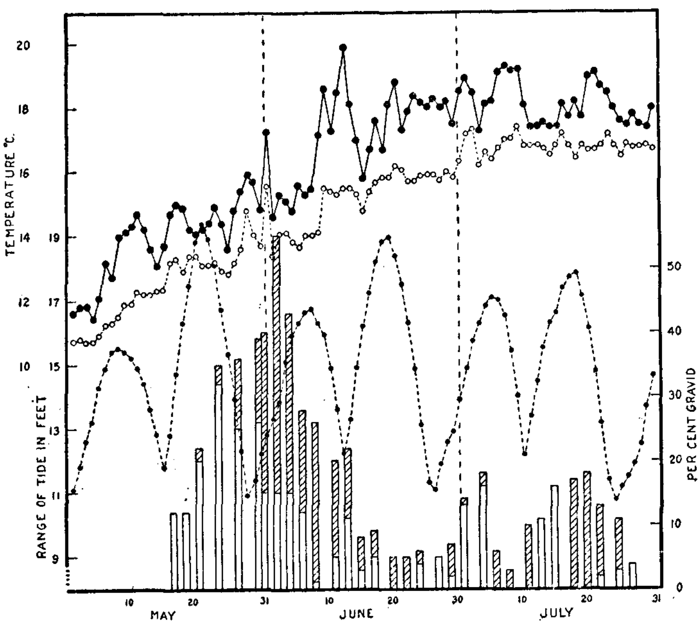

FIGURE 15.—Daily average and minimum temperature in Oyster Bay during summer of 1932 as related to the frequency of spawning and range of tide. Open portions of columns refer to white larvae or embryos, shaded portions to conchiferous larvae.

During the same year, in Mud Bay, the beginning of spawning may be more closely correlated with a rise in minimum temperature from about 12° to over 13° C. (see fig. 17). The average temperature, at the same time, was about 14° C. The spring rise in temperature in Mud Bay is characteristically late in comparison with Oyster Bay and the entire breeding season is therefore later. In 1935, in Oyster Bay (fig. 18), spawning started just after the minimum temperature reached a level of 13° C., although the average was between 15° and 16° C.

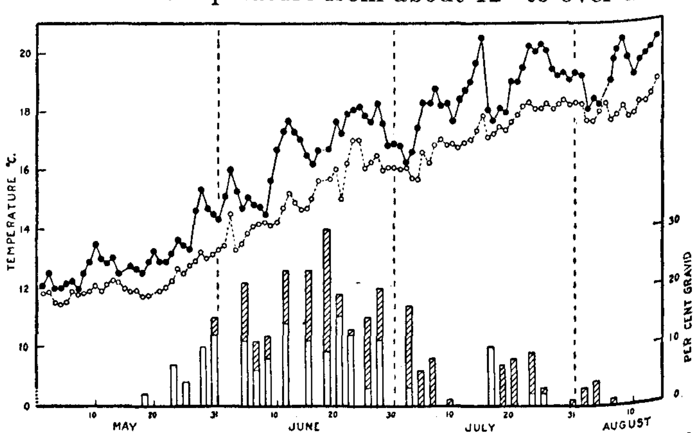

FIGURE 16.—Daily average and minimum temperature in Oyster Bay during summer of 1933 as related to frequency of spawning. Compare figures 15 and 18.

These four series are selected for reproduction because they represent the most complete data at hand referring to specific localities. It is certain that it is not the low-tide temperature which initiates spawning in spring, for on many days preceding the time of beginning of spawning the water in the dikes would warm to 20° or 25° C. and remain so for several hours. It may be noted that, in the four cases presented, the average temperature varied over a wide range at the critical time. The minimum temperature occurs commonly during the higher high tide and this shows a striking relationship to the onset of spawning. Prytherch's (1929) conclusion that the high-tide temperature must be adequate before spawning will begin appears to apply equally well to this species. Judging from these data, the critical temperature for spawning may be placed at about 13° C., possibly from 12.5° to 13° C.

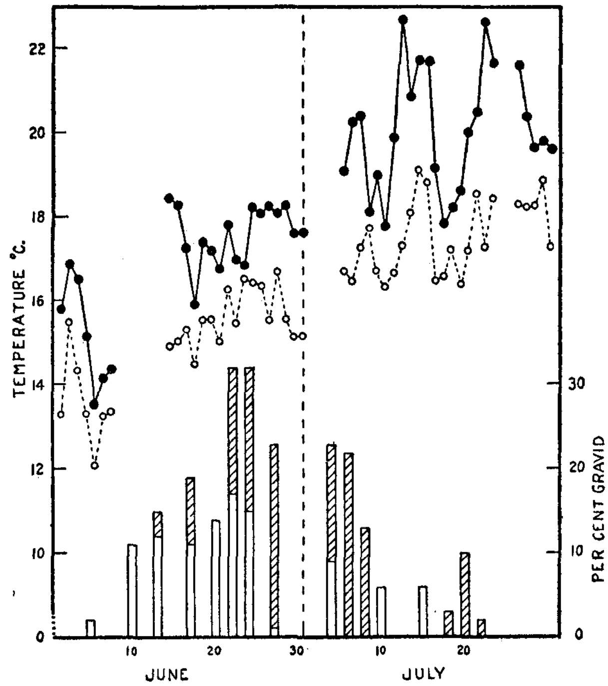

FIGURE 17.—Daily average and minimum temperature in Mud Bay during summer of 1933 as related to frequency of spawning. Compare figures 16 and 18.

It has frequently been noted that spawning is most likely to begin during or shortly after a period of neap tides. In spring and early summer, as shown in figure 15, at such times the minimum temperature is at a relatively high level. During a period of spring, or extreme tides, the tide flats warm in the sunshine and raise the temperature of the water coming in with the flood tides. The great range of tide in this place, 18 to 19 feet during a spring tide period, causes the colder water of the deep channels down the bays to reach the oyster grounds at high tide, while the warmer water is forced toward the head of the bay. During the neap tides a week later, however, the range may be only 11 or 12 feet, permitting the relatively warm water, resulting from the preceding low tide period, to remain over the oyster grounds. While the highest temperature is to be found in the dikes at low tide during a period of spring tides, the highest high-tide temperature may frequently occur in the neap-tide period, thereby inducing spawning.

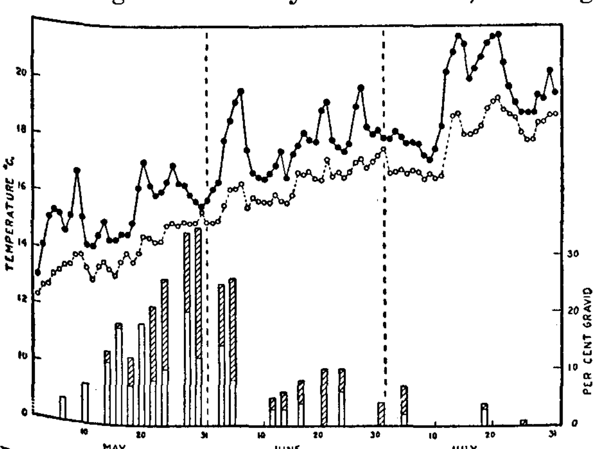

FIGURE 18.—Daily average and minimum temperature in Oyster Bay during summer of 1935 as related to frequency of spawning.

It is probable that this estimate of the critical temperature for spawning is not out of harmony with the results of Hori (1933) and Coe (1931a), who stated that the water temperature during spawning was at least 14° and 16°, respectively. Their measurements appear to refer either to the average temperature or to that indicated by more or less frequent readings. As shown above, the average temperature at the time of the initial spawning is generally 14° to 16°.

SPAWNING SEASON

The spawning period of the Olympia oyster appears to be quite different from that of *O. virginica* in Long Island Sound, as described by Prytherch (1929). In that place the oysters spawned prolifically on a particular day, when water conditions were favorable, so that the time of setting of the larvae could be exactly determined with reference to the time of discharge of the eggs. During several years, according to Prytherch, the first spawning was relatively light, and was followed about 2 weeks later, during the next period of spring tides when the water was warmer, by more general spawning.

The native oyster, as described by Stafford (1914), spawns during a period of about 2½ months. According to this author, in 1913, in British Columbia waters, spawning occurred from about May 20 until the end of July, with the maximum spawning activity at the middle of June. On the coast of southern California Coe (1931a–1932b) found that spawning in this species continues for a period of about 7 months of the year. In the same manner, *O. virginica* on the Gulf coast spawns during many months (Hopkins, 1931b).

TABLE 13.—*Percentage of oysters bearing larvae in Oyster Bay*

Date	Number opened	Number gravid	Number not gravid	Percent gravid	Date	Number opened	Number gravid	Number not gravid	Percent gravid
1931					1931				
May 25	15	7	8	47	July 2	30	4	26	13
May 27	15	6	9	40	July 8	37	3	34	8
May 29	10	2	8	20	July 9	64	3	61	5
June 12	27	4	23	15	July 10	28	3	25	11
June 19	34	8	26	24	July 15	53	0	53	0
June 21	20	3	17	15	July 24	30	0	30	0
June 22	11	1	10	9	July 27	21	3	18	14
June 27	29	2	27	7	Aug. 8	20	0	20	0

TABLE 14.—*Percentage of adult oysters bearing embryos (E) and conchiferous larvae (C) in dikes 5 and S (Oyster Bay) and dike B (Mud Bay) during 1932*

Date	Dike 5		Dike S		Dike B		Date	Dike 5		Dike S		Dike B	
	E	C	E	C	E	C		E	C	E	C	E	C
May 17	12						July 1	13	1	4	6		
19	12						2					5	1
21	20	3					4	13	4	8	4		
24	32	3					5						5
27	25	11					6		6		10		
30	26	13					8		3	6	12		
31	15	25					9					9	2
June 2	15	40					11		10		8		
3					14	[2] 13	12					6	1
4	15	28					13	11			8		
6	12	16					14						10
8	1	25					15	16			6		
10					7	30	16						5
11	5	15					18	17		4	8		
13	11	12	4	[1] 12			19						7
14					7	19	20		18	4			
15	3	5	2	8			21					5	2
16					2	11	22	2	11		4		
17	5	4		4			25	3	8	4	6		
18					4	10	26						6
20		5	12	4			27		4		6		
21						5	28						8
22		5					30						6
23					5	4	Aug. 1				2		
24	4	2	4	2			2						10
27		5		12			4					1	
28						5	5		1	4			
29	2	5					8	2					
							31		1				

[1] No oysters opened before June 13.
[2] No oysters opened before June 3.

TABLE 15.—*Percentage of adult oysters bearing embryos (E) and conchiferous larvae (C) in dikes 5 and S (Oyster Bay) and dike B (Mud Bay)*

Date	Dike 5		Dike S		Dike B		Date	Dike 5		Dike S		Dike B	
	E	C	E	C	E	C		E	C	E	C	E	C
1933							1933						
May 19	2	----	----	----	----	----	June 27	----	----	----	----	1	22
24	7	----	6	----	----	----	28	11	9	2	12	----	----
26	4	----	6	----	----	----	July 3	3	14	----	12	----	----
29	10	----	10	2	----	----	4	----	----	----	----	9	14
31	10	4	10	8	----	----	5	----	6	----	4	----	----
June 5	10	11	22	6	----	----	6	----	----	----	----	----	22
6	----	----	----	----	2	----	7	----	8	4	6	----	----
7	6	4	8	14	----	----	8	----	----	----	----	----	13
9	8	4	4	20	----	----	10	----	1	2	4	6	----
10	----	----	----	----	11	----	15	----	----	----	----	6	----
12	14	10	4	22	----	----	17	10	----	----	4	----	----
13	----	----	----	----	12	3	18	----	----	----	----	----	3
16	11	13	----	----	----	----	19	----	----	6	----	----	----
17	----	----	----	----	11	8	20	----	----	----	----	----	10
19	9	21	----	32	----	----	21	----	8	12	----	----	----
20	----	----	----	----	----	14	22	----	----	----	----	----	2
21	15	4	8	20	----	----	24	2	7	----	6	----	----
22	----	----	----	----	17	15	26	2	1	2	----	----	----
23	12	1	----	20	----	----	31	----	1	----	----	----	----
24	----	----	----	----	15	17	Aug. 2	----	3	----	4	----	9
26	3	12	----	10	----	----							

TABLE 16.—*Percentage of adult oysters bearing embryos (E) and conchiferous larvae (C) in dikes 5 and T (Oyster Bay) and dike B (Mud Bay) during 1934*

Date	Dike 5		Dike T		Dike B		Date	Dike 5		Dike T		Dike B	
	E	C	E	C	E	C		E	C	E	C	E	C
Apr. 19	----	----	7	----	----	----	June 1	5	6	6	2	----	----
27	----	----	6	5	----	----	7	----	----	----	----	3	8
28	----	----	----	----	3	[2] 1	8	----	6	----	4	----	----
May 1	----	----	----	----	8	7	9	----	----	----	----	----	8
2	14	[1] 20	19	6	----	----	11	1	2	----	5	----	----
9	----	----	----	----	18	3	12	----	----	----	----	3	6
10	2	17	9	17	----	----	13	----	3	5	1	----	----
11	----	----	16	29	----	----	14	----	----	----	----	3	8
12	----	----	----	----	10	3	15	9	1	----	7	----	----
14	9	18	13	18	----	----	16	----	----	----	----	6	----
17	----	----	----	----	14	15	22	----	2	----	4	----	----
18	10	23	5	18	----	----	25	1	6	----	3	----	----
19	----	----	----	----	11	24	29	----	4	4	2	----	----
25	1	10	1	20	----	----	July 6	----	----	----	1	----	----
26	----	----	----	----	----	18	9	----	1	4	3	----	----
28	----	6	7	9	----	----	10	----	----	----	----	3	----
29	----	----	----	----	1	17	13	1	1	----	2	----	----
30	----	7	4	6	----	----	21	----	----	----	----	----	1
31	----	----	----	----	----	15	25	----	----	1	----	----	----

[1] No oysters opened until May 2.   [2] No oysters opened until Apr. 28.

TABLE 17.—*Percentage of adult oysters bearing embryos (E) and conchiferous larvae (C) in dikes 5 and T (Oyster Bay) and dike A (Mud Bay) during 1935*

Date	Dike 5		Dike T		Dike A		Date	Dike 5		Dike T		Dike A	
	E	C	E	C	E	C		E	C	E	C	E	C
May 6	4	----	----	----	----	----	June 1	----	----	----	----	14	12
10	7	----	----	----	----	----	3	14	11	27	21	----	----
14	11	2	----	----	----	----	4	----	----	----	----	1	24
15	----	----	----	----	8	----	5	8	14	11	22	----	----
16	17	1	[1] 4	----	----	----	6	----	----	----	----	8	14
17	----	----	----	----	12	----	12	3	2	----	----	1	[2] 18
18	7	5	4	----	----	----	14	3	3	----	----	----	----
20	18	----	10	1	----	----	17	4	4	4	3	----	----
21	----	----	----	----	18	10	21	----	10	----	----	----	----
22	8	13	6	8	----	----	24	6	4	3	4	----	----
24	10	16	10	6	----	----	July 1	----	4	3	2	----	----
28	20	14	----	----	----	----	5	2	5	7	2	----	----
29	----	----	----	----	17	24	19	3	1	----	----	----	----
30	12	23	10	26	----	----	26	----	----	1	----	----	----

[1] No oysters opened until May 16.   [2] Sampling discontinued.

TABLE 18.—*Number of spat caught on plane glass surfaces as determined by the angle of the surfaces: 0°, under horizontal; 90°, vertical; 180°, upper horizontal*

Angle of surface	Area square inches	Number of spat	Average number of spat per 2,400 square inches
0°	2,400	1,195	1,195
[1]45°	1,200	42	181
[2]45°	1,200	139	
[1]90°	2,400	6	11
[2]90°	2,400	16	
[1]135°	1,200	1	3
[2]135°	1,200	2	
180°	2,400	1	1

[1] Perpendicular. [2] Parallel to general direction of current.

A correct estimate of spawning activity of functional females was obtained by opening 100 adults two or three times weekly throughout the season on selected typical beds. This mode of sampling has been carried on in two bays during 4 consecutive years. In 1931, the work was not begun in time to permit exact determination of the entire duration of the spawning season, but in table 13 the results of miscellaneous samples are given for comparison with later years. The table indicates, however, that after the end of May the proportion of adults bearing larvae became continuously less, until in July and August gravid specimens were only occasionally found.

More complete data were obtained during the years 1932 to 1935 in both Oyster Bay and Mud Bay. Tables 14 to 17 summarize the results. In Oyster Bay two grounds were employed for sampling, one well up the bay, the other some distance below, or one high ground (dike 5) and one low ground (dike T). In Mud Bay samples were taken from dike B, a ground which is closely similar in all respects to most of those in the bay. The oysters were opened at the beds to eliminate the possibility of confusion due to the occurrence of spawning or abortion during transportation. In the tables the gravid specimens are divided into two groups, according to whether they bear unshelled embryos (E) or conchiferous larvae (C), in order to indicate more exactly the rate of spawning. While the complete data are given in the tables, a more significant picture of spawning activity may be obtained from figures 15 to 18, in which the percentage of gravid specimens on each day is shown as a column, the shaded portion of which represents conchiferous larvae, the open portion the embryos up through the trochophore stage. The tables and figures are not quite complete in that they do not include the very occasional gravid specimens that may be found as late as October, but these are too few to warrant any attention.

In the tables it may be noted that the time when spawning begins varies over a period of about a month, depending upon climatic conditions which control the temperature of the water. While, in Oyster Bay, the first oysters bearing larvae were found at about the middle of May in 1932 and 1933, in 1934 spawning started a full month earlier. In Mud Bay the oysters generally start spawning some time later than in Oyster Bay, even early in June during some years.

Spawning goes on at a significant rate for a period of about 6 weeks, although larvae may be found in some adults for as long as 5 or 6 months. The reproductory activity is best shown in figures 15 to 18, which indicate that after it once begins, the frequency of spawning slowly increases to a maximum, then gradually diminishes until gravid individuals are found only occasionally. During most years, the rate of spawning may be represented with fair accuracy by a simple symmetrical distribution curve, though sometimes (fig. 15) there is a later, secondary wave of spawning. In 1932, in Oyster Bay this later spawning was considerable, though not as important as the original activity early in the season. In other years it was not apparent that there was any definite renewed spawning activity.

In his work on *O. edulis*, Moebius (1883) said that as many as 20.6 percent of the adults bore larvae at once, and estimated from frequent observations, that at least 44 percent of the oysters produced broods during the season. Stafford's (1914) results indicate a comparable proportion bearing larvae at the same time, though he did not estimate the proportion of the population which produced broods. The data obtained during the sampling described above provide a means of estimating with some degree of certainty the total spawning activity throughout several seasons.

Because of the frequency of the samples, it is possible to analyze the rate of development of the larvae, as is described below, and to detect the relative number of oysters bearing newly spawned eggs. From this one may reach an estimate of the total number of adults which bear broods. In 1932, as shown in table 14 and figure 15, the oysters spawned prolifically in Oyster Bay. At one time as many as 55 out of 100 carried broods. By referring each age group back to the date of spawning and then determining the total percentage of individuals spawning during the season it was possible to demonstrate that at least 1.5 broods per oyster were produced. That is, apparently all of the individuals bore one brood and at least half were gravid for the second time.

In 1933, however, at the same place only about 75 percent of the individuals became gravid (fig. 16). During most years it appears that approximately 100 percent of the adults bear larvae, but only in 1932 was much greater spawning activity noted. Judging from all data available, it is probable that the variation in number of broods produced during different seasons is between about 75 and 150 per 100 adult oysters. In addition, the specimens would also spawn as males, as described by Coe (1931a, b). A source of error in such estimates is the possibility of abortions of young embryos which would, therefore, not be counted. It would be difficult to determine how frequently abortion of a brood occurs, but it is clear that it sometimes happens.

DEVELOPMENT OF LARVAE

Although Stafford (1914) reached the conclusion that the larvae develop normally for a period of 16½ days within the maternal brood chamber it is probable that the method he employed was unsatisfactory. He would periodically pry the valves of a gravid specimen partly open and take a sample of the larvae. Such handling of the specimen might readily result in a disturbance of normal function and interfere with larval development. A strictly biological method, therefore, would not appear to be adequate to solve the problems related to rate of development under natural conditions.

It was necessary to use a system of sampling the oyster population and determining at frequent intervals the stage of development of larvae in the various broods. On each of two typical grounds in Oyster Bay 100 adults were opened 3 times weekly. Larvae from gravid specimens were separately preserved in vials for later laboratory examination to determine their size or stage of development. By taking samples at frequent intervals throughout the season it was possible to organize the results so that gravid specimens bearing broods of the same stage of development could be grouped and followed through the various stages. If on 1 day 10 percent of the oysters bore newly spawned eggs, 2 days later about the same number would be found with embryos of a certain stage. In subsequent samples the group would continue to recur until the larvae reached the size at which they are discharged. A single brood was found to consist of larvae of approximately the same stage, within relatively narrow limits. In no case were larvae of widely different stages found in a brood, and it may be concluded that an individual seldom, if ever, spawns as a female while carrying a brood of larvae.

Records of the larvae taken in such collections were arranged in tabular form (fig. 19) to show the percentage of adults bearing larvae of different stages of development. By connecting the values from date to date and stage to stage, the age of each group is made clear. Division of the developmental process into 10 stages is largely arbitrary but at the same time convenient. While the embryonic stages, up through the trochophore, are well defined, the only significant difference between straight-hinge larvae of different ages is in size. Measurements with an ocular micrometer were made of the larvae in each sample and while there is necessarily some uncertainty as to exact size, because of the variation among the larvae themselves, this is not great enough to be confusing.

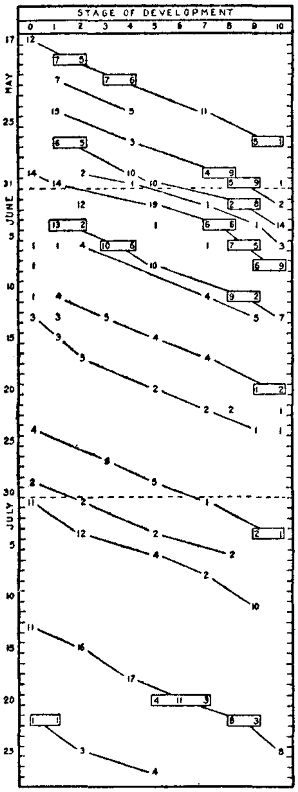

FIGURE 19.—Graph showing percentage of adult oysters bearing broods of larvae of each of 10 stages, as follows: 0, eggs, or early segmentation; 1, blastulae; 2, gastrulae; 3, trochophores; 4, first conchiferous larvae with incomplete valves; 5 to 10, straight μ-hinge veliger larvae classified according to approximate length of valves: 5, 110–120μ; 6, 120–130μ; 7, 130–140μ; 8, 140–155μ; 9, 155–170μ; 10, 170–185μ. The percentage values of larvae of definite size groups are connected to indicate rate of development. See text.

The example reproduced (fig. 19) is only one of many which are at hand but there is little difference between them. In the first place it will be noted that a total period of 9 to 11 days is required for development from eggs to the largest straight-hinge larvae. The general embryology has been well described by Stafford (1914) and is essentially the same as in *O. virginica*, so that it is not necessary to describe it here. To illustrate some of the important stages there is reproduced in figure 20 a series of drawings from Hori (1933), an original copy of which Professor Hori kindly prepared for the writer. The figures are drawn accurately to scale so that they may be employed for the identification of larvae of the species.

When they are discharged from the gonad the eggs are 100 to 105μ in diameter, as stated by Stafford (1914) and Hori (1933). Development proceeds much more slowly than in the case of oviparous species. On the day after the eggs are discharged into the brood chamber they have become blastulae. At the age of 2 days they are usually in the gastrula stage, and 1 day later they have developed the swimming organ, or prototroch, and are actively swimming trochopore larvae. Usually on the fourth day the small valves may be seen developing on the dorso-lateral surfaces as a pair of clearly defined structures about 30 to 40μ long. This may be called the first conchiferous stage, and in figures 15 to 18 they are considered as such and included in the shaded portions of the columns. On the fifth day the valves have become complete and enclose the larvae entirely except when they are swimming with the velum protruding. In *O. virginica*, as stated by Stafford (1913), "The age at which swimming begins may be considered to be about 5 hours, reckoned from fertilization * * *." As indicated above, the early embryology proceeds much more slowly in the viviparous *O. lurida*, requiring between 3 and 4 days to reach the swimming stage.

Larvae carried in the brood chamber are commonly spoken of as being either white or black. The expressions, "white-sick" and "black-sick" are frequently used in this respect. It is true, in general, that the young embryos show as pure white in the branchial chamber adjacent to the gills, and that older larvae in the well-advanced straight-hinge stage appear as a dark-gray or bluish-black mass. Yet one may not judge accurately the stage of development by estimating the depth of color. The

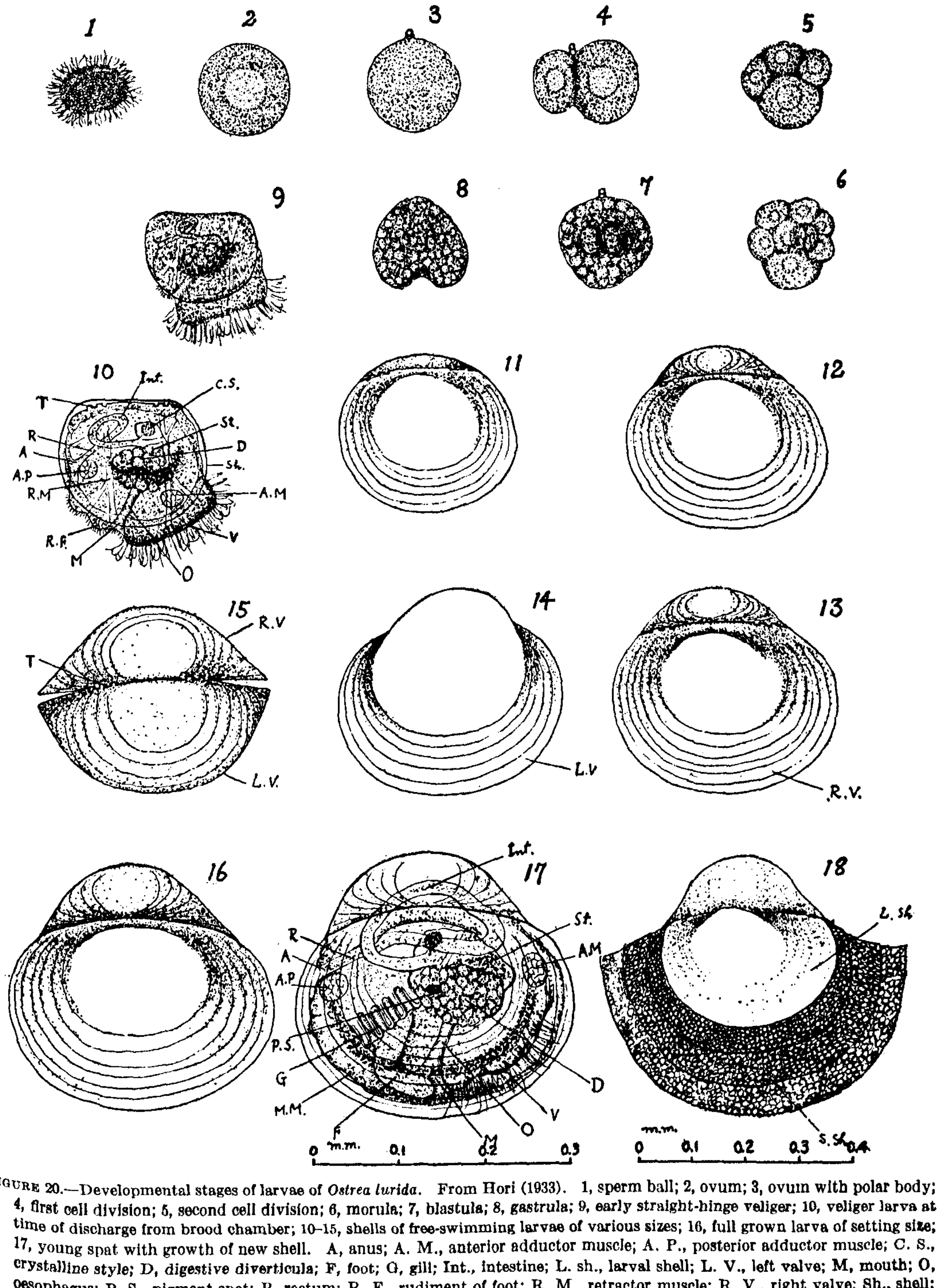

FIGURE 20.—Developmental stages of larvae of *Ostrea lurida*. From Hori (1933). 1, sperm ball; 2, ovum; 3, ovum with polar body; 4, first cell division; 5, second cell division; 6, morula; 7, blastula; 8, gastrula; 9, early straight-hinge veliger; 10, veliger larva at time of discharge from brood chamber; 10–15, shells of free-swimming larvae of various sizes; 16, full grown larva of setting size; 17, young spat with growth of new shell. A, anus; A. M., anterior adductor muscle; A. P., posterior adductor muscle; C. S., crystalline style; D, digestive diverticula; F, foot; G, gill; Int., intestine; L. sh., larval shell; L. V., left valve; M, mouth; O, oesophagus; P. S., pigment spot; R, rectum; R. F., rudiment of foot; R. M., retractor muscle; R. V., right valve; Sh., shell; S. Sh., spat shell; St., stomach; T, teeth; V, velum.

pure whiteness of the eggs and young embryos slowly changes toward the gray after development of the valves. As the larvae grow older the mass becomes darker and darker, while the valves develop and pigment forms in the tissues. Frequently the largest larvae appear as black with a somewhat bluish tint, but it often happens that larvae of the largest size ever found in the brood chamber are only a medium gray.

After 5 days of development in the brood chamber the larval valves become complete and the larvae are in the straight-hinge stage, so called because the dorsal border of the valves is straight, in contrast with the later pronounced umbo in the hinge region. The further developmental stages are arbitrarily arranged according to length of the larval valves, as measured under the microscope.

These results appear not to be out of harmony with those of Stafford (1914) save that in the present case development is somewhat more rapid. His estimate of a period as long as 16½ days may be correct for the locality in which he worked, or it may be due to his method of analysis. His data on water temperature, though incomplete, appear not to differ greatly from those taken in the present instance. Coe's (1931a) estimate of a period of about 10 to 12 days required for development within the branchial chamber is more in accord with the records described above, which indicate a period of about 10 days, on the average.

In his work on *O. edulis* Orton (1926) estimated the gestation period, and stated (p. 219):

> An analysis of the spawning oysters into those with young embyros and those with mainly shelled larvae brings out the fact statistically that oyster larvae under natural conditions are retained in the mantle cavity a period of only 1 to 1½ weeks from the date of their extrusion as fertilized eggs from the parent.

In a later paper (1936) he wrote:

> The white-sick stage is thus normally of about 3 to 3½ days duration, the grey-shelled stage about 1½ to 2 days or less, and the black-sick stage of variable duration, probably 4 days or less. It seems probable that the oyster larva becomes fully developed normally in the sea in a period of 6 or 7 days and is expelled at an age between 7 and 10 days.

Apparently his samples were not taken with sufficient frequency to permit analysis in the manner described above. Nevertheless it is probable that the period of larval development within the maternal brood chambers is not greatly different in the two species.

Stafford used the word "swarming" to designate the final release of larvae from the maternal brood chamber, in contrast to the original spawning whereby the eggs are released from the gonad. It may be considered, in viviparous species, that swarming is the delayed completion of the spawning process which in oviparous oysters, as described by Nelson (1928c) and Galtsoff (1930b–1932), is accomplished at once by means of rhythmic contractions of the adductor muscle. Whether discharge of the larvae is accomplished in the same manner is not known, but it has been observed that during abortions the embryos are forcibly ejected by means of shell movements.

After discharge the larvae live and grow as free-swimming organisms for a period of approximately 1 month. The largest larvae found in the brood chambers are 180 to 185μ long, as described by Stafford (1914) and Hori (1933). The smallest straight–hinge larvae, 5 days after fertilization of the eggs, are about 110 to 120μ long. Growth in length of the valves within the brood chamber proceeds at a rate of about 12μ per day. At the time of setting the larvae are almost constant in size, of a length very close to 320μ. As is described in the following section, at least 30 days elapse between the time of discharge of the first larvae and the time when the first spat are found. During this period the larvae grow in length from 180μ to 320μ, or an average rate of about 5μ per day.

Quantitative observations were not made on the abundance of larvae in the water, though plankton samples were frequently taken. In the case of this species it is not necessary to estimate the frequency and intensity of spawning from the age and abundance of larvae in the plankton, for this was more readily and accurately accomplished by opening oysters periodically, as has already been described. Correlation between time of spawning and setting is considered below.

Stafford (1914) wrote that the largest larvae found in plankton samples, and the smallest spat found on shells soon after attachment, had a length of 255μ. Hori (1933), in a series of experiments on the artificial propagation of the species, stated that the length of newly-set spat is 320μ. He worked with oysters imported into Japan from Puget Sound, and was able to grow the larvae to maturity in dishes by feeding them ground sea lettuce (*Ulva*). Setting under the artificial conditions was successfully accomplished and his measurements of the spat are identical with those of the writer. A great many spat have been measured during these experiments and in no case has an attached spat been seen which was significantly less than 320μ long. It is of interest also that Stafford's (1913) measurements of larvae of *O. virginica* at setting size are different from those of other observers. While he stated that newly-set spat are 380μ long, Prytherch (1934) measured them as 330μ "across the shell at its greatest diameter."

Whether these differences are due to error in measurement or to actual differences in the size of the setting larvae may not be determined from Stafford's works. It is certainly not impossible that under other environmental conditions the larvae of *O. lurida* may be ready to attach at a smaller size. Stafford's (1914) figures of older larvae and of newly-set spat do not show the umbo of the left valve to be as prominent as those of Hori (1933), which are in exact accord with observations of the writer. It is a possibility, also, that differentiation may proceed, under some circumstances, more rapidly than growth, with the result that the organs of the larvae reach the stage of maturity at a size smaller than that observed during the present work. There is, in addition, the possibility that the oysters studied by Stafford are of a distinct variety, having different characteristics from those of the Olympia oyster, though such is hardly likely. However, the fact remains that the measurements of Hori and the writer agree perfectly for both larvae and spat. Stafford's measurements are exactly the same only up to the time of swarming.

SETTING

As was described in the preceding section, spawning is a long-continued process, and not as in some places an occurrence confined to a period of a day or two. It would therefore be expected that setting of larvae would also continue during a considerable period of time. It is important to know the frequency of attachment of larvae throughout the season and the relation of this to the rate of spawning.

However, before describing the methods employed to analyze the results of setting during the different seasons it is necessary to consider the matter of cultch. Various questions have frequently arisen as to what constitutes the most favorable cultch and why oyster larvae attach as they do to certain surfaces. This phase of the investigation is of importance in throwing light upon the results described later.

EFFECT OF ANGLE OF SURFACE

Practical oyster growers have often noticed that most of the spat are to be found on the under surfaces of shells or other objects in the water. The question therefore arose as to whether this was due to some specific reaction of the mature larvae or merely to the fact that sedimentation and growth of algae and other organisms on the upper surfaces ordinarily prevent attachment of larvae. The opinion is frequently encountered that larvae seek the shadows and migrate to the relatively dark under surfaces. In order to determine, in the first place, whether larvae actually attach more abundantly to lower surfaces even when upper surfaces are equally clean an experiment was performed which provided various angles for comparison. Some of these results have already been published (Hopkins, 1935).

Wire frames were made of galvanized hardware cloth of ½-inch mesh, each frame holding three 8- by 10-inch panes of clear glass 1 inch apart and parallel. Some of the frames were designed to hold the panes in either a vertical or a horizontal position, others were so constructed that the panes were held at an angle of 45°. Thirty plates were used in each of the three positions, horizontal, vertical, and at the 45° angle. These were placed in the water of a dike at low tide on one day and removed the following day when the dike was exposed. They were in the water only 24½ hours and may be considered as all equally clean since the time was too short for any considerable amount of fouling. Half of the vertical and 45° plates were placed perpendicular to the general direction of tidal flow, the other half parallel, in order to indicate the effect of current.

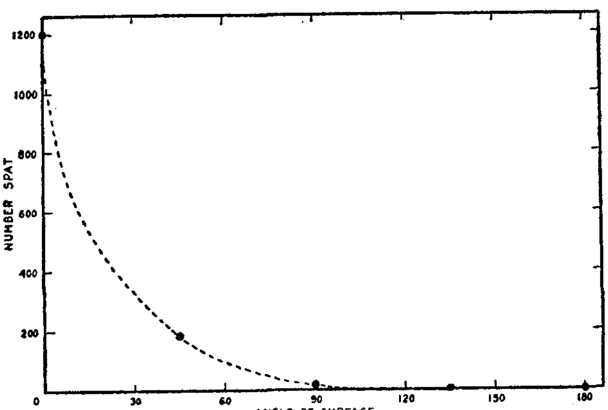

FIGURE 21.—Number of spat caught per 2,400 square inches of glass surface at different angles: 0°, under horizontal; 180°, upper horizontal; 90°, vertical.

After removal from the water the plates were allowed to dry, removed from the frames, and the number of spat caught on all surfaces carefully counted with a binocular microscope. In the analysis of the results the different angles are referred to as follows: 0°, under horizontal; 180°, upper horizontal; 45°, under, and 135°, upper, surfaces of the 45° panes; and 90°, vertical. In table 18 the results are presented in detail. The effect of the angle of the surface on its efficiency as a collector of spat is further illustrated in figure 21, in which the average values in table 18 are plotted graphically. The correlation between angle and number of spat caught is remarkably close, when it is considered that in each case, except for the vertical plates, the area of surface was only 2,400 square inches.

It may be noted in the table that the panes which were parallel to the direction of flow of tide caught definitely more spat than those perpendicular to the current. This would appear to indicate that setting may be proportional to the rate of current. Prytherch (1929) noted that larvae of *Ostrea virginica* set most abundantly on the leeward side of objects in the water, where the current is reduced to a minimum, and concluded that the heaviest setting takes place when the current is least. The above results suggest that the larvae of the native oyster react differently.

The values represented in the graph (fig. 21) are the totals, including plates which were both perpendicular and parallel to the current. It might possibly be a more exact picture of setting behavior if only the results obtained with the parallel series were plotted. However, to do so would hardly alter the curve, since the difference in efficiency of the various angles is tremendously greater than that between plates of the same angle but in different positions with reference to tide. Also, in its present form, the curve is more typical of natural conditions, considered from an ecological point of view.

The results of these experiments have an obvious practical application, for they point out the desirability of furnishing cultch which has a large amount of the ideal under horizontal surface. It is also of practical importance to know that the more freely the current flows along the surfaces the more spat will be caught, presumably because more water, bearing larvae, comes into contact with the surfaces. A comparison of the efficiency of two types of manufactured spat collectors serves to illustrate well the commercial application of the results described above.

Prytherch, in 1929, used the egg crate filler, coated thinly with concrete, as a collector of seed oysters on the Atlantic coast. (See Bureau of Fisheries Document 1076, Improved Methods for the Collection of Seed Oysters.) These fillers, made of cardboard, provide a large amount of surface for the attachment of larvae, and the rough concrete surface is particularly favorable for setting. Such spat collectors are spread on the seed grounds at the correct time and have proven to be highly effective. The method is in use on some of the Olympia oyster beds where the fillers remain covered at low tide because of the dikes (see fig. 2).

However, the experiments described above show that the best surface for the catching of spat of the Olympia oyster is the under-horizontal, and the egg crate filler lies on the bed with all partitions in the vertical position. Also, the filler, lying on the oyster ground, does not permit the free flow of water over the surfaces and the individual cells contain relatively still water, frequently resulting in their filling with silt. In order to develop an efficient collector for Olympia oysters it was, therefore, necessary to design a modification of the egg crate filler which would provide a large amount of under-horizontal surface and also permit the water to flow freely over all the surfaces.

This special collector was made like the egg crate filler, but the individual partitions are twice as wide, and consists of two rows of six cells each. The cells are 2 inches square by 4 inches long (see fig. 22). It lies naturally on the ground in a position which is at an angle of 90° to that of the egg crate filler. Both vertical and horizontal surfaces are present, and the water flows freely through the cells. As they are now used they consist of two rows of seven cells, making the total area almost the same as that of the egg crate filler, but the counts of spat which were made for comparison refer to the original type.

TABLE 19.—*Comparison of efficiency of 2 types of manufactured spat collectors*

	Number of spat per 1,000 cm²			Total area (cm²)	Total number of spat	Average number of spat per 1,000 cm²
	Under-horizontal	Vertical	Upper-horizontal			
Egg crate filler	----------	427	----------	4,724	2,064	427
Special collector	3,235	1,066	28	3,464	4,775	1,378

Table 19 gives the results of counts of spat caught on egg crate fillers and special collectors which were put on the same grounds at the same time and removed together 3 months later. Each series is the average obtained by analysis of three collectors.

The table shows that the average number of spat caught on 1,000 square centimeters of the egg crate filler is 427, while on the special collector the average is 1,378. This value refers to all surfaces, which in the egg crate filler are vertical, and in the special collector both vertical and horizontal. It was conclusively demonstrated that the special design is more than three times as effective as the standard filler.

It is to be expected that the difference between the numbers of spat caught on horizontal and vertical surfaces would not be as great for concrete-coated paper as for plane glass, as described above, since the roughness of the concrete provides a large amount of surface which may be at all angles. The vertical concrete wall has a large horizontal component in the projecting grains of sand which are large in proportion to the oyster larvae. Therefore, the values in table 19 do not exactly fit the curve obtained with plane glass (fig. 21), but the points fall along a more gently sloping curve. The significance of the observation cited above, that flow of water along surfaces is necessary for most efficient setting, is well demonstrated by the difference between the numbers of spat caught per 1,000 square centimeters of vertical surface on the two types of collectors. The special collector is about two and one-half times as effective, considering only the vertical walls.

On most grounds egg crate fillers collect large quantities of silt which fills the cells and kills the spat. Frequently only those caught on the upper edges survive. In the case of the special collector, however, the water is able to flow through the cells and prevent deposition of silt. Even on soft ground only the bottom layer suffers a loss as the collector settles into the surface. Such an example is shown in the upper photograph of figure 22, while the lower surface of a collector placed on firm ground shows little mortality.

It would appear that the habit of attaching primarily to an under surface has the function of protecting the delicate young spat from various unfavorable conditions, such as hot sunshine, and deposition of silt. Immediately suggested by the results is the possibility that the larvae are photosensitive and react negatively, causing them to collect in the shadows where they set. Such a view would imply that setting takes place almost entirely during the day, and that at night the larvae would not concentrate on under surfaces.

To determine whether light is a factor in the setting behavior of larvae, two sets of wire frames, each containing 15 glass plates, were placed on an oyster ground so that the plates were horizontal and allowed to remain for about 24 hours. The plates of one set were painted black on the upper surfaces, the others left clear. Both surfaces of each pane of glass were carefully examined with a binocular miscroscope and all spat counted. On the lower surfaces of the black glass 435 spat had caught, while on similar surfaces of the clear glass 616 were counted. Not one was found on the upper surfaces of either group. It is not considered significant that the clear glass caught more spat than the black, but it is important that the shadow under the latter did not result in any increase in the catch.

In other expèriments, which are described in a later section, it was demonstrated that larvae set as well at night as during the day, and that in all cases the lower surfaces of horizontal panes receive almost all of the spat. It is therefore obvious that light is not an orienting factor in the setting behavior of larvae of this species. The pigment spots of mature larvae have often been looked upon as possibly sensitive to light, but Prytherch (1934) concluded that larvae are not photosensitive, and that the pigment spots have an entirely different function. The present results confirm his conclusion.

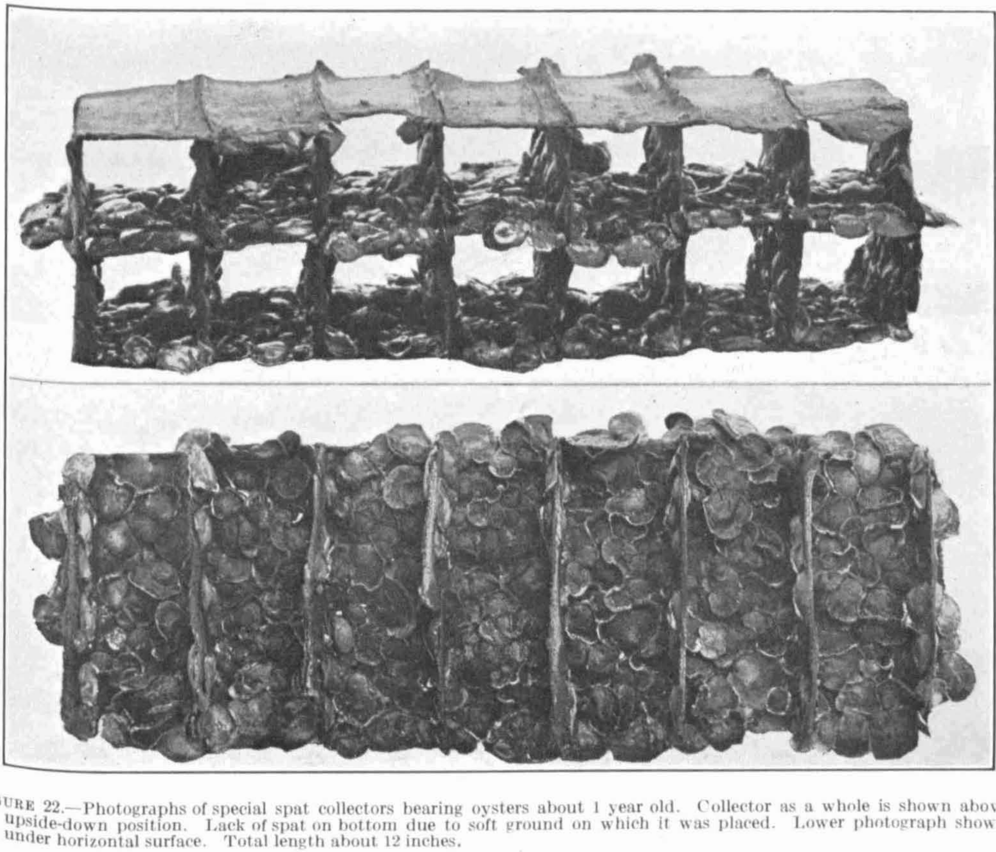

FIGURE 22.—Photographs of special spat collectors bearing oysters about 1 year old. Collector as a whole is shown above in upside-down position. Lack of spat on bottom due to soft ground on which it was placed. Lower photograph shows an under horizontal surface. Total length about 12 inches.

The graph (fig. 21) suggests that the effect of angle of surface on the number of spat caught is purely mechanical and not due to any definitely biological reactions of the larvae. Hori (1933) stated that swimming larvae commonly are in an inverted position, with the velum uppermost. This has been observed also by the writer and is well illustrated in Prytherch's (1934) work on larvae of *Ostrea virginica*. The velum projects through the valves as a flattened, ciliated swimming organ, while the heavier shell hangs downward. The foot with which the larvae must adhere is beside the velum and projects more or less upward, although it is extensible in all directions. It is most likely that the swimming larva, as it comes into contact with a surface from below, is able to hold on with the foot, while on coming down upon a surface it is the hinge portion of the shell that touches. In this manner, as the angle of the surface departs more and more from the under horizontal there is constantly less chance of the foot touching. This interpretation, in effect, is that the observed results are due to accidental contact of the foot with the surface as the larvae is swim ming and being washed about by tidal currents. Prytherch's descriptions of setting, as directly observed with the microscope, suggest that larvae of *O. virginica* may react differently in this respect.

If the above-described interpretation is correct it would be expected that in places where the water is highly turbulent the larvae would frequently be turned over so that they might also catch on upper surfaces. It has frequently been observed on oyster grounds near Olympia, in places where the water flows over dikes, that the rocks and shells close to the dikes bear spat also on upper surfaces.

METHOD OF DETERMINING FREQUENCY OF SETTING

It is of considerable importance to know the duration of the setting season and the times when maxima are reached. For this purpose it was necessary to plant cultch periodically during the entire season. The system finally adopted, after the first year, was to plant a wire bag of shells on each experimental ground and allow it to remain for 7 days. It was then removed and brought to the laboratory. As one bag was taken from the ground a new one was planted and allowed to remain for the following 7 days. It was found necessary, however, to carry on at each place two such 7-day series so that one overlapped the other. In one series, for example, the bags would be in the water from Monday until the following Monday; in the other series, from Friday until the next Friday. A clean lot of shells was therefore put into the water every 3 or 4 days.

After being brought from the grounds the shells were allowed to dry and counts made of the number of spat caught. Bags were made of 1-inch mesh galvanized wire netting and were about 30 inches long by about 8 inches in diameter. Each held something over three-quarters of a bushel of Japanese oyster shells. These shells were preferable because of their large size, generally 4 to 6 inches long, and the white color of the inside surfaces. In the bags the shells were held at all possible angles, eliminating any error that might be traceable to the angle of the surfaces.

Counts were made only of the spat on the inside surfaces, because of their color and smoothness and because the outside surfaces are too rough, and often lamellate, so that all spat are not readily seen. This is not difficult to understand when it is realized that the shells were in the water only 7 days and the oldest spat a millimeter or less in diameter. Two bags of shells were left in the water for a month and a half to allow the spat to grow to a large enough size to permit accurate counts of the number on inside and outside surfaces. The results are summarized in table 20. In one case 33 percent were on inside surfaces, and in the other, 36.1 percent. The larger number on the outside surfaces is probably due to roughness as well as to greater area. The two series average 34.6 percent inside and 65.4 percent outside. In calculating the number of spat caught in a bag the counts made on inside surfaces are considered as 35 percent of the total. This proportion would not be correct if the shells were spread directly upon the grounds, for most of them, because of curvature, fall with the outer surfaces down.

TABLE 20.—*Number of spat caught on inside and outside surfaces of shells in wire bags*

Bag no.	Date planted	Date removed	Number of spat on inside surfaces (25 shells)	Number of spat on outside surfaces (25 shells)
Dike 1				
2810	June 16	July 30	237	352
			163	268
			85	260
			100	287
			66	200
			127	196
			80	200
			129	237
Total (200 shells)			987	2,000
Percentage			33.0	67.0
Dike 5				
2966	June 16	July 30	144	344
			178	258
			118	250
			115	289
			189	246
			172	274
			178	254
			196	372
Total (200 shells)			1,290	2,287
Percentage			36.1	63.9
Average percentage			34.6	65.4

Records were kept on the basis of a standard-size bag of shells, and at the time of counting the shells were carefully measured in a box of definite dimensions. Although some bags were fuller than others, the remeasurement eliminated any error from this source. It is true, of course, that it is impossible to obtain exactly uniform shells, and that at times they might be relatively smaller or larger than the average. It was noted, however, that this had little to do with the results. Generally, a standard bag contained 125 to 150 shells, though some held as many as 200 or as few as 100. When the shells are small they provide more surface per unit of volume, but impede the free circulation of water. When extra large, the water flows freely among them, though the area of surface is not so great. These factors appear to offset one another, in the case of bags of small diameter such as were used, and the resultant averages are relatively consistent.

To standardize the system of counting and calculating the total number of spat caught by this method, 100 unselected shells from each bag were examined carefully, on their inside surfaces, with a binocular miscroscope, and every spat counted. To avoid error, circles were drawn around the spat as they were counted, for in some cases as many as 600 or 700 spat were found on the inside surface of a shell. The number of spat on the inside surfaces of 100 shells was used as a basis for calculating the number on both surfaces of all shells as described above. The variation between the different shells, with respect to the number of spat caught on the inside surfaces, was tremendous. In one typical case the extremes were 0 and 730. This was obviously due to differences in the angles at which the shells are held as well as to their size and their position in the bag. On the shells in this particular bag, which was selected for description because it was in the water during a period of abundant setting, an average of 358 spat per shell were caught.

During the first season the method employed was somewhat different. Bags of shells were left in the water for various lengths of time, the spat counted, and a great many of them measured for the purpose of determining from their size distribution the time at which setting took place. The method of measurement was discarded because of the large error, due chiefly to differences in rate of growth during periods of spring and neap tides, which affect the low-tide temperature, and also probably to specific peculiarities of the different spat. The records for 1931 are therefore not as exact as those for the following years.

Experimental series of this kind were carried on in the two principle oyster-producing bays near Olympia during five consecutive seasons. In addition, two other bays were studied for one season. The results of the analyses are given in detail in the following section. The time of beginning of setting was determined by daily examination of shells on the grounds until spat were found.

SETTING SEASONS, OYSTER BAY

SEASON OF 1931

Observations were not begun in 1931 in time to permit obtaining of complete data on spawning, though it is evident (table 13) that most of the larvae were discharged during May and early June, for after this time few gravid specimens were to be found. Bags of shells, however, were left in the water for various periods throughout the season. The first spat were found on June 12, and they were of the size of mature larvae, with no new growth, so that this date may be considered as the time when larvae began to attach.

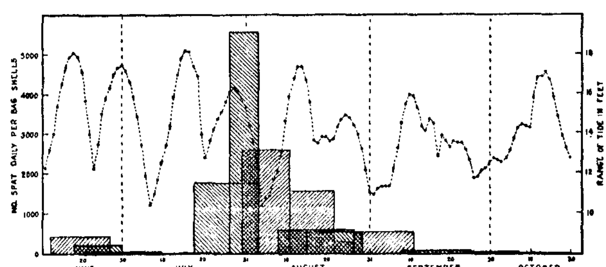

FIGURE 23.—Average number of spat caught daily on bags of shells left in dike 5 (Oyster Bay) for different periods during 1931. Daily range of tide is also shown.

The results of counts of spat on the shells are given in table 21. Only two grounds were studied in detail, and the samples from only one of these (dike 5) were thoroughly analyzed. The other series was checked sufficiently to show that the course of the setting season was identical on the two grounds. Figure 23 gives a better picture of the abundance of larvae setting during different portions of the season. After setting had started on June 12, it continued for a period of about two weeks. Comparison of the graph (fig. 23) with table 21 is necessary for reaching an understanding of the season as a whole. The first bag of shells which caught spat was in the water for 15 days, from June 12 to 27, and caught a total of 6,065 spat, or an average of 404 per day. The bag which was in the water from June 30 to July 24 caught a negligible total of only 35 spat, and none at all was caught between July 10 and 18. The actual significant period of setting, therefore, was between June 12 and 30, and during the last 10 days of this time the average daily catch was very slight.

After this period, during which almost no larvae attached, a very profuse set began to take place. The table shows that the beginning of the second setting period was probably just after July 24, since the shells removed on that date bore a few spat. Between this date and August 3, when shells were brought in again, a great amount of setting occurred. The bags which were in the water from July 30 to August 11 caught fewer spat than those in between, indicating that the peak of frequency of setting was probably between July 24 and 30. During the remainder of the season the rate of setting became gradually slower.

TABLE 21.—*Number of spat caught on bags of shells on two grounds in Oyster Bay, 1931*

Date planted	Date removed	Number of days	Dike 1		Dike 5	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
June 12	June 27	15	7,286	485	6,065	404
June 18	June 30	12	1,900	158	2,480	207
June 20	July 10	20			697	35
June 30	July 24	24			35	1
July 10	July 18	8			0	0
July 15	July 24	9			30	3
July 18	Aug. 3	16	22,320	1,395	28,071	1,754
July 27	do	7	40,520	5,789	39,040	5,577
July 30	Aug. 11	12	35,980	2,998	31,063	2,588
Aug. 8	Aug. 27	19			10,863	571
Aug. 11	Aug. 22	11	14,277	1,298	16,866	1,533
Aug. 15	Aug. 29	14	6,957	497	7,240	517
Aug. 22	Aug. 27	5			1,340	68
Aug. 27	Sept. 11	15			7,769	518
Sept. 8	Sept. 25	17	2,691	150	1,474	87
Sept. 24	Oct. 7	13	1,163	89	817	63
Oct. 7	Oct. 20	13			10	0.77

TABLE 22.—*Number of spat caught on bags of shells on 3 grounds in Oyster Bay throughout the season of 1932*

[Counts were made on only a few of the dike 5 series for comparison]

Date planted	Date removed	Number of days	Dike 1		Dike 5		Dike S	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
June 24	June 27	3	4,286	1,429			527	176
June 27	July 1	4	21,694	5,423			3,913	978
June 29	July 4	5	30,083	6,016			3,463	693
July 1	July 8	7	42,037	6,005	42,040	6,006	5,342	763
July 4	July 11	7	38,156	5,451			16,263	2,323
July 8	July 15	7	36,657	5,237			3,494	499
July 11	July 18	7	19,981	2,854	19,963	2,852	4,756	679
July 15	July 22	7	9,577	1,368			1,888	269
July 18	July 25	7	2,654	379	2,960	423	281	54
July 22	July 29	7	2,614	373			1,220	174
July 25	Aug. 1	7	3,352	479			1,474	210
July 29	Aug. 5	7	4,981	712	4,043	577	1,986	284
Aug. 1	Aug. 8	7	7,146	1,021	4,206	601	1,820	260
Aug. 5	Aug. 12	7	13,132	1,876	10,951	1,564	2,665	381
Aug. 8	Aug. 15	7	11,229	1,604			2,214	216
Aug. 12	Aug. 19	7	25,618	3,659	18,420	2,631	2,086	298
Aug. 15	Aug. 22	7	31,406	4,486	31,694	4,528	3,315	473
Aug. 19	Aug. 26	7	31,824	4,546			6,891	984
Aug. 22	Aug. 29	7	51,877	7,411	37,023	5,289	4,894	699
Aug. 26	Sept. 2	7	15,591	2,227			1,521	217
Aug. 29	Sept. 5	7	6,419	917			1,389	198
Sept. 2	Sept. 9	7	10,694	1,528			333	48
Sept. 5	Sept. 12	7	4,441	634			803	115
Sept. 9	Sept. 16	7	2,029	289			423	60
Sept. 12	Sept. 19	7	563	80	1,374	196	843	120
Sept. 16	Sept. 23	7	983	140			311	44
Sept. 19	Sept. 26	7	1,468	209	1,802	257	651	93
Sept. 23	Sept. 30	7	1,466	209			655	93
Sept. 26	Oct. 3	7	211	30			307	44
Sept. 30	Oct. 7	7	534	76			141	20
Oct. 3	Oct. 11	8	471	59			374	47
Oct. 7	Oct. 14	7	160	23			360	51
Oct. 11	Oct. 17	6	69	11				

Although not as complete as the results for later years, these records proved that two well-defined periods of setting occurred with their maxima about 6 weeks apart. The finding was particularly significant since the later setting was so much more profuse than the earlier, although the oyster growers had planted cultch only early in the season. It appears to have been a common idea that only by planting cultch in time for the initial setting could a good catch be obtained. In 1931 this was certainly not the case. The larvae continued to set in small numbers up until about the middle of October.

Either dike 5 or dike 1 (Olympia Oyster Co.) was used for experimentation during all five seasons. The former is at a level of about 1.5 feet above the zero tide, while the latter has a height of about 3.5 feet. Both grounds are considered as excellent seed-catching areas. According to the results obtained in these experiments the 2 grounds are almost equally favorable. As may be seen in table 21 the number of spat caught on bags of shells which were in the water at the same time is almost identical for the two dikes. Considering only those bags which were in the dikes during the same periods, the total number of spat caught was 137,074 in dike 5, and 136,581 in dike 1.

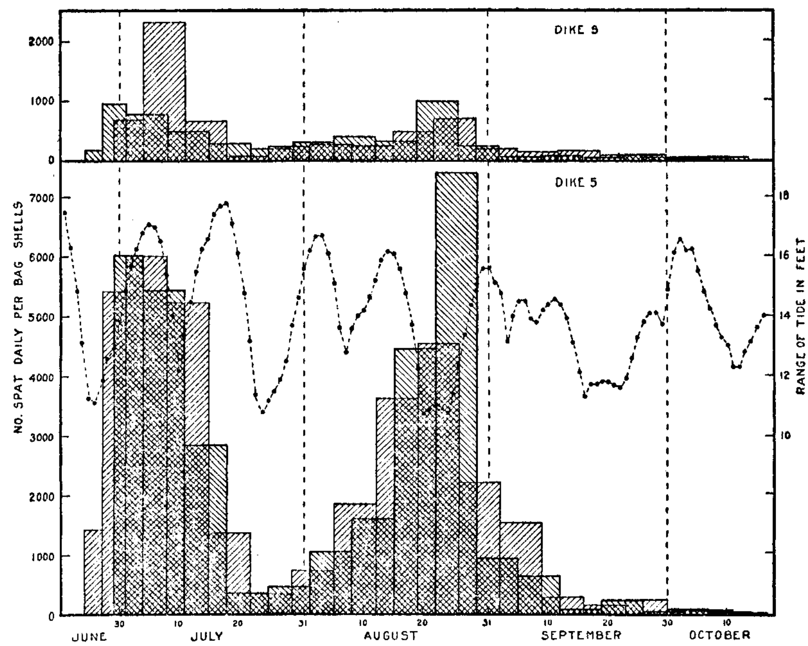

FIGURE 24.—Average number of spat caught daily per bag of shells on two grounds in Oyster Bay, 1932. Each bag was in the water for 7 days. Range of tide is also shown.

SEASON OF 1932

In 1932 the system of carrying on two overlapping series of bags of shells for each ground was put into effect. Although involving the counting of spat on a great many more shells the results well justify the effort because of the increased accuracy obtained, permitting more exact determination of the times of maximum and minimum frequency of setting. Complete counts were made of two series and on sample bags of another (table 22). No spat were found until June 26, although daily observations were made. After this date setting continued until the middle of October, a total period of over 3½ months.

Represented graphically (fig. 24) the more numerous samples make an excellent picture of setting activity. Dike S (Steele ground) is about 2 miles down the bay from dike 1 and is removed from the larger area in which most of the beds are located. The total number of larvae caught is therefore considerably less than on grounds up the bay. There are two distinct major periods of setting having their maxima during the first few days of July and near the end of August respectively. The graphs representing the two grounds are substantially alike with respect to the times of the maxima and minima and differ only in the total number of spat caught at any time. As was found in the previous year the season consists of two distinct setting periods, with the maxima in the present case approximately 8 weeks apart.

TABLE 23.—*Number of spat caught on bags of shells on two grounds in Oyster Bay during the season of 1933*

Date planted	Date removed	Number of days	Dike 5		Dike S	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
June 26	July 3	[1] 7(1)	951	951	196	196
June 30	July 7	[1] 7(5)	16, 200	3, 240	1, 815	363
July 3	July 10	7	27, 566	3, 978	9, 416	1, 345
July 7	July 14	7	23, 248	3, 321	5, 455	779
July 10	July 17	7	9, 900	1, 414	2, 450	350
July 14	July 21	7	11, 480	1, 640	2, 225	318
July 17	July 24	7	14, 483	2, 069	1, 060	151
July 21	July 28	7	20, 082	2, 869	3, 144	449
July 24	July 31	7	16, 302	2, 329	4, 745	678
July 28	Aug. 4	7	8, 320	1, 189	4, 196	599
July 31	Aug. 7	7	9, 551	1, 364	6, 619	945
Aug. 4	Aug. 11	7	8, 167	1, 167	1, 297	185
Aug. 7	Aug. 14	7	7, 277	1, 039	2, 838	405
Aug. 11	Aug. 18	7	23, 040	3, 291	16, 872	2, 410
Aug. 14	Aug. 21	7	16, 766	2, 395	12, 954	1, 850
Aug. 18	Aug. 25	7	16, 778	2, 397	5, 928	847
Aug. 21	Aug. 28	7	15, 784	2, 255	2, 040	291
Aug. 25	Sept. 1	7	6, 003	858	823	117
Aug. 28	Sept. 4	7	3, 602	514	343	49
Sept. 1	Sept. 8	7	573	82	----	----
Sept. 4	Sept. 11	7	467	67	----	----
Sept. 8	Sept. 15	7	120	17	----	----
Sept. 11	Sept. 18	7	100	14	----	----

[1] Bags in water for 7 days, but setting started some time after they were planted.

TABLE 24.—*Number of spat caught on bags of shells on grounds in Oakland Bay and Little Skookum in the season of 1933*

Date planted	Date removed	Number of days	Oakland Bay		Little Skookum	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
June 30	July 7	7	240	34	----	----
July 3	July 10	[1] 7	1, 640	234	480	80
July 7	July 14	7	982	140	577	82
July 10	July 17	7	920	131	246	35
July 14	July 21	7	1, 630	233	428	61
July 17	July 24	7	4, 731	676	243	35
July 21	July 28	7	10, 620	1, 517	791	113
July 24	July 31	7	5, 650	807	440	63
July 28	Aug. 4	7	1, 340	191	403	58
July 31	Aug. 7	7	680	97	157	22
Aug. 4	Aug. 11	7	297	42	----	----
Aug. 4	Aug. 18	14	----	----	1, 560	112
Aug. 7	Aug. 14	7	0	0	----	----
Aug. 7	Aug. 21	14	----	----	3, 563	255
Aug. 11	Aug. 18	7	200	28	----	----
Aug. 14	Aug. 21	7	2, 591	370	----	----
Aug. 18	Aug. 25	7	2, 614	373	709	101
Aug. 21	Aug. 28	7	1, 131	161	----	----
Aug. 21	Sept. 21	31	----	----	86	3
Aug. 25	Sept. 1	7	0	0	----	----
Aug. 28	Sept. 5	8	185	23	----	----

[1] In Little Skookum 6 days.

SEASON OF 1933

In 1933 complete counts were made on shells planted in the same periodic manner in dikes 5 and S, and in addition two other adjacent bays were included (see tables 23 and 24). The three bays are treated together because of the similarity of the setting periods. Little Skookum (Skookum Inlet) is a small bay which branches off from Oyster Bay about half way between the mouth and the upper end, and well down from most of the oyster grounds (see chart, fig. 4). The mouth of Oakland Bay is very near to that of Oyster Bay and it would therefore not seem improbable that the water entering the two bodies of water is almost identical. As a result of pollution of the water in this region by waste liquor from a pulp mill several years before, the oyster beds in Oakland Bay and Little Skookum had been seriously depleted and the supply of spawning oysters reduced to a low level. For this reason the catch of seeds could not be expected to be as great as in the upper end of Oyster Bay, which retained more spawners.

The results obtained on two grounds in Oyster Bay (dikes 5 and S) and on one typical ground each in Oakland Bay and Little Skookum are presented graphically in figure 25. On all of the grounds there were three periods during which setting was especially profuse. The graphs show the three maxima as occurring early in July, at the end of July, and at the middle of August. The last maximum was somewhat later in Oakland Bay than in the other areas, but the first two were in all cases at almost the same time. The total length of the setting season was only about 2½ months, from the beginning of July until the middle of September, a full month shorter than in 1932. The first spat were found in Oyster Bay on July 3, and in Little Skookum the next day. In Oakland Bay the exact date was not noted, but the first bag of shells to bear spat was in the water from June 30 until July 7, indicating that setting began at almost the same time as in Oyster Bay.

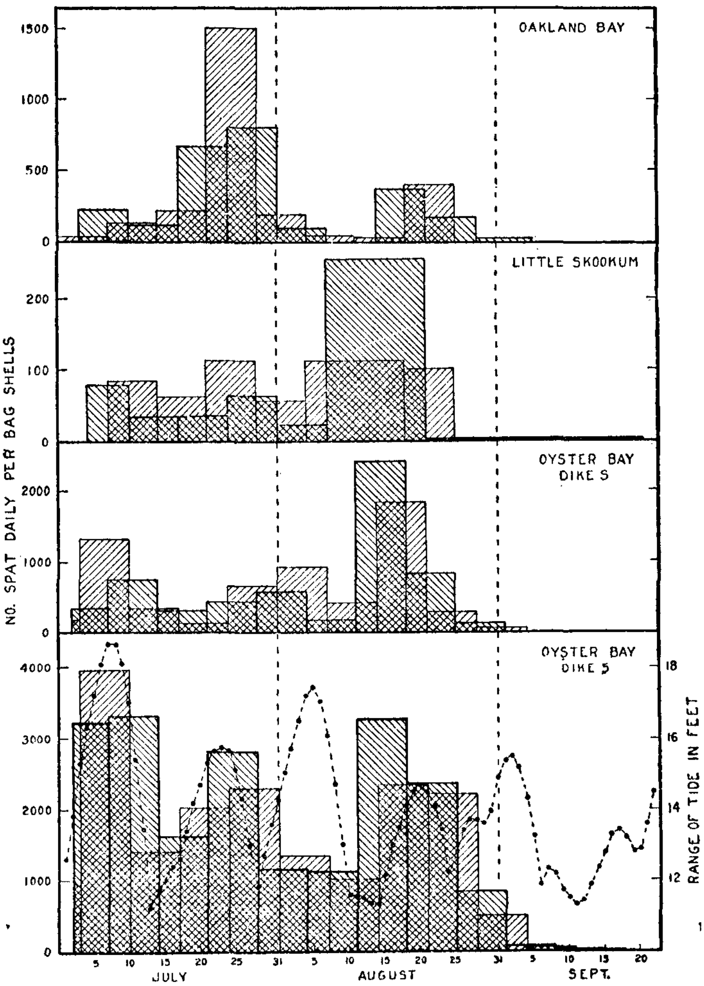

FIGURE 25.—Average number of spat caught daily per bag of shells on two grounds in Oyster Bay and one each in Skookum Inlet and Oakland Bay, 1933. Range of tide is also indicated.

In the season of 1933 setting started later and stopped earlier than during any of the other years. The reason for this short season may be seen in the records of water temperatures (see table 1, fig. 7). The water warmed to the spawning temperature much later in the spring, and did not reach as high a level by the end of the summer as during other years, thus reducing the length of the spawning season. Also, as was pointed out in the section on spawning, fewer adults bore broods of larvae.

SEASON OF 1934

In the summer of 1934 setting started on June 4, a month earlier than in the preceding year, and continued until the end of September (see table 25, fig. 26). In both dikes (5 and S) there were again two distinct periods of setting, during June and early August, respectively. However, each period was of considerable duration and consisted of two minor maxima. In each instance the two submaxima are approximately 2 weeks apart, while the two peaks of the second period are about 6 weeks later than those of the first period. While in some seasons the second setting period is the greater, as in 1931, during 1934 the first was by far the more important. In 1932, however, the two were roughly equal. The results obtained in dike S are similar, but the submaxima do not show so clearly, possibly because the number of spat was too small to indicate such details. At the middle of July there was a period of about 2 weeks during which only an occasional larva attached. The figure shows that between July 9 and July 23 the number of spat caught was insignificant. A similar cessation of setting was also noted in 1931 for an even longer time in between the two major divisions of the setting season. As will be discussed later, this does not appear to be directly correlated with a similar variation in the frequency of spawning.

TABLE 25.—*Number of spat caught on bags of shells of 2 grounds in Oyster Bay during the season of 1934*

Date planted	Date removed	Number of days	Dike 5		Dike S	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
May 28	June 4	[1] 7(1)	218	218	(2)	----------
June 1	June 8	[1] 7(5)	2,267	453	(2)	----------
June 4	June 11	7	3,569	510	549	78
June 8	June 15	7	47,229	6,761	3,430	490
June 11	June 18	7	44,825	6,403	8,510	1,216
June 15	June 22	7	39,053	5,579	8,610	1,230
June 18	June 25	7	34,051	4,864	10,487	1,498
June 22	June 29	7	48,309	6,901	8,000	1,143
June 25	July 2	7	48,600	6,943	6,855	979
June 29	July 6	7	28,671	4,096	5,407	772
July 2	July 9	7	16,448	2,349	4,307	615
July 6	July 13	7	4,386	626	936	133
July 9	July 16	7	398	57	79	11
July 13	July 20	7	55	8	(2)	----------
July 16	July 23	7	100	14	(2)	----------
July 20	July 27	[1] 7 (4)	2,132	533	160	40
July 23	July 30	7	6,193	885	892	127
July 27	Aug. 3	7	20,785	2,969	2,204	315
July 30	Aug. 6	7	13,728	1,961	1,360	194
Aug. 3	Aug. 10	7	14,694	2,099	2,453	350
Aug. 6	Aug. 13	7	24,823	3,546	1,737	248
Aug. 10	Aug. 17	7	8,200	1,171	526	75
Aug. 13	Aug. 20	7	6,634	948	377	54
Aug. 17	Aug. 24	7	2,731	390	503	72
Aug. 20	Aug. 27	7	1,047	149	417	59
Aug. 24	Aug. 31	7	3,528	504	31	4
Aug. 27	Sept. 3	7	2,497	357	192	27
Aug. 31	Sept. 7	7	1,480	211	69	10
Sept. 3	Sept. 10	7	1,303	186	130	18
Sept. 7	Sept. 14	7	1,471	210	178	25
Sept. 10	Sept. 17	7	1,403	200	351	50
Sept. 14	Sept. 21	7	123	17	34	5
Sept. 17	Sept. 24	7	257	37	34	5
Sept. 21	Sept. 28	7	----------	----------	62	9

[1] Bags in water for 7 days, but setting started some time after they were planted.
[2] Only occasional spat; too few to warrant counting.

TABLE 26.—*Number of spat caught on bags of shells in dike 5 in Oyster Bay during the season of 1935*

Date planted	Date removed	Number of days	Total number of spat	Number of spat daily	Date planted	Date removed	Number of days	Total number of spat	Number of spat daily
June 14	June 21	[1] 7(3)	7,991	2,664	Aug. 9	Aug. 16	7	22,751	3,250
June 17	June 24	[1] 7(6)	20,451	3,408	Aug. 12	Aug. 19	7	52,810	7,544
June 21	June 28	7	48,848	6,979	Aug. 16	Aug. 23	7	62,110	8,872
June 24	July 1	7	86,034	12,291	Aug. 19	Aug. 26	7	33,628	4,808
June 28	July 5	7	25,114	3,587	Aug. 23	Aug. 30	7	19,008	2,715
July 1	July 8	7	44,311	6,330	Aug. 26	Sept. 2	7	18,672	2,667
July 5	July 12	7	17,890	2,555	Aug. 30	Sept. 6	7	15,800	2,257
July 8	July 15	7	9,506	1,358	Sept. 2	Sept. 9	7	5,942	848
July 12	July 19	7	16,505	2,357	Sept. 6	Sept. 14	8	694	87
July 15	July 22	7	27,751	3,964	Sept. 9	Sept. 16	7	171	24
July 19	July 26	7	28,097	4,013	Sept. 14	Sept. 20	6	380	76
July 22	July 29	7	16,157	2,308	Sept. 16	Sept. 27	11	514	46
July 26	Aug. 2	7	3,791	540	Sept. 20	---do----	7	122	17
July 29	Aug. 5	7	274	39	Sept. 27	Oct. 5	8	108	13
Aug. 2	Aug. 9	7	817	116	Oct. 5	Oct. 12	7	211	30
Aug. 5	Aug. 12	7	2,394	342					

[1] Bags in water for 7 days, but setting started some time after they were planted.

SEASON OF 1935

Records for this year were analyzed completely only in dike 5, since it had already been well demonstrated that different portions of the bay differ only in the number of spat setting, while the time is the same. The results are given in table 26, and figure 27, and they show a marked similarity to those of previous years in that there are two major divisions of the setting season. After starting on June 17 setting increased in frequency, reaching the first maximum at the end of the month. A second, smaller maximum centered about July 20. From July 29 until August 9 there was a time when almost no larvae attached, and then the second major setting period started, reaching a peak soon after the middle of August. Although the season was practically over early in September a few spat were caught up until mid-October, making a total setting season of nearly 4 months.

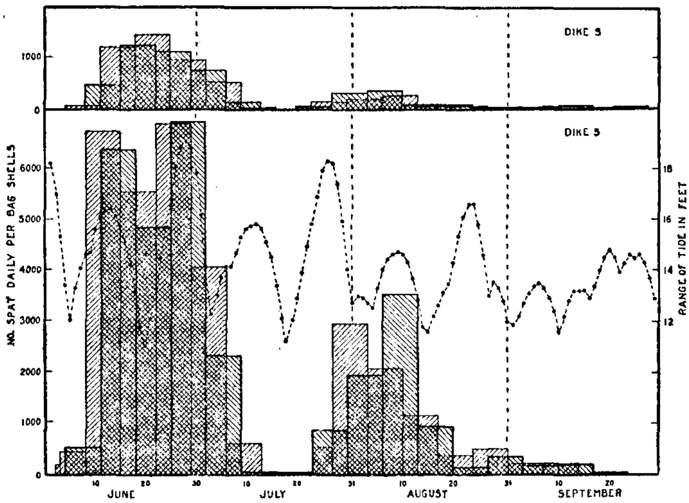

FIGURE 26.—Average number of spat caught daily per bag of shells on two grounds in Oyster Bay, 1934. Range of tide is indicated also.

Other bags of shells were planted in the same dikes at more frequent intervals, in order to give more exactly the times of the maxima. This series will be considered below with respect to the analysis of the significance of the results.

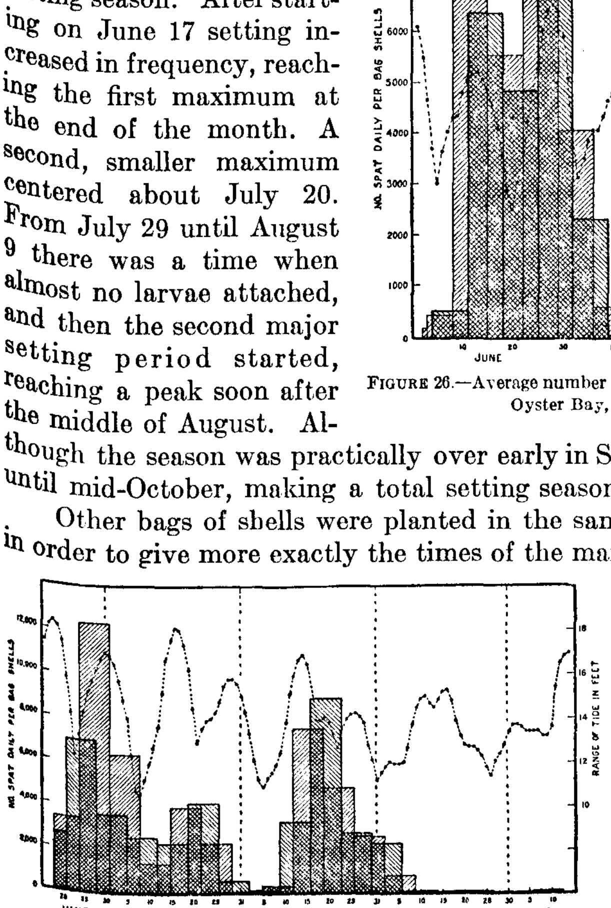

FIGURE 27.—Average number of spat caught daily per bag of shells in dike 5 (Oyster Bay) in 1935. See also figure 33 for results with more frequently planted cultch.

SETTING SEASONS, MUD BAY

Although parallel to Oyster Bay and separated from it by only a few miles, Mud Bay is somewhat different hydrographically, as was indicated above. Also, the spawning and setting activities of the oysters are so different in the two bodies of water that they must be treated separately. It was shown in tables 14 to 17 that spawning does not begin until relatively late in Mud Bay, sometimes as much as 3 weeks later than in Oyster Bay. Setting is therefore similarly later.

TABLE 27.—*Number of spat caught per bag of shells on two grounds in Mud Bay, 1931*

Date planted	Date removed	Number of days	Dike B: Total number of spat	Dike B: Number of spat daily	Dike D: Total number of spat	Dike D: Number of spat daily	Date planted	Date removed	Number of days	Dike B: Total number of spat	Dike B: Number of spat daily	Dike D: Total number of spat	Dike D: Number of spat daily
June 17	June 29	12	6,626	552	6,240	520	June 29	Aug. 7	9	0	0	0	0
June 25	July 1	6	7,390	1,231	3,120	520	Aug. 7	Aug. 21	14	120	8	414	30
June 29	July 9	10	6,949	695	10,037	1,003	Aug. 21	Aug. 26	5	60	12	323	65
July 9	July 17	8	3,021	377	3,709	463	Aug. 26	Sept. 10	15	331	22	628	42
July 13	July 25	12	331	27	228	19	Sept. 5	Sept. 26	21	871	41	1,988	95
July 20	Aug. 7	18	0	0	0	0	Sept. 26	Oct. 8	12	0	0	103	8

SEASON OF 1931

Bags of shells were planted and removed periodically for spat counting on two grounds. Dike *B* is near the shore and dike *D* is next to the small channel which remains at low tide (see chart, fig. 4). As in Oyster Bay during this year a system of planting shells for regular intervals was not employed and the results are not as accurate as in later seasons. Setting began on the 16th of June and the maximum was reached at the end of the month, after which it diminished gradually in intensity (see table 27, fig. 28). From soon after the middle of July until early in August no spat were caught, but after this time a few were found on every bag of shells until the end of September. The total number of seeds caught was small as compared with Oyster Bay during the same season. The first setting period was by far the more important, as shown in the figure, while in Oyster Bay the later period of setting was more significant. All tests in Mud Bay were made in dikes *A*, *B*, *C*, *D* (J. J. Brenner Oyster Co.) and *E* (Charles Brenner).

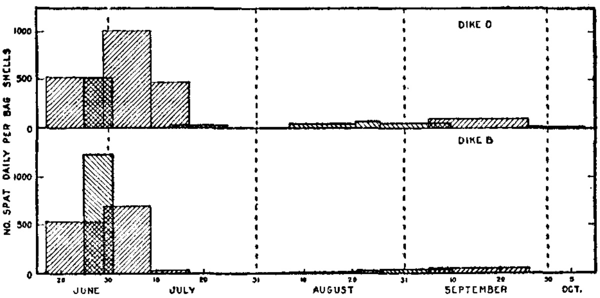

FIGURE 28.—Average number of spat caught daily per bag of shells left in dikes B and D (Mud Bay) for different periods during 1931.

SEASON OF 1932

During this year the improved method of sampling was employed and complete counts were made on the shells tested in dike *B*. For comparison, some counts were made on shells planted in dikes *D* and *E*. The latter is across the channel from dike *D*. The original results are given in table 28, and the dike *B* values are represented graphically in figure 29. The picture is in some respects different from that obtained during 1931, but the 2 years are alike in that there were two separate setting periods. In the graph the first period falls into two maxima. The late setting, though not as intense, was sufficient to be of commercial importance, although it continued only until early in September.

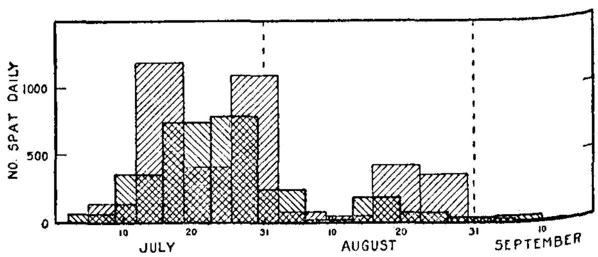

FIGURE 29.—Average number of spat caught daily per bag of shells in dike B, Mud Bay, 1932.

SEASON OF 1933

The results for this year are given in table 29 and figure 30, and consist of complete counts on two series of bags of shells. The graphs are very similar save that the number of spat caught in dike *E* is only a small fraction of that obtained in dike *B*. It was necessary to double the scale in plotting the results in the former case in order to make the values distinct. It has generally been found that the catch of seeds in dike *E* and grounds nearby is much less than in other places a short distance away.

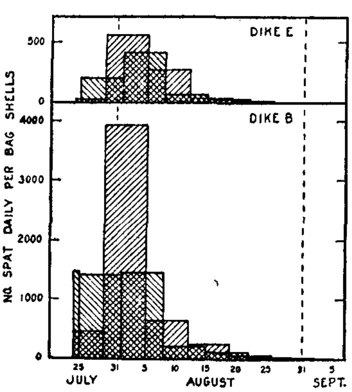

FIGURE 30.—Average number of spat caught daily per bag of shells in dikes B and E, Mud Bay, 1933.

TABLE 28.—*Number of spat caught on bags of shells planted periodically in Mud Bay during 1932*

[Counts were completed on the dike B series, and representative samples from dikes D and E were studied for comparison]

Date planted	Date removed	Number of days	Dike B		Dike D		Dike E	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
July 2	July 9	7	441	63			466	66
July 5	July 12	7	935	134			609	87
July 9	July 16	7	2,521	360			3,663	523
July 12	July 19	7	8,350	1,193	7,626	1,089	3,469	496
July 16	July 23	7	5,153	736			4,034	576
July 19	July 26	7	2,843	403	2,275	325		
July 23	July 30	7	5,590	798				
July 26	Aug. 2	7	7,692	1,099	5,520	789	6,047	864
July 30	Aug. 6	7	1,705	243	2,126	304		
Aug. 2	Aug. 9	7	442	63			354	51
Aug. 6	Aug. 13	7	50	7				
Aug. 9	Aug. 16	7	269	38				
Aug. 13	Aug. 20	7	1,238	177			1,391	199
Aug. 16	Aug. 23	7	2,902	427	4,057	579	4,271	610
Aug. 20	Aug. 27	7	530	76			1,395	140
Aug. 23	Aug. 30	7	2,463	352	5,177	739		
Aug. 27	Sept. 3	7	220	31				
Aug. 30	Sept. 6	7	175	25				
Sept. 3	Sept. 10	7	320	46	860	123		
Sept. 6	Sept. 13	7	45	6				

TABLE 29.—*Number of spat caught on bags of shells on 2 grounds in Mud Bay, 1933*

[Dike B is more favorable seed ground, although the time of most profuse setting is the same on both beds]

Date planted	Date removed	Number of days	Dike B		Dike E		Date planted	Date removed	Number of days	Dike B		Dike E	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily				Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
July 18	July 25	[1] 7(1)	1,494	1,494			Aug. 12	Aug. 19	7	1,836	262	234	33
22	29	[1] 7(5)	2,318	464	157	31	15	22	7	913	130	163	23
25	Aug. 1	7	9,933	1,419	1,417	202	19	26	7	530	76	55	8
29	5	7	27,678	3,954	3,877	554	22	29	7	226	32	([2])	
Aug. 1	8	7	10,011	1,430	2,951	421	26	Sept. 2	7	183	26	([2])	
5	12	7	8,154	1,165	1,892	270	29	5	7	61	9	([2])	
8	15	7	1,565	223	463	66							

[1] Bags in water for 7 days, but setting started some time after they were planted.
[2] Only occasional spat; too few to warrant counting.

TABLE 30.—*Number of spat caught on bags of shells on 2 grounds in Mud Bay, 1934*

Date planted	Date removed	Number of days	Dike B		Dike E		Date planted	Date removed	Number of days	Dike B		Dike E	
			Total number of spat	Number of spat daily	Total number of spat	Number of spat daily				Total number of spat	Number of spat daily	Total number of spat	Number of spat daily
June 9	June 16	[1] 7(1)	39	39	7	7	June 26	July 3	7	729	104	137	19
June 12	June 19	[1] 7(4)	377	94	123	31	June 30	July 7	7	1,360	194	355	50
June 16	June 23	7	2,134	305	248	35	July 3	July 10	7	788	112	85	12
June 19	June 26	7	1,998	285	343	49	July 7	July 14	7	401	57		
June 23	June 30	7	1,562	223	266	38	July 10	July 17	[2] 7(4)	66	17		

[1] Bags in water for 7 days, but setting started some time after they were planted.
[2] Setting stopped 4 days after planting.

The figure shows only one period of setting, which started between July 24 and 25, reached a maximum about a week later, then gradually declined until early in September when it reached the zero level. The entire length of the setting season was only about 1½ months. Nevertheless, oyster growers obtained a highly satisfactory catch of seeds, for during a short time the frequency of attachment was greater than was found in this bay during any of the other years.

SEASON OF 1934

This was a relatively poor seed year in this bay, as may be seen in table 30 and figure 31. Even for the dike *B* results it was necessary to employ a scale 10 times as great as that used in most of the figures in order to obtain a satisfactory graph. After starting to set on about June 16 the larvae never attached in great numbers, so that at the time of the maximum the bags of shells caught an average of only about 300 spat per day in dike *B* and only about 50 per day in dike *E*. The entire setting period

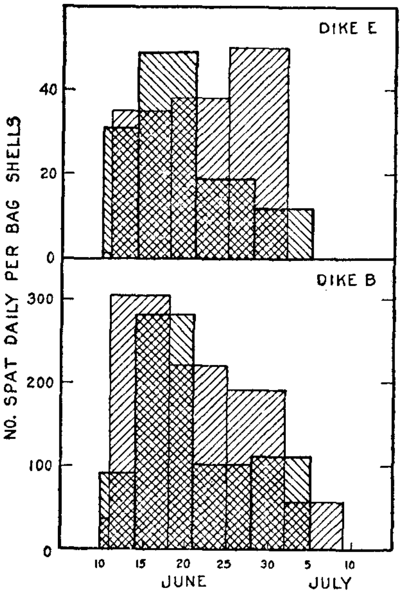

FIGURE 31.—Average number of spat caught daily per bag of shells in dikes B and E, Mud Bay, 1934.

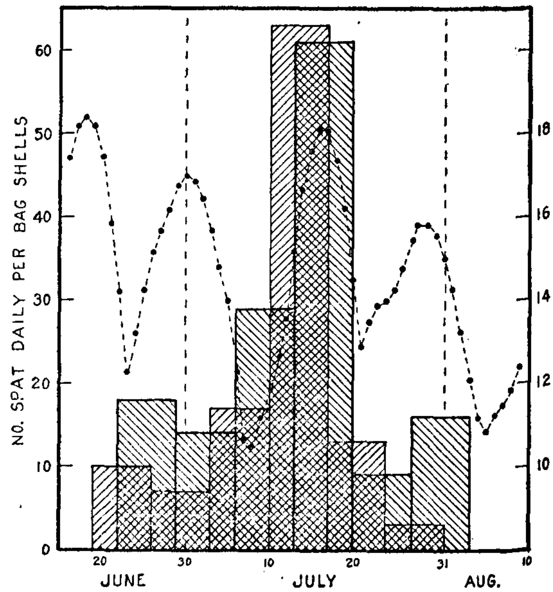

FIGURE 32.—Average number of spat caught daily per bag of shells in dike E, Mud Bay, 1935.

occupied only about 1 month, and no larvae became attached after the middle of July, although bags of clean shells were planted twice weekly until the end of September.

TABLE 31.—*Number of spat caught on bags of shells in dike E in Mud Bay during the season of 1935*

Date planted	Date removed	Number of days	Total number of spat	Number of spat daily	Date planted	Date removed	Number of days	Total number of spat	Number of spat daily
June 19	June 26	7	74	10	July 13	July 20	7	428	61
June 22	June 29	7	128	18	July 17	July 24	7	94	13
June 26	July 3	7	54	7	July 20	July 27	7	68	9
June 29	July 6	7	102	14	July 24	July 31	7	22	3
July 3	July 10	7	122	17	July 27	Aug. 3	7	115	16
July 6	July 13	7	203	29	July 31	Aug. 7	7	0	0
July 10	July 17	7	445	63					

SEASON OF 1935

Because of more concentrated investigations in Oyster Bay little attention was paid in 1935 to Mud Bay. One series of bags of shells was completed in dike *E*, which is not good seed ground. The catch in dike *B*, judging from records of previous years, was probably at least five times as great. The trend of the setting season is shown in table 31 and figure 32. Setting started at the last of June, reached a maximum at the middle of July, and stopped at the first of August. Even during the time of most abundant setting the bags of shells caught an average of only about 50 spat per day. There was some later set after the middle of August, but it was of small significance and samples taken are not complete enough to be included in the table and graph.

Mud Bay is different from Oyster Bay in time of spawning, time of beginning of setting, time of maximum intensity of setting, and duration of the setting season. While Oyster Bay, Little Skookum, and Oakland Bay are closely similar with respect to setting seasons, Mud Bay is entirely different, and the results have to be presented separately.

PERIODICITY OF SETTING

In the foregoing account it was described, particularly with reference to Oyster Bay, that several periods of setting may occur during each season. Attempts to correlate these periods with conditions of salinity, pH, or temperature have resulted in no significant relationship. Local weather conditions appear to have little or no influence upon the setting of larvae, save in their effect upon water temperature which controls spawning and rate of larval development. A period of setting occurs generally as a matter of many days duration, seldom less than 2 weeks. In this locality it is not concentrated within a few days, as described by Prytherch (1929) for Long Island Sound. Ordinarily, only a few spat are found when a setting period begins, but during the following days the larvae attach more and more abundantly.

The oyster growers have the problem of deciding when to plant cultch so that it will not be silted over or covered with organic growth before the larvae are able to attach. The system has always been in use to plant the cultch in advance of the time of setting, after it is known that spawning has started, so as to be certain that the cultch is in the water when setting begins. Naturally, it frequently occurred that cultch was planted far too early and the maximum catch of seeds was not obtained. During 1931, an opportunity was afforded to test roughly the depreciation in efficiency of cultch after being in the water for some time.

TABLE 32.—*Loss in percentage of efficiency of cultch after 9 days*

Bag number	Date planted	Date removed	Number of spat	Difference
Dike 1				*Percent*
3578	July 18	Aug. 3	22,320	44.91
3515	July 27	Aug. 3	40,520	
Dike 5				
3577	July 18	Aug. 3	28,071	28.09
3516	July 27	Aug. 3	39,040	
Average percent difference				36.50

During the middle of the summer the water is typically relatively free of silt and organic growth, as compared with spring and early summer. In 1931 the second major period of setting began between the 25th and the 28th of July. Two bags of shells had been planted on July 18 and two on the 27th. All were removed on August 3. The counts of spat on the two groups are given in table 32. It is assumed, for convenience, that the bags planted July 27 were placed in the water just at the correct time to obtain the maximum catch, though they may have been a little too late to get all of it. The other bags were planted 9 days earlier. When all bags were removed at the same time and the number of spat counted there was found to be a remarkable difference. One bag planted in dike 1 on July 18 caught a total of 22,320 spat, while the bag planted beside it on the 27 caught 40,520 spat. Similarly, in dike 5 the earlier bag caught 28,071 spat, and the later, 39,040. The average difference between the two groups is 36.5 percent, indicating that the earlier shells had lost one-third of their efficiency as spat collectors in 9 days, even during the time when the bay water was most free from fouling materials and organisms. The shells in wire bags are less subject to fouling than those thrown directly upon the grounds, for they are well supported above the silt of the bottom and tidal flow serves to keep them clean. The depreciation in effectiveness of shells thrown on the grounds is probably very rapid, particularly during early summer when there is still considerable silt. An understanding of the setting periods should serve to make it possible to eliminate much of the loss due to fouling of cultch.

It was noted that setting periods appeared to be approximately 2, 4, or 6 weeks apart, rather definitely spaced, suggesting that tidal periodicity might be concerned. By plotting the daily range of tide throughout each setting season (fig. 23 to 27) this suggestion was shown to be well founded. In almost every case the time of maximum frequency of setting is near to the time of greatest tidal range; and in many cases it may be observed that during neap tides, when the range of tide is small, the frequency of setting is also low. In some of the series in which 7-day bags were used it is difficult to decide from the graphs the exact dates of maximum frequency of setting. To throw more light upon the nature of the periodicity and the possible relation to tidal conditions a series of bags of shells was tested in one dike in 1935 in such a manner that each bag generally remained in the water only 2 or 3 days.

TABLE 33.—*Number of spat caught on bags of shells planted at frequent intervals in Oyster Bay, dike 5, 1935*

Date planted	Date removed	Number of days	Total number of spat	Number of spat daily	Date planted	Date removed	Number of days	Total number of spat	Number of spat daily
June 18	June 20	2	1,120	554	July 23	July 25	2	4,786	2,393
June 19	June 21	2	1,840	920	July 24	July 26	2	2,788	1,394
June 20	June 22	2	4,123	2,061	July 25	July 27	2	2,851	1,425
June 21	June 24	3	6,909	2,303	July 26	July 29	3	3,231	1,077
June 24	June 25	1	5,471	5,471	July 27	...do....	2	883	441
June 22	June 24	2	3,226	1,613	Do...	July 30	3	1,220	407
June 25	June 26	1	1,186	1,186	July 29	July 31	2	177	88
June 26	June 27	1	4,131	4,131	July 30	Aug. 1	2	88	44
June 27	June 28	1	8,703	8,703	July 31	Aug. 2	2	37	18
June 28	July 1	3	8,211	2,737	Aug. 1	Aug. 3	2	83	41
June 29	...do....	2	37,704	18,852	Aug. 2	Aug. 5	3	122	41
Do...	July 2	3	10,157	3,386	Aug. 3	Aug. 6	3	191	64
July 1	July 3	2	24,120	12,060	Do...	Aug. 5	2	57	28
July 2	July 4	2	29,149	14,574	Aug. 5	Aug. 7	2	60	30
July 3	July 5	2	31,043	15,021	Aug. 6	Aug. 8	2	34	17
July 4	July 6	2	20,360	10,180	Aug. 7	Aug. 9	2	57	28
July 5	July 8	3	16,640	5,547	Aug. 8	Aug. 10	2	191	95
July 6	...do.....	2	7,500	3,750	Aug. 9	Aug. 12	3	1,200	400
Do...	July 9	3	8,805	2,935	Aug. 10	...do....	2	360	180
July 8	July 10	2	2,914	1,457	Do...	Aug. 17	7	45,314	6,473
July 10	July 12	2	1,080	540	Aug. 12	...do.....	5	47,968	9,593
July 11	July 13	2	622	311	Aug. 17	Aug. 19	2	17,126	8,563
July 12	July 15	3	3,162	1,054	Do...	Aug. 20	3	19,571	6,524
July 13	...do.....	2	4,520	2,260	Aug. 19	Aug. 21	2	9,694	4,847
Do...	July 16	3	6,168	2,056	Aug. 22	Aug. 24	2	4,351	2,175
July 15	July 17	2	4,617	2,308	Aug. 23	Aug. 26	3	4,783	1,594
July 16	July 18	2	4,445	2,222	Aug. 24	Aug. 27	3	9,434	3,145
July 17	July 19	2	4,200	2,100	Aug. 26	Aug. 28	2	4,662	2,331
July 18	July 20	2	4,831	2,415	Aug. 27	Aug. 29	2	6,225	3,112
July 19	July 22	3	10,460	3,487	Aug. 28	Aug. 30	2	3,663	1,831
July 20	July 23	3	5,723	1,908	Aug. 29	Aug. 31	2	2,757	1,378
Do...	July 22	2	3,448	1,724	Aug. 30	Sept. 2	3	5,794	1,931
July 22	July 24	2	2,843	1,421	Aug. 31	Sept. 3	3	6,791	2,263

Smaller units make the graph (fig. 33) more complete and permit a more certain statement of the correlation between frequency of setting and tidal periods. The results of the counts are given in detail in table 33. On the graph the daily range of tide is also plotted, and it may readily be seen that the maximum of the first setting period is centered almost exactly during a period of extreme, or spring, tides. Setting started on June 17, at the time of maximum range of the preceding tidal period, and reached a peak 2 weeks later. The first wave of setting may be considered as having ended about July 10, during neap tides, and a new set started immediately afterward, not reaching a definite sharp peak. It is to be noted that while this setting period continued until the end of the month, for a total time of about 3 weeks, the intervening neap tides had a high minimum range of 13 feet. The difference between spring and neap tides in this case was small, and little difference in rate of setting is to be observed.

The next major setting cycle is concentrated during the extreme spring tides, having started at the time of the preceding neap tides. The following neap tides were not markedly different in range, and the effect is slight, though obvious. During the prominent neap tide period at the beginning of August almost no spat were caught.

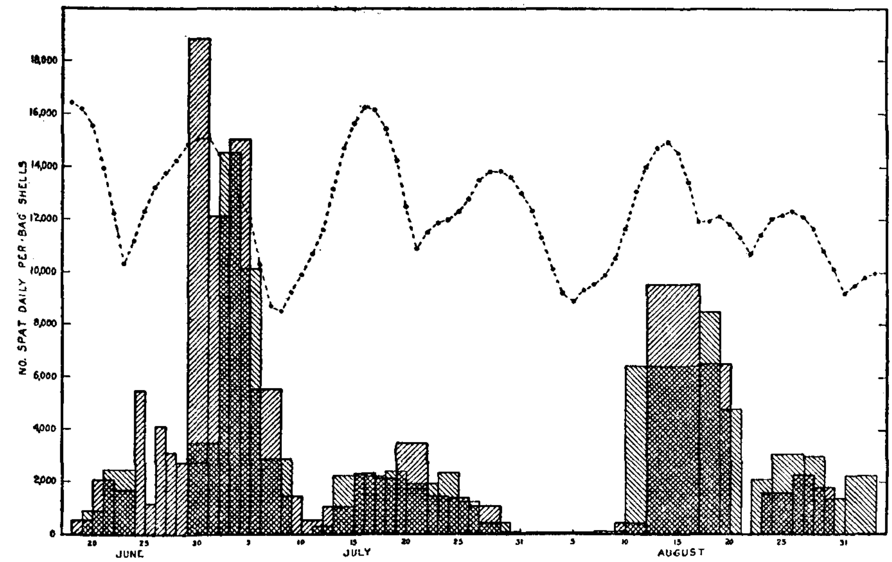

FIGURE 33.—Average number of spat caught daily per bag of shells left in water (dike 5, Oyster Bay) for periods of usually 2 or 3 days, 1935. Tidal range is also shown to illustrate correlation. Compare with figure 27.

This series shows on a more exact basis that the previous interpretation of results obtained with weekly bags is generally correct.

An important source of possible error in reaching an understanding of the significance of counts of spat on the shells in bags is the fact that the shells are clean and thoroughly efficient as spat collectors only at the time they are put into the water. During the next 7 days they become increasingly less efficient. The error is overcome to some degree by using overlapping series. It is to be noted, for example, in figures 27 and 33 that the average number of spat caught daily during any time is greater on the shells that were in the water 2 or 3 days than on those kept for 7 days. In interpreting weekly series it is necessary to take the factor of fouling into consideration, for it would not be correct to say that the exact center of the highest column in any case represents the day of most abundant setting.

STAGES OF TIDE AND SETTING

Since periods of spring tides were shown above to provide most favorable conditions for the attachment of larvae it is of interest to determine the effect of different stages of tide. In Milford Harbor, Conn., Prytherch (1929) found for *Ostrea virginica* that—

"Heaviest setting occurs in the surface layer during the period of low slack water, which is the zone in which the oyster larvae were found to be most abundant. Setting continues as the tide begins to run flood, gradually becoming less intense as the velocity of the current increases, and finally ceasing altogether when the current attains a velocity of 10 centimeters, or one-third foot, per second."

Where this investigator worked the range of tide is less than half of that in southern Puget Sound and it is hardly to be expected that setting habits of larvae would be identical in the two places.

When experiments on this subject were begun it was desired to determine at what stages of tide setting is most intense and the possible effect of such factors as daylight and darkness, salinity, temperature, and pH. Glass plates, supported in wire frames as previously described, were arranged in units of fifteen 8- by 10-inch plates, making a total area of under surface of 1,200 square inches, almost 1 square yard. At low tide the frames were just covered by the water retained in the dikes. A set of frames was placed upon the ground and allowed to remain for a definite interval, then removed, allowed to dry and the number of spat counted.

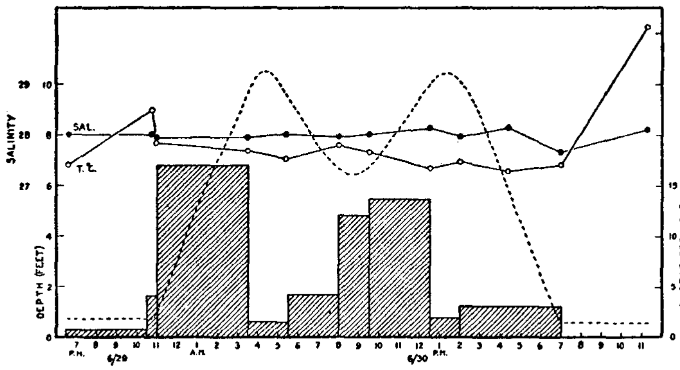

FIGURE 34.—Number of spat caught hourly per unit of cultch with relation to stage of tide, temperature, and salinity. (Oyster Bay, dike 5, June 29 and 30, 1932.)

In the first series, plates were planted in the dike soon after it was exposed by the receding tide, at 6:30 a. m., and allowed to remain until just before the flood-tide water came over the dike (fig. 34). During this time the plates caught but 3 spat. The next set was in the water for a total time of 30 minutes, from near the end of the exposed period until the water was about 1 foot deep over the dike. Throughout the rest of the tidal cycle it was arranged to have a set of plates in the water during each major tide except for about 1½ or 2 hours at the times of high and low tides, which were separately tested.

In figure 34 the results are given as number of spat caught hourly on each of the sets of plates. Shown also are depth of water throughout the period and values of temperature and salinity obtained each time samples were changed. The fewest spat were caught at low tide when the dike was exposed, the most on the two flood tides, although at, or near, the time of the higher low tide spat were also caught. During ebb tide few larvae set, in proportion to the activity at flood tide. It is of interest that salinity and temperature were quite uniform during the experimental period, save that the exposed dike permitted warming of the water at low tide. It is also clear that attachment of larvae is not markedly influenced by daylight or

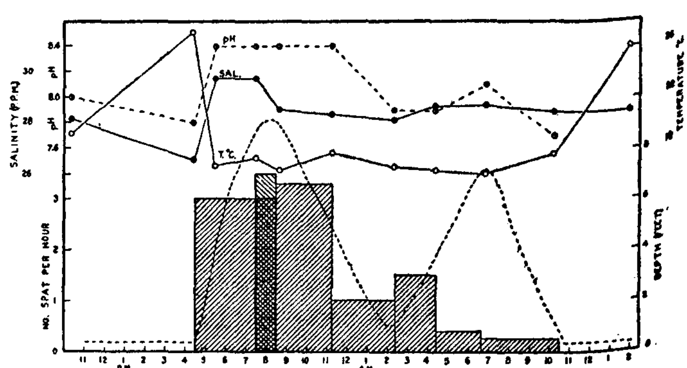

FIGURE 35.—Number of spat caught hourly per unit of cultch with relation to stage of tide, temperature, salinity, and pH. (Oyster Bay, dike S, July 6 and 7, 1932.)

darkness. The two high tides in this case were almost identical and setting was almost equally heavy on the two floods, one day, the other night.

In the next experiment, about 2 weeks later, made on a different ground, the first high tide was more than 4 feet higher than the second. Whether the different picture obtained (fig. 35) is due to the large difference between the two tides is uncertain though it would not seem unlikely that the greater flow of water in the former may account for the heavier set. On neither day was a single spat caught when the dike was exposed. Setting was about equally profuse on flood and ebb of the first tide, and it is suggested that the very low tide after midnight, which almost left the ground exposed, caused rate of current or other factors on the ebb and flood tides to be similar. The following secondary high tide produced few spat, most of which set during the flood.

Except when the ground was exposed the temperature varied only slightly. It is of interest that the most prolific setting took place when both pH and salinity were quite high. The water in the dike at the end of the period of exposure had a pH of 7.8, while about an hour later it was 8.4. At the same time the salinity rose from a little over 26 to more than 29 parts per mille.

In an attempt to reach a more definite conclusion a similar experiment was made in a later year with the additional help of an electric current meter. The boat was anchored in the channel near the oyster ground and the current meter suspended from a framework directly in the dike. The meter hung just above the oysters, at the level of the panes of glass, and the transmission line was led to the boat where counts of revolutions were made. The results are shown in figure 36. Spat were caught only at three well separated times: During the first flood and the following small ebb, and during the major ebb of the next day. The first and the last coincide definitely with the times of swift current. In the second case the current was not particularly rapid, but it is true that the heaviest setting took place about half way between high and low tide, when the current during this ebb was swiftest. Why no spat were caught on the second flood is not known, though it must be realized that in an experiment of this kind, necessarily carried on over a limited area and with a relatively small amount of cultch, chance is a large factor in determining whether the water in the particular place happens to contain larvae. For this reason the error involved in the tests is considerable. Nevertheless, the results are, within certain limits, of great interest.

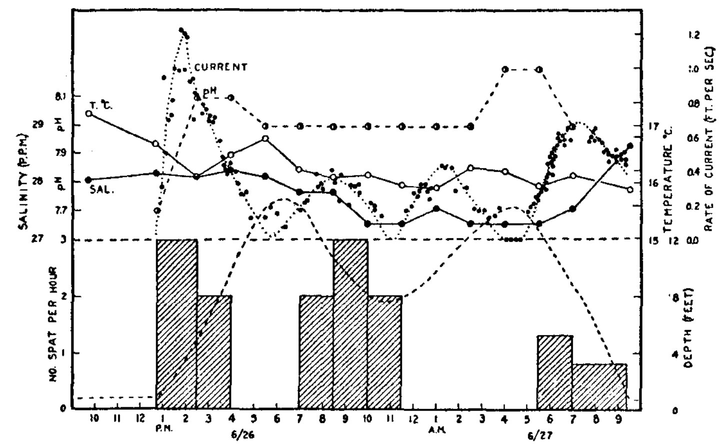

FIGURE 36.—Number of spat caught hourly per unit of cultch with relation to stage of tide, rate of current, temperature, salinity, and pH. (Oyster Bay, Made Ground, June 26 and 27, 1934.)

The final series to be described here is shown in figure 37. The experiment consisted of two parts. One set of plates was in the water for an entire tide, from high to low or low to high. In the other group two overlapping series of plates were used, each set being left in the water 3 hours. The lower portion of the graph represents the first group. Although spat were caught during all four tides, only during the two floods did very many larvae set. By far the most were caught during the major flood tide following the extreme low of the first day.

The sets of plates which were in the water for 3 hours each gave generally similar results. Those which caught most spat were exposed during the time when the flood tide was most rapid, from 1½ hours after the water came over the dike, in the first case, until 1½ hours before high tide. During the first, or small, ebb fewer spat were caught than on the major ebb the next morning. The current records are incomplete in two places, because seaweed became entangled in the current meter. The pH was remarkably constant throughout the period, save that at low tide it dropped from 8.4 to 7.8, due to respiratory activity of the oysters in the shallow, warm water. Salinity and temperature also varied but slightly.

Prytherch (1934) made the important finding that larvae of *Ostrea virginica* may vary over a wide range in the time required for completion of the setting process, and stated that:

> The most rapid setting was observed at salinities of 16 to 18.6 per mille and was completed in from 12 to 19 minutes.

He also determined that:

> In solutions that were above or below this salt concentration, the time for setting increased and reached a maximum of 140 and 144 minutes in salinities of 5.6 and 32.2 per mille respectively.

It is of great significance that the time required for a larva to complete the process of setting may vary from 12 to 144 minutes, for it would therefore appear that a number of environmental conditions might become limiting factors.

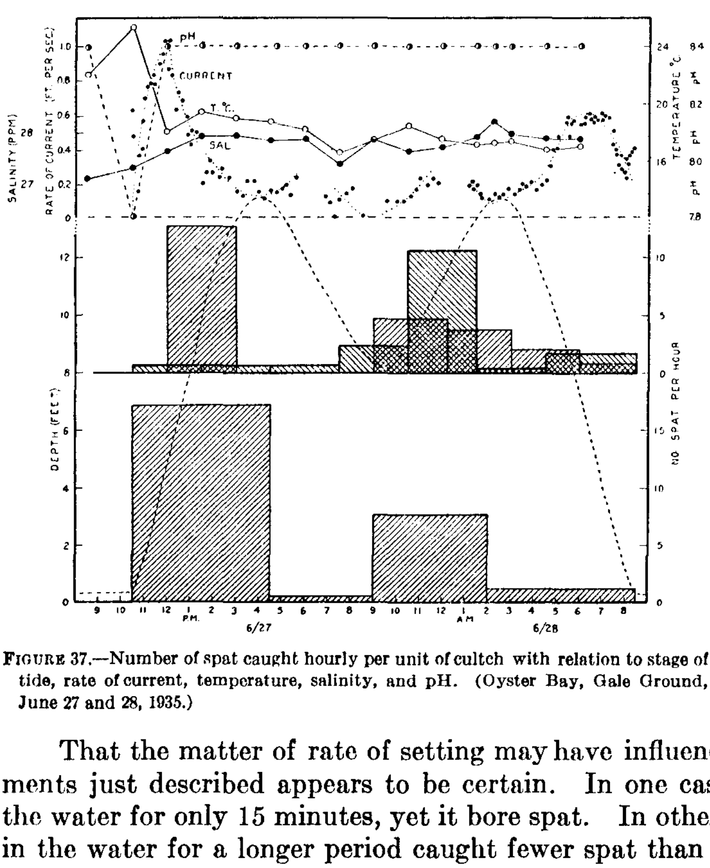

FIGURE 37.—Number of spat caught hourly per unit of cultch with relation to stage of tide, rate of current, temperature, salinity, and pH. (Oyster Bay, Gale Ground, June 27 and 28, 1935.)

That the matter of rate of setting may have influenced the results of the experiments just described appears to be certain. In one case a set of plates was left in the water for only 15 minutes, yet it bore spat. In other cases the plates which were in the water for a longer period caught fewer spat than expected. In the last series described (fig. 37) the plates which were exposed during the major flood tide for a period of 6 hours caught a total of 103 spat. The three sets shown in the upper graph, covering the same period of time, caught a total of only 42 spat. It is suggested that those larvae which had not completed the setting process released their hold when the plates were withdrawn from the water, so that possibly only those that began to set soon after the plates were immersed were able to attach permanently. More clearly to illustrate the point it may be stated that a set of plates, left in the water during the entire 24 hours caught a total of 199 spat, while the four sets of the lower graph caught 151, and all of the double series of 3-hour plates caught but 129 spat.

This information is of assistance in interpreting the results of the four experiments for it indicates that the first portion of the time that the plates are in the water must be given most weight. In such an instance as that shown in the upper graph of figure 37 the first 3-hour set of plates caught few spat; the next one, planted 1½ hours later caught many; the third, still 1½ hours later caught few. It would seem safe to assume that most of this set occurred between 12 and 1:30 o'clock, or the third set would have caught a larger number.

Summarizing these experiments it may be said that almost no spat are caught when the tide is low and the water in the dike is still. At this time the water is warmest, the salinity lowest, though only 1 to 2 per mille below that of the maximum, and the pH lowest, especially after the ground has been exposed for some time. As the tide comes in setting increases in intensity, most of it occurring when the water is 6 to 8 feet deep over the beds on which the tests were made. At this time the pH and salinity are relatively high and the temperature low. In some cases there appears to be a correlation between rate of current and frequency of setting. There seems to be no obvious parallel with conditions observed by Prytherch (1929) in Connecticut.

DEPTH OF SETTING

Most of the favorable grounds for the collection of spat are relatively high, at a level of 3 to 8 feet above the average lower low tide. While usually not so good as producers of the best oysters for market the higher grounds are used almost entirely for the collection of seeds. To the practical oystermen, who have always believed that most of the larvae set when the tide is low and the water on the grounds clear and warm, the highest grounds offered the warmest water at low tide and for this reason were especially favorable for catching seeds. However, as was shown in a preceding section, setting takes place at a lower frequency at low tide than at any other time.

Only when the tide is as much as half high are some of the best seed beds completely covered, except for the few inches of water held by the dikes. Because they are covered by deep water so much less of the time and are closer to the warmer surface water the seed beds are best for obtaining rapid growth of the spat, while on lower grounds, where growth is slower, the oysters fatten better but not so many spat are caught. It is probably true that cultch becomes fouled with organic growth more quickly on the lower grounds, thus preventing a heavy set of spat, but it appeared possible that some other factor might be concerned in determining that higher grounds are so much more effective.

TABLE 34.—*Number of spat caught on shells in four series of wire baskets suspended at fixed distances from surface of water*

[A basket covered a depth of 5 inches]

Depth (inches)	Series 1 number of spat	Series 2 number of spat	Series 3		Series 4	
			Depth (inches)	Number of spat	Depth (inches)	Number of spat
0-5	402	228	0-5	338	0-5	182
6-11	1,029	517	6-11	612	8-13	696
14-19	1,393	640	14-19	662	16-21	664
24-29	779	392	24-29	723	24-29	654
39-44	757	417	42-47	624	32-37	544
64-69	718	447	71-76	591	----	----
99-104	530	495	----	----	----	----

Several series of experiments were performed for the purpose of finding at what depths the larvae set most profusely. Wire baskets were constructed 12 by 12 inches wide and 5 inches deep, filled with clam shells, suspended in series one above the other, and the entire series hung from a float which was anchored in the channel. The baskets were supported so that each was in a horizontal position, occupying 5 inches of depth. They were placed so as to be well separated in the series and to maintain a constant distance from the surface for periods of from 2 weeks to 2 months, and the spat then counted.

The results of four series are given in table 34. In two series the baskets were at depths ranging from the surface down to 104 inches. The others reached only to 37 and 76 inches, respectively. In each basket 30 unselected shells were gone over carefully and every spat counted. The results are relatively uniform, considering the impossibility of measuring the exact area of individual shells, and when the results of the two longer series are averaged and plotted as number of spat per unit of cultch at different depths it becomes evident that the most spat were caught within the first 20 to 30 inches from the surface. In all cases the sample at the surface (0 to 5 inches) caught fewest spat, possibly because of the scouring action of waves, partly, perhaps, because larvae do not set as profusely within that area as they do a short distance below. On the bags suspended below this level of maximum setting fewer and fewer spat were caught. About twice as many spat were taken on the shells at a depth of 14 to 19 inches as on those at 99 to 104 inches.

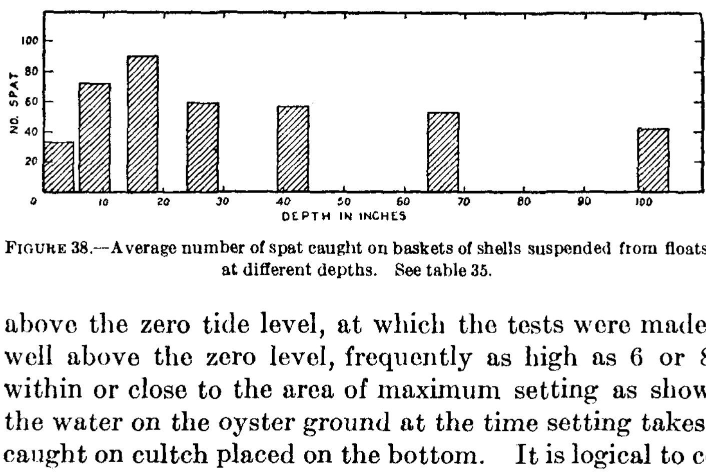

FIGURE 38.—Average number of spat caught on baskets of shells suspended from floats at different depths. See table 35.

It was shown above that most of the larvae set when the water has a depth of about 6 to 10 feet or more above the zero tide level, at which the tests were made. The best seed grounds are well above the zero level, frequently as high as 6 or 8 feet, thereby placing them within or close to the area of maximum setting as shown in figure 38. The deeper the water on the oyster ground at the time setting takes place the fewer spat will be caught on cultch placed on the bottom. It is logical to conclude that this is one of the reasons why the higher grounds are best adapted to the catching of spat.

Difficult to understand in view of these results is the fact that all natural beds in the region are located between low- and high-tide levels, or in shallow channels which are almost dry at low tide. The graph shows that the number of spat caught diminishes gradually with increasing distance from the surface. Tests were made only down to about 8.5 feet and the results suggest that larvae would set to some extent at much greater depths. It appeared likely that beds of oysters might be found in the deep channels well down the bay but extensive dredging in such places failed to disclose a single oyster. It may be that there is little clean cultch to which the larvae might attach, but clam shells were found abundantly in some places. The factor responsible for this localization of natural oyster beds is not clear, but in Yaquina Bay, Oreg., oysters of the same species occur almost exclusively in the deeper waters.

These experiments have served a more immediately practical purpose. Following the original observations in 1931, which demonstrated that a very heavy set of spat could be obtained by employing floats, it was suggested to oyster growers that they try the method on a commercial scale. One of them tried it with a float made of two logs and a wire bottom, filled with Japanese oyster shells, in 1932. He was quite successful and during the following years others have started catching seeds in

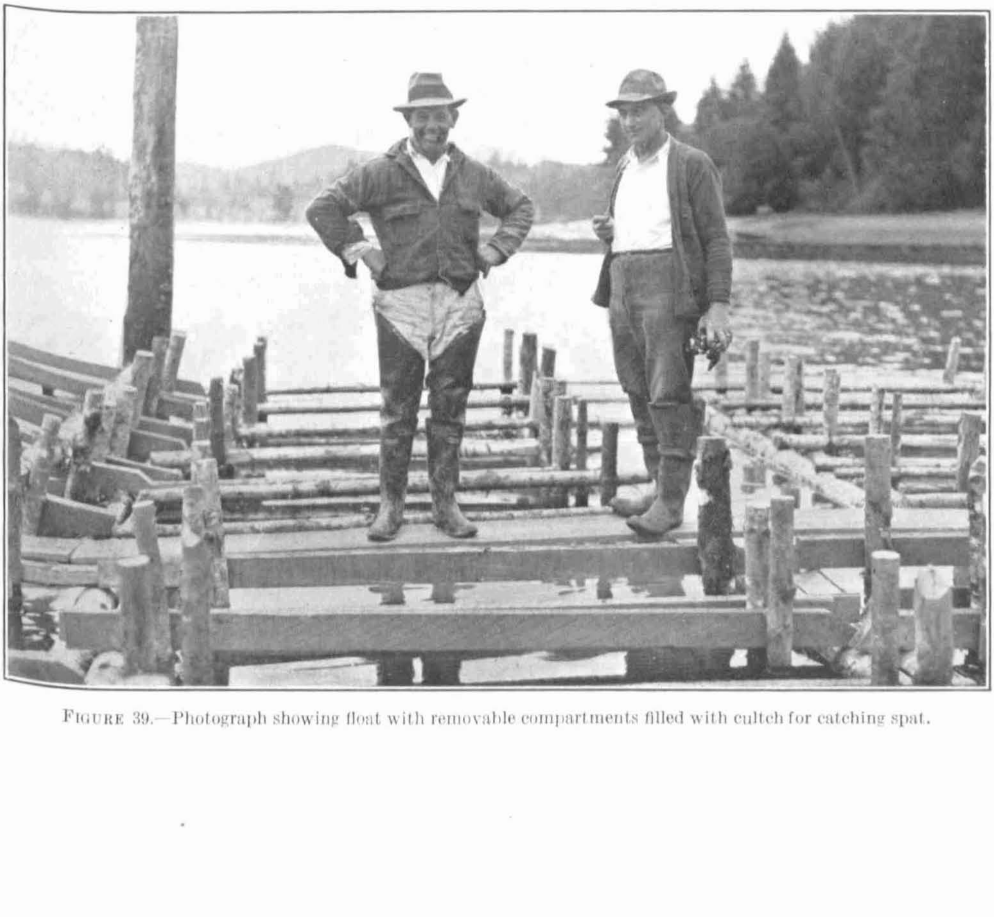

FIGURE 39.—Photograph showing float with removable compartments filled with cultch for catching spat.

this manner. In 1935 and 1936 the method has been put into practice on a large commercial scale, with floats filled with shells or manufactured collectors. Some of the growers have worked out a system of dividing the floats into a series of removable compartments, in which the cultch is placed, thus facilitating handling and minimizing possible storm damage. (See fig. 39.) Counts made on typical egg crate fillers or special-type collectors in 1935 showed that they caught an average of 5,000 to 10,000 spat each.

These floats may be anchored in the channels or pot holes of Oyster Bay, where they get a swift current of water. The manufactured collectors are always placed so that water will flow through the cells bringing abundant larvae and washing out silt. Most of the growers using the method at the present time are those who have satisfactory growing ground but lack adequate seed beds. Formerly these growers purchased what seeds they were able to get, but in recent years, since almost complete destruction of oysters on the State-owned seed beds of Oakland Bay following the beginning of operations of a nearby pulp mill, almost no seeds have been purchasable. The float method now makes it possible for anyone with growing ground to obtain abundant seeds at a cost considerably less than would be required to maintain seed ground for the purpose.

CORRELATION BETWEEN SPAWNING AND SETTING

In the foregoing account detailed descriptions have been given of observations of spawning activities and on setting of larvae throughout the several seasons under different conditions. It is of interest to consider reproductory activities in their entirety in order to correlate the initial spawning with the somewhat later setting and metamorphosis of the larvae. Coe (1932 a, b) stated that spawning in this species continues during at least 7 months of the year on the coast of southern California, while in British Columbia waters, according to Stafford (1914), "The spawning season appeared to extend from about May 20 to about the last of July, and to have reached its maximum about the middle of June." This is a total spawning period of about 2½ months, and he observed a setting period of about the same length, from early July until nearly the middle of September. The investigations described above indicate a total spawning period of 3 to 4 months, although the most intense spawning activity is confined to a much shorter time.

Stafford estimated that at least a month is required between spawning and setting, while Coe (1932a) stated:

> Shortly after they have been spawned into the water these young bivalves attach themselves to almost any kind of solid objects. The free-swimming stage is thus very short and the opportunities for dispersal are limited.

In a similar manner Galtsoff (1929) wrote:

> It is noteworthy that, although the whole development of the Pacific oyster is about twice as long as that of the eastern oyster, the duration of the free-swimming stage, when the organism is subjected to the vicissitudes of life in the open water and is not protected by the mother's body, in both cases lasts for about a fortnight. Thus, the fact that *Ostrea lurida* spends half of the period of its development within the brood chamber of its mother is of no particular advantage, and the free swimming larvae of both species have an equal chance to become prey to plankton-feeding organisms or to be carried away by the tides.

Because of the fact that the free swimming larval period lasts for a month or more, as was noted above, it is obvious that there is great opportunity for dispersal; and in view of the fact that the maternal individuals protect their larvae until they have developed to an advanced bivalve stage at which they are presumably able to protect themselves from many of the unfavorable environmental factors it must be considered that the chances of survival are greater than in the case of oviparous species, which cast the unprotected eggs into the open water.

TABLE 35.—*Dates on which first spawning and first setting occurred*

Date	Oyster Bay			Mud Bay		
	Spawn	Spat	Number of days	Spawn	Spat	Number of days
1931		June 12			June 16	
1932	May 17	June 26	40	May 25	July 7	43
1933	do	July 3	47	June 4	July 25	51
1934	Apr. 17	June 4	48	Apr. 24	June 16	53
1935	May 5	June 17	44	May 13	June 29	47

The only accurate estimate available of the duration of the free swimming period of larval life is that obtained by Hori (1933) who grew the larvae in the laboratory by feeding them macerated sea lettuce (*Ulva*). He removed black larvae from the brood chambers and kept them in dishes of seawater at a temperature of about 20° C. and found that they reached full size and attached after 22 days. The temperature of the water in Puget Sound is generally considerably lower and it is to be expected that development of larvae would proceed more slowly.

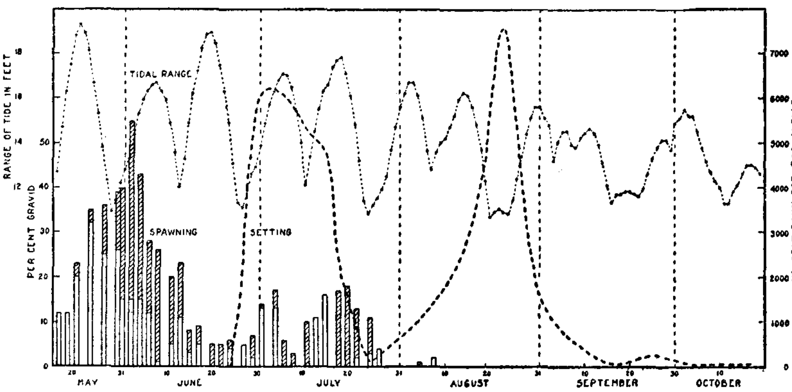

FIGURE 40.—Frequency of spawning and setting during season of 1932 in Oyster Bay. Setting is indicated by a trend line derived from values given in figure 24. Tidal range is also shown.

Field observations on the time when the first larvae and the first spat were found each season are summarized in table 36. In Oyster Bay the interval varied during 4 years from 40 to 48 days, while in Mud Bay the extremes were 43 and 53 days, or about 4 days longer each year. Available data do not permit an exact statement of the total time from spawning until setting, for it is most probable that natural conditions may cause it to vary from year to year. Water temperature necessarily is concerned in determining rate of growth and it is probable that development may be affected by the abundance of food material. Hori (1933) was able to grow larvae of *Ostrea gigas* by feeding them *Chlorella pacifica*, but larvae of *O. lurida* did not thrive on this alga. The experiments of Amemiya (1926) indicated that salinity, also, is an important factor in the development of larvae of several species. It has been described that during the first 10 days larval development takes place within the maternal brood chamber and the free swimming period in Oyster Bay is therefore some 30 or more days in length.

Although tables and graphs of both spawning and setting activities have already been described, a complete picture of the season of propagation is better presented, as in figures 40 and 41, by including measurements of both spawning and setting on the same graph. In figure 40, referring to Oyster Bay in 1932, the frequency of occurrence of gravid adults is shown as a histogram while the time and abundance of larvae setting is indicated by a trend line derived from the results obtained by sampling with bags of shells as previously described. Range of tide is also given. During this year most of the spawning took place from the middle of May until the middle of June, and during July there was some further active spawning. In some respects the record of setting resembles that of spawning, though the break between the two setting periods may not readily be correlated with a comparable cessation of spawning. If the second setting period is traceable to larvae resulting from July spawning the mortality of larvae produced during the first spawning period was tremendously larger, for the later period of setting was very intense.

In the graph referring to the year 1934 (fig. 41) the picture is somewhat similar, though one can hardly consider that there was a second distinct period of spawning. In this figure the correlation between tidal periods and setting is strikingly shown, while in figure 40 the second setting period appears to be correlated with the neap tides. However, in the latter case it is not quite correct to plot tides in this manner, for at the time of the second major set there were very low tides, but the high tides were not great, so that the total range shown is small. In both years, which were selected for presentation because they represent marked differences in time of spawning and setting, the seasons of reproduction cover about 5 months.

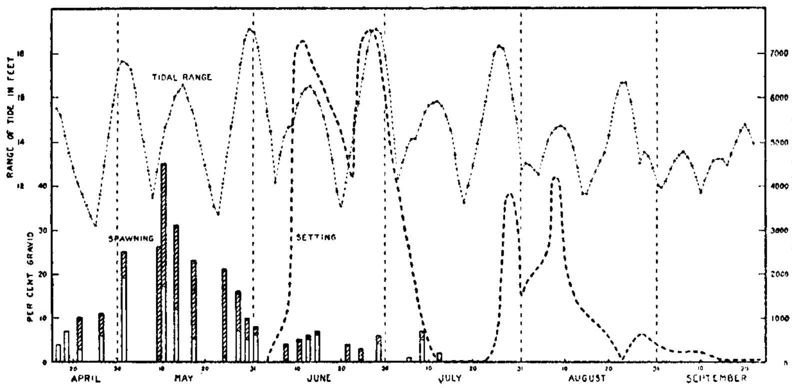

FIGURE 41.—Frequency of spawning and setting during season of 1934 in Oyster Bay. Setting is indicated by a trend line derived from values given in figure 26. Tidal range is also shown.

It may be noted that setting begins during the third period of tides following the beginning of spawning, and also that for 5 seasons, the second major setting period takes place during the third and fourth spring tide periods following that when the first set occurs. The time intervals seem to be predetermined, either by the spawning activity or by cyclic changes in the water which are correlated with tidal periodicity.

DISCUSSION

In the foregoing account various phases of the spawning and setting activities of the Olympia oyster have been described with particular reference to their application to commercial cultivation. Larvae of this viviparous species develop slowly within the maternal brood chamber, or that portion of the mantle chamber which contains the palps and the anterior ends of the gills, and require an average time of about 10 days before they reach the size at which they are normally discharged into the open water. While eggs spawned by the female of *O. virginica* and other viviparous species develop to the trochophore, or earliest swimming stage, within a few hours, in the case of *O. lurida* the same stage is not reached for about 4 days. Rapid early development is characteristic of those species which discharge the eggs directly into the open water, in contrast with the viviparous Olympia oyster which protects the embryos.

Oyster culture in Puget Sound is somewhat different from that in other parts of the United States in that the range of tides is greater, with a maximum range of 20 feet. The oyster grounds are above the extreme low-tide level and are surrounded by dikes which hold enough water to protect the oysters from freezing and drying, while at high tide they may be covered by as much as 16 or 18 feet of water. Such tides involve the movement of great quantities of water and swift currents, but most of the beds are located in the upper ends of the bays where currents are not so rapid. The interchange of cold water from the very deep portions of the Sound with that in the upper ends of the oyster-producing bays prevents the temperature from rising to a high level even during an exceptionally warm season. For this reason eastern oysters, transplanted to Puget Sound, were never able to spawn, since the high-tide temperature on the oyster beds does not reach the critical level of 20° C.

The spawning season is of several months duration and, although in no case has a sudden burst of spawning been observed in which a great number of oysters were involved, as occurs frequently with oviparous species, it has been found that smaller numbers of individuals often bear embryos or larvae of the same age, indicating that favorable conditions may cause spawning to take place in a considerable portion of the population at the same time. Alternation of sexual phases (Coe, 1931a, b; 1932a) probably is responsible for the rather slowly developed wave of spawning, for different individuals are at any time in different stages of maturity. Sometimes as many as 12 to 15 percent of the adults bear larvae of the same age, so that a system of statistical sampling serves to show the rate of growth. Whether sperms or sperm extract will stimulate discharge of eggs by functional females (Galtsoff, 1930b, 1932) has not been demonstrated in this species, but it is considered probable.

It is hardly to be expected that the small native oyster would discharge as many eggs as the larger oviparous species (Galtsoff, 1930), not only because of difference in size but also because the eggs are held within the mantle chamber where they grow into larvae almost twice the diameter of the eggs, and space alone probably acts as a limit. Although an individual produces in one brood only about 250,000 to 300,000 larvae, all individuals are capable of bearing at least one brood each season, while the eastern oyster is generally functional as only of one sex during a single season (Coe, 1932c, d). In some years as many as 150 broods are produced per 100 oysters, indicating that a large number bear second broods, while in other seasons as few as 75 broods per 100 individuals are produced. The degree of success of a spawning season depends upon the number of larvae per brood and the total number of broods produced.

A problem which has never before been attacked is that of the relationship between angle of surface and frequency of attachment of larvae, although Prytherch (1934) observed that larvae in a dish set more abundantly on the vertical sides than on the bottom. It was shown in preceding pages that most larvae attach to under horizontal surfaces and that as the angle departs from this the larvae set in smaller numbers. It was demonstrated that this behavior of the larvae is not due to the effect of light, but the suggestion was put forward that in the normal swimming position of the larva the foot is projecting upward and therefore is able to take hold most readily to the under horizontal surface. Actual setting, according to Prytherch, is a specific process, and larvae may crawl for some time before definitely attaching themselves, but the foot must take hold before final attachment. It would seem probable, from considerations of structure, that the larvae of other species may also attach most abundantly to under horizontal surfaces. Various factors, however, may influence the reaction, and it would be of interest to determine the activities of other species in this respect. Incidentally, Prytherch's (1934) observation that the pigment spots are not light-sensitive organs but have another function is in accord with the present results in that no evidence of a directive influence of light was noted.

By planting cultch periodically throughout each season and allowing each unit to remain in the water for only a few days it was possible to obtain a picture of the frequency of setting at all times. The results, of course, represent the potential catch at any time, rather than the number of larvae setting on the commercial beds, for in the experimental work new shells were planted twice weekly to provide clean cultch at all times, while the older shells on the grounds are usually fouled and unfavorable. In this manner it was shown that in most oyster-producing bays the setting season is not limited to a short period early in the summer, as thought by many oyster growers, but is of several months duration. This information has resulted favorably for the growers for they no longer plant cultch well in advance of the beginning of setting, as was the previous practice. The fact that after setting starts there is still a week or more before the time of maximum setting gives them sufficient time for the planting of cultch.

The setting season consists of several distinct periods which in certain bays are remarkably uniform from year to year. The first period of the season is followed by a second major setting period 6 to 8 weeks later. There is a marked parallel between tidal periodicity and periodicity in the setting of larvae. The peak of a setting period coincides generally with the maximum tidal range of a run of spring tides. Therefore, after setting begins, one may determine from the tide tables the time of the following extreme tides when the rate of setting will be at a maximum. It is probable that the total tidal range is not so much the important factor, but the incidence of extreme low tides without regard to the height of the following high tides. Of practical importance is the very prolific late setting period, which follows the first on the next third and fourth spring tide periods; for oyster growers are able to plant cultch at this time, also, thereby improving their chance of obtaining a satisfactory catch of seeds.

The exact reason for the control of setting by tidal periods is not now definitely known. The beginning of spawning, however, is associated with the tides, for the water warms more rapidly during spring tides. After the minimum water temperature reaches the critical level for spawning there appears to be no connection between further spawning and tides. Orton's (1926) observation that a maximum of spawning occurred at about the time of full moon may in some instances apply also to the Olympia oyster, but analysis of data on spawning during several years indicates that maxima of spawning, as judged from the findings of newly spawned eggs or young embryos, occur during neap tides as well as during full-moon and new-moon tidal periods. The relation between setting of larvae and tidal periods appears not to be traceable to a similar correlation between spawning and tidal periods.

It appears most likely that Prytherch's (1934) work on the effect of copper brought into the bays with land drainage may be applicable to the Olympia oyster, also. He reached the conclusion, from both laboratory experimentation and field observation, that precipitation of copper from solution in the inflowing river water permits the mature larvae to absorb this substance which is required for setting and metamorphosis. For this reason natural oyster beds are always found in relatively enclosed bodies of water which receive a considerable inflow of land drainage. A period of extreme low tides permits a more effective mixing of the fresh water with the sea water, providing the required mineral for the larvae. He found that most larvae attached during low and early flood tides in the surface layer of the water when the salinity was lowest and the rate of current very slow.

In the present work it was found that the best set of spat was caught, on floating cultch, within about 2 feet of the surface of the water, and that with increasing depth the frequency of attachment became less and less. Although during summer there is very little salinity difference from surface to bottom it may be sufficient to account for the results on the basis of Prytherch's conclusion. More difficult to understand, however, is the fact that on the oyster grounds most spat are caught at relatively high tide, when the water is deep and of the maximum salinity, while at low tide, when the salinity is lowest and the amount of mineral from land drainage presumably in highest concentration, almost no larvae set. At this time other factors, such as low pH, may inhibit setting. It is clear, also, that during a period of extreme tides the fresher water entering the upper end of a bay goes farther down the bay and is most thoroughly mixed with the sea water.

These results appear to permit interpretation in the light of Prytherch's conclusion, though the specific factor involved is not definitely known. Although copper may be the controlling factor in the bays studied it is not difficult to conceive that other substances may act in a similar manner. That is, copper may be only one of a number of factors which may control the setting process. As a result of field observations near Galveston, Tex., (Hopkins, 1931b), it was concluded that setting occurred only when the salinity was relatively high, in the neighborhood of 20 p.p.m., for in that place the salinity was frequently very low. Prytherch (1934) disagreed with this conclusion, although he demonstrated experimentally that the setting process proceeds most rapidly at a salinity of 15 to 25 p.p.m. Very slow completion of attachment may be of considerable disadvantage to the larvae and thereby constitute the reason for the writer's observation that spat were caught chiefly when the salinity was high. In addition to salinity and copper there may be other factors which determine the time and frequency of setting under different conditions.

It is not possible to give an exact statement of the number of days required for larvae to reach the setting stage, though it was demonstrated that they develop for about 10 days within the maternal branchial chamber before being discharged. The free-swimming period appears to be 30 to 40 or more days, depending largely, perhaps, on water temperature, so that the total larval life is at least 40 days. This is about three times as long as that of *Ostrea virginica* (Prytherch, 1929). The long larval life permits wide dispersal but also subjects the larvae to various plankton-feeding organisms as well as to the effects of tides and storms.

Mortality of larvae is necessarily large in any species. It may be estimated that oyster growers catch and grow not more than about one out of a million larvae produced, when it is considered that the 4-year-old oysters discharge about 300,000 eggs and all of the younger individuals also propagate on a smaller scale. Mortality of spat is also tremendous. It was shown that during a period of profuse setting as many as 12,000 spat per day might be caught on the shells in one bag. Since there were generally only about 125 shells in a bag, each shell caught several hundred spat within a few days. Yet, after 1 year it is remarkable to find a shell with as many as 50 spat. Most of the mortality appears to take place within the first few weeks after setting, and while some of it is due to overcrowding it cannot all be traced to this cause.

SUMMARY

1. Grounds on which Olympia oysters are grown are surrounded by dikes to retain a few inches of water over the oysters at low tide. The maximum range of tide at this place is about 20 feet, the average about 14 feet, and most grounds are located between the minus 2 foot and plus 4 foot tide levels.

2. Average water temperature varies between a winter low of 6° to 9° C. and a summer high of 18° to 20° C. In summer the temperature is highest when the tide is

low, and the shallow water often reaches 30° C., while during winter low tides occur at night and a temperature as low as about −2° C. has been recorded.

3. Salinity of the water on the oyster beds at high tide varies, in Oyster Bay, between about 26 p. p. m. in winter and about 29 p. p. m. in summer; in Mud Bay the range is about 27 to 29.5 p. p. m. Salinity of the surface water, however, is subject to greater variation.

4. Hydrogen-ion concentration varies throughout the year from a pH of 7.7 to 7.8 in midwinter to about 8.4 in late spring. It is probable that prolific growth of algae in spring, in the presence of fertilizing substances brought in by the winter rains, accounts for the high pH at this time.

5. Market-size oysters bear broods of 250,000 to 300,000 larvae. The number of larvae per brood depends generally upon the size of the maternal oyster.

6. Generally each oyster produces one brood per season, but in some years as many as 50 percent bear second broods while in other seasons as few as 75 percent of the individuals spawn as females. Abortions of embryos frequently occur, however.

7. Spawning of functional females begins in the spring when the minimum, or high tide, temperature reaches 12.5° to 13° C.

8. Most broods of larvae are produced during a period of about 6 weeks at the beginning of the spawning season, though an occasional gravid individual may be found as late as October.

9. An average period of 10 days is required for development within the branchial chamber from the time the eggs (diameter, 100μ to 105μ) are extruded from the gonad until straight-hinge veliger larvae (length of valves, 180μ) are discharged.

10. As compared with oviparous species, development of the larvae of *O. lurida* is very slow, and the age of the various stages may be stated approximately as follows: 1 day, blastulae; 2 days, gastrulae; 3 days, trochophores; 4 days, first conchiferous larvae with incomplete valves; 5 days, straight-hinge veliger larvae completely enclosed by valves 110μ–120μ long; 10 day, veliger larvae with valves 180μ-185μ long.

11. The free-swimming period is 30 or more days in length and varies from year to year, probably according to water temperature.

12. Larvae set most frequently on an under horizontal surface, while fewest catch on upper horizontal surfaces. A definite relationship exists between angle of surface and number of spat caught.

13. This setting behavior of larvae is not due to a directive influence of light but to the swimming position whereby the larval foot projects upward.

14. A special type of manufactured spat collector, designed to take advantage of these habits, is now in use commercially.

15. In Oyster Bay the setting season consists of two distinct periods, 6 to 8 weeks apart. Secondary periods of setting may occur between these two or after the second.

16. Setting seasons in Oakland Bay and Skookum Inlet are similar to those in Oyster Bay. In Mud Bay seasons are shorter and maxima occur at different times.

17. Times of maximum frequency of setting fall within periods of spring tides when tidal range is greatest.

18. On cultch suspended from floats most spat are caught at a distance of 1 to 2 feet from the surface. This appears to be one reason why high grounds catch the most seeds. Floats filled with cultch are now being employed commercially to take advantage of these results.

19. Few spat are caught at low tide, most when the tide is about half high. Frequency of setting appears to be associated with swiftness of current.

20. Setting of larvae begins in the third tidal period following that during which spawning starts. Setting later in the season appears to depend upon larvae remaining in the water from earlier spawning as well as upon larvae resulting from late spawning.

LITERATURE CITED

AMEMIYA, IKUSAKU. 1926. Notes on experiments on the early developmental stages of the Portuguese, American, and English native oyster, with special reference to the effect of varying salinity. Jour. Mar. Biol. Ass'n., vol. 14 (N. S.), pp. 161–175. Plymouth.

CHURCHILL, E. P. 1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. Rept. U. S. Com. of Fish., 1919 (1920), appendix VIII, 51 pp. Washington.

COE, WESLEY, R. 1931a. Sexual rhythm in the California oyster (*Ostrea lurida*). Science, vol. 74, pp. 247–249.

COE, WESLEY R. 1931. Spermatogenesis in the California oyster (*Ostrea lurida*). Biol. Bull., vol. 61, pp. 309–315.

COE, WESLEY R. 1932a. Development of the gonads and the sequence of the sexual phases in the California oyster (*Ostrea lurida*). Bull. Scripps Inst. of Oceanography, Univ. of Calif., Technical Series, vol. 3, pp. 119–144. Berkeley.

COE, WESLEY R. 1932b. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, California. Bull. Scripps Inst. of Oceanography, Univ. of Calif., Technical Series, vol. 3, pp. 37–86. Berkeley.

COE, WESLEY R. 1932c. Sexual phases in the American oyster (*Ostrea virginica*). Biol. Bull. vol. 63, pp. 419–441.

COE, WESLEY R. 1932d. Histological basis of sex changes in the American oyster (*Ostrea virginica*). Science, vol. 76, pp. 125–127.

DEAN, BASHFORD. 1890. The present methods of oyster-culture in France. Bull. U. S. Fish Com., vol. X, pp. 363–388. Washington.

ELSEY, C. R. 1933. The Japanese oyster in Canadian Pacific waters. Fifth Pacific Science Congress, section B8, pp. 4121–4127.

ELSEY, C. R. 1935. On the structure and function of the mantle and gill of *Ostrea gigas* (Thunberg) and *Ostrea lurida* (Carpenter). Trans. R. Soc. Canada, section V, pp. 131–160.

GALTSOFF, PAUL S. 1929. Oyster industry of the Pacific coast of the United States. Report U. S. Com. Fish., 1929, appendix VIII, pp. 367–400.

GALTSOFF, PAUL S. 1930a. The fecundity of the oyster. Science, vol. LXXII, pp. 97–98.

GALTSOFF, PAUL S. 1930b. The rôle of chemical stimulation in the spawning reactions of *Ostrea virginica* and *Ostrea gigas*. Proc. Nat. Acad. Sci., vol. 16, pp. 555–559.

GALTSOFF, PAUL S. 1932. Spawning reactions of three species of oysters. Jour. Wash. Acad. Sci., vol. 22, pp. 65–69.

GALTSOFF, PAUL S., and R. O. SMITH. 1932. Stimulation of spawning and cross fertilization between American and Japanese oysters. Science, vol. 76, pp. 371–372.

GUTSELL, J. S. 1924. Oyster cultural problems of Connecticut. Report U. S. Com. Fish., 1923, appendix X, pp. 1–10.

GUTSELL, J. S. 1926. A hermaphroditic viviparous oyster of the Atlantic coast of North America. Science, vol. LXIV, p. 450.

HOPKINS, A. E. 1931a. Temperature and the shell movements of oysters. Bull. U. S. Bur. Fish., vol. XLVII, pp. 1–14.

HOPKINS, A. E. 1931b. Factors influencing the spawning and setting of oysters in Galveston Bay, Tex. Bull. U. S. Bur. Fish., vol. XLVII, pp. 57–83.

HOPKINS, A. E. 1935. Attachment of larvae of the Olympia oyster, *Ostrea lurida*, to plane surfaces. Ecology, vol. 16, pp. 82–87.

HOPKINS, A. E. 1936. Ecological observations on spawning and early larval development in the Olympia oyster (*Ostrea lurida*). Ecology (in press).

HOPKINS, A. E., PAUL S. GALTSOFF, and H. C. MCMILLIN. 1931. Effects of pulp mill pollution on oysters. Bull. U. S. Bur. Fish., vol. XLVII, pp. 125–186.

HORI, JUZO. 1933. On the development of the Olympia oyster, *Ostrea lurida* Carpenter, transplanted from United States to Japan. Bull. Jap. Soc. Sci. Fish., vol. 1, pp. 269–276.

MCGINITIE, G. E. 1930. The natural history of the mud shrimp, *Upogebia pugettensis* (Dana). Annals and Magazine of Natural History, ser. 10, vol. 6, pp. 36–44.

MOEBIUS, KARL. 1883. The oyster and oyster-culture. Report U. S. Com. Fish., 1880, appendix XXVII, pp. 683–751.

NELSON, T. C. 1922. Report, Dept. of Biol., New Jersey Agr. Exp. Sta., year ending June 30, 1921, pp. 287–299.

NELSON, T. C. 1928a. Relations of spawning of the oyster to temperature. Ecology, vol. IX, pp. 145–154.

NELSON, T. C. 1928b. On the distribution of critical temperatures for spawning and for ciliary activity in bivalve molluscs, Science, vol. LXVII, pp. 220–221.

NELSON, T. C. 1928c. Report, Dept. of Biol., New Jersey Agr. Exp. Sta., year ending June 30, 1927, pp. 77–83.

NELSON, T. C., and E. B. PERKINS. 1931. Report, Dept. of Biol., New Jersey Agr. Exp. Sta., year ending June 30, 1930, pp. 1–47.

ORTON, J. H. 1920. Sea-temperature, breeding, and distribution in marine animals. Jour. Mar. Biol. Assoc., United Kingdom, vol. XII (N. S.), pp. 339–366. Plymouth.

ORTON, J. H. 1926. On lunar periodicity in spawning of normally grown Falmouth oysters (*O. edulis*) in 1925, with a comparison of the spawning capacity of normally grown and dumpy oysters. Jour. Mar. Biol. Assoc., United Kingdom, vol. XIV (N. S.), pp. 199–225. Plymouth.

ORTON, J. H. 1936. Observations and experiments on sex-change in the European oyster, *Ostrea edulis* L. Part 5. A simultaneous study of spawning in 1927 in two distinct geographical localities. Mémoires du Musée Royal D'Histoire Naturelle de Belgique, Deuxième Série, Fasc. 3, pp. 997–1056.

PRYTHERCH, H. F. 1929. Investigation of the physical conditions controlling spawning of oysters and the occurrence, distribution and setting of oyster larvae in Milford Harbor, Conn. Bull. U. S. Bur. Fish., vol. XLIV, pp. 429–503.

PRYTHERCH, H. F. 1934. The rôle of copper in the setting, metamorphosis, and distribution of the American oyster, *Ostrea virginica*. Ecological Monographs, vol. 4, pp. 47–107.

STAFFORD, J. 1913. The Canadian oyster, its development, environment and culture. Commission of Conservation, Canada. Committee on Fisheries, Game and Fur-bearing Animals. 159 pp. Ottawa.

STAFFORD, J. 1914. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Province of British Columbia, Report, Com. of Fish., year ending December 31, 1913, pp. 79–102.

STAFFORD, J. 1915. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Province of British Columbia, Report, Com. of Fish., year ending December 31, 1914, pp. 100–119.

STAFFORD, J. 1916. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Province of British Columbia, Report, Com. of Fish., year ending December 31, 1915, pp. 141–160.

STAFFORD, J. 1917. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Province of British Columbia, Report, Com. of Fish., year ending December 31, 1916, pp. 88–120.

STAFFORD, J. 1918. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Province of British Columbia, Report, Com. of Fish., year ending December 31, 1917, pp. 91–112.

TOWNSEND, C. H. 1893. Report of observations respecting the oyster resources and oyster fishery of the Pacific coast of the United States. Report, U. S. Com. of Fish. for 1889 to 1891, pp. 343–372. Washington.

O