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ABUNDANCE AND GROWTH OF *Venus mercenaria* AND *Callocardia morrhuana* IN RELATION TO THE CHARACTER OF BOTTOM SEDIMENTS

BY

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ABSTRACT

The distribution patterns of *Venus mercenaria* and *Callocardia morrhuana* in Narragansett Bay are shown to be related to the character of the bottom. *Venus* is most abundant where the dominant sediments are fine, but its abundance in these sediments is strongly related to the presence of large particles such as shell and rocks as minor constituents of the substratum. The numbers of *Callocardia* are consistently correlated with the fineness of bottom sediments. A theory is advanced to explain these distribution patterns in terms of bottom current velocities, in so far as these velocities can be inferred from sediment particle sizes. It has been shown that the growth rate of *Venus* depends directly or indirectly on the nature of the substratum; populations living in sand grew 24% faster than did those living in an adjacent plot of sandy mud containing much organic matter.

INTRODUCTION

The quahog, *Venus mercenaria* L., is one of the most widely distributed and successfully adapted species of bivalves on the Atlantic Coast. In spite of a heavy fishery, it is abundant from the Gulf of St. Lawrence to the Gulf of Mexico, and it probably owes its continued success in part to a high tolerance for variations in such ecological factors as temperature, salinity and type of substratum. Its occurrence in a wide variety of substrata suggests that it is equally well adapted to several bottom types, and perhaps it is this apparent lack of preference which has led us to overlook the possible influences of sediment type on the biology of the species. There appear to be no published quantitative statements that relate the abundance or growth rate of *Venus* to the character of the bottom.

A dredging survey of Narragansett Bay has shown that the quahog is the most abundant animal of its size in or on the bottom in the estuarine waters of Rhode Island. In certain areas it is replaced by another bivalve, *Callocardia (Pitar) morrhuana* (Lindsley). The distribution patterns of these two species appear to be strongly related

1 Contribution No. 5 from the Narragansett Marine Laboratory.
to the nature of the bottom sediments. Furthermore, the results of an experiment in which quahogs were grown in different bottom types indicate that the character of the substratum materially affects the growth rate of *Venus*.

**ABUNDANCE OF *VENUS* AND *CALLOCARDIA* IN RELATION TO BOTTOM SEDIMENT TYPES**

An approximately quantitative survey of the quahog populations in Narragansett Bay was conducted in 1949 and 1950. At 123 stations based on a grid of one-mile interval, samples were taken by the 37-foot dragger *Lil-Joy* and a commercial quahog dredge of the Fall River type. The dredge was provided with removable lead weights so that its total weight could be adjusted to approximately 200, 250 or 300 pounds, depending on the hardness of the bottom. Eight 7-inch teeth were so set that they cut a swath approximately 14 inches wide. The dredge was lowered and raised on the vessel’s winch wire, but the actual towing was done on a one-inch manila line. The elasticity of the rope enhanced the efficiency of the drag. For this work, the chain-link bag which caught and sifted the material dredged by the teeth was lined with a twine bag of such a mesh that a quahog 36 by 31 mm could barely be forced through it. Drags were standardized to four minutes at a fixed setting of the vessel’s throttle which gave a speed of approximately three knots. The skilled assistance of Captain R. E. Sutcliffe throughout this work is gratefully acknowledged.

There are three disadvantages to this dredge as a sampling device. (1) In this and similar dredges (as opposed to grabs) the spatial relationships between different materials sampled are destroyed by thorough mixing; that is, two or more strata of different sediments are so mixed that they lose their identities. (2) Where there are insufficient amounts of cohesive materials, such as clay or organic silt, fine particles are washed out and hence the sediment sample obtained is not representative. Fortunately, in most parts of Narragansett Bay the dominant sediment is a mud high in organic content. From such bottoms the dredge always recovered large sediment samples (usually more than a bushel) in which the minor constituents such as sand and shell fragments were retained. It is believed that relatively few of the samples collected in this survey suffered serious alteration through washing. (3) Its efficiency is reduced on rocky bottoms, where the dredge digs and bounces, as evidenced by the alternate straining and relaxation of the towline. Thus the amount of material dug and passed through the bag is relatively less than that taken in a normal drag on soft bottom. This last drawback is more serious than
the first two in that it concerns the reliability of sampling objects (such as adult quahogs) which are theoretically large enough to be captured quantitatively.

However, this type of dredge is advantageous in that it is possible to secure a large sample of the bottom and its populations in a single operation. Experience of quahog fishermen has shown that the distribution of individuals in a bed is spotty, the numbers often varying greatly from one square yard to the next; hence a large number of grab samples is required to make an adequate census. In the dredge sample this unevenness is averaged out. Thus, in spite of its failings, the dredge appears to be especially suited to rapid and approximately quantitative quahog sampling in an extensive area such as Narragansett Bay. Repeated sampling at various localities has produced consistent results; except where rocks were numerous, the dredge sample gave a reliable index (if not an absolute census) of the relative concentration of quahogs.

The character of the bottom was judged by gross inspection of the dredged material. Five types were distinguished by appearance and feel: clay, mud, sand, shell, and rocks, the last defined as stones bigger than a man's fist. A description of the bottom at each station consisted primarily of one of these, usually with one or more additional materials as minor constituents. Although no quantitative measurements were made of particle size distribution, it is felt that the classification of the five sediment types is based upon differences which are readily appreciable without refined means of measurement. The distinction between clay and mud may be questionable. The term "clay," rarely used, was applied only to decidedly plastic matter. A proper sedimentological study of the area would likely reveal considerably greater amounts of clay, particularly as a minor constituent.

_Venus mercenaria_

This survey showed that the main centers of quahog abundance are concentrated in the inner (northern) areas of the Bay. No doubt its distribution reflects the influence of salinity (and possibly temperature) as well as several other factors, one of which appears to be the character of the bottom.

The average number of quahogs captured per standard drag in each of the types of bottoms sampled is given in Table I. In several cases the dragging time exceeded four minutes, and many of the stations were sampled more than once. In Table I all samples are reduced to numbers per four minute drag, and all drags at each station are averaged to give a single figure for the station. All told, approximately 9,000 quahogs were taken in the course of the survey.
Of the five types of bottom materials, only three occurred as major constituents: mud, sand and rocks. In Table I the quahog abundance is correlated with these three in the order just named: bottoms chiefly of mud yielded an average of 39 quahogs per four-minute drag; sand, 36; rocks, only 8. Due to the relatively inefficient operation of the dredge in rocky bottoms, it is probable that all of the figures given for quahog numbers in such locations are low. This conclusion is supported by the opinion, universal among local fishermen, that rocky areas, while difficult to work, are frequently rich in quahogs.

The data may also be used for a comparison of the average population density in bottoms containing each of the different sediment types, i.e. by calculating the average numbers in all bottoms that include clay, the average in bottoms containing mud, and so forth. This comparison (see Fig. 1) shows that, on the average, bottoms containing clay support the sparsest populations, those containing shell the densest populations, with mud and sand intermediate.

<table>
<thead>
<tr>
<th>Bottom Materials</th>
<th>Venus</th>
<th>Callocardia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean number</td>
<td>Mean number</td>
</tr>
<tr>
<td></td>
<td>per drag</td>
<td>per drag</td>
</tr>
<tr>
<td>MUD</td>
<td>39</td>
<td>13</td>
</tr>
<tr>
<td>sand</td>
<td>15</td>
<td>8</td>
</tr>
<tr>
<td>rocks</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>clay</td>
<td>2</td>
<td>45</td>
</tr>
<tr>
<td>shell</td>
<td>50</td>
<td>7</td>
</tr>
<tr>
<td>sand, rocks</td>
<td>16</td>
<td>6</td>
</tr>
<tr>
<td>sand, clay</td>
<td>14</td>
<td>5</td>
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<tr>
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<tr>
<td>rocks, shell</td>
<td>81</td>
<td>1</td>
</tr>
<tr>
<td>sand, rocks, clay</td>
<td>191</td>
<td>3</td>
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<tr>
<td>sand, rocks, shell</td>
<td>37</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>Mean 83</td>
<td>Total 68</td>
</tr>
<tr>
<td></td>
<td>Mean 39</td>
<td>Mean 14</td>
</tr>
</tbody>
</table>

| SAND             | 36       | Mean 4      |
| mud              | 4        |             |
| rocks            | 9        |             |
| shell            | 3         |             |
| mud, rocks       | 34       |             |
| mud, shell       | 52       |             |
| rocks, shell     | 2         |             |
| mud, rocks, shell| 129      |             |
| Total            | Mean 34  | Total 30    |
|                  | Mean 36  | Mean 4      |

| ROCKS            | 8        | Mean 2      |
| sand             | 0        |             |
| shell            | 1         |             |
| sand, shell      | 15       |             |
| Total            | Mean 6   | Total 6     |
|                  | Mean 8   | Mean 2      |

Grand Totals and Averages

123 Mean 36 104 Mean 11
again the average number given for bottoms that include rocks is probably low. "Shell" consists of fragments and whole shells of a number of mollusks including Crepidula, Anomia and Venus, as well as Ensis, Callocardia, Mya, Ostrea, and others. Although the quahog shells were outnumbered in most cases by those of other species, we have here a good example of an animal's presence altering the environment so as to render it more favorable to its progeny.
In a third comparison (Fig. 2), numbers of quahogs are correlated with the presence of clay, sand, shell and rocks as minor constituents of bottoms consisting mainly of mud. This figure closely resembles the preceding one because mud is the dominant sediment of the Bay, and the great majority of quahogs were taken from such bottoms. As noted above, bottoms with mud as the major constituent maintain, on an average, the densest populations. From Fig. 2, however, it is clear that the virtue of mud bottoms depends largely on sand and shell as
minor constituents, since mud alone appears to be a poor environment, scarcely better than mud + clay. Rocks might also prove to be a beneficial minor constituent of mud if truly representative samples could be dredged from areas containing them.

The abundance of quahogs is correlated with particle size of the bottom sediments in a consistent if somewhat complex fashion. Population density is negatively correlated with the particle size of the major bottom constituent: greatest average concentration in predominantly muddy grounds, less in sandy bottoms, and least in rocky areas—see Table I. However, when bottoms are classified on the basis of the inclusion of each of the five materials, as in Fig. 1 (in which sediment types are arranged in series from fine to coarse particles), quahog abundance increases with increasing particle size (again with the exception of rocks). The same relationship holds between population density and particle size of the minor constituents when bottoms consisting chiefly of mud are compared *inter se* (Fig. 2). To sum up, quahogs are most abundant in predominantly fine sediments, but in such sediments their abundance is generally a function of the coarseness of the minor constituents.

Whether this relationship of quahog numbers to sediment particle size results from an active selection of substratum by the settling larvae or from factors quite beyond their control is a question that cannot be answered from available information. However, an explanation of the observed distribution in terms of entirely passive behavior seems plausible. In the absence of current measurements along the bottom of Narragansett Bay, it is reasonable to assume that in general fine bottom sediments indicate low current velocities, coarser sediments progressively greater velocities. At any given locality the abundance of quahogs of the sizes sampled by the dredge must have been determined by the numbers of viable larvae which set and survived, and the speed of the bottom currents probably affected both setting and survival. Presumably a low current velocity favors setting, but it probably also results in three conditions adverse to survival: (1) rapid deposition of fine silt which may bury or smother the young set, (2) low rate of supply of food and oxygen, and (3) slow removal of metabolic wastes. On the other hand, a high current velocity probably allows only limited setting of the larvae and may cause a grinding action of coarse particles severe enough to injure the spat, but undoubtedly it favors survival by high rates of food and oxygen supply and waste removal.

If quahog distribution with reference to sediment types is related to these current effects, then current velocities which produce the optimal combined effect on setting and survival are somewhere in the
range of those that occur over predominantly muddy grounds. By comparison, currents which are fast enough to reduce setting and survival, particularly of the spat, occur over sandy areas and dominantly rocky bottoms.

Pursuing these ideas further, let us consider the varying abundance of quahogs in bottoms constituted primarily of mud. Theoretically, bottoms of mud + clay (followed in close sequence by mud alone) would be associated with minimal currents which contribute to heavy setting but low survival. Mud + sand would be related to somewhat faster currents whose combined effects should result in much denser populations. The presence of shell and rocks would indicate currents of sufficient speed to prevent the burial of these larger constituents by finer sediments. However, in such situations, where rocks and shells break the bottom surface to form pockets and hollows, small depressions probably result in very local but sharp reduction of the current velocity, thus assisting the deposition of larvae and affording protection against molar action. Shell and rocks would thus make it possible for quahogs to profit from the favorable effects of high current velocities while escaping their unfavorable effects.

Theoretically, by comparison with bottoms of mud only, one should expect to find greater average concentrations in each of the following types of mud bottom: (1) mud (major constituent) + sand (minor constituent), (2) mud + rocks, (3) mud + shell, (4) mud + sand and rocks, (5) mud + sand and shell, (6) mud + rocks and shell, and (7) mud + sand, rocks and shell. The data in Table I bear out these expectations, possibly with the exception of (2) and (4), in which the population densities are not as high as anticipated. However, failure to support the theory in these cases may have been due to the inadequacy of the dredge in rocky grounds. If mud + clay signifies slower currents than mud alone, one should expect quahogs to be scarcer in mud + clay. This is indeed the case. The combination of clay with any other minor constituent in mud gives contradictory indications of current velocity and cannot be interpreted according to the theory. Indeed, it is possible that clay has some special effect on quahogs that is not related to current speed—an effect on behavior such that spat avoid clay when setting, or a detrimental effect on postlarval survival.

Areas containing sand as a major sediment and mud as a minor constituent can be interpreted as indicating slower currents than those in areas containing only sand. If, as already assumed above, the optimal current velocities for the development of adult populations is of the order that results in predominantly muddy deposits, then sandy bottoms containing mud should be more suitable than those lacking mud. As in muddy bottoms, the presence of shell or rocks in
sandy bottoms should render the substratum more favorable for quahogs. Thus the addition of mud, shell or rocks should increase the average quahog capacity of sandy habitats. Table I shows seven types of sandy bottoms so modified, and in all but one (sand + rocks and shell) the expectations are confirmed. The interference of rocks in the operation of the dredge may account for the exception.

The data for quahog numbers in primarily rocky bottoms are too scanty to warrant analysis or interpretation according to current speed.

The attempt to relate quahog abundance to current velocity rests on the plausible assumption that current velocity is statistically related to sediment particle size. If we then take into account the fact that the population figures for bottoms containing rocks are probably erroneously low, the dual relationship of quahog numbers to sediment types can be explained to a large extent and in consistent detail on the basis of the combined effects of current velocity upon set and survival.

It should be noted that the highest mean concentrations of quahogs occur only in the presence of shell, usually accompanied by rocks. Provided that quahog abundance is truly related to current velocity as postulated, this fact would indicate that shell and rocks are indeed effective in inducing set and probably in affording protection to the young spat.

*Callocardia morrhua*

Early in this survey, *C. morrhua*, which closely resembles small specimens of *Venus*, attracted attention because of its abundance and distribution, which appeared to complement that of *Venus*. One or the other species was taken at all but 15 stations, usually in reciprocal numbers, which were clearly related to the character of the bottom.

The abundance of *Callocardia* with reference to sediment types has been analyzed in the same fashion as that of *Venus*, and the results are presented in Table I and Figs. 1 and 2. The information for this species is less complete than that for *Venus*, since no record of *Callocardia* numbers was kept in the early phase of the survey. The distribution of *Callocardia* is similar to that of *Venus* in two respects: (1) both species occur in greater average numbers in predominantly muddy bottoms than in sandy or rocky areas, and (2) where sand is the major constituent, the presence of mud favors both species. Here the resemblance in distribution ends. If the sediment type is judged on the basis of inclusion of each of the five bottom materials (Fig. 1), then *Callocardia* population density decreases steadily with increasing sediment particle size. Likewise, where the major bottom constituent is mud, *Callocardia* is progressively less abundant with increasing particle size of the minor constituents (Fig. 2).
Thus the abundance of *Callocardia* is consistently correlated with fineness of bottom sediments. If this distribution pattern is also interpreted on the basis of presumed current velocities, the data suggest that minimal currents produce the optimal effect upon set and survival of *Callocardia*. Under this interpretation it might be assumed that minimal currents result in maximal setting, that survival under these conditions is not reduced as in the case of *Venus*, and that faster currents with their attendant molar action do not result in greater survival of *Callocardia*, even when shell and rocks are present. According to this view, the observed differences in distribution between *Callocardia* and *Venus* result, at least in part, from such factors as: (1) differences in resistance to silting and low rates of food and oxygen supply in slow currents, and (2) differences in ability to withstand molar forces in faster currents.

However, factors other than current speed may well have been influential in bringing about the contrasting patterns of distribution. There may be differences in behavior of the larvae of the two species at the time of setting, including the active selection or avoidance of certain substrata because of textural or other qualities. This possibility seems particularly strong where clay is involved as a minor constituent of the bottom. It seems unlikely that the presence or absence of clay in predominantly muddy bottoms indicates significant differences in current velocities. For this reason the considerable effect which clay has on the relative numbers of the two species strongly suggests active selection by *Callocardia* and avoidance by *Venus* of substrata containing clay. For an excellent discussion and review of literature on the active selection of substrata by the planktonic larvae of benthonic invertebrates, see Wilson (1952).

**GROWTH OF VENUS IN RELATION TO BOTTOM TYPE**

A problem that has been largely neglected is whether the nature of the substratum has any influence, direct or indirect, upon the growth rate of *Venus*. Apparently the only study of this problem is one conducted by Kerswill (1941) in the course of an extensive investigation of environmental factors that affect the growth of *Venus*. Two groups of 50 quahogs were grown in adjacent plots, one consisting of "sandy mud," the other of "clean sand." At the end of one growth season no significant difference in growth was observed.

To compare more amply the growth of quahogs in two different types of bottom materials under otherwise theoretically identical conditions, the following experiment was performed. In mid-November of 1950, eight bottomless wooden frames, each four feet square and eight inches deep, were forced into the bottom of Wickford Harbor.
until their tops were nearly flush with the bottom surface. They were
so placed as to be exposed on only the extreme low tides. The sedi-
ment here was classified, on gross inspection, as sandy mud (see below
for analysis), black with added organic matter, and smelling rather
strongly of \( \text{H}_2\text{S} \). For simplicity this material will be referred to as
"mud." In four of the frames the indigenous mud was replaced with
sand of a medium coarseness; the mud in the remaining frames was
left unaltered except for the removal of native quahogs. Four
hundred measured quahogs ranging from 20 to 50 mm long, with a
sharp length-frequency mode at about 30 mm, were planted in each
frame. The water temperature at the time averaged about 10° C,
below which quahog growth is negligible (Belding, 1931; Kerswill,
1941). To determine the amount of growth during different parts of
the growing season as well as in an entire year, the animals from one
sand frame and one mud frame were removed, measured and replaced
on June 18, 1951, those from a second pair of frames were observed
on July 16, from a third pair on September 14, and all were removed
and measured on November 27, 1951. This schedule left one sand
frame and one mud frame undisturbed for an entire year so that any
interruption in growth due to the temporary removal of the animals
from the other frames during the growing season could be detected.
In every digging more than 85% of the quahogs were recovered; in
most cases more than 90%.

At the end of the year's observations, sediment samples from the
frames were analyzed for particle size distribution by Mr. Ivory A.
Canty, to whom I am indebted. By this time the surface layer in
the sand frames (about one inch or so) had received from the water
an admixture of finely divided black organic matter such as that
which characterizes the local bottom. The samples, after purging of
the organic matter with \( \text{H}_2\text{O}_2 \), were analyzed by a combination of sieve
and hydrometer methods. The results (Table II), after removal of
the organic content, showed that the "mud" was actually half sand
and half silt-plus-clay, while 96% of the "sand," both at the surface
and below, consisted of particles classed as sand or larger. The only
conspicuous change that occurred during the year in these surface
layers was not detected by this analysis, viz., the addition of organic
matter.

Growth was determined by measuring the total shell length of each
individual recovered in each frame, by plotting the length-frequency
curve for comparison with the original curve, and by noting the shift
of identifiable peaks. In most of the comparisons there were seven
or more positive features common to the two curves, hence growth
increments over the entire range of sizes could be read with ease.
Since these increments usually varied by less than 2 mm in any given comparison of curves and since they showed no consistent relation to the absolute length, they have been averaged to obtain a single mean increment for each frame in each growth period.

For the four populations living in sand, the means of annual growth varied from 15.3 to 16.3 mm, and the mean for the population left undisturbed throughout the year was 16.1 mm. For the populations in mud frames, the annual mean increments ranged from 11.7 to 13.7 mm, and the population left undisturbed grew 13.2 mm. Since the means of growth in the undisturbed frames were not the highest observed in either sand or mud, evidently the temporary removal of animals from other frames in midseason did not seriously interrupt their growth. In growth studies of Venus, therefore, we conclude that measurements of progress during various parts of the growing season can be made without fear of influencing the outcome of the investigation.

### TABLE II. PARTICLE SIZE DISTRIBUTION OF SEDIMENTS IN EXPERIMENTAL FRAMES

<table>
<thead>
<tr>
<th>Particles</th>
<th>Size range</th>
<th>&quot;Mud&quot; top inch</th>
<th>Sand, subsurface</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pebbles</td>
<td>&gt;3.96 mm</td>
<td>1.2% 4.1%</td>
<td>6.9</td>
</tr>
<tr>
<td>Granules</td>
<td>3.96-1.98</td>
<td>0.1 3.2</td>
<td>8.3</td>
</tr>
<tr>
<td>Sand</td>
<td>1.98-.062</td>
<td>50.7 89.2</td>
<td>81.2</td>
</tr>
<tr>
<td>Silt</td>
<td>.062-.004</td>
<td>34.2 2.6</td>
<td>2.1</td>
</tr>
<tr>
<td>Clay</td>
<td>&lt;.004</td>
<td>13.8 1.0</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Growth Relative to Type of Sediment. To obtain a comparison of growth in the two kinds of bottom materials, all of the individual measurements of annual increment in sand and in mud were averaged. Twenty-three measurements of annual increment, obtained from the four populations in sand, yielded a grand average of 15.93 mm, with a standard deviation of 0.968. Populations in mud (28 measurements) showed a grand average annual growth of 12.89 mm, standard deviation 1.071. The standard error of the difference is 0.292. The observed difference between the means is more than ten times the standard error and thus can hardly have arisen from chance variation.

On an average, the quahogs in sand grew 24% faster than did those living in mud, and this difference is shown to be highly significant. No observations were made which might have explained the difference in growth. Since the frames were contiguous, the water cannot have varied from one frame to the next, except as it may have been locally influenced by the sediments in the frames. Therefore the difference
in growth rate must have arisen directly or indirectly from benthonic factors. What these might be we can only surmise. Loosanoff and Tommers (1948) have shown that suspended silt has a marked effect on the pumping rate and hence on the feeding of oysters; as little as 0.1g of silt per liter of water reduced the average pumping rate 57%, and the oysters expelled large amounts of silt as pseudo-feces. Quahogs probably react to suspended silt in a similar manner. The necessity of frequent clearing of the animal's filtering apparatus might seriously interfere with the process of feeding, thus reducing appreciably its total nutrition. In the mud frames the currents may have kept the water along the surface of the bottom roiled with silt, whereas in the sand frames this thin but important layer of water may have been relatively free of suspended silt. Such a difference in the microenvironment and in the relative feeding efficiency of the quahogs might account for the observed difference in annual growth. The amounts of dissolved oxygen in the water just above the bottom may also explain the difference: perhaps the mud bottom, rich in decomposing organic matter, reduces the oxygen content of the water much more than does the sand.

Growth by Season. As noted above, the populations in mud and in sand showed somewhat various annual increments. These variations must be taken into account in calculating the increments for the different parts of the growth season in order to arrive at figures representative of all four populations in each bottom type. Accordingly the partial increments have been adjusted to the grand averages for the year's growth in sand and in mud. Each increment (Table III) bears the same ratio to the mean annual growth in sand or in mud as the observed partial increment bears to the observed annual growth in the given population.

If we can assume that the period of constructive growth coincides approximately with that in which water temperatures are 10° C or higher, the growth season in 1951 lasted from mid-April to mid-November according to a semiweekly temperature record kindly supplied by Mr. Warren S. Landers of the U. S. Fish and Wildlife Service. During mid-April to mid-July the animals living in sand put on more than 50% of their year's growth, those in mud about 75%. Furthermore, plankton studies by Mr. Landers show that the great bulk of the year's quahog spawning at this locality occurred in June and early July. The period of most rapid growth came earlier in the season than it does in the waters of Cape Cod, where, according to Belding (1931), August and September show the fastest growth. In the Bideford River, Prince Edward Island, more than half of the
year's growth occurs between mid-July and mid-September (Kerswill, 1941). Annual differences may account in part for these discrepancies.

In an attempt to explain the distribution of growth in the growing season, the temperature record and a series of weekly plankton samples from mid-April to mid-November have been analyzed without satisfactory results. The temperature record yields a fairly symmetrical curve with a maximum 2-week average of 24.0° C in the latter half of July (absolute maximum of 25.7° August 13). Temperatures of 10°–

<table>
<thead>
<tr>
<th>TABLE III. GROWTH BY PARTS OF THE YEAR, ADJUSTED TO THE MEAN ANNUAL GROWTH IN SAND AND IN MUD (SEE TEXT).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period</td>
</tr>
<tr>
<td>---------------------------------</td>
</tr>
<tr>
<td>Before 18 June</td>
</tr>
<tr>
<td>18 June–16 July</td>
</tr>
<tr>
<td>16 July–14 Sept.</td>
</tr>
<tr>
<td>After 14 Sept.</td>
</tr>
</tbody>
</table>

22.5° were associated with the rapid growth between mid-April and mid-July, and with growth at a much lower rate (especially in mud) from September 1 to mid-November. The plankton samples, preserved in 1% neutralized formalin, were collected by pouring 50 gallons of water through a net in which the mesh apertures averaged approximately 45 µ in their greatest diameter; for these I am again indebted to Mr. Landers. Qualitative and quantitative studies of these samples have failed to yield an explanation for the more rapid growth in spring and early summer than in subsequent months. Indeed, several categories of objects, notably the plants and animals with greatest dimension less than 75 µ, were counted and were found to be relatively scarce until late August, after which they reached great maxima in September and October when quahog growth was slow. It is quite possible that particles too small to be retained quantitatively by the net, particularly nannoplankton forms which disintegrate even in dilute preservations, constitute an important part of the quahog diet.

Mortality of quahogs during the experiment was light and appeared to be randomly distributed as regards size and seasons. Totals for the year were: sand, 59 (3.7%); mud, 77 (4.8%).

As in studies by other investigators, size and growth of quahogs in this experiment are expressed in terms of a linear dimension of the shell. Such measures can be made rapidly, easily, and exactly, and they bear a fairly constant relationship to total volume. However, other possible measures, such as weight or carbon content of meats, would probably give more meaningful indices of size and growth, particularly in inter- and intra-seasonal studies. Growth of soft
parts, i. e. excess of assimilation over catabolism, in a given interval of time is perhaps not reflected in increased shell dimensions until after a lag of unknown duration. If this is true, measurements of the shell cannot give an accurate record of growth of the soft parts by months or other subdivisions of the annual cycle.

**SUMMARY**

1. The distribution patterns of *Venus mercenaria* and of *Callocardia morrhua* in Narragansett Bay are complementary in general and show decided correlations with the character of the bottom. *Venus* is most abundant in bottoms consisting principally of fine sediments, but its abundance in these sediments is strongly related to the presence of large particles such as shell and rocks as minor constituents of the substratum. Again, if bottoms are classified on the basis of the inclusion of each of the recognized sediment types, quahog numbers vary directly with particle size. The abundance of *Callocardia* shows a consistent inverse correlation with the particle size of bottom sediments.

2. It has been shown that the growth rate of *Venus* depends directly or indirectly on the nature of the substratum: populations living in sand grew 24% faster than did those living in an adjacent plot of sandy mud containing much organic matter.

**REFERENCES**

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