Macrofouling community structure in Kanayama Bay, Kii Peninsula (Japan)

T.V. RAVEENDRAN[1] and EIJI HARADA

Seto Marine Biological Laboratory, Shirahama, Wakayama 649-2211, Japan

Abstract An investigation on the macrofouling community in Kanayama Bay, Kii Peninsula, Japan was undertaken from June 1994 to May 1995 by exposing fiber reinforced plastic (FRP) panels at subsurface and bottom (2.2 m) depths. The composition and abundance of fouling organisms were monitored at monthly intervals. Fortnightly variations in hydrographic parameters were also noted simultaneously. The fouling community at this bay was a complex assemblage of bryozoans, ascidians, polychaetes and barnacles comprising more than 40 species. The faunal elements exhibited distinct seasonal trends in abundance closely associated with fluctuations in temperature, i.e. maximum abundance was recorded in summer and the reverse in winter. Greater faunal abundance was generally observed on the subsurface panels. Significant depth wise variation in abundance seems to be the result of predation, competition and the effect of residents on recruits. Succession in the community was divided into three stages by dendrogram analysis. First stage was characterized by polychaetes (*Protohydroides elegans* and *Dexiospira foraminosa*) on panels from both depths. The encrusting bryozoan, *Watersipora subtorquata* dominated on the subsurface panels and a mixed dominance of *W. subtorquata*, barnacles, *P. elegans* and the ascidian, *Polyclinum constellatum*, on bottom panels in second stage. Third stage was characterized by a mixed dominance of *W. subtorquata, Bugula neritina* (an erect bryozoan) and *P. constellatum* at the subsurface and *B. neritina* at bottom depths.

Key words: Macrofouling community; succession, colonization curve; Kanayama Bay

Introduction

The term macrofouling is commonly applied to the recruitment and growth of sessile organisms on man-made structures in the marine environment. Macrofouling, due to its extensive economic impact, has received considerable attention during the past several decades (see WHOI, 1952; Costlow and Tipper, 1984). Fouling community structure depends on environmental and biological interactions comprising competition and predation (Kawahara, 1965; Sutherland, 1974; Osman, 1977; Russ, 1980, 1982; Nandakumar, 1995; Anil *et al*; 1990 a, b). It often undergoes sequential structural change, *i.e.* succession (Sutherland, 1974; Sutherland and Karlson, 1977; Osman, 1977; Field, 1982; Greene *et al.*, 1983; Okamura, 1986; Hirata, 1991; Underwood and Anderson, 1994; Zvyaintsev and Ivin, 1995). The present study was intended to elucidate the fouling community structure in Kanayama Bay, Kii Peninsula, Japan. An attempt was also made to find out whether the community undergoes succession during the developmental process.

Materials and methods

The following four seasons are recognized here as: summer (June to August), autumn (September to November), winter (December to February) and spring (March to May). We considered recruits to be all sessile organisms that settled and survived on the panel long enough to be observed (Keough and Downes, 1982).

---

[1] Address for Correspondence: National Institute of Oceanography, Dr. Salim Ali Road, P.B.No-1616, Kochi-682014, India.

Study site

The study site is located in Kanayama Bay on the Pacific coast (33° 41'N; 135° 21' E), where the local fisheries department places rafts with cages for culturing fish. Being a semi-enclosed bay, it is well protected from heavy swells and waves. The maximum depth near the raft is ~2.5 m and the maximum depth at the center of the bay is ~6 m during the lowest low tide.

Experimental design

Artificial substrates are commonly employed in biofouling studies as it is easy for handling and observation in the lab, can provide information regarding the period and rate of recruitment and can be conveniently retrieved and replaced at desired depths to follow community progression and succession. We used Fiber Reinforced Plastic (FRP) panels because of its industrial as well as marine applications. FRP panels measuring 20 x 20 cm were submerged vertically at subsurface and bottom (2.2 m) depths by securing back-to-back in pairs on FRP bar each of 75 x 4 x 1.5 cm. A single bar was holding a maximum of six panels at a time. These bars were suspended from the raft using nylon ropes. Lead weights of ~2.5 kg were suspended at the end of the ropes to reduce the movement of the bars. A set of 48 panels (2 depths X 2 replicates X 12 months), representing long-term panels, was submerged in June 1994 to follow the development of the community for 1 year (Fig. 1). The short-term panels (*i.e.* of 1, 2, and 3 months duration), in duplicates, were

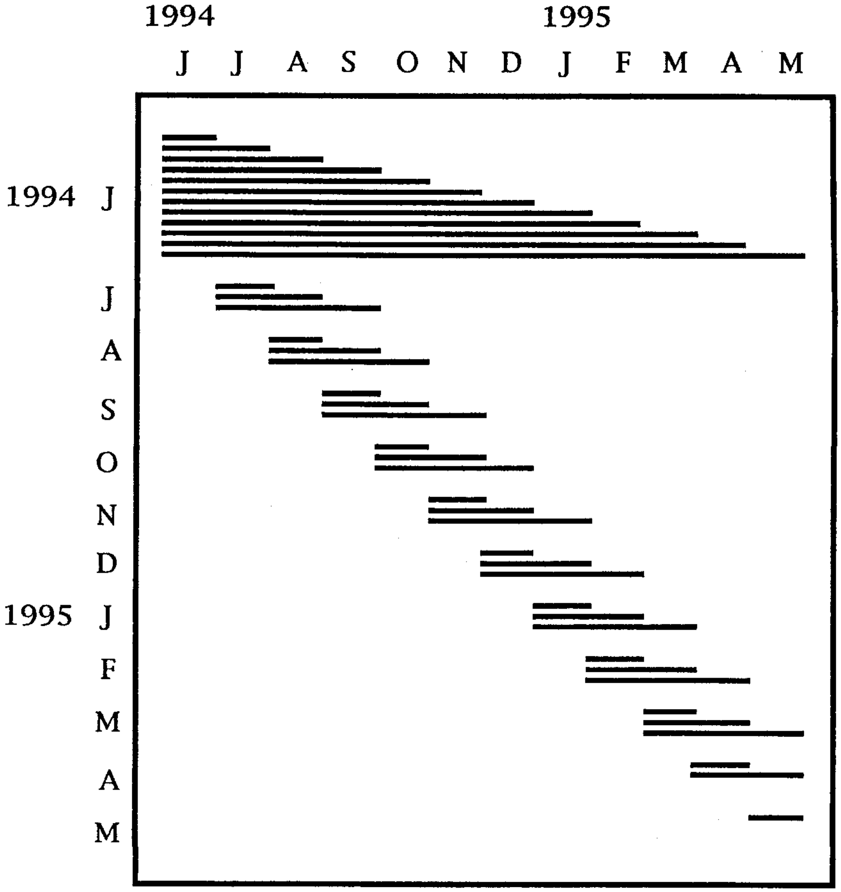

Fig. 1. Panel exposure pattern.

submerged at the subsurface and bottom depths, sequentially every month starting from July 1994 to March 1995 to study the effect of period of initiation on settlement.

Observation and measurement

On retrieval, the panels were brought back to the laboratory and kept in running seawater until observation and measurement. The percentage cover of colonial forms and numerical abundance of solitary forms occupying the central 15 x 15 cm area of the panels were recorded. Percentage cover was measured using 10 x 10 grids of 225 cm^2 area so that each grid represents 1% cover. Since the canopy cover was measured in the case of the arborescent bryozoan, *Bugula neritina*, more than 100% cover was possible on some of the panels. For the numerical abundance of solitary forms, total count was taken whenever possible. However, during the periods of intense recruitment, 5 grids of 16 cm^2 area (one in the center and four at each corner of the central 225 cm^2 area) were counted and their mean value was converted into abundance per m^2. The basal diameter of barnacles and *Dexiospira foraminosa* and tube length of *Protohydriodes elegans* were noted. In the case of barnacles, only total count was taken due to the practical difficulties in identification to species level on short-term panels. However, individual species were noted for their presence on all panels.

Hydrographic parameters such as water temperature and salinity were monitored at fortnightly intervals.

Data analysis

To distinguish successive stages of community development, the samples were subjected to cluster analysis using Horn's coefficient of similarity (Horn, 1966), based on Shannon-Wiener information theory and the group average method. The mean percentage cover of sessile invertebrates on the central area of the long-term panels was used for this analysis.

Results

Analysis of the hydrographic data revealed the prevalence of typical marine conditions at this station (Fig. 2). Temperature showed wide fluctuations, ranging from 14.6°C (February 1995) to 30.2°C (September 1994). Salinity was above 33 during the major part of the study period. Drop in salinity during July-August is due to precipitation.

Composition of fouling organisms

The faunal elements of the macrofouling community are presented in Table 1. Bryozoans, ascidians, barnacles and polychaetes were the major contributors to the fouling community. The encrusting bryozoan, *Watersipora subtorquata*, was the most important and dominant species in terms of its occurrence and coverage on the panels. Recruitment of this species occurred almost round the year (Table 1). It occupied more than 60% area on 3-monthly panels initiated in September as well as on long-term panels exposed for June-January and June-April period at subsurface (Figs. 3, 4). The erect bryozoan, *Bugula neritina* was another important fouling species observed at this station. Recruitment of this species was generally absent during the summer (June-July) months, but abundant recruitment occurred during the autumn season. Canopy coverage of 63±17% at subsurface and 45±5% at bottom on 3-monthly panels initiated in October was notable (Fig. 3). A maximum coverage of 88±12% was recorded on June-February panels (Fig. 4). *Rhynchozoon* sp. showed very poor cover with a maximum of 8±1% on a long-term panel (June-March) at bottom depth (Figs. 3, 4).

Ascidians showed very poor area cover on short-term panels during the entire study period. The maximum recorded for *Didemnum moseleyi* was 11±2% on a 2-monthly panel and for *Diplosoma mitsukurii* was 16±14% on a 3-monthly panel, both initiated in September (Fig. 5).

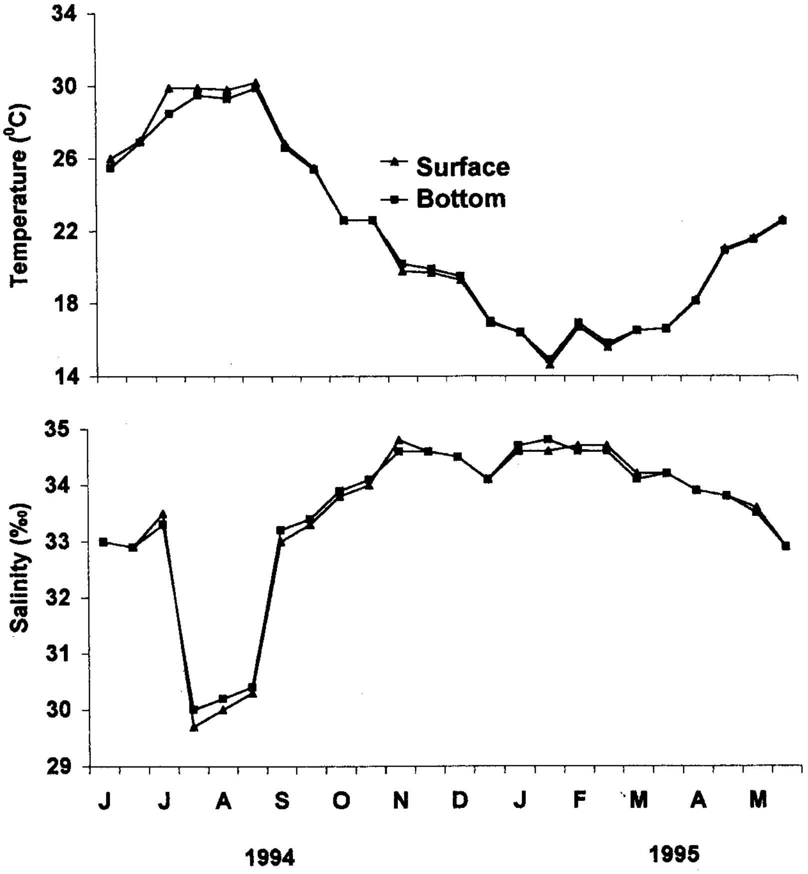

Fig. 2. Fortnightly variations in hydrographic parameters.

Polyclinum constellatum and *Aplidium yamazii* were generally absent on short-term panels but were recorded on long-term panels. *Polyclinum constellatum* showed its appearance immediately after October. Maximum cover recorded was 24±4% on June-February panels exposed at subsurface (Fig. 4). *Aplidium yamazii* was observed only on long-term panels that were still in the field after March. Maximum cover recorded was 33±26% on June-March subsurface panels.

Polychaetes were observed round the year with peak recruitment observed in summer (Fig. 6). Among them, *Protohydroides elegans* and *Dexiospira foraminosa* were important. Barnacles, in general, showed very poor representation on the panels. Only notable recruitment occurred on 2 and 3-monthly panels during spring at bottom depth (Fig. 6) and was dominated by *Balanus trigonus*. Barnacles were completely absent during the winter season.

Community development

Colonization curve

The colonization of sessile invertebrates proceeded rapidly after submergence of the panels (Fig. 7). There was a significant increase in the number of species during the first 7 months at subsurface ($p<0.05$) and 8 months at bottom ($p<0.001$). Thereafter, non-significant variation prevailed at both depths ($p>0.05$).

Table 1. Occurrence of taxa on 1, 2, 3-monthly and cumulative panels submersed during June 1994 to May 1995.

Species	1-m onthly																								2-monthly																						3-monthly																				J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-	J-
	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	J	J	A	S	O	N	D	J	F	M	A	J	J	A	S	O	N	D	J	F	M	J	J	A	S	O	N	D	J	F	M	S	O	N	D	J	F	M	A	M	S	O	N	D	J	F	M	A	M
	Subsurface												Bottom												Subsurface											Bottom											Subsurface										Bottom										Subsurface									Bottom								
Porifera																																																																																						
Sycon sp.	·												·													·	·	·	·	·				·	·						·	·		·	·	·	·	·	·	·	·	·			·	·				·	·	·	·	·	·	·	·	·	·	·	·							·	·	·	·			
Grantia sp.																																													·	·									·								·		·								·	·	·					·	·		·	·
Clathrina mutsu																																																																															·			
Callyspongia murex																																																																													·				·	
Acervochalina sp.																										·																																									·															
Haliclona sp.																																																																					·			·						·				·
Coelenterata																																																																																						
Eudendrium capillare					·	·																						·		·						·					·	·		·						·	·	·								·	·	·									·	·	·					·			·			
Clytia sp.		·																											·											·										·																		·															
Obelia dichotoma				·		·	·		·	·	·	·							·		·	·			·				·	·		·		·	·			·		·	·							·			·				·	·					·						·		·	·		·												
Polychaeta																																																																																				
Protohydroides elegans	·	·	·	·		·			·		·	·	·	·	·	·	·	·				·	·	·	·	·	·	·	·	·				·	·	·	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·			·	·	·	·	·	·	·	·		·	·	·		·	·	·	·			·	·	·	·	·	·				·
Pomatoleios kraussii																										·																					·	·									·										·	·	·	·	·		·			·	·	·	·	·	·	·	·	·
Hydroides exaltata																																																							·																	·	·								·		·	
Filograna implexa																								·																																									·											·						·	·	·
Dexiospira foraminosa	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·	·	·	·			
Bryozoa																																																																																					
Zoobotryon pellucidum																									·																						·																												·									
Membranipora serrilamellata						·	·											·												·																		·	·		·	·	·						·		·							·															
Bugula neritina					·	·	·	·	·	·	·	·					·	·	·	·	·	·	·		·			·	·	·	·	·	·	·	·				·	·	·	·	·	·	·	·			·	·	·	·	·	·	·	·				·	·	·	·	·	·	·			·	·	·	·	·	·	·			·	·	·	·	·	·	·
Bugula stolonifera						·																							·					·						·			·		·					·		·			·							·			·	·			·	·									·		·			
Tricellaria occidentalis																								·			·																																																									
Rhynchozoon sp.						·	·		·			·	·					·	·	·	·	·		·	·		·	·	·	·	·	·		·	·	·			·	·	·	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·	·
Watersipora subtorquata	·	·	·	·	·	·	·	·	·	·	·	·	·		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Hippothoa divaricata																											·	·	·																			·	·	·									·	·	·					·	·	·	·							·		·				
Petralia japonica																																		·	·											·							·	·	·	·							·	·		·						·									·		·	
Bivalvia																																																																																				
Musculus japonica									·													·																								·	·							·			·												·		·	·												
Hormomia mutabilis		·	·		·									·	·											·										·	·																															·													
Pinctada fucata				·																																																							·										·				·		·			·	·					·	
Crassostrea gigas	·																																																																					·		·						·	·							
Crassostrea nipponica																																																																						·									·							
Dendostrea folium																																																																																|·|				
Dendostrea rosacea																																																																						·									·	·						
Cirripedia																																																																																						
Balanus trigonus																								·											·											·										·										·					·									·	·	·	·	·
Balanus amphitrite		·		·	·														·				·		·	·	·	·	·					·	·	·		·	·	·					·		·	·	·	·	·	·	·		·			·	·	·	·				·		·		·	·	·		·			·	·	·	·	·	·	·		·
Balanus improvisus		·		·																				·													·	·	·																	·		·	·	·															·	·	·	·			·		·	·
Megabalanus volcano												·												·											·											·								·	·			·		·									·						·	·	·	·					
Ascidia																																																																																					
Policlinum constellatum	·		·																							·	·	·	·	·					·		·	·		·	·						·	·	·	·	·	·				·	·	·		·	·	·					·	·	·	·	·	·	·	·	·	·	·	·	·	·	·		·	·
Aplidium yamazii																																																																	·						·	·	·	·							·	·	·
Didemnum moseleyi	·		·		·								·					·					·		·	·	·	·	·	·				·	·		·	·	·	·	·	·	·	·		·	·	·	·	·	·					·				·	·	·	·		·		·	·	·	·	·	·	·		·		·	·	·	·	·	·	·	
Diplosoma mitsukurii	·																			·	·	·	·				·		·					·	·				·				·	·	·	·			·	·			·		·							·			·	·	·	·			·	·						·	·				
Lissoclinum sp.								·																																																																													
Botrylloides simodensis																								·			·						·		·	·		·							·	·	·					·	·			·	·					·				·	·			·	·		·		·					·	·	·	·	·	·
Styela canopus																							·			·																					·			·																		·	·	·	·	·	·	·			·		·	·				·
Herdmania sp.																																					·																																															

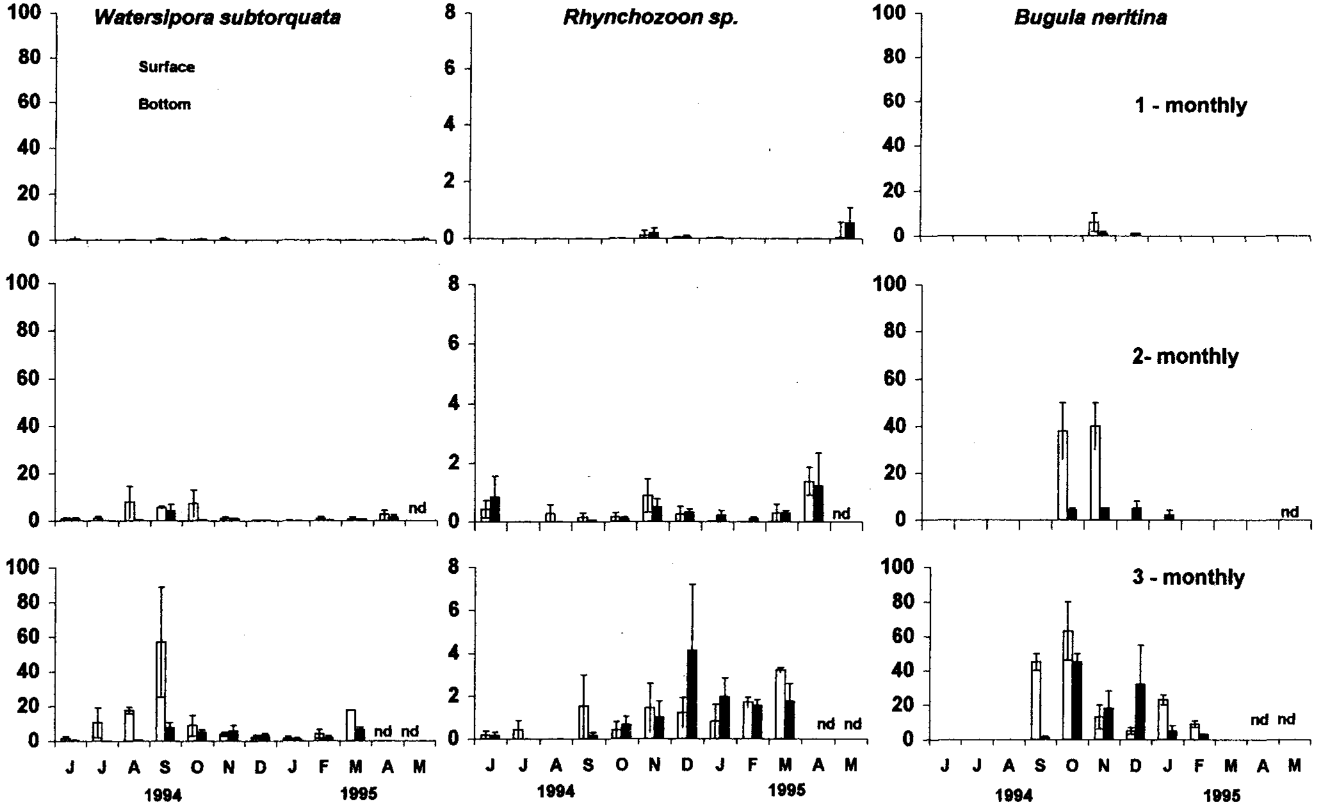

Fig. 3. Percentage cover (mean ± se, $n=2$) of bryozoans on 1,2 and 3-monthly panels.

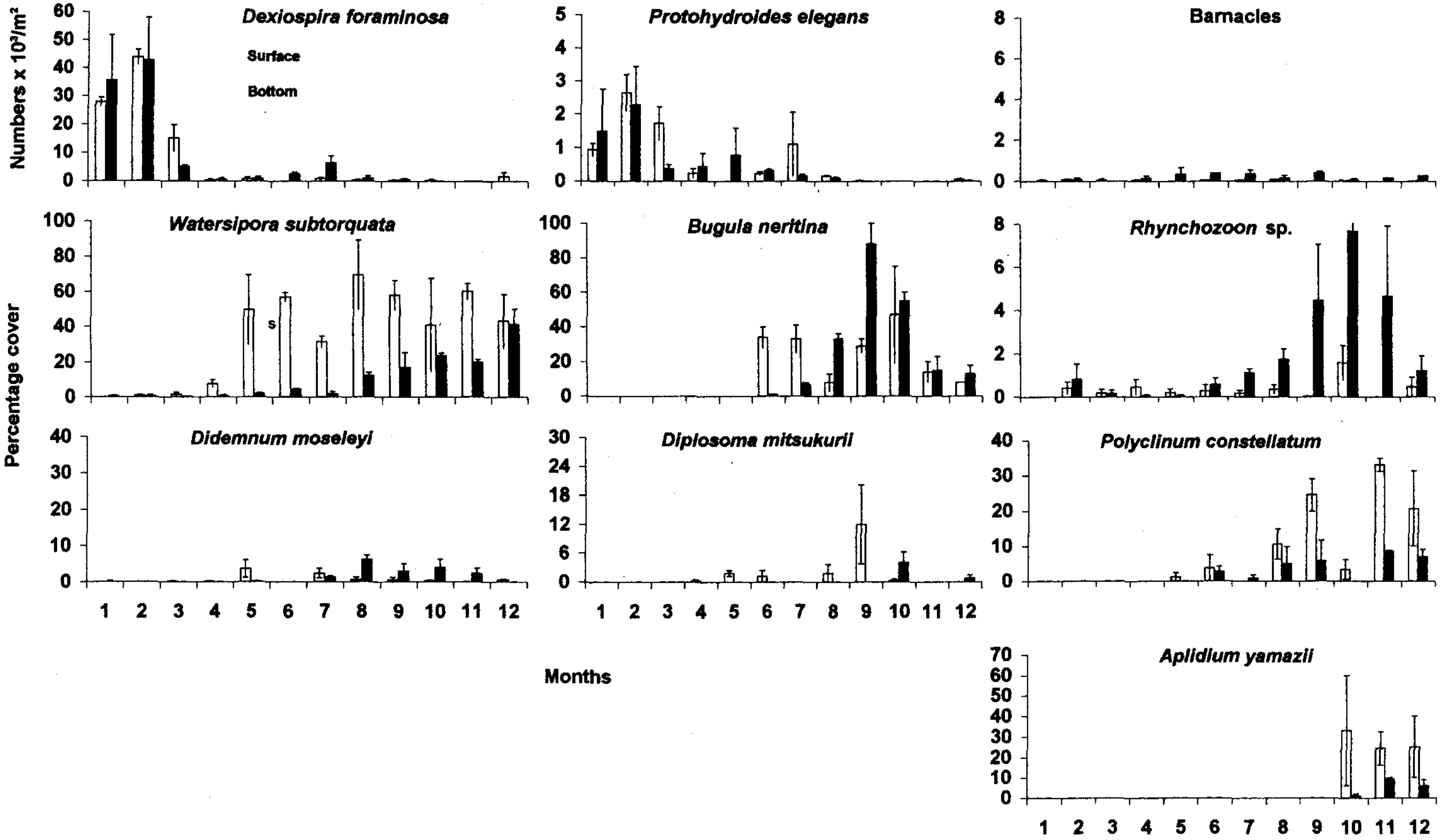

Fig. 4. Numerical abundance of polychaetes and barnacles and percentage cover of bryozoans and ascidians (mean ± se, $n=2$) on cumulative panels.

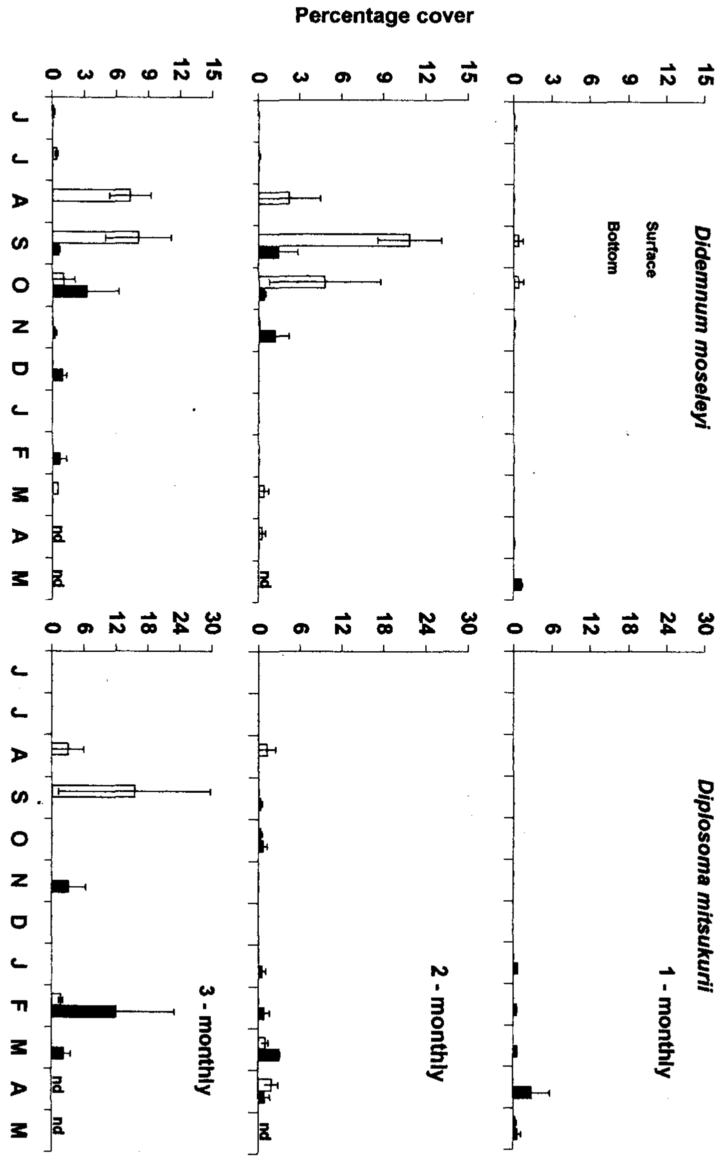

Fig. 5. Percentage cover of ascidians (mean±se, $n=2$) on 1,2 and 3-monthly panels.

Progression in community development

The succession sequence of colonization by sessile invertebrates is illustrated in the dendrogram (Fig. 8). Where in three major clusters can be distinguished at a similarity level of 0.50. The clusters were generally following the time sequence. The separation of sub-clusters based on the depth of the panels is notable.

In the following section, 3 major clusters were identified as representing the 3 successive stages of development. The features of these stages are summarized in Table 2. First stage was characterized by the dominance of *P. elegans* and *D. foraminosa* during summer and the second stage by *W. subtorquata* after 4-5 months submersion, *i.e.* from early autumn, at subsurface (Figs. 4, 8; Table 2, sub-cluster 2a). Simultaneously, settlement of colonies of *B. neritina* also occurred.

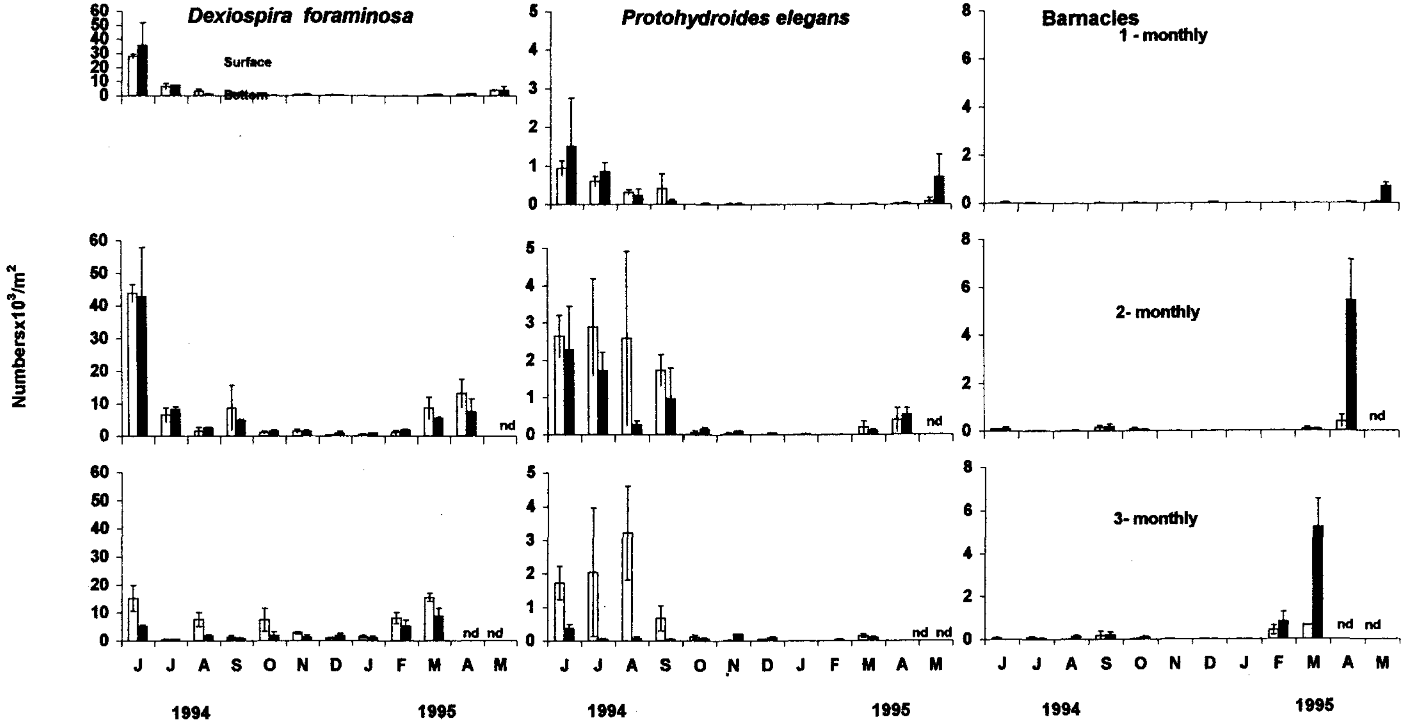

Fig. 6. Numerical abundance of polychaetes and barnacles (mean±se, $n=2$) on 1,2 and 3-monthly panels.

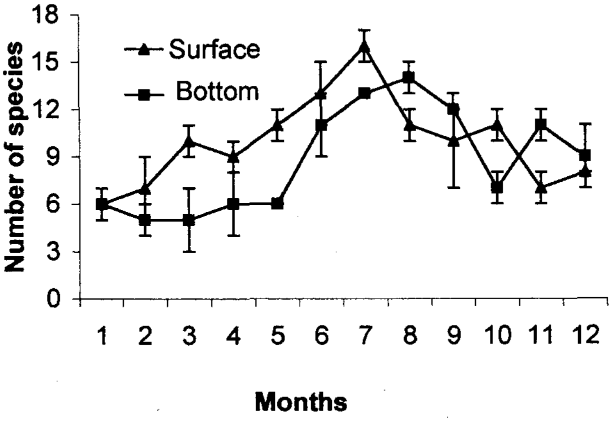

Fig. 7. Colonization curves of sessile species. Vertical bars indicate standard error.

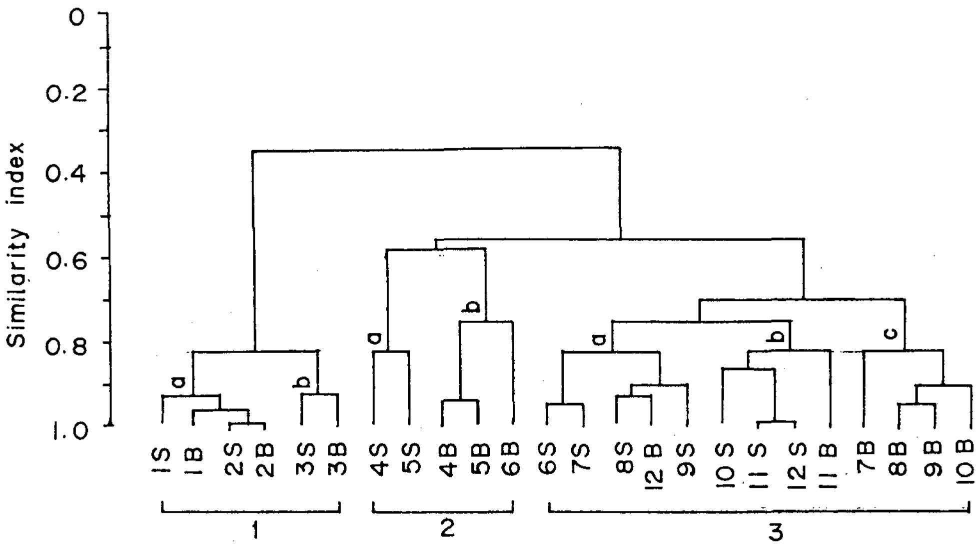

Fig. 8. Dendrogram of fouling community using nearest neighbour method and similarity index. S - subsurface, B - bottom, Numericals denote exposure durations in months.

The third stage was characterized by a mixed dominance of bryozoans and ascidians during late autumn through winter (Figs. 4, 8; Table 2). In the initial phase of this stage (Fig. 8; Table 2, sub-cluster 3a), *W. subtorquata* continued to maintain its dominance on the panels. Simultaneously, *P. constellatum* appeared on the panel. It was followed by the appearance of *A. yamazii* during spring (Figs 4, 8; Table 2, sub-cluster 3b).

The bottom panels also showed an almost similar trend of succession during the first stage of community development thereby, clustering with the subsurface panels. However, the formation of separate sub-clusters by bottom panels in the second and third stages indicates a certain degree of dissimilarity from those of subsurface panels. Thus, unlike the complete dominance of *W. subtorquata* on subsurface panels during the second stage, a mixed dominance of *W. subtorquata*, barnacles, *P. elegans* and *P. constellatum* was observed on bottom panels (Figs. 4, 8; Table 2, sub-

Table 2. Successional stages derived from the dendrogram shown in Fig. 10. The degree of domination is ranked by the relative abundance of species. The species are arranged in their order of dominance in each cluster.

Stages	Dominant species	Relative abundance (% cover)
I.	*Protohydroides elegans*	49
	Dexiospira foraminosa	35
	Watersipora subtorquata	9
	Rhynchozoon sp.	4
	Barnacles	2
IIa.	*Watersipora subtorquata*	80
	Hippothoa divaricata	7
	Didemnum moseleyi	5
	Diplosoma mitsukurii	3
	Polyclinum constellatum	2
IIb.	*Watersipora subtorquata*	32
	Barnacles	23
	Protohydroides elegans	14
	Polyclinum constellatum	13
	Oysters	6
IIIa.	*Watersipora subtorquata*	59
	Bugula neritina	18
	Polyclinum constellatum	15
	Diplosoma mitsukurii	5
	Aplidium yamazii	3
IIIb.	*Watersipora subtorquata*	38
	Aplidium yamazii	21
	Bugula neritina	20
	Polyclinum constellatum	15
	Botrylloides simodensis	3
IIIc.	*Bugula neritina*	62
	Watersipora subtorquata	18
	Rhynchozoon sp.	5
	Didemnum moseleyi	5
	Polyclinum constelletum	4

cluster 2b). Similarly, in the third stage, the bottom panels were dominated by *B. neritina.* The clustering of 11 and 12-monthly bottom panels with subsurface panels was mainly due to a greater cover of *W. subtorquata* and the presence of *A. yamazii* (Fig. 4).

Discussion

The macrofouling community in Kanayama Bay is rich and diverse, comprising more than 40 species from 7 major taxa. *Watersipora subtorquata* dominated on the panels due to their faster growth-rate. *Bugula neritina* needs only a relatively small basal area for attachment because of its arborescent growth form, and therefore, could easily invade and persist in established communities. *Polyclinum constellatum* appeared immediately after the recruitment of *B. neritina. Aplidium yamazii* was a latecomer at this station. *Dexiospira foraminosa* never formed an important member of the fouling community during later successional stages of community development due to their small size and high susceptibility to overgrowth by other fouling organisms. Barnacles (*B. trigonus*) were generally abundant on bottom panels, but were absent in winter as reported by Anil *et al.* (1990a, b).

The major faunal elements seem to be common along the coasts of Japan. For example, *W. subtorquata* and *D. mitsukurii* have been reported from the fouling community in Nabeta and Tomioka Bays, *B. neritina* from Tomioka and Matoya Bays; *B. trigonus* from Nabeta, Tomioka and Matoya Bays and from Lake Hamana, *B. amphitrite* in all these bays, except Nabeta Bay and *D. foraminosa* common in all these sites (Kawahara, 1965; Hirata, 1987; Anil *et al*; 1990a, b; Nandakumar, 1995). However, a precise comparison of individual species abundance is impossible due to the difference in substratum choice (Anderson and Underwood, 1994).

The species richness of an island community (which is equivalent to artificial substrata) depends on the immigration of new species and extinction of existing ones (MacArthur and Wilson, 1967). In the present site, the colonization curve attained its peak within 7 to 8 months after submersion of the panels due to rapid recruitment as the panels were submerged in the beginning of summer. Osman (1975) made similar observations off temperate Massachusetts. The curve exhibited a declining tendency because the peak colonization period was immediately followed by the winter season. At the same time, the existing colonies of *W. subtorquata* and *P. constellatum*, which can withstand low winter temperatures, enhanced their dominance and continued to occupy space and overgrow other species. Thus, the increased dominance by resident species inhibited potential invasion of competitively inferior species during spring when larval recruitment was taking place as evidenced from the short-term panels. Sutherland and Karlson (1973, 1977) also have suggested that certain temperate species inhibit subsequent colonization. Thus, lack of immigration coupled with increased extinction leads to a decrease in species richness. The recovery in the curve in the end was the result of decline in the cover by bryozoans and ascidians, thereby creating open space for new recruits. According to Sutherland and Karlson (1977), North Carolina fouling-plates require more than a year to reach their equilibrial species numbers. At the same time, fouling panel studies conducted in Massachusetts by Osman (1977) and in Nabeta Bay, Japan, by Hirata (1991) suggest that one-year is a sufficient interval for approaching the equilibrium.

Whether the term "succession" (Odum, 1969) can be applied to a marine fouling community is a subject of controversy (Drury and Nisbet, 1973; Horn, 1974; Connell and Slatyer, 1977). Succession is defined here as "the changes in the occurrence and relative abundance of different species over time, regardless of the underlying mechanisms which brought about these changes" (Foster, 1975; Underwood and Adnerson, 1994). In this sense, the fouling community in Kanayama Bay seems to undergo succession as evidenced from the dendrogram analysis. First stage, on subsurface panels, was characterized by initial colonizers such as *P. elegans* and *D. foraminosa*. These species were easily overgrown by the encrusting bryozoan, *W. subtorquata*. The continued presence of *D. foraminosa* in the community (Table 1) can be attributed to its regular recruitment (Hirata, 1987) and requirement of minimum space for attachment due to their small size. The *P. elegans* can overcome overgrowth by simply extending their tubes (accretion) in such a way that their feeding ends are always kept clear of an overgrowing species (Osman, 1977). Abundant growth of *W. subtorquata* was the characteristic of the second stage. The colonies of *W. subtorquata* rarely overgrew each other, but exhibited intraspecific competition and extended their growth by attaching the basal portion of the adjacent colonies each other showing flower petal like growth. In the initial phase of third stage, *P. constellatum* began to grow in between *W. subtorquata* under the canopy cover of *B. neritina*. Subsequently, *B. neritina* cover declined so exposing the ascidians to predation by *Ostracion immaculatus. Polyclinum constellatum* is highly susceptible to predation by *O. immaculatus*, a trunk fish that was commonly observed at the present site (Raveendran and Harada, 1996). The effect of predation by fish on fouling communities has also been reported by Sutherland (1974) and Russ, (1980). *Polyclinum constellatum*, because of its massive growth form, often was observed loosely attached on the panels creating the possibility for "slough-off". Similar "slough-offs" in fouling communities have been reported by Boyd (1972); Sutherland and Karlson (1977). Thus, the decrease in abundance of *P. constellatum* may have resulted from the combined effects of "slough-off" and predation. With the appearance of *A. yamazii* towards the end of the third stage, a mixed bryozoan-ascidian community was observed on the panels after one year of submersion.

The community on bottom panels also followed similar trends in succession in the first stage as on subsurface panels. During the second stage and initial phase of third stage both sets of panels had similar species composition, but with different relative abundance. Ultimately they converged to produce almost identical communities. This indicates that the panels at both depths had a similar potential for community development. The observed differences may have been due to a greater predation pressure at bottom depth, as mentioned elsewhere.

Acknowledgements

The authors wish to thank the following taxonomists for their help in identifying: sponges, Dr. Van Soest of the University of Amsterdam, Netherlands; hydroids, Dr. S. Kubota of Kyoto University; bryozoans, Dr. P.S.R. Nair of the Australian Museum, Sydney; polychaetes, Dr. H. Uchida of Kushimoto Marine Park; barnacles, Dr. K. Mori of Kyushu University; bivalves, Dr. K. Torigoe of Hiroshima University and ascidians, Dr. T. Nishikawa of Nagoya University. Thanks are due to Dr. A.C. Anil for his comments on the manuscript and to Mr. K. Okita for his assistance in the field. This investigation may not have been carried out successfully without the support of all the staff of SMBL. The kind co-operation extended by the late Mr. Masaki of the Fishermen's Co-operative of Shirahama is gratefully acknowledged here. The first author (T.V.R.) is grateful to the Director, National Institute of Oceanography and the Government of India for providing this opportunity to study in Japan and to the Ministry of Science and Education, Japan for awarding a scholarship.

Literature Cited

Anderson, M.J. and Underwood, A.J. 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. Journal of experimental Marine Biology and Ecology, 184: 217-236.

Anil, A.C., Chiba, K and Okamoto, K. 1990a. Macrofouling community structure and ecology of barnacles in Hamana Bay (Japan). Biofouling, 2:137-150.

Anil, A.C., Chiba, K., Okamoto, K. and Hirano, R. 1990b. Macrofouling prospects of Lake Hamana, Japan. In: Hirano, R. and Hanyu, T. (eds.) The Second Asian Fisheries Forum, Asian Fisheries Society, Manila, Phillipines, pp. 907-910.

Boyd, M.K. 1972. Fouling community structure and development in Bodega harbour, California. Ph.D thesis, University of California.

Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalists, 111: 1119-1144.

Costlow, J. D. and Tipper, R.C. 1984. Marine Biodeterioration: an Interdisciplinary Study. Naval Institute Press, Annapolis, Maryland, USA.

Drury, W.H. and Nisbet, I.C.T. 1973. Succession. Journal of the Arnold Arboretum, 54: 331-368.

Field, B. 1982. Structural analysis of fouling community development in the Damariscotta River estuary, Maine. Journal of experimental marine Biology and Ecology, 57: 25-33.

Foster, M.S. 1975. Algal succession in a *Macrocystis pyrifera* forest. Marine Biology, 32: 313-329.

Greene, C.H., Schoener, A. and Corets, E. 1983. Succession on marine hard substrata: The adaptive significance of solitary and colonial strategies in temperate fouling communities. Marine Ecology Progress Series, 13: 121-129.

Hirata, T. 1987. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan, II. Succession of invertebrates. Marine Ecology Progress Series, 38: 25-35.

Hirata, T. 1991. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan, IV Temporal changes in metabolism, biomass and maturity of community.

Ecological Research, 6: 347-362.

Horn, H.S. 1966. Measurement of 'overlap' in comparative ecological studies. American Naturalists, 100: 419-424.

Horn, H.S. 1974. The ecology of secondary succession. Annual Review of Ecology and Systematics, 5: 25- 37.

Kawahara, T. 1965. Studies on marine fouling communities III. Seasonal changes in the initial development of test block communities. Report of Faculty of Fisheries, Prefectural University of Mie, 5: 319-364.

Keough, M.J. and Downes, B.J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia, 54: 348-352.

MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography, Princeton University Press, Princeton.

Nandakumar, K. 1995. Competitive interactions among sessile organisms in Tomioka Bay, south Japan: importance of light conditions on the panels surface. Marine Biology, 121: 713-719.

Odum, E.P. 1969. The strategy of ecosystem development. Science, 164: 262-270.

Okamura, B. 1986. Formation and disruption of aggregations of *Mytilus edulis* in the fouling community of San Francisco Bay, California. Marine Ecology Progress Series, 30: 275-282.

Osman, R.W. 1975. The establishment, development and maintenance of a marine epifaunal community in Woods Hole, Massachusetts. Doctoral dissertation, University of Chicago, Illinois, USA.

Osman, R.W. 1977. The establishment and development of a marine epifaunal community. Ecological Monograph, 47: 37-63.

Raveendran, T.V. and Harada, E. 1996. Intense predation on ascidians by a trunk fish, *Ostracion immaculatus* (Temminck et Schlegel) (Pisces: Ostraciidae). Publication of the Seto Marine Biological Laboratory, 37: 193-200.

Russ, G.R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. Journal of experimental Marine Biology and Ecology, 42: 55-69.

Russ, G.R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. Oecologia, 53: 12-19.

Sutherland, J.P. 1974. Multiple stable points in natural communities. American Naturalists, 108: 859-873.

Sutherland, J.P. and Karlson, R. H. 1973. Succession and seasonal progression in the fouling community at Beaufort, North Carolina. In: 3rd International congress on marine corrosion and fouling. Northwestern University Press, Illinois, USA, pp. 906-929.

Sutherland, J.P. and Karlson, R.H. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecological Monograph, 47: 425-446.

Underwood, A.J. and Anderson, M.J. 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. Journal of Marine Biological Association of U. K., 74: 563-584.

Woods Hole Oceanographic Institution 1952. Marine Fouling and its Prevention, 388 pp., George Banta Publishing, Wisconsin.

Zvyagintsev, A.Y. and Ivin, V.V. 1995. Study of the biofouling of the submerged structural surfaces of offshore oil and gas production platforms. Marine Technological Society Journal, 29: 59-62.