# SEASON OF ATTACHMENT AND RATE OF GROWTH OF SEDENTARY MARINE ORGANISMS AT THE PIER OF THE SCRIPPS INSTITUTION OF OCEANOGRAPHY, LA JOLLA, CALIFORNIA

BY WESLEY R. COE

(Contribution from the Osborn Zoological Laboratory, Yale University, in cooperation with the Scripps Institution of Oceanography)

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INTRODUCTION

It is the purpose of this paper to report the studies which have been in progress during the past four and one-half years on the organisms, particularly invertebrate animals, which attached themselves to experimental blocks submerged at frequent intervals throughout the year.

The life cycles of relatively few of these forms have as yet been fully investigated; even those animals that are of economic importance require further study. Because of their accumulated growths the entire community of these organisms presents an economic problem whenever they attach themselves to ships, boats, and scows, thereby "fouling" the bottoms and thus retarding progress through the water.

It is to this group of economic importance that the investigations here recorded were particularly directed, and it seems not improbable that information regarding the seasons at which the various fouling organisms attach themselves and the rate at which they grow may prove of service in devising means for preventing or, at least, decreasing their troublesomeness.

At the suggestion of Professor W. E. Allen, of the Scripps Institution of Oceanography, the writer attempted to gain some information on this subject by making observations at the Institution pier from October, 1926, to June, 1927. During that period records were kept of the times at which the various species of invertebrates attached themselves to wooden and concrete blocks sunk to low-water level at distances of about sixty feet apart along the thousand-foot pier. By putting down new blocks at regular intervals throughout the year or by cleaning off the accumulated growths of some of those already in the water, the season or seasons of attachment could be determined accurately. By allowing the growths on other blocks to remain undisturbed for long periods the rate of growth at different seasons could be measured and the age at sexual maturity accurately determined.

The original program called for a weekly inspection of all the blocks, and the collection of one sample every two weeks. In collecting the sample, one side of one of the blocks was scraped clean with a knife, after which the block was reset in the water to serve as a new surface for the attachment of a succeeding crop of organisms. In this way a new surface was exposed to the free-swimming stages of the
organisms every two weeks, while the number of blocks was sufficiently great to allow some of the faces on the blocks to mature their growths for periods ranging from one to six months or more.

During the first year the program as outlined met with many vicissitudes, owing mainly to the writer’s inexperience with the powerful force of the breaking surf on an exposed sea-shore. In the first really heavy surf of the autumn months several of the in-shore blocks were carried away in spite of the heavy wires by which they were attached. In a midwinter storm still others were lost or scoured free of their accumulated growths. Eventually only those set in deep water near the end of the pier remained.

In the writer’s absence Professor Allen generously offered to supervise the setting of the blocks and the collection of samples during the following year (1927–1928). With the aid of his assistant, Mr. Horace M. Buley, a nearly complete series was obtained during the first half of the year. Since that time, and continuing through 1931, Professor Allen has personally made the collections at regular intervals. During 1930 he obtained material for comparing the rates of attachment and growth on wood and cement surfaces by immersing, in close proximity for various periods, blocks made of each of these materials. After a block had remained submerged for the desired interval of time the accumulated growths were carefully and completely scraped from one face and preserved in formalin. Thus, through Professor Allen’s generous cooperation, it has been possible for the writer to continue at Yale University the studies undertaken while he was a guest at the Scripps Institution of Oceanography in 1926–27.

SCOPE OF THE INVESTIGATION

Only meager data have as yet been published relative to the season of the year at which the free-swimming larvae of these sedentary organisms appear on the California coast, although Vischer (1928) gives a few figures obtained from an examination of test panels submerged by the U. S. S. “Sirius.”

According to these records one panel set in San Diego harbor from May 31 to June 5 showed “slimy scum; few barnacles”; while two other panels set during the same period received a “few barnacles and hydroids.” Three similar panels submerged from July 23 to 28 received a “few minute barnacles,” “barnacles and a few hydroids,” and “a single hydroid” respectively. In a third test at San Diego, November 22 to 28, all the panels remained “clean.”

This rather scanty evidence would indicate that barnacles and hydroids are in the free-swimming stage in that locality from the end
of May to the end of July, but that the set is completed before the end of November. This is not in accord with the findings from the experimental blocks at La Jolla where the set of barnacles may extend from February to near the end of December, while the hydroids produce new colonies during all the cooler months of the year. But further tests conducted in San Diego harbor in the spring of 1930 are said to agree more closely with the records at La Jolla.

A similar test at Mare Island, June 10 to 18, showed a "single hydroid," "few hydroids," and "seem only." In the same locality, October 21 to 30, three similar panels obtained respectively "500 minute barnacles," "25 barnacles and a few minute hydroids," and "1000 barnacles and a few hydroids."

These two tests at Mare Island are plainly indicative of a marked periodicity in the swarming of barnacle larvae in that locality, and it is obvious that conditions for the fouling of ships' bottoms in June and in October are entirely different. Protection against fouling organisms would thus be required at one season, but not at the other, assuming that the samples obtained fairly represent average conditions over a series of years. But it will be necessary to supplement these meager data by similar tests made throughout the year and, indeed, for several years, before any such assumption is fully justified.

On the Atlantic coast much more reliable information is available, but even that is incomplete. From an examination of ships' bottoms and from test panels, Visscher (1928) determined the periods of attachment of the various types of fouling organisms at Boston, New York, Norfolk, and Beaufort. For algae, this period extends from February to April at Boston and from January to March at Beaufort. For hydroids, likewise, the principal season for attachment is, in both localities, January to April. The set of barnacles at Boston appears to be most abundant in August and September, while at Beaufort the period extends from January to September. Tunicates attach themselves from June to September, as do also the bryozoa, while oysters breed only in midsummer. At New York and at Norfolk the periods are intermediate between those given for Boston and for Beaufort.

For the complete understanding of the life cycles of these sedentary organisms, observations on the growth stages after attachment must be supplemented by a study of the free-swimming larvae in the plankton. On the coast of southern Massachusetts Fish (1925) found a marked periodicity in the occurrence of the larvae of the three native species of rock barnacles. In one of these the free-swimming stages were found mainly during August; the larvae of the second appeared during June and July, while those of the third species occurred from December to June. Similar conditions hold for other sedentary invertebrates.
On the California coast the seasonal changes in temperature are much less than in the same latitudes on the Atlantic coast and in general the breeding periods of the representatives of the various groups of organisms are much longer. Two or more generations in a single year more frequently occur, especially on the coast of southern California. Toward the northern end of the range of certain species the reproductive period is relatively brief, as Späroch (1925) and Orton (1927) have shown for the European oyster and Nelson (1928) and Galtsoff (1930) for Ostrea virginica. Each of these species is found to have a critical temperature, below which spawning is inhibited.

At La Jolla the spawning season of the native oyster (Ostrea lurida) extends over a period of at least seven months and that of the striped barnacle (Balanus tinidinabulum californicus) over more than ten months. The critical temperature for both these forms is about 16° C. Some of the other invertebrates, however, reproduce mainly or wholly during the cooler months of the year, as will be more fully explained in the chapter dealing with the monthly sequence of organisms.

It should be emphasized in this connection that the waters along the coast of southern California are sufficiently warm to encourage not only the continued growth but also the multiplication of organisms throughout the entire year. The evidence from the investigations recorded in this paper indicates that there is not a single day in the year when the water bathing the Scripps Institution pier does not carry the free-swimming stages of some organisms ready to attach themselves to the piles or to other submerged objects.

Consequently it might be expected that a submerged block would receive these organisms the very day it is lowered beneath the surface. As a matter of experience, however, the block may remain apparently free from attached organisms for several days, or even for a week or more in rough weather. And as for the blocks which are placed so as to receive the full force of the surf, the scouring action of the breaking waves, carrying sand in suspension, may in a few hours clean off growths already well established. Furthermore, the minute size of the newly established organisms makes them very difficult to detect and identify. In practice, an exposure of at least two weeks is desirable in order to allow the young organisms to grow large enough to be easily distinguished, and of four weeks if they are to be scraped off for later study.

The statement that free-swimming stages of sedentary organisms occur throughout the year must not be assumed to imply that many of the species have so long a reproductive period. On the contrary, each species has a more or less definite cyclical periodicity of its own.
Each month of the year has a characteristic group of free-swimming organisms, as shown by the species which attach themselves to the blocks at that time. After a little experience one can confidently place the time of the year when a particular growth was scraped from the blocks without looking at the label which accompanies the collection.

The writer is fully aware that the population found on the smooth surfaces of the wood and cement blocks may differ considerably from the communities living naturally on the relatively uneven surfaces of the rocks along the shore and on piles already densely covered with growths of mussels, barnacles, algae, and other organisms. Not only are the conditions for attachment different but there is a difference in the distribution of natural enemies.

It was repeatedly observed that the blocks exposed to the surf were in a few hours freed from barnacles that had reached a diameter of several millimeters, and there is no doubt that the protected spaces between large mussels and barnacles offer the delicate young larvae a much better protection for attachment than do the exposed surfaces of the blocks. In this respect the cement blocks are far superior to wood in obtaining a somewhat earlier set and a more rapid growth of barnacles, while the growth of hydroids, oysters, and algae is almost always greater upon the wood.

WOOD COMPARED WITH CEMENT SURFACES

In order to test the relative suitability of wood as compared with cement for the attachment and growth of organisms, Professor Allen, during the year 1930, placed a series of wood and cement blocks in closely associated pairs.

At the end of five weeks from March 3, the growths on the corresponding faces were compared. Very little difference was noted in the amount per unit area of the *Ectocarpus, Obelia*, diatoms, annelids, and caprellids which had become attached to the two blocks.

After eight weeks (April 28) the situation was quite different. *Ectocarpus, Scytosiphon,* and *Leathesia* appeared to find a better attachment on the wood surface. *Obelia, Bugula,* and *Crisia* were equally abundant on both blocks. *Pecten* and *Lichenopora* were found on the wood only, while other forms were attached to the cement only. The barnacles, however, made the most interesting comparison, for on the wood face there were only 8 individuals, the largest of which was 3 mm. in diameter, while on the cement face with less than half as great an area there were 62, and the largest of these was 5.5 mm. wide.
### TABLE 1

**Comparison of Wood and Cement Blocks with Reference to Number of Barnacles Per Square Inch of Surface**

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of weeks</th>
<th>Wood</th>
<th>Cement</th>
<th>Ratio</th>
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<tbody>
<tr>
<td>1930</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 3 to April 1930</td>
<td>7</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
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<td>March 3 to April 1930</td>
<td>23</td>
<td>8</td>
<td>0.12</td>
<td>2.2</td>
</tr>
<tr>
<td>March 3 to May 1930</td>
<td>13</td>
<td>10</td>
<td>0.2</td>
<td>3.3</td>
</tr>
<tr>
<td>March 3 to May 1930</td>
<td>19</td>
<td>11</td>
<td>0.5</td>
<td>10.5</td>
</tr>
<tr>
<td>March 12 to July 1930</td>
<td>20</td>
<td>50*</td>
<td>50*</td>
<td>1:1   *</td>
</tr>
<tr>
<td>April 20 to May 1930</td>
<td>28</td>
<td>4</td>
<td>1.36</td>
<td>53</td>
</tr>
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<td>April 29 to June 1930</td>
<td>23</td>
<td>8</td>
<td>15</td>
<td>143</td>
</tr>
<tr>
<td>May 19 to June 1930</td>
<td>9</td>
<td>3</td>
<td>20</td>
<td>71</td>
</tr>
<tr>
<td>May 19 to June 1930</td>
<td>30</td>
<td>6</td>
<td>97</td>
<td>200</td>
</tr>
<tr>
<td>May 26 to July 1930</td>
<td>21</td>
<td>8</td>
<td>45</td>
<td>96</td>
</tr>
<tr>
<td>June 9 to June 1930</td>
<td>30</td>
<td>3</td>
<td>5</td>
<td>10.7</td>
</tr>
<tr>
<td>June 9 to July 1930</td>
<td>7</td>
<td>4</td>
<td>30</td>
<td></td>
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<tr>
<td>June 9 to July 1930</td>
<td>23</td>
<td>7</td>
<td>21</td>
<td>115</td>
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<tr>
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<td>4</td>
<td>8</td>
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<td>68.5</td>
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<tr>
<td>June 9 to August 1930</td>
<td>23</td>
<td>11</td>
<td>12</td>
<td>25</td>
</tr>
<tr>
<td>July 7 to August 1930</td>
<td>4</td>
<td>4</td>
<td>4.5</td>
<td>29.3</td>
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<tr>
<td>July 7 to August 1930</td>
<td>25</td>
<td>7</td>
<td>16.6</td>
<td>24</td>
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<tr>
<td>July 7 to September 1930</td>
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<td>July 7 to October 1930</td>
<td>27</td>
<td>10</td>
<td>10*</td>
<td>10*</td>
</tr>
<tr>
<td>August 5 to September 1930</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>August 4 to September 1930</td>
<td>8</td>
<td>1.3</td>
<td>3</td>
<td>1:2.3</td>
</tr>
<tr>
<td>August 4 to December 1930</td>
<td>21</td>
<td>20</td>
<td>1.7</td>
<td>5.4</td>
</tr>
<tr>
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<td>15</td>
<td>3</td>
<td>0.62</td>
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<td>0.5</td>
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<td>1.5</td>
<td>3.5</td>
</tr>
<tr>
<td>August 25 to November 1930</td>
<td>24</td>
<td>13</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>September 15 to October 1930</td>
<td>13</td>
<td>4</td>
<td>0.5</td>
<td>2.5</td>
</tr>
<tr>
<td>September 29 to October 1930</td>
<td>27</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>October 27 to November 1930</td>
<td>24</td>
<td>4</td>
<td>0.5</td>
<td>2</td>
</tr>
<tr>
<td>October 27 to December 21</td>
<td>8</td>
<td>0.7</td>
<td>1.2</td>
<td>1:1.7</td>
</tr>
<tr>
<td>November 24 to December 21</td>
<td>4</td>
<td>0.5</td>
<td></td>
<td></td>
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* Limiting factor is the available area of surface rather than the material of which it is composed. These figures represent only the survivors after a long competitive struggle for the space necessary for growth.
During the progress of the tests throughout the year the collections from the two types of surfaces could almost invariably be distinguished without reference to the labels, because of the greater abundance of algae, oysters, and hydroids on the wood and of most other organisms on the cement. Essentially similar results were obtained in 1931.

Table 1 shows the average number of barnacles per square inch of surface found on pairs of wood and cement blocks set in close proximity on the same day. The numbers show the relative frequency of attachment at different periods of the year, while the ratios indicate the comparative adaptability of the two kinds of material for the attachment and continued growth of barnacles. Each of the four faces of the wood blocks contained 66 square inches, while the corresponding faces of the cement blocks contained 28 square inches. The total number on each face may, therefore, be obtained by multiplying the number given in the table by 66 or 28, as the case may be.

The numbers given include the smaller barnacles which are often attached to the larger ones but do not indicate the very minute individuals of which large numbers are sometimes crushed into an unrecognizable mass by the scraping knife. Examination of the block with a hand lens is always necessary for complete accuracy.

A few cases require special comment. The pair of blocks set April 29 and examined four weeks later (May 26) was exceptional in the amount of disparity between wood and cement, for the face of the wood block bore only 90 small barnacles while the corresponding face of the cement block, with less than half as great a surface area, had 1480—a ratio per square inch of 1 to 35. On the bottom of the cement block the barnacles were more numerous than on any of the sides. Moreover, the average size of the barnacles was considerably greater on the cement surface than on the wood.

In the three weeks, from May 19 to June 9, about 2000 barnacles attached themselves to one face of a cement block—an average of over 71 per square inch of surface. The number on a wood block in close proximity was only about 1300, or approximately 20 per square inch.

Another pair of blocks, examined June 23, after having been in the water for eight weeks, showed an average of nearly ten times as many barnacles on the cement block as on an equal area on the wood. On the cement surface the 4000 barnacles were so closely crowded together that they were compelled to assume the form of slender columns, while many of those which appeared subsequently attached themselves as a crown around the apices of the earlier settlers. Those of a third crop later attached themselves to the second.

Attached to one face of a wood block which had been in the water for the six weeks ending June 30, were about 6400 barnacles, including
many smaller ones attached directly to the larger. On a face of the associated cement block there were about 5600, also including similar smaller ones. The number of those growing directly and indirectly upon the wood surface thus averaged 97 per square inch and on the cement surface 200. This number is twenty-five to fifty times as great as the maximum population which can reach sexual maturity on any square inch of surface, indicating that 95 to 98 per cent must be destroyed by over-crowding and subsequent suffocation before reaching the reproductive period. As additional young individuals appear day after day the percentage mortality becomes still higher.

After a period of several months the numbers on the wood block may equal those on an equal area of the cement block, for the number of survivals depends not so much on the number of organisms that originally became attached as on the space available for continued growth.

Even during the season when young barnacles are daily attaching themselves to the blocks the rate of mortality may exceed the increment owing to new arrivals, with a progressive decrease in the population following an early maximum. This is well illustrated by the successive collections from the four faces of a single block. The cement block set June 9, for example, had about 300 barnacles per square inch on one of its faces after four weeks, while an adjacent face had only 115 individuals per square inch after an additional interval of three weeks. After one week more the corresponding number had become reduced to 68.5 and three weeks later (eleven weeks after the block was set) there were only 25 per square inch, or only one-twelfth as many as were found on a similar face of the same block seven weeks previously. The process of elimination continues until only three or four barnacles remain on any square inch of surface, for no larger number can find space to grow to sexual maturity.

Blocks set early in the year, when growth is slower because of the cooler water and when relatively few individuals are ready for attachment, may show quite different relations. On the faces of blocks set March 3, there is an increase in numbers on both wood and cement from the eighth to the eleventh week, and likewise from the fourth to the eighth week on blocks set April 29, as well as from the third to the sixth week on the blocks set May 19. When the series is approaching the height of the breeding season the new arrivals exceed the mortality rate, but after the peak is reached, the reverse appears to be true.
SEQUENCE OF ORGANISMS APPEARING UPON THE EXPERIMENTAL BLOCKS FROM MONTH TO MONTH THROUGHOUT THE YEAR

The period of attachment and the rate of growth of the animals and plants with which this report is concerned may be most clearly shown by first considering briefly the evidence furnished by an examination of blocks set at monthly periods.

The life histories of the most abundant or economically important species will be discussed in more detail later.

January.—This month is chosen for the beginning of the cycle, not only because it is the first month of the calendar year, but especially because it represents the period when the smallest number of animal forms are in the free-swimming stage.

Algae and hydroids comprise the characteristic growths upon the blocks during this month. Of the former, 

*Ectocarpus granulosus, E. mitelli, E. conservoides, E. cylindricus, Leathesia difformis, Scytosiphon lomentaria, and Herposiphonia verticellata* are the most abundant, while *Obelia dichotoma* and *Plumularia setacea* are the commonest hydroids. Diatoms of many species are always found.

Of the annelids, *Nereis agassizii* is always present, while *Caprella scaura* is the most common representative of the crustacea. *Pecten latissimus*, now grown to a length of 10 to 15 mm., appears frequently, and nudibranch mollusks are always found whenever there are hydroids on which they may browse.

The mean temperature of the water during January is about 14°.

February.—The average water temperature during the month is still about 14°, favoring the multiplication of algae and hydroids, but the growth of most of the other organisms on the pier is retarded. A small number of barnacles may appear in certain years.

March.—The temperature of the water still remains between 14° and 15°, and the appearance of the growths on the blocks is but little different from that of January and February, although the increase in size of the various organisms is somewhat more rapid. New arrivals, however, include the tube-building annelids, *Eupomatus, Serpula*, and *Spirorbis*.

April.—Although the algae, particularly several species of *Ectocarpus*, still continue to constitute the predominant growth on blocks set early in this month, the hydroids, principally *Obelia dichotoma*,
now compete for supremacy. Bugula and other bryozoa make their first appearance at this time. Balanus tinimnabulum californicus settles upon the blocks in considerable numbers. The first crop of young oysters appears, sometimes early in the month when the water temperature has reached 16°.

May.—With the advent of longer days and warmer water comes a great increase in the diversity of animal forms which appear upon the blocks, while the algae are correspondingly diminished.

Shortly after submersion the blocks are covered with colonies of Obelia dichotoma, interspersed with an abundance of Ectocarpus and with diatoms in great profusion. Barnacles and oysters become more numerous. Colonies of bryozoa rapidly establish themselves, the most common forms being Bugula neritina, Crisia geniculata, and Membranipora membranacea, with a few groups of Menippea occidentalis and Thalmoporella rosieri. Copepods, amphipods, and ostracods also become more abundant.

In addition to the algae which were so plentiful earlier in the year, the delicate, branching coralline (Corallina gracilis) now appears, becoming very abundant on some of the blocks later in the summer.

The mean water temperature during May is a little above 17°.

June.—By the first week in June the temperature of the water has risen to about 18°, making the conditions favorable for a very rapid growth of the entire animal population on the pier. The food supplies which have been accumulating during the winter and spring months through the metabolic activities of the algae and diatoms now become available for nourishing the animal life which springs into full activity.

Many of the animals which have themselves been slowly accumulating reserve materials are now maturing their reproductive cells. This is the month, therefore, when the barnacles produce the largest number of larvae, when the bryozoa and the sponges, the tunicates and the mollusks, the anemones and other forms are most likely to become sexually mature, and the first of the three months during which the oyster spawns most abundantly.

Although the hydroids, particularly Obelia dichotoma, continue to form new colonies, they are no longer the dominant animal population on the blocks but have been largely replaced by the bryozoa. Of the latter group the most abundant forms are Bugula neritina, B. eburnea, Crisia geniculata, C. franciscana, C. pacifica, and Scrupocellaria diegensis. All of these form branching, mosslike colonies, while other bryozoa, particularly Thalmoporella, Membranipora, and Hippothoa form thin incrustations, usually upon the oysters, barnacles, scallops,
algae, and other organisms growing upon the block, or sometimes directly upon the surface of the block itself.

Among the numerous new arrivals during this month, are the simple calcareous sponge *Grantia*, the sand-covered ascidian *Molgula verrucifera*, *Ascidia californica*, and the compound ascidians *Didemnum cornulum* and *Distaplia occidentalis*.

*July.*—The water temperature for this month averages above 20°, favoring the rapid growth of most of the inhabitants of the block, with the notable exception of the hydroids and algae. Reproduction in the oysters, barnacles, mussels, scallops, bryozoa, and serpulids continues at its height and the water about the pier is swarming with larvae.

Blocks that have been in the water for eight or ten months are now crowded and overgrown by the rapid growth of the vast assemblages of organisms which have accumulated upon them. The older oysters are almost fully grown and are discharging their young; others are half grown, and still others have recently become attached; several species of bryozoa are at the height of their reproductive cycle; the sponges and tunicates are also fully mature; and the various crops of barnacles are in rapid growth or in the midst of spawning, as the case may be. The younger organisms which become attached upon the older are, in turn, furnishing support for still younger individuals, so that the population of the block consists of several irregular layers of living organisms, with the youngest at the top.

From such a block large numbers of eggs and larval stages are daily set free into the water. But, in compensation, the block receives daily accumulations of the same or other larval forms, perhaps in even greater numbers.

*August.*—The temperature of the water averages only slightly less than 21°, being somewhat higher than in July. This brings to full development those individuals of the various species which have for some reason failed to mature earlier in the summer. Other individuals continue to discharge their successive crops of sexual products or of living young, as in the case of hermaphroditic animals such as the oysters and the barnacles.

*September.*—During the first half of this month there is a continuation of the summer reproductive season of many of the species, the individuals with delayed development spawning at this time. Others with a more prolonged breeding season or with two generations a year now bring to maturity their final crop of sexual products or of free-swimming young.

Blocks set in the water during the early part of this month will therefore receive nearly a complete set of the sedentary forms which
breed in summer, while similar blocks immersed near the end of the month will obtain a somewhat less varied population.

The mean water temperature for the month is slightly above 19°.

October.—The oyster, barnacle, and some of the bryozoa continue spawning, but less abundantly than during the preceding month. The average temperature of the water has dropped to somewhat below 18°, making the conditions more favorable for the growth of hydroids and algae.

November.—The algae, particularly Ectocarpus, and the hydroids, chiefly Obelia, are the most common organisms on blocks placed in the water during this month, for the water temperature has fallen to an average of about 16°. Barnacles arrive less frequently and only a few oysters appear.

December.—The algae, principally Ectocarpus, but associated with Leathesia and Herposiphonia, and the hydroid Obelia are the only organisms, with the exception of enormous numbers of diatoms of many species, which attach themselves in any considerable numbers to the blocks during this month. A few barnacle larvae may appear from time to time throughout the month.

The mean temperature of the water has fallen to about 15°, checking the reproduction of most of the animal life and reducing the rate of growth.

SEASON OF ATTACHMENT AND RATE OF GROWTH OF EACH GROUP OF ORGANISMS

ALGAE

It not infrequently happens that various species of algae have established themselves upon the blocks before the first of the animal occupants have arrived. Although the spores of some of these algae are present in the water at all seasons of the year, there is a marked periodicity in the luxuriance of their growths.

The most favorable season for the rapid growth of most species is late winter and early spring. A block placed in the water at that time is quickly covered with a luxuriant growth of algae, with relatively few forms of animals. If the block was placed in the water earlier in the year the algae already established show a rapid increase in size.

The most abundant of all the algae and the first to appear upon the blocks are four species of Ectocarpus, E. granulosus, E. mitchellae, E. cyliniicus, and E. confervoides. Of these, the first named forms the most luxuriant growth, while E. confervoides occurs only spar-
ingly. All of them are found at all seasons of the year, but reach their maximum growth in February, March, and April. Thereafter they continue in greatly diminished quantities, to become conspicuous again the following autumn.

The bladder weed (Leathesia disformis) is also found on all of the blocks during the cooler seasons of the year. Starting as a tiny solid globule, some of the plants become irregular, thin-walled vesicles an inch or more in diameter within six or seven weeks. Reproduction occurs at all seasons of the year, although the blocks indicate a marked periodicity in abundance.

Another common and conspicuous alga, sometimes becoming an inch thick and six inches or more in diameter is Hydroclathrus clathrus. This flourishes on the blocks especially from March to June.

The tubular Scytophron lomentaria is also very common. Small plants are abundant in January and February, and these may reach the length of a foot or more early in May. Reproduction evidently occurs throughout the year. The young plants may reach a length of 35 mm. within four weeks.

The lovely red Heterophyton verticellata was present at all seasons of the year but only relatively small plants were found on any of the blocks.

The delicate branching coralline (Corallina gracilis, or C. cuvieri, var. caliptera) occurred in great abundance on some of the blocks which were in the water during the warmer months of the year. It covers large areas on the adjacent rocks.

Among the other algal growths which were kindly identified by Professor W. L. Gardner, of the University of California, and Dr. E. M. Howe, of the New York Botanical Garden, are: Egregia laevigata, Gigantia spinosa, Colpomenia sinuosa, Itea Fascia, Hypnea sp. and two species of Ceramium.

DIATOMS

Growing upon the stems of hydroids, bryozoa, and algae, as well as upon the block itself, were innumerable diatoms belonging to a considerable number of species. These have not yet been studied. They show a marked periodicity in abundance, as Allen (1922) has reported for the plankton.

PROTOZOA

No attempt has been made to identify all the protozoa, but attention may be called to the presence of vast colonies of acetarians on the hydroid stems and to the abundance of foraminifera, especially from
June to October. Dr. Joseph A. Cushman kindly examined a single lot of the latter group collected during the month of August and found it to contain representatives of the following species:

- *Quinqueloculina Lamarckiana* d’Orbigny
- *Trioculina circularis* Bornemann
- *Trepostomphalus bulloides* (d’Orbigny)
- *Cornuspira involvens* Reuss
- *Patelloïda corrugata* Williamson f. juv.
- *Discorbis isabelleana* (d’Orbigny)
- *Planulina ornata* (d’Orbigny)
- *Globigerina conglomerata* Schwager.

Many additional species were undoubtedly present on other blocks.

**Sponges**

The simple calcareous sponge *Grantiæ* sp. was frequently found on blocks which had been placed in the water from June to September. Growth occurs throughout the winter and spring, but reproduction is limited to the warmer months of the year.

A white encrusting sponge may reach a diameter of six inches or more from the first week in September to the following July.

**Hydroids**

The most common species of hydroids have two seasons of maximum abundance each year, one being in April and the other in September and October. Although the colonies are present throughout the winter, multiplication and growth are most rapid in early spring, after which they mostly disappear, to return again in August and September.

*Obelia dichotoma* is more abundant on the blocks than is any other hydroid. In September and October it may constitute 90 per cent of the entire population, including both plants and animals. It is immediately attacked by nudibranch mollusks which browse upon it throughout the winter. By the end of March only the stalks of the hydroids remain in some cases, the heads having entirely disappeared. Such stalks are often thickly covered with minute suetorians. On adjacent blocks, however, the growth may continue during April and May.

*Plumularia setacea* is less abundant. It is found from September to the end of May. The ostrich-plume hydroid, *Aglaotheca struthioides* was found occasionally, as was also *Campanularia gelatinosa*. Other hydroids, as *Clytie* sp., *Orthopyx substratulata*, and *O. evera* grow abundantly upon the larger algae and upon the stems of *Obelia*. 
ANNELEDS

Various species of chaetopods appear upon the blocks as soon as the growths of algae and barnacles have become established. Some of these have kindly been identified by Prof. A. L. Treadwell, of Vassar College.

Several species build tubes directly upon the wood or concrete block but appear to select in preference the shells of oysters, scallops, or barnacles if any are present. Individuals of other species move about freely or conceal themselves beneath the other growths.

The most abundant of the tube builders is *Eupomatus gracilis*, the calcareous tubes of which twist about irregularly, as shown in figures 21 and 22, plate 3; in figures 31, 32, 35, plate 4; and in figures 47a, 48, 49, plate 5. *Serpula columbiana* has similar habits, and a species of *Spirorbis* is found occasionally. The U-shaped, parchment-like tubes of *Chaetopterus* sometimes reach a large size.

Another annelid, *Branchiomma disparoculatum*, frequently lives among colonies of barnacles and oysters, constructing its tubes of sand particles cemented together by a firm mucous secretion.

Whenever Ectocarpus has attained a considerable growth upon any of the blocks, the nest-building *Nereis agassizi* is always present. This annelid binds the algae into tubular nests, within which it is well protected from its enemies. The worms are gregarious and are sometimes present in such numbers as to mat together the entire growth of algae into an irregular mass of twisted tubes. Large worms are always associated with a heavy growth of the algae, but there is doubtless free migration between the block and the adjacent pier. If removed from its tube the worm can form a new one within a few minutes by the secretion of the numerous glands in its parapodia. If no algae are available, bits of sand and shells are utilized, and if the worm is placed in a glass of clean water its tube consists of firm, translucent secretion only. The young worms appear on the blocks in great numbers in late winter and early spring and again in August.

Young individuals of two other species of the same genus, *Nereis latecens* and *N. vezilosa*, appear in considerable numbers as soon as the other growths have become established upon the blocks. Both species, but especially the latter, are very abundant on the adjacent piles. The scaly annelid *Halosydna brevisetosa* conceals itself beneath tufts of bryozoa.
Bryozoa

Growing abundantly on all of the blocks which have been in the water for a few weeks during the warmer months of the year are the mosslike colonies of several species of bryozoa. On the same blocks other species will frequently be found which form encrusting sheets of calcareous materials, covering particularly the shells of such bivalves or barnacles as may be present, and occurring commonly upon the larger algae.

Not only are the colonies of bryozoa abundant but the species are numerous, and not all of those found on the blocks have been identified. It is probable that some of them are as yet undescribed. Not infrequently as many as six or more species have been found upon a single block. Dr. R. S. Bassler of the U. S. National Museum, has kindly assisted in the identification of a considerable part of the collection.

New colonies of some of the species may be established at any time between April and November, while other forms multiply only during the summer. As a general rule, however, the new colonies make their appearance rather late in the spring, after the hydroids and algae have begun to decline.

As soon as the oysters, scallops, and barnacles have formed shells of sufficient size, the bryozoa use these as the most suitable places for attachment. Since the bryozoa grow more rapidly than do their hosts the latter are frequently completely obscured and sometimes smothered by them. In all cases there is competition for the minute organisms which all of them use for food, so that the bryozoa may greatly interfere with the nutrition as well as with the respiration of their hosts.

Bugula neritina is the most abundant of all the bryozoa found in the neighborhood of the Scripps Institution, and it occurs on all the blocks set from April to October or November. When established in the autumn, the colonies increase in size during the winter and multiply rapidly in the early spring. It is absent only from the blocks exposed to the full force of the surf, and sometimes constitutes fully 50 per cent of the total animal life on the block. On blocks set in September the reddish brown or purple, mosslike colonies may reach a height of 40 mm. within three months. The following spring, some of the large bushy tufts may be nearly double this height. Bugula eburnea has similar habits.

During the warmer months of the year the growth and reproduction of the Bugula colonies are very rapid, as Grave (1930) has recently shown to be the case with B. flabellata on the Atlantic coast.
Within three weeks after the attachment of the larva the colony of *B. noritina* may reach a height of 8 mm., with 8 branches and more than 50 zooids. At the age of six weeks some of the colonies are 12 mm. in height, with 32 to 64 dichotomous branches and about 300 zooids. Two weeks later a colony may have more than 200 branches. Sexual reproduction begins at the age of six to eight weeks, with three or four complete generations each year.

One colony at the age of only four weeks had reached a height of 15 mm. and consisted of 72 branches, with nearly 500 zooids. This remarkable growth occurred on a new cement block during the period between June 9 and July 7. But none of the other colonies on this block had more than 32 branches.

Another very common species is *Crissa pacifica*; the erect, calcareous tufts of numerous colonies sometimes cover the greater part of the block and grow in such luxuriance on the oysters, scallops, and barnacles as to completely obscure them. *Crissa pacifica* and *C. franciscana* are also abundant and of similar habit.

A closely related form, *Crissetia occidentalis*, is occasionally abundant during the summer and autumn, as are also *Cellaria diffusa* and *C. mandibulata*. The prostrate tufts of *Menippe occidentalis* and *Scurpocellaria diogenes* are also frequently plentiful, while *Eucratea chetata* is found occasionally. *Zoobotryon pellucidus* often appears in midsummer.

The calcareous encrusting forms, *Membranipora membranacea* and *M. tehuelcha* spread over the other animals and plants previously established on the blocks and not infrequently destroy them either by suffocation or by adding so greatly to their weight as to loosen them from their attachments. The circular patches of *Hippothoa hylina* are often found on the shells of oysters and upon the larger algae, as well as on the block itself. *Thalmaparella rosier californiensis*, *Smittia roticulata*, and *S. colisfera* are other encrusting forms, sometimes associated with the delicate *Lichenopora radiata*.

**Mollusks**

**The Oyster**

The Pacific coast oyster (*Ostrea lurida*) is found on the supports of the Scripps Institution pier, as well as on some of the rocks in the vicinity. Consequently, the larvae of these sedentary mollusks attach themselves upon the experimental blocks during all the warmer months of the year (Coe, 1930).

The reproductive period extends through seven or more months of the year at La Jolla, for the recently attached young appear on the blocks early in April, when the temperature of the water has
reached about 16° C, and they are present as well on those which are set as late as October (fig. A). Although seldom found on blocks set in November, the water temperature is higher during that month than in April, so that the spawning season may extend into November in some years.

The oyster grows very rapidly during the warmer months of the year, as is shown by the fact that the young which settle upon the blocks in April become sexually mature in August and September of the same year, at the age of about five months. Those which become attached in August may have ripe gonads the following February, although spawning is usually delayed until April. A length of 10 to 16 mm. may be reached in eight weeks during midsummer and 30–37 mm. in sixteen weeks.

On the coast of British Columbia spawning takes place during July and August (Stafford, 1913); some of the young oysters reaching a length of 6 mm. early in August and 20 mm. by the middle of September. Galtsoff (1929) found the spat at Willapa Bay, Washington, to be about 15 mm. long in October, while at the mouth of the Nasel River the length was only 6 to 9 mm. at the same date.

Perhaps it should be mentioned in this connection that *O. lurida*, like the European oyster, but unlike the species on the Atlantic coast of the United States, is hermaphroditic and regularly protandric. The eggs are fertilized within the mantle cavity of the parent, and there the larvae develop until the young mollusks have completed their transformations and have secreted delicate bivalve shells. These young oysters are then discharged from the body and after floating in the water for a brief period attach themselves to any solid objects with which they come in contact (Stafford, 1913; Galtsoff, 1929).

The height of the spawning season at La Jolla extends through June, July, and August; there may be several spawning periods for each individual participating. All individuals appear to function as males at the beginning of their reproductive cycle. After the discharge of the sperm a large number of eggs ripen and are set free into the mantle cavity, where they are fertilized by sperm from the same or other individuals. After reaching the bivalve condition the young spat leave the parent's body, whereupon the parent reassumes the male phase of sexuality. Sometimes this second male phase is postponed until after a second ovulation has taken place (Coe, 1931). Occasionally a succeeding crop of eggs appears before all the young have left, and in such cases the mantle cavity may contain embryos as well as bivalve young.

The accompanying table 2 indicates the rates of growth at different seasons during the year. It should be emphasized, however, that the
periods under the heading "Date" represent the time between setting the block and collecting the material. The actual period of growth will be consequently somewhat less than the time in weeks as stated, depending on the length of time which may have elapsed after the block was set in the water and before the attachment of the first individuals which remained when the block was examined. On the block set March 3, for example, it is improbable that any attachment of oysters occurred for at least five weeks. Data from blocks on which attachment was obviously long delayed are not included, nor are the smaller and presumably younger individuals found with those that have evidently had a period of growth approximating the entire time that the block was in the water.

The data have also been compiled in the graph shown in figure A. Each curve of growth is plotted either from the four faces of one block or from two or more blocks set at the same time. Hence, each curve is composite, the segments being compiled separately from the larger individuals of a single collection. Since the numbers are small no attempt has been made to plot the normal curve of growth.

GROWTH ON BLOCKS PLACED IN THE WATER DURING MARCH, APRIL, AND MAY

The young oysters are seldom found on the blocks earlier than April. By the end of that month the shells have reached a length of 2 to 3 mm., and by the middle of May, 5 mm. As the temperature of the water rises in June and July, the growth rate is accelerated. By the end of August the largest individuals of this first spring set measure 25 to 33 mm. in length and the animals are approaching sexual maturity at an age of approximately four and one-half months (fig. A; table 2).

Spawning by well-nourished individuals of this set may take place during September and October, when the shell has reached a length of 30 to 40 mm. (Plate 5, figs. 48, 49, 49a, 49b). The young of the second generation, if spawned in September, may become sexually mature during the winter and will be ready to spawn in May. Two generations may thus be possible within a year, but such an occurrence is probably limited to a very small proportion of the population. As a rule, the young of one summer shed their first crop of sperm-balls early the following spring and later spawn as females. It is only the first broods in the spring that become sexually mature and spawn before the close of the breeding season in the autumn, and then only when the environmental conditions are favorable.
### Table 2

**Rate of Growth of Ostrea lurida**

<table>
<thead>
<tr>
<th>Date</th>
<th>Weeks</th>
<th>Length, mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1930</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 3 to April</td>
<td>28</td>
<td>8 (3)</td>
</tr>
<tr>
<td>March 3 to May</td>
<td>12</td>
<td>10 (5)</td>
</tr>
<tr>
<td>March 3 to July</td>
<td>25</td>
<td>21 (10)</td>
</tr>
<tr>
<td><strong>1929</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1 to August</td>
<td>30</td>
<td>30 (21)</td>
</tr>
<tr>
<td>April 26 to October</td>
<td>4</td>
<td>23</td>
</tr>
<tr>
<td>May 15 to October</td>
<td>25</td>
<td>23</td>
</tr>
<tr>
<td><strong>1930</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 9 to July</td>
<td>28</td>
<td>7</td>
</tr>
<tr>
<td>June 9 to August</td>
<td>40</td>
<td>8</td>
</tr>
<tr>
<td>June 9 to August</td>
<td>25</td>
<td>11</td>
</tr>
<tr>
<td><strong>1930</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 7 to August</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>July 7 to August</td>
<td>11</td>
<td>5</td>
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<tr>
<td>July 7 to August</td>
<td>25</td>
<td>7</td>
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<td>July 7 to September 1</td>
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<td>8</td>
</tr>
<tr>
<td>July 7 to September 15</td>
<td>10</td>
<td>10-12</td>
</tr>
<tr>
<td>July 7 to September 23</td>
<td>12</td>
<td>15-20</td>
</tr>
<tr>
<td>July 7 to October 27</td>
<td>16</td>
<td>25-41*</td>
</tr>
<tr>
<td><strong>1930</strong></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>4</td>
<td>4</td>
</tr>
<tr>
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<td>August 4 to February 16</td>
<td>28</td>
<td>25-41*</td>
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<td><strong>1927</strong></td>
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<td></td>
</tr>
<tr>
<td>September 6 to November 15</td>
<td>10</td>
<td>2-3</td>
</tr>
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<td>14</td>
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<td>20-25</td>
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<tr>
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<td>30-35*</td>
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</tr>
<tr>
<td>September 6 to May 30</td>
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</tr>
<tr>
<td>September 6 to June 14</td>
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</tr>
<tr>
<td>September 6 to July 12</td>
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<td>35-46*</td>
</tr>
<tr>
<td><strong>1927</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>October 4 to November 15</td>
<td>6</td>
<td>3-4</td>
</tr>
<tr>
<td><strong>1926</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>October 8 to June 26</td>
<td>37</td>
<td>30-45*</td>
</tr>
</tbody>
</table>

* Sexually mature
GROWTH ON BLOCKS PLACED IN THE WATER FROM JUNE TO OCTOBER

The young spat which settle upon the blocks in early summer grow much more rapidly than those of earlier or later spawnings, as shown in figure A and by the photographs on plate 6 (figs. 50–53). Figures 19–27, plate 8, represent in natural size the growth of spat attached to blocks which were placed in the water September 6, 1927. During the autumn and winter the rate of growth is relatively slow, but as the water becomes warmer growth is accelerated and by the middle of May the largest shells are 35 to 38 mm. long and 30 mm. wide (fig. 24), and the animals have become sexually mature. During the spawning season, which continues during June, July, and August, there is but little increase in size, for the nutritive materials are used mainly for the elaboration of the sexual products, and not for growth (table 2).

Figures 25, 25a, and 25b show some of the variations in shape which the oysters on a single block may assume. After the first of June the shells become densely covered with growths of encrusting organisms (fig. 26) and these doubtless interfere considerably with the oysters’ supply of food and oxygen. Barnacles, bryozoans, sponges, ascidians, and hydroids may thus compete with the oysters for the minute organisms which constitute the food of all. Growth and reproduction may thereby be inhibited for a long period and in extreme cases the death of the oyster or of its parasites, or of both, may follow.

The largest individual found on any of the blocks measured 53 mm. in length and 38 mm. in width. This was only 31 weeks of age. Although it is known that some individuals live to be several years old, there is evidently only a very slow increment of growth after the first year, for but few of the individuals living naturally on the supports of the pier are larger than those found on the experimental blocks at the age of 8 to 10 months. Specimens up to 60 mm., or even 70 mm., in length, however, have been recorded from other localities.

Examination of large individuals at the end of February, and, hence, shortly before the earliest spawning, shows all three types of sexuality: (a) those which are predominantly female, with apparently ripe ova and few, if any, sperm-balls; (b) males filled with spermatids and ripe spermatozoa but no large ova; (c) hermaphrodites, with varying proportions of follicles containing both large ova and spermatids.

In case the male phase is completed during the autumn of the oyster’s first year the animal will function as a female at the beginning of the following season. Other individuals are then in the male phase. Such irregularities in the sex physiology, associated with several
successive spawnings during the reproductive season, will account for
the presence of the young spat in the water through seven or more
months of the year. The interpolation of a partial or complete second
generation also aids in extending the spawning season.

Fig. A. Graph to show rate of growth of Ostrea lurida on blocks placed in
the water at different seasons of the year. The ordinates represent length of
shell. Comparison with the temperature curve indicates that no attachment
occurred while the water was below 10°.

SEQUENCE OF SEXUAL PHASES

Examination of microscopic sections of more than two hundred
oysters of known ages shows that there is a rhythmical sequence of
female and male phases, following an initial male phase. Due to the
long seasonal reproductive period and the consequent overlapping of
generations, animals in all sexual phases are found in the population
at all seasons of the year.
The length of any sexual phase may be greatly prolonged by low
temperature and other environmental conditions, for any phase may be
interrupted in the autumn by the lowering of the water temperature
to the critical point of about 16°, the animal remaining through the
winter in the incompletely phase. When the temperature again becomes
suitable the following spring the interrupted phase is completed and
the succeeding phases follow (Coe, 1931).

At the end of the seasonal reproductive period of each animal the
body is soft and watery, and the visceral mass, which was previously
plump and firm and of a pale yellowish color, now becomes thin,
flabby, and translucent.

THE BROAD-EARED SCALLOP

Although capable of moving about from place to place occasionally,
and therefore not strictly a sedentary animal, one of the species of
Peeten (P. latiauritus) occurs so frequently upon the experimental
blocks that it should be included among the regular inhabitants. It
was represented in about half of the entire number of collections from
blocks that had been in the water six weeks or more. The foot of the
scallop is evidently able to find a secure attachment only on those
blocks which are covered with a growth of other organisms, such as
barnacles, oysters, and bryozoa, all of which are fastened to the blocks
by secretions.

Sometimes only a few specimens were present, more often from
ten to twenty; in one case about fifty and in another case more than
a hundred individuals were found on the 66 square inches composing
one face of a block. The species is abundant on the adjacent piles, and
from this stock the blocks are presumably supplied.

In spite of this tendency to migrate, the rate of growth throughout
the year may be determined with some accuracy by comparing the
collections made in successive months as indicated in table 3. The
youngest stages, measuring only 1½ to 2 mm. in greatest diameter
appear on the blocks from July to October, while the fully mature
individuals are found from May to August, after which the adult
animals disappear from the blocks to spawn in other situations.

The sequence of the growth stages is shown by the photographs in
natural size on plate 4. In each group are shown both the smallest
and the largest individuals from the same block. All are from blocks
placed in the water during the first week in September.

After the middle of May (36 weeks) the sexual products in the
larger individuals are in process of formation and further growth is
arrested. Incrustations of barnacles, bryozoa, and annelid tubes now
thickly cover the upper valve of the shell (fig. 36) and doubtless hamper the animal’s activities.

On plate 5 are shown certain growth stages which appeared on blocks set at various periods of the year. These agree rather closely with those described above for corresponding seasons, but with some interesting deviations. Attached to a block which was in the water from January 10 to February 22 were the specimens shown in figure 43. These are of about the same size as the small individuals shown in figure 30, proving that migration occurs even in midwinter. The shells shown in figures 44 and 45 are from blocks set in February, the former collected at the end of that month, and the latter early in May. These likewise prove the migratory tendency of immature individuals.

**TABLE 3**

**RACE OF GROWTH OF PROTEUS LATIURUS**

<table>
<thead>
<tr>
<th>Date</th>
<th>Weeks</th>
<th>Diameter, mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1927</td>
<td></td>
<td></td>
</tr>
<tr>
<td>September 6 to November 15</td>
<td>10</td>
<td>2-5</td>
</tr>
<tr>
<td>September 6 to December 13</td>
<td>14</td>
<td>10-12</td>
</tr>
<tr>
<td>September 6 to February 8</td>
<td>22</td>
<td>16-20</td>
</tr>
<tr>
<td>September 6 to March 6</td>
<td>26</td>
<td>25-28</td>
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<tr>
<td>September 6 to May</td>
<td>34</td>
<td>25-28</td>
</tr>
<tr>
<td>September 6 to May</td>
<td>36</td>
<td>25-28</td>
</tr>
<tr>
<td>September 6 to May</td>
<td>38</td>
<td>25-28*</td>
</tr>
<tr>
<td>September 6 to June</td>
<td>40</td>
<td>25-28*</td>
</tr>
<tr>
<td>October 8 to June</td>
<td>37</td>
<td>25-32*</td>
</tr>
</tbody>
</table>

* Sexually mature.

The evidence from these observations indicates for this species an annual cycle, the age at which sexual maturity occurs in well nourished individuals being nine to twelve months. Migration from place to place presumably occurs at all seasons of the year, perhaps frequently. The animals’ hold on the wooden block is so insecure that some of the shells are doubtless washed off in every storm, to be replaced by others from the neighboring pier. It is thus uncertain whether any individual remains for more than a few days or a few weeks in the same situation.

**MUSSELS**

Of the several species of mussels occurring on the coast of California, only the two edible species, *Mytilus edulis* and *M. californianus*, have been found upon the experimental blocks. Although these species form enormously thick growths on the neighboring piles, only
a few individuals of the former species (pl. 5, figs. 39–41) and only
two of the latter (figs. 37, 38) were found attached to the blocks. The
smooth surface evidently does not afford a suitable attachment for the
byssus of the young mollusks, for the water is often swarming with
the free-swimming larvae of both species during the warmer months
of the year. The two species live closely associated upon the supports
of the pier, but no very young individuals of either species were found,
and data can be given as to the rate of growth only within certain
limits.

Plate 5 illustrates some of the individuals found on blocks which
were placed in the water in September and October and remained
submerged over the winter. Figure 37 shows that attachment of M.
californianus takes place at least as late as October 8 and that the
young mollusk may attain a length of at least 30 mm. during the ensu-
ing nine months. In figure 38, from a block set about a month earlier,
a slightly larger size is attained by the end of May.

Measurements by Richards (1928) of nearly 1200 specimens taken
from a restricted area in Monterey Bay indicate an average length of
40 mm. at the end of the first year and 80 mm. at the age of two years.

Mytilus edulis found attachment on only two of the blocks, both of
which had been in the water from early September to June and
July. The smallest of the nine specimens was about 7 mm. in length
and the largest 16 mm. (figs. 39, 40, 41). This would indicate an age
of between two and four months, as Field (1922) has shown that on
the southern coast of Massachusetts the young of this species may
reach a length of 18 mm. within four months. It may, therefore, be
assumed that the individuals found on the blocks attached themselves
in early spring, although the blocks had been in the water since the
preceding September. At the time of attachment the blocks were
already provided with heavy growths of oysters, barnacles, and bryoz-
zoa, among which the young mussels could find suitable places for
fastening the byssus.

OTHER MOLLUSKS

Saxicava pholadis.—This pretty pink, red, or reddish-brown bivalve
occurs abundantly during the summer on blocks which are already
covered with a growth of other organisms.

Botula (Adula) diegensis.—A few individuals of this "pea-pod"
mollusk (figs. 39a, 41a) were found on blocks which had been in the
water from September until the following summer.

Nudibranchs.—Any account of the sequence of life upon the
experimental blocks would be incomplete without mention of the nudi-
branchs which are invariably present when the hydroid colonies are
flourishing. Several species of these beautifully colored mollusks browse among the hydroids, devouring the zooids. Flabellina iodinea, beautifully and contrastingly colored with orange and violet, is one of the most common species.

Vermetids.—The scaly worm-mollusk, Aletes squamigerus, frequently becomes established on the shells of oysters and barnacles during midsummer.

Pecten circularis var. acquisulatus and Crucibulum spinosum are found occasionally.

CRUSTACEA
BARNACLES

Of the many species of animals which attached themselves to the experimental blocks the most numerous and frequently the most conspicuous were the barnacles. Several species of these crustaceans occur abundantly upon the rocks of the adjacent seashore, but only one of them, the California striped barnacle (Balanus tintinnabulum californicus), is commonly found attached to the blocks.

Successively submerged blocks show that the free-swimming stages of this species are present in the water during almost the entire year, for the young barnacles first attached themselves to the blocks as early as the middle of February (in 1931), and they continued to arrive until near the end of December in other years. Developing embryos are found in the brood pouches of some of the adult animals at all times of the year. The fact that no new set appeared on the blocks in January does not indicate that the larvae were not then present in small numbers, for they would have found a more protected refuge in the interstices among the larger growths upon the adjacent piles. Moreover, the area of the block is relatively minute as compared with other equally suitable places for attachment.

This species of barnacle appears to have a critical temperature of about 16° C, below which spawning is inhibited (fig. B). A temporary warm period may in some years induce a limited amount of spawning a month or more before the seasonal mean of 16° is reached.

During the warmer months of the year the young barnacles, when not overcrowded, increase in size with greater rapidity, as shown in table 4 and figure B. Sexual maturity may occur in less than three months after attachment and developing larvae may be found in the brood pouch a few days later. Two complete generations may thus occur in one calendar year. The rapidity of their growth during successive weeks of their first year is shown by the photographs on plates 1, 2, and 6.
<table>
<thead>
<tr>
<th>Date</th>
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<th>Diameter, mm.</th>
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<tbody>
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<td>April 14 to April</td>
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<td>May 18 to June</td>
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<tr>
<td>1930</td>
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<td></td>
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<tr>
<td>June 9 to June</td>
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<td>3</td>
</tr>
<tr>
<td>June 9 to July</td>
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<td>June 9 to August</td>
<td>25</td>
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<td>1930</td>
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<td>July 7 to July</td>
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<tr>
<td>July 7 to August</td>
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<td>40</td>
</tr>
<tr>
<td>September 6 to July</td>
<td>12</td>
<td>44</td>
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</table>

* Sexually mature; eggs or embryos in brood chamber. † All dead.
TABLE 4—(Concluded)

<table>
<thead>
<tr>
<th>Date</th>
<th>Weeks</th>
<th>Diameter, mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>October 4 to November 15, 1927</td>
<td>6</td>
<td>3-4</td>
</tr>
<tr>
<td>October 8 to May, 1926</td>
<td>4</td>
<td>20-25*</td>
</tr>
<tr>
<td>October 8 to June, 1930</td>
<td>37</td>
<td>20-25*</td>
</tr>
<tr>
<td>October 27 to January, 1926</td>
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<td>10-12</td>
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<tr>
<td>November 24 to January, 1926</td>
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<td>5-8</td>
</tr>
<tr>
<td>November 24 to March, 1926</td>
<td>18</td>
<td>15-18*</td>
</tr>
<tr>
<td>December 10 to May, 1926</td>
<td>22</td>
<td>20-25*</td>
</tr>
<tr>
<td>December 10 to June, 1930</td>
<td>28</td>
<td>20-25*</td>
</tr>
<tr>
<td>December 22 to January, 1930</td>
<td>4</td>
<td>1-2</td>
</tr>
</tbody>
</table>

It should be remembered in this connection that the barnacle is hermaphroditic and apparently capable of self-fertilization. The fertilized eggs are retained within the brood pouch of the parent until they have completed their development to the free-swimming larval (nauplius) stage. These larvae are then discharged from the body and swim near the surface of the water until, after further transformations, they are ready for attachment to some solid object.

On blocks immersed early in the year the number of barnacles remains small until the middle of May (fig. C). Thereafter new arrivals appear in relatively vast numbers until the middle of July, when a rapid decrease occurs. After the individuals of the first set have reached a diameter of 5 to 10 mm, many of the later arrivals (fig. C) attach themselves at the summit of the rostrum of the older individuals in preference to the surface of the block itself. A circle of eight to twenty of these small barnacles may quickly form around the apex of each of the larger individuals (pl. 6, fig. 56, 56a).

The numerous young may thus seriously interfere with the growth of the original settlers by depriving the latter of sufficient food and oxygen. By the middle of summer the oldest individuals may be no larger than some of those which have grown as parasites upon them, if, indeed, they have not already been destroyed by starvation or suffocation.

Where favorably situated the first set reaches sexual maturity in July (fig. B). The size is then hardly more than 15 mm. in diameter and 15 to 20 mm. in height, although fully grown individuals on the neighboring piles may exceed 30 mm. in diameter. It is stated that individuals of this species may sometimes reach a diameter of 57 mm.
and a height of 34 mm., but such specimens are veritable giants as compared with young animals during their first spawning season.

During July and August the barnacles of this first set of the year are themselves discharging young. These pass through the free-swimming stages and become sexually mature in time to discharge their own young before the water has become cool enough to inhibit spawning in November and December. If conditions are somewhat less favorable the first young of this second generation may not be discharged until the following April.

Fig. B. Graph to show rate of growth of Balanus tintinnabulum californicus on blocks placed in the water at different seasons of the year. The ordinates represent diameter of shell at base.

Two complete generations may thus occur in a single year, and under very favorable conditions both generations may be completed within a period of less than nine months. But the numbers of larvae produced by these young animals are relatively small as compared with those of animals a year or more of age and of vastly greater size.

If attachment takes place in May or June, growth is even more rapid. Sexual maturity may occur within eleven weeks. In August the brood pouches of the more favorably situated individuals are filled
with developing embryos. The young of this later generation, after passing through the free-swimming stages, may reach sexual maturity during November and some of the individuals may, perhaps, begin spawning early in December. Presumably, however, the great majority of animals of this second generation retain their sexual products or their larvae until the following April or May.

Growth on Blocks Placed in the Water in July and August

During these months the water temperature averages above 20°, and the rate of growth is more rapid than at any other season of the year. An increase of more than 1 mm. per week in diameter is usual and those that are favorably situated may grow at twice that rate. Larvae from this crop will be spawned in October and may settle on the blocks in November (pl. 6, figs. 63-65).

It is not at all improbable that many of the barnacles which attach themselves during August and September represent the second generation of the crop which became attached in April and May. If the parent’s nutritive conditions are highly favorable there may be a rapid attainment of sexual maturity, but if the environmental factors are less suitable, increase in size is extremely slow and reproduction may be postponed indefinitely. It is because of the overlapping of the reproductive cycles of different individuals that the water surrounding a colony of these barnacles contains free-swimming larvae during most of the year.

Growth on Blocks Placed in the Water in September and October

Although growth is somewhat slower during the winter, sexual maturity is reached in March and April (fig. B, table 4). After completing the free-swimming stages the larvae will be ready to attach themselves to new blocks or other objects during May. A period of six to eight months is thus required for a complete winter generation as compared with three to four months for the summer life cycle. Two generations within twelve months are still possible however. The actual rate of growth during their first year is shown by the series of photographs on plate I.

Growth on Blocks Placed in the Water Later Than October

Many of the young barnacles which settle upon the blocks during November and December fail to survive. Those that are favorably situated, however, may reach maturity in time to spawn in April or May (pl. 2, figs. 14, 15; fig. B).
Relative Abundance of Young Barnacles at Different Seasons of the Year

The accompanying graph (fig. C) constructed from the data given in table 1, page 43, shows the relative frequency with which young barnacles attached themselves to cement blocks during the year 1930. It is seen that the height of the spawning season occurs toward the end of June and falls off rapidly after the end of July. Although all the curves are in essential agreement, the one for four weeks is obviously more reliable than the others, as the lag will be less than in those which were compiled from blocks which had been in the water for a longer period and, in consequence, carried barnacles of many different ages.

In making these computations all the barnacles were counted, not only those which were attached directly to the surface of the block but also those which were situated upon the shells of older individuals. On blocks which have been long in the water the latter may be several times as numerous as the former.

The maximum abundance in early summer is presumably explained not only as the result of the spawning of the young barnacles of the preceding summer and autumn but also of those much larger and vastly more prolific individuals which are two or more years of age. The relatively large number of young animals which spawn at a few months of age serves to keep a small supply of larvae in the water throughout the autumn.

The actual numbers found on both wood and cement blocks in 1930 are indicated in table 1, page 43. The first larvae in that year reached the blocks about the middle of April. Near the end of the month a mean total of 2.2 young barnacles per square inch of surface had settled upon a cement block while only about one-twentieth as many had succeeded in fastening themselves to the corresponding wood block. During the week from May 12 to 19 the numbers increased very rapidly, the new arrivals being more than twice as numerous as those which had attached themselves during the previous five weeks, and bringing the total up to 10.5 per square inch.

From the middle of May to the early part of July the rate of attachment reached its climax, a total of 53 per square inch being recorded for the four weeks ending May 26, 143 per square inch for the eight weeks ending June 23, 200 for the eight weeks preceding June 30, and 300 per square inch for the four weeks ending July 7. Thereafter the number of new arrivals decreased gradually to the end of August and rapidly during September and October. In November and the first half of December not more than 2 barnacles
per square inch have been found after an immersion period of four weeks.

The table shows that there is a curious consistency in the preference which the young barnacles show for the cement surface as contrasted with wood, although both blocks were placed in close proximity. It was noticed repeatedly that the areas near the edges of the wood block are chosen in preference to other parts of the surface.

Fig. C. Graph to show relative frequency with which young Balanus t. californicus attached themselves to cement blocks during the year 1930. The ordinates represent the mean number of barnacles found on each square inch of surface of one face of blocks which had been in the water for four, six, seven, and eight weeks. Comparison with the temperature curve shows that no attachment took place while the water was below 16°, but that the maximum abundance occurs more than a month previous to the highest temperature of the water.

Sometimes there are relatively more on the bottom than on any of the lateral faces. The enormous number of larvae which must be present in the water surrounding the pier during the height of the
spawning season is indicated by the fact that no less than 8400 small barnacles were found upon the 28 square inches of surface constituting one face of a cement block that had been in the water for the four weeks preceding July 7. About half of these had attached themselves directly upon the surface of the cement; an equal number, being later arrivals, had settled upon the shells of the others. In other words, an average of about 300 young barnacles had found this one small cement face for each day that it had been in the water.

Since only three or four barnacles can reach sexual maturity on any square inch of surface, the mortality after attachment must be very great. With 200 to 300 young per square inch, even if regularly spaced, the mortality due to overcrowding must approximate 98 to 99 per cent. The process of overcrowding and subsequent suffocation continues from day to day throughout the summer if the block remains in the water. New arrivals continually settle upon those already established, to become themselves parasitized by still younger ones. A small fraction of 1 per cent of these may reach sexual maturity, the others being gradually suffocated as layer after layer of young attach themselves to the few survivors.

Moreover, in competition with the barnacles for solid surfaces upon which to attach themselves are many other organisms, particularly oysters, mussels, scallops, bryozoa, sponges, hydroids, ascidians, and algae. All of these may appear in vast numbers at the time when the young barnacles are ready for attachment and any of them may avail themselves of the shells of barnacles already established, just as do the younger set of barnacles. The new arrivals then act as parasites in depriving the earlier settlers of food and oxygen. Growth is thereby retarded, sexual maturity delayed, and eventual starvation or suffocation may result.

The evidence thus indicates that in normal years a vessel in the vicinity of the Scripps Institution pier would receive the heaviest set of barnacles during the months of May to September inclusive, with a maximum in June and July, and a lighter set in April, October, November, and the first half of December. There would be very little infestation during the last half of December and the first half of April, and still less in the first three months of the calendar year.

OTHER CRUSTACEA

In addition to the barnacles, the blocks formed a suitable environment for great numbers of crustacean visitors. Copepods, amphipods, isopods, and true crabs were frequently met with, but only a few of these can be considered as permanent residents. The amphipod
Caprella scabra, however, swarmed upon all the blocks on which Ectocarpus was abundant. Several hundred have been collected from one side of a block. It is found throughout the year, but is most abundant from January to the end of May. From September to January or later the brood pouches are filled with embryos.

Of the isopods, only Synidotea harfordi can be listed as a regular visitant.

Ascidians

Three species of simple ascidians were found on the blocks. One of these, the sand-covered ascidian, Molgula verrucifera, is often very abundant. It frequently occurs in groups of a dozen or more individuals, wedged between and growing upon the oysters as well as between the colonies of bryozoa. Ascidia californica and Styela montereyensis are less common.

Appearing first as small, irregular, grayish-white patches, the common encrusting ascidian, Didemnum cornutum, is often seen on the shells of the oysters about the end of May. A month or two later these patches may have grown to a diameter of several inches, covering both oysters and barnacles, but often leaving openings through which these animals may secure their food and breathe. Distasia occidentalis was found to have similar habits. Botrylloides diegensis was found on several blocks in summer. Two other composite ascidians, identified as Amaroucius californicum and Euherdmanninia claviformis, likewise appear in early summer.

Conclusions

The foregoing sections of this report show that the principal growths upon the experimental blocks consist mainly of mixed populations of barnacles, oysters, bryozoa, algae, hydroids, scallops, ascidians, sponges, mussels, and annelids. In the fouling of vessels in the vicinity of La Jolla these would undoubtedly likewise be the principal organisms concerned, their importance in this respect being, presumably, in the order named.

A more or less distinctly marked seasonal periodicity is characteristic for each group of organisms and for each of the species within the group. But in general it is evident that the algae and the hydroids form the principal new growths during the cooler months of the year; all the others attach themselves to the blocks most abundantly or exclusively during the summer.
At no season of the year can an unpainted wood or cement surface be exposed beneath the surface of the water without having at least some of these groups of organisms implanted upon it within a few days. In heavy seas the young growths are easily dislodged, but after some of the organisms have secured a firm attachment they are almost immune to the effects of the surf. After the earliest growths have become well established, however, the later arrivals find secure places of attachment upon them or between them. Several successive layers of growing organisms may thus be built up within a few months, and these may include many different species of both plants and animals (pl. 1, figs. 10, 11, 12; pl. 3, figs. 26, 27; pl. 4, fig. 36; pl. 5, fig. 49).

It not infrequently happens that more individuals, even of a single species, attach themselves within a few days than can possibly find space for continued growth. This overcrowding forces an intense competition for the available food and oxygen, resulting in the suffocation or starvation of all except a minute fraction of the original population. As newcomers continue to arrive, they frequently attach themselves directly to the growths already present, eventually forming a superficial layer of living organisms upon the dead shells of the earlier settlers. Barnacles and oysters are thus destroyed in vast numbers.

Within a few months these successive growths may have formed a dense covering an inch or more in thickness, from which protrude bushy tufts of bryozoa, and streamers of algae, the latter often a foot or more in length. It is such irregular surfaces that result in the fouling of vessels.

Since some of these fouling organisms are in the water and ready for attachment at all seasons of the year in the vicinity of La Jolla, it follows that, unless preventive measures are undertaken, the surface of a vessel below the water line will promptly acquire a coating of the particular species which are reproducing at the time. If the season of reproduction is known for each of the organisms which form the thickest growth, and thereby cause the most serious trouble, the type of fouling for any period of the year can be predicted.

The following table indicates the principal reproductive season for each of these groups of organisms, although it is quite possible that in certain seasons, owing to variations in the temperature of the water, the limits may vary somewhat from those here given, which are based on the evidence obtained during the past four years. Nor is it improbable that a relatively few individuals in every year may extend their reproductive period beyond the limits here given. More detailed evidence concerning each species has been given on the preceding pages.
Reference to the above table will show that the only fouling organisms which are reproducing abundantly during the winter are various species of algae, hydroids, protozoa, and annelids. None of these, except some of the algae, grow to a size sufficient to cause serious trouble, and, in fact, a growth of Ectocarpus is desirable in that it retards the attachment of oysters and barnacles. Consequently no precautions against fouling need to be taken during the first three months of the calendar year.

At any time during the remainder of the year, however, the entire submerged surface, if unprotected, will be quickly covered with barnacles, oysters, and bryozoa, which cause the principal trouble, while from June to September the attachment of fouling organisms will be most abundant and of the greatest variety.

June is probably the month of maximum reproduction, for as a general rule the rate of reproduction for each species reaches its maximum rather rapidly after the beginning of the reproductive season and then slowly diminishes as the successive spawning periods of different individuals ensue.
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References to the literature pertaining to the biology and systematics of the various groups of invertebrates may be found in Johnson and Snook’s Seashore Animals of the Pacific Coast (Macmillan Co., 1927).
EXPLANATION OF PLATES
PLATE 1

Rate of growth of Balanus tianshanbulum californicus on blocks submerged September 6, 1927, with the exception of figure 8. Natural size.

Fig. 1. Size after 9 weeks; November 8.
Fig. 2. Size after 12 weeks; November 29.
Fig. 3. Size after 14 weeks; December 13.
Fig. 4. Size after 16 weeks; December 27.
Fig. 5. Size after 20 weeks; March 6.
Fig. 6. Size after 30 weeks; April 3.
Fig. 7.* Size after 34 weeks; May 1.
Fig. 8.† Size after 29½ weeks; May 4. Small individuals represent new set.
Fig. 9. Size after 36 weeks; May 15. Small individuals represent new set.
Fig. 10. Size after 38 weeks; May 30. Small individuals represent new set.
Fig. 11. Size after 40 weeks; June 14. Covered with new set and with bryozoa.
Fig. 12. Size after 44 weeks; July 12. Covered with encrusting organisms.

* Block set in unfavorable situation.
† Block submerged from October 8, 1926, to May 4, 1927.
PLATE 2

Rate of growth of Balanus tinctusbalbus californicus on submerged blocks. Natural size.

Fig. 13. February 8 to May 5, 1927; 12 weeks.
Fig. 14. December 10, 1926, to May 12, 1927; 22 weeks.
Fig. 15. December 10, 1926, to June 26, 1927; 28 weeks.
Fig. 16. October 8, 1926, to June 26, 1927; 37 weeks. Covered with incrustations of bryozoa and other organisms.
Fig. 17. April 26 to October 4, 1929; 23 weeks.
Fig. 18. May 15 to October 25, 1929; 23 weeks.
PLATE 3

Rate of growth of *Ostrea lurida* on blocks submerged September 6, 1927. Natural size.

Fig. 19. Size after 10 weeks; November 15.
Fig. 20. Size after 14 weeks; December 13.
Fig. 21. Size after 22 weeks; February 8.
Fig. 22. Size after 30 weeks; April 3.
Fig. 23. Size after 34 weeks; May 1.
Fig. 24. Size after 36 weeks; May 15.
Fig. 25. Size after 38 weeks; May 30.
Fig. 26. Size after 40 weeks; June 14. Covered with incrusting organisms.
Fig. 27. Size after 44 weeks; July 12.
PLATE 4

Rate of growth of *Pecten latiscutitus* on blocks submerged September 6, 1927. Natural size.

Fig. 28. Size after 10 weeks; November 15.
Fig. 29. Size after 14 weeks; December 13.
Fig. 30. Size after 22 weeks; February 8.
Fig. 31. Size after 26 weeks; March 6.
Fig. 32. Size after 30 weeks; April 3.
Fig. 33. Size after 34 weeks; May 1.
Fig. 34. Size after 36 weeks; May 15.
Fig. 35. Size after 38 weeks; May 30.
Fig. 36. Size after 40 weeks; June 14. Covered with bryozoa.
PLATE 5

Rate of growth of Mytilus californianus (figs. 37, 38), M. edulis (figs. 39–41), Patula diegensis (figs. 39a, 41a), Pecten lactarius (figs. 42–47), and Ostrea larida (figs. 48, 49) on submerged blocks. Natural size.

Fig. 37. October 8, 1926; to June 26, 1927; 37 weeks.
Fig. 38. September 6, 1927; to May 80, 1928; 38 weeks.
Figs. 39, 39a. September 6, 1927; to June 14, 1928; 40 weeks.
Fig. 40. September 6, 1927; to July 12, 1928; 44 weeks.
Figs. 41, 41a. September 6, 1927; to July 13, 1928; 44 weeks.
Fig. 42. October 4 to November 15, 1927; 8 weeks.
Fig. 43. January 10 to February 22, 1928; 6 weeks.
Fig. 44. February 1 to February 28, 1929; 4 weeks.
Fig. 45. February 8 to May 5, 1927; 12 weeks.
Fig. 46. October 8, 1926 to May 4, 1927; 30 weeks.
Fig. 47. October 8, 1926; to June 26, 1927; 37 weeks.
Fig. 48. April 26 to October 4, 1929; 23 weeks. Covered with barnacles and bryozoa.
Fig. 49. May 15 to October 25, 1929; 23 weeks.
PLATE 6

Rate of growth of *Ostrea lurida* (figs. 50–53) and *Balanus tinctinabulum californicus* (figs. 54–65) at different seasons of the year.

Fig. 50. June 9 to July 23; 7 weeks.
Fig. 51. June 9 to August 4; 8 weeks.
Fig. 52. June 9 to August 25; 11 weeks.
Fig. 53. July 7 to September 20; 12 weeks.
Fig. 54. March 3 to April 25; 8 weeks.
Fig. 55. March 3 to May 12; 10 weeks.
Fig. 56. March 3 to May 19; 11 weeks. Each large individual has a crown of smaller barnacles.
Fig. 57. May 18 to June 30; 6 weeks.
Fig. 58. June 9 to June 30; 3 weeks.
Fig. 59. June 9 to July 7; 4 weeks.
Fig. 60. June 9 to July 23; 7 weeks.
Fig. 61. June 9 to August 4; 8 weeks.
Fig. 62. June 9 to August 25; 11 weeks.
Fig. 63. August 4 to September 20; 8 weeks.
Fig. 64. August 25 to September 20; 5 weeks.
Fig. 65. August 25 to October 29; 65 days. These were sexually mature, some of them having the brood chamber already filled with young embryos.