BIOLOGY OF THE CALIFORNIA SEA-MUSSEL (MYTILUS CALIFORNIANUS). III. ENVIRONMENTAL CONDITIONS AND RATE OF GROWTH [1]

WESLEY R. COE AND DENIS L. FOX

(*Scripps Institution of Oceanography, University of California, La Jolla*)

In the cultivation of oysters, clams and other mollusks, as well as in studies on their rates of growth under natural conditions, it has been frequently observed that certain years are more favorable than others for rapid increment in size. But there has been no satisfactory analysis of the environmental conditions responsible for the observed differences in growth rates. For this reason an experimental study, extending over four years, has been made of the growth of the California sea-mussel at the pier of the Scripps Institution of Oceanography. At this station daily records are made of the temperature of the water and of the numbers of dinoflagellates, diatoms and bacteria present and potentially contributory to the mussels' ultimate food supply. For the temperature records the writers are indebted to Capt. S. W. Chambers; for the data on phytoplankton to Prof. W. E. Allen, and for those on bacteria to Prof. C. E. ZoBell. They also appreciate the technical assistance of Miss Harriet Dunn and Mr. Carl Johnson.

In two previous papers (Coe and Fox, 1942; Fox and Coe, 1943) the writers have presented evidence relative to the normal rates of growth in this species at different seasons and at different ages and sizes, the different rates in the two sexes, the nature of the food materials and the influence of environmental conditions on the rates of growth. It was concluded from these observations that there is a generally positive correlation of the growth rates both with temperature changes and with the abundance of dinoflagellates present in the water. No similar correlation was found relative to the numbers of diatoms or bacteria. It was emphasized however that the correspondence between the size of the dinoflagellate populations and the growth rates of the mussels was not to be interpreted as the direct effect of dinoflagellates as potential food material, since a large proportion of the living dinoflagellates ingested usually pass apparently unchanged through the mussel's digestive tract. Furthermore the total supply of living phytoplankton which the mussel could possibly obtain is estimated to be so small in amount that even if all the constituents could be fully utilized they would furnish less than one-fifth of the mussels' nutritive requirements. The principal portion of the food was shown to consist of finely divided organic detritus, derived from the disintegration of many kinds of marine animals and plants, including both unicellular and multicellular forms (Fox and Coe, 1943).

Continuation of those observations during three additional years has shown that there are wide variations in the mussels' growth rates, not only from month to

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month but also from year to year. It is the object of this paper to record these variations and particularly to present such evidence as has now been obtained as to their causes. For this purpose the changes in the environmental conditions from month to month have been analyzed as fully as possible. Since there are no rivers in the vicinity and the annual rainfall is small, there is but little variation in salinity. The principal effective variables are the temperature and the food supply.

The experimental mussels were kept in wire-screened boxes immersed in the sea below the low-tide level. Since the increment in size was found to vary with the age of the individual under identical environmental conditions (Coe and Fox, 1942), it was necessary to have the same ages represented at all times. This required the addition of young individuals from month to month and the removal of the oldest.

The experiment was continued from January 1940, to January 1944, with the exception of the first five months of 1942. At nearly all times the experimental boxes contained from 100 to 400 or more individuals, each age group being in a separate compartment. The average age remained nearly constant and all were sexually immature. When the individuals of a group were separately numbered, it was found that some grew rapidly for a period and were then overtaken by others; some became leaders for several months, while others remained dwarfs. For statistical purposes it was therefore desirable to follow the growth of 20 or more individuals of each age group. The mean monthly increments in size for all groups are shown in Figures 1 to 4.

In any consideration of the environmental conditions, it must be kept in mind that these conditions are constantly changing, due to the water currents that continually sweep past the pier at rates averaging from four to five miles per day. Consequently these conditions may vary considerably from day to day and even from hour to hour. The monthly means, however, will give a reasonably close approximation to the prevailing environments.

A comparison of the graphs in Figures 1 to 4 shows that the growth rates of the mussels have varied considerably, not only from year to year but also for the corresponding months of the years. The mean monthly increment in length for all groups was 3.43 mm. in the year 1940, 3.96 mm. in 1941, 5.43 mm. during the last seven months of 1942 and 5.11 mm. in 1943. It is evident from these figures that 1942 and 1943 were more favorable for rapid growth than either of the other two years and that 1940 was the least favorable. The lowest rate for any month of the four years was in August 1940. During that month the mean increment in length was only 1.6 mm., which was less than one-third as great as in the corresponding month of each of the three other years. The maximum rate occurred during April in 1940, during June in 1941, during July in 1942 and during May and July in 1943 (Figs. 1–4).

An examination of the environmental conditions, particularly as concerns temperature, storms and abundance of the phytoplankton during these years, will give some indication of the influence of each on the observed growth rates of the mussels.

First Year, 1940

The monthly growth rates of the mussels during this year were exceptional in that they showed fewer positive correlations with the temperature and with the abundance of dinoflagellates than in any of the other years. Following a decrease in the rate during February there was a rapid increase to a maximum in May, fol-

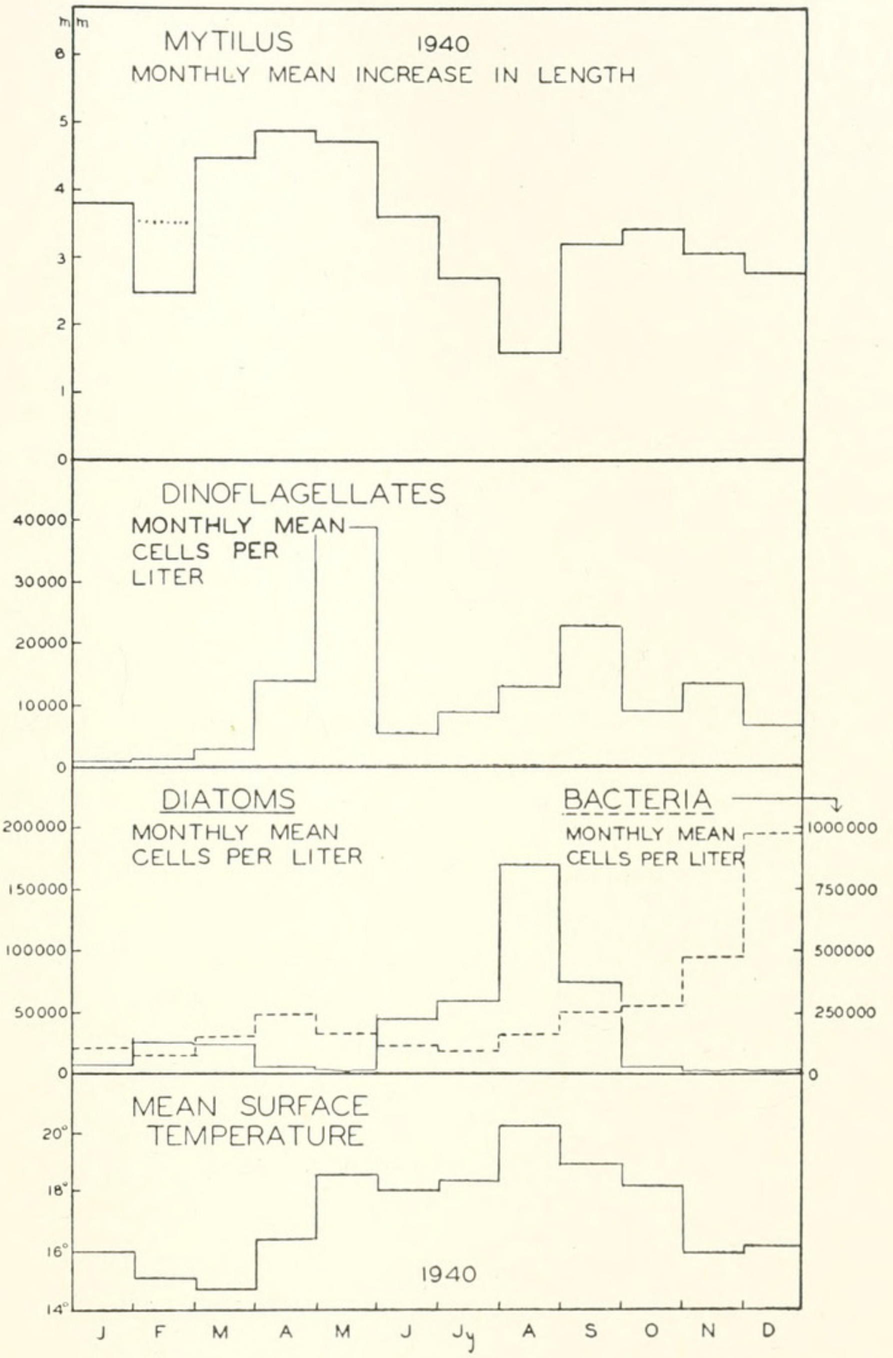

FIGURE 1. Graphs showing the average monthly growth rate of 453 mussels, divided into 11 groups according to age, and the abundance of dinoflagellates, diatoms and bacteria, as well as the average monthly temperature of the water during the year 1940. The depression of the growth rate in February was mainly due to a reduction of the feeding period to 22 days because of accidents caused by storms; the dotted line indicates the estimated increment if the accidents had not occurred. It was necessary also to estimate the growth in December because of an accident due to storm. The numbers of dinoflagellates shown in the graph differ in several cases from those indicated in Figure 4 of our previous paper (1942) because of erroneous data supplied to us at that time.

With some exceptions the growth rates were highest during those months having large dinoflagellate populations and in which the temperature exceeded 16° C.

lowed by a continuous decline to the lowest rate for any month of the four years in August (Fig. 1). The only explanation that can now be given for this exceptionally low rate in August is that for some unknown reason the organic detritus which furnishes the greater part of the mussel's nutrition was not present in sufficient quantity. The sharp drop in February was in part due to storms which necessitated removing the mussels from the sea and keeping them in the aquarium for six days. Since no increase in size occurs in the aquarium except when additional food is supplied (Coe and Fox, 1942), there was a possible feeding period of only 22 days during that month. Computed on the basis of the growth during that period, the estimated increase per day in February would be but slightly less than during the preceding month, as indicated by the dotted line in the graph (Fig. 1). A sharp rise in the growth rate in September and an additional increase in October was followed by the usual decline during the last two months of the year.

As a general rule, but with some conspicuous exceptions, the most rapid increment in size occurred during those months in which a large population of dinoflagellates was present and in which the temperature exceeded 16° C. Neither the diatoms nor the bacteria showed definite correlations with the growth rates of the mussels (Fig. 1).

Second Year, 1941

During the second year the growth rate was somewhat higher than in the preceding year, although the average number of dinoflagellates was smaller and the diatoms were less than half as abundant as in 1940. With the exception of February there was a continuous rise in the growth rate to a maximum in June, with a steady decrease thereafter (Fig. 2). The dinoflagellate population correspondingly reached a maximum in July, followed by a continuous decline to a minimum in December. Neither the diatoms nor the bacteria showed similar trends. The rate indicated for December is lower than it would have been except for a severe storm which allowed a feeding period of only 27 days.

Third Year, 1942

The experiment was interrupted for the first five months of 1942, but the last seven months of the year showed a greater increment in growth than in the corresponding months of any of the other years. The maximum rate occurred in July, followed by a continuous decrease during the rest of the year, with the exception of a slight rise in November, followed by a small decrease in December (Fig. 3). The water during those months contained an average of more than five times as many dinoflagellates as in the last seven months of the preceding year and the average monthly increment in the lengths of the mussels was 5.4 mm. as compared with 4.3 mm. in the corresponding period of 1941. The average number of diatoms was smaller than in any of the other three years.

Fourth Year, 1943

During the year 1943 the average monthly increment in size was considerably greater than in 1940 or 1941 but somewhat less than in 1942 (Fig. 4). By comparing the rate for December 1942 (Fig. 3), with that of January 1943, it will be seen that a sharp drop occurred during the latter month. The cause of this decrease in growth rate may have been due to a severe storm which necessitated transferring the experimental box from the sea to the aquarium, where it remained for four days.

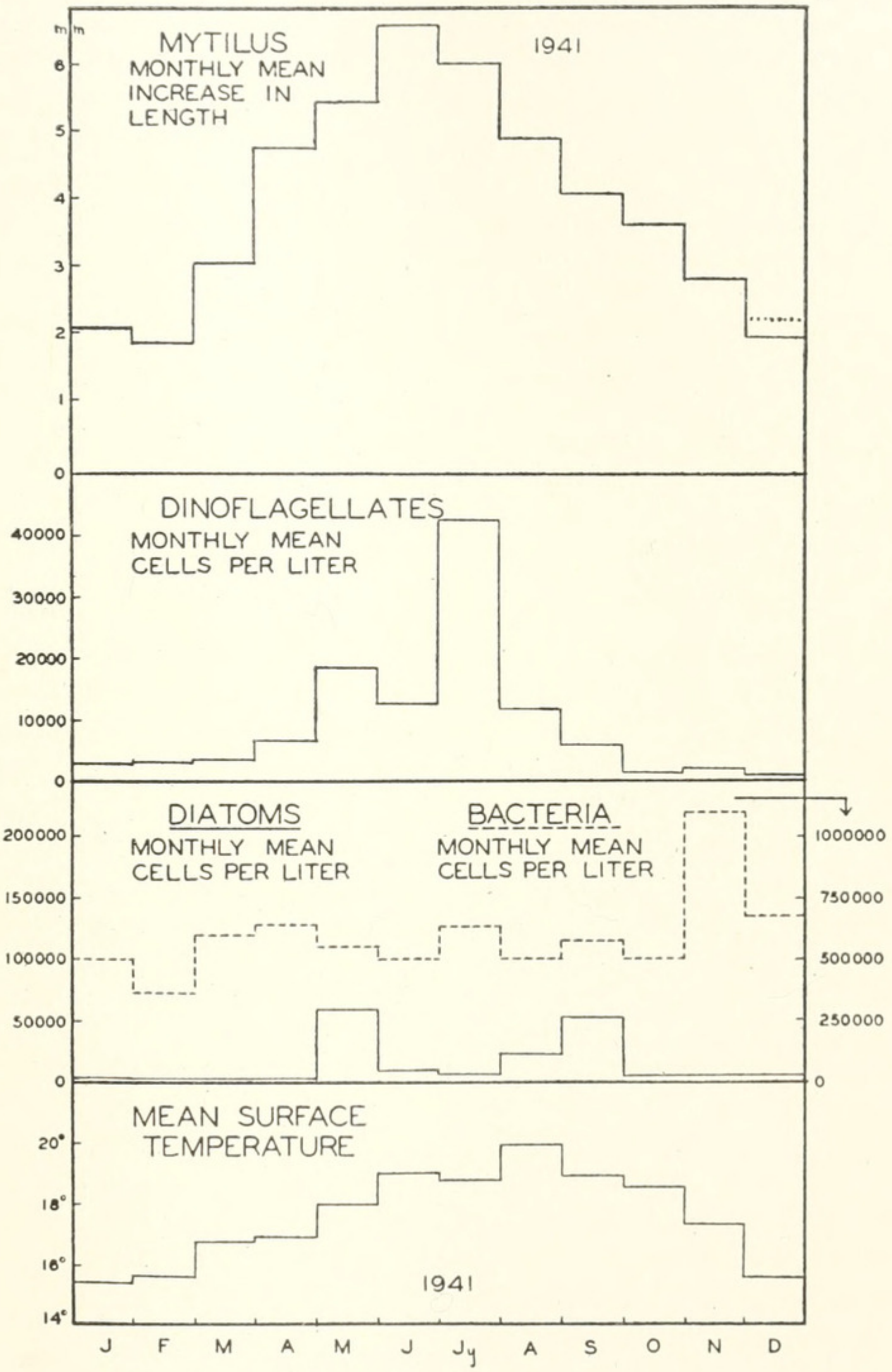

FIGURE 2. Graphs showing average monthly growth rate of mussels and abundance of dinoflagellates, diatoms and bacteria, as well as average monthly temperature of the water during the year 1941. The growth indicated for December represents a feeding period of only 27 days; the dotted line indicates the computed increase for a month of 31 days.

The most rapid increment in size occurred in those months having large populations of dinoflagellates, accompanied, presumably, by an abundance of organic detritus.

From this depression in January, the growth rate increased continuously until May, when the average increment was 6.4 mm. (Fig. 4). An unaccountable drop in the growth rate during June was followed by an average increment of 6.6 mm.

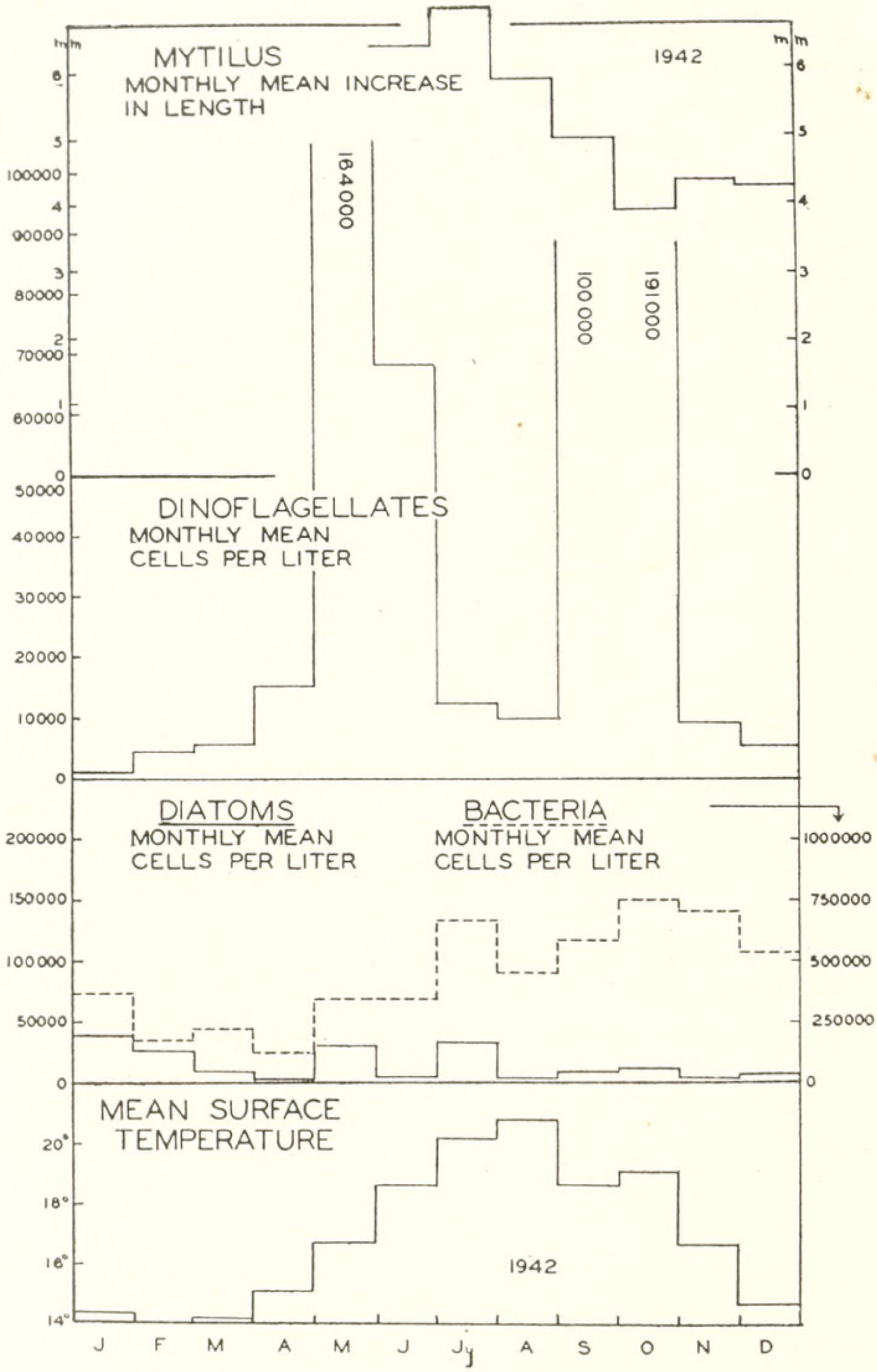

FIGURE 3. Graphs showing the mean monthly growth of mussels, the mean monthly temperature of the water and the mean monthly abundance of dinoflagellates, diatoms and bacteria during 1942.

in July, which was the highest rate for the year. Following the usual decrease in August, the rate continued high and steady during the two succeeding months; then, instead of the usual decline in November, there was a rise to an average of 6 mm., as compared with about 3 mm. in the corresponding month of 1940, 2 mm.

in 1941 and 4.3 mm. in 1942. In December the rate was but little more than half as great as during the preceding month (Fig. 4).

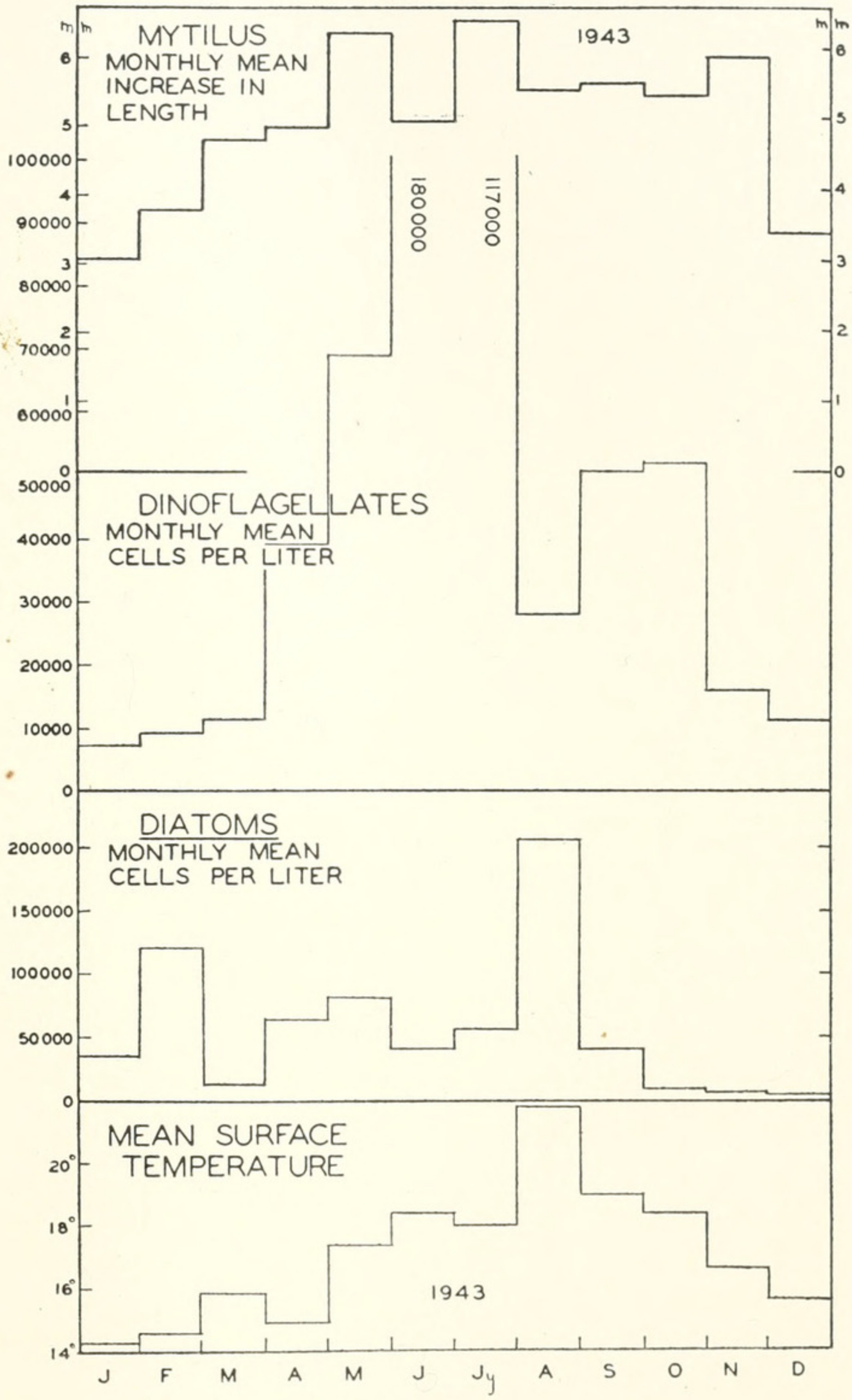

FIGURE 4. Graphs showing the mean monthly growth of mussels, the mean monthly temperature of the water and the mean monthly abundance of dinoflagellates and diatoms during the year 1943.

The average monthly increment in length was 5.1 mm. as compared with 3.43 mm. in 1940 and 3.96 mm. in 1941. This increased rate of growth was accompanied by populations of dinoflagellates more than four times as great as in either

1940 or 1941. The diatoms were also four times as numerous as in 1942, but again it should be emphasized that neither the dinoflagellates nor the diatoms furnish more than a small proportion of the food supply of the mussel.

Environmental Influences

The observations described on the foregoing pages show how great a variation was found in the growth rates of the mussels in different years and in different months of each year. The comparisons of these rates with the temperature and with the abundance of dinoflagellates, diatoms and bacteria are shown in Figures 1 to 4. There are obviously many other environmental conditions which are constantly exerting their influence on the growth of the mussels. Some of these may be of great importance but they are so sporadic in their action or so difficult to measure that no precise evaluation of their influence has as yet been possible.

There is little variation in salinity throughout the year and there is often a correlation between the amount of oxygen and the relative abundance of phytoplankton.

1. *Temperature*

As a general rule the rate of growth in mollusks increases with the temperature to a certain optimum and then rapidly decreases. Consequently the annual increment in length is greater in southern than in more northern localities because of the longer season favorable for rapid growth. The observations of Weymouth, McMillan and Rich (1931) on Siliqua, of Newcombe (1936) on Mya, of Chamberlain (1931) on Lampsilis, of Orton (1926–27) on Cardium and of Coe (1938) on Ostrea support this conclusion. The size eventually reached by the individual however is commonly much greater in the north because of the greater length of life.

At the pier of the Scripps Institution of Oceanography, where the experiment was conducted, the variation in the mean monthly surface temperature of the water during the year seldom exceeds 8° C. Both the low point of about 14° in winter and the high of about 22° in summer are well within range of the normal activities of the mussel. The highest temperature recorded at any time during these four years was 22.9° C., in August 1943, and the lowest was 13.4° in January 1943. Consequently growth continues throughout the year in this locality, although the rate of increment in length is only about half as great in midwinter as it usually is in the early summer. This decreased rate in winter is presumably due both to a lower state of metabolic activity and a decreased supply of nutritive materials.

In *M. californianus*, as in *M. edulis* (Loosanoff, 1942), feeding continues at temperatures both lower and higher than the extremes mentioned in the preceding paragraph. Under experimental conditions the California mussel will secrete byssus threads, ingest food and discharge feces at temperatures as high as 24 to 26° C. and to a less extent at 27 to 28°. The individuals subjected to the highest of these temperatures however died within 5 to 7 days. The lowest temperature at which ingestion and fecal discharge were found to occur was 7 to 8°. Since these mussels were subjected to the temperatures mentioned without any period of acclimatization from an aquarium temperature of 15°, it is considered probable that the figures given do not represent the extreme range of the mussels' potential metabolic activities.

Experiments previously made in this laboratory indicate that the maximum rate of filtration and maximum oxygen consumption take place at about 20° C., with distinctly lower rates below 15°. A decreased growth rate has occurred in August, the month of highest temperature, in each of the four years. But in 1940 the decrease began in June and reached its lowest rate in August, while in 1941 the highest growth rate occurred in June and in 1942 in July. In 1943 maxima occurred in May and July. The variability in the growth rates at corresponding temperatures in different years indicates that the food supply is more influential than small variations in temperature in determining the rates of growth. The prevalence of storms and high seas common in winter are doubtless detrimental to active growth.

2. *Food*

The mussel is essentially a scavenger, utilizing as food not only small unicellular organisms and dissociated cells but also the particulate disintegration products of any of the animals and plants which die in the vicinity or similar products which are brought from a distance by currents. Even the bacteria which cause the decomposition may themselves be utilized as an additional source of nourishment (Coe and Fox, 1942; Fox and Coe, 1943).

The constituents of the ingested materials have been ascertained at frequent intervals by examination of the stomach and intestinal contents and of the feces. The substances most commonly present are finely divided organic detritus, dinoflagellates, diatoms, silicoflagellates and bacteria; also tintinnids, flagellates, ciliates and other protozoans, as well as algal cells and fragments, algal spores, spermatozoa and ova (including those of its own species), together with inorganic substances such as particles of sand and shells. At times the organic materials may be ingested in amounts much greater than the mussels' capacity for assimilation. The excess, if not too great, may pass unchanged through the digestive system but in case of a very great surplus most of the material is rejected by the palps and is discharged from the mantle cavity as pseudofeces. No satisfactory evidence of selection, except as to size, from among these small cells and particles has been obtained, although chemically injurious substances are rejected, together with the larger cells and other objects.

Digestion in the mussel, with the exception of starch and glycogen, appears to be mainly or wholly intracellular. Many of the smallest objects and particles are phagocytized by the cells lining the digestive diverticula. Others are ingested by phagocytic cells which migrate into the lumens of the stomach and intestine and later return with their ingested materials through the epithelial lining of the digestive tract and thence to the connective tissues of the body, as Yonge (1926, 1931) has so fully described for the oyster. Most of the local dinoflagellates and many of the diatoms are far too large to be assimilated in this manner. Some of the starch and glycogen, on the contrary, undergoes extracellular digestion in the stomach through the action of enzymes in the style. No evidence of the digestion of cellulose, which forms the covering walls of most neritic dinoflagellates, nor of any cells with completely closed cellulose walls, has been obtained (Fox and Coe, 1943).

Diatoms. These organisms, either living or dead, furnish a small portion of the mussels' nutrition. Their disintegration products are also utilized. They are usually present in numbers ranging from 1000 to 200,000 per liter but the large and spiny ones are not ingested. Many of those that enter the digestive tract are seized and digested by the phagocytic cells mentioned in a preceding paragraph, while others pass through the tract without apparent change.

The mean number of diatoms, as counted by the settling method, per liter of water for each month of the four years is shown in Figures 1 to 4 and the combined monthly averages for 1940, 1941 and 1943 in Figure 5. In none of these years has there been a direct correlation between the diatom populations and the mussels' growth rate, although positive correlations have been reported by Newcombe (1935) for Mya and by Nelson (1942) and others for oysters.

The number of diatoms in the water about the mussel beds has varied greatly from year to year. The average in 1940 was 38,700 per liter, in 1941 16,600, in 1942 12,600 and in 1943 54,300 (Figs. 1–4). The average monthly increase in the lengths of the mussels for the same years was 3.43 mm., 3.96 mm., 5.43 mm. and 5.10 mm., respectively. It is obvious that there was in these four years no direct correlation in the two groups of data. In spite of a four-fold increase in the number of diatoms in 1943 as compared with 1942 there was nevertheless a somewhat lower rate of growth in the mussels. This should not be surprising when it is realized that even if these organisms had been uniformly distributed in the water throughout the year, instead of occurring in dense swarms, the rate of filtration by the mussel is such that an adult animal could have secured no more than 200 million to 800 million per year. If all of these could have been fully utilized they would have furnished only a minute fraction of the material required for the upbuilding of the mussel's tissues and gametes. Such of these organisms as can be ingested by the mussel are so minute that it would require some 600 million to supply one gram of organic matter, while the adult mussel is estimated to need about 40 grams annually (Fox and Coe, 1943).

Bacteria. Bacteria are ingested in vast numbers (Figs. 1–3) but their total mass is so small that they have little quantitative influence on the mussels' nutrition (Fox and Coe, 1943).

Dinoflagellates. It has been mentioned that in each of the four years there was generally, but with some conspicuous exceptions, a rather close correspondence between the monthly and yearly growth rates of the mussels and the abundance or scarcity of dinoflagellates in the water. In 1940 the average daily number of these organisms per liter of water was 12,100, as compared with 9880 in 1941, 54,750 in 1942 and 49,500 in 1943. The corresponding average monthly growth rates of the mussels were 3.43 mm. in 1940, 3.96 mm. in 1941, 5.43 in 1942 and 5.10 in 1943. From these figures alone it may be concluded that the mussels grow most rapidly in those years in which the populations of dinoflagellates are the largest.

More precise evidence as to this association however is furnished by an inspection of the monthly data as shown in Figures 1–4. It has been emphasized in a foregoing paragraph however that a large proportion of the living dinoflagellates, which may be ingested in vast numbers, usually pass apparently unchanged through the intestinal tract and often constitute much of the fecal material. Their cellulose walls cannot be digested by the secretions in the stomach or intestine and there is no satisfactory evidence that they are phagocytized by the cells of the digestive diverticula in any considerable numbers. Following the death of these unicellular organisms however, either before or after entering the mussel's digestive tract, they doubtless form particulate disintegration products which are readily assimilated. It is well known that species of Gonyaulax and less frequently of some other genera may be ingested in such numbers and the contained toxic substance accumulated in such quantity as to cause sickness or even death when the mussels are eaten by man.

It has been shown by Fox and Coe (1943) that the mussel filters the water at such a rate that the available supplies of dinoflagellates, even if they could be fully utilized, would furnish only a small fraction of the food which the mussels require for their growth and reproduction. Assuming a filtration rate of 2.5 liters per hour, or 22,000 liters per year, it would be necessary to have an average population of about 2000 of these cells per liter in order to supply one gram of organic matter in a year. This is only about two and one-half per cent of the amount which an adult mussel is estimated to require annually for the upbuilding of its tissues and gametes. During these four years the water has contained averages of 10,000 to 54,750 of these cells per liter but a large proportion of these were present in such dense swarms that relatively few of those that were drawn into the mantle cavities of the mussels could have been actually ingested; the others were presumably discharged as pseudofeces. Furthermore, as has been stated, many of those that are ingested usually pass through the digestive tract without visible change, while the large and spiny forms are seldom ingested.

Therefore any correlation between the abundance of dinoflagellates and the growth rates of the mussels must be merely indicative of other, associated sources of nutrition. The principal source is organic detritus.

Detritus. The organic detritus ingested by the mussel consists of various fragments of cells or of entire cells of minute size, as well as suspended proteins, lipids and polysaccharides. It may be recalled that the mussel obtains its food by secreting over its gills a thin sheet of mucus to which the particles are adsorbed. The mucus sheet with its attached particles is then drawn into the mouth. There is no evidence that the mussel is capable of securing substances in true solution until these have first been changed to particulate form through the agency of various unicellular organisms (Fox and Coe, 1943).

Consequently it may be concluded that, with the exception of refractory humus materials, cellulose, chitin and other indigestible substances, the total organic constituents of all marine organisms, from the smallest to the largest, are potential sources of nutrient for the mussel. After the death and disintegration of the animal or plant, the residual organic matter, or detritus, may remain suspended in the water for an indefinite period before it chances to enter the digestive system of the mussel. The amount available is obviously subject to great variation locally and it is to this variation that many of the differences in growth rates are ascribed.

Inspection of Figure 5, which indicates the combined average monthly growth rates for three years, will show that the rate increases from a low in January or February to a maximum in May, June and July. This period corresponds with the increasing reproduction of many of the invertebrates in the vicinity and elsewhere along the coast. The striped barnacle (*Balanus tintinnabulum*), for example, has minimum and maximum periods of reproduction coinciding almost precisely with the low and high growth rates of the mussels (Fig. 5). These reproductive periodicities are undoubtedly associated with similar variations in the detritus which the barnacles yield, since a large proportion of the free-swimming larvae die without finding a place of attachment and presumably less than one per cent of those which succeed in transforming to the adult stage survive to reach sexual maturity

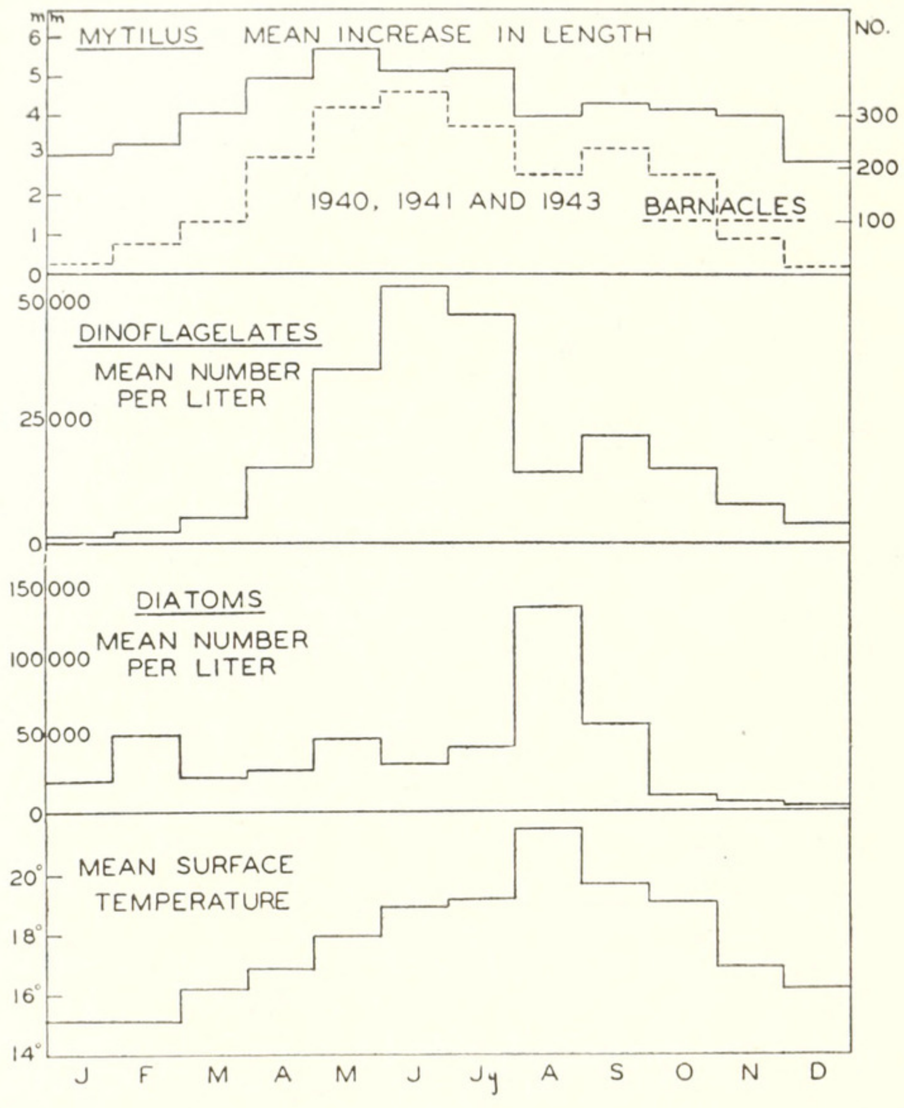

FIGURE 5. Correlations between the mean monthly increment in length of the experimental groups of mussels for the years 1940, 1941 and 1943, the mean numbers of dinoflagellates and diatoms per liter and the mean temperature of the water. The year 1942 is not included because of lack of complete data for the first five months of that year. Except for the decrease both in growth rate of the mussels and numbers of dinoflagellates during August, when the temperatures were highest, the general correspondence of three of these groups of data is evident. But this correspondence does not hold for the diatoms.

As indicative of the relative amount of organic detritus presumably available in each month, the estimated average numbers of barnacles which became attached to each square inch of surface of submerged plates in previous years have been included. These numbers indicate a close correlation with the growth rates of the mussels.

(Coe, 1932). The disintegrated bodies of those that perish doubtless supply more nutritive material to the mussel than can be obtained from the living phytoplankton.

In some years the growth rate has been more or less distinctly bimodal, rising to a maximum in late spring or early summer, followed by an invariable decrease in

August and in three of the four years with another rise preceding the decrease at the end of the year. In three of the four years the dinoflagellates showed somewhat similar bimodal periodicities, with distinct spring and autumn maxima, and this has been shown to be the average condition of these organisms for the twenty preceding years (Allen, 1941). The diatom populations, on the contrary, reached a conspicuous maximum in August in 1940 and in 1943, although in many other years that has been a month of extremely low production.

The bimodal periodicities in the growth rates of the mussel are closely parallel with similar periodicities in the reproduction of many of the associated invertebrates, including the mussels themselves. The growth rates of the entire mussel population would obviously be complicated by the reproductive processes but these complications were avoided in this experiment by using sexually immature individuals.

It is unfortunate that no precise measurements are available relative to the local variations in the amount of organic detritus, but the seasonal differences in the rates of growth of the mussels and other detritus feeders presumably afford a fairly reliable criterion.

Summary

This study offers additional evidence as to the complexity of the environmental conditions found along the shores of the ocean and which affect so profoundly the lives of the organisms residing there. Variations in the growth rates will obviously depend upon the interaction of several of these conditions, not the least important of which are the temperature and the character and abundance of the food supply.

Furthermore these environmental conditions are constantly changing, due in part to the continual motion of the water. At the locality where the foregoing observations were made, there are not only the variable currents caused by wind and tidal changes, but there is also a drift along the coast at a rate averaging four to five miles per day. Consequently the water in which the mussels are living and the conditions associated therewith may differ not only from month to month but also from day to day and even from hour to hour. In one week there may be ten to fifty times as much phytoplankton in the water as in the following week. The yearly averages are more stable but these may vary by more than five fold.

Monthly correlations, extending over four years, between the growth rates of the mussels and the prevalent environmental conditions offer conclusive evidence that the most rapid increase in size takes place at temperatures from 17 to 20° C., although growth continues less rapidly at 14° or lower. Feeding continues at a temperature as low as 7 to 8° and as high as 27 to 28°.

The average number of diatoms per liter was 38,700 in 1940, 16,600 in 1941, 12,600 in 1942 and 54,300 in 1943. The average number of dinoflagellates for the same years was 12,100, 9880, 54,750 and 49,500, respectively. The average monthly increment in the lengths of the mussels was 3.43 mm. in 1940, 3.96 in 1941, 5.43 mm. in 1942 and 5.11 mm. in 1943, indicating a yearly variation of more than 50 per cent.

It is obvious that the two years with the largest dinoflagellate populations have been conducive to the most rapid growth of the mussels, but an increase of four fold in abundance has been associated with an increased growth rate of only 42 per cent. The correlation noted is evidently not direct, since the living dinoflagellates

can supply only a small fraction of the mussels' nutritive requirements. Both mussels and dinoflagellates appear to thrive under the same environmental conditions. That the living diatoms and bacteria are of even less importance in the life of the mussel is indicated not only by the small amount of organic matter that they contain but also by the fact that the mussels grew most rapidly in the year with the smallest number of diatoms and least rapidly in the year when the number was three times as great.

More direct correlations with the growth rates of the mussels are found in the reproductive periodicities of various invertebrate populations which contribute so largely to the available organic detritus and thereby to the mussels' nutrition.

The principal food supply of this species of mussel consists of minute particles of organic detritus derived from the disintegration of the cells of all kinds of marine organisms, both animals and plants, supplemented by living and dead unicellular organisms of minute size as well as living and dead gametes. There is no evidence that organic matter in true solution can be utilized until after it has been changed into particulate form by the action of unicellular organisms.

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