SYNECOLOGICAL STUDY ON INTERTIDAL, COMMUNITIES III. AN ANALYSIS OF INTERRELATION AMONG SEDENTARY ORGANISMS ON THE ARTIFICIALLY DENUDED ROCK SURFACE

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SYNECOLOGICAL STUDY ON INTERTIDAL COMMUNITIES III. AN ANALYSIS OF INTERRELATION AMONG SEDENTARY ORGANISMS ON THE ARTIFICIALLY DENUDED ROCK SURFACE[1)]

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Previously from the observation on the zonation of intertidal animals on the cliff of a headland it was suggested that since the dead shells of *Chthamalus challengeri* and *Balanus amphitrite albicostatus* were found beneath the shells of *Mytilus edulis* and *Crassostrea gigas*, and *C. gigas* beneath the *M. edulis* zone, the vertical range of the apparent zones of *C. challengeri* and *B. a. albicostatus* might be narrowed by the covering of *C. gigas* and the distribution of *C. challengeri*, *B. a. albicostatus* and *C. gigas* might be modified by the concealing of *M. edulis* (Hoshiai 1958). While, on the tuff cliff (TN) (Hoshiai 1959) neither barnacles nor oysters were found beneath the mussel zone.

In this study an analysis of the covering process was attempted. To ascertain the order of the successive covering among animals and the difference between the vertical range of each constituent species in the natural apparent zone and the specific character of the vertical range which may be expected if each animal settles independently without interspecific relations, it is necessary to know whether the covering can reappear artificially. Thus, some artificially denuded vertical belts were made on the cliff and rock, where the successive observations were done. Denudations were performed in May, August and December, 1956, and the observations were quantitatively done in June, August and December, 1956; May, 1957; May, 1958 and April, 1959.

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OBSERVATIONS

At the outer coast of Matsushima Bay, *Chthamalus challengeri* Hoek, *Balanus amphitrite albicostatus* Pilsbry, *Crassostrea gigas* (Thunberg) (= *Ostrea gigas*) and *Mytilus edulis* Linné arrange generally in the order from the upper downwards in the intertidal region of the cliffs and rocks. The observed surfaces were subjected to rather strong currents and exposed to the air during the low spring tide.

I

(1) At Station 5 of Tobi-ga-Saki (Hoshiai 1958), the animals found in the vertical belt (50 cm in width) were completely removed in May, 1956, to clear the rock surface.

As shown in Fig. 1A, before denudation two separated *C. challengeri* zones were

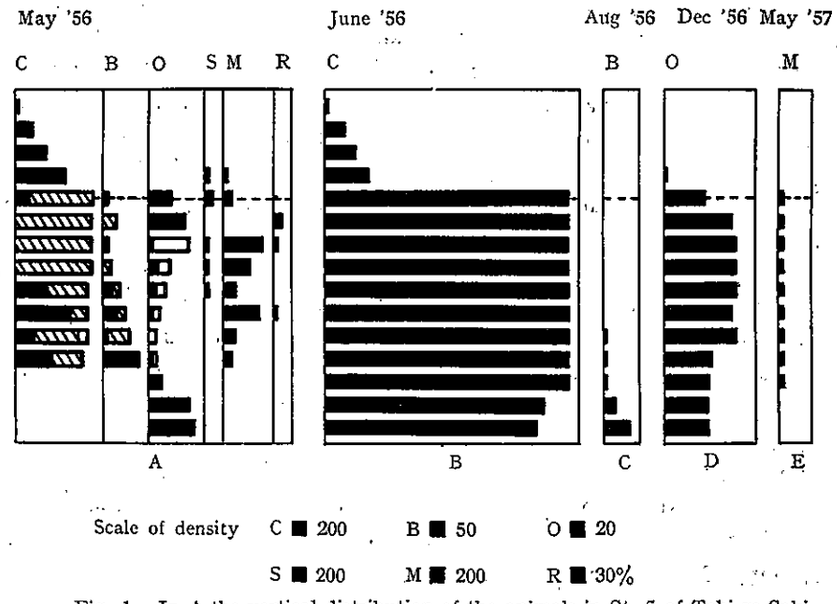

Fig. 1. In A the vertical distribution of the animals in St. 5 of Tobi-ga-Saki is illustrated with the individual number in an area of 10×50 cm and, for *R. japonica* with the percentage of the covered area to the above unit area.

The present number is represented by the black bars, the number covered with *C. gigas* by the shaded bars and that covered with *M. edulis* by the white bars.

In B-E the distributions of the new arrivals found in each observation are shown.

Broken line shows high-water level.

The abbreviations used in the figure are;
C-*C. challengeri* B-*B. a. albicostatus* O-*C. gigas* S-*S. virgatus*
M-*M. edulis* R-*R. japonica*

found above the high-water level and at the middle part of the intertidal region. *B. a. albicostatus* and *M. edulis* distributed from about the high-water level to the middle part of the intertidal region. *C. gigas* appeared below the high-water level and again at the lower part of the intertidal region.

The distribution and the abundance of the new arrivals on the denuded rock surface are also shown in Fig. 1.

In June, 1956 a dense population of *C. challengeri* appeared on the aforesaid cleared rock surface, and the lower limit of the *C. challengeri* zone descended downwards as compared with that in May. At the adjacent part of the same rock several individuals attached only to the shell of *M. edulis* in the upper part of the *M. edulis* zone and no *C. challengeri* settled on the old shells of *C. challengeri* or *C. gigas*. In August at the lower part of the newly formed *C. challengeri* zone, *B. a. albicostatus* settled on the denuded rock surface but not on the shells of *C. challengeri*. As shown in Fig. 1, the newly formed *B. a albicostatus* zone descended and was narrowed as compared with the previous zone. In December the spats of *C. gigas* (1–3 cm in shell length) which might attach in the summer of that year, had become conspicuously perceptible on the shells of *C. challengeri*. By May, 1957 *M. edulis* (about 1 cm in shell length) had appeared around the rim of the shells of *C. gigas*. By May, 1958 *C. challengeri* had decreased in number owing to the detachment and the covering of *C. gigas*, on the other hand, *M. edulis* increased and began to conceal *C. gigas*. By April, 1959 *Septifer virgatus* had become distinguished from *M. edulis* in the upper part of the *M. edulis* zone, but no *Reniera japonica* appeared and thus the general state of the newly formed zonation was considered to rather resemble that in May, 1956.

In August, 1956 another belt was denuded and *C. challengeri* and *B. a. albicostatus* settled on successively, but few *C. gigas* attached. The *C. gigas* zone had become recognizable and *M. edulis* had settled by May, 1958.

The third belt was denuded in December, 1956 and few *Balauns cariosus* which was scarcely found in this neighbourhood settled on the lower part of that belt by April, 1957. The conspicuous *C. challengeri* zone appeared in May, 1957 and *C. gigas* and *M. edulis* had become recognizable by May, 1958.

(2) The next observation was carried out on the smooth vertical surface of a granite rock close beside the headland and the results are illustrated in Fig. 2.

As shown in Fig. 2A, on the aforementioned surface there were previously the *C. challengeri* zone and the *M. edulis* zone. In the *C. challengeri* zone small individuals of *C. gigas* appeared and calcareous chips of shells of dead *C. challengeri* were found among the byssal threads of *M. edulis*.

In May, 1956 all animals were detached to make a vertical belt (10 cm in width). In June, 1956 the denuded part was covered with the dense population of *C. challengeri* whose lower limit descended remarkably, and this belt did not change

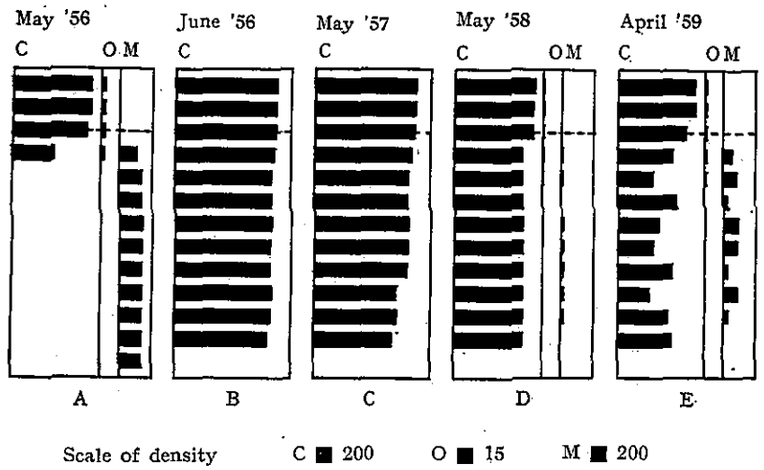

Fig. 2. A: The distribution of animals in the vertical belt (10 cm in width) on a granite rock before denudation.

B-E: The newly formed zonation subsequent to denudation. Broken line shows high-water level.

The abbreviations used in the figure are;

C-*C. challengeri* O-*C. gigas* M-*M. edulis*.

to May, 1957 (Fig. 2B, C). The surface of the *C. challengeri* bed became uneven by the difference of growth rate owing to the crowding (Katô *et al.* 1959). By May, 1958 *C. gigas* and *M. edulis* settled on the shells of *C. challengeri*; the former at the upper part and the latter at the middle and lower parts of the *C. challengeri* zone. By April, 1959 the population density of *C. challengeri* had remarkably decreased, on the other hand, *M. edulis* had increased and its clumps became larger than in May, 1958 (Fig. 2D, E).

On a belt adjacent to the above-mentioned one which was denuded in August, 1956 *C. challengeri* settled and continued to dominate till May, 1957. The successive change in the constituent species resembled that in the former experiment.

In December, 1956 the denudation was performed on the same rock. The zonation of the animals is shown in Fig. 3A. Here, *B. cariosus* had formed a distinct zone by May, 1957 (Fig. 3B), but no *B. cariosus* attached to the shells of *C. challengeri* or *M. edulis* of the adjacent natural rock surface. As the upper limit of the vertical distribution of *B. cariosus* was lower than that of the normal *C. challengri* zone, the rock surface above the upper limits of the former zone remained free from settling of animals. In May, 1957 *C. challengeri* appeared at this bare layer whose lower limit of settlement was higher than that in the belt denuded in May (Fig. 3C). It is noted that no *C. challengeri* settled on the newly

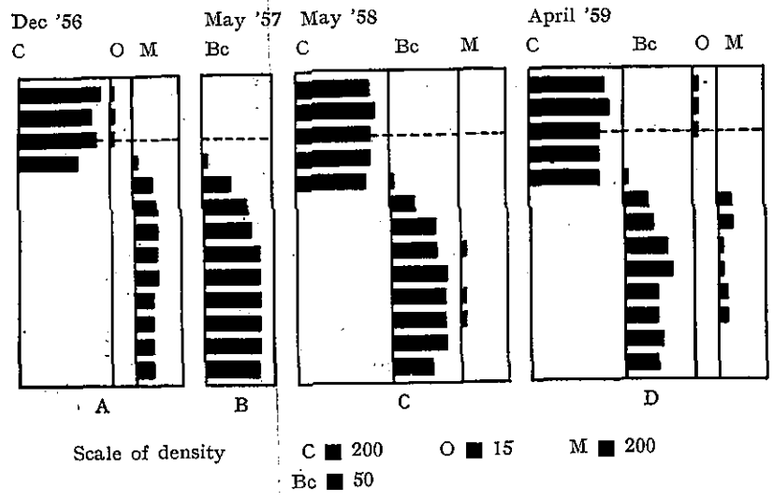

Fig. 3. A: The distribution of animals in the vertical belt (10 cm in width) on the same surface as in Fig. 2 before denudation.

B-D: The newly formed zonation subsequent to denudation. Broken line shows high-water level.

The abbreviations used in the figure are;

C-*C. challengeri* c-*B. cariosus* O-*C. gigas* M-*M. edulis*.

arrived *B. cariosus* shells nor on the *C. challengeri* shells of the adjacent rock. By May, 1958 *B. cariosus* had grown and *M. edulis* appeared as distinct patches on the *B. cariosus* shells.

(3) The denudation was carried out on the tuff cliff (TN) which was observed in the previous work (Hoshiai 1959). At this station on the belt denuded in May, 1956 some *C. challengeri* settled at the upper part and then below them *Ulva* sp. attached. The present belt and that denuded in August, 1956 were similarly covered with the algal community dominated by *Endarachne* sp. and *Grateroupia* spp. in December. By May, 1957 these algae flourished on these denuded belts but details of the flora were not observed. By May, 1958 *M. edulis* had attached to algae.

II

To know the details of the covering process, another observation was tried on a different granite rock near the stations mentioned above.

The experimental belts were set on the vertical surface of the rock, where the dominant species had been *M. edulis*, which blanketed *C. gigas* which in turn encrusted *C. challengeri*. In one of these belts the animals were completely removed and in the other *C. gigas* concealed by *M. edulis* was exposed and remained

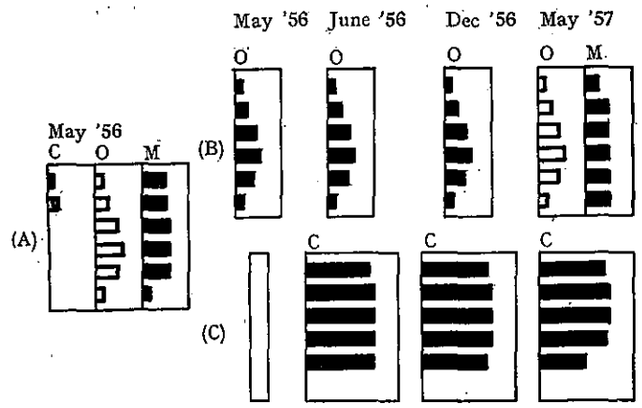

Fig. 4. In (A) the distribution of animals before denudation on a granite rock is illustrated with the individual number. In (B) series, the successive change of animals in the belt where *C. gigas* was left is represented and in (C) series, that in the bared belt.

The present number is represented by the black bars, the number covered with *C. gigas* by the shaded bars and that covered with *M. edulis* by the white bars.

The abbreviations used in the figure are;
C-*C. challengeri* O-*C. gigas* M-*M. edulis*.

as it was.

On the bare rock *C. challengeri* settled in June, 1956, but no individual settled on the shells of the remaining *C. gigas* (Fig. 4). The state of the animals on this rock did not change to December, 1956. By May, 1957 the exposed *C. gigas* belt was completely concealed again by *M. edulis*, while, *C. challengeri* remained as it was.

The same results were aquired from the further experiment repeated from May, 1957 to May, 1958.

DISCUSSION

Hewatt (1935) reported the ecological succession in the *Mytilus californianus* habitat. According to his observation, at the denuded square barnacles appeared prior to the settlement of *M. californianus*. In the present paper it was ascertained that the order of the covering was based on the change of the prominent species which arrived subsequent to the denudation, namely at first barnacles attached and oysters settled on the shells of the barnacles and then mussels attached to the preceding inhabitants. With respect to the attachment of *Mytilus*, Bokenham and Stephenson (1938) reported that *Mytilus perna* settled on the barnacles and algae which occurred after the clearance of the rock surfaces. The fact observed

on the tuff cliff (TN) may show that *M. edulis* smothered not only animals but also algae consequently neither barnacles nor oysters were found beneath the *M. edulis* zone.

If the apparent zone of barnacles is modified by the covering of oysters and mussels and that of oysters by mussels, it must be expected that the state of the animal zone newly formed on the denuded belt differs from that of the natural zones. Concerning this it is interesting that *B. cariosus* which was rare in this neighbourhood formed a distinct zone at the belt denuded in December. As previous instances excepting (3), at the denuded belt the population density of *C. challengeri* remarkably increased and the lower limit of the newly formed *C. challengeri* zone descended lower than that of the normal apparent *C. challengeri* zone. In (1), in spite of that before denudation the *C. gigas* zone had been separated into two layers, *C. gigas* formed a continuous zone at the denuded belt and the pattern of the newly formed *C. gigas* zone rather resembled the pattern of the *C. gigas* zone given by removing of *M. edulis*.

While, it is noteworthy that *C. challengeri* did not settle on the shells of *B. cariosus* or *B. a. albicostatus*, and *B. cariosus* did not on the *C. challengeri* shell. Furthermore, *C. challengeri* did not attach to the old shell of itself. On the other hand, *C. gigas* and *M. edulis* may prevent barnacles and oysters from settling. Accordingly it is found that few barnacles settled on the shells of these bivalves covering the barnacles and also *C. gigas* did not settle on the shell of *M. edulis* which covered *C. gigas*.

As for the belts denuded in May, *C. challengeri* appeared in June on the denuded surfaces. At St. 5, *C. gigas* settled on the shells of *C. challengeri* and *M. edulis* had attached by May, 1957. At the belt set on the granite rock *C. gigas* and *M. edulis* had appeared by May, 1958, and in this case *M. edulis* settled directly on the shells of barnacles. On the other granite rock, the vertical belt where *C. gigas* was exposed, was completely covered with *M. edulis* by May, 1957, though it did not appear at the denuded belt by that time. Accordingly, it is probable that *C. gigas* seems to provide more suitable foundations for the settlement of *M. edulis* than barnacles. However, for the settlement of *M. edulis*, *C. gigas* was not always necessary and sometimes *M. edulis* attached directly to the shells of barnacles as mentioned above. In this case the dead shells of barnacles were found as the small chips of shells on the granite rock.

Thus it is concluded that the order of the covering may be determined by such a process of settling and growth of the organisms as mentioned above.

SUMMARY

At the outer coast of Matsushima Bay, to examine the interrelation among sedentary organisms, artificial denudation was tried.

On the denuded rock surface three covering courses among the sedentary organisms were distinguished, namely, 1. barnacles settle and oysters cover them and then mussels attach to the oysters; 2. mussels cover directly the barnacles which settle on the denuded rock surface; 3. the algal community appeared and is smothered by mussels.

In the course of appearance of the prominent species, *C. challengeri* prevents the other species of barnacles from settling and also itself. Barnacles do not attach to the shells of *C. gigas* and *M. edulis*.

C. gigas provides more suitable foundations for the settlement of *M. edulis* than barnacles.

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