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FLUCTUATIONS IN POPULATIONS OF LITTORAL MARINE INVERTEBRATES

BY

WESLEY R. COE
Scripps Institution of Oceanography
University of California
La Jolla, California

ABSTRACT

Fluctuations in populations of various species of marine invertebrates, several of them over many years, are recorded. Some of the data are quantitative, but most of them are merely estimates of relative abundance at the same season in successive years. Records of local fluctuations in populations of the Pismo clam extend over 25 years, those of dinoflagellates 20 years, and of Donax 58 years; records of the set of young oysters cover 70 years and those of the local production of oysters 100 years. These data offer no satisfactory evidence of persistent rhythmical periodicity in any of the species. Changes that have occurred in local populations of littoral invertebrates due to constantly changing environmental conditions and to the introduction of foreign species during the past half-century are recorded. Some of these changes have been catastrophic.

INTRODUCTION

The term annual fluctuation is used in this report to designate variations in the relative number of individuals of a particular species in the same locality in successive years. The estimated amount of fluctuation is based on samples which have been taken at the same season each year in order to avoid the complication of seasonal variations, which are often of considerable magnitude. The number of individuals usually have been largest shortly after periods of reproduction. Fluctuations have varied simultaneously in different parts of the range of a species, since they are largely dependent on local environmental conditions, including diseases.

The writer has recorded many observations of changes which have taken place in populations of various species of littoral invertebrates during the past half-century along the coasts of southern New England and southern California. Most of these changes have been minor fluctuations in numbers while others have been catastrophic, with the total elimination over considerable areas of all members of sus-
ceptible species or even of the entire littoral fauna. Catastrophic changes have obviously resulted from wide deviations in environmental conditions or from diseases, but no satisfactory explanations have been found for many of the observed fluctuations.

**ANNUAL FLUCTUATIONS**

Kemp (1938), Dexter (1944), Burkenroad (1946) and many others have published numerous examples of fluctuations among marine invertebrates, and others are known to every naturalist who is acquainted with the seashore.

At present many long-term records are available. Some of these are quantitative or semiquantitative in nature, while others are mere estimates of relative abundance which record whether many, few or none of a species were present. Some of these records were obtained in a survey of a particular locality at the same season in successive years. Some have reference to the entire local population of a species and others to only a single year-class. Also, annual records of the production of some commercial species are available for a long series of years. It seems desirable to examine a few of these records in order to determine the magnitudes and intervals observed.

1. Pismo Clam.—In the population of the Pismo clam (*Tivela stultorum*) at La Jolla, California, changes which occurred in each year-class during five successive years (1945–1949) were determined by collections taken at monthly intervals, beginning at the time when the young clams first appeared on the beach. Of the average total of 297 individuals found on a restricted portion of the beach in September of these years, 214 were in the first year-class, 71 in the second, 8 in the third, and 4 in the fourth. The population on the beach in those five years indicated that there was an annual loss of 67 to 75% for each year-class and that less than 1% of the young individuals reached the age of four years (Coe, 1947; Coe and Fitch, 1950). A few individuals of more than 20 years of age have been found on the same beach.

Fig. 1 shows not only the number of individuals in each year-class at the end of September from 1945 through 1949 but estimates of the total population from 1938 to 1952 as well. It will be observed that the number of those one year of age increased rapidly in 1946 and decreased in 1949, that those aged two years increased in each successive year, and that the reduced populations of older clams remained nearly stationary. The estimated total population increased about six-fold during the five years preceding 1943. This
was followed by a considerable decrease in numbers, with a resurgence in 1946. From 1949 through 1952 there was a rapidly declining population because of the failure of young clams to establish themselves on the beach at the end of the free-swimming larval periods. In 1953 the species had disappeared almost completely from the intertidal zone, not only locally but also in other formerly well populated areas. No significant deviation from average in temperature or salinity and no evidence of disease have been observed. Although some of the larger individuals were taken by poachers, it is concluded that deviations in the currents along the coast were mainly responsible for this pronounced decline. The larvae apparently have a pelagic

**Figure 1.** The constituent year-classes in the Pismo clam population on a restricted portion of the beach at La Jolla, California, during the last week in September of each year, 1938–1953. The numbers indicated for 1945 through 1949 are strictly quantitative and indicate an annual mortality rate of 67 to 75%. The total mortality from the first to fourth years was 97.5%. For the other years the population is estimated. No new set arrived in 1951 and the entire population disappeared in 1952.

life of two to three weeks or more, and during this period they may be carried far from their place of spawning by the ocean currents which on that part of the coast have an average velocity of four to five miles a day. Consequently the young clams in any locality may originate from populations living several, or even many, miles distant and the larvae are dependent upon favorable currents to bring them to the beach at the exact time when they are ready for transforming and settling in the sand. Presumably diseases similar to those recorded in this paper for *Donax* and oysters were responsible for many deaths; however, the causative agents were not determined. In some localities, every large clam observed showed macroscopic evidence of disease; some were moribund and others had died recently.

The greater range in the fluctuations of the young as compared with older individuals is shown in the records of the Pismo clam
populations at Pismo Beach, California, for the years 1923 through 1950. The samples were standard in that the same areas of the beach were covered in November of each year. The constituents of this population were described by Coe and Fitch (1950) but several of the data require further analysis. The first year-class is of particular interest. The numbers of young clams which settled in the measured areas and survived until the census was taken each year are shown in Fig. 2. The figures indicate variations ranging from 0 in 1934 and 1950, 1 in 1949, 6 in 1928, and 9 in 1938 to 743 in 1937, 758 in 1935, and 871 in 1931. The total of 4111 in the first year-class during the 19 years was 50% of the entire population not exceeding four years of age. Thus a high rate of mortality is indicated.

It will be noted that during most of this period there was a biennial rhythm in the set or survival of young clams, the numbers in each alternate year being greater than those in the preceding year (Fig. 2). It seems possible that this may have been a chance occurrence due to variations in the water currents, but why there should have been five years in succession with no appreciable set on this beach remains unexplained (Fitch, 1952).

In order to avoid the possible influence of strictly local fluctuations, the collections were made in three well separated sections of the long beach (Fig. 3). The Pismo section was 1.4 miles from the Oceano section and 6.5 miles from the Le Grande section. The data compiled by Fitch (1952) show that, in spite of the distances separating the three sections, the fluctuations were generally parallel at each date of sampling (Fig. 3). This is presumably indicative of nearly uniform
environmental conditions along the entire extent of the beach in any given year although such conditions undoubtedly varied in different years.

The life span of individuals of this species may exceed ten years
under favorable conditions, and each adult female may produce from 5 to 20 million eggs annually. During the years in which practically no young appeared there were many thousands of adults on the same beach, hence it is concluded that the immense numbers of potential young either failed to survive or were carried to other beaches, perhaps some miles distant. Presumably a large proportion of the young perished by being carried too far from shore; Johnson (1940) found larvae of the sand crab Emerita more than 90 miles from the nearest coast although the adults live only in the intertidal zone. Some were undoubtedly devoured, some probably died because of adverse temperature or lack of suitable nutrition, and possibly others succumbed to parasitic disease either before or after setting.

The older year-classes were less variable in numbers, the second year-class fluctuating from 2 in 1935 to 297 in 1947, the third year-class from 3 in 1946 to 245 in 1937, and the fourth year class from 4 in 1930 to 200 in 1946.

2. Oysters.—A quantitative study of variations in the number of young oysters (Crassostrea virginica) which set on 100 oyster shells in Long Island Sound has been made by Dr. Victor L. Loosanoff during 15 summers, 1937 through 1951, and by his permission the unpublished data are shown in Fig. 4. It will be noted that in two

![Figure 4. Yearly variation in the average set of young oysters on 100 oyster shells placed at various depths. Long Island Sound. Unpublished data supplied by Dr. V. L. Loosanoff.](image)

of these years the numbers were 40 times greater than those in the preceding year and were correspondingly larger than any set during the last five years. It appears that the number of survivors which reached the places for attachment fluctuated widely, but there is no evidence as to the number of larvae produced.

The longest continuous record concerning fluctuations in popula-
tions of any American marine invertebrate may be found in the estimates of the relative abundance of the set of young oysters in the large oyster producing areas in Long Island Sound. It is obvious that a heavy set is generally, but not always, indicative of a large future population of adults. These records for the past 70 years have been compiled by Loosanoff and Engel (1940) and have been supplemented by personal communications from Dr. Loosanoff. Fig. 5 indicates that heavy sets were reported in 12 of the 18 years prior to 1900 whereas in only six years of the present century has the set been considered heavy. From 1906 to 1924 there were continual failures and light sets; medium sets occurred in 1926, 1934, 1937, 1941 and 1945, and heavy sets in 1904, 1925, 1928, 1930, 1939 and 1940.

Note that in four of these years heavy sets occurred in the year immediately following one in which the set was a failure and that in only one year (1931) did a failure occur immediately following a heavy set. A sequence of six heavy sets was reported at the beginning of the record and a sequence of four failures followed 1914. In other years a maximum of three heavy sets or four failures followed in sequence. A cyclical periodicity in abundance is not evident. It is obvious that a light set accompanied by a low rate of mortality may be more productive than a heavy set with high mortality.

3. Starfish.—A quantitative study of the variations in the rate of attachment of young starfish (Asterias forbesi) on planted oyster shells for the years 1937 through 1951 was made by Dr. Loosanoff, who has kindly supplied the data indicated in Fig. 6. It will be seen that the numbers were much larger in 1938 and 1941 than in more recent years. It was mentioned in a preceding paragraph that the
associated set of young oysters was also much reduced in the five most recent years.

A cyclical periodicity has been reported by Burkenroad (1946) for the same species of starfish. From an examination of published reports of the oyster industry, of newspaper accounts and of testimony of oyster growers, he concluded that this starfish, which is the chief enemy of the adult oyster on the southern coast of New England, has been particularly destructive at intervals of about 14 years during the past 90 years. To Burkenroad the records seemed to indicate an interval of approximately 7 years between the periods of minimum and maximum abundance in each cycle. It seems doubtful, however,

![Figure 6](image_url)

Figure 6. Fluctuations in the average seasonal set of young starfish on 100 oyster shells placed at various depths in Long Island Sound in the years 1937-1948. Unpublished data supplied by Dr. V. L. Loosanoff. The graph shows young populations in 1938 and 1941 which were many-fold larger than those in subsequent years.

whether the data from the diverse sources mentioned, although of much interest, are sufficient to justify the conclusion that such definite periodic cycles prevail. He estimated that the population at peak periods might be 20 times that at trough periods.

The term “Resurgent Populations” is appropriately used for such populations as experience only minor fluctuations for a number of years and then increase rapidly to many times their former numbers with an increment of a hundred or even thousands. After one or several years of increase the population usually returns to approximately its former size. Such a resurgent population for the Pismo clam is shown in Fig. 1 and for the mussel *Septifer bifurcatus* in Fig. 8. Every naturalist familiar with seashore life must have noticed such resurgent populations, for they are common to all groups of invertebrates. A species formerly considered scarce suddenly becomes abundant and soon becomes scarce again.

4. *Donax.*—Conspicuous examples of this type of population are found in certain species of the little “bean clam,” *Donax*. Of the two
species found in California, *D. californica* usually occurs only in small populations while *D. gouldii* remains relatively scarce locally for a number of years and then appears in countless millions. At such times the shells lie in contact or even in several layers in the intertidal zone over many miles of the sandy beaches.

After a life span of three years or less, the clams have sometimes disappeared so completely that not a single individual could be found in the intertidal zone on an extent of beach which was occupied by millions a few months earlier. Fig. 7 shows that these resurgent populations have been recorded at La Jolla in 1894–95, 1909–10, 1913–15, 1931–32, 1934, and 1937–38.

During the summer of 1949 there arrived a resurgent population which seems to have been of unprecedented magnitude. In the autumn of that year the beach had an average population of more than 20,000 young clams per square meter in a zone 2 to 5 meters wide which extended with some interruptions for more than five miles along the coast.

This dense population continued, but with considerable mortality, for almost two years. In July 1951 approximately half of the individuals died after spawning, but those remaining still formed a dense population in many areas. As soon as spawning began the following spring the mortality increased until about mid-July 1952, when only about 20 individuals per square meter, 0.1% of the early population, remained. The major portion of the mortalities occurred within a few days. The deceased included not only members of the resurgent population, which had then attained the ripe old age of nearly three years, but also most of the younger individuals which had reached the beach in the two intervening years and which had managed to
survive in less crowded situations until the final catastrophe. Extended search along the beach, both in the intertidal zone and below, failed to reveal a dozen individuals, old or young, excepting one small area in which all members of the resurgent population died; the younger year-classes survived a few months longer. The miles of sandy beaches thickly strewn with empty shells bore vivid testimony as to what had occurred.

Samples of the population had been examined microscopically once each month or oftener throughout the 3-year history of this phenomenon. Infestation with trematode parasites was common, but no evidence of truly pathogenic organisms appeared during the first two years. Thereafter the moribund individuals lay fully exposed on the surface of the sand for several days before death, apparently too feeble to bury themselves after having been washed out by the surf. The bodies were thin and watery, often with greenish exudations of blood and blood corpuscles, together with many minute unicellular parasites in the connective tissues, blood vessels, epithelium of gut and other tissues. On this evidence it is presumed that the minute parasites caused the epidemic.

In the year preceding this resurgence the population did not exceed one clam per square meter in the same area, although it is probable that some individuals were present below the tidal zone. It is not known whether this resurgent population originated from these few local individuals or were brought as larvae from a distance of many miles by ocean currents, as mentioned earlier. During the months preceding the appearance of this resurgent population at La Jolla there were populations of spawning adults at Coronado, about 12 miles south, at Sunset Beach, 65 miles north, and probably at other localities along the coast. With favorable current velocities of 2–5 miles per day, the larvae could have reached La Jolla from either of these localities during the larval period.

The occasional occurrence of these resurgent populations is presumably due to the chance combination of suitable conditions during the pelagic larval period and to favorable currents which bring the swarms of larvae to the beach at the exact time when they are ready for transforming and setting.

5. Mussels.—Not infrequently an introduced species multiplies with great rapidity for a few years and then declines or disappears. The bay-mussel (*Mytilus edulis diegensis*) offers an excellent example of the rise and fall of such a newly arrived population. In 1940 this subspecies attracted considerable attention in Newport Bay, California, because of its great abundance, and three years later, in August
1943, a small colony was found on the pier at the Scripps Institution of Oceanography, about 60 miles south of Newport Bay. Within a few months they multiplied so that by the following summer these mussels covered all available spaces in the intertidal zone on the pier as well as on adjacent rocks. Later they were found in Mission Bay, San Diego Bay and elsewhere along the coast, and soon they became a nuisance by clogging the intake pipes of salt-water systems. In many situations there were so many young that they could not possibly have grown to maturity because of lack of space. Thus

![Comparison of populations of three species of mussels on the pier and rocks at La Jolla, California. The bay-mussel (Mytilus edulis diegensis) represents the temporary exuberance of a newly introduced stock. The sea-mussel (Mytilus californianus) has maintained an essentially maximum population with only minor fluctuations except in the years when the bay-mussel pre-empted the more favorable situations or when starfish were unusually numerous. The population of the ribbed mussel (Septifer bifurcatus) has been sparse except for a slight resurgence in 1938 to 1940.](image)

vast colonies sprang up in situations unsuitable for long survival (Coe, 1946). Following the maximum during the second year after arrival, the numbers diminished slightly and then declined rapidly to a relatively sparse population in the seventh year (Fig. 8).

In contrast with this briefly exuberant population, the native sea-mussel (Mytilus californianus) has long maintained maximum numbers, with only small fluctuations except for the years when many of the situations suitable for attachment of the young were pre-empted by the bay-mussel (Fig. 8).

A third species of mussel, Septifer bifurcatus, which occupies the same habitat, has maintained a sparse population except for a brief resurgence from 1938 through 1942 (Fig. 8).
6. Dinoflagellates.—Since the productivity of the sea is so largely dependent on phytoplankton for the nutrition of marine animals, it would naturally be expected that conditions favoring large phytoplankton populations would likewise be associated with large animal populations. An abundant crop of phytoplankton is normally accompanied by a large crop of grazing zooplankton which in turn serves directly or indirectly as food for larger animals, invertebrates as well as vertebrates. Thus the phytoplankton primarily, together with other marine plants and a comparatively small amount of detritus from the land, supplies the nutrition of all marine organisms. Hence if a rhythmical periodicity actually occurs in the production of phytoplankton over a series of years, associated changes in the animal populations should be predictable.

Statistical studies by Allen (1941) on the abundance of dinoflagellates on the coast of southern California, extending over a period of 20 years, have shown that the populations of dinoflagellates indicate an inverse correlation with the temperature of the water during the first quarter of the year. Low temperatures on that portion of the Pacific coast often indicate upwelling of deeper oceanic water which brings with it phosphates and other inorganic nutrients required for the growth of phytoplankton and animals. His data, however, do not show satisfactory evidence of cyclical periodicity.

![Figure 9. Fluctuations in the populations of diatoms and dinoflagellates as correlated with mean annual temperature of the water and increment in growth rate of mussels at the pier of the Scripps Institution of Oceanography, La Jolla, California. Low average temperature is associated with upwelling oceanic water, with large populations of dinoflagellates and relatively few diatoms, as well as with rapid growth of mussels.](image-url)
In studies from 1940 through 1943, Coe and Fox (1944) found that the largest dinoflagellate populations occurred during 1942 when the lowest annual water temperature was recorded and that there was a more rapid growth of mussels in the same locality in 1942 than in the three years of higher temperatures. On the other hand, the populations of diatoms in 1942 were smaller than those of the other three years (Fig. 9).

CATASTROPHIC CHANGES

The littoral fauna, in contrast with fauna of the open ocean, is subject to great vicissitudes. During the half-century under observation there have been occasions when excessive cold in winter or heat in summer has destroyed all or nearly all individuals of susceptible species of the population over large areas.

Along the coast of southern New England during certain winters, particularly that of 1918, extensive populations of invertebrates were killed when the intertidal zone was exposed to temperatures far below the freezing point of sea water. Allee (1923) has shown that species having a more southerly range suffered greater losses than those which have a normal range extending farther northward. Blegvad (1929) described the high mortality among littoral invertebrates along the northern coasts of Europe during unusually cold winters. Heat combined with excessive salinity often produce similar catastrophes, as Gunter (1947) observed in the Gulf of Mexico.

MacGinitie (1939) has reported that the heavy rains and freshets of 1927, 1938, and 1941, and presumably of other years, lowered the salinity of the water in some of the bays along the coast of southern California to such an extent that only the more tolerant invertebrates in the intertidal zone were able to survive.

Severe storms and violent surf have in many winters washed out the intertidal substrate, thus destroying the associated invertebrates or crushing them as the surf pounded the rocks on or beneath which they had maintained flourishing colonies.

Epidemics of parasitic diseases have destroyed populations of sponges, oysters, clams, mussels and other invertebrates along many miles of seacoast within a single year. The epidemics in the bean clam, Donax, at La Jolla, California have been mentioned earlier. Diseases of an apparently similar nature, which have been destructive to oysters on the southern Atlantic and Gulf coasts of the United States in recent years, have long been known from other parts of the world (Mackin, 1951).

Sedentary invertebrates with a pelagic larval life are subjected
to great vicissitudes because of their dependence upon favorable currents, as noted earlier. On both the Atlantic and Pacific coasts adverse currents have evidently caused the complete failure of young oysters and clams to establish themselves in many formerly populous localities.

Many marine invertebrates are more or less dependent upon vegetation for support or protection, and without it they perish. Mention may be made of the bay scallop (*Pecten irradians* = *P. gibbus*) which formerly lived in vast colonies in eelgrass (*Zostera marina*) in protected areas over a great extent of the Atlantic coast. Though not limited to such situations, the scallop populations suffered a rapid decline in numbers in 1931–1933 following destruction of the eelgrass by disease. A lucrative fishery disappeared in many localities. With the scallop went also many of the ophiurans, annelids, nemerteans, echinoids, crustaceans, bivalves and other invertebrates that had found congenial homes in and beneath the vegetation. In some areas, however, the populations of scallops have more recently increased again in spite of the absence of eelgrass (Marshall, 1947).

The most spectacular catastrophes to both invertebrates and vertebrates along many miles of seacoast have been caused by a sudden heavy bloom of poisonous dinoflagellates, commonly referred to as “red water.” These phenomena occur frequently in areas of upwelling. Brongersma-Sanders (1948) has shown that on some coasts they may be expected annually but that in most regions they occur at irregular intervals and cannot be predicted.

On the coast of southern California red tide has been observed either locally or over an extent of 100 to 200 miles or more in 1894, 1901, 1907, 1917, 1924, 1933, 1938, 1939, 1945 and 1952; thus the intervals have been 7, 6, 10, 7, 9, 5, 1, 6 and 7 years, with an average of nearly 6.5 years. Some of these occurrences have been highly destructive to both vertebrates and invertebrates while others have caused little injury. Although several species have been involved, the greatest destruction occurred when *Gonyaulax polyhedra* was the predominant organism. Not infrequently in years other than those noted above, the water has become more or less distinctly discolored locally in midsummer by populations of species of *Prorocentrum*, *Ceratium* and other dinoflagellates, but the populations did not reach the density characteristic of red water.

There are many records of the rapid elimination of flourishing populations due to pollution by oil and industrial wastes. Harbors and estuaries which formerly supported a vast assemblage of invertebrates have become barren wastes except for a few of the more resistant species. The effluent from sewers of certain communities, however,
supplies additional nutrition for bivalve mollusks and other forms which feed on particles in suspension.

INTRODUCTION OF FOREIGN SPECIES

Some of the populations under observation have maintained themselves for many years with relatively little apparent change while others have fluctuated widely. Certain mussel beds, for example, with their associated invertebrates, have the same appearance today as they had 50 years ago whereas others have disappeared completely or have disappeared and repopulated repeatedly.

With few exceptions the species that constitute the marine invertebrate fauna of southern New England today are the same as those that were reported by Verrill (1873), although they have varied greatly in local abundance during the past 80 years. New species have been described each year, but most of these have been inconspicuous creatures that Verrill did not study or did not find. Changes in the local distribution of some of the species have been profound, due in large measure to the increased demand for seafood, the encroachment of industry, and the development of seashore properties, but none of the species appears to have been exterminated. Only three conspicuous species have become common since the publication of Verrill’s report. The edible periwinkle (Littorina littorea L.) of European coasts was first noticed at Woods Hole in 1875 and soon became abundant along the coast as far south as Virginia. Another conspicuous, and sometimes abundant, species not reported by Verrill is the medusa Gonionemus murbachi Mayor; this was first found in the Eel Pond at Woods Hole in 1894. The sea-anemone Aiptasianomorpha (Sagartia) luciae (Verrill), discovered in 1887 on the southern coast of New England, became one of the most abundant constituents of the littoral fauna as far south as Florida and the Gulf of Mexico; it has fluctuated widely in abundance and local distribution in subsequent years.

Frequently the result of the introduction of a species of marine invertebrate, either accidentally or intentionally, into a foreign locality has been its speedy elimination. Even when environmental conditions seemed suitable for the existence of introduced individuals, conditions have seldom been favorable for reproduction and continuation of the species. Hence most of the attempts to introduce useful marine invertebrates have met with failure, but there have been some exceptions; a few of the useful species have been successful in establishing themselves in their new environments and have supplemented the human food supply.
The accidentally introduced Japanese little-neck clam (*Protothaca philippinarum*, also known as *Tapes semidecussata*) is an example. This highly palatable bivalve was first noticed on the coast of British Columbia in 1936. During the ensuing eight years it spread widely and in 1944 it had extended along the coast for a distance of more than 80 miles. It is stated by Neave (1944) that in some areas only two seasons of spawning were required to make it more abundant than any of the edible species of native clams. The species is now established at many localities along the Pacific coast and has become commercially important.

The intentional introduction of the soft-shell clam (*Mya arenaria*) of the Atlantic coast furnished the stock from which large crops of these succulent bivalves are now harvested commercially each year in many areas on the Pacific coast. Other introductions from the Atlantic to the Pacific include the horse mussel (*Volsella demissa*) and the quahog (*Venus mercenaria*). The snails *Ilyanassa obsoleta*, *Crepidula plana*, *C. glauca*, *C. fornicata*, *Busycon pyrum* and the gem clam (*Gemma gemma*) are among the immigrants who were transported from east to west coasts as stowaways among oysters.

Attempts to establish reproductive colonies of the Atlantic oyster (*Crassostrea virginica*) on the Pacific coast have not generally met with success; however, when the spat has been introduced it has grown to maturity in some localities, and it is said that normal reproduction occurs occasionally. Plantings of the lobster from the Atlantic coast have always failed.

Only a single species of marine invertebrate has been transported intentionally across the continent in the opposite direction, the reason being that edible invertebrates of the Atlantic coast are almost invariably more succulent than their relatives of the Pacific. Experimental plantings of the Japanese oyster have been made on the coast of New England in the hope that this species will thrive in situations that are unfavorable for the growth of the superior native species.

For many years on the Pacific American coast the Japanese oyster (*Crassostrea gigas*) has been successfully cultivated from young imported each year from Japan. This procedure has been necessary because of its failure to reproduce in the new localities. More recently, however, normal reproduction has occurred in certain areas at intervals of a few years, but most of the commercial crop is still grown from the imported young.

Unless great care is exercised there is always danger of introducing harmful species with beneficial species, and the former sometimes multiply more rapidly and prove to be even more injurious than they
were in their native home. For example, in its native southern New England habitat the snail *Crepidula fornicata* is only occasionally injurious to the oyster beds, but on both shores of the English Channel it has become a great nuisance since it was accidentally introduced with American oysters. The snails quickly established themselves but the oysters did not. The boring snail or drill (*Urosalpinx cinerea*), which is so destructive to oysters and other bivalves, was brought to the Pacific coast and to the coasts of England in futile attempts to introduce oysters from the American Atlantic coast. The similarly destructive Japanese drill (*Tritonalia japonica*) has also become established on the American Pacific coast. The barnacle *Elminius modestus* from the southern hemisphere has now become a pest on British oyster beds, and species of *Teredo*, *Bankia* and *Limnoria*, which destroy wooden marine structures, have established themselves on all sea coasts except in the far north and far south.

**PRODUCTION RECORDS**

A summary of the commercial production in the various groups of marine organisms may be found in "Marine Products of Commerce" by Tressler, *et al.* (1951). However, these records of production do not afford reliable evidence as to the relative size of the population in any year or in any locality because they are influenced in large measure by economic factors such as demand, price and available manpower. Thus, from such records it may appear for a limited time that production is increasing when the population is actually being rapidly depleted. Records of oyster production in Maryland for more than a century, published by Beavan (1945), are typical of the production of most other invertebrates of economic importance. During the periods of maximum production between 1875 and 1892, 10 to 15 million bushels were harvested in that area annually. Then during the ensuing 13 years the rate of production declined rather rapidly, and more recently it has fluctuated irregularly between 2 and 3 million bushels a year, or one-fifth the previous maximum. In this case the production has been correlated with the size of the oyster population, since both have declined to about the same extent.

In most of the other oyster-producing areas on the Atlantic and Gulf coasts there has been a somewhat similar decrease in the past quarter century, but there have been some exceptions, such as that in Louisiana where the annual production has fluctuated widely but where there has been no downward trend during the 20 years preceding 1949 (Gunter, 1949).

Recently the commercial production of the various species of clams in most areas has declined even more rapidly than the production
of oysters. On the contrary, lobster production in the New England and Middle Atlantic states has more than doubled in the 20 years between 1929 and 1949 (Scattergood and McKown, 1951).

POPULATION CYCLES

Many reports have been interpreted as indicating regular and predictable periodicities in the abundance of certain species of insects and mammals, and supposed cycles have been reported for commercial fish catches. However, the evidence is not conclusive, since there is always the possibility of chance coincidence. Irregularity in the periods of fluctuations is certainly the general rule. Cole (1951) and others have shown that purely random variations in environmental conditions would be consistent mathematically with practically all numerical maxima and minima observed in vertebrate populations and with variations in tree-ring width. The evidence presented by Burkenroad (1946) concerning a 14-year periodicity in the abundance of starfish has been noted previously.

From an examination of temperature variations in surface water off New Brunswick, Canada from 1921 to 1947, Hachey and McLellan (1948) concluded that cycles of 3.3, 9 and 15 years were involved, and they have indicated similar trends for other localities along the Atlantic coast. Four years of warmer water have alternated more or less regularly with similar periods of colder water, but the deviations have not been extensive and random fluctuation would seem to be a more plausible explanation.

Hutchinson (1950) concluded from a study of the guano deposits on the Peruvian coast that a well marked 7-year cycle in the inshore movement of warm water and in associated biological catastrophes had occurred regularly from 1864 to 1939; he found no evidence of such a cycle prior to 1864. He concluded therefore that this rhythm is nonpersistent, as are so many meteorological cycles. The deposits on one of the islands showed no trace of this periodicity.

If it should be proved that there are predictable long-term periodic cycles in meteorological conditions or in the physical and chemical phenomena of the environment, then it might be expected that populations of plants and animals would fluctuate accordingly (Allee, et al., 1949; Dice, 1952), but thus far the available information on population abundance seems to indicate that nearly all of the fluctuations have occurred at irregular intervals and have resulted from irregular changes in one or more of the environmental conditions.

A full discussion of this subject may be found in “Symposium on cycles in animal populations” (Hewitt, 1954).
SUMMARY AND CONCLUSIONS

The foregoing examples of fluctuations in populations of marine invertebrates indicate that annual changes of considerable magnitude are of general occurrence. Some of these are evidently due to concurrent changes in environmental conditions (including chemical and physical alterations of the water), to enemies, to disease, and to changes in substrate and in ocean currents. Others are due to migration or introduction to new localities.

Records of local populations of dinoflagellates, starfish, oysters, clams and mussels over long periods show that maximum and minimum populations have sometimes followed each other immediately but that populations of medium size are more numerous than those with either extreme.

Maximum and minimum populations generally occur at irregular and unpredictable intervals with no satisfactory indication of long-term periodic or rhythmical cycles; it is concluded that the supposed periodicities are the result of random variations in the complex environmental conditions, including diseases.

The records show that the reproductive capacity of many marine invertebrates is such that relatively few individuals under favorable conditions can produce a maximum population in a single generation. Overpopulation has been frequent and has often been followed by a rapid decline in numbers, since the competition for space or food was too severe for survival.

Resurgent populations have sometimes resulted from the arrival of vast numbers of pelagic larvae transported from localities several miles distant by ocean currents. Except in bays and partially confined bodies of water, there is little chance that a large proportion of the larvae will settle in the immediate vicinity of their place of origin.

Introduction of a species to a new locality has sometimes resulted temporarily in a high rate of multiplication and territorial expansion, usually followed by a rapid decline in numbers. More frequently the introduced species has found the new locality unsuitable for reproduction and has been rapidly eliminated.

The populations of most commercially important species, with the exception of lobsters, have declined more rapidly during the past decade than at any earlier period of similar length.

Useful as well as harmful species, when introduced intentionally or accidentally, have sometimes become permanent members of the local fauna.

On the Pacific coast an inverse correlation was found between the mean annual temperature of the water and the growth rate of mussels, as well as the populations of dinoflagellates.
Catastrophic changes in the populations have been observed occasionally or at irregular intervals. These have resulted from excessive heat or cold, heavy rains and floods, heavy surf, adverse ocean currents, loss of associated vegetation, industrial wastes, excessive abundance of dinoflagellates, or epidemics of parasitic diseases, with the destruction of many or nearly all individuals of susceptible species over large areas.

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