Population Dynamics in a Sublittoral Epifauna

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AT PRESENT we have little evidence that successional changes following predictable patterns occur among epifaunal communities living on natural rock-reefs in the shallow sublittoral of the open ocean. If this phenomenon does occur here, it can be detected by sustained observations at a single study site. In the period from 1957 to 1960 I conducted an intensive study of the epifaunas of two submarine hogbacks located at different depths off the coast of Corona del Mar, California. Some observations made during this period indicate that both gradual and disruptive changes do occur in these epifaunal communities. Attention is called in this paper to an abrupt change in population density of a predominant species that occurred on part of the shallower reef, and to the widespread biotal adjustments that ensued.

The epifauna of the deeper reef (9.5–18.5 m) remained quite stable throughout the study period (Fig. 1, Reef 500). Nevertheless, this is a dynamic stability with an appreciable flow of individuals through the community structure. For example, in the rock oyster, *Chama pellucida*, which is dominant on the upper part of this reef, natality and growth counterbalance mortality from all causes and such erosive factors as *Lithophaga* burrowings, resulting in a stable community as determined by consecutive samplings over a prolonged period. Some seasonal population fluctuations were observed, especially among sponges and ectoprocts, but I have not detected there any changes that can be construed as serial stages moving toward a climax differing from any extant community.

But this stability appears not to be characteristic of a significant part of the epifauna that

was present on the shallower reef (2–11.2 m) when the first observations were made (Fig. 1, Reef 200). Although the temporal changes in communities observed here cannot be presented as a typical ecological succession, they have had profound influences upon the composition of the epifauna of this rock-reef. My purpose in calling attention to these changes is to stimulate other investigators to follow the course of similar population shifts that may occur in regions under their purview. Additional data may make it possible to delineate the role of successional heterochrony in creating the complex epifauna present on submarine reefs at any given point in time.

The central species in the present study is the common mussel, *Mytilus edulis*. Beginning in late January, 1959, the *Mytilus* population on the inshore reef began a decline in density, which was not recognized as of singular importance at the time. However, before this decline leveled off it resulted in an almost complete disappearance of this species from the reef. The basic cause is unknown, although the early sharpness of decline suggests that disease may have been a contributing factor. Still, the decline did not occur on the deeper reef, some 300 m distant, although it must be pointed out that the maximum population densities here were only a hundredth of those on the shallower reef. In addition to the possibility of disease, it is known that an unusually large population of *Pisaster giganteus* was preying on the dense mussel population during preceding weeks. Although the decline extended through a year, the bulk of the *Mytilus* population disappeared in half this time. Unfortunately observations were not made during part of this period, nor has it been possible to follow developments after *Mytilus* was nearly wiped out. Nevertheless, sufficient data are available to provide a picture of the biotal shifts that accompanied the decline. The dis-
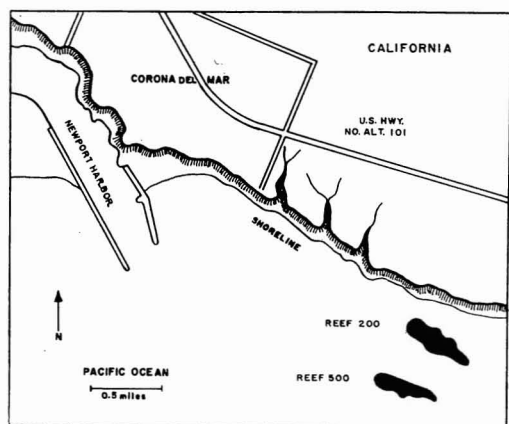
FIG. 1. Location of the two sublittoral rock-reefs under study, in relation to the city of Corona Del Mar and the entrance to Newport Harbor, Orange County, California.

appearance of certain predominant species apparently triggered increases and decreases in associated species. And these changes proved to be very extensive, involving some species that would not have been expected to react to changes in *Mytilus* populations.

STUDY SITE

The rock mass under study is composed of siltstone that has been subjected to complex folding. Gorsline (1962) advises that these promontories may properly be called submarine hogbacks. The dip of the strata ranges from a few degrees to 90°, but the larger part exhibits the latter dip. Because it is located approximately 200 m offshore, I shall refer to it hereinafter as Reef 200.

Situated about 2.5 km southeast of the entrance to Newport Harbor, Reef 200 (Fig. 1) rises from a sand bottom at a greatest depth of 11.2 m to a shallow point of 2 m at standard mean sea level. It has a minimum surface area of 1,200 m² distributed over a length of 58 m and an average width of 27 m (ranges from 8 to 44 m). Because its long axis parallels the shore, the hogback lies athwart the direction of surface wave propagation. This results in interference with wave transmission and a high degree of turbulence at shallow points. The magnitude of turbulence is inversely related to

depth; hence it falls off rapidly down the walls and is barely perceptible at the reef base on days of average swell.

Most of the *Mytilus* population was confined to the reef's flat top, between depths of 2 and 4 m. The same was true of such brown algae as *Eisenia arborea, Egregia australis,* and *Laminaria farlowi.*

STUDY METHODS

Samples of the *Mytilus* populations of Reef 200 were obtained under water by using SCUBA. Quadrats were established by placing metal rings encompassing 0.1 m² against the biota and removing all components by hand. Where required, hammers, chisels, and forceps were also utilized. All specimens were placed in canvas bags, which were sealed prior to ascent and returned to the laboratory. Subsequently species were identified, and individuals of numerable species (noncolonial) were counted and measured.

Prior to the *Mytilus* decline, study sites were selected by dropping metal rings onto the reef from a moving boat. Samples were removed from the sites where the rings came to rest. During and after the decline, conscious attempts were made to remove samples within a few meters of predecline quadrats. This was possible since chisel marks were still evident on the rocks. The first samples were taken on October 29, 1958, and the last on February 22, 1960. The longest period without samples extended from February 15 to August 19, 1959, when the author was in Europe. For most purposes I have divided the dates of sampling into three periods of time: Predecline (October, 1958, to January 15, 1959), Decline (January 16 to October 15, 1959), Postdecline (October 16, 1959, to February, 1960). Although *Mytilus* had not disappeared completely from the reef at the end of the study, its average population per 0.1 m² quadrat was then only 0.5% of its original value. Twelve 0.1 m² quadrats were studied during the above periods.

Large species, such as *Pisaster giganteus, Strongylocentrotus purpuratus,* and *Parastichopus parvimensis,* were sampled with metal rings encompassing 1 m². Specimens of these species were not removed from the reef. Samples were

taken at random distances along transverse and longitudinal transects. Some 100 sq m quadrats were established during this study.

RESULTS

During the decline, the *Mytilus edulis* population at depths of 2 m dropped from an average of about 1,100 to less than 10 individuals per 0.1 m^2. Even more drastic reduction eventually occurred at greater depths (Table 1). And as *Mytilus* declined at specific sites, populations of the red alga *Corallina chilensis,* which are stated in terms of percentage of rock surface covered in Table 1, increased on the same sites, particularly above depths of 4 m. There was, however, a considerable lag between *Mytilus* depletion and the spread of *Corallina*. This lag permitted rapid population increases of a few invertebrates. But, as will be discussed later, some of these increases were cut back after the encroachment of *Corallina* got underway. In turn these population shifts triggered other reciprocal changes among less noticeable species, especially among platyhelminths, nemerteans, mollusks, annelids, and crustaceans (Table 2). Fortunately sufficient samples had been taken prior to, or early in, the *Mytilus* decline to establish a basis of comparison with subsequent unforeseen events. The samples of November, 1958 (Table 1), reveal (1) that most of the *Mytilus* population lived on horizontal surfaces at depths between 2 and 4 m, (2) that its density decreased sharply with increasing depth to the 7-m level, and (3) that

it was absent from this point downward. These relationships persisted unchanged as late as January 15, 1959. Soon thereafter, however, it was noted that *Mytilus* shells were beginning to accumulate in unusual numbers on the shoreward bottom of the reef. Unfortunately an impending trip to Europe precluded additional sampling for several months. But by August, 1959, the *Mytilus* population at the 2-m level (samples were taken only a few meters horizontally from the predecline quadrats) had dropped about 80%. And, as can be seen in Table 1, by February, 1960, considered here to be early postdecline, *Mytilus* had almost disappeared from the entire reef. Apparently at depths below 2 m the initial rate of decline was not as rapid, but complete disappearance eventually occurred. The later occurrence of small individuals at depths of 8 and 9 m is probably explained by dislodgment of small clumps from the reef-top. As seen in Table 1, *Corallina* increased markedly during this time, and came to form a uniform mat, some 6 cm thick, over much of the reef's upper surface. This trend continued until at the culmination of the study it covered 65% of the shallowest part of the reef with a mat some 9 cm thick.

Meanwhile significant changes occurred in molluscan populations. Whereas an average of 25 molluscan species per plot (among a total of some 35 species on all plots) occurred with *Mytilus* (at 2-m depths) prior to the decline, this average dropped to 11 by September, 1959

TABLE 1

CHANGES IN POPULATION DENSITIES, WITH DEPTH AND TIME, OF *Mytilus* AND *Corallina*
(Dashes indicate absence of data)

DEPTH (m)	*Mytilus edulis:* IND /0.1 M^2* BY DATE				*Corallina chilensis:* % COVER† BY DATE			
	11/58	9/59	10/59	2/60	11/58	9/59	10/59	2/60
2	1,086	176	95	5	5	25	50	65
4	180	90	0	0	5	10	15	35
6	95	50	0	0	–	5	5	10
7	7	20	0	0	5	–	–	0
8	0	0	7	0	–	5	5	–
9	0	7	0	0	0	0	0	–

* Individuals per quadrat.
† Per cent of quadrat surface covered by plant.

TABLE 2

DATA GATHERED FROM 0.1 M² QUADRATS AT 2-M LEVEL BEFORE, DURING, AND
AFTER MAJOR PART OF *Mytilus* DECLINE

PHYLA	NO. SPECIES IN PHYLA (Average)		
	Predecline	Decline	Postdecline
Porifera	2.5	1.5	2
Coelenterata	3	3	3
Platyhelminthes	2	3	4
Endoprocta	1	0.5	0
Ectoprocta	5	3.5	6
Sipunculoidea	1	1	1
Nemertea	1	1	3
Mollusca	25	11	25
Annelida	12	7	21
Arthropoda (Crustacea)	8	6.5	11
Echinodermata	4	2.5	5
Chordata (Ascidiacea)	1	1	1
TOTAL ANIMAL SPECIES	66	48.5	82
Numerable Species	56	42	72
Motile Species	36	28	47
TOTAL ANIMAL INDIVIDUALS/0.1 M²	1759	1754	841

(Table 2). Then, as the result of the encroachment of different molluscan species, it increased again to an average of 25 by February, 1960. Four types of population shifts were exhibited by molluscan species during this time: (1) the numbers of one species originally present increased, (2) several species declined but persisted, (3) others declined in numbers and eventually disappeared, and (4) previously absent species invaded the *Corallina* mat. *Chama pellucida* is the only species that increased and retained its population gain, although, as would be expected, the new individuals were very small. Twelve of the original 35 species suffered severe population drops, but were still present in February, 1960. Illustrative of these, in addition to *Mytilus edulis,* are *Hiatella arctica,* which dropped from an average of 135 to 10 individuals / 0.1 m², and *Pterorytis nuttalli,* which dropped from an average of 16 to 2 / 0.1 m². Twenty species of mollusks that were originally present disappeared completely. Among the more prominent of these are *Mytilus californianus, Modiolus capox, Tegula ligulata, Amphissa bicolor,* and *Glans carpenteri.* Among the 15 invading species are *Anomia peruviana, Chlamys hastatus, Flabellina iodinea, Doriopsilla fulva,*

and *Erato vitellina.* The following three species were unaffected by the other changes: *Crepipatella lingulata, Pholadidea penita,* and *P. ovoidea.*

Similar changes took place among the polychaetes. Whereas an average of 12 species occurred on *Mytilus* quadrats (2-m depth) prior to the decline, this dropped to 7 in October, 1959, and then rose sharply to 21 by February, 1960 (Table 2). The greatest increase was exhibited by *Nereis grubei,* which shot from an early average of 8 to 96 individuals / 0.1 m² by October, 1959. It persisted at or above 80 / 0.1 m² into February, 1960. The populations of *Anaitides mucosa* and *Platynereis* sp. more than doubled in this time. *Arabella iricolor* declined at first, but recovered its earlier population size by February, 1960. On the other hand, *Eunice rubra, Typosyllis pulchra, Polycirrus* sp., and *Polydora* sp. declined sharply and eventually disappeared. Eleven species of polychaetes, not previously present, invaded the *Corallina* mats. Among the more interesting of these are *Lumbrinereis zonata, Anaitides* sp., and *Nainereis dendritica.* None of the invading species came to be represented by many individuals.

Among the crustaceans, *Balanus tintinnabulum* displayed a marked population surge from

a predecline average of 30 individuals to 800 / 0.1 m² during the decline. This dropped back to an average of 350 living individuals per 0.1 m² by February, 1960. Curiously, *Balanus tri-gonus* populations remained unchanged throughout the period, as did those of *Pachycheles rudis, P. holosericus,* and *Crangon dentipes.* Four species of crustaceans disappeared during the *My-tilus* decline: *Paraxanthias taylori, Cirolana harfordi, Lophopanopeus leucomanus,* and *L. diegensis,* the latter of which had been represented only by young. These losses were more than offset by the appearance of six species, among which are *Pelia clausa* and *Pugettia dalli.*

Among the smaller echinoderms, *Ophiactis simplex* reacted quickly by nearly doubling its population at the 2-m level, going from 180 individuals to 340/0.1 m² by October, 1959. This dropped back to an average of 154/0.1 m² by February, 1960. The plankton-feeding holothuroid *Cucumaria lubrica* appeared on the 2-m level for the first time.

While working with the above data I was struck by the fact that throughout the entire period from November, 1958, to February, 1960, over 72% of the numerable individuals at the 2-m level were found in only four species (Table 3). We see, however, that the relative percentages that each contributed to the total shifted considerably during the decline.

Now let us turn to an analysis of shifts among the larger species existing on Reef 200. Not only did populations of some of these decline significantly, but there were also shifts of population centers on the vertical axis. One might easily have predicted some, but not all, of these changes. Prior to the decline, 70% of the *Pisaster giganteus* population was found on the upper half of the reef in close association with *Mytilus* (Table 4). Subsequently this percentage dropped to 46. At the same time the *Pisaster* population on the entire reef dropped about 45%, presumably as a result of emigration to new sites. Most of the *Pisaster* emigrants must have come from the upper reef. Quite unexpectedly the sea urchin *Strongylocentrotus purpuratus* appears to have been markedly affected by the *Mytilus* loss. Its population dropped 34% and data in Table 4 point also to a downward movement on the reef. *Strongylocentrotus franciscanus,* on the other hand, suffered only a small loss of total population, and the center of population remained on the lower reef as before. The quadrat densities of the sea cucumber *Parastichopus parvimensis* dropped 30% during the *Mytilus* decline, but the center of population remained on the lower half of the reef.

DISCUSSION

Four kinds of population changes occurred during the *Mytilus* decline: (1) some species previously present with the mussel increased in numbers and held their gains; (2) some species

TABLE 3

PERCENTAGE OF TOTAL INDIVIDUALS OF NUMERABLE SPECIES ON
EACH QUADRAT PROVIDED BY ONLY FOUR SPECIES

SPECIES*	PERCENTAGES OF TOTAL POPULATION BY DATE†				
	11/21/58	1/16/59	9/4/59	10/4/59	2/14/60
Mytilus edulis	61	62	10	5	0.2
Balanus tintinnabulum	2	2	40	46	42
Nereis grubei	0.2	0.7	4	5	10
Ophiactis simplex	11	10	20	22	20
PERCENTAGE OF POPULATION	74.2	74.7	74	78	72.2
NO. OF OTHER NUMERABLE SPECIES	53	50	50	26	68

* Note that these four species accounted for an average of 75% of the total animal population, but their relative contributions to the total changed markedly during the decline.

† Data obtained prior to (11/21/58) and during the *Mytilus* decline on the dates heading columns. All quadrats situated at depths of 2 m and within 3 m of the first.

TABLE 4

RELATIVE POPULATION DENSITIES OF LARGE, MOTILE SPECIES BEFORE AND
DURING THE DECLINE OF *Mytilus* POPULATIONS

SPECIES	INDIVIDUALS / M^2*			
	Predecline		During Decline	
	depth (m)†		depth (m)†	
	2–7	7.1–11.2	2–7	7.1–11.2
Pisaster giganteus	3.3	1.7	1.2	1.5
Strongylocentrotus purpuratus	3.7	0.5	1.6	1.0
Strongylocentrotus franciscanus	0.5	5.8	1.1	4.8
Parastichopus parvimensis	0.1	0.6	0	0.5

* Average number of individuals per square meter.
† Reef is divided roughly into upper (2–7 m depth) and lower parts to show some redistribution of individuals of some species with depth.

appeared only after *Corallina* became predominant; (3) others maintained their populations at previous levels, though most underwent temporary fluctuations; and (4) still others decreased and, in some instances, disappeared. Most of the major population shifts occurred where *Mytilus* was previously dominant, but a few significant shifts were noted below the 4-m line. The degree of these effects may provide some measure of the closeness of relationship of individual species to the mussel (and to *Corallina*), both in positive and negative (inhibitory) ways. Our knowledge of these relationships will be increased significantly when careful studies are made of the feeding habits of the many species involved.

Some species increased in numbers simply because space became available and they had the reproductive capacity to spread out. *Balanus tintinnabulum* exemplifies this; its larvae were available to settle prior to the encroachment of *Corallina*. It is apparent, also, that *Corallina* is unable to invade an established *Mytilus* bed, but when the latter is gone the alga moves in after a few weeks' lag. Other species increased after this alga had become established, apparently because it provided a more suitable milieu. Quite possibly some species increased as a result of the withdrawal of predators not adapted to living in algal mats. The marked decrease in *Pisaster giganteus* resulted from an abrupt loss of food. The shift of remaining individuals to the lower

part of the reef is probably related to the presence there of *Chama pellucida,* an alternate food source. The anemone *Anthopleura* sp. dropped from an average of 40 individuals to 17/0.1 m^2 because of a reduction of substratum rather than of food. Prior to the decline most anemone individuals lived on mussel valves, with a few living in the rock niches. The number increased on the rock as the mussel declined, but the total available space was not sufficient to sustain the previous populations. The reduction of *Parastichopus parvimensis* may be accounted for by the greater production of detritus by *Mytilus* than *Corallina*, but this is purely conjectural. The different reactions of the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus* to the *Mytilus* decline indicate that broad generalizations are not appropriate. Whereas *S. purpuratus* suffered a severe decline, the other species was unaffected. It is perhaps significant that *S. purpuratus* existed primarily on the upper half of the reef, whereas *S. franciscanus* held forth on the lower half. The withdrawal of *S. purpuratus* may have resulted from the reduction of niches provided by the *Mytilus* beds and the fact that *Corallina* produced a very compact cover over the rocky surface.

Some interesting relationships between the numbers of species and individuals occurred during this disruptive change in community structure. These can be ascertained from the last four line items of Table 2. Note, for example,

that while the number of numerable (non-colonial) species per quadrat dropped about 25% during the decline, the total of individuals persisted unchanged for many months. But, as can be seen, by the beginning of the postdecline the total number of individuals in the numerable species fell markedly, in spite of the marked increase in numbers of species per quadrat. We find part of the explanation of this in the fact that when *Mytilus* was at its peak there was an average of 31 individuals per numerable species (aside from *Mytilus*) on each quadrat; that during the decline this jumped to 41, and then dropped to 12 in the early postdecline. These phenomena are based upon the following occurrences: (1) the rapid population increases of a few such species as *Nereis grubei, Balanus tintinnabulum,* and *Ophiactis simplex;* while (2) other species were leaving the sites; (3) formerly absent species, principally motile ones (Table 2), invaded the sites, resulting in an increase of 30% over the original number of species; (4) those species that underwent rapid population increases overshot the mark and dropped back; and (5) all of the invading species, at least during the period of this study, were represented by a small number of individuals. It is of interest that no single animal species equalled the former population density of *Mytilus. Balanus* came closest, but it is only a fraction the size of the mussel. This indicates that the animal contribution to the total biomass in the Hyperbenthal Zone (Pequegnat, 1961) was markedly reduced; the emigrations of the echinoderms mentioned above also account for a considerable loss. Reciprocally, the plant component must have risen through the *Corallina* increase.

For several reasons the appearance of the *Corallina* mat and associated species appears to comprise an unstable complex. Judging from the population changes discussed above and from observations made elsewhere in the subtidal and intertidal, one gains the impression that extremely dense growths of *Corallina* are associated with disturbed conditions. Though one might expect this predominance of the corallines to be temporary, Dawson (1959) points to the distinct possibility that the corallines encroach upon and later dominate areas subject to pollution from human wastes. Hence interest is heightened in obtaining additional samples in the future.

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