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SUCCESSION OF SESSILE ORGANISMS ON EXPERIMENTAL PLATES IMMERSED IN NABETA BAY, IZU PENINSULA, JAPAN

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INTRODUCTION

Communities of sessile organisms are suitable for the study of succession, because the sessile nature of those organisms makes observations and manipulation easy, their turnover rates are high, and their community development is rapid.

Margalef (1968) and Odum (1969) proposed a hypothesis on the changes through succession of the structural and functional attributes of communities such as species composition, community structure, community metabolism, community biomass and community maturity. The hypothesis predicted that these community attributes would develop into a stable, mature state dominated by large, low metabolic and _K_-selected species in stable environments, while they would remain in an immature state dominated by small, high metabolic and _r_-selected species in unstable environments suffering physical or biological disturbances. However, this remains controversial (Drury and Nisbet 1973, Horn 1974, Connell and Slatyer 1977).

It has been shown that the determination and maintenance of the community structure of sessile organisms are influenced by several factors such as desiccation (Dayton 1971), waves and scouring by storm (Kitching 1937), exposure to wave action (Hoshiai 1965), shading (Kain 1969), log damage (Dayton 1971), sedimentation (McDougall 1943), grazing (Bakus 1966), herbivory (Randall 1961), predation (Stephenson and Searles 1960), and overgrowth (Hoshiai 1959, 1960, 1965). Besides, it is thought that morphological, physiological and ecological characteristics of species appearing during succession influence the process of succession. Nevertheless, the correlation between the structural and functional attributes of communities through succession remains indistinct because studies on the changes of the functional attributes are still few. Thus, a comprehensive understanding of succession needs investigating the changes of the structural and functional attributes of communities through succession in stable environment as well as in unstable one.

I investigated the succession of sessile organisms by suspending experimental plates at four fixed depths of the subtidal zone regarded as more stable than in the intertidal zone. The changes in species composition, community structure, community metabolism, community biomass and community maturity of sessile organisms through community development were investigated for the purpose of testing the hypothesis of Margalef (1968) and Odum (1969), and clarifying the general characteristics in the community development of sessile organisms.

MATERIALS AND METHODS

Study site

The study site was in Nabeta Bay adjacent to Shimoda Bay located at the southern end of the Izu Peninsula, Japan (34°39'40"N; 139°56'35"E). This site has a water depth of 6.0 m at lowest low tide and is located ca. 400 m from Shimoda Marine Research Center (S.M.R.C.) of University of Tsukuba where various observations and measurements were carried out (Fig. 1). Surface water temperatures in Nabeta Bay varied between 13.6 °C (February) and 24.8 °C (August) during the study period. Surface salinities varied little, ranging from 32.6‰ in July to 34.2‰ in January. These data were supplied from S.M.R.C. of University of Tsukuba.

Immersion of plates

In the first series of experiment (series 1), concrete plates (20 cm x 20 cm x 2 cm) were set at depths of 1.0, 2.5, 4.0 and 5.5 m below sea level on July 9, 1974 to investigate the changes of the above-mentioned structural and functional attributes of communities through succession (Table 1 and Fig. 2a). These depths are respectively designated as Depth A, B, C and D in the following description. In the second series (series 2), plates were set at the same four depths on August 8, 1975 to investigate the effect of light intensity on community metabolism, and in the third series (series 3), plates were set at Depth B on August 8, 1975 and August 9, 1978 to investigate the effect of temperature on community metabolism (Table 1). On each setting occasion, a set of 4 plates was fixed with concrete cement to a polypropylene rope at the position corresponding to each depth, and plates were suspended vertically at each depth (Fig. 2b).

In series 1, 8 ropes with 16 plates were tied, in the sea, to a galvanized pipe floated by several buoys so as to maintain the plates at the four fixed depths below the sea surface (Fig. 2a). This pipe was oriented northwest and southeast and held with several anchors to avoid the action of waves or swells, especially during typhoons in summer (Fig. 2a). A round iron bar was attached to the bottom ends of the ropes to avoid mutual contact of plates (Fig. 2a). The distance between vertical ropes was 70 cm. In series 2 and 3, experimental plates were suspended in emptied positions after sampling of several plates of series 1 by using the same galvanized pipe.

Sampling

Sampling of the plates of series 1 was carried out four times in the first year (Aug. 23-Sept. 2, 1974; Nov. 8-17, 1974; Jan. 10-18, 1975; May 1-13, 1975) and then three times in the late summers or early autumn of subsequent years (Aug. 9-15, 1975; Sept. 6-23, 1976; Aug. 7-18, 1977); the immersion period from setting out plates until each sampling time is represented by the approximate number of elapsed months, i.e., 2, 4, 6, 10, 13, 26 and 37 months (Table 1). In series 1, a total of 112 plates were detached from the ropes for investigation. One rope with 16 plates was left in place to investigate further biotic changes. Sampling of the plates of series 2 and 3 was carried out in 1977 and 1978, respectively (Table 1).

On each sampling occasion, a set of 4 plates at the deepest depth was first detached from the rope and raised carefully, so as not to damage the organisms on the plates. The plates were carefully detached from the rope with a hammer and screwdriver. They were transported to the laboratory at S.M.R.C., and kept in a running seawater tank until observation and measurement.

Observation and measurement

Fig. 3 is a flowchart showing the procedure of observations and measurements carried out on the plates of series 1. At each sampling, samples taken from Depth D were dealt with according to this procedure. Metabolic rates of the samples were first measured as soon as possible to investigate community metabolism. The plates were then photographed in color and the positions of sessile organisms on the plates were sketched briefly to estimate their coverages (%). All the organisms on one half of each plate were stripped off with a hammer and paint scraper, and were used for the measurement of community biomass, i.e., chlorophyll *a*, organic carbon, organic nitrogen, dry mass, ash dry mass, and ash-free dry mass. All the organisms on the other half of the plate were preserved in a 70% ethanol solution for identification. Subsequently, the plates removed from Depths C, B and A were treated in the same manner as described above. Three of 4 plates at each sampling were used for the above-mentioned observations and measurements, but in some cases only 2 plates were used. The remaining plate was used for identification.

(1). Coverage

The coverages of sessile organisms in the central area (16 cm x 16 cm) of plates were estimated by the analysis of photographs (Fig. 2c). The peripheral area was excluded from counting because of a possible edge effect caused by sessile organisms or possible damage occurring during the experiment. The photographs were projected onto 1 cm x 1 cm graph paper, and the coverage of each species was calculated by counting the number of squares occupied by the attachment sites of sessile organisms.

(2). Metabolic rates

Total metabolic rates of organisms existing on plates (20 cm x 20 cm), i.e., net primary production of community (Pn) and community respiration (R), were measured by using a metabolism measurement apparatus as shown in Fig. 4. Their measurements were made under constant light or in darkness at constant water temperature. The water temperature at each measurement was set according to the mean surface water temperature in Nabeta Bay during each sampling time in the past 5 years (Table 1). Before measurement, all the organisms on the four lateral faces of each plate were stripped with a hammer, chisel and whetstone. Immediately, the plates were placed in a water bath of 300 liter kept at fixed temperature within a variation of 0.2 °C, and then the organisms were acclimated to constant temperature and to constant light or darkness at least for 15 minutes. Three respiro-chambers (3.9 or 5.65 liter) fitted with a stirrer are set on the inside wood rack of its bath (Fig. 4). The respiro-chambers are made of clear acrylic plastics and are able to be closed tightly by silicone rubber tube and several pinchcocks during measurement. A 500-watt candescent floodlight installed 37 cm over each plate provided its surface with 23,000 lx. The amount of dissolved oxygen in the water within the respiro-chamber was determined with Winkler's method at the beginning and the end of each measurement. The duration of measurement was 5 to 30 minutes. This duration was arbitrarily determined, taking account of both biomass of each sample and temperature at measurement. During measurement, oxygen concentration was never allowed to supersaturate the water or to decrease to less than 4.22 mg O_2/l. Measurements were all carried out in the daytime to exclude the influence of diurnal rhythm of organisms. When large algae, Codium latum, C. fragile, C. divaricatum and Eisenia bicyclis, were very massive on plates, they were cut from their holdfasts before measurement, and then E. bicyclis was divided into the blades and stipe. The metabolic rates of these four species were measured by using the whole of separated parts or were estimated by using the small portion.

(3). Biomass

After measuring community metabolism and sketching the positions of sessile organisms on the plates for the estimation of their percent cover, the organisms on one half of each plate were all stripped off with a hammer and paint scraper, were homogenized with a juice mixer, and were used for the measurements of chlorophyll *a*, organic carbon, organic nitrogen, dry mass, ash dry mass, and ash-free dry mass. The amount of chlorophyll *a* in the homogenate was determined by a modified routine method (SCOR-UNESCO 1964); the absorbance at 430, 630, 645 and 665 nm of the 90% acetone extracts of samples which were left at 3 to 5 °C in the dark for 24 hours was measured with a spectrophotometer.

The remainders of the extracted samples were dried in a hot-air drier at 80 °C, and then were powdered with an electric-powered coffee mill. The amounts of organic carbon and organic nitrogen were determined from a small part of its powder by Tyulin's and micro-Kjeldahl's method, respectively. A small part of the rest was burnt in a muffle stove at 500 °C for 6 hours. Ash-free dry mass was then determined by subtracting ash dry mass from total dry mass.

Effect of light intensity on photosynthetic metabolism

Effect of light intensity on photosynthetic metabolism was examined on the plates of series 2 immersed for ca. 2 years (Table 1). Plates were exposed to seven different light intensities from 5,800 to 36,500 lx at 24 °C to determine net primary production of community (Pn) and to darkness at 24 °C to determine community respiration (R). At the biginning and the end of these measurements, the amount of dissolved oxygen in the water within a respiro-chamber was determined with Winkler's method. The acclimating time and the measuring duration of samples under those conditions were the same as the samples of series 1. The measurement of oxygen concentration in water was made under the condition without supersaturation or depletion of oxygen in a respiro-chamber.

Effect of temperature on metabolism

Effect of temperature on community metabolism was examined on several plates of series 1 and on 16 plates of series 3 (Table 1). In this measurement, plates were exposed at four or five different temperatures from 12 to 24 °C under 23,000 lx or in darkness. Acclimating time of samples was at least 15 minutes. The measuring duration was 10 to 40 minutes, taking account of both biomass of each plate and temperature at measurement. At the beginning and the end of each measurement, the amount of dissolved oxygen in the water within a respiro-chamber was determined with Winkler's method. The measurement of oxygen concentration in water was made under the condition without supersaturation or depletion of oxygen in a respiro-chamber.

RESULTS

1. Species composition and percent cover of algae

Macroalgae were not found on any of the plates immersed for up to 2 months. Though articulated and non-articulated coralline algae of the family Corallinaceae were found on all plates immersed longer than 2 months, they are not included in this study because of difficulty in discriminating their presence or absence accurately in the photographic analysis. During the period from 4 to 37 months after immersion, a total of 17 species of algae were observed. The changes in mean cover (%) of these 17 species during the period of study are summarized in Table 2. The time of appearance of each species and changes of its percent cover during community development are described below for each phylum.

(1). Chlorophyta

Cladophora wrightiana, *Ulva pertusa*, *Codium adhaerens*, *Codium fragile* and *Codium latum* were early colonizers, all having recruited by 4 months after immersion. *C. wrightiana* was a fugitive, not being found again after appearing at Depths A and B after 4 and 6 months. Four months after immersion, *U. pertusa* showed the highest percent cover at all depths; higher at Depths

A and B than at Depths C and D. It was also highest in frequecy, having recruited on all plates at Depths A, B and C and 1 of 3 plates at Depth D. Subsequently it declined gradually in cover until it disappeared almost completely from the plates; 13 months after immersion it was found only at Depth D and was absent at all depths 26 months after immersion. It appeared again at Depths C and D only, 37 months after immersion.

The mossy alga *Codium adhaerens* recruited 4 months after immersion at Depths A and B and 6 months after immersion at Depths C and D. Its coverage reached a maximum 10 months after immersion at all depths except Depth C. The coverage had decreased at 13 months, and this species was not found again on any plate except for a single reappearance at Depth C after 37 months.

Codium fragile and *C. latum* are taller algae, becoming large at maturity. They first appeared 4 or 6 months after immersion and were found more frequently at Depths A and B until 13 months after immersion. These two species often occurred outside the central area of plate. They reached a maximum size in the late spring 10 months after immersion or in the late summer 13 months after immersion. However their coverage was low because of the small size of their holdfasts. None of them were present 26 and 37 months after immersion. The remaining species, *Chaetomorpha spiralis*, was a fugitive, being found transiently during the experimental period.

(2). *Rhodophyta*

Pterocladia capillacea and *Grateloupia sparsa* appeared as early colonizers 4 months after immersion. The former species occurred continuously, but the latter was a fugitive and never found during the period from 10 to 37 months after immersion.

At 6 months after immersion, *Gracilaria textorii*, *Champia parvula* and *Ceramium paniculatum* first appeared as early colonizers; *G. textorii* was found 6 to 10 months after immersion, and the others were fugitive appearing only at 6 months after immersion. Their coverage was low except for one appearance of a small filamentous *C. paniculatum* at Depth C after 6 months. The occurrence of these three species was restricted to the period from 6 to 10 months after immersion, so that they and *Grateloupia sparsa* are considered to be absent in summer.

Unlike the above-mentioned four species, *Pterocladia capillacea*, *Plocamium telfairiae* and *Grateloupia livida* were found in summer. They were first found on the plates immersed for 4, 6 and 10 months, respectively. *P. capillacea* was continuously found 4 to 26 months after immersion at Depths A and B and 4 to 13 months after immersion at Depths C and D. *P. telfairiae* was found 13 and 26 months after immersion at Depth A. *G. livida* was a fugitive, but was able to colonize even more than a year after the start of immersion since it appeared first 26 months after immersion at Depth C. It is not clear whether the other two species survived as perennials or whether they had newly recruited 13 to 26 months after immersion.

Gelidium amansii appeared transiently 10 or 13 months after immersion. It also appeared on one Depth D plate immersed for 37 months; no other species of red algae were found 37 months after immersion. *G. amansii* can survive during the summer like the three species mentioned above, but it differs from them in that it shows later recruitment in succession.

(3). Phaeophyta

Colpomenia sinuosa was an early colonizer, being found on the plates immersed for 4 months at Depths A, B and C and a little later, on plates immersed for 6 months, at Depth D. It was subsequently found at up to 10 months after immersion, and more abundantly at shallower depths. But it was not found on any plate in late summers during the period from 13 to 37 months after immersion.

Padina arborescens grows larger than the previous species. It was occasionally found on plates immersed for 6 or 10 months but not found on any plate immersed for 13 months. It was found on only one plate at each of Depths A to C 26 months after immersion. It was also found on only one plate at each of Depths A and B 37 months after immersion. This species was never found at Depth D.

Eisenia bicyclis grows much larger with its broad blades, long stipe and large holdfast. This species appeared earlier at greater depths: it was first found on plates of Depths A and B immersed for 26 months, on plates of Depth C immersed for 13 months and on plates of Depth D immersed for 6 months. Recruitment occurred in the period from 13 to 26 months after immersion at Depths A and B. The values of coverage at Depths A and B increased with time to reach 11.2 or 6.9% respectively, 37 months after immersion. On the other hand, the pattern of change in coverage with time at Depths C and D was reversed: at Depth C the coverage decreased to 1.8% 37 months after immersion, and at Depth D it was totally absent 26 months after immersion. Nevertheless, one young individual of this species appeared again on one of Depth D plates immersed for 37 months.

2. Species composition and percent cover of sessile invertebrates

Throughout the period from 2 to 37 months after immersion, a total of 28 species of invertebrates were observed (Table 3). The barnacles *Megabalanus volcano* and *M. rosa* were counted as the same species because of difficulty in identifying their young individuals in the photographic analysis. The changes in mean cover (%) of these 28 species during community development are summarized in Table 3. The time of appearance of each species and changes of its percent cover during community development are described below for each taxon.

(1). Cirripedia

Balanus trigonus was found on all plates sampled. The coverage of this species was 97.9 to 100.0% 2 months after immersion; higher at Depths C and D than at Depths A and B. After that, its coverage decreased until 6 or 10 months after immersion, but increased again 10 or 13 months after immersion. At Depths A and B, though there was a slight increase in coverage from 13 to 26 months after immersion, the coverage at 37 months after immersion decreased to the lowest level of 79.8 or 87.6%. On the other hand, at Depths C and D, the coverage decreased slightly 26 months after immersion, and increased to 99.4 or 99.6% 37 months after immersion. This high values in coverage at Depths C and D approximate to those of younger plates immersed for 2 or 4 months.

Megabalanus volcano and *M. rosa* were the earliest colonizers like *B. trigonus*, but they showed much lower coverage. Their coverage increased until 4 or 6 months after immersion unlike *B. trigonus*. At Depths A and B, *Megabalanus* coverage decreased successively to reach a minimum 37 months after immersion. At Depths C and D, it temporarily increased 10 to 13 months after immersion. And then, it decreased at Depth C, but increased 26 to 37 months after immersion at Depth D. Another species *Balanus eburneus* was rare, being found only on one plate immersed for 4 months.

(2). *Tunicata*

The tunicates identified are all colonial ascidians except for a solitary species *Styela plicata*. *Botrylloides violaceus*, *Botrylloides simodensis*, *Botryllus primigenus*, *Symplegma reptans* and *Styela plicata* appeared first in the period from 2 to 6 months after immersion. The occurrence of these five species was restricted to the period from 2 to 13 months after immersion. Though the coverages of these species were low, *B. violaceus* and *B. simodensis* were slightly high in coverage, especially 6 months after immersion.

Diplosoma mitsukurii, *Didemnum moseleyi* and *Trididemnum savignii* more often dominated plates. These three species appeared first 2 or 4 months after immersion, and they were continuously found until 37 months after immersion. The coverage of _D. mitsukurii_ increased to a maximum of 61.6 to 77.4% 10 months after immersion at Depths A, B and C, and to that of 89.1% earlier at 6 months after immersion at Depth D. And 13 months after immersion, its coverage decreased to 9.6 to 47.7%. In the period from 13 to 37 months after immersion, its coverage decreased after an increase at Depth A, while increased at Depths B, C and D. The coverage at 37 months after immersion showed a higher value of 85.5% at Depth D. _D. moseleyi_ showed the maximum coverage of 24.2 to 50.1% 13 or 26 months after immersion. But, the coverage at 37 months after immersion decreased to 5.3 to 21.1%. This decrease was remarkable at Depths C and D. _T. savignii_ showed the maximum coverage of 12.8 to 32.2% 13 or 26 months after immersion at Depths A, B and C. But the coverage at 37 months after immersion decreased to 0.8 to 3.8% at these depths. At Depth D, this species showed low coverage throughout the period of study, and was absent 37 months after immersion.

Amaroucium multiplicatum and _Leptoclinides_ sp. were rare and appeared at Depth A or B 37 months after immersion. But the latter species was also found on one of Depth D plates immersed for 6 months.

(3). Porifera

Halichondria japonica appeared first 4 or 6 months after immersion. Though this species was found only on one of Depth B plates 10 months after immersion, it occurred at all depths 13 months after immersion. Its coverage showed a maximum 26 months after immersion, much higher at Depths C and D. And 37 months after immersion, it was not found at Depth A but showed low coverage at Depths B, C and D. Halichondria panicea was transiently found 4 and 10 months after immersion, appearing earlier at Depths A and B and later at Depths C and D. Mycale plumosa was rare, being found only on one of Depth B plates immersed for 37 months.

(4). Bryozoa

The bryozoans identified are of encrusting types except for Amathia distans having a stoloniferous form. Watersipora subovoidea was found at all sampling times and more often dominated the plates. This species appeared first 2 or 4 months after immersion. At Depths A and B, though there was a transient decrease in coverage 10 months after immersion, the coverage increased to reach the highest value of 39.8 or 44.8% 13 months after immersion. At Depths C and D, the coverage did not show such a high value at this time. In the period from 13 to 37 months after immersion, the coverage decreased at Depth A, but increased greatly 26 to 37 months after immersion at Depths B, C and D. The coverage at 37 months after immersion showed a gradual increase with depth. Depth D plates immersed for 37 months showed the maximum of 82.8% in coverage.

Amathia distans often dominated the plates like *W. subovoidea*. This species appeared first 6 months after immersion at Depths C and D, and later 10 months after immersion at Depths A and B. It was continuously found until 37 months after immersion. The coverage at 13 months after immersion reached a maximum or was close to it, being higher at Depths C and D. The coverage temporarily decreased 26 months after immersion, but increased again 37 months after immersion, especially high at Depths C and D.

Schizoporella unicornis appeared first 4 or 6 months after immersion. This species was continuously observed until 13 months after immersion, but was absent 26 and 37 months after immersion. *Parasmittina trispinosa*, *Membranipora savartii* and *Celleporaria columnaris* appeared first on the plates immersed for 4 or 6, 6 or 10, and 10 months, respectively. These three species were transient and restricted also to the period from 4 to 13 months after immersion.

(5). Polychaeta

The serpulid *Hydroides ezoensis* appeared first 4 months after immersion. Its coverage showed a maximum 10 months after immersion though there was a decrease 6 months after immersion. This species was continuously found until 37 months after immersion at Depths A, B and C, where the coverage increased 26 to 37 months after immersion. At Depth D, though absent 13 and 26 months after immersion, it reappeared 37 months after immersion.

The spirorbid *Dexiospira foraminosus* appeared first 2 months after immersion, when the coverage was higher at greater depths. This species was not found on the plates immersed for 6 months. Nevertheless, it reappeared 26 months after immersion at Depth A, 37 months after immersion at Depth B, and earlier 13 months after immersion at Depths C and D. After that, it disappeared at Depths C and D, earlier at the latter depth.

(6). Bivalvia

Pinctada fucata, *Mytilus edulis* and *Crassostrea nippona* become fairly large at maturity. *P. fucata* appeared only at Depths A and B. It appeared first on one of Depth A plates immersed for 6 months. Though not found 13 and 26 months after immersion, it was present on 2 of 3 Depth A plates and 1 of 3 Depth B ones 37 months after immersion.

M. edulis appeared at Depths A, B and C. It appeared first on Depth A to C plates immersed for 6 months, but its coverage decreased temporarily 10 months after immersion. Subsequently, the coverage increased to reach 22.9% 37 months after immersion at Depth A, but this species was not found at all 26 and 37 months after immersion at Depths B and C.

C. nippona appeared also at Depths A, B and C. It appeared first on one of Depth A plates immersed for 10 months. And 13 months after immersion, it was found on all plates at Depths A and B and on one plate at Depth C. The coverage at 37 months after immersion increased to 59.6 or 52.5% at Depths A and B, while it decreased to 21.7% at Depth C after having reached a maximum of 50.4% 26 months after immersion.

3. Stages in community development inferred from dendrogram analysis

(1). Dendrogram analysis

To discriminate successive stages of community development, the samples were subjected to cluster analysis using Horn's coefficient of similarity (Horn 1966), based on Shannon-Weaver information theory and the weighted group average method. The data used for this analysis were the mean percent cover of sessile organisms in the central area of plates. The results of the analysis are shown as a dendrogram in Fig. 5, in which three major clusters and four sub-clusters can be discriminated. The level of percentage similarity for this division was arbitrarily determined to be between 81.2 and 83.6% (Fig. 5). The samples showed a general tendency to be clustered in the order of duration of immersion. But Depth D samples immersed for 6 to 37 months which formed a sub-cluster together were similar to younger Depth A to C samples immersed for 4 to 10 months than those immersed for 13 to 37 months. This suggests that these Depth D samples are at an early stage of community development. The 26D and 37D samples differed from younger Depth D samples immersed for 6 to 13 months, probably showing a return to earlier stage of community development. On the other hand, Depth A to C samples immersed for 13 to 37 months which were clustered together were evidently different from those immersed for 2 to 10 months. This suggests that these older samples are at the later stage of community development. Of these, the 26 and 37 months' samples formed a sub-cluster together. In it, the 37A sample differed evidently from other samples. This dissimilarity indicates that the sample is probably at the latest stage of community development studied here.

(2). Transition of developmental stages

In the following, the major three clusters in Fig. 5 are regarded as three stages in community development, and the four sub-clusters in the second and third major clusters were regarded as sub-stages. Based on the results of this cluster analysis, the samples can be arranged according to depth and time and partitioned into the three stages and four sub-stages as shown in Fig. 6.

As seen in this diagram, Depth A to C communities shifted successively from Stage 1 to Stages 2 and 3 with time. In Stage 2, Depth C community was in one sub-stage differing from Depth A and B communities 6 and 10 months after immersion. On the other hand, Depth D community shifted from Stage 1 to Stage 2 without advancing to Stage 3, staying at Stage 2 throughout the period from 4 to 37 months after immersion. In Stage 2, Depth D samples immersed for 6 to 37 months were in one sub-stage (Fig. 6). From this long staying at Stage 2, it is inferred that the Depth D samples is at an immature stage of community development.

Furthermore, 37A sample differed from others in one sub-stage of Stage 3. It is inferred from this that the 37A sample is at a mature stage of community development. On the other hand, 26D and 37D samples differed from others in one sub-stage of Stage 2. This is regarded as a return to a more immature stage of community development owing to the decrease in coverage or disappearance of *Eisenia bicyclis* and *Crassostrea nippona* dominated finally in this study, the reappearance of the early colonizers, *Ulva pertusa* and *Codium adhaerens*, and the increase in coverage of early colonizer *Balanus trigonus*.

(3). Features of developmental stages

Features of the first stage and the four sub-stages of the second and third stage distinguished in this study are summarized in Table 4. The first stage and four sub-stages are characterized by the species which occupied the top to third rank in the mean coverage (%) of species in the central area of plates at each immersion period and depth. However, the top to third species were always sessile invertebrates, but not algae. Thus, the characterization of stage and sub-stages was also made on algae in the same manner (Table 5). In all samples, *B. trigonus* always occupied the top rank.

In Stage 1, *Dexiospira foraminosus* was sub-dominant, always occupying the second rank; *Megabalanus volcano* and *M. rosa* were next dominant species, occupying the third rank except for one sample. Macroalgae visible with the naked eye were not observed at all, but the existence of some algae is inferred from the presence of chlorophyll *a* in 90% acetone extracts of samples or by the production of oxygen when exposed to light. This suggests the presence of macroalgae at the germination stage or of microalgae such as diatoms or filamentous brown algae (e.g., *Ectocarpus* spp.). Bacteria, diatoms, *Ectocarpus* spp. and hydroids have been observed as a sheet-like film in the earliest stage of succession on marine substrata (e.g., Zobell and Allen 1935, Coe and Allen 1937, Itô 1959, Kawahara 1962, Kazihara 1964, Fager 1971, Foster 1975). Samples at this stage have thin, uneven surface structure formed by the shells of barnacles and by a sheet-like film, which consists of the species mentioned above, on the shells of barnacles or plate surface. This stage is, therefore, characterized by the earliest colonizers mentioned above, especially by *B. trigonus* and *D. foraminosus*.

In the first sub-stage of Stage 2 (Sub-stage 2-1), *Diplosoma mitsukurii* was sub-dominant, always occupying the second rank; *Watersipora subovoidea* dominated next, occupying the third or fourth rank except for one sample. As to algae, *Pterocladia capillacea*, *Ulva pertusa*, *Codium adhaerens* and *Colpomenia sinuosa* were dominants. Samples at this sub-stage have sheets of colonial animals formed on the shells of barnacles and a stand of shorter algae. This sub-stage is characterized by the early colonizers of these four algal species and by the colonial animals of *D. mitsukurii* and *W. subovoidea*.

In the second sub-stage of Stage 2 (Sub-stage 2-2), Diplosoma mitsukurii was sub-dominant, always occupying the second or third rank; Amathia distans dominated next, occupying the second to fourth rank. As to algae, Ceramium paniculatum dominated in addition to the four species of Sub-stage 2-1. Samples at this sub-stage were similar to ones at Sub-stage 2-1. This sub-stage is additionally characterized by C. paniculatum and A. distans.

In the first sub-stage of Stage 3 (Sub-stage 3-1), Amathia distans was sub-dominant, always occupying the second or fourth rank; Didemnum moseleyi dominated next, occupying the third to the fifth rank. As to algae, Pterocladia capillacea, Codium adhaerens and Eisenia bicyclis were dominants. Samples at this sub-stage have sporadically massive, rough surface structure formed by the shell of Crassostrea nippona ranking the fifth, on which there was the overgrowth of sessile invertebrates, mainly of barnacles, ascidians and bryozoans. The occupation of three-dimensional space by the large algae Codium latum and E. bicyclis was seen on the plates. This sub-stage is characterized by D. moseleyi as well as P. capillacea and A. distans.

In the second sub-stage of Stage 3 (Sub-stage 3-2), Diplosoma mitsukurii was sub-dominant, always occupying the second to fifth rank; Crassostrea nippona dominated next, occupying the second to fifth rank. As to algae, *Eisenia bicyclis* occupied the top rank except for one sample, and *Padina arborescens* and *Pterocladia capillacea* dominated next. Samples at this sub-stage have more massive, rough surface structure formed by the shell of *C. nippona* than at Sub-stage 3-1. On its shell, there was also the overgrowth of sessile invertebrates, mainly of barnacles, ascidians and bryozoans. The water column near the plates was occupied predominantly by *E. bicyclis*. Especially, the 37A sample consisted of the double layers of *C. nippona*. This sub-stage is characterized by *E. bicyclis* and *C. nippona*.

4. Community structure

To examine the transition of community structure of sessile organisms (i.e., whether or not their community structure develops into a stable, converged state with succession), several analyses were made on diversity, evenness, dominance and similarity, as well as the number of species. That is, the following five parameters were computed basing on the data of the coverages of sessile organisms in the central area (16 cm x 16 cm) of plates: the number of species (S), Shannon-Weaver diversity index (H') (Shannon and Weaver 1949), information theory evenness index (J') (Pielou 1966a), McNaughton's dominance index (MDI) (McNaughton 1967) and Horn's similarity index (HSI) (Horn 1966). $\underline{H}'$ is an index evaluating both the total number of species and the degree of apportionment in coverage among species; $\underline{J}'$ evaluating only the latter; MDI evaluating the degree of domination in dominant and subdominant species; and HSI evaluating the degree of similarity in both the number of species and the apportionment of coverage between plates sampled at the same immersion period and at the same depth.

The temporal changes of these five parameters are shown in Fig 7. To confirm statistically the trend of their changes along the lapse of time, Spearman's rank correlation coefficients were obtained for three sample periods which were arbitrarily assigned from the pattern of their changes (Table 6).

(1). Species richness (S)

The colonization of sessile organisms proceeded rapidly after submerging experimental plates, and S increased rapidly to reach a maximum in mean 6 months after immersion (Fig. 7). Spearman's rank correlation coefficients were all significantly positive in the period from 2 to 6 months after immersion (Table 6). In the period from 6 to 13 months after immersion, there was a tendency for S to decrease with a significant correlation at Depth C (Fig. 7 and Table 6). In the period from 13 to 37 months after immersion, the pattern of change in S differed among depths; S remained almost constant at Depths A and B, while decreasing significantly at Depths C and D (Fig. 7 and Table 6). The values of S of Depth D samples immersed for 26 and 37 months were much lower than those at other depths (Fig. 7).

(2) Species diversity (H')

Shannon-Weaver diversity index (H') (Shannon and Weaver 1949) originating from information theory, is defined as

$$H' = -\sum_{i=1}^{s} P_i \log P_i$$

where P_i and s are the relative abundance of the i-th species to total abundance and the total number of species, respectively, and it is computed in natural logarithm. This index increases with a more even apportionment of abundance among species as well as an increase of the number of species (Pielou 1966b). An increase of H' in the community of sessile organisms means an increase in species number and a high degree of apportionment in coverage among their species.

H' increased rapidly at all depths after immersion

(Fig. 7). Spearman's rank correlation coefficients were all significantly positive in the period from 2 to 6 months after immersion (Table 6). In the period from 6 to 37 months after immersion, though there was no significant correlation, the pattern of change in H' differed among depths (Fig. 7 and Table 6). At Depths A and B, after there was a temporary decrease in mean 10 months after immersion, the mean at 13 months after immersion was so high as at 6 months after immersion, and this high H' remained almost constant during the period from 13 to 37 months after immersion (Fig. 7). At Depth C, the mean decreased also 10 months after immersion, and then remained almost constant until 26 months after immersion. But there was a decrease in mean from 26 to 37 months after immersion (Fig. 7). At Depth D, the mean increased until 10 months after immersion, and decreased after that. The values of H' of Depth D samples immersed for 26 and 37 months were much lower than those at other depths (Fig. 7).

(3). Evenness (J')

Information theory evenness index (J') (Pielou 1966a), defined as

$$J' = -\sum_{i=1}^{s} p_i \log_s p_i$$

indicates an adjustment of relative abundance among species, evaluating the degree of relative apportionment in coverage among the species of sessile organisms in this study. This index varies from 0 to 1, and is 1 when there is an even apportionment of abundance among species.

$\underline{J}'$ increased rapidly after immersion (Fig. 7). In the period from 2 to 6 months after immersion, it increased significantly at all depths (Table 6). After that, the mean at Depths A and B showed a maximum 13 months after immersion and then remained almost constant until 37 months after immersion (Fig. 7). At Depth C, after reaching a high mean earlier 6 months after immersion, it also remained almost constant until 37 months after immersion (Fig. 7). On the other hand, at Depth D, it did not reach so high values within the first year after immersion as at Depths A, B and C, and then increased significantly in the period from 13 to 37 months after immersion (Fig. 7 and Table 6).

(4). Dominance (MDI)

McNaughton's dominance index (MDI) (McNaughton 1967), defined as

$$\mathrm{MDI} = (\underline{n}1 + \underline{n}2)/\underline{N}$$

where _n_1, _n_2 and _N_ are respectively the abundance of species ranking the top and second in abundance and the total abundance, evaluates the degree of domination in coverage by dominant and subdominant species in this study.

MDI decreased significantly at all depths in the period from 2 to 6 months after immersion (Fig. 7 and Table 6). In the period from 6 to 13 months after immersion, the mean temporarily showed a high value 10 months after immersion at Depths A, B and C, while remained high even 13 months after immersion at Depth D (Fig. 7). In the period from 13 to 37 months after immersion, it remained almost constant at Depths A, B and C, while there was an increase from 13 to 26 months after immersion at Depth D (Fig. 7).

(5). Similarity (HSI)

The above-mentioned four parameters provided some information for the structural organization of the community, but give no insight into differences in relative abundance among species between samples. Similarity index accounts more specifically for the changes in abundance of each species, as well as the total number of species and the apportionment of abundance among them. By Horn's similarity index (HSI) (Horn 1966), similarity between plates sampled at the same immersion period and at the same depth was examined. This index basing on Shannon-Weaver information theory is defined as

$$\mathrm{HSI} = \left[\sum_i (x_i + y_i)\log(x_i + y_i) - \sum_i x_i \log x_i - \sum_i y_i \log y_i \right] \Big/ \left[(X + Y)\log(X + Y) - X\log X - Y\log Y \right]$$

where X and x_i are the sum of abundance of all species and the abundance of the i-th species in one sample respectively, and Y and y_i are the same abundance in another sample, which evaluates the similarity of not only species composition but also differences in relative coverage among species between the two samples. It ranges from 0 when there is no common species between two samples, to 1 when both species composition and relative coverage between them are quite equal. Natural logarithm is used for this calculation.

HSI showed a maximum at all depths 2 months after immersion (Fig. 7). At Depths A, B and C, it decreased significantly in the period from 2 to 6 months after immersion to reach a minimum 6 months after immersion (Fig. 7 and Table 6). In the period from 6 to 13 months after immersion, there was no significant correlation at these three depths, and it increased transiently 10 months after immersion only at Depth C (Fig. 7 and Table 6). At Depth D, it decreased in the period from 2 to 13 months after immersion (Fig. 7). This decrease was significant in the period from 6 to 13 months after immersion (Table 6). In the period from 13 to 37 months after immersion, though the coefficients showed a significant increase only at Depth B (Table 6), its pattern of change was not so much different among depths (Fig. 7). But it showed an increase from 13 to 26 months after immersion at Depth D (Fig. 7). The mean at 37 months after immersion showed a gradual increase with depth (Fig. 7).

5. Community metabolism

Gross primary production of community (Pg) was estimated by summing net primary production of community (Pn) measured in light and community respiration (R) measured in darkness, assuming the respiration rates of organisms in darkness to be equivalent to those in light. To estimate daily energy budget of community, Pg in a day was calculated by multiplying Pg per hour by the number of hours equivalent to the mean day length during the period in which the metabolic rates were measured (Table 1), and R in a day was calculated by multiplying R per hour by 24 hours. The daily energy budget was estimated as the ratio of Pg to R in a day, which is expressed below as Pg/R. Temporal changes of Pg, R and Pg/R are shown in Fig. 8. To confirm statistically the trend of their changes along the lapse of time, Spearman's rank correlation coefficients were obtained for three sample periods which were arbitrarily assigned from the pattern of their changes (Table 7).

(1). Light intensity and gross primary production of community

Relation of Pg to light intensity in ca. 2 years' samples of series 2 is shown in Fig. 9. Saturation point of Pg was 10,000 to 13,000 lx at Depth A, while 28,000 to 36,000 lx at Depths B, C and D. This low saturation point at Depth A is due to the paucity of algae appearing on the plates, because dominant *E. bicyclis* inhibited other algae and this alga which was restricted on the lateral faces of plates was all removed from the plates before measurement. Therefore, the Depth A samples were fully exposed to experimentally given light. The saturation point of the Depth A samples was equivalent to that of ca. 7 months' plates set up experimentally in the intertidal rocky shore near the present study site by Yamagami and Mishima (1974). The surfaces of these intertidal samples were almost all covered with short articulated corallines *Corallina pilulifera* (A. Yamagami, *personal communication*), so that experimentally given light was fully able to penetrate into them. On the other hand, the Depth B to D samples had the spread foliage of large algae, Eisenia bicyclis, Padina arborescens and Pterocladia capillacea on the plates. All short algae having situated below these algae would not have fully been exposed to the light. The short algae are considered not to attain their saturation points because of the shading caused by the large algae. This suggests why the saturation point of Depth B to D samples became higher than that of Depth A ones.

The following values of Pg were all measured at 23,000 lx lower than the saturation point of the Depth B to D samples. The values of Pg in saturation of the Depth B to D samples were higher approximately by 10% than those at 23,000 lx (Fig. 9). Therefore, when the foliose of large algae spread over the plates, the values of Pg at 23,000 lx are estimated to be lower by 10% than those in saturation. In this study, samples immersed longer than 10 months is often applicable to this case.

(2). Gross primary production of community (Pg)

Pg at 2 months after immersion was 197 to 382 mg $O_2/hr/m^2$ in mean, higher at Depths A and B than at Depths C and D (Fig. 8). This high values at Depths A and B were due to the rapid recruitment of microalgae such as diatoms. In the period from 2 to 6 months after immersion, it showed no significant change along the lapse of time, though tending to decrease at Depths A and B and to increase at Depths C and D (Fig. 8 and Table 7). At 6 months after immersion, the difference in Pg among depths became small to reach 251 to 360 mg $O_2/hr/m^2$ in mean (Fig. 8). After that, it increased, especially at Depths A to C, to reach a maximum of 388 to 1,276 mg $O_2/hr/m^2$ 10 or 13 months after immersion (Fig. 8). The high variation in Pg at these two immersion periods was due to the sporadic occurrence of large green algae, *Codium fragile*, *C. latum* or *C. divaricatum* on the plates, of which the third species occurred only in the peripheral area of plates. In the period from 13 to 37 months after immersion, it showed a significant decrease at all depths (Table 7). At 37 months after immersion, its mean showed lower values of 86 to 200 mg $O_2/hr/m^2$ (Fig. 8). The sporadic occurrence of large brown alga *Eisenia bicyclis* on the plates also produced a high variation in Pg at Depth C 26 months after immersion.

(3). Community respiration (R)

R at 2 months after immersion was 144 to 450 mg $O_2/hr/m^2$ in mean, higher at Depths C and D than at Depths A and B (Fig. 8). This high values at Depths C and D were due to the rapid recruitment of sessile invertebrates such as barnacles. In the period from 2 to 6 months after immersion, there was no significant correlation at Depths A and B, while it decreased significantly at Depths C and D (Fig. 8 and Table 7). This constancy or decrease in R in spite of the growth of sessile organisms is attributable to a fall in water temperature lowering metabolic rates of organisms on plates. In the period from 6 to 13 months after immersion, it increased significantly at Depths A, C and D (Fig. 8 and Table 7). This increase is attributable to both the growth of organisms on plates and a rise in water temperature from winter to summer. At 10 or 13 months after immersion, it reached a maximum of 404 to 834 mg $O_2/hr/m^2$ in mean (Fig. 8). At these two immersion periods, R varied greatly like Pg (Fig. 8). This great variation is also due to the sporadic occurrence of large Codium spp. In the period from 13 to 37 months after immersion, it decreased significantly only at Depth C (Fig. 8 and Table 7). At 37 months after immersion, it was 267 to 559 mg $O_2/hr/m^2$ in mean, higher at Depths A and B than at Depths C and D (Fig. 8). This high values at Depths A and B are attributable to abundant epifaunas and infaunas on the plates.

(4). Daily energy budget (Pg/R)

Pg/R at 2 months after immersion showed an autotrophic state (Pg/R greater than 1) at Depth A, a slightly heterotrophic state (Pg/R a little less than 1) at Depth B, and a strongly heterotrophic state (Pg/R much less than 1) at Depths C and D (Fig. 8). Pg/R at Depths A and B showed a decrease (change to heterotrophic state) transiently 4 months after immersion, returned to an autotrophic value 6 months after immersion, and finally showed a much more heterotrophic value; while Pg/R at Depths C and D showed a significant increase in the period from 2 to 6 months after immersion to reach an autotrophic state 6 months after immersion, and then remained in a heterotrophic state until 37 months after immersion (Fig. 8 and Table 7). In the period from 13 to 37 months after immersion, it decreased significantly at Depths A, B and C (Table 7). At 37 months after immersion, it was much more heterotrophic at shallower depths (Fig. 8).

6. Community biomass

Temporal changes of community biomass represented by the following six parameters of dry mass, ash dry mass, ash-free dry mass, organic carbon, organic nitrogen and chlorophyll *a* are shown in Fig. 10. To confirm statistically the trend of their changes along the lapse of time, Spearman's rank correlation coefficients were obtained for two sample periods which were arbitrarily assigned from the pattern of their changes (Table 8).

(1). Dry mass (DM) and ash dry mass (ADM)

The patterns of changes in DM and ADM were similar to each other (Fig. 10). They showed a significant increase at all depths in the period from 2 to 13 months after immersion (Table 8). In the period from 13 to 37 months after immersion, they increased significantly at Depths A and B, while decreased significantly at Depth D (Table 8). The means of DM at 37 months after immersion were 26.8 and 16.5 kg/m^2 at Depths A and B respectively, which were much higher than those of 7.9 and 4.6 kg/m^2 at Depths C and D, respectively (Fig. 10). The ratio of the mean value of 37 months' samples to that of 13 months' samples was 2.3, 1.8, 0.8 and 0.6 at Depth A, B, C and D, respectively. The same comparison on ADM showed the same relationship as DM.

(2). Ash-free dry mass (AFDM) and organic carbon (C)

AFDM and C were similar to each other in the pattern of change (Fig. 10). They showed a significant increase at all depths in the period from 2 to 13 months after immersion (Table 8). Though their means at Depths A and B decreased 13 to 26 months after immersion (Fig. 10), they showed a significant increase at Depth A in the period from 13 to 37 months after immersion (Table 8). On the other hand, their means at Depths C and D showed a tendency to decrease in this period, being significant at

Depth D (Fig. 10 and Table 8). The means of AFDM at 37 months after immersion were 1.2 and 0.8 kg/m^2 at Depths A and B respectively, which were much higher than those of 0.3 and 0.2 kg/m^2 at Depths C and D, respectively (Fig. 10). The means of C at 37 months after immersion were 507 and 285 g/m^2 at Depths A and B respectively, which were much higher than those of 122 and 83 g/m^2 at Depths C and D, respectively (Fig. 10). The ratio of their mean value of 37 month's samples to that of 13 months' samples was 1.8, 1.2, 0.4 and 0.6 in AFDM and 2.0, 1.1, 0.5 and 0.7 in C at Depth A, B, C and D, respectively.

(3). <u>Organic nitrogen (N)</u>

The pattern of change in N resembled those of AFDM and C (Fig. 10). It showed a significant increase at all depths in the period from 2 to 13 months after immersion (Table 8). In the period from 13 to 37 months after immersion, it increased significantly at Depth A, while decreased significantly at Depth D (Table 8). The means at 37 months after immersion were 114 and 59 g/m^2 at Depths A and B respectively, which were much higher than those of 21 and 14 g/m^2 at Depths C and D, respectively (Fig. 10). The ratio of the mean value of 37 months' samples to that of 13 months' samples was 2.5, 1.6, 0.6 and 0.6 at Depth A, B, C and D, respectively.

(4). Chlorophyll a (Chl. a)

Chl. *a* increased significantly at all depths in the period from 2 to 13 months after immersion, beginning with means of 24 to 71 mg/m^2 2 months after immersion and attaining the highest means of 221 to 2,939 mg/m^2 10 or 13 months after immersion (Table 8 and Fig. 10). This wide variation in Chl. *a* at 10 and 13 months after immersion was due to the sporadic occurrence of large green algae of *Codium fragile*, *C. latum* and *C. divaricatum* on the plates. In the period from 13 to 37 months after immersion, Chl. *a* showed a tendency to decrease, being significant at Depth D (Fig. 10 and Table 8). At 37 month after immersion, its mean showed lower values of 106 to 280 mg/m^2. Depth C samples immersed for 26 months also showed wide variation, that was due to the sporadic occurrence of *Eisenia bicyclis* on the plates. The pattern of change in Chl. *a* was similar to that of gross primary production.

7. Indices of community maturity

To examine the degree of community maturity of samples during community development, the four ratios of gross primary production/organic carbon (Pg/C), gross primary production/chlorophyll *a* (Pg/Chl. *a*), organic carbon/organic nitrogen (C/N) and the pigment diversity of Margalef (1961, 1967) (D430/D665) were examined as indices of community maturity. By choosing organic carbon as a measure representative of community biomass, Pg/C was regarded as the ratio of gross primary production of community to community biomass. This index is expected to shift from a high to a low value with succession for the reasons that Pg does not necessarily become higher in the later stage of succession and that community biomass increases with succession. The second index Pg/Chl. a which means the photosynthetic ability of chlorophyll a is expected to shift from a high to a low value with succession, because of the aging of chlorophyll a in large algae dominating in the later stage of succession and the lowered penetration of light into the bodies of their algae. The third index C/N means the relative abundance of organic carbon to organic nitrogen, and this was employed as a biochemical diversity index indicated by Odum (1969). The fourth index D430/D665 which is the ratio of 430 to 665 nm in absorbance of the 90% acetone extracts of samples is regarded as a simple "yellow-green" index, and is expected to shift from a low to a high value with succession, because rapidly growing immature communities such as young forests and algal assemblages show bright green color in contrast to the yellow-green color of mature communities such as older forests or kelp forests.

Temporal changes of these four parameters are shown in Fig. 11. To confirm statistically the trend of their changes along the lapse of time, Spearman's rank correlation coefficients were obtained for two sample periods which were arbitrarily assigned from the pattern of their changes (Table 9).

(1). Gross primary production/organic carbon (Pg/C)

At Depths A and B, Pg/C showed a maximum in mean 2 months after immersion and then decreased rapidly until 6 months after immersion (Fig. 11). In the period from 2 to 13 months after immersion, it showed a significant decrease, though there was a transient increase in mean 10 months after immersion (Table 9 and Fig. 11). In the period from 13 to 37 months after immersion, there was also a significant decrease at these two depths (Table 9). On the other hand, at Depths C and D, the mean at 2 months after immersion was much lower than at Depths A and B (Fig. 11). In the period from 2 to 13 months after immersion, its changes were not significant (Table 9). In the period from 13 to 37 months after immersion, it decreased significantly at Depth C (Fig. 11 and Table 9). At Depth D, its variation was small through this study period. The mean at 37 months after immersion showed a gradual increase with depth (Fig. 11).

(2). Gross primary production/chlorophyll a (Pg/Chl. a)

Pg/Chl. *a* showed a maximum in mean 2 months after immersion (Fig. 11). It decreased significantly at all depths in the period from 2 to 13 months after immersion, though increasing slightly 10 or 13 months after immersion (Table 9 and Fig. 11). In the period from 13 to 37 months after immersion, it decreased significantly except for Depth C (Table 9). The mean at 37 months after immersion showed a gradual increase with depth (Fig. 11).

(3). Organic carbon/organic nitrogen (C/N)

C/N showed a maximum in mean 2 months after immersion, higher at Depths A and B than at Depths C and D (Fig. 11). At this immersion period, there was wide variation of values at Depths A and B (Fig. 11). This wide variation was due to the high values of C rather than N (Fig. 11). After that, it decreased and then remained almost constant until 37 months after immersion except for several high values at 10 or 13 months after immersion (Fig. 11). However, at Depth D, it decreased significantly in the period from 2 to 13 months after immersion, and then increased significantly in the period from 13 to 37 months after immersion (Table 9). At 37 months after immersion, the mean showed a gradual increase with depth (Fig. 11).

(4). Pigment diversity (D430/D665)

In the period from 2 to 13 months after immersion, D430/D665 showed little variation ranging from 2.09 to 3.02 (Fig. 11). But, there was a significant decrease at Depth A (Table 9). In the period from 13 to 37 months after immersion, it increased significantly at Depths A and B, while decreased significantly at Depth D (Table 9). The mean at 37 months after immersion showed a gradual increase with depth (Fig. 11). Of these four indices, D430/D665 showed the least variation.

8. Relation of community metabolism to temperature

In order to consider the relation of metabolic rates (Pg and R) to temperature, regressions of Pg and R in common logarithm on temperature were calculated for the samples of series 1 at different sampling times (Table 1). All of 44 samples examined showed a significant positive regression of R on temperature, and the 36 samples of them (82%) also showed a significant positive regression of Pg on temperature (Table 10). Regression equations on temperature are expressed as follows,

$$\text{Log Pg} = a_P\, t + b_P$$

and

$$\text{Log R} = a_R\, t + b_R$$

, where a_P and a_R are regression coefficients of Pg and R respectively, and t is water temperature. When a_P and a_R have lower values, both Pg and R become more independent of temperature. Temporal changes of a_P and a_R indicating a significant regression on temperature are shown in Fig. 12. They showed no definite changes along the lapse of time among four depths (Fig. 12a). But a_P and a_R showed very similar value each other in several samples. This similarity was remarkable in the samples immersed longer (Fig. 12b).

Subtracting the regression equation of R from that of Pg produces another equation:

$$\mathrm{Log}\ Pg{:}R = (a_P - a_R)\ t + (b_P - b_R)$$

, consequently turning into a regression equation of the ratio of Pg to R on temperature. The regression coefficient of $a_P - a_R$ is that of Pg:R ratio on temperature in common logarithm. When a_P is equal to a_R, the ratio of Pg:R always becomes constant on temperature. This means that the Pg:R is entirely independent of temperature. Fig. 12b shows the changes in value of $a_P - a_R$ along the lapse of time. Its values were apt to become closer to zero in the older samples, though there was an approximation to zero at Depth A 10 months after immersion. At 37 months after immersion, Depth A to C samples showed an approximation to zero rather than Depth D ones (Fig. 12b).

This relation of community metabolism to temperature was further investigated using 16 Depth B samples of series 3 which were immersed approximately for 2 to 3 months and 37 to 38 months (Table 1). The regression coefficient of Pg or R on temperature was also significantly positive (Table 11).

Assuming the changes of the regression coefficients of Pg and R on temperature to be independent of differences among the altitudes of the regression lines, Pg and R regression coefficients can be each compared statistically between samples at two different immersion periods. Means and standard deviations of regression coefficients are given in Table 11. But the regression coefficients of a_P and a_R each showed no significant difference between the young and old samples (two-tailed $\underline{t}$ test, $\underline{P}<0.60$ in Pg; $\underline{P}<0.10$ in R).

The Pg:R ratio is a dimensionless number which provides an estimate of the degree to which algal production of organic material exceeds consumption by plants and animals. This parameter is potentially useful because it normalizes biomass and allows comparisons independent of absolute levels of metabolic activity, assuming that Pg and R are similarly size-related. Pg:R regression coefficients on temperature were not significant except for one of 16 samples (Table 11). And the values of $a_P - a_R$ at the two different immersion periods were also compared statistically but were not different significantly (two-tailed *t* test, $P<0.30$).

The values of $a_P - a_R$ of 2 to 3 months' samples of series 3 were higher than those of 4 months' samples of series 1. These two kinds of samples differed each other in species number and biomass as well as species composition. The former samples were fewer in species number and less in biomass than the latter ones. Besides, the former had a little number of barnacles (less than 5% in percent cover) and was dominated by microalgae such as diatoms (no less than 100% in percent cover), while the latter was dominated by barnacles (percent cover of more than 98%). On the other hand, 37 to 38 months' samples of series 3 were similar to 37 months' ones of series 1 in biomass as well as dominant species (i.e., the oyster *Crassostrea nippona*; the barnacle *Balanus trigonus*; the kelp *Eisenia bicyclis*). The means of the regression coefficients of Pg:R of their samples on temperature both showed very similar value each other (Table 11 and Fig. 12).

Fig. 13 shows the relation of log Pg:R values on water temperature in 2 to 3 months' samples of series 3 and 37 to 38 months' ones of the same series. Neither of their regression coefficients was significant, but the regression coefficient of the 37 to 38 months' samples were closer to zero. This indicates that the Pg:R ratio of the ca. 3 years' samples is apt to be more independent of temperature.

DISCUSSION

1. Community development and ecological and physiological characteristics of algae

The process of algal colonization is influenced by various physical environmental factors as well as ecological and physiological characteristics of algae such as their life cycles, growth rates, tolerance for shading in germination or growth, growth forms, tissue robustness, and interactions with colonial animals.

(1). Early developmental process

Most of the green algae observed were earlier colonizers. The fact that their presence was restricted to the first 13 months after immersion indicates that they are ephemeral and have an annual life cycle. Among green algae, *Ulva pertusa* with foliose form is well known as an early ephemeral colonizer (e.g., Haderlie 1968, Kawahara 1969, Kennelly 1983, Sousa 1984). It showed high coverage in the initial stage of community development, but in later stages its percent cover decreased (Table 2). *Codium adhaerens*, which appeared a little later, increased in percent cover (Table 2). The higher percent cover of *C. adhaerens* seems to be due to its peculiar morphological form which differs from that of *Ulva pertusa*. *U. pertusa* grows upward from the small holdfast and its body is flimsy and flexible, but *C. adhaerens* spreads like a moss and its body is more robust. Moreover, the holdfast of *U. pertusa* does not become large with growth. Therefore, the young individual of *U. pertusa* is likely to be overgrown by colonial animals such as ascidians and bryozoans, which frequently dominated the plates examined in this study. On the other hand, a small, flexible alga such as *Cladophora wrightiana* disappeared soon after its appearance. This disappearance was thought to be caused by the overgrowth of colonial animals. Dayton (1971) observed that the growth of the shells of barnacles weakens the holdfasts of non-encrusting algae. However, such dislodgement was not observed in this study. Barnacles were first colonizers having abundant recruits, and grew rapidly all over the plates immersed for up to 4 months (Table 3). The barnacle shells provided attachment sites for non-encrusting algae. Two large-sized species, *Codium latum* and *C. fragile*, also have holdfasts larger in size than *U. pertusa*, and became mature 10 or 13 months after immersion, dominating the water column on plates with their large thalli. Strong survival abilities of *Codium* spp. may be due to their thicker and more robust tissues and ability to grow rapidly. Because of these characteristics, they would not have been overgrown by colonial animals.

The first time of appearance of red algae differs with species: *Pterocladia capillacea* and *Grateloupia sparsa* appeared 4 months after immersion as the earliest colonizers; *Gracilaria textorii*, *Champia parvula*, *Ceramium paniculatum* and *Plocamium telfairiae* 6 months after immersion; *Grateloupia livida* and *Gelidium amansii* 10 months after immersion. Though their reproductive seasons are not known, the timing of first colonization suggests that they each have peculiar physiological characteristics for attachment or germination. The red algae can be classified into two groups from the pattern of their appearances. The first group includes the species which appeared within the first year after immersion. These species were unable to survive the next summer. The second group includes those species which could be observed in the late summer, 13 months after immersion, but often appeared even after this time. The former species are considered to be ephemeral or annual. On the other hand, the second group species are not necessarily perennial, because of the possibility of repeating recruitment every year. Northcraft (1948) indicated that red algae generally appear later in the colonization process than green and brown algae, perhaps because red algae produce non-motile spores whereas green and brown algae produce motile ones.

The brown alga *Colpomenia sinuosa* is known to be an early colonizer (e.g., Wilson 1925, Kawahara 1962, Murray and Littler 1978), and its appearance was restricted to the first 10 months after immersion. Moreover, it was never observed in late summer. It is also known that *C. sinuosa* is an annual species; it propagates from spring to summer and then dies in summer in Nabeta Bay (K. Matsue, *personal communication*). *Eisenia bicyclis* and *Padina arborescens* were able to colonize in the first year after immersion, and were found earlier at greater depths. This suggests that low light intensity at greater depths is suitable for their attachment, germination, or subsequent growth. Light intensity-photosynthesis curves suggest that *E. bicyclis* is a shade-adapted alga (Yokohama 1977). Generally, it is known that the germination of spores of red and brown algae is not inhibited at low light intensity, and the growth of these algae is good in those conditions (Arasaki 1953). The appearance of several kelp species including *E. bicyclis* was observed on artificial or cleared natural substrata at depths of 5 to 35 m within the first year of fouling experiments (Itô 1959, Iwahashi 1968, Fager 1971, Foster 1975, Dayton et al. 1984, Reed and Foster 1984). A condition of low light intensity seems necessary for their germination and growth. The absence of *E. bicyclis* until 13 months after immersion at

Depths A and B may be due to the inhibiting effect of high light intensity (Table 2).

At 10 or 13 months after immersion, large-sized *Codium latum* and *C. fragile* dominated the water column at Depths A and B, but not at Depths C and D, where young individuals of *E. bicyclis* predominated. The large-sized *Codium* species seem unable to grow successfully at greater depths. This suggests that their growth is inhibited by *E. bicyclis* because the latter absorbs light near plates. *Padina arborescens* appeared transiently at Depths B and C in the first year after immersion. Light conditions at these depths would be suitable for the recruitment and growth of this alga. However, it was not always observed during the first year after immersion. The sporadic occurrence of this species may have been caused by overgrowth of colonial animals before reaching its mature size. When it was observed, it was always found on only one of the plates at each depth. This suggests that its recruitment is also essentially poor.

(2) Later developmental process

At Depths A and B, after the decline of *Ulva pertusa* and several other green algae, large-sized *Codium* spp. occupied space from spring to late summer in the first year after immersion. Next, the perennial kelp *Eisenia bicyclis* appeared and finally dominated available space

(Table 2). At Depths C and D, no distinct dominant species was observed (Table 2).

E. bicyclis was observed from the middle to late stage of community development. This may be because: it has a robust stipe and holdfast; it forms a canopy which ensures its escape from shading; and it has a perennial life cycle with considerable longevity. The longevity of this species is known to be at least more than 5 years from the growth rings on the stipe (Maegawa and Kida 1984). These characteristics also made it possible to dominate finally both in area covered and in the water column near the plates at Depths A and B.

On the other hand, *Eisenia bicyclis* decreased in percent cover or disappeared entirely at Depths C and D in the late stage of community development. Early colonizers, *U. pertusa* and *C. adhaerens*, and a middle colonizer appearing later in the first year after immersion, *Gelidium amansii*, appeared again at Depths C and D 37 months after immersion (Table 2). This reappearance indicates that such communities return to an early stage of community development. The pattern of this return at Depth D was different from that at Depth C. In Depth D samples, one young individual of *E. bicyclis* was observed 37 months after immersion, but not found 26 months after immersion (Table 2). Furthermore, *U. pertusa* and *G. amansii* existed simultaneously at Depth

D 37 months after immersion (Table 2). This indicates that a recovery from a secondary early stage to a later stage of community development occurred during the period from 26 to 37 months after immersion.

The decrease in cover or disappearance of Eisenia bicyclis at Depths C and D mentioned above may have been caused mainly by sand scouring due to wave action. The removal of other algae by sand scouring is probably the cause for a return to the early stage of community development. There is the additional possibility that this decrease in cover or disappearance was also caused by contact of plates with the sand bottom due to the change of sea level with the tide or by the action of waves. Even at extreme low tides in May and December, the lower edges of the deepest sets of plates were about 30 cm off the sand bottom, since this study site is 6 m deep and the deepest sets of plates are maintained 5.5 m below the sea surface as already mentioned. Therefore, there seems little possibility that contact of plates with the bottom occurred at the low tide. On the other hand, while this study site is ordinarily calm with waves less than about 30 cm in height throughout the year, in stormy weather waves of 1 to 2 m in height were observed. Therefore, the deepest sets of plates might have come in contact with the sand bottom in some unfavorable conditions.

2. Community development and ecological characteristics of sessile invertebrates

Physical or biological disturbance, such as caused by log damage, storm-waves, scouring, sedimentation, grazing or predation, has been known to affect the community structure of sessile organisms (e.g., Dayton 1971, Foster 1975, Aleem 1957, McDougall 1943, Bakus 1966, Stephenson and Searles 1960). All the plates examined had not come in contact with the sand bottom but only with ropes supporting them, so that predators common on neighboring rocky reefs, such as starfish, crabs and snails, were rarely observed on plates except their young individuals. By underwater observations during the day, I confirmed the following predators were foraging near the raft which carried the plates: surgeon-fish *Navodon modestus* and *Stephanolepis cirrhifer*, blowfish *Ostracion cubicus*, and young individuals of false parrot fish *Oplegnathus fasciatus*. These predatory fish were observed in the warmer season from late spring to mid autumn. However, they had little influence on the present community structure of sessile organisms. Besides, grazing by sea urchins or snails common on neighboring rocky reefs was negligible for the same reason as the case of predators. But, the scouring of sand from the bottom seems to have some effect on the community structure of sessile invertebrates as mentioned already in the case of algal community.

It is well known that the overgrowth by sessile invertebrates is an important agent affecting the community structure of sessile organisms (e.g., Hoshiai 1959, 1960, 1965). Besides, the process of community development, i.e., appearance and transition of sessile invertebrates, is also influenced by other various ecological characteristics of sessile invertebrates such as their sizes, life forms, reproduction, growth rates, life spans, quality of tissue or shell, and ability to escape the overgrowth of colonial animals. The earliest colonizers having a solitary form, *Balanus trigonus*, *Megabalanus volcano*, *M. rosa* and *Dexiospira foraminosus*, decreased in coverage or disappeared with community development by the effect of the overgrowth of colonial ascidians, bryozoans, and sponges having recruited a little later (Table 3). The decrease in coverage of *B. trigonus* at 6 or 10 months after immersion was primarily brought by the overgrowth of colonials, and secondarily by the predation of a polyclad *Pseudostylochus* sp. which was frequently observed in the shells of barnacles. The increase in coverage of *B. trigonus* at 13 months after immersion is attributable to abundant recruitment in warmer season (Table 3). The percent cover of *M. volcano* and *M. rosa* increased until 6 months after immersion unlike *B. trigonus* (Table 3). These two species grow larger in size than *B. trigonus*, making an escape from the overgrowth of colonials more possible. Overgrowth by colonials also caused the disappearance of *D. foraminosus* of much smaller size from the plates immersed for 6 months (Table 3). Osman (1977) showed a hierarchy in interspecific competition among several species of sessile invertebrates, in which solitary species of limited size (*Balanus amphitrite niveus* and *Spirorbis pagenstecheri*) were easily overgrown by colonial species of ascidians, bryozoans and sponges. Like the Osman's hierarchy, the earliest colonizers of four species observed were covered easily by colonials, and their percent covers generally decreased with time. However, the complete disappearance from the plates did not necessarily occur. The barnacles *B. trigonus*, *M. volcano* and *M. rosa* were found on the plates throughout this study. The spirorbid *D. foraminosus* reappeared in the period from 13 to 37 months after immersion (Table 3). The incomplete disappearance of these four species seems to be due to their essentially abundant recruits, and due to free space produced secondarily by the shells of *Crassostrea nippona*, *Mytilus edulis* and *Pinctada fucata* which finally occupied three-dimensional space on the plates at Depths A and B.

Ascidians observed can be classified into three groups from the pattern of their appearances. The first group includes the species which appeared in the period from 2 to 13 months after immersion. The second group includes the species which were continuously found from the first appearance until the end of this study. The third group includes the species which appeared mainly 37 months after immersion. The species of the first group showed low percent cover (Table 3). This low percent cover is considered to have been brought by their low growth rates and by the intensive overgrowth of the colonial species with higher growth rates which belong to the second group. The solitary ascidian *Styela plicata*, which belongs to the first group, may have sloughed off from the plates like the cases observed by Sutherland (1974, 1978), Sutherland and Karlson (1977) and Mook (1981). *Diplosoma mitsukurii* of the second group spreads on plates earlier by high growth rate and showed a maximum in coverage 6 or 10 months after immersion. But the percent cover of this species decreased in the summer at 13 months after immersion (Table 3). The season of sexual reproduction of this species seems to be year-round centering the period of June to August (Kitazawa 1967, Yamaguchi 1975, Iwaki et al. 1977, Tsuchiya and Osanai 1978). The decrease in coverage of *D. mitsukurii* in summer may be due to the atrophy of vegetative growth as a result of the aging of the colonies after sexual reproduction. *Didemnum moseleyi* and *Trididemnum savignii* showed high percent cover 10 or 13 months after immersion later than *D. mitsukurii* (Table 3). These two species grow more slowly than *D. mitsukurii*, but they have the robust tunic containing hard spicules. Their robust tunics may have ensured their presence until the end of this study. These three species of ascidians play an important role in the present community structure because of their intensive overgrowth. *Amaroucium multiplicatum* and *Leptoclinides* sp. belong to the third group (Table 3).

Sponges can be classified into three groups in appearance pattern like ascidians: *Halichondria panicea* appears to have been unable to avoid the overgrowth of colonials because it appeared only 4 and 10 months after immersion; *Halichondria japonica* appears to have been able to avoid the overgrowth of colonials because this species was continuously found until 37 months after immersion; *Mycale plumosa* was a later colonizer, being found only 37 months after immersion (Table 3).

Bryozoans belong to the first or second group of appearance pattern which is typified by the case of ascidians. *Watersipora subovoidea* and *Amathia distans* showed frequently high percent cover (Table 3). The percent cover of *W. subovoidea* decreased 6 or 10 months after immersion at Depths A and B, and a little later 13 months after immersion at Depth D, while it remained low at Depth C (Table 3). This decrease or lowness in coverage is primarily attributable to the overgrowth of *Diplosoma mitsukurii*. On the other hand, the percent cover of *D. mitsukurii* decreased in the summer at 13 months after immersion. This decrease brought an increase in coverage of *W. subovoidea* and *A. distans* (Table 3). However, the percent cover of *D. mitsukurii* did not decrease greatly at this time at Depth D, because lower water temperature at greater depths would have delayed the sexual reproduction of this species. At this depth, the percent cover of *W. subovoidea* was lower, while that of *A. distans* was higher (Table 3). These two species differ in life form: the former is encrusting, the latter stoloniferous. *A. distans* was found abundantly on the holdfasts of the kelp *Eisenia bicyclis* which was found only on Depth C and D plates immersed for 13 months (Table 2). Bryozoans observed differ in the first time of appearance. The earliest species appeared 2 or 4 months after immersion, the latest ones 10 months after immersion: *W. subovoidea*, *Schizoporella unicornis*, *Parasmittina trispinosa*, *Membranipora savartii*, *A. distans*, and *Celleporaria columnaris* appeared in this order (Table 3). But, the reason of this difference in the first time of appearance is not clear.

The above-mentioned classification of ascidians, sponges and bryozoans into three groups from the pattern of their appearances seems to reflect the differences in their growth rates or reproductive ability. The species belonging to the first group have lower growth rates, and some species produce abundant recruits but others poor ones in the season of sexual reproduction. On the other hand, the species belonging to the second group have higher growth rates producing probably abundant recruits. Therefore, the latter species would have completely defeated the former species by overgrowing within the first year after immersion. Once the latter dominated, the former would be unable to survive on the plates for intensive overgrowth by the latter, even though the former frequently produced abundant recruits. The occurrence of the species of the third group at Depths A and B 37 months after immersion may be due to the scantiness of their larvae around the study site. Besides, the communities at Depths A and B were dominated by the kelp *Eisenia bicyclis* as well as the oyster *Crassostrea nippona* (Tables 2 and 3). The canopy and shell produce shading and free space on the plates, respectively. It is inferred that these two factors seem necessary for the settlement of the species of the third group.

The bivalves *Pinctada fucata*, *Mytilus edulis* and *Crassostrea nippona* could recruit within the first year of immersion. The third species was later in the first time of appearance (Table 3). These three species settled and grew on barnacles, and finally dominated Depth A plates immersed for 37 months. Therefore, they are considered to have ability to escape the overgrowth of colonials. The first and second species can detach themselves from their byssuses and move from their attachment sites. The opening and closing movement of shells of these three species is also considered to prevent the overgrowth of colonials. In the first year after immersion, P. fucata appeared sporadically, and the percent cover of M. edulis decreased temporarily 10 months after immersion (Table 3). This discontinuous appearance or decrease in coverage of these two species seems to be due to the overgrowth of colonials as well as their slow growth rates and poor recruitment.

Pinctada fucata appeared again at Depths A and B 37 months after immersion (Table 3). This indicates that the complicated surface structure of Crassostrea nippona is necessary for the establishment and survival of P. fucata. Mytilus edulis existed only at Depth A 26 and 37 months after immersion. This may indicate that other depths are not suitable for its survival because its natural distribution is generally restricted to the range from intertidal to shallower subtidal zone. C. nippona can grow to have a massive and robust shell and can escape the overgrowth of colonials. Therefore, it finally occupied three-dimensional space with large coverage. It has the following characteristics advantageous for its survival; robust shell, great adhesive power to substratum, great opening and closing power of shell, and a long life span. Therefore, this species will be able to survive until its natural death unless it is killed by such disturbance as scouring, log damage or predation. This suggests that the domination of *C. nippona* at Depths A and B lasts for a fairly long time. The life span of *C. nippona* is not certain, but I confirmed that it could live more than 10 years.

3. Factors affecting the transition of algae

Fifteen algal species had appeared on the plates within 6 months after immersion (Table 2). Of these, perennial and shade-adapted species of algae are considered to have outcompeted the ephemeral, annual and more sun-adapted species through interspecific competition for light. The algae surviving until the later stages of community development are considered to be species more tolerant of low light intensity. *Eisenia bicyclis* can be regarded as a representative of perennial and shade-adapted algae. The later recruitment of the remaining two species might be facilitated by low light intensity brought about by the early colonizers. On the other hand, they may be regarded as tolerant species resistant to reduced light intensity during community development, if they had recruited simultaneously on plates with the early colonizers and then survived throughout community development. The first time of appearance of *E. bicyclis* differs with depth. It appeared first in the first to second year after immersion at Depths A and B, later than at Depths C and D. This suggests that it was probably assisted by low light intensity brought about by resident algae. At Depths A and B 37 months after immersion where *E. bicyclis* occurred as a dominant, no algae other than this species and *Padina arborescens* were present in spite of the existence of the free spaces on the shells of *Crassostrea nippona*, *Balanus trigonus*, *Megabalanus volcano* and *M. rosa* (Table 2). At Depths C and D where colonial animals dominated, only four algal species were observed 37 months after immersion (Table 2). This suggests that at Depths A and B the recruitment and growth of other algae is inhibited by *E. bicyclis* and at Depths C and D by the overgrowth of colonial animals. It has been suggested that space is a main limiting factor in the community development of sessile invertebrates, because interspecific competition among them through smothering has a great effect on the determination of community structure (Connell 1961, Dayton 1971, Emerson and Zedler 1978, Dean and Hurd 1980). Also in an algal community, space seems to be a limiting factor in some cases. But light, inducing a depth stratification in the algal community, seems to be a much more important limiting factor for the recruitment, germination and growth of algae than space, because interspecific competition among algae through shading has a great effect on the determination of the community structure.

4. Stability and end point in community development

The oyster often forms an assemblage with many associated animals on underwater stones or rocky reefs (Möbius 1877, Tsuchiya and Hirano 1985). As to the succession of communities of sessile invertebrates, there have been few studies having investigated the domination by oysters. On the other hand, the domination of free space by mussels has been indicated by many studies since the investigation by Hewatt (1935). The mussel remains dominant on rocky reefs by the occupation of space through overgrowing other species and inhibiting the colonization of other sessile species, when physical or biological disturbance is not effective (Paine 1966, 1971, 1974, Dayton 1971, Menge 1976). In this study, an assemblage dominated by *Crassostrea nippona* was found at

Depths A and B where there was no effective disturbance such as scouring by the bottom sand. On the other hand, at Depths C and D where such physical disturbance acted effectively, the domination by C. nippona never occurred. The number of species at Depths A and B remained almost constant in the period from 13 to 37 months after immersion, while that at Depths C and D showed a tendency to decrease in this period (Fig. 7 and Table 6). Besides, though samples immersed for 13 to 37 months were not divided into two stages distinctly between Depths B and C in the diagram of Fig. 6, the species which occupied high ranks of the top to third in Stage 3 showed mean percent cover similar to one another except for Balanus trigonus, while those in Stages 1 and 2 did not show such similarity among them (Table 4). These facts suggest that communities at Depths A and B are stable in community structure showing an equal apportionment of percent cover among high ranked species, while communities at Depths C and D are unstable in community structure, having simpler community structure owing to the domination by a few species. Connell (1978) also indicated that when disturbance is strongly effective, community structure becomes simpler. Especially, the 37A sample may be regarded as more matured community because of more massive growth of C. nippona.

As to the endpoint of communities of sessile invertebrates on artificial plates, Sutherland and Karlson (1977), Sutherland (1974, 1978) and Osman (1977) observed that the communities were dominated by bryozoans, sponges or solitary ascidians, but not by oysters or mussels. From the facts that the same single species does not dominate experimental plates, they indicated that the historical differences in colonization or disturbance occurring during community development allow the domination of different species. From these results, Sutherland (1974) pointed out that multiple stable points are an undeniable reality in his system, while Osman (1977) described that dominance by a single species is a stable endpoint and unless disturbed this composition will persist, and that the historical differences will allow different species to dominate, therefore allowing a group of stable endpoints. Sutherland (1974) and Osman (1977) immersed the plates at different seasons throughout the year. I did not try to immerse the plates at other seasons than summer. The unidirectional change of community structure such as the transition from Stage 1 to Stages 2 and 3 at Depths A, B and C (Fig. 6) does not necessarily occur if the experiment was started at winter season. The abundant recruitment of barnacles which characterized Stage 1 occurs mainly in warmer season in Nabeta Bay, so that an initial stage of community development initiated in cooler season will be probably dominated by other species. But, it is not likely that the other species continue to inhibit the recruitment of barnacles completely over one year, because an abundance of barnacles' larvae probably makes it possible for them to recruit even on a slightly opened space. The settlement of *Crassostrea nippona* more frequently occurred on the shells of barnacles. Therefore, it is thought that the recruitment of *C. nippona* on the shells of barnacles will surely occur in the near future, so long as there are the shells of barnacles on plates. *C. nippona* can settle easily on the shells of barnacles having high ability of recruitment, it can escape the intensive overgrowth of colonials and it has a long life span. These facts suggest that, unless effectively disturbed, communities of sessile invertebrates will be gradually converging on an oyster assemblage with time and then the oyster assemblage will become a persistent, stable endpoint of community development in spite of the seasonal difference in the start of immersion of experimental plates. This single endpoint of community development dominated by *C. nippona* differs from the results of Sutherland (1974) and Osman (1977) which indicated the destination of their community development as multiple stable points and a group of stable points, respectively. Basically, communities of sessile organisms submerged at different times should converge on an equilibrium assemblage of the longest-lived species, if its species is not disturbed by physical factor or biological interactions (Glasser 1982). The domination by C. nippona has not been observed on neighboring natural rocky reefs, but artificial structure such as the concrete breakwaters showed frequently the monoculture by C. nippona over their surface.

Like the case of oysters mentioned above, mussels also possess a fairly long life span and can escape the intensive overgrowth of colonials, so that they appear similarly to be able to bring a single endpoint dominated by only one species when there is no effective disturbance (Paine 1966, 1971, 1974, Dayton 1971, Menge 1976). However, mussels could not dominate plates immersed in the subtidal zone in this study, the reason of which must be made clear in future investigation.

The plates were dominated by C. nippona as mentioned above, while the water column near them by the kelp Eisenia bicyclis. The latter species has a long life like the former, and ordinarily dominates neighbouring natural rock reefs as well as artificial structure unlike the former. Though the recruitment time of this alga was later than other algae because of a shade-adapted alga, it is thought that the reducion of light by its large-sized blades on plates would have inhibited the recruitment or germination of other algae. If once this alga recruits and establishes on plates, it will finally come to dominate the water column through interspecific competition for light with the growth when there is no effective disturbance such as scouring from the bottom sand or no continuous, extensive overgrowth by colonial animals. Thus, it is considered that unless effectively disturbed, communities of sessile organisms develop into a stable, persistent assemblage of oysters and kelps.

5. Developmental process of community structure

(1). Colonization curve

MacArthur and Wilson (1963, 1967) suggested that the number of species on an island is the outcome of two opposing processes: immigration, adding new species, and extinction, subtracting existing species. In time, the resultant number of species is thought to become fairly constant, varying slightly around an equilibrium value. The curves expressing the changes of the number of species against time from initiation are represented as "colonization curve". As pointed out by Schoener (1974), Schoener et al. (1978) and Osman (1977, 1978), a set of plates employed in this study was regarded as an island isolated truly.

By using the data drawn from the several published panel studies, Schoener (1974) assessed the shapes of colonization curve over ca. 13 months' period in marine environment (i.e., whether the number of species approaches an equilibrium value and what effect the seasonal recruitment of sessile organisms has on the shapes). She divided these colonization curves into three types: the first increases throughout its observed period (Type A); the second tends to become horizontal toward the end of observed period (Type B); and the third becomes horizontal well before the end of observed period (Type C). She concluded that in most of these colonization curves the number of species does not approach an equilibrium value during colonization like Type A.

These curves assessed by Schoener (1974) showed seasonal variations in temperate regions; they rose more rapidly in the initial portion of warmer months than in that of cooler ones. Substantial seasonal variation relates closely to the reproductive season of potential colonizers (e.g., Woods Hole Oceanographic Institution 1952, and others). Difference in reproductive season among sessile organisms has an effect on the rate of increase in the number of species in the initial portion of colonization curve (Schoener 1974, Osman 1977). Osman's (1977) experiments on panels submerged at the various times of year clearly demonstrated that more rapid colonization occurs during warmer months, resulting earlier in a higher equilibrium number of species.

Furthermore, Schoener et al. (1978) compared one year's colonization curves on identical panels submerged at the similar time of year at several shallower-water Northern Hemisphere localities ranging from tropical to subtropical, temperate, and subarctic regions, restricting their comparisons to the surveys initiated in the warmer months of spring to early summer. They reported that the tropical Thailand curve rises rapidly to reach a peak in the number of species and then begins to descend, that the subtropical Hawaii curve reaches a maximum number of species later and then decreases, that temperate and subarctic regions show slowly rising curves which become horizontal afterwards, and that the numbers of species on the panels from all regions finally approach the similar values at the end of observed period. Besides, Schoener et al. (1978) pointed out that the colonization curve in Korea of several temperate localities resembles the subtropical curve rather than the other temperate ones because of the influence of a warmer-water westward flowing branch of the Kuroshio (the Yellow Sea Warm Current) which mitigates water temperatures of northerly latitudes.

It is appropriate to ask whether these colonization curves are, in fact, approaching their equilibrium values within one year's period. Schoener et al. (1978) describes "Because this study had terminated after one year, we hope that future experiments conclude at some less arbitrary point than the end of one calendar year after submergence". As to the equilibrium number of species, there are two opposite results; Sutherland and Karlson (1977) found out that their North Carolina fouling-plates require more than one year's time to reach an equilibrium number of species, while Osman (1977) suggested that one year's time is a sufficient period for the equilibrium to be approached on his Massachusetts panels.

The plates of series 1 in this study were suspended in July of warmer month. The number of species per plate increased significantly through the period from 2 to 6 months after immersion (Table 6). Particularly, from 2 to 4 months after immersion the rate of increase of the number of species was high (Fig. 7). This high rate suggests that reproductive seasons of many of sessile organisms found in the present study area are in the warmer months of late summer to late autumn as in the results of Schoener (1974) and Osman (1977). In this study, the number of species at each depth became horizontal after reaching a maximum 6 months after immersion and showed similar values in mean 10 and 13 months after immersion (Fig. 7). This suggests that one year's time in this study is a sufficient period for the equilibrium number of species. This attainment to an equilibrium number of species within one year from initiation coincided with the results of Osman's Massachusetts panels (1977). Though Sutherland and Karlson (1977) indicated that equilibrium number was not attained within one year after immersion, their North Carolina communities were dominated by *Styela* or *Schizoporella* after one or two years from initiation. But, their community structure is considered to have been destroyed because of sloughing of *Styela* in summer. Though the domination of another species *Schizoporella* often persisted when the preemption of plates by this species occurred before being overgrown by other species, there were sometimes cases where the monopoly of plates by *Schizoporella* was inhibited by *Styela* (Sutherland 1977, 1978). It is thought that the attainment to an equilibrium number within one year after immersion was made impossible probably by sloughing of *Styela* or overgrowing of *Styela* onto *Schizoporella*.

Though there are no data showing seasonal changes in the number of species during the period from 13 to 37 months after immersion, the number of species in two late summers and one early autumn at 13, 26 and 37 months after immersion remained almost constant at Depths A and B (Fig. 7). In this period, four species (*Codium* *adhaerens*, *C. latum*, *Botrylloides violaceus* and *Schizoporella unicornis*) occurred only 13 months after immersion at Depths A and B, while other four species (*Amaroucium multiplicatum*, *Leptoclinides* sp., *Mycale plumosa* and *Pinctada fucata*) only 37 months after immersion at the same depths (Tables 2 and 3). This difference in species composition suggests that the attained, stable equilibrium number is maintained by the replacement of species among these eight species. Finally, compared with the types of colonization curve of Schoener et al. (1978), the present colonization curve resembled that of their subtropical type; the influence of the Kuroshio along the Pacific coast of Japan may have brought the increase of the number of species like the case of Korea studied by Schoener et al. (1978).

(2). Developmental process at Depths A and B

At Depths A and B, the three parameters of S, H' and J' increased in the period from 2 to 6 months after immersion (Fig. 7 and Table 6). This indicates that in the initial stage of community development, Depth A and B communities come to have many species of sessile organisms and to show an even apportionment of coverage among the species. After that, the high values of H' which occurred 6 months after immersion remained constant in the period from 13 to 37 months after immersion, though there was a temporary decrease 10 months after immersion (Fig. 7). This similar high value of *H*' between these two phases does not mean an analogy in community structure between them. The high value of *H*' at 6 months after immersion results from the high value of S rather than *J*', while that in the period from 13 to 37 months after immersion results from the high value of *J*' rather than S (Fig. 7). This indicates that 13 to 37 months' samples at Depths A and B come to show a more even apportionment of coverage among species rather than an increase in the number of species. On the other hand, the temporary decrease of *H*' at 10 months after immersion results from the low value of S (Fig. 7). The overgrowth of the colonial ascidian *Diplosoma mitsukurii* which dominated at this immersion period is considered to have mainly caused the extinction of species showing low percent cover. A temporary increase of MDI at 10 months after immersion (Fig. 7) is also considered to reflect the domination of *D. mitsukurii*. In the period from 13 to 37 months after immersion, the values of S, *H*', *J*' and MDI at Depths A and B also remained almost constant. From the constancy of these four parameters, it is inferred that Depth A and B communities are stable in community structure after immersion for ca. one year. In this stable state, an equilibrium number of species is attained, and the high value of *J*' rather than S is responsible for the high value of _H_' as indicated by the low value of MDI.

The low value of HSI at Depths A and B at 6 and 10 months after immersion (Fig. 7) shows a difference in community structure among samples. The difference at 6 months after immersion when S was maximum seems to be due to the variability in the recruitment of sessile organisms, while that at 10 months after immersion when S temporarily decreased seems to be due to the extinction of several species of sessile organisms showing low coverage by the overgrowth of colonials, especially of _D. mitsukurii_. In the period from 13 to 37 months after immersion, HSI also remained almost constant at Depths A and B (Fig. 7). However, the lowest mean of HSI in Depth A samples immersed for 37 months (Fig. 7) is considered to show much difference in community structure among the samples. Depth A and B samples immersed for 37 months are characterized by three-dimensional, complicated surface structure of the shell of _Crassostrea nippona_ which provided a new open space for the recruitment and growth of colonials as well as solitaries, and by the rare two species _Amaroucium multiplicatum_ and _Mycale plumosa_ which occurred only in these samples through this study. The variability in the recruitment of these rare species may be responsible for the difference in community structure. And, the inconsistency in rank of the species ranking from the top to fourth among 37 months' Depth A samples is considered to be responsible for the difference in the similarity of community structure; the 37 months' Depth A samples had two common species of *Balanus trigonus* and *Amathia distans* in the ranks, but the 37 months' Depth B to D samples had three or four common species consisting of *B. trigonus*, *D. mitsukurii*, *C. nippona*, *W. subovoidea* and *A. distans* (Fig. 14). Besides, the final dominant species *Eisenia bicyclis* and *Crassostrea nippona* did not show such high ranks together on the same plate at Depth A (Fig. 14). These two species may have relatively equal or high competitive ranks for space. The following two processes have been thought to bring a difference in community structure between samples: one is that the recruitment of sessile organisms is a universally variable and unpredictable process (Sutherland and Karlson 1977); the other is that there are some species with relatively equal or high competitive rank (Osman 1977, Sutherland and Karlson 1977). As mentioned above, the former seems to occur in the initial and later stages of community development, and the latter in the later stage of community development.

(3). Developmental process at Depths C and D

At Depths C and D, the three parameters of S, *H*' and

J' increased with the rapid recruitment of sessile organisms in the period from 2 to 6 months after immersion as occurred at Depths A and B (Fig. 7). But a temporary decrease of H' which occurred 10 months after immersion at Depths A and B did not occur especially at Depth D. At this immersion period, H' at Depth D showed a maximum (Fig. 7). This maximum of H' was due to the low values of S and J' at 6 months after immersion. The overgrowth of *D. mitsukurii* which dominated 6 months after immersion earlier than other depths is considered to have brought the low values of S and J' at this immersion period.

In the period from 13 to 37 months after immersion, community structure at Depths C and D differed greatly from that at Depths A and B (Fig. 7). At Depths C and D, S decreased significantly in this period, and H' showed a tendency to decrease though not significant (Fig. 7 and Table 6). From the low values of S and H', it is inferred that Depth C and D communities in this period are much simpler in community structure than Depth A and B communities in the same period. The low value of H' results from the low value of S rather than J'. Besides, the decrease of S and H' in this period occurred earlier at Depth D and later at Depth C, and a rise of MDI similarly occurred earlier at Depth D and later at Depth C (Fig. 7). This suggests that the simplification in structure of Depth C and D communities occurs earlier at Depth D than at Depth C. The communities of sessile organisms which showed this simplification are regarded as a return to an immature stage of community development, because there were the reappearance of the early colonizers of green algae *Ulva pertusa* and *Codium adhaerens*, the increase in coverage of the early colonizers of barnacles *Balanus trigonus*, *Megabalanus volcano* and *M. rosa*, and the decreases in coverage or disappearance of the kelp *Eisenia bicyclis* and the oyster *Crassostrea nippona* which finally dominated at Depths A and B (Tables 2 and 3).

On the other hand, a high mean value of J' was seen in Depth D samples immersed for 37 months (Fig. 7). This high value of J' was brought by the high similarity of coverage among the species having high coverage rather than among the ones having low coverage (Fig. 14). The low value of MDI also suggests a low degree of domination (Fig. 7). These changes in J' and MDI at Depth D from 26 to 37 months after immersion are regarded as a recovery from a secondary immature stage to a mature stage of community development. This recovery is reflected by the appearance of the young individual of the later colonizer *Eisenia bicyclis* in the community (Table 2).

The lowest mean of HSI occurred 6 months after immersion at Depth C and 13 months after immersion at

Depth D (Fig. 7). The low value at 6 months after immersion seems to be due to the variability in the recruitment of sessile organisms, while that at 13 months after immersion seems to be due to the extinction of several species of sessile organisms by the overgrowth of colonials, especially of _D. mitsukurii_. In the period from 13 to 37 months after immersion, HSI was higher at 26 and 37 months after immersion at Depth D (Fig. 7). This rise of HSI from 13 to 26 months after immersion at Depth D is also regarded as a return to an immature stage of community development because the high similarity in community structure between the samples results from the simplification of community structure mainly by an increase in coverage of the early colonizers of barnacles, while a little decrease in mean of HSI from 26 to 37 months after immersion also seems to reflect a recovery to a mature state of community development.

6. Stability of community structure

In the period from 13 to 37 months after immersion, the pattern of transition of sessile organisms differed greatly with depth; Depth A and B communities were finally dominated by _Eisenia bicyclis_ and _Crassostrea nippona_, while Depth C and D communities finally showed the decrease in coverage or disappearance of these two species, followed by the occurrence of a mixture of the early, middle and late colonizers of algae and by the increase in coverage of the early colonizers of barnacles. These changes at Depths C and D seem to be brought mainly by the sand scouring due to wave action. A disturbance such as scouring of bottom sand to community is regarded as an agent making it return to an immature stage of community development.

Physical or biological disturbance to communities has been proved to operate on the determination or maintenance of community structure in intertidal zones (Johnson 1970, Dayton 1971, Sousa 1979, Paine and Levin 1981, Dethier 1984), in subtidal zones (Moran 1980, Ayling 1981, Hay 1984) and in coral reefs (Connell 1978, Woodley et al. 1981). And it has been indicated that its determination or maintenance is controlled by the magnitude, frequency and length of disturbance (Sutherland 1981, Dethier 1984). Though this study did not measure the magnitude, frequency and length of disturbance at all, the instability of the external environment for sessile organisms on the plates at greater depths such as scouring from the bottom sand probably have made the Depth C and D communities stay in a particular immature stage of community development. Besides, these immature communities may be explicable by a stability-time hypothesis of Sanders (1968), which tries to explain differences in species diversity between communities. Communities at Depths A and B may be regarded as approximation to a biologically accommodated community being the one of both ends in the continuum of his hypothesis, while communities at Depths C and D as a stay in a physically controlled community being the other of those ends.

In this study, communities at Depths A and B where there was no effective physical or biological disturbance, reached a more mature stage of community development dominated by *Eisenia bicyclis* and *Crassostrea nippona* with superior competitive abilities peculiar to themselves through biological interactions of interspecific competition for light or space. Thus, when physical or biological disturbance is not effective on community, the following morphological, physiological or ecological characteristics of these two species (i.e., the kelp's morphological form, robustness of tissue, tolerance for shading in germination or growth, and a long life span; and the oyster's robust shell, great adhesive power to substratum, great strength in opening and shutting movement of shell, and a long life span) are considered to be important for the determination and maintenance of community structure in the future community development of sessile organisms. When disturbance is more effective on a community of sessile organisms, it is thought that it forces the community to stay in an immature stage of community development.

7. Developmental process of community metabolism

The relation between Pg and R values which reversed along the gradient of depth at 2 months after immersion was due to abundant recruitment of microalgae such as diatoms at Depths A and B and of barnacles at Depths C and D. Therefore, Pg was higher at Depths A and B, R was higher at Depths C and D, and estimated energy budget in a day (Pg/R) suggested an autotrophic state at Depth A, a slightly heterotrophic state at Depth B, and a more heterotrophic state at Depths C and D (Fig. 8). In the period from 2 to 6 months after immersion, Pg and R showed no increase with time in spite of the growth of organisms (Fig. 8). This is attributable to the fall in water temperature from summer to winter. In this period, the decrease of R rather than Pg was great, so that Pg/R indicated an autotrophic state, especially in midwinter at 6 months after immersion (Fig. 8). In the period from 6 to 13 months after immersion of winter to summer, Pg and R increased together to reach a maximum 10 or 13 months after immersion, at which Pg/R was approximate to 1 or it showed a value in a heterotrophic state (Fig. 8). R seems to be more affected by water temperature than Pg;

the regression coefficients of Pg and R with temperature of young samples within the first year after immersion were generally higher in R than in Pg (Tables 10 and 11). Therefore, Pg/R is considered to have decreased 6 to 13 months after immersion.

In the period from 13 to 37 months after immersion, Pg showed a decrease (Fig. 8 and Table 7). This decrease is attributable to differences in the total mass of the photosynthetic tissues of dominant algae among samples. The large-sized *Codium latum* which dominated 10 or 13 months after immersion was most massive in the mass of photosynthetic tissue per individual among algae appearing in this study, so that this alga brought the maximum of Pg at 10 or 13 months after immersion. As to *Eisenia bicyclis* of final dominant species, its stipe was scarcely active in photosynthesis, so that its blades are regarded as photosynthetic tissue. The smallness of *E. bicyclis* more than *C. latum* in the mass of photosynthetic tissue per individual is thought to be the primary reason for bringing the low value of Pg in the late stage of community development. The secondary reason is that *E. bicyclis* often occurred on the edges (lateral faces) of plates. At this time, *E. bicyclis* was stripped from them before metabolism measurement. A wide variation of Pg values in Depth C samples immersed for 26 months was also due to the frequent occurrence on the edges of this species. Thus, when experimental plates with a larger area than in this study were used, Pg in the later stage of community development would probably become much higher because there is no edge effect on *E. bicyclis*.

R showed a tendency to decrease at Depths C and D in the period from 13 to 37 months after immersion (Fig. 8 and Table 7). This decrease is attributable to the decrease in biomass of sessile organisms by falling from the plates. However, the values of R at Depths A and B in this period were not finally so low as at Depths C and D, increasing 26 to 37 months after immersion (Fig. 8). This increase is attributable to not only the growth of finally dominated *Crassostrea nippona* and *Eisenia bicyclis* but also the increases of epifaunas dwelling on these two dominant species and infaunas dwelling in the former massive shells and among the latter holdfasts.

Odum (1969) made a suggestion about the change of bioenergetics in ecosystem during succession: Pg exceeds R in the early stage of succession, in which Pg/R becomes greater than 1; although Pg/R is reversely less than 1 in a special case of organic pollution, Pg/R finally approaches 1 with the progress of succession in both cases. And he suggested that the ratio of Pg/R is an excellent functional index of the relative maturity of the system. And then, from comparing the pattern of a 100 days' autotrophic succession in a microcosm based on the data of Cooke (1967) and the hypothetical model of a 100 years' forest succession presented by Kira and Shidei (1967), he indicated that the two patterns show a characteristic process in change of Pg/R along succession, that is, Pg exceeds R in the early stage of succession, in which Pg/R becomes greater than 1, and then Pg/R finally approaches 1.

In this study, the pattern of change in Pg during community development paralleled to the above-stated two cases which showed a decrease after a maximum, but that of R paralleled to the microcosm's case which showed decrease after a maximum rather than the forest's one which showed stabilization after a maximum. But Pg and R did not finally approach each other, and Pg/R indicated a more heterotrophic state in more developed Depth A and B communities (Fig. 8). This development into a more heterotrophic state differs from Odum's prediction. Communities of sessile organisms are an open system in the water for energy resource of light or food. Almost all sessile invertebrates are filter feeders and depend on particulate organic matter suspended in the water, so that they exploit plankton or organic suspension from surrounding water mass as energy source to support their lives. Margalef (1968) indicated that this exploitation of surrounding organic matter occurs in plankton communities. Much more heterotrophic state at Depth A 37 months after immersion suggests that there is the strong exploitation of organic matter from the water in the present communities of sessile organisms. Fisher et al. (1982) investigated the transition of community attributes following succession after a flood in a desert stream with the purpose of testing the hypothesis of Odum (1969) and Margalef (1968) on succession, and indicated that Pg and R increase rapidly after the flood and that Pg/R exceeds 1 by 5 days but does not approach 1 afterwards as predicted by Odum (1969). Fisher et al. (1982) suggested that a criterion in Pg/R of approaching 1 which derived from relatively closed ecosystems by Odum (1960), Beyers (1963), Cooke (1967) and Gordon et al. (1969) is inadequate to describe succession in such open system as streams. The results of this study agreed with those of Fisher et al. (1982) in that Pg/R did not always approach 1 with succession, but showed a tendency becoming heterotrophic state with succession. Furthermore, Odum (1969) proposed that Pg/R deviates greatly from 1 when community returns to an immature stage of community development, but this study showed that the Pg/R values of the Depth C and D communities which showed a return to an immature stage from 13 to 37 months after immersion indicates a heterotrophic state like the Depth A and B communities which showed development to a mature stage, but the former communities were higher in value than the latter ones (Fig. 8). Though the Pg/R did not finally approach 1 in this study, the Pg/R more heterotrophic at Depths A and B indicates a mature stage of community development because of the strong exploitation of organic matter from the surroundings of plates, while the slightly high value of Pg/R at Depths C and D than at Depths A and B indicates a deviation from the mature state of community which means a return to an immature stage of community development.

8. Developmental process of community biomass

As described already, a great difference was confirmed between Depths A and B and Depths C and D in the changes of percent cover, community structure and community metabolism during the period from 13 to 37 months after immersion. Community biomass except chlorophyll *a* at Depths A and B generally increased with succession, while that at Depths C and D increased until 13 months after immersion and then decreased in the period from 13 to 37 months after immersion (Fig. 10). After barnacles *Balanus trigonus*, *Megabalanus volcano* and *M. rosa* colonized plates immediately as earlier colonizers, they covered most of bare space rapidly and formed a layer on the plates 2 months after immersion. The barnacles, especially *B. trigonus*, attached to each other and formed one to three layers on the plates. Their shells provided new attachment sites for sessile organisms, and then were covered mostly by colonial animals as a result of vegetative reproduction. The colonials could scarcely grow to the direction perpendicular to the plates. But the bryozoan *Watersipora subovoidea* occasionally showed its growth to the direction perpendicular to plates along the lateral surface of the shell of barnacles or the foliose of *Ulva pertusa*. The tissue of *W. subovoidea* is fairly fragile, so that it was difficult for its species to extend its own structure to the three-dimensional space. The sessile organisms which contributed to the increases of community biomass were not colonial animals but the large macroalgae, *Codium latum*, *C. fragile*, *C. divaricatum* and *Eisenia bicyclis*, and the large bivalve, *Crassostrea nippona*, which were able to dominate three-dimensional space on the plates by escaping the overgrowth of colonials.

The oyster *C. nippona* covered most of sessile organisms' species with the growth to occupy large cover on the plates by its massive body, and the kelp *E. bicyclis* occupied the water column near the plates by its blades. Besides, the surfaces of the shells of its grown oyster were occupied extensively by newly recruited barnacles and colonial animals and partially by newly recruited bivalves including *C. nippona* and the growth of *C. nippona*, and the expansion of three-dimensional space by them contributed to the increases of community biomass except chlorophyll *a*. The complicated, rugged massive structure constructed on the plates by sessile organisms is considered to be suitable for dwelling of mobile infaunas such as polychaetes and for accumulation of organic detritus or sediment.

Community biomass at Depths A and B generally increased with time except for chlorophyll *a* (Fig. 10). In Depth A samples immersed for 37 months, DM was 26.8 kg/m^2, ADM comprised 95.5% of DM, and AFDM was 1.2 kg/m^2. On the other hand, community biomass at Depths C and D increased until 13 months after immersion but decreased from 13 to 37 months after immersion (Fig. 10). This decrease was significant at Depth D (Table 8). Compared with DM, ADM and AFDM of 37 months' Depth A sample, those of 37 months' Depth D sample were 0.17, 0.17 and 0.20 times, respectively. This suggests that the matter accumulated on plates until 13 months after immersion had fallen off from them from 13 to 37 months after immersion at Depths C and D. At Depth C, the percent cover of *Crassostrea nippona* decreased from 13 to 37 months after immersion (Table 3). At Depth D, the barnacles *Balanus trigonus*, *Megabalanus volcano* and *M. rosa* and the colonial animals *Diplosoma mitsukurii*, *Watersipora* subovoidea and Amathia distans had formed a thin layer on plates in the absence of C. nippona (Table 3). As to a factor causing the falling of the accumulated matter from plates, I confirmed by underwater observations that the effects of grazers or predators are not important, and the sand scouring from the bottom seems to be an agent bringing the decrease of community biomass.

9. Developmental process of community maturity indices

(1). Gross primary production/organic carbon (Pg/C)

Pg/C showed high values 2 months after immersion at Depths A and B (Fig. 11). This high values of Pg/C resulted from both the high value of Pg by abundant microalgae and the low value of C by a small number of barnacles at these two depths at this time (Figs. 8 and 10). On the other hand, there were earlier and more abundant recruitment of barnacles and less recruitment of microalgae at Depths C and D than at Depths A and B, so that Pg/C was low at Depths C and D (Fig. 11). The changes of Pg/C with community development showed a decrease at Depths A and B but were almost constant at Depths C and D (Fig. 11).

In the period from 13 to 37 months after immersion, communities at Depths C and D showed a return to an immature stage of community development, which was accompanied with the falling of matter from plates and by the reappearance of early colonizers Ulva pertusa and Codium adhaerens and the increase in coverage of an early colonizer Balanus trigonus. This return to immature communities was not accompanied with the increase of Pg/C, but the values of Pg/C at Depths C and D were higher than at Depths A and B (Fig. 11). Spearman's rank correlation coefficients of Pg/C values of 37 months' samples on the gradient of depth showed a significant increase with depth (Fig. 15).

In a closed ecosystem, Pg is the sole energy influx and is used for maintaining organisms or accumulating biomass. However, the present community of sessile organisms is an open system in the water, so that energy influx coming into the community is the algal production by photosynthesis and the taking of foods by animals from the water. Odum's hypothesis on Pg/C is thought to be appropriate to a more closed ecosystem, but the low value of Pg/C in the later developmental stage of the present community as an open system was also brought by the accumulation of biomass and the decrease of Pg.

(2). Gross primary production/chlorophyll a (Pg/Chl. a)

Pg/Chl. a generally decreased with community development after reaching its high values at 2 months after immersion (Fig. 11). This decrease is attributable to differences in life form of transitional algae in community development, in which they changed from microalgae, to foliose, to branching and to kelp macroalgae. In this series of life form, light given experimentally to small algae will almost all reach chlorophyll *a* in their tissues without being weakened by absorption, while that to large algae will be weakened more strongly by absorption before reaching chlorophyll *a* in their tissues. The high value of Pg/Chl. *a* at 2 months after immersion was due to the presence of microalgae, because the chlorophyll *a* within them is apt to be exposed more fully to light. But the kelp *E. bicyclis* is considered not to be more fully exposed by the light reaching its surface than foliose algae, *Ulva pertusa* and *Codium latum*, and branching ones, *Codium fragile* and *Pterocladia capillacea*, because of the partial absorption of light by its thick tissue before reaching chlorophyll *a*. Depth A and B communities immersed for 37 months which were dominated by *E. bicyclis* showed the lowest values of Pg/Chl. *a* (Fig. 11). A return to an immature stage of community development which occurred at Depths C and D after 13 months from immersion was not accompanied with an increase in value of Pg/Chl. *a*, but Pg/Chl. *a* in 37 months' samples was slightly high at Depths C and D than at Depths A and B (Fig. 11). This slightly high value of Pg/Chl. *a* is attributable mainly to the reappearance of the foliose alga *Ulva pertusa* of early colonizer (Table 2). Spearman's rank correlation coefficients of Pg/Chl. *a* values of 37 months' samples on the gradient of depth showed a significant increase with depth (Fig. 15).

(3). Organic carbon/organic nitrogen (C/N)

The wide variation of C/N at Depths A and B at 2 months after immersion (Fig. 11) was caused by various degrees of exposure of plates to sunlight. Microalgae such as diatoms formed their mat on sunny plates, and barnacles were abundant on shadowy ones. From the probability that the N content of organic matter in algae is higher than that in invertebrates because of the possession of cell wall of algae, the ratios of C/N in algae is generally regarded as higher than those in invertebrates, so that the difference in recruitment between microalgae and barnacles which was caused by various degrees of exposure of plates to sunlight is thought to have brought this wide variation of C/N. At this time, the values of C/N were higher at Depths A and B than at Depths C and D (Fig. 11), indicating more abundant microalgae and less barnacles at the former depths. After that, C/N decreased and then remained almost constant until 37 months after immersion except for a few high values at 10 or 13 months after immersion

(Fig. 11). But, at Depth D, it showed a significant decrease in the period from 2 to 13 months after immersion, and then a significant increase in the period from 13 to 37 months after immersion (Table 9). Though both C and N showed similar changes in amount with community development, this decrease of C/N in the former period at Depth D was due to the increase in amount of N rather than C (Fig. 10). This suggests that there is an increase of organic matter including N in this period. A return to an immature state of community development which occurred at Depths C and D in the period from 13 to 37 months after immersion was accompanied with a significant increase of C/N at Depth D. This increase at Depth D was due to more decrease in N than in C (Fig. 10). This suggests that there is a decrease of organic matter including N rather than C. Spearman's rank correlation coefficients of C/N values of 37 months' samples on the gradient of depth showed a significant increase with depth (Fig. 15). The existence of large invertebrates such as bivalves rather than large alga, Eisenia bicyclis may be one cause producing the high value of the ratio of C to N.

(4). Pigment diversity (D430/D665)

Margalef (1961, 1967) suggested an index of D430/D665 as a criterion for the degree of maturity of plankton communities. Niell (1979) showed that D430/D665 of sessile organisms in an intertidal rocky shore does not increase with community development, and Fisher et al. (1982) showed the same results of D480/D666 for the community development of organisms in a stream. Besides, communities of sessile organisms formed on the artificial concrete plates set up experimentally for ca. 5 years in intertidal rocky shore near the present study site do not also show an increase of value of D430/D665 (A. Yamagami, *personal communication*). Pigment diversity of communities indicated by D430/D665 or D480/D666 seems not to be appropriate to a criterion for the degree of maturity of the communities in intertidal rocky shores or streams.

In the present communities of sessile organisms formed on artificial plates immersed in the sea, D430/D665 showed almost no variation during the first year after immersion but increased significantly at Depths A and B in the period from 13 to 37 months after immersion (Fig. 11 and Table 9). On the other hand, there was a significant decrease at Depth D in the period from 13 to 37 months after immersion (Table 9). Spearman's rank correlation coefficients of D430/D665 values of 37 months' samples on the gradient of depth showed a significant decrease with depth (Fig. 15). The D430/D665 values of 37 months' Depth A sample corresponded to those of older plankton communities of Margalef (1968). Furthermore, the values of D430/D665 during the first year after immersion in this study also corresponded to those of Niell (1979) and Yamagami (*personal communication*) or of younger plankton communities of Margalef (1968).

It can be considered that communities investigated by Niell (1979), Yamagami (*personal communication*) and Fisher et al. (1982) are staying at an immature state of community development, because the pigment diversity showed constantly low values through community development. Though these communities stayed in such an immature state, this immature state is considered to be an upper limit of community development reached in those environments. This limit of community development in intertidal zones or streams is thought to be brought by frequent or occasional physical disturbances such as continued wave-actions, regular desiccation by the tide and occasional strong wave-actions by typhoon in the former environment and continued flows of water and occasional dryness or floods in the latter environment.

Those environments are severer in water movement or desiccation than the underwater environment in which this study was carried out. Such severe environmental factors would have determined the upper limit of D430/D665 or D480/D666 values in the community development of sessile organisms in intertidal rocky shores or streams. However, the pigment diversity observed in older plankton communities of Margalef (1968) as well as Depth A and B communities of this study exceeded this upper limit in a mature state of community development, when there was no recognizable effective disturbance.

10. Relation of community metabolism to temperature

Metabolic rates of poikilothermal sessile organisms strongly depend on temperature. Beyers (1962) compared the respiration rate on temperature of a stabilized fresh-water laboratory microcosm, which was taken from a river and then had been cultured over a year previous to experiments, with that of a single organism Daphnia and that of a sewage community. Beyers (1962) indicated that the respiration rate of Daphnia is more dependent on temperature than that of the sewage community, that the latter is more dependent on temperature than the nighttime respiration rate of the stabilized microcosm, and that the nighttime respiration rate of the stabilized microcosm is practically independent of temperature. Furthermore, Beyers (1962) suggested that the estimated gross primary production of the stabilized microcosm is not certainly stimulated by the increase of temperature. From the results of Beyers (1962), Odum (1971) suggested that various optimum responses to a change in the temperature among many species constituting community would make the accomplishment of reciprocal adjustment and acclimation to a change in the temperature possible so as to enable the whole of stabilized community to compensate for a change in the temperature.

The relations of Pg and R with temperature in the present communities of sessile organisms both showed a significantly positive linear regression in common logarithm in almost all of samples examined (Tables 10 and 11). The regression coefficients of Pg and R in the samples of series 3 did not show a significant difference between the young and old samples. This indicates that Pg and R in the present communities which reached a mature stage of community development do not become independent of temperature.

On the other hand, the regression coefficients of Pg and R with temperature became closer each other in old samples (Fig. 12b). This mutual approach of these two regression coefficients suggests that they are apt to become equal each other in the later stage of community development. Subtracting the regression equation of R from that of Pg produces a linear regression in common logarithm of Pg:R on temperature. The mutual approach of the two regression coefficients of Pg and R in the present mature community indicates that the regression coefficient of Pg:R which is represented as $a_P - a_R$ becomes closer to zero (Figs. 12 and 13). This suggests that the Pg:R in mature community becomes independent of temperature and that the acquirement and exhaustion of energy of mature community come to have a balance to the surrounding changes of water temperature occurring through one year. This balance between Pg and R may be regarded as one homeostatic community attribute of mature community, though there are no seasonal data for the relation of Pg:R with temperature in mature community.

CONCLUSION

The community attributes, i.e., species composition, community structure, community metabolism, community biomass and community maturity showed a gradual progress through community development at the upper two depths where there was no recognizable effective physical or biological disturbance, while they showed some irregular progress indicating a return from a mature to an immature state of community development in the period from 13 to 37 months after immersion at the lower two depths where there was probably effective disturbance such as sand scouring from the bottom.

The changes of community attributes observed in this study are in most cases explicable by the hypothesis on succession suggested by Margalef (1968) and Odum (1969), with some exceptions. A more heterotrophic state suggested by Pg/R values in a mature state of community development at the upper two depths is not explicable by the hypothesis of Odum (1969) that Pg/R value approaches 1 with the progress of succession, becoming 1 at a mature state, but explicable by the hypothesis of Margalef (1968) that there is a case indicating Pg/R value less than 1 in mature state when a part of energy necessary for maintaining a system can be obtained from the surrounding. Besides, Odum (1969) suggested that the evenness ($\underline{J}'$) on community structure becomes high with the progress of succession, but it becomes low when the development of a community is disturbed by some factors. In this study, however, $\underline{J}'$ was maintained high even when a community becomes immature by some disturbance, as seen at the lowest depth in the period from 13 to 37 months after immersion.

SUMMARY

1. Succession of sessile organisms over ca. 3 years on concrete plates suspended at the depths of 1.0, 2.5, 4.0 and 5.5 m in Nabeta Bay, Shimoda, Pacific coast of Japan, was investigated from the changes of percent cover, community structure, community metabolism, community biomass and community maturity for the purpose of testing the hypothesis on succession suggested by Margalef (1968) and Odum (1969) and clarifying the general characteristics in the community development of sessile organisms.
2. A total of 45 species of sessile organisms (17 algal and 28 invertebrate species) appeared during colonization.
3. The transition of algae began with the recruitment of green algae *Ulva pertusa* and *Codium adhaerens*, and ended in the domination of the kelp *Eisenia bicyclis* at the upper two depths and in a mixture of early (*U. pertusa* and *C. adhaerens*), middle (red alga *Gelidium amansii*) and late (*E. bicyclis*) colonizers at the lower two depths.
4. The transition of sessile invertebrates began with the recruitment of barnacles, especially of *Balanus trigonus*, followed by the recruitment of colonial animals having a great effect on community structure through

overgrowth, and ended in the domination of the oyster *Crassostrea nippona* at the upper two depths and in the domination of *B. trigonus*, an ascidian *Diplosoma mitsukurii* and bryozoans *Watersipora subovoidea* and *Amathia distans* at the lower two depths.

5. The process of succession was divided into three stages and four sub-stages by dendrogram analysis. Communities at the three upper depths shifted successively from Stage 1 to Stages 2 and 3 with time, while community at the lowest depth shifted from Stage 1 to Stage 2 without advancing to Stage 3, staying at Stage 2 throughout the period from 4 to 37 months after immersion. By dividing each of Stages 2 and 3 into two sub-stages, Stage 1 and four sub-stages were characterized by high-ranking sessile organisms as shown in Tables 4 and 5.

6. As to colonization curve, the number of species at each depth became horizontal after reaching a maximum at 6 months after immersion, and its mean values at 10 and 13 months after immersion closely resembled each other. This stabilization in the number of species suggests that in this study one year is a sufficient period for the equilibrium number of species. And the stable equilibrium number which continued through the period from 13 to 37 months after immersion was maintained by the replacement of several species.

7. The changes of the five parameters on community structure, i.e., the number of species (S), Shannon-Weaver diversity index ($\underline{H}'$), information theory evenness index ($\underline{J}'$), McNaughton's dominance index (MDI) and Horn's similarity index (HSI), were investigated throughout community development. Communities at the upper two depths indicated the stability of community structure under the maintenance of high S, $\underline{H}'$ and $\underline{J}'$ values in the period from 13 to 37 months after immersion, while those at the lower two depths indicated the simplification of community structure accompanied with the decrease of S and $\underline{H}'$ in the same period. At the lowest depth, $\underline{J}'$ showed an increase in this period, due to the high similarity of coverage among the species having high coverage. Besides, HSI at 37 months after immersion showed low values at the upper three depths, while a high value at the lowest depth. This high similarity among the samples at the lowest depth was due to the strong domination by few species.

8. As to the end point of community development, at the upper two depths where there was no recognizable effective physical or biological disturbance, communities of sessile organisms were considered to come to converge on a persistent, stable assemblage of oysters and kelps because of their superior competitive abilities through biological interactions of interspecific competition for

space or light.

9. The pattern of change of gross primary production of community (Pg) during community development showed a decrease after reaching a maximum, and that of community respiration (R) showed stabilization after reaching a maximum. Estimated energy budget in a day (Pg/R) finally indicated a more heterotrophic state (Pg/R less than 1) at the upper two depths than at the lower two ones.

10. The six parameters on community biomass, i.e., dry mass (DM), ash dry mass (ADM), ash-free dry mass (AFDM), organic carbon (C), organic nitrogen (N) and chlorophyll a (Chl. a), increased with succession at the upper two depths except for Chl. a showing the pattern of change similar to Pg, while those at the lower two depths increased in the first year after immersion and then decreased until 37 months after immersion.

11. The changes of the four indices evaluating the degree of community maturity, i.e., the ratios of gross primary production/organic carbon (Pg/C), gross primary production/chlorophyll a (Pg/Chl. a), organic carbon/organic nitrogen (C/N) and pigment diversity (D430/D665), were investigated throughout community development. Pg/C showed a significant decrease at the upper two depths with succession, but was almost constant at the lower two depths throughout it. Pg/Chl. a and C/N changed from high to low values with succession. C/N

showed a significant increase at the lowest depth in the period from 13 to 37 months after immersion. D430/D665 showed almost no variation during the first year after immersion, and then, in the period from 13 to 37 months after immersion, it increased significantly at the upper two depths but decreased significantly at the lowest depth. The values of these four indices in 37 months' samples showed a significant change on the gradient of depth. This gradient of values indicated attainment to a mature state of the upper two depths' communities and a return to an immature state of the lower two depths' communities.

12. Relation of community metabolism to temperature was investigated throughout community development. In mature communities, Pg and R were not independent of temperature at any depths, but the ratio Pg:R tended to become independent of temperature at the upper three depths.

13. The changes of community attributes observed in this study are in most cases explicable by the hypothesis on succession suggested by Margalef (1968) and Odum (1969), with some exceptions.

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Table 1. Date of start of immersion, sampling time, immersion period, mean surface water temperature during sampling time, water temperature at measurement of metabolic rates and mean day length at its measurement. Plates in series 1 were immersed at the four depths of 1.0, 2.5, 4.0 and 5.5 m. Plates in series 2 were immersed at the same four depths for investigating the relation of gross primary production of community to light intensity. Plates in series 3 were immersed only at the depth of 2.5 m for investigating the metabolism-temperature relationships of the community.

Series	Date of start of immersion	Sampling time	Immersion period (months)	Mean surface water temp. (°C)	Water temp. at measurement (°C)	Mean day length at measurement (hours)
1	July, 9 1974	Aug. 23-Sept. 2, 1974	2	24.2	24	13.0
		Nov. 8-17, 1974	4	18.4	20*	10.5
		Jan. 10-18, 1975	6	14.5	14	10.1
		May 1-13, 1975	10	18.1	18*	13.8
		Aug. 9-15, 1975	13	24.5	24*	13.6
		Sept. 6-23, 1976	26	24.5	24*	12.4
		Aug. 7-18, 1977	37	24.5	24*	13.6
2	Aug. 8, 1975	Aug. 23-Sept. 24, 1977	25-26	24.5	24	12.6
3	Aug. 8, 1975	Aug. 10-Sept. 15, 1978	37-38	24.5	*	12.9
	Aug. 9, 1978	Sept. 23-Oct. 30, 1978	2-3	24.4-21.0	*	11.5

*used for measuring metabolism-temperature relationships at different temperatures from 12 to 24 °C.

Table 2. Changes in the mean percent cover of algae observed in the central area (16 cm x 16 cm) of experimental plates at four depths. P: occurrence in the peripheral area of the plate. The hyphenated sequence of four values represents mean cover (%) of Depth A-B-C-D (i.e., 1.0-2.5 4.0-5.5 m).

Species	Immersion period (months)					
	4	6	10	13	26	37
CHLOROPHYTA						
Cladophora wrightiana	1.8- 0.2- 0 - 0	5.3- 1.7- 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Ulva pertusa	3.1- 4.4- 1.8- 0.9	2.5- 1.7- 1.6- 0.1	0.3- P - P - 0.1	0 - 0 - 0 - 0.4	0 - 0 - 0 - 0	0 - 0 - 0.1- 0.1
Codium adhaerens	2.1- 2.7- 0 - 0	5.1- 6.6- 3.8- 3.3	11.9-19.7- 1.6- 6.3	0.7- P - 3.1- 2.2	0 - 0 - 0 - 0	0 - 0 - 0.5- 0
Codium fragile	0 - 0.7- 0 - 0	0.7- P - 0.4- P	P - P - 0 - 0	P - P - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Codium latum	0 - 0 - 0.4- 0	0 - P - 0 - 0	P - 0.9- 0 - 0	1.3- 1.0- 0 - P	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Chaetomorpha spiralis	0 - 0 - 0 - 0	0 - P - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0.4- 0 - 0 - 0	0 - 0 - 0 - 0
RHODOPHYTA						
Pterocladia capillacea	5.3-12.9- 3.1- 4.0	1.8- 0.8- 0.3- 0.3	5.8- 3.5- 0.6- 3.0	0.7- 3.9-18.1- 6.1	0.5- 1.2- 0 - 0	0 - 0 - 0 - 0
Grateloupia sparsa	0 - 0.5- 0 - 0	0.3- 0 - P - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Gracilaria textorii	0 - 0 - 0 - 0	0.4- 0.5- 0.9- 0	1.7- 1.2- 0.6- 2.1	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Champia parvula	0 - 0 - 0 - 0	0 - 0.1- 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Ceramium paniculatum	0 - 0 - 0 - 0	0 - 0 -11.5- 3.9	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Plocamium telfairiae	0 - 0 - 0 - 0	0 - 4.3- 7.8- 0.9	0 - 0 - 0 - 0	0.7- 0 - 0 - 0	0.5- 0 - 0 - 0	0 - 0 - 0 - 0
Grateloupia livida	0 - 0 - 0 - 0	0 - 0 - 0 - 0	P - P - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0.4- 0	0 - 0 - 0 - 0
Gelidium amansii	0 - 0 - 0 - 0	0 - 0 - 0 - 0	P - P - 0 - 0	0 - 0 - P - 3.9	0 - 0 - 0 - 0	0 - 0 - 0 - P
PHAEOPHYTA						
Colpomenia sinuosa	4.0- 5.9- 2.0- 0	23.7- 2.7- 0.1- 3.9	2.7- P - P - 0.3	0 - 0 - 0 - 0	0 - 0 - 0 - 0	0 - 0 - 0 - 0
Padina arborescens	0 - 0 - 0 - 0	0 - 0 - 1.4- 0	0 - P - 0 - 0	0 - 0 - 0 - 0	1.2- 1.0- 3.5- 0	P - 4.3- 0 - 0
Eisenia bicyclis	0 - 0 - 0 - 0	0 - 0 - 0 - 0.5	0 - 0 - 0 - 1.0	0 - 0 - 3.8- 1.4	4.6- 2.7- 3.3- 0	11.2- 6.9- 1.8- P

Table 3. Changes in the mean percent cover of sessile invertebrates observed in the central area (16 cm x 16 cm) of experimental plates at four depths. P: occurrence in the peripheral area of the plates. The hyphenated sequence of four values represents mean cover (%) of Depth A-B-C-D (i.e., 1.0-2.5-4.0-5.5 m).

Species	Immersion period (months)						
	2	4	6	10	13	26	37
Cirripedia							
Balanus trigonus	99.9-97.9-100.0-100.0	98.3-99.8-99.8-100.0	87.6-92.8-94.3-97.4	92.5-90.0-94.9-91.8	92.1-97.3-98.4-98.4	96.7-98.4-97.5-97.3	79.8-87.6-99.4-99.6
Balanus eburneus	0-0-0-0	0-0-1.0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
*Megabalanus volcano**	0.7-3.5-1.7-1.8	10.7-3.8-3.9-3.5	19.9-9.0-5.1-1.4	8.0-5.3-1.8-1.0	6.6-4.9-7.2-5.9	1.7-1.7-2.7-0.4	0.5-1.0-0.3-2.1
Tunicata							
Botrylloides violaceus	0-0-0-0	11.8-9.3-5.1-6.8	10.4-19.1-5.5-2.3	P-P-1.8-2.9	3.1-0-4.1-0	0-0-0-0	0-0-0-0
Botrylloides simodensis	0-0-0-0	0-0-0-0	0-8.3-6.6-0	0-0-5.5-0	0-0-0-0	0-0-0-0	0-0-0-0
Botryllus primigenus	0-1.2-0-0	1.3-1.6-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
Symplegma reptans	0-0-0-0	0-0-0-0	0-0-2.2-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
Diplosoma mitsukurii	0-0-0-0	33.3-26.4-21.9-34.8	58.7-56.4-53.4-89.1	77.4-61.6-62.6-67.7	16.3-14.5-9.6-47.7	57.6-52.6-37.5-66.4	21.4-56.6-51.6-85.5
Didemnum moseleyi	0-0-0-0	17.1-12.9-13.3-17.7	10.9-18.4-19.0-19.8	19.5-28.1-40.2-20.7	44.3-26.6-50.1-24.2	22.7-37.1-6.6-3.3	21.1-13.3-5.5-5.3
Trididemnum savignii	0-3.5-0-0	1.8-1.2-0.4-1.4	0-2.0-1.2-0.9	3.5-3.6-0.8-3.0	32.2-3.5-12.8-0.8	8.6-17.7-4.9-2.5	2.0-3.8-0.8-0
Amaroucium multiplicatum	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	4.8-2.0-0-0
Leptoclinides sp.	0-0-0-0	0-0-0-0	0-0-0-0.5	0-0-0-0	0-0-0-0	0-0-0-0	2.0-0-0-0
Styela plicata	0-0-0-0	0-0-0.8-0	0-0-0-0	0-0-P-0	P-0-0-0	0-0-0-0	0-0-0-0
Porifera							
Halichondria japonica	0-0-0-0	0-0.9-0-5.3	0.9-7.0-1.3-2.1	0-P-0-0	2.2-8.8-0.9-2.9	4.6-9.1-34.4-28.7	0-1.6-4.4-6.9
Halichondria panicea	0-0-0-0	0.3-P 0-0	0-0-0-0	0-2.5-17.6-9.1	0-0-0-0	0-0-0-0	0-0-0-0
Mycale plumosa	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-1.7-0-0
Bryozoa							
Watersipora subovoidea	0-3.4-2.1-0	25.1-25.3-14.1-10.3	20.7-29.4-9.0-12.5	11.2-3.1-9.0-20.1	44.8-39.8-12.0-12.7	22.0-6.5-11.3-3.7	7.7-25.3-37.2-82.8
Schizoporella unicornis	0-0-0-0	1.2-0.9-P-0	2.1-1.2-2.1-0.9	2.9-0.3-0-0.7	1.4-0-0.5-0.8	0-0-0-0	0-0-0-0
Parasmittina trispinosa	0-0-0-0	0.1-0-0-0	0-0-0.7-0.1	0-0-0-0	0-0-1.6-0	0-0-0-0	0-0-0-0
Membranipora savartii	0-0-0-0	0-0-0-0	8.5-0.4-0.5-0	0-0-0-0.8	0-0-0-0	0-0-0-0	0-0-0-0
Celleporaria columnaris	0-0-0-0	0-0-0-0	0-0-0-0	0.1-0-0-0.4	0-0-0-0	0-0-0-0	0-0-0-0
Amathia distans	0-0-0-0	0-0-0-0	0-0-38.0-89.7	P-1.8-22.7-26.8	49.9-32.2-68.1-87.3	9.1-25.4-16.8-19.3	40.9-26.6-47.3-48.8
Polychaeta							
Hydroides ezoensis	0-0-0-0	6.5-3.5-1.8-2.1	2.7-4.0-1.3-1.0	6.3-6.8-7.2-4.7	1.3-2.5-0.5-0	1.0-0.8-0.6-0	1.2-3.3-1.8-0.3
Dexiospira foraminosus	8.5-14.1-21.1-23.2	0.4-1.4-0.4-0.3	0-0-0-0	0-0-0-0	0-0-1.0-1.0	0.3-0-1.4-0	0.4-0.1-0-0
Bivalvia							
Pinctada fucata	0-0-0-0	0-0-0-0	0.5-0-0-0	P-0-0-0	0-0-0-0	0-0-0-0	7.2-2.9-0-0
Mytilus edulis	0-0-0-0	0-0-0-0	6.1-1.4-0.8-0	0.7-P-0.4-0	2.5-3.3-0.1-0	16.5-0-0-0	22.9-0-0-0
Crassostrea nippona	0-0-0-0	0-0-0-0	0-0-0-0	9.2-0-0-0	19.9-48.4-6.6-0	39.6-42.2-50.4-0	59.6-52.5-21.7-0

*Including *Megabalanus rosa*.

Table 4. Developmental stages derived from the dendrogram analysis shown in Fig. 5. One stage and four sub-stages are characterized by the species of sessile invertebrates which occupied the top to third rank in mean percent cover in the central area of plates at each immersion period and depth. The degree of domination is ranked by the average of the two ranks of mean percent cover and frequency of appearance. Numerator: number of samples in which species were observed. Denominator: total number of samples.

Stage or sub-stage	Dominant or subdominant species	Mean percent cover	Appearance frequency	Rank of domination
1	*Balanus trigonus*	99.5	4/4	1
	Dexiospira foraminosus	16.7	4/4	2
	*Megabalanus volcano**	1.9	4/4	3
	Watersipora subovoidea	1.4	2/4	4
	Trididemnum savignii	0.9	1/4	5
2-1	*Balanus trigonus*	95.1	8/8	1
	Diplosoma mitsukurii	46.3	8/8	2
	Watersipora subovoidea	17.4	8/8	3
	Didemnum moseleyi	17.2	8/8	4
2-2	*Balanus trigonus*	96.2	7/7	1
	Diplosoma mitsukurii	67.5	7/7	2
	Amathia distans	47.5	7/7	3
	Watersipora subovoidea	21.4	7/7	4
	Didemnum moseleyi	18.9	7/7	5
	Halichondria japonica	6.0	5/7	6
3-1	*Balanus trigonus*	95.9	3/3	1
	Amathia distans	50.1	3/3	2
	Didemnum moseleyi	40.3	3/3	3
	Watersipora subovoidea	32.2	3/3	4
	Crassostrea nippona	25.0	3/3	5
3-2	*Balanus trigonus*	93.2	6/6	1
	Diplosoma mitsukurii	46.2	6/6	2
	Crassostrea nippona	44.3	6/6	3
	Amathia distans	27.7	6/6	4

* including *Megabalanus rosa*.

Table 5. Developmental stages derived from the dendrogram analysis shown in Fig. 5. One stage and four sub-stages are characterized by the algal species which occupied the top to third rank in mean percent cover in the central area of plates at each immersion period and depth. The degree of domination is ranked by the average of the two ranks of mean percent cover and frequency of appearance. +: less than 0.1%. Numerator: number of samples in which algal species were observed. Denominator: total number of samples.

Stage or sub-stage	Dominant or subdominant species	Mean percent cover	Appearance frequency	Rank of domination
1	NO MACROALGAE			
2-1	*Pterocladia capillacea*	4.7	8/8	1
	Codium adhaerens	6.0	6/8	1
	Colpomenia sinuosa	5.1	6/8	3
	Ulva pertusa	1.8	7/8	4
	Cladophora wrightiana	1.1	4/8	5
	Gracilaria textorii	0.5	4/8	6
	Plocamium telfairiae	0.5	1/8	7
2-2	*Codium adhaerens*	2.5	5/7	1
	Pterocladia capillacea	1.5	5/7	2
	Ceramium paniculatum	2.2	2/7	3
	Ulva pertusa	0.3	5/7	4
	Colpomenia sinuosa	0.6	3/7	4
	Plocamium telfairiae	1.2	2/7	6
	Gracilaria textorii	0.5	3/7	7
	Gelidium amansii	0.6	1/7	8
3-1	*Pterocladia capillacea*	7.6	3/3	1
	Codium adhaerens	1.3	2/3	2
	Eisenia bicyclis	1.3	1/3	3
	Codium latum	0.8	2/3	3
	Plocamium telfairiae	0.2	1/3	5
3-2	*Eisenia bicyclis*	5.1	6/6	1
	Padina arborescens	1.7	4/6	2
	Pterocladia capillacea	0.3	2/6	3
	Plocamium telfairiae	+	1/6	4
	Codium adhaerens	+	1/6	4
	Grateloupia livida	+	1/6	6
	Ulva pertusa	+	1/6	7

Table 6. Spearman's rank correlation coefficients showing the tendency of changes in the five parameters of community structure (S, H', J', MDI and HSI) in the central area (16 cm x 16 cm) of plates. Sample size (number of plates examined) is shown in parentheses. **: highly significant ($P<0.01$); *: significant ($P<0.05$); ns: not significant ($P>0.05$). See the legend of Fig. 7 for explanation of parameters.

Parameter	Depth	Immersion period (months)		
		2-6	6-13	13-37
S	A (1.0 m)	0.973 (9) **	-0.581 (9) ns	0.093 (9) ns
	B (2.5 m)	0.718 (9) *	-0.539 (8) ns	0.299 (8) ns
	C (4.0 m)	0.950 (8) **	-0.715 (8) *	-0.835 (8) **
	D (5.5 m)	0.973 (9) **	-0.257 (8) ns	-0.818 (7) *
H'	A (1.0 m)	0.791 (9) **	-0.053 (9) ns	0.105 (9) ns
	B (2.5 m)	0.791 (9) **	-0.299 (8) ns	0.113 (8) ns
	C (4.0 m)	0.945 (8) **	-0.602 (8) ns	-0.567 (8) ns
	D (5.5 m)	0.896 (9) **	0.050 (8) ns	-0.397 (7) ns
J'	A (1.0 m)	0.794 (9) **	0.527 (9) ns	-0.053 (9) ns
	B (2.5 m)	0.843 (9) **	0.416 (8) ns	0.113 (8) ns
	C (4.0 m)	0.882 (8) **	0.038 (8) ns	-0.063 (8) ns
	D (5.5 m)	0.791 (9) **	0.548 (8) ns	0.794 (7) *
MDI	A (1.0 m)	-0.791 (9) **	-0.316 (9) ns	0 (9) ns
	B (2.5 m)	-0.738 (9) *	-0.063 (8) ns	-0.517 (8) ns
	C (4.0 m)	-0.945 (8) **	0.216 (8) ns	0.252 (8) ns
	D (5.5 m)	-0.949 (9) **	0.529 (8) ns	-0.302 (7) ns
HSI	A (1.0 m)	-0.949 (9) **	0.422 (9) ns	0.105 (9) ns
	B (2.5 m)	-0.896 (9) **	0.058 (7) ns	0.759 (7) *
	C (4.0 m)	-0.926 (7) **	0.694 (7) ns	0.386 (7) ns
	D (5.5 m)	-0.590 (9) ns	-0.810 (7) *	0.447 (5) ns

Table 7. Spearman's rank correlation coefficients showing the tendency of changes in the three parameters of community metabolism (Pg, R and Pg/R) in the whole area (20 cm x 20 cm) of plates. Sample size (number of plates examined) is shown in parentheses. **: highly significant (P<0.01); *: significant (P<0.05); ns: not significant (P>0.05). See the legend of Fig. 8 for explanation of parameters.

Parameter	Depth	Immersion period (months)		
		2-6	6-13	13-37
Pg	A (1.0 m)	-0.158 (9) ns	0.580 (9) ns	-0.949 (9) **
	B (2.5 m)	-0.211 (9) ns	0.316 (9) ns	-0.843 (9) **
	C (4.0 m)	0.580 (9) ns	0.474 (9) ns	-0.738 (9) *
	D (5.5 m)	0.264 (9) ns	0.105 (9) ns	-0.791 (9) *
R	A (1.0 m)	-0.212 (9) ns	0.791 (9) *	-0.422 (9) ns
	B (2.5 m)	-0.580 (9) ns	0.580 (9) ns	-0.474 (9) ns
	C (4.0 m)	-0.959 (9) **	0.896 (9) **	-0.685 (9) *
	D (5.5 m)	-0.949 (9) **	0.791 (9) *	-0.474 (9) ns
Pg/R	A (1.0 m)	-0.211 (9) ns	-0.738 (9) *	-0.896 (9) **
	B (2.5 m)	0.316 (9) ns	-0.264 (9) ns	-0.685 (9) *
	C (4.0 m)	0.949 (9) **	-0.474 (9) ns	-0.738 (9) *
	D (5.5 m)	0.949 (9) **	-0.949 (9) **	-0.264 (9) ns

Table 8. Spearman's rank correlation coefficients showing the tendency of changes in the six parameters of community biomass (DM, ADM, AFDM, C, N and Chl. *a*) in the whole area (20 cm x 20 cm) of plates. Sample size (number of plates examined) is shown in parentheses. **: highly significant ($P<0.01$); *: significant ($P<0.05$); ns: not significant ($P>0.05$). See the legend of Fig. 10 for explanation of parameters.

Parameter	Depth	Immersion period (months)	
		2-13	13-37
DM	A (1.0 m)	0.895 (15) **	0.843 (9) **
	B (2.5 m)	0.796 (15) **	0.632 (9) *
	C (4.0 m)	0.731 (15) **	-0.580 (9) ns
	D (5.5 m)	0.687 (15) **	-0.791 (9) **
ADM	A (1.0 m)	0.884 (15) **	0.843 (9) **
	B (2.5 m)	0.807 (15) **	0.685 (9) *
	C (4.0 m)	0.731 (15) **	-0.474 (9) ns
	D (5.5 m)	0.676 (15) **	-0.791 (9) **
AFDM	A (1.0 m)	0.895 (15) **	0.632 (9) *
	B (2.5 m)	0.906 (15) **	0.316 (9) ns
	C (4.0 m)	0.862 (15) **	-0.518 (9) ns
	D (5.5 m)	0.884 (15) **	-0.896 (9) **
C	A (1.0 m)	0.873 (15) **	0.685 (9) *
	B (2.5 m)	0.884 (15) **	0.158 (9) ns
	C (4.0 m)	0.731 (15) **	-0.158 (9) ns
	D (5.5 m)	0.513 (15) *	-0.791 (9) **
N	A (1.0 m)	0.906 (15) **	0.685 (9) *
	B (2.5 m)	0.873 (15) **	0.264 (9) ns
	C (4.0 m)	0.796 (15) **	-0.527 (9) ns
	D (5.5 m)	0.496 (15) *	-0.949 (9) **
Chl. *a*	A (1.0 m)	0.775 (15) **	-0.422 (9) ns
	B (2.5 m)	0.807 (15) **	-0.053 (9) ns
	C (4.0 m)	0.937 (15) **	-0.527 (9) ns
	D (5.5 m)	0.753 (15) **	-0.685 (9) *

Table 9. Spearman's rank correlation coefficients showing the tendency of changes in the four indices showing the degree of community maturity (Pg/C, Pg/Chl. *a*, C/N and D430/D665). Sample size (number of plates examined) is shown in parentheses. **: highly significant (*P*<0.01); * significant (*P*<0.05); ns: not significant (*P*>0.05). See the legend of Fig. 11 for explanation of indices.

Index	Depth	Immersion period (months)	
		2-13	13-37
Pg/C	A (1.0 m)	-0.644 (15) **	-0.896 (9) **
	B (2.5 m)	-0.556 (15) *	-0.791 (9) **
	C (4.0 m)	0.291 (15) ns	-0.791 (9) **
	D (5.5 m)	0.109 (15) ns	-0.316 (9) ns
Pg/Chl. *a*	A (1.0 m)	-0.742 (15) **	-0.738 (9) *
	B (2.5 m)	-0.818 (15) **	-0.949 (9) **
	C (4.0 m)	-0.818 (15) **	-0.369 (9) ns
	D (5.5 m)	-0.731 (15) **	-0.632 (9) *
C/N	A (1.0 m)	-0.240 (15) ns	-0.158 (9) ns
	B (2.5 m)	0.044 (15) ns	-0.474 (9) ns
	C (4.0 m)	-0.269 (15) ns	0.211 (9) ns
	D (5.5 m)	-0.513 (15) *	0.791 (9) **
D430/D665	A (1.0 m)	-0.491 (15) *	0.896 (9) **
	B (2.5 m)	0.306 (15) ns	0.843 (9) **
	C (4.0 m)	0.273 (15) ns	-0.264 (9) ns
	D (5.5 m)	-0.098 (15) ns	-0.632 (9) *

Table 10. Regression coefficients of gross primary production of community (Pg) and community respiration (R) in common logarithm on temperature for several samples immersed in 1974. **: highly significant ($P<0.01$); *: significant ($P<0.05$); ns: not significant ($P>0.05$).

Immersion period (months)	Depth (m)	Pg		R	
		Regression coefficient	Significance level	Regression coefficient	Significance level
4	1.0	0.023	**	0.050	**
	4.0	0.023	**	0.058	**
10	1.0	0.041	ns	0.059	**
		0.050	*	0.054	**
		0.053	*	0.059	*
	4.0	0.046	**	0.054	**
		0.037	**	0.056	**
		0.024	**	0.041	**
13	1.0	0.053	*	0.066	**
		0.032	*	0.068	**
		0.052	*	0.060	*
	2.5	0.021	ns	0.045	**
		0.035	**	0.058	**
		0.039	**	0.052	**
	4.0	0.081	ns	0.076	**
		0.036	**	0.060	**
		0.050	**	0.071	**
	5.5	0.043	*	0.057	**
		0.022	ns	0.047	**
		0.020	*	0.035	**
26	1.0	0.041	**	0.064	**
		0.024	ns	0.063	*
		0.023	*	0.048	**
	2.5	0.013	**	0.051	**
		0.028	**	0.052	**
		0.017	*	0.041	**
	4.0	0.051	ns	0.034	**
		0.038	*	0.031	**
		0.018	*	0.030	*
	5.5	0.029	*	0.048	*
		0.031	*	0.043	**
		0.035	**	0.043	**
37	1.0	0.045	ns	0.066	**
		0.032	*	0.040	**
		0.123	ns	0.073	*
	2.5	0.040	**	0.041	**
		0.053	**	0.047	**
		0.031	ns	0.057	**
	4.0	0.030	*	0.049	**
		0.042	*	0.036	**
		0.041	*	0.047	**
	5.5	0.037	**	0.051	**
		0.045	**	0.050	**
		0.034	*	0.048	**

Table 11. Regression coefficients of gross primary production of community (Pg), community respiration (R) and the ratio of Pg to R in common logarithm (log Pg:R) on temperature for 2 to 3 months' samples immersed in 1978 and 37 to 38 months' ones immersed in 1975. SD: standard deviation. **: highly significant ($P<0.01$); *: significant ($P<0.05$); ns: not significant ($P>0.05$).

Immersion period (months)		Regression coefficient		
		Pg	R	log Pg:R
2-3		0.0455 **	0.0369 **	0.0085 ns
		0.0411 **	0.0464 **	-0.0053 ns
		0.0349 **	0.0449 **	-0.0101 ns
		0.0339 **	0.0493 **	-0.0154 ns
		0.0461 **	0.0365 **	0.0096 ns
		0.0457 **	0.0458 **	-0.0002 ns
		0.0493 **	0.0707 **	-0.0215 **
		0.0610 **	0.0731 **	-0.0120 ns
	mean	0.0447	0.0505	-0.0058
	(SD)	(0.0086)	(0.0140)	(0.0111)
37-38		0.0783 *	0.0504 **	0.0279 ns
		0.0348 **	0.0422 **	-0.0074 ns
		0.0274 **	0.0217 **	0.0057 ns
		0.0415 **	0.0358 **	0.0057 ns
		0.0174 *	0.0235 **	-0.0061 ns
		0.0334 *	0.0368 **	-0.0034 ns
		0.0468 **	0.0433 **	0.0035 ns
		0.0422 *	0.0531 **	-0.0109 ns
	mean	0.0402	0.0384	0.0019
	(SD)	(0.0180)	(0.0114)	(0.0122)

Fig. 1. Map showing the study site (★) in Nabeta Bay, where experimental plates were immersed. S.M.R.C: Shimoda Marine Research Center of University of Tsukuba.

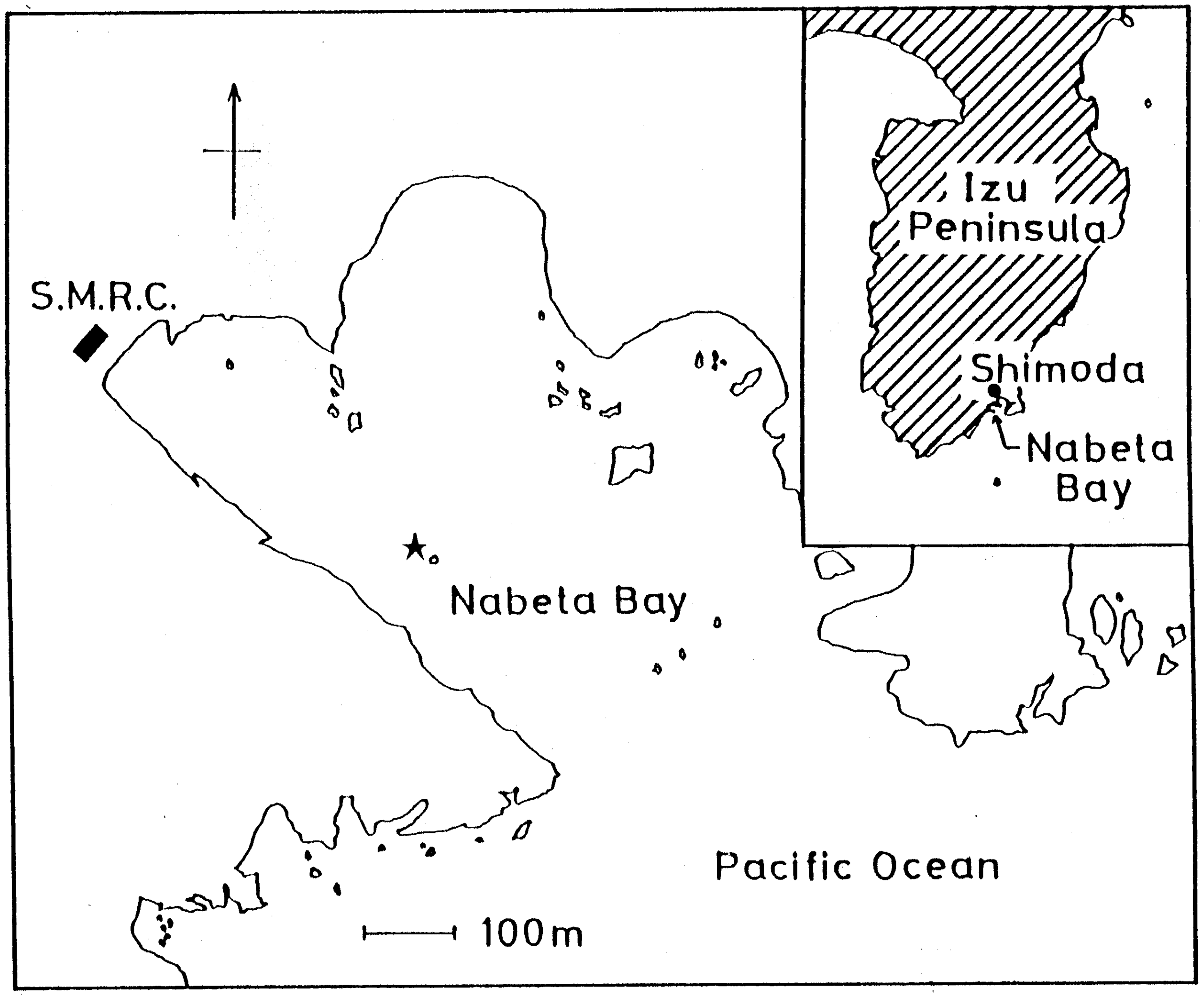

S.M.R.C.
Nabeta Bay
Pacific Ocean
100m
Izu
Peninsula
Shimoda
Nabeta
Bay

Fig. 2. (a) Diagram showing setting of experimental concrete plates in the sea. Eight ropes attached with plates are suspended from a galvanized pipe which is floated with buoys. Rope movement is limited by an iron bar. Four plates are fixed on each rope at each depth. This diagram is not drawn to scale.

(b) Diagram showing a set of four plates fixed to a rope.

(c) Diagram showing the central area (16 cm x 16 cm) of a plate, within which sessile organisms were examined for the calculation of percent cover.

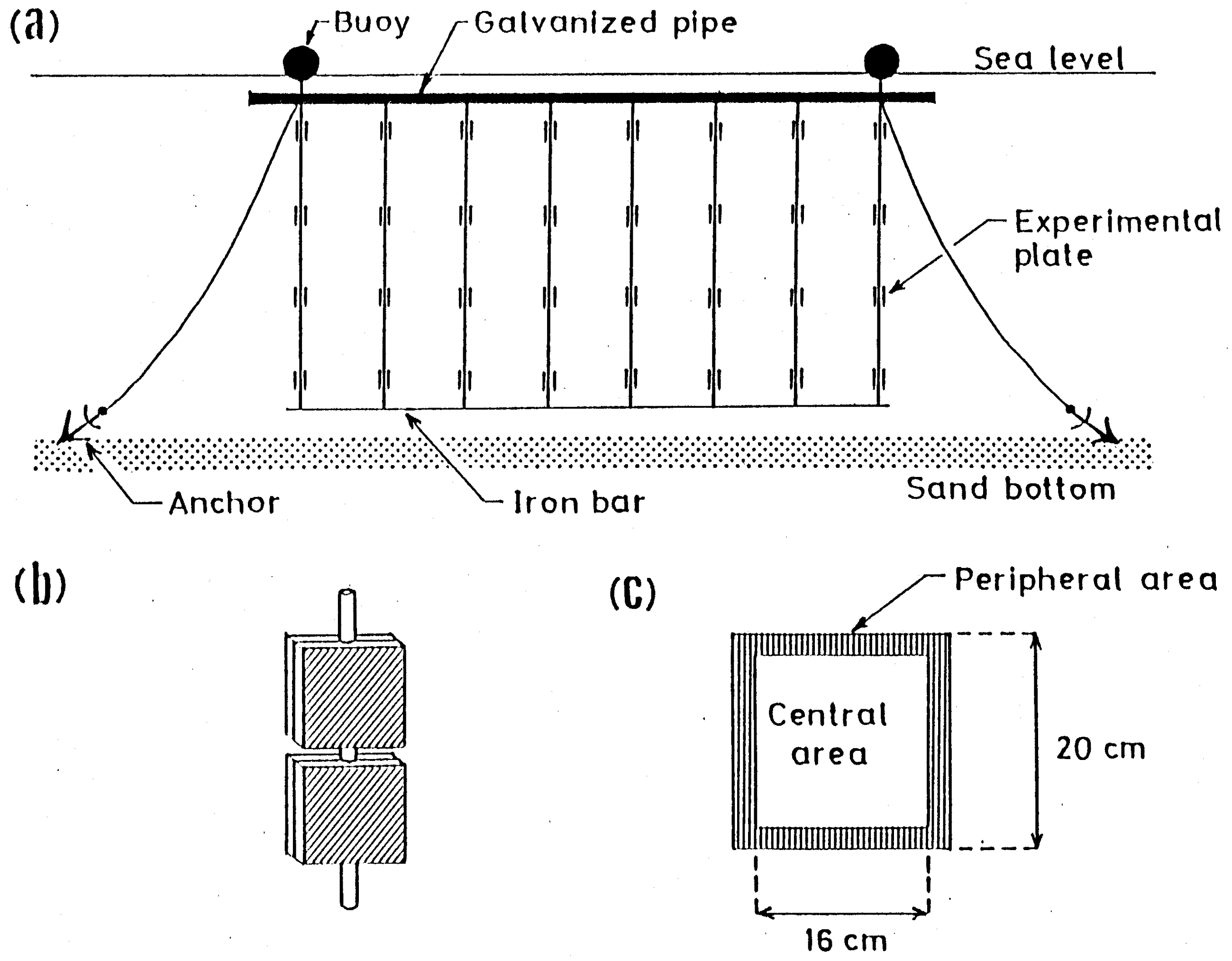

(a)
Buoy
Galvanized pipe
Sea level
Experimental plate
Anchor
Iron bar
Sand bottom
(b)
(c)
Peripheral area
Central area
20 cm
16 cm

Fig. 3. Flowchart showing the procedure of observations and measurements.

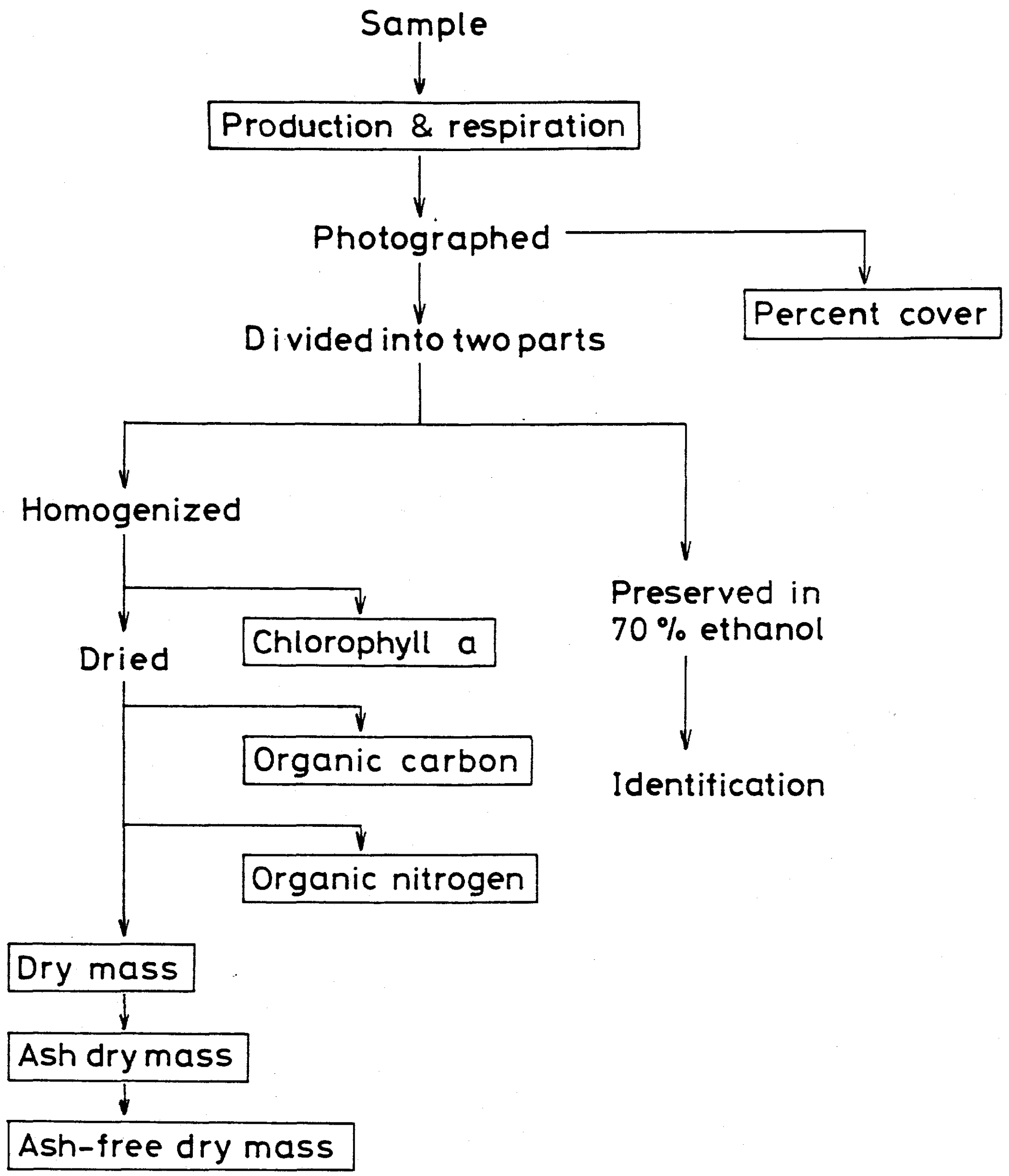
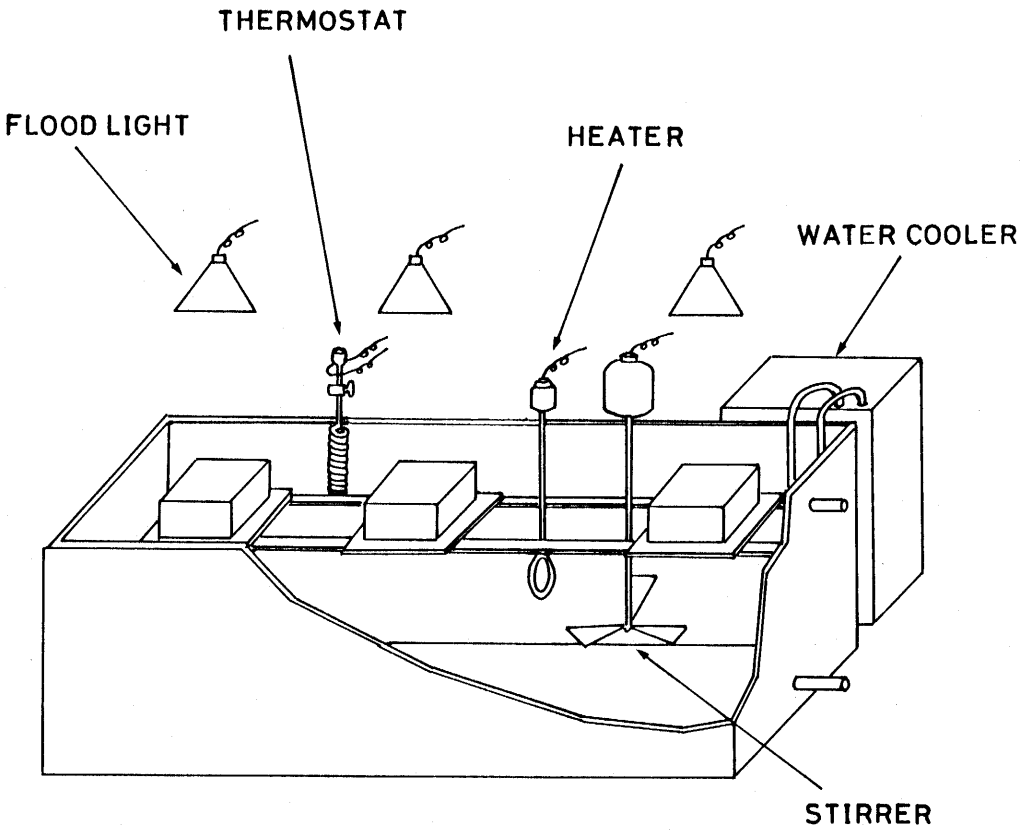

Sample
Production & respiration
Photographed
Percent cover
Divided into two parts
Homogenized
Preserved in 70 % ethanol
Chlorophyll a
Dried
Identification
Organic carbon
Organic nitrogen
Dry mass
Ash dry mass
Ash-free dry mass

Fig. 4. (a) Diagram showing the apparatus for measuring community metabolism of sampled plates, in which light and temperature can be kept constant.

(b) Diagram showing the respiro-chamber with three outlet pipes for taking water samples, one air inlet to compensate the amount of sampled water, and a stirrer, into which one plate is set.

(a)


THERMOSTAT
FLOOD LIGHT
HEATER
WATER COOLER
STIRRER

(b)

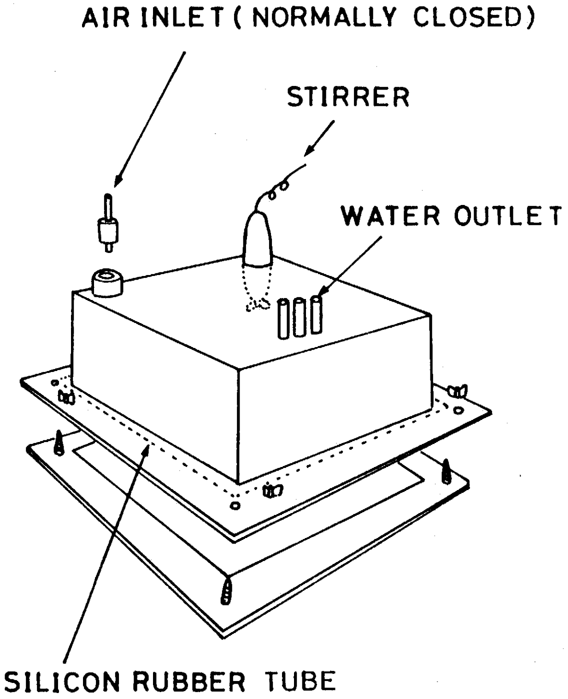

AIR INLET (NORMALLY CLOSED)
STIRRER
WATER OUTLET
SILICON RUBBER TUBE

Fig. 5. Dendrogram constructed from Horn's similarity coefficients based on the mean percent cover of sessile organisms in the central area (16 cm x 16 cm) of a plate at each immersion period and depth. Major clusters are indicated by numbers and sub-clusters by the letters. Samples are indicated at right by months and their immersed depth (e.g., 2A indicates the sample immersed for 2 months at Depth A). See text for further explanation.

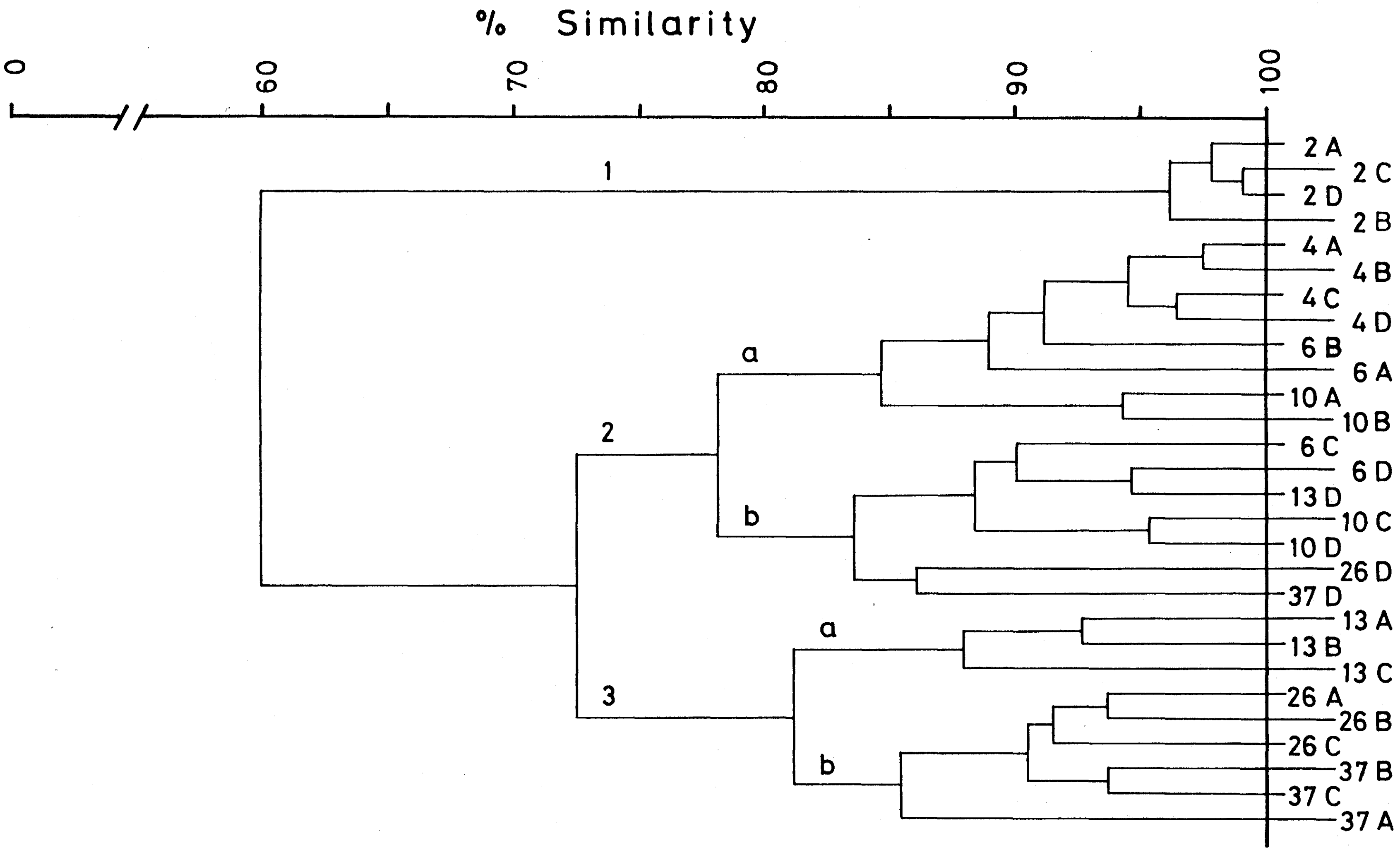

% Similarity
0
60
70
80
90
100
1
2
3
a
b
a
b
2 A
2 C
2 D
2 B
4 A
4 B
4 C
4 D
6 B
6 A
10 A
10 B
6 C
6 D
13 D
10 C
10 D
26 D
37 D
13 A
13 B
13 C
26 A
26 B
26 C
37 B
37 C
37 A

Fig. 6. Diagram showing the processes of community development at four depths, inferred from the results of dendrogram analysis shown in Fig. 5. Three kinds of hatched areas represent three developmental stages divided by the dendrogram analysis. Four kinds of areas without hatching represent four sub-stages. Boxes in the sub-stages represent clusters subordinate to their sub-stages. Black arrows indicate transition from one developmental stage to the next. White arrows indicate transition from one sub-stage to the other. Narrow arrows indicate transition from one subordinate cluster to the other. Code the same as in Fig. 5

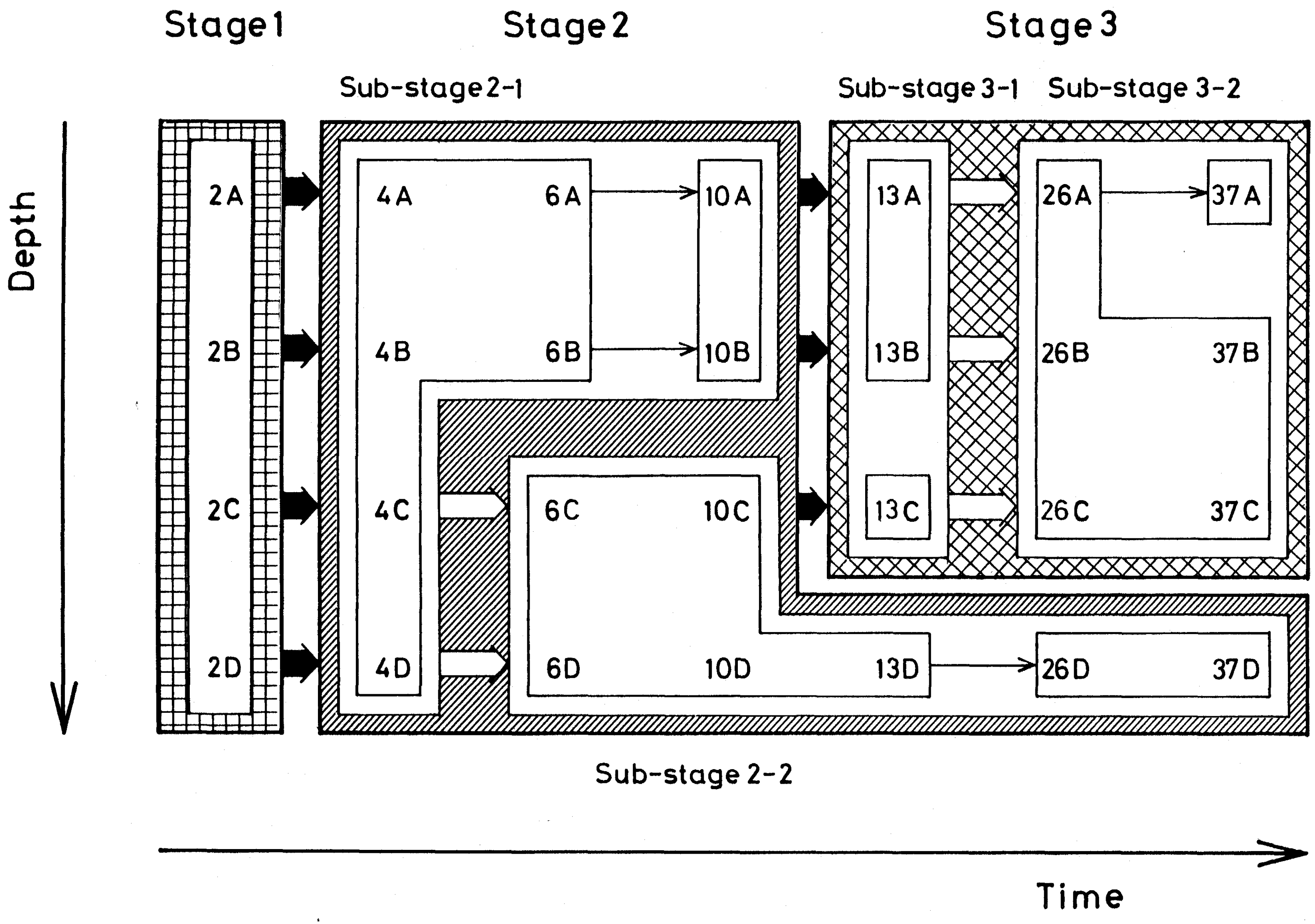

Stage 1
Stage 2
Stage 3
Sub-stage 2-1
Sub-stage 3-1
Sub-stage 3-2
Depth
2A
2B
2C
2D
4A
6A
10A
4B
6B
10B
4C
6C
10C
4D
6D
10D
13D
13A
13B
13C
26A
37A
26B
37B
26C
37C
26D
37D
Sub-stage 2-2
Time

Fig. 7. Changes in the five parameters of community structure (S, _H_', _J_', MDI and HSI) in the central areas (16 cm x 16 cm) of plates during community development at four depths. Curves show the change of average of each parameter. Small solid circle represents a measurement for an individual plate, and large solid circle represents two or three samples having the same values. Numbers near them indicate number of samples. S: number of species; _H_': Shannon-Weaver diversity index; _J_': information theory evenness index; MDI: McNaughton's dominance index; and HSI: Horn's similarity index. See text for detailed explanation of the parameters.

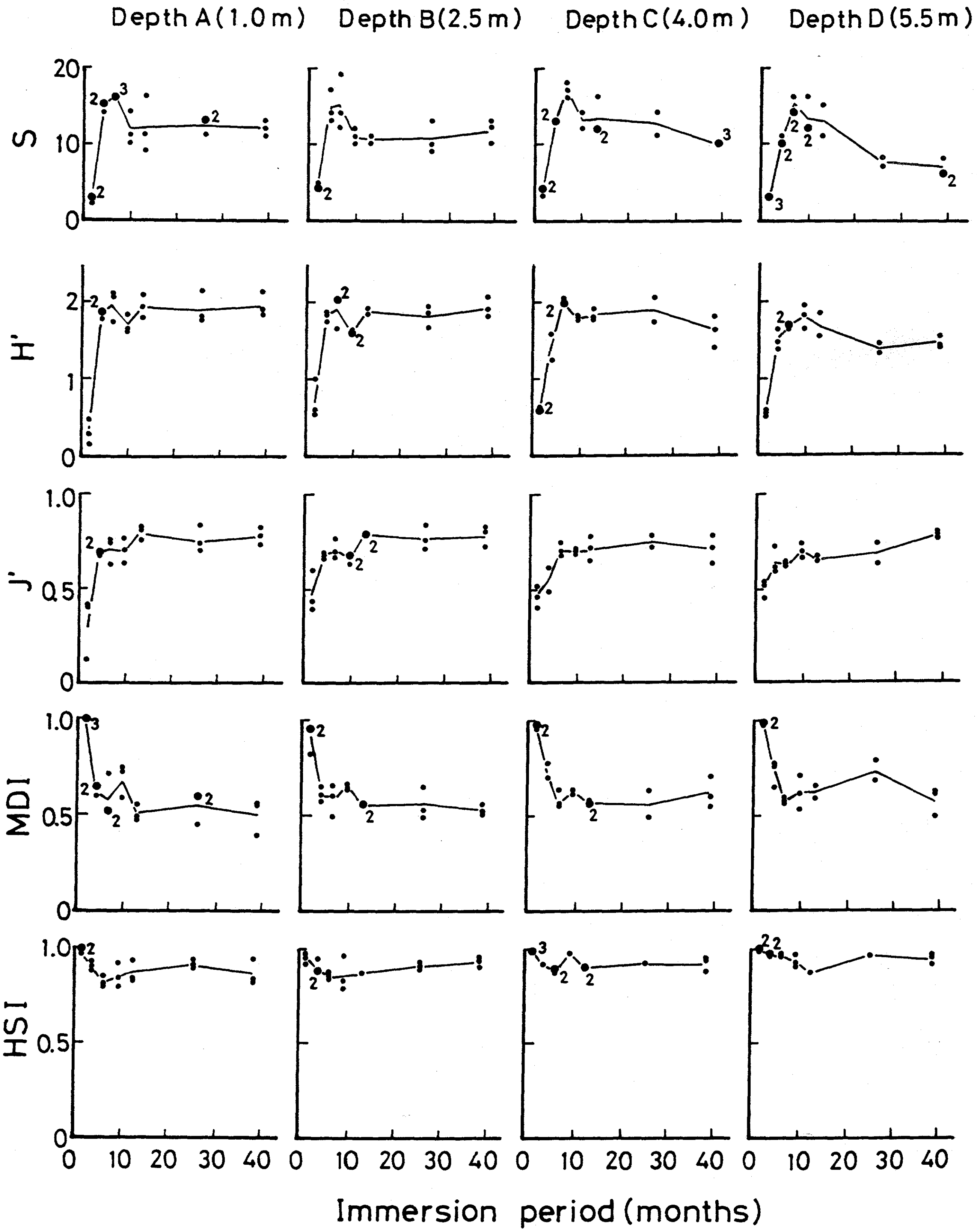

Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
S
H'
J'
MDI
HSI
0
10
20
1
2
0.5
1.0
0
10
20
30
40
Immersion period (months)

Fig. 8. Changes in the three parameters of community metabolism (Pg, R and Pg/R) in the whole areas (20 cm x 20 cm) of plates during community development at four depths. Curves show the change of average of each parameter. Small solid circle represents a measurement for an individual plate, and large solid circle represents two or three samples having the same values. Numbers near them indicate number of samples. Pg: gross primary production of community; R: community respiration; and Pg/R: daily community energy budget.

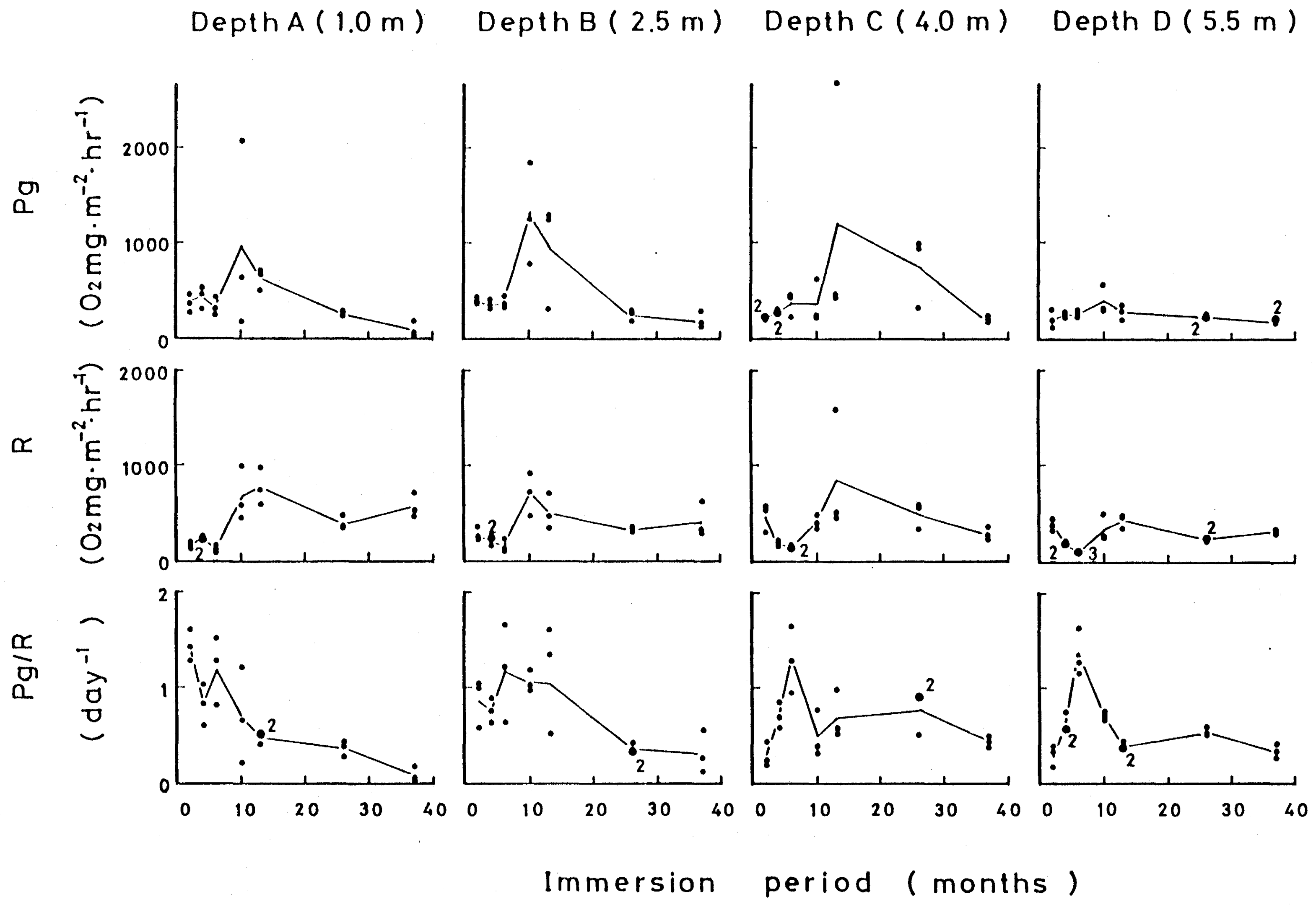

Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
Pg
(O_2 mg · m^{-2} · hr^{-1})
R
(O_2 mg · m^{-2} · hr^{-1})
Pg/R
(day^{-1})
2000
1000
0
2
1
0
0
10
20
30
40
2
3
Immersion period (months)

Fig. 9. Relation between gross primary production of community (Pg) and light intensity in 25 to 26 months' samples immersed in 1975 at four depths.

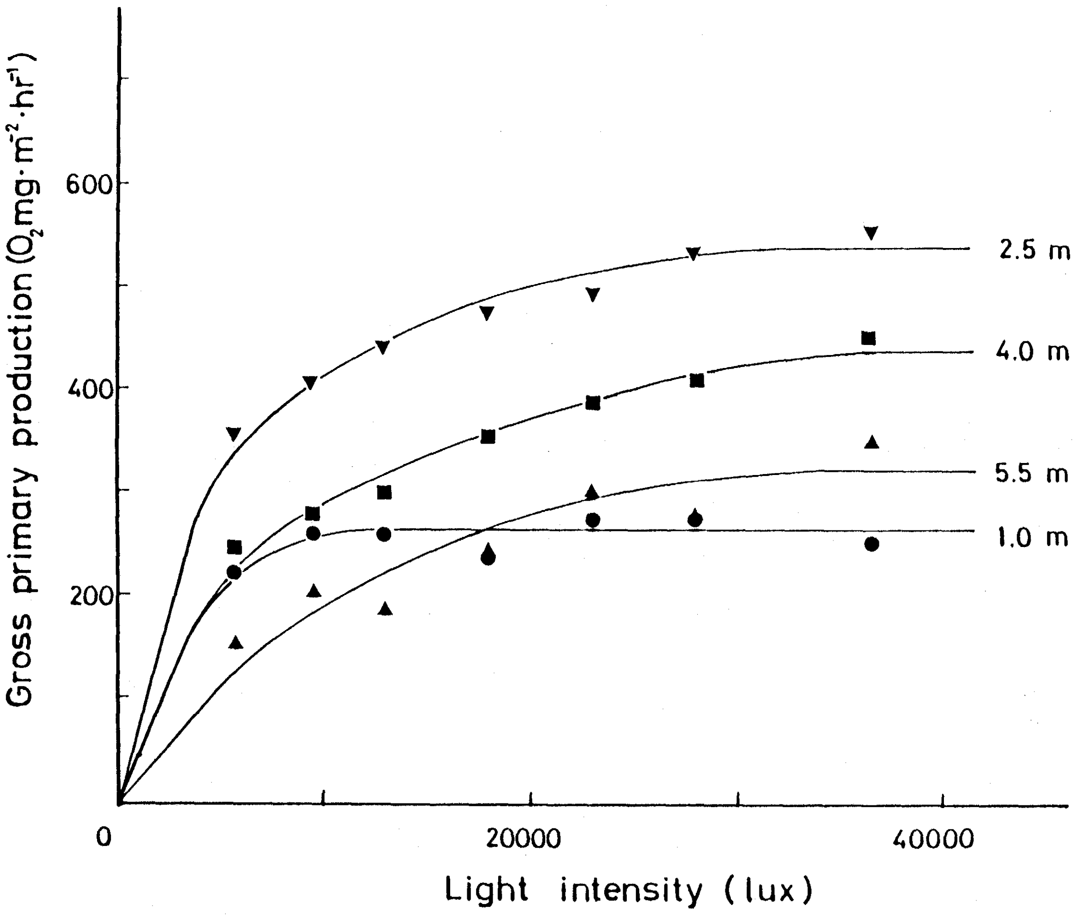

Gross primary production (O_2 mg·m^{-2}·hr^{-1})
600
400
200
0
20000
40000
Light intensity (lux)
2.5 m
4.0 m
5.5 m
1.0 m

Fig. 10. Changes in the six parameters of community biomass (DM, ADM, AFDM, C, N and Chl. *a*) in the whole areas (20 cm x 20 cm) of plates during community development at four depths. Curves show the change of average of each parameter. Small solid circle represents a measurement for an individual plate, and large solid circle represents two or three samples having the same values. Numbers near them indicate number of samples. DM: dry mass; ADM: ash dry mass; AFDM: ash-free dry mass; C: organic carbon; N: organic nitrogen; and Chl. *a*: chlorophyll *a*.

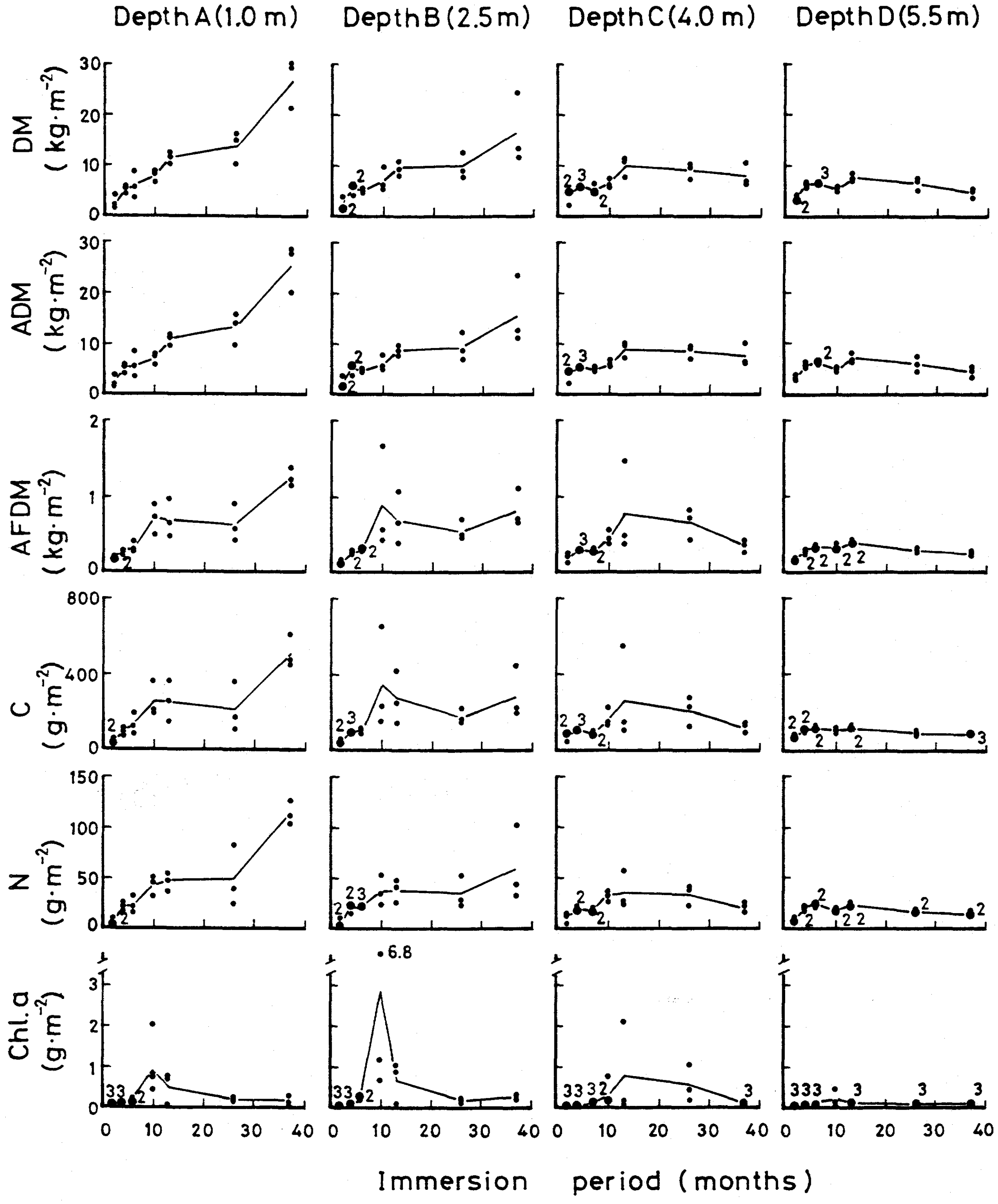

Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
DM (kg·m^{-2})
ADM (kg·m^{-2})
AFDM (kg·m^{-2})
C (g·m^{-2})
N (g·m^{-2})
Chl. a (g·m^{-2})
0
10
20
30
0
10
20
30
0
1
2
0
400
800
0
50
100
150
0
1
2
3
•6.8
0
10
20
30
40
Immersion period (months)

Fig. 11. Changes in the four indices showing the degree of community maturity (Pg/C, Pg/Chl. a, C/N and D430/D665) in the whole areas (20 cm x 20 cm) of plates during community development at four depths. Curves show the change of average of each parameter. Small solid circle represents a measurement for an individual plate, and large solid circle represents two or three samples having the same values. Numbers near them indicate number of samples. Pg/C: ratio of gross primary production to organic carbon; Pg/Chl. a: ratio of gross primary production of community to chlorophyll a; C/N: ratio of organic carbon to organic nitrogen; and D430/D665: ratio of absorbance at 430 and 665 nm of acetone extracts of samples.

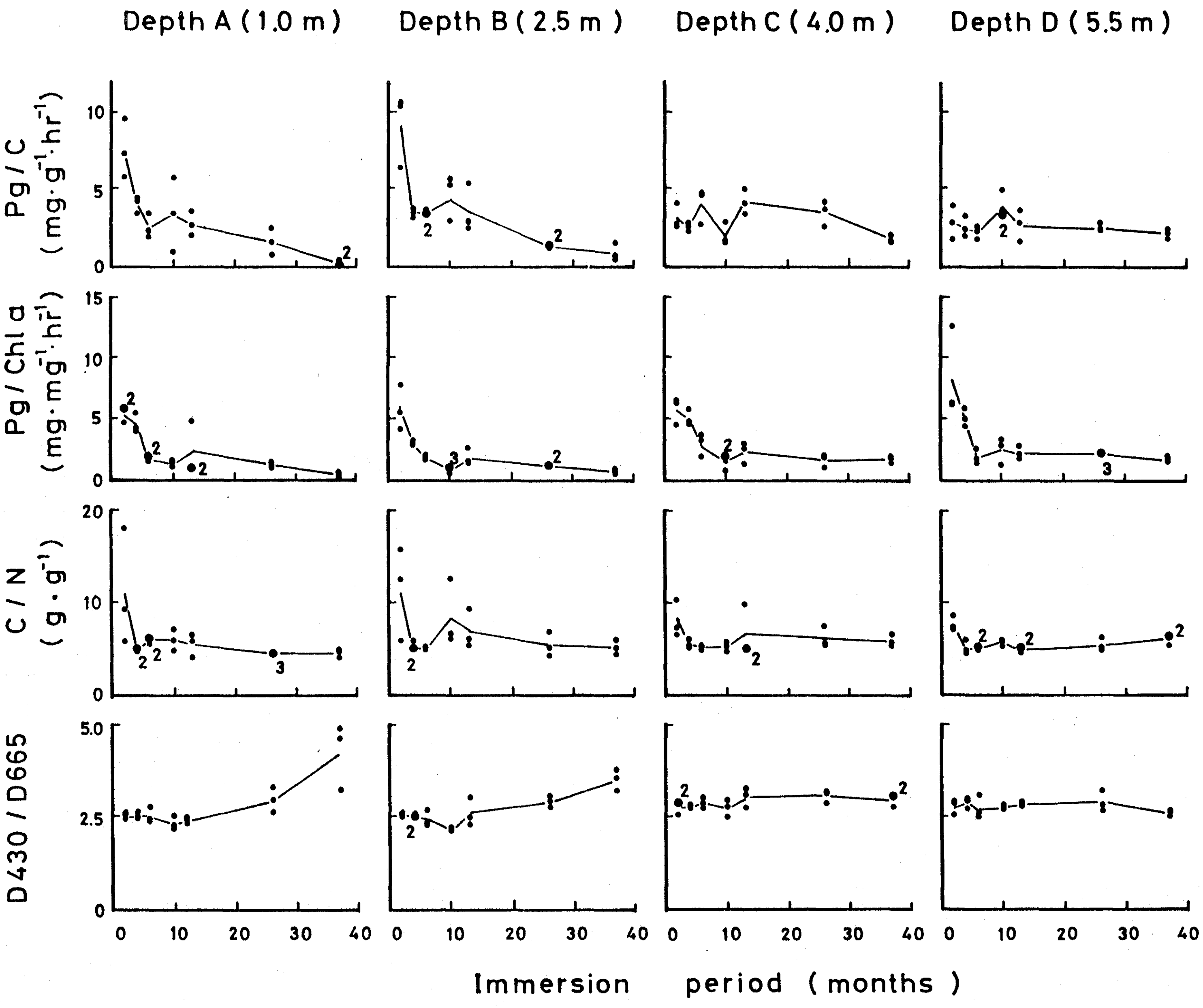
Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
Pg / C
(mg · g⁻¹ · hr⁻¹)
Pg / Chl a
(mg · mg⁻¹ · hr⁻¹)
C / N
(g · g⁻¹)
D430 / D665
0
5
10
15
20
2.5
5.0
2
3
0
10
20
30
40
Immersion period (months)

Fig. 12. (a) Temporal changes of the regression coefficients of gross primary production of community (Pg) and community respiration (R) in common logarithm on temperature in the samples showing a significant correlation coefficient. a_P: regression coefficient of Pg; a_R: that of R.

(b) Temporal changes of the difference between a_P and a_R values of the samples which showed a significant correlation coefficient in both regressions of Pg and R.

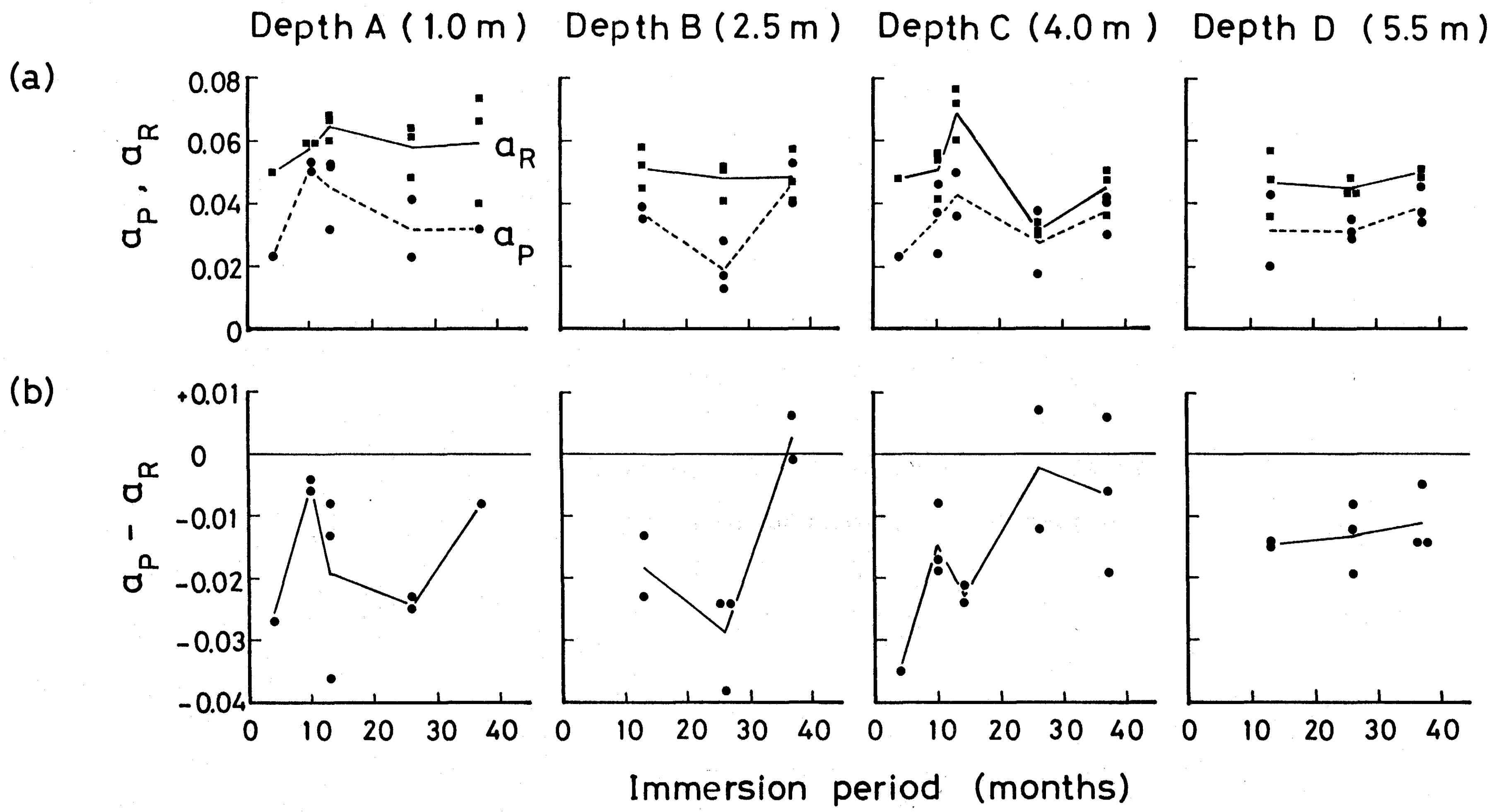

Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
(a)
a_P , a_R
0.08
0.06
0.04
0.02
0
a_R
a_P
(b)
$a_P - a_R$
+0.01
0
-0.01
-0.02
-0.03
-0.04
0
10
20
30
40
Immersion period (months)

Fig. 13. Temperature-log Pg:R relationships for 2 to 3 months' samples immersed in 1978 at the depth of 2.5 m and 37 to 38 months' ones immersed in 1975 at the same depth. Their regressions and correlation coefficients are each calculated by lumping log Pg:R values of eight samples.

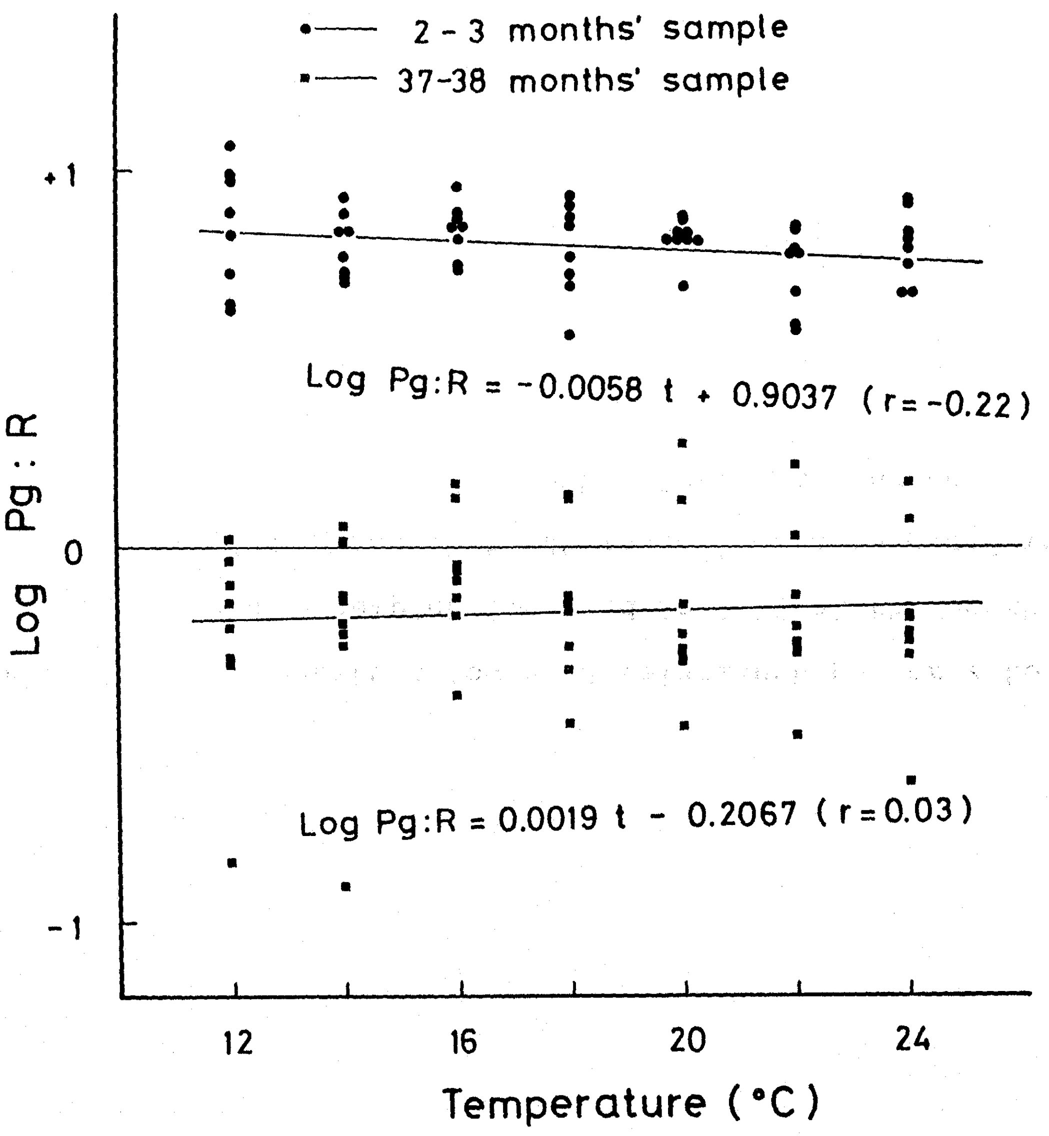

•—— 2 - 3 months' sample
▪—— 37-38 months' sample
Log Pg:R = -0.0058 t + 0.9037 (r = -0.22)
Log Pg:R = 0.0019 t - 0.2067 (r = 0.03)
Log Pg : R
+1
0
-1
12
16
20
24
Temperature (°C)

Fig. 14. Relative abundance in percent cover of sessile organisms in the central areas (16 cm x 16 cm) of 12 plates immersed for 37 months at four depths, which is shown by the species ranking from the top to fourth in percent cover in each sample and by the others consisting of remaining species.

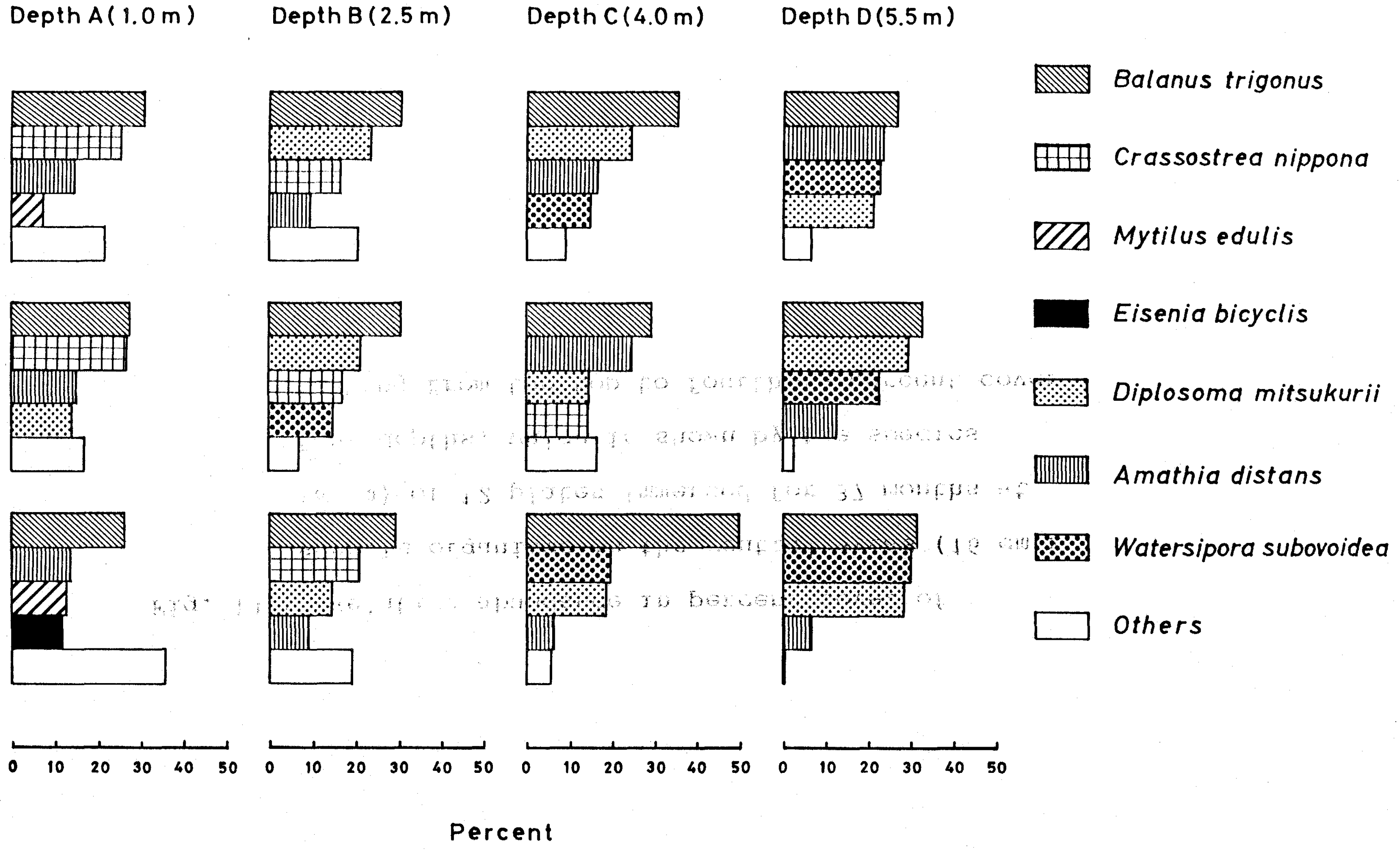
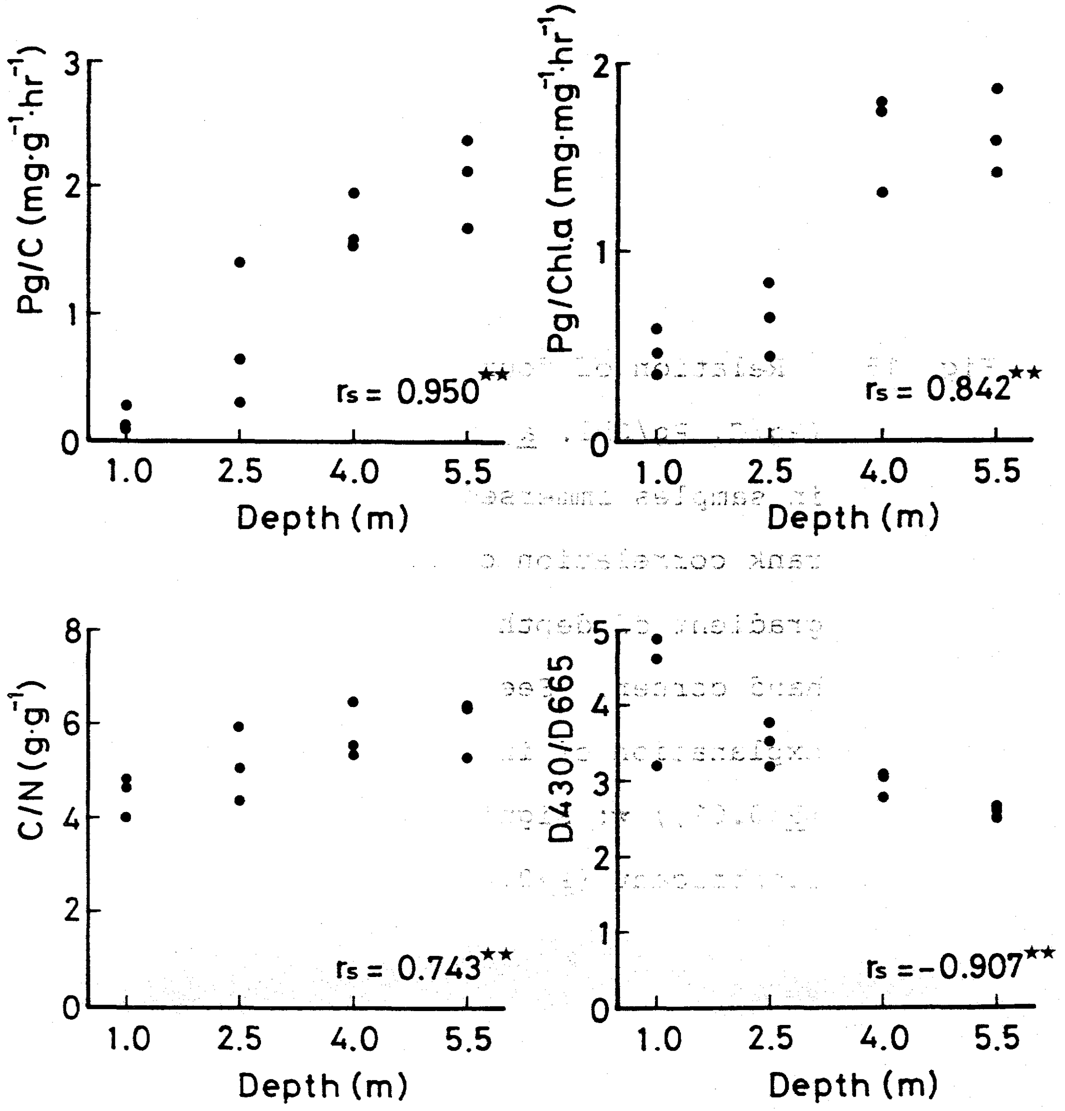
Depth A (1.0 m)
Depth B (2.5 m)
Depth C (4.0 m)
Depth D (5.5 m)
▨ Balanus trigonus
⊞ Crassostrea nippona
▨ Mytilus edulis
■ Eisenia bicyclis
░ Diplosoma mitsukurii
▥ Amathia distans
▩ Watersipora subovoidea
□ Others
0
10
20
30
40
50
Percent

Fig. 15. Relation of four community maturity indices (Pg/C, Pg/Chl. *a*, C/N and D430/D665) to depth in samples immersed for 37 months. Spearman's rank correlation coefficients (r_s) on the gradient of depth is each given to the right-hand corner. See the legend of Fig. 11 for explanation of indices. ★★: highly significant ($P<0.01$); ★: significantly ($P<0.05$); ns: not significant ($P>0.05$).


Pg/C (mg·g⁻¹·hr⁻¹)
3
2
1
0
rs = 0.950**
1.0
2.5
4.0
5.5
Depth (m)
Pg/Chl.a (mg·mg⁻¹·hr⁻¹)
2
1
0
rs = 0.842**
1.0
2.5
4.0
5.5
Depth (m)
C/N (g·g⁻¹)
8
6
4
2
0
rs = 0.743**
1.0
2.5
4.0
5.5
Depth (m)
D430/D665
5
4
3
2
1
0
rs = -0.907**
1.0
2.5
4.0
5.5
Depth (m)