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Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization*

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ABSTRACT: Community structure of the associated animals of low intertidal patches of *Mytilus edulis* L. with different age structure was investigated at Asamushi, northern Japan. Each patch was composed of similar components i.e. live *M. edulis*, byssal threads, shell fragments, sediments, algae and associated animals. The amounts of sediments, shell fragments and byssal threads were greater in the periphery (MP) and central part (MC) of adult mussel patches than in patches of young (Y) and old (O) mussels. Total organic matter within sediments increased in the following order: O, MC, MP and Y. Algal growth was luxuriant in Y and this supported abundant amphipods. Species richness was higher in older patches and species diversity (H') and equitability (J') were higher in MP and MC than in Y and O. Sediments, shell fragments and byssal threads seemed to play an important role in increasing heterogeneity of environments and thus species diversity. Similarities in species compositions among MP, MC and O were high, but those between Y and other patches extremely low. This fact is probably caused both by the presence of a large number of epiphytic animals in Y and the difference in the composition of creeping fauna among the patches. Based on these results, the processes controlling community organization of *Mytilus* islands are discussed.

INTRODUCTION

It is well known that in the rocky intertidal zone, patches of *Mytilus* spp. harbour a variety of small animals (Hewatt 1935, Suchanek 1979, 1985, Tsuchiya 1979, Tsuchiya & Nishihira 1985). A community composed of *M. edulis* plus associated organisms is designated here as a *Mytilus* community. The dynamic process of *Mytilus* community organization and the effect of *Mytilus* age composition on the associated fauna have not been well studied. In Japan, *Mytilus edulis* frequently forms aggregations in discrete patches of various sizes (hereafter such patches are designated as *Mytilus* islands). *Mytilus* islands have common components in addition to live *M. edulis*, i.e. byssal threads, shell fragments, sediments, algae and associated animals (Tsuchiya & Nishihira 1985). Moreover, amounts of these components vary among patches according to differences in age (or size) composition. It is likely that the *Mytilus* island as a habitat for associated organisms is steadily changing, because it is composed of living mussels. Dynamic aspects of this community, therefore, should be studied in relation to the change in *M. edulis* population (growth and death).

For *Mytilus* islands composed of young mussels of similar age class (<20 mm in shell length), Tsuchiya & Nishihira (1985) discussed the effect of island size on the community structure of the associated animals. In the present paper, we describe the effects of the physical structure of *Mytilus* islands with different age composition on the community structure and discuss the process of community development within *Mytilus* islands.

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MATERIALS AND METHODS

Patches of *Mytilus edulis* L. with different age compositions were studied on a concrete slope in the lower intertidal (5 to 20 cm above MLWS, inclination of 10°) in a small harbour of the Marine Biological Station, Tohoku University (40°55′ N, 140°50′ E). Among such *Mytilus* islands, 3 patches were sampled during daytime low tides in June 1980. The first patch of mussels (<30 mm in shell length) was irregularly shaped measuring about 15 to 30 cm width by 70 cm length. The second patch was an ellipsoid (1.0 m × 5.0 m) consisting of mussels 25 to 45 mm in length, and the third was of larger mussels (35 to 55 mm long) with eroded shells and of 20 cm × 30 cm in patch size. Five samples (each 10 cm × 10 cm) were collected from the central part of each patch and from the periphery of the second patch after taking photographs and measurements of patch thickness (height above substratum). Hereafter we refer to samples from the first patch as 'Y' (young), those of the second 'M' (medium) and those from the third 'O' (old). The central and peripheral samples of the second patches are designated by adding the letters 'C' (central) and 'P' (peripheral), respectively. Age was determined using shell characteristics such as size, color and degree of erosion.

Total displacement volume was measured first for each total sample wrapped in a thin polyethylene sheet and then for each constituent; i.e. live *Mytilus edulis*, byssal threads, shell fragments, sediments, algae attached to mussels and associated macrobenthic animals. Space in the *Mytilus* patch was estimated by subtracting the volume of all constituents of the patch from the total displacement volume. Associated animals were identified and counted. Species diversity (H′ using $\log_2$) and Pielou's equitability (J′) in each patch, and similarity of species composition between patches (Kimoto's C_Π) were calculated. The formula for C_Π (Kimoto 1967) is as follows;

$$C_\Pi = \frac{2\sum_{i=1}^{s} n_{1i}\cdot n_{2i}}{(\Sigma\,\Pi_1^2 + \Sigma\,\Pi_2^2)\,N_1\cdot N_2} \qquad 0 \leqq C_\Pi \leqq 1$$

$$\Sigma\,\Pi_1^2 = \frac{\sum_{i=1}^{s} n_{1i}^2}{N_1^2},\quad \Sigma\,\Pi_2^2 = \frac{\sum_{i=1}^{s} n_{2i}^2}{N_2^2}$$

where N_1 and N_2 = total number of individuals occurring in the 1st and 2nd areas; n_{1i} and n_{2i} = number of individuals of ith species in each area; s = total number of species occurring in both areas. If overlap is complete, the index is 1, and if there is no overlap, it is 0. Total organic content of the sediments was estimated from weight loss on ignition (500 °C, 2 h).

RESULTS

Nature of the patches

Table 1 shows patch size and volume of each component. MC had the largest volume of each component except algae and associated animals. The algae were mostly *Chondria crassicaulis* and *Laurencia okamurai* and were abundant in Y. Associated animals were most abundant in O. Sediments accumulated more in MP and MC than in Y and O, and their total organic content was largest in MP and least in Y. Shell fragments were extremely scarce in Y. Volume of space (total displacement volume minus volume of all components) varied widely among patches. The relative amount of space (space volume/total displacement volume) was fairly constant (38.1 to 44.5 %).

Size distribution of *Mytilus edulis*

Young *Mytilus* patches (Y) contained nearly an order of magnitude more very small (<5 mm) mussels than the medium aged (MC and MP) or old (O) patches

Table 1. Patch size and volume of components of the *Mytilus* patch (10 cm × 10 cm). Y: young; MP: medium age/periphery; MC: medium age/center; O: old

	Y	MP	MC	O
Thickness (mm)	27.1 ± 5.1	42.8 ± 6.0	56.2 ± 7.7	42.2 ± 1.2
Total volume (cm^3)	233.1 ± 70.2	407.4 ± 70.8	532.2 ± 62.8	354.3 ± 82.5
Components (cm^3)				
Mytilus edulis	133.9 ± 39.6	185.5 ± 27.4	259.9 ± 61.7	168.2 ± 26.0
Byssal threads	1.6 ± 0.6	3.5 ± 0.8	4.2 ± 0.7	2.4 ± 0.6
Shell fragments	1.3 ± 0.7	12.6 ± 4.1	19.7 ± 6.3	11.7 ± 5.0
Sediments	2.1 ± 0.6	20.9 ± 15.2	23.6 ± 13.2	4.2 ± 1.9
(Loss on ignition, %)	(0.8 ± 0.2)	(2.8 ± 0.4)	(3.2 ± 0.5)	(3.6 ± 1.6)
Space	88.9 ± 24.2	181.3 ± 46.1	220.4 ± 20.8	159.1 ± 51.1
Algae	3.8 ± 1.7	0.9 ± 0.7	0.5 ± 0.3	0.4 ± 0.5
Associated animals	1.5 ± 0.7	2.7 ± 1.8	3.9 ± 1.0	8.3 ± 2.6

(Fig. 1). In Y, young mussels of 10 to 30 mm shell length were also found together with many recently settled smaller ones. Size distributions in MP and MC were comparable having many larger mussels (25 to 45 mm long). The O samples were composed of a monolayer of large mussels (35 to 55 mm) and few small ones. The peaks in the size-frequencies are to be taken as year classes. The mussels attached to one another in MC, and those in Y and MP were multilayered.

Associated animals in each patch

A species-area curve based on 5 samples of increasing area was drawn for each island (Fig. 2). Although none of the curves reached a plateau, it is considered that our samples (in total 500 cm^2 for each island) include about 80 % of species expected to be found in the island. Tsuchiya (1979) listed macrobenthic fauna of the rocky intertidal at Asamushi area. About 80 species were expected to be seen in a *Mytilus* bed. We collected 69 species in the present study, and they were mostly included in the faunal list. These facts suggest that our samples describe well the species richness of each *Mytilus* island.

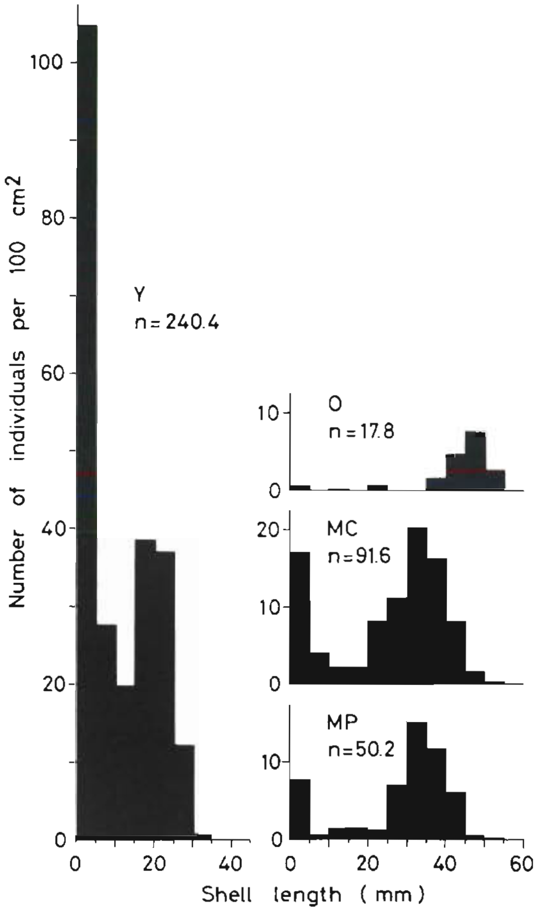

Fig. 1. *Mytilus edulis*. Size composition for each patch. n: total number of *M. edulis* per 100 cm^2

Table 2 shows the species-number relation of the associated animals for each patch. Number of species increased with age, but the number of individuals of associated animals were more abundant in MP and MC than in Y and O. The number of individuals per area was nearly equal in both Y and O, but on a per volume basis was larger in Y. The number of species per volume was largest in Y. Species diversity (H') and equitability (J') were larger in MP and MC than in Y and O.

Table 3 shows the members of associated fauna established in the patches of different age class. Although animals belonging to 8 phyla appeared, 93.9 % of total specimens were shared by 2 phyla: Annelida and Arthropoda. The most abundant species was the orbiniid polychaete worm *Nainereis laevigata*, which was extremely abundant in O, but not seen in Y. The arabellid polychaete *Arabella iricolor* was also abundant in O and rather large specimens (>200 mm long) were collected. This explains the largest volume of associated animals in O (Table 1). In other patches, only small worms were seen. On the other hand, the amphipod *Hyale grandicornis* was extremely concentrated in Y. A similar trend was observed in the amphipod *Mellita* sp. and the nereid worm *Nereis pelagica*. Several species which were restricted to O

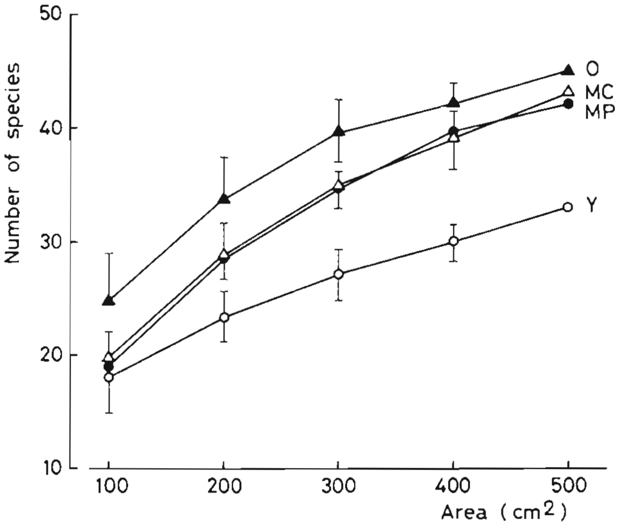

Fig. 2. Species-area relation in *Mytilus* islands composed of mussels of different ages. Y: *Mytilus* island with young mussels; MP: peripheral part of the island of adult mussels; MC: central part of the island of adult mussels; O: island consisting of old mussels. Bars indicate SD; we collected 5 samples in each patch and mean values of possible combinations for each area were calculated, so we have only 1 sample for 500 cm^2

Table 2. Relation between numbers of species and individuals (species diversity and equitability) in each patch (500 cm^2). Means (± SD) (100 cm^2) are also shown in parentheses. Y: young; MP: medium age/peripheral; MC: medium age/center; O: old

	Y	MP	MC	O
Number of species	33	42	43	45
	(18.0 ± 3.16)	(19.0 ± 0)	(19.8 ± 2.22)	(24.8 ± 4.26)
Number of individuals	595	251	292	554
	(119.0 ± 28.65)	(50.2 ± 12.56)	(58.4 ± 6.86)	(110.8 ± 21.74)
Number of species cm^{-3} *	0.074	0.046	0.039	0.057
	(0.20 ± 0.07)	(0.09 ± 0.03)	(0.08 ± 0.01)	(0.20 ± 0.09)
Number of individuals cm^{-3} *	1.339	0.277	0.265	0.696
	(1.25 ± 0.38)	(0.24 ± 0.06)	(0.22 ± 0.04)	(0.69 ± 0.34)
H'	3.154	4.274	4.245	3.537
H'_{max}	5.044	5.392	5.426	5.524
J'	0.625	0.793	0.782	0.640

* Volume of space

Table 3. Faunal list collected in each patch. Total number of individuals in 5 quadrats (100 cm^2 each) are shown for each species

Species	Y	MP	MC	O
COELENTERATA	(0)	(1)	(2)	(0)
Anthopleura japonica	0	0	2	0
Unidentified actiniarian sp. 1	0	1	0	0
PLATYHELMINTHES	(0)	(2)	(1)	(0)
Notoplana humilis	0	2	1	0
NEMERTINEA	(1)	(7)	(7)	(7)
Emplectonema gracile	0	1	3	0
Amphiporus cervicalis	0	2	1	3
Unidentified nemertinean sp. 1	1	0	0	4
Unidentified nemertinean sp. 2	0	0	2	0
Unidentified nemertinean sp. 3	0	4	1	0
SIPUNCULOIDEA	(0)	(1)	(0)	(3)
Unidentified sipunculid sp. 1	0	1	0	3
ANNELIDA	(131)	(139)	(149)	(357)
Harmothoe imbricata	4	10	25	2
Lepidonotus sp. 1	3	4	1	9
Lepidonotus sp. 2	1	0	0	1
Halosydna brevisetosa	0	1	0	0
Chrysopetalum occidentale	0	2	1	4
Unidentified syllid sp. 1	1	0	0	0
Unidentified syllid sp. 2	8	2	1	1
Unidentified syllid sp. 3	1	3	0	9
Genetyllis castanea	2	2	6	3
Euralia viridis	1	1	0	1
Eteone longa	0	0	1	0
Nereis pelagica	35	0	3	0
Nereis heterocirrata	4	6	0	0
Nereis sp.	60	14	12	3
Lumbrineris latreilli	0	2	1	4
Arabella irricolor	1	12	8	29
Arabella sp.	7	0	0	1
Dorvillea matsushimaensis	0	0	0	8
Spio sp.	0	1	7	0
Cirriformia tentaculata	0	6	9	4
Cirratulus cirratus	0	0	0	1
Nainereis laevigata	0	64	66	249
Stylarioides plumosa	0	1	2	0
Nicolea gracilibranchis	0	1	3	6
Unidentified sabellid sp. 1	3	7	3	12
Hydroides ezoensis	0	0	0	5
Hydroides elegans	0	0	0	5
MOLLUSCA	(35)	(40)	(52)	(91)
Ischonochiton (s.s.) computus f. *computus*	0	3	3	8
Tonicella liniata	0	1	0	0
Acanthochiton rubrolineatus	3	9	8	10
Collisella (Conoidacmea) heroldi	19	19	21	44
Notoacmea schrenckii	0	0	3	0
Littorina brevicula	0	3	1	0
Temanella turita	7	1	0	2
Mitrella tenuis	4	1	8	4
Septifer (Mytilisepta) virgatus	0	4	7	0
Septifer (Mytilisepta) keenae	0	0	0	19
Modiolus modiolus difficilis	0	0	0	4
Hiatella flaccida	2	0	1	0
ARTHROPODA	(428)	(59)	(77)	(93)
Unidentified pycnogonid sp. 1	0	1	0	1
Chthamalus challengeri	0	0	0	30
Paranthura japonica	5	0	1	1
Exosphaeroma ovata	0	1	0	1
Dynoides dentisinus	8	6	0	1
Allorchestes plumicornis	28	4	1	5
Hyale grandicornis	218	21	1	4
Amphithoe lacertosa	22	1	34	5
Melita sp.	127	18	15	29
Elasmopus japonicus	3	0	0	0
Jassa falcata	6	0	1	2
Unidentified amphipod sp.	1	0	1	1
Caprella acutifrons	6	0	0	0
Orchonemella sp.	2	0	0	1
Pagurus germinus	1	5	15	7
Oedignathus inermis	0	0	7	5
Hemigrapsus sanguineus	1	2	1	0
ECHINODERMATA	(0)	(1)	(4)	(2)
Ophiophragmus japonicus	0	0	0	2
Unidentified ophiuroid sp. 1	0	1	1	0
Aphelasterias japonica	0	0	1	0
Cucumaria chronhjemi	0	0	2	0
Number of species	33	42	43	45
Number of individuals	586	252	283	556

were divided into 3 groups owing to their mode of life; (1) epizoic sessile animals such as the barnacle *Chthamalus challengeri* and the serpulids *Hydroides ezoensis* and *H. elegans;* (2) the mussels *Septifer (Mytilisepta) keenae* and *Modiolus modiolus difficilis;* (3) creeping fauna, the dorvilleid *Dorvillea matsushimaensis* and the ophiuroid *Ophiophragmus japonicus.*

Table 4 shows similarities of species composition (C_π) between patches. Table 4a shows values for whole animals. Patches MP, MC and O were highly similar in community structure. Table 4b shows indices for animals excluding epiphytic species (e.g. amphipods and the gastropod *Temanella turita* living on algal thalli). Similarity between Y and other patches decreased when compared with the entire fauna, but increased among MP, MC and O.

Table 4. Similarity of species composition between patches. C_π indices are calculated (a) on total animals and (b) on animals excluding epiphytal species. Y: young; MP: medium age/peripheral; MC: medium age/center; O: old

		Y	MP	MC	O
(a)	Y	1	0.3819	0.1728	0.0874
	MP			0.8458	0.8250
	MC				0.7424
	O				1
(b)	Y	1	0.2598	0.2381	0.0625
	MP			0.9426	0.8724
	MC				0.8025
	O				1

DISCUSSION

In *Mytilus* islands, some biological activities such as filtering, biodeposition and growth of *M. edulis* undoubtedly affect the process of community organization of associated animals. There may be biological reasons for a low recruitment by mussel larvae into the patch, e.g. predation by associated fauna or filtering by the patch-forming mussels. This may explain the low density of juvenile mussels in the patches MP, MC and O, because these patches were constructed by large mussels with high filtration rates (Winter 1973, 1978, Jørgensen 1975). Recruitment might be more successful in the younger patch (Y).

Physical structure created by sessile organisms is an important characteristic of the system for associated fauna (Dean 1981). After larval settlement on the rock, a monolayer mussel bed is formed in the early stage of patch growth (Y). With growth, mussels require more space for attachment, and some individuals on the periphery of the patch are pushed out while some inside the patch are shifted up. This results in the formation of a double or multi-layered mussel bed (MC). With time, some mussels die, but some of the dead shells and fragments remain in the patches. The structure of *Mytilus* islands may change with growth and recruitment of the mussels. Hosomi (1967) reported a similar change in the physical structure of *M. edulis* populations with time on a breakwater in Osaka Bay, Japan. If further settlement of mussel larvae does not occur, only large mussels make up a monolayered bed (O). In such situations, the volume of patch per unit area becomes small and the height of a patch is less than that of double or multilayered younger patches.

The fact that the monolayered old patch (O) had a smaller amount of sediments and shell fragments than younger patches (MP and MC) and were poorer in species richness may suggest that more space and larger amounts of sediments and shell fragments in the patches may be needed for an increase in species diversity. Increase of sediments, shell fragments and byssal threads accelerate an increase of heterogeneity of habitat structure. In MP and MC, feeding habits of the associated animals were diverse including herbivores, deposit feeders, carnivores and suspension feeders. Organic matter in the sediments was richer in MP, MC and O than in Y. Deposit feeders use environments rich in organic matter, e.g. the cirratulid *Cirriformia tentaculata,* which is an indicator species of such an environment, was seen in these patches.

In the oldest patch (O), sessile animals such as barnacles and serpulids were found on *Mytilus edulis* shells. Growth of older mussels is slower than that of younger ones (Seed 1976). Because older part of shells do not grow, they are suitable substrates for sessile organisms.

On the other hand, there is a possibility that the sediment accumulation affects adversely the associated fauna, because super-abundant sediments prevent *Mytilus edulis* larvae from settling to patches (Field 1982) and generate a reducing environment (Tsuchiya 1979).

Species composition in Y differed from those of other patches. Because Y is the youngest patch, it had provided the shortest period for invasion by associated animals. Since it is considered that those species found in Y settled also in older patches, interactions between inhabitants or early settlers and new settlers might cause the death of the latter. Dynamic processes in a *Mytilus* island community, with reference to the immigration and recruitment of associated fauna, need to be studied in future. On the other hand, environmental traits may be unsuitable for animals inhabiting older patches because the patches may be affected by wave action or predators.

It has been reported that the *Mytilus* community is

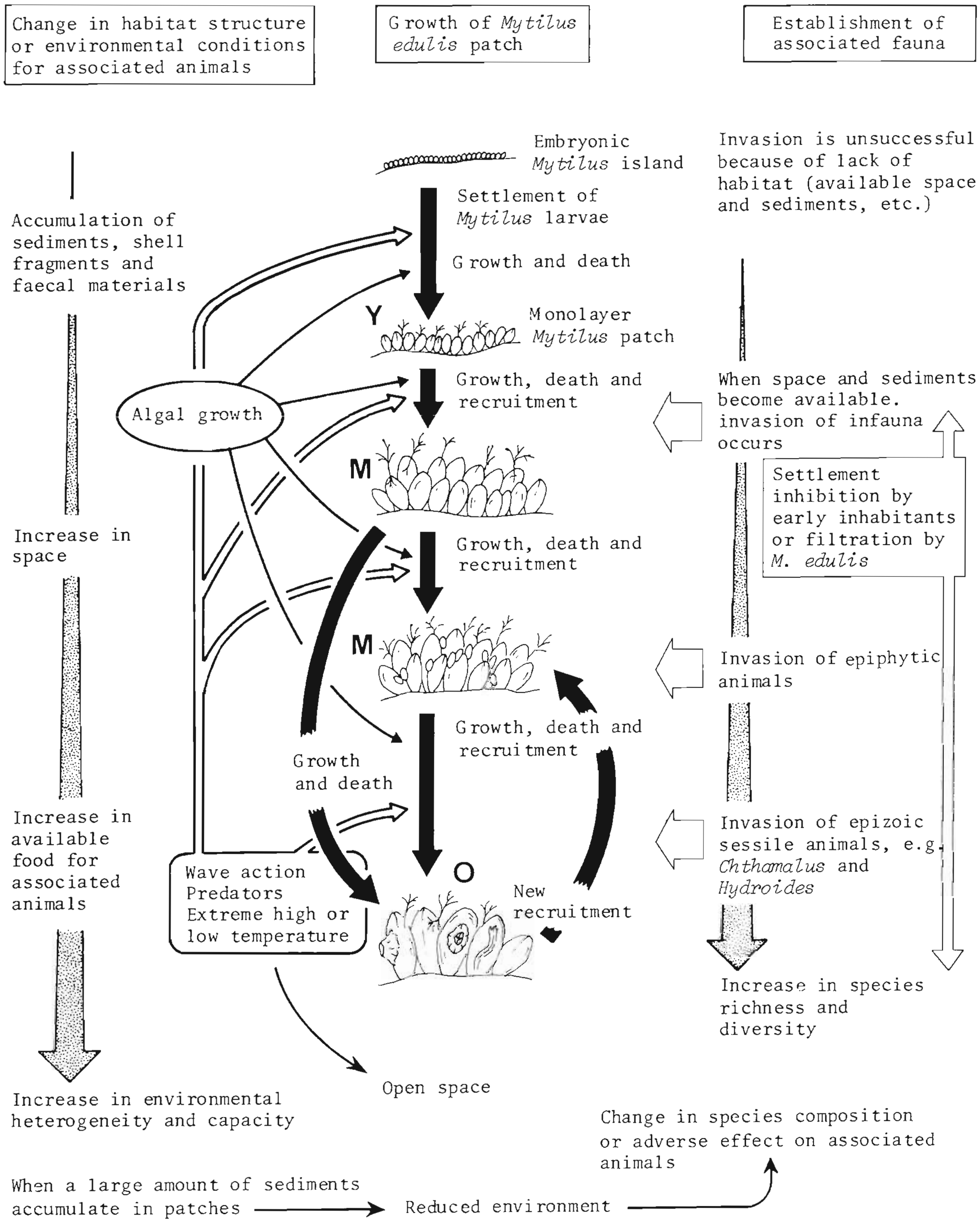

Fig. 3. Possible process of community organization in *Mytilus* islands. Y: *Mytilus* island composed of young mussels; M: *Mytilus* island of adult mussels; O: *Mytilus* island of old mussels. For detailed explanation, see text

relatively stable (Sheer 1945, Dean & Hurd 1980), because the mussel bed confers protection from external perturbations (Connell 1972). However, the periphery of patches is greatly affected by forces from outside, e.g. wave action and predators, etc. If so, it is conceivable that there are differences in faunal composition between peripheral and central parts in a patch. However, the species composition in MP and MC was very similar (C_n based on all inhabitants being 0.8458). Environmental differentiation of the *Mytilus* island may occur only at a very peripheral part.

The role that algae growing in the patches play in community structure requires special attention. Many epiphytic amphipods were collected in Y, which was characterized by much algae (Table 1). Scarcity of amphipods in older patches could be explained by the poor algal growth.

Fig. 3 shows the possible process of community organization in *Mytilus* islands, which emerged from the results obtained in previous (Tsuchiya & Nishihira 1985) and the present studies. The volume of each component of a *Mytilus* island varies from patch to patch. In Y, dead shells seem to be removed more easily by wave action than in the other older patches, because, presumably, the latters' insides are protected from wave action. Shell fragments may be accumulated in these patches, snared by byssal threads. *M. edulis* produces faeces and pseudofaeces which accumulate in the *Mytilus* bed (Seed 1976, Tsuchiya 1980). Because some resuspended bottom materials are present in shallow waters (Kiørboe et al. 1981), these may also be deposited in the patches. There is a possibility that detritus and micro-organisms on the shell surface are used as food for deposit feeders in the patch. Accumulations of sediments, shell fragments and faecal materials may play important roles in increasing species diversity through increasing environmental heterogeneity. Impacts from outside the *Mytilus* island may play an important role in community organization. *Mytilus* beds frequently receive adverse affects of some factors such as extreme temperatures or desiccation (Suchanek 1978, Tsuchiya 1983), wave action or drift logs (Dayton 1971, Paine & Levin 1981) and predators (Paine 1974, Menge 1976). In such cases, open rock surface may appear on the intertidal and opportunistic species can invade it (Connell & Slatyer 1977). In northern Japan, the barnacle *Chthamalus challengeri* is considered to be such an opportunistic species, because invasion of *C. challengeri* into the bared rock surface has frequently seen (Hoshiai 1960, 1965, Tsuchiya 1983).

In order to confirm these speculative processes of community organization, we must conduct many experimental analyses both in the field and laboratory.

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