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Response of macrobenthic community to seasonal sediment environmental parameter changes in a tidal estuary of the Seto Inland Sea, Japan

Nittaya CHAIYANATE* and Shigeru MONTANI*†

Abstract : Changes in macrobenthic communities were studied in a tidal estuary of the Seto Inland Sea, Japan from November 1998 to February 2000 at eight stations. Selected chemical components in sediments and the abundance and biomass of five dominant macrobenthos species were determined. High abundance of species indicative in unstable bottom, such as the bivalve *Theora fragilis* and the polychaete *Lumbrineris* were recorded. Moreover, stations nearest the facility have continuous input of organic matter, and gross structure changes in the macrobenthic communities (e.g. reduced specific richness, diversity, and dominance of opportunistic species *Capitella* sp.I). And changes in seasonal pattern of macrobenthic communities were observed. The community structural changes were analyzed by means of univariate and multivariate techniques.

Key words : *Macrobenthic community, total organic carbon (TOC), Acid Volatile Sulfide (AVS), Seto Inland Sea, univariate measures, cluster analysis, Abundance Biomass Comparison (ABC) plot*

1. Introduction

Estuaries are the major conduits between land and sea, through which the flow of large amount of soluble and particulate materials derived from the nearby area of each estuary. These loads deposited to the benthos and changes in benthic environments characteristically. Dissolved oxygen is rapidly depleted and aerobic respiration is limited to a narrow zone at the surface of non-bioturbated sediments. The activity of heterotrophic organisms maintains reducing conditions below a thin oxidized surface layer in most coastal sediments. The stratification provides the basis for bacterial sulfate reduction in the deeper anoxic sediment where sulfate is reduced to toxic sulfide. Sulfide results from inhibition of the electron transport chain in aerobic respiration may be important for the distribution and density variations of benthic organisms. In organically polluted sediments are generally assumed to be characterized by macrofauna with small

body sizes and infauna living at or near the sediment-water interface (WESTON 1990; MIRON and KRISTENSEN 1993; DRAKE and ARIAS 1997; Marvin-DiPasquale and Capone 1998; Trimmer *et al.* 2000).

Tidal estuary in front Yashima mount at Takamatsu, Japan is now surrounded by densely populated urban residential neighborhoods, quay, industries and river runoff from Tsumeta, Kasuga and Shin rivers which carry huge amount of particle matters. And several large sewage effluents also plus street runoff and combined sewer overflows continuing major impacts. It has been a progressive increase of opportunistic green macroalgae *Ulva* sp. on the intertidal flat where is near by the present study sampling site. In this areas MAGNI and MONTANI (1998) found that *Ulva* sp. shown recurrent seasonal patterns, growing heavily in spring and summer and decomposing in late summer to early autumn. Consequently, strong increase in biomass of bivalves *Ruditapes philippinarum* and *Musculista senhousia* indicated a highly production during spring-summer. After the decomposition of high amounts of the macroalgae, a massive

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mortality of the bivalve *R. philippinarum* on the intertidal flat and a drastic reduction of the macrobenthic biomass on an adjacent subtidal station were observed. In this context, the aim of this research was to detect and follow the changes in the macrobenthic communities. We report on patterns of macrobenthic communities' structure and diversity related to sediment characteristic.

2. Materials and methods

We divided the sampling site into three transect lines for 8 sampling stations. First three sampling stations were set on the tidal flat area (Stns. 1, 2 and 3), next other three sampling stations (Stns. 4, 5, 6 and 7), on quay area and one sampling station (Stn. 8) which was placed in the seagrass area and beside domestic communities. For transaction classify, the study area was considered to two areas from the shore as intertidal area (Stn. 4), and subtidal area which component with the inner stations (Stns. 2, 3, 5 and 6) and outer stations (Stns. 1, 7 and 8) (Fig. 1). Sampling of the benthic environment at a tidal estuary was conducted every three months at 8 stations from November 19, 1998 to February 7, 2000. At each station, vertical profiles of temperature and dissolved oxygen (DO) were measured at intervals of 1 m in depth with a STDDO (Alec, Model ADO 1050-D) and sediment samples were obtained by two 4-cm diameter gravity core samplers for chemical analysis. The surface layer of the sediment sample up to 2 cm in depth from each gravity core was determined the Acid Volatile Sulfide (AVS) level of the sediment with an AVS test column (Gastec, Hedorotec 201H and 201L) and the total organic carbon (TOC) level of the sediment with a CHN analyzer (Yanaco, MT-500). One sediment grab for particle size distribution study by re-suspending sediment in pure ionexchanged water and wet sieving through a range of stainless steel meshes (2000, 1000, 500, 250, 125 and 63 μ m pore sizes). Each fraction was collected, re-dried and re-weighed. Particle size was expressed as a percentage of the total dry weight.

Benthic samples were collected two grab samples with 0.04m⁻² Eckman-Birge grab sam-

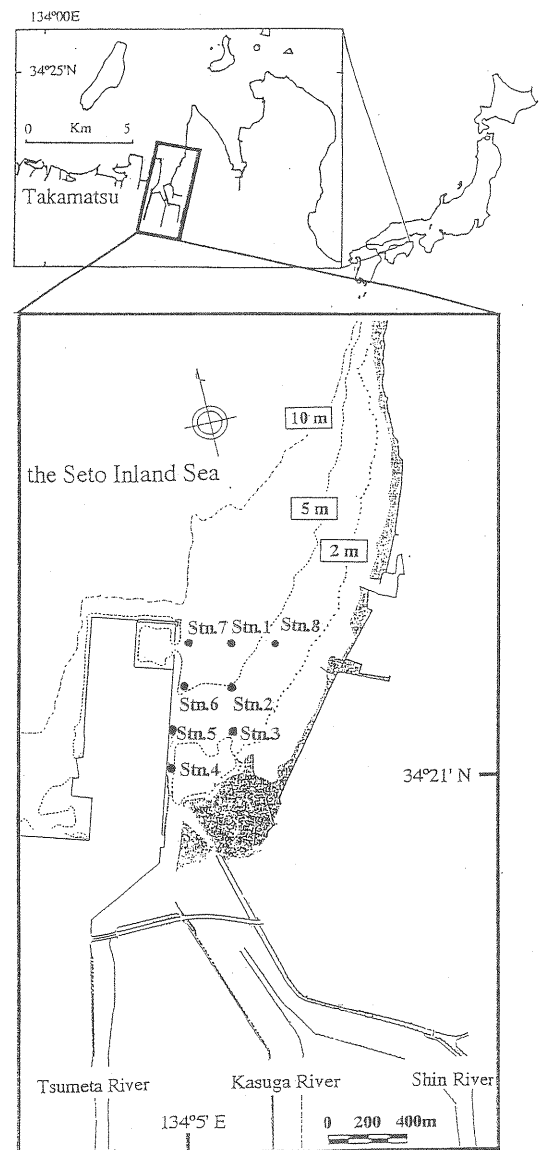


Fig. 1. Map of the study site in tidal estuary of the Seto Inland Sea.

pler. Samples were screened through a 1.0-mm mesh sieve to separate macrofauna animals from sediments. After screening, organisms were sorted under a dissecting microscope, identified to the lowest possible taxonomic levels, counted and weighed.

Several traditional univariate measures (abundance, biomass, specific richness, evenness (J') and diversity (H') indices) were

employed in the analysis of the community structure. And using a multivariate ordination technique, the Bray Curtis similarity index coefficient for double square root transformed species abundance data. Multivariate patterns of assemblages were visualized using metric multidimensional scaling plots (MDS). The identified assemblages were tested by the ABC (abundance, biomass comparison) method to judge the degree of environmental disturbance (CLARKE and WARWICK, 1994).

3. Results

Spatial patterns of macrobenthos and environmental factors

Table 1 showed the summary of the particle

size distribution at each sampling station. The bottom have moderately sorted fine median particles with high percentage of silt clay at Stns. 1, 2, 3, 5 and 6 (73, 61, 76, 81 and 76 %, respectively) but there was high percentage of sand at Stn. 4 (77%) and about 50 to 60 percent sand at Stns. 7 and 8. Because of sampling stations were situated in shallow waters. Therefore water column showed vertical well mixed throughout the water depth at all sampling stations. Thus mean temperature, salinity and dissolved oxygen values for each seasonal sampling at the sampling site are shown in Fig. 2. During the study period, the pattern of temperature was increased from $18 \pm 0.14^\circ\text{C}$ in May 1999 to $27 \pm 0.06^\circ\text{C}$ in August 1999 and de-

Table 1. Average of particle size distribution in eight sampling stations at tidal estuary of the Seto Inland Sea (expression in percentage)

Size class ^a	Station							
	1	2	3	4	5	6	7	8
Silt/clays	73.03	60.72	75.97	23.23	81.22	75.54	44.79	39.54
Very fine sands	15.13	10.27	8.25	26.62	13.12	11.52	13.89	42.71
Fine sands	7.74	6.37	5.62	20.59	4.82	7.51	7.03	5.09
Medium sands	3.49	1.56	3.76	22.95	0.84	3.84	13.4	3.51
Course sands	0.61	2.54	6.4	6.61	-	1.59	20.89	9.15

^a Wentworth classification (Mudroch and Bourbonniere, 1991) : median sands, 500 to 250 μm ; 250 to 125 μm ; very fine sands, 125 to 63 μm ; silt/clay, < 63 μm .

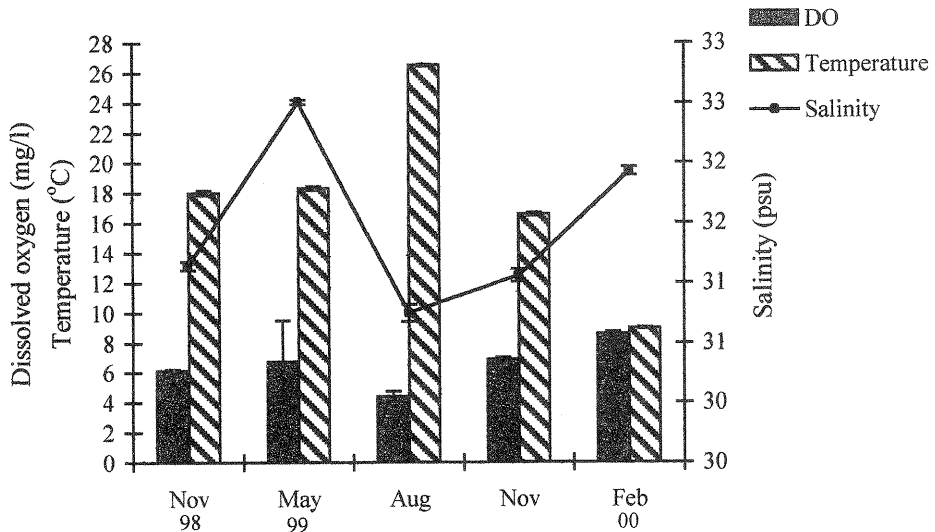


Fig. 2. Mean values of temperature(°C), salinity (psu) and dissolved oxygen (mg/l) of bottom waters at the sampling sites.

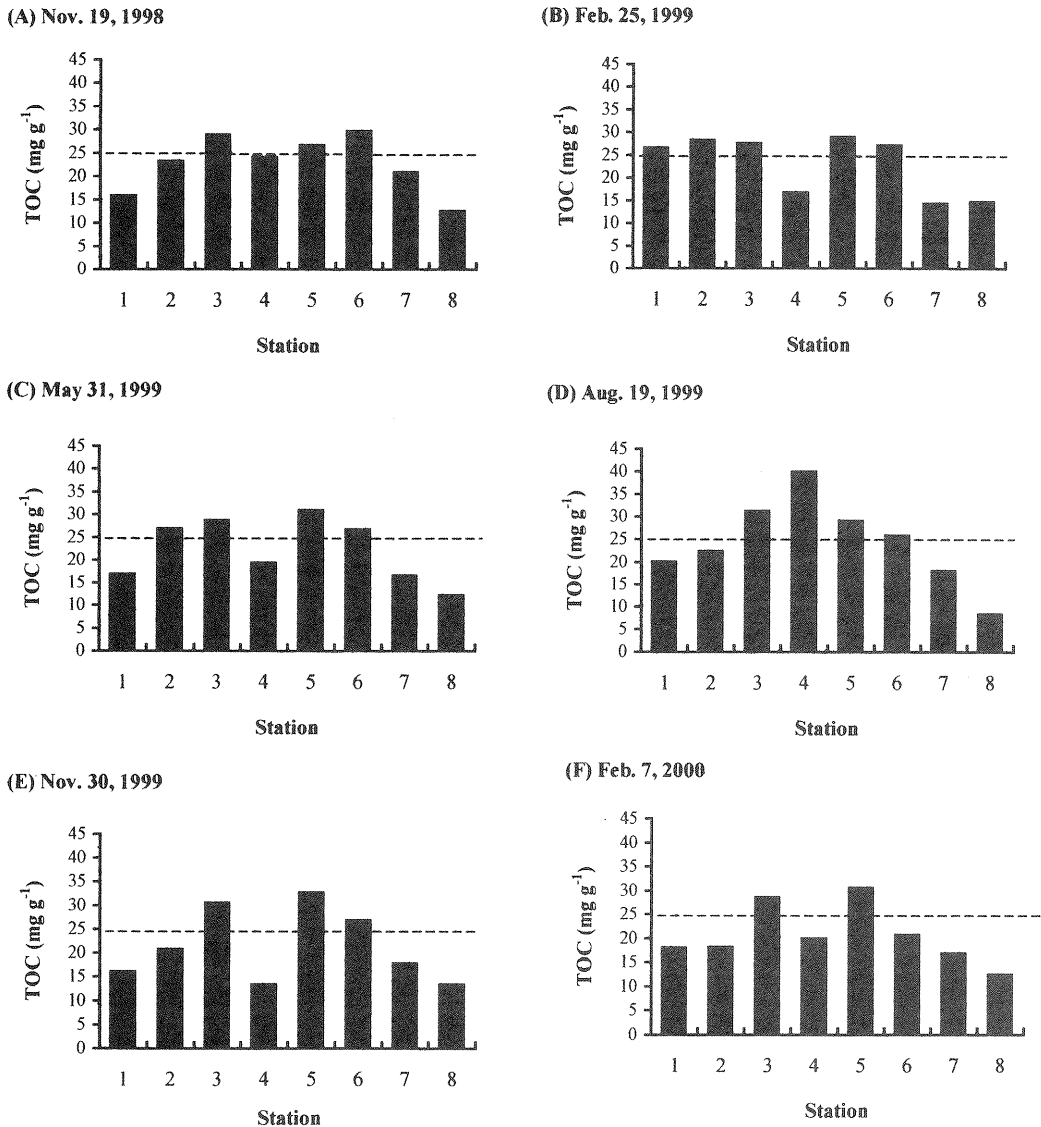


Fig. 3. Seasonal fluctuation in sediment TOC level at eight sampling stations in the tidal estuary.

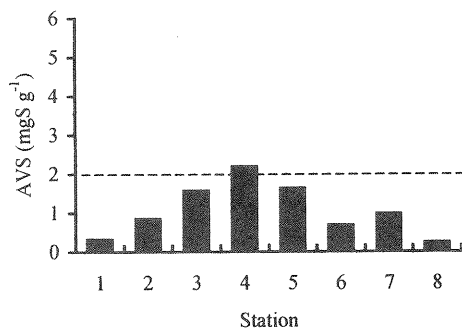
creased to the lowest ($9 \pm 0.04^\circ\text{C}$) in February 2000. Salinity ranged between 30 ± 0.07 and 33 ± 0.02 psu while dissolved oxygen was saturated or oversaturated within a range 4 ± 0.34 to 8.5 ± 0.15 mg l^{-1} .

The surface layer sediment TOC levels at all sampling stations were shown in Fig. 3. Station 3 and 5 showed stability of sediment TOC levels throughout sampling period. While sediment TOC levels at Stn. 4 was evidently increase from 20 mg g^{-1} in May 1999 to 40 mg g^{-1} in April 1999 and decrease drastically in November 1999 (14 mg g^{-1}). The remaining stations slightly fluctuated in sediment TOC levels.

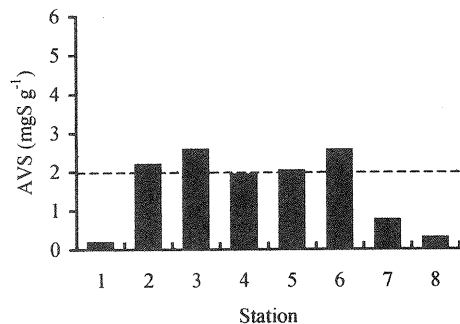
There was a fluctuation of surface layer sediment AVS levels at sampling site also. At Stns. 2, 3, 4, 5, and 6 sediment AVS levels ranged between 2 to 2.5 mg g^{-1} in February 1999 and slightly decreased within range 0.7 to 1.7 mg g^{-1} in May 1999 (Fig. 4). As sediment TOC levels, sediment AVS levels at Stn. 4 was rapidly

decrease drastically in November 1999 (14 mg g^{-1}). The remaining stations slightly fluctuated in sediment TOC levels.

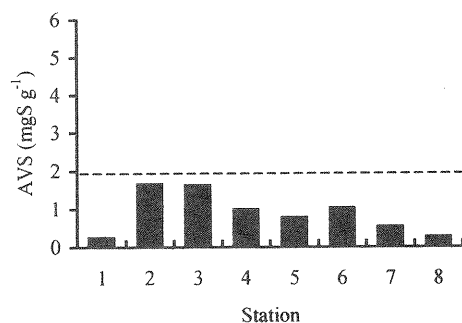
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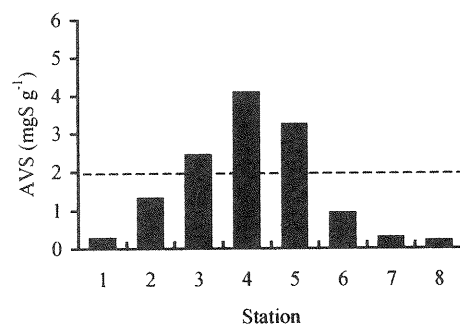
(B) Feb. 25, 1999



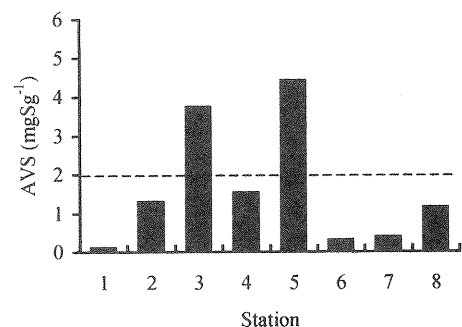
(C) May 31, 1999



(D) Aug. 19, 1999



(E) Nov. 30, 1999



(F) Feb. 7, 2000

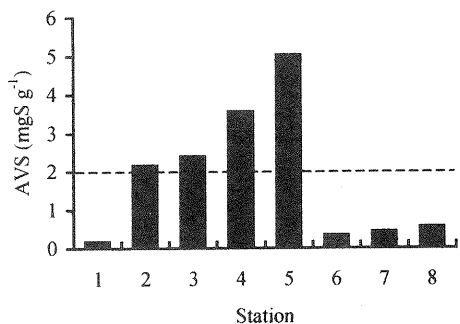


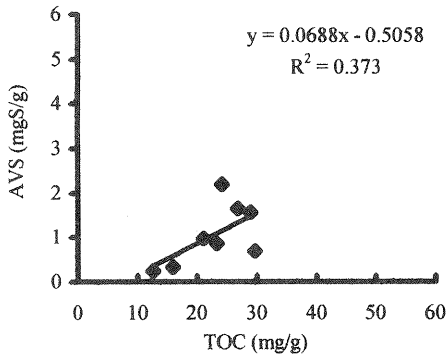
Fig. 4. Seasonal fluctuation in sediment AVS level at eight sampling stations in the tidal estuary.

increase from May to August 1999 (1 mg g^{-1} to 4 mg g^{-1}) and decrease to 1.7 mg g^{-1} in November 1999. While continued develop of sediment AVS level to high value was occurred at Stn. 3 (1.7 to 3.6 mg g^{-1}), from May to November 1999 before it decreased in February 2000. However, sediment AVS level was continued developing and reach to the highest value in February 2000 at Stn. 5 (0.8 to 5 mg g^{-1}). The low

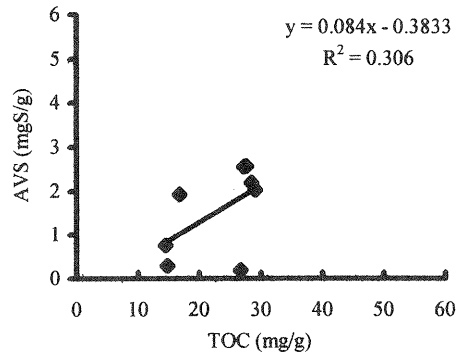
sediment AVS levels were occurred at Stns. 1 and 8 (Fig. 4). There was positive relationship between sediment TOC and AVS level only Stn. 4 ($r = 0.73$, data not shown). But significant increased in sediment AVS levels with sediment TOC levels were found in seasonal sampling (Fig. 5).

The high number of individuals was recorded in February 1999 and 2000 (47,303 and

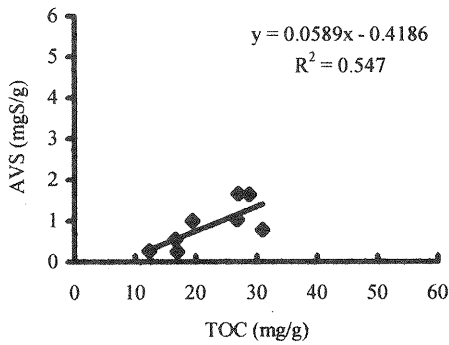
(A) Nov. 19, 1998



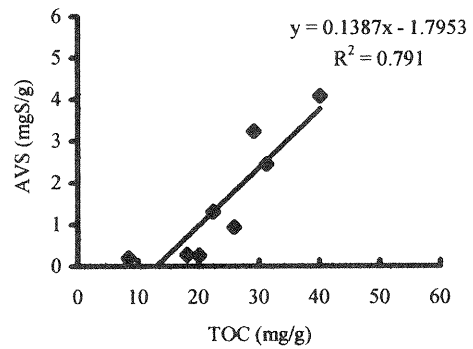
(B) Feb. 25, 1999



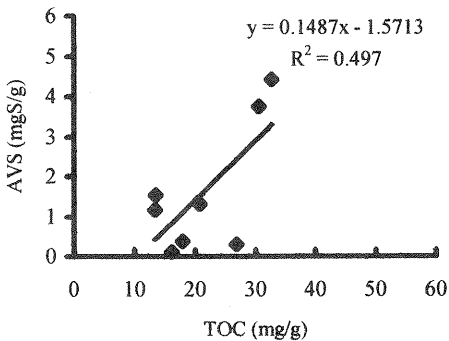
(C) May 31, 1999



(D) Aug. 19, 1999



(E) Nov. 30, 1999



(F) Feb. 7, 2000

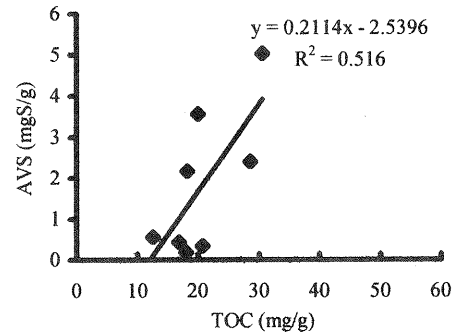


Fig. 5. Relationship between seasonal sediment TOC and AVS levels.

55,889 ind m^{-2}) while biomass was obtained in August and November 1999 (865 and 701 gWW m^{-2} , approximately 80% of which was *M. senhousia*). The polychaetes, *Capitella* sp. I, *Pseudopolydora kempfi* and *Rhynchospio* sp., occurred dominantly with numbers in February

1999 and 2000. Changes in community structure throughout the whole period of study are shown in Figs. 7 and 8. The total number of species ranged over the stations from 3 to 25 ($3 \leq S \leq 25$). Evenness (J') and diversity (H') showed a similar pattern throughout the study period.

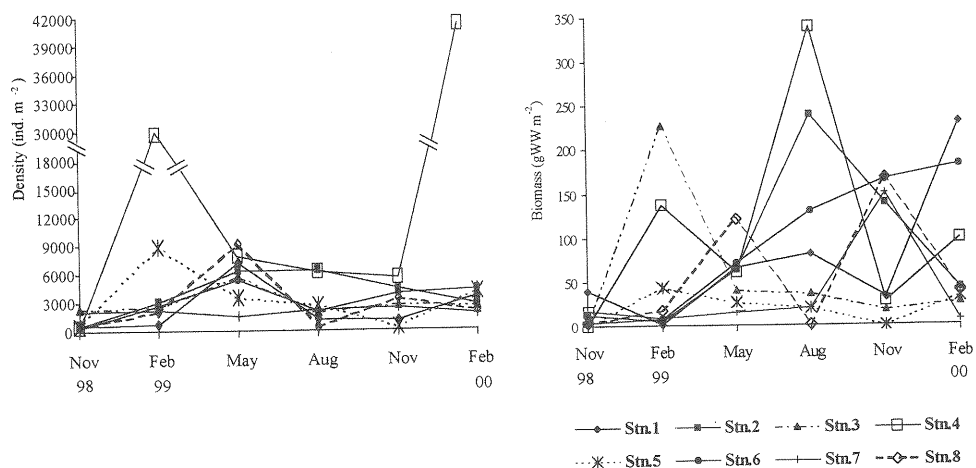


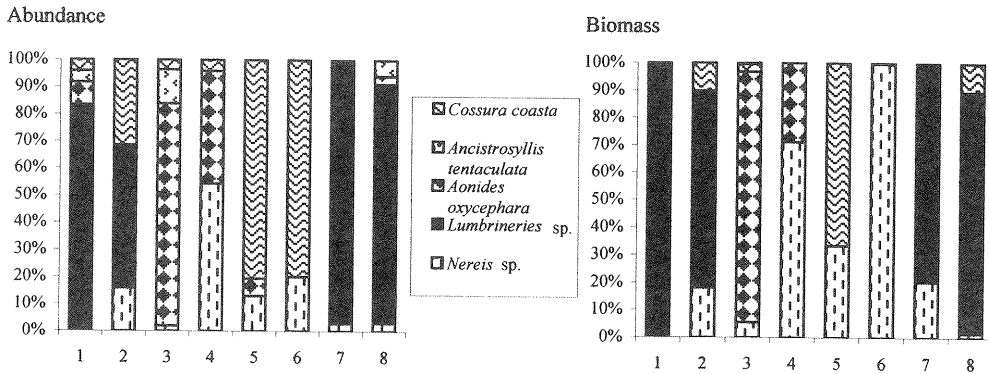
Fig. 6. Seasonal fluctuations in density (ind./m²) and biomass (gWW/m²) at eight sampling stations in the tidal estuary.

The range of evenness over all sampling stations was from 0.23 to 0.9 ($0.23 \leq J' \leq 0.9$) and diversity was from 0.68 to 3.93 ($0.68 \leq H' \leq 3.93$). Seasonal fluctuation in the species diversity indices reflected the recovering and subsequent degenerating processes of the macrofauna. During the earliest stage in the faunal recovery, diversity (H') was low at Stns. 3, 4 and 5 (Fig. 8) due to the occurrence of only a few pioneer species and the dominant of *Capitella* sp. I in November 1999 (Stns. 3 and 5), February 1999 (Stn. 5) and February 1999 and 2000 (Stn. 4). Which accounted for 90 and 95% in February 1999 (Stn. 4 and 5, respectively), 95 and 99% in November 1999 (Stns. 3 and 5, respectively) and 40% and 65% in February 2000 (Stns. 4 and 5, respectively) of the abundance. As subsequent species recruited, the specific richness increased with the dominance by single species reduced, increases of the evenness (J') occurred in May and August 1999 (Fig. 9).

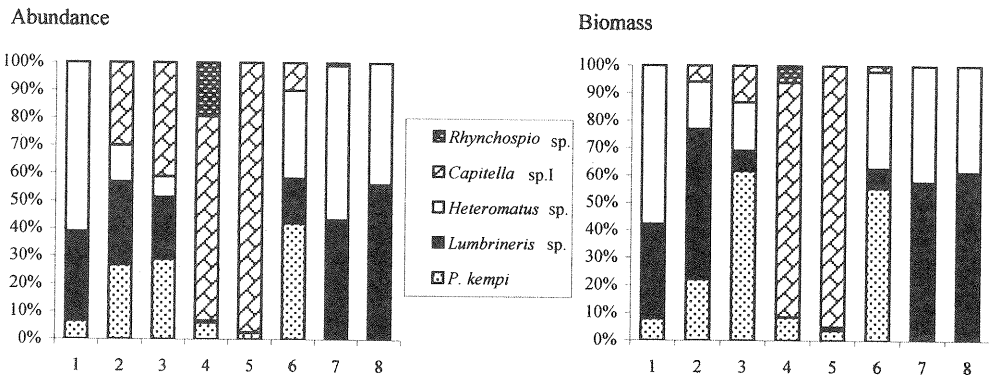
Consequently, a change of dominant species was occurred in May 1999 (Fig. 8). During this changes the bivalves *Theora fragilis* (Stns. 3, 5 and 6) and *M. senhausia* (Stns. 1, 2 and 8) and the polychaete *Lumbrineris* sp. (Stns. 2, 3, 6, 7 and 8) became to main composition of abundance species and play up to increase of biomass values. *Capitella* sp. I was decreased at Stns. 4 and 5 in both number and biomass. In August 1999, *M. senhausia* was dominated at

Stns. 1, 2, 4 and 6 (90, 80, 35 and 75 %, respectively) and showed the highest biomass values (99, 95, 90 and 95%, respectively). In this sampling month, the beginning of sediment AVS accumulation was appeared at Stns. 3 and 5. *Lumbrineris* sp. (43% at Stn. 3), *Cossura coasta* (75% at Stn. 5) and *T. fragilis* (33 and 20 % at Stns. 3 and 5, respectively) were dominated in abundance, only *T. fragilis* (63 and 80% at Stns. 3 and 5, respectively) was played on biomass dominator. When sediment AVS level was decreased in November 1999 at Stn. 4, *Heteromatus* sp. and *Rhynchospio* sp. became dominator (70 and 10%, respectively) and small number of *Capitella* sp. I was observed. Presented with *Heteromatus* sp. were *Lumbrineris* sp. and *M. senhausia* at Stns. 1, 2, 6, 7 and 8 where *M. senhausia* was biomass dominator. While *Capitella* sp. I dominated at Stns. 3 and 5 more than 90% of abundance and biomass and associated with reduced of diversity (H'), evenness (J') and specific richness. Due to sediment AVS levels kept relatively high values at these stations. As February 1999, *Capitella* sp. I increased in number to the highest values at Stn. 4 (from 10% to 40%) and dominated at Stn. 5 (65%). When the rapidly increased of sediment AVS level occurred at Stn. 4 and increased to the highest value at Stn. 5. Two polychaetes, *P. kempfi* and *Rhynchospio* sp., presented in large number with *Capitella*

(A) November 19, 1998



(B) February 25, 1999



(C) May 31, 1999

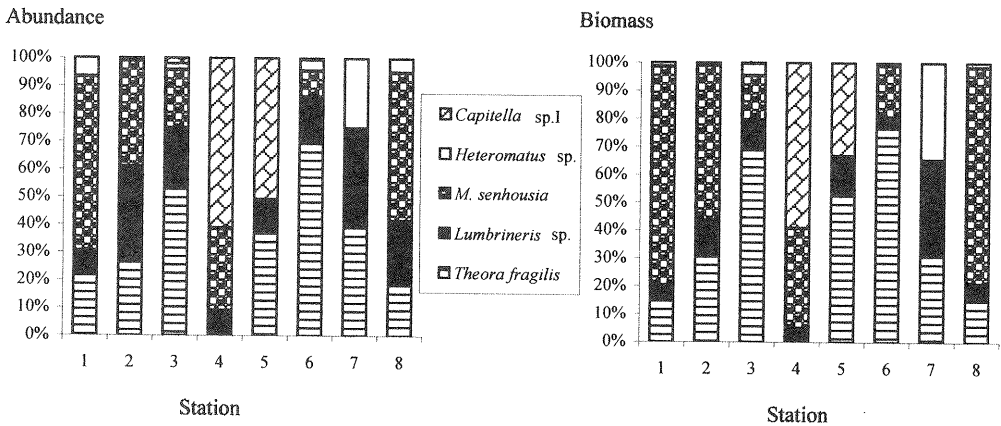
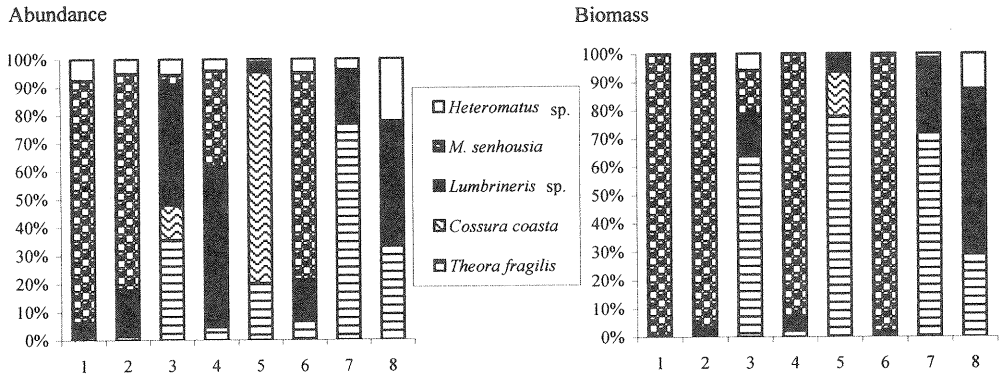
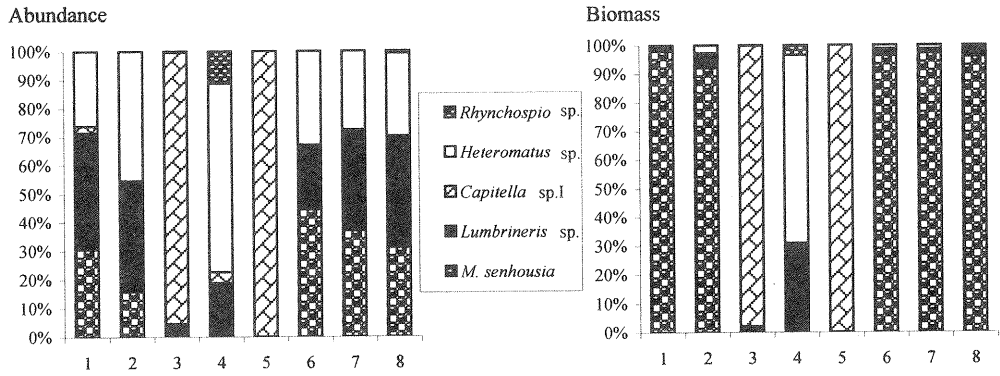


Fig. 7. Percent composition of abundance and biomass of five dominant macrobenthic animal species at the eight stations. (A) on November 19, 1998, (B) on February 25, 1999, (C) on May 31, 1999.

(D) August 19, 1999



(E) November 30, 1999



(F) February 7, 2000

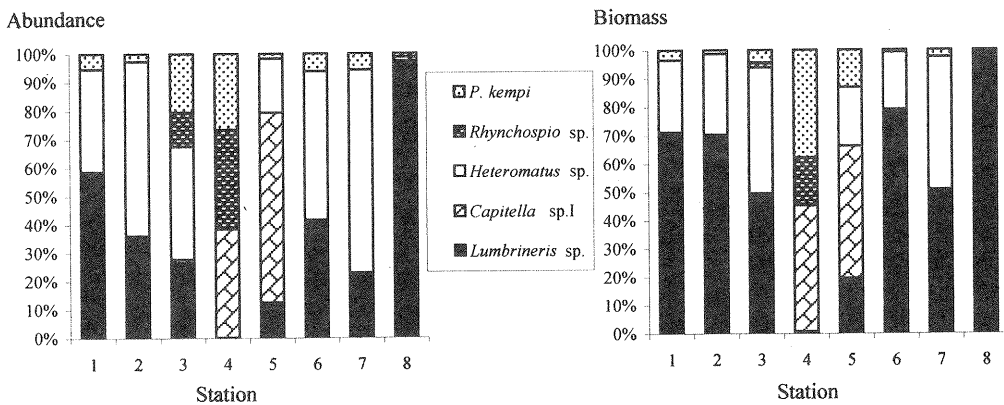


Fig. 7 (continued). Percent composition of abundance and biomass of 5 dominant macrobenthic animal species at the eight stations. (D) on August 19, 1999, (E) on November 30, 1999, (F) on February 7, 2000.

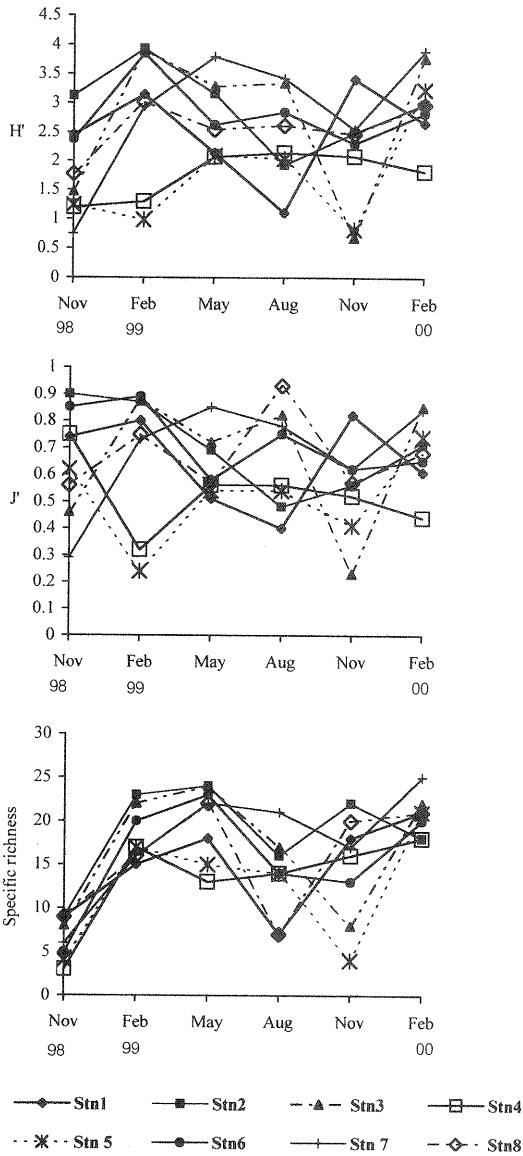


Fig. 8. Seasonal fluctuations in specific richness, evenness (J'), and diversity (H') at eight sampling stations in the tidal estuary.

sp. I at Stn. 4 and small number at Stn. 3. Specific richness, diversity (H') and evenness (J') increased at Stns. 3 and 5 (Fig. 8). While other two polychaetes, *Heteromatus* sp. and *Lumbrineris* sp. were dominated in number and biomass at other stations in February 2000 (Fig. 7).

Abundance-Biomass Comparison

Figure 9 shows the classification analysis for species abundance, the dendrogram for the samples were divided into four distinct clusters, lettered A through D, which were considered to represent different communities on the basis of their geometric means. The first cluster includes 4 stations (2, 3, 6 and 7) in the subtidal zone (quay and tidal flat transect). The most abundance species found at these stations were two polychaetes (*Lumbrinereis* sp. and *Heteromatus* sp.) and two bivalves (*M. senhousia* and *T. fragilis*). The second cluster had 2 stations at the outer stations in subtidal zone (Stns. 1 and 8) and characterized by the most abundant four species as same as those in the first two clusters but recognized the difference in density. The third and fourth clusters were Stns. 5 and 4 where opportunistic polychaetes like *Capitella* sp. I, *P. kempfi* and *Rhynchospio* sp. were dominated in autumn and reached to the peak in winter (Figs. 6 and 7). MDS model exhibited the similar patterns described previously, with the stations-points of the four clusters. According to criteria proposed by WARWICK (1986) for detecting the severity of disturbance in the macrobenthic community. Then the response of four major macrobenthic assemblages to environmental disturbance was tested by the ABC method (Fig. 10). Species are ranked in order of dominance on the abscissa (logarithmic scale), and cumulative percentage composition is plotted on the ordinate. The assemblage "A" showed the undisturbed condition with the biomass curve above the abundance curve of its length. While contrary position of the two curves in assemblages "C" indicates grossly state of disturbance, respectively. Under moderate disturbance, the 2 curves will tend to be superimposed, often crossing one another in assemblages "B" and "D".

4. Discussion

The discharged loads in the watershed and the run-off loads are the loads that actually reach the Seto Inland Sea through rivers and gutters (OKAICHI and YANAGI, 1997). The determinants of community composition and abundance were related to natural features in the

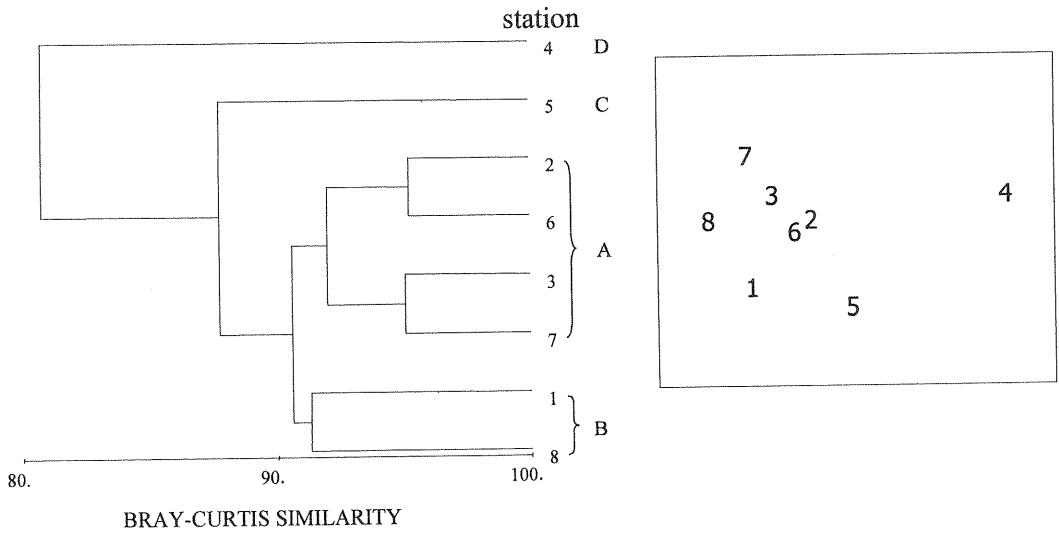


Fig. 9. Cluster analysis of the macrobenthos assemblage similarity in tidal estuary. And two-dimensional non-metric multi-dimension scaling plot of stations based on similarity matrix abundance; Stress=0.05. Dendrogram showing similarity between the stations, division of estuary into zones A-D.

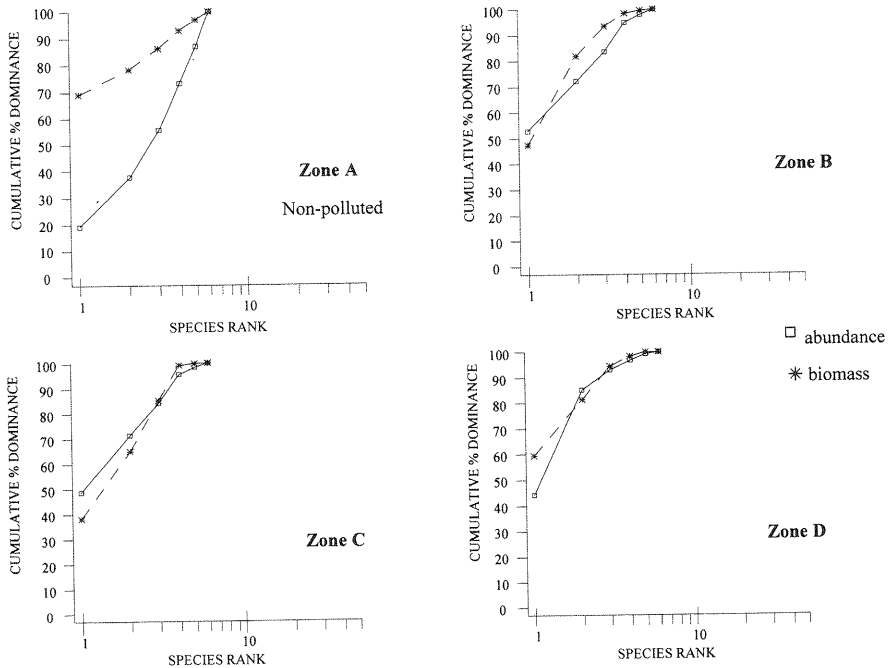


Fig. 10. Combined k-dominance curve for species biomass (crosses and dashed lines) and abundance (squares and continuous lines) in four zone in tidal estuary.

study area and sediment characteristics. Alteration of sediment chemistry as a result of organic enrichment was evidently only at Stn. 4. Because this station was placed in intertidal area where *Ulva* sp., from adjacent tidal flat, grows heavily in spring and summer and decompose from late summer to early autumn. Therefore sediment AVS level was highly related to sediment TOC level. In *Palude della Rosa*, Italy, the accrual phase of *Ulva rigida* was followed, in summer, by a massive decline of the algae biomass (TAGLIAPIETRA *et al.*, 1998). When macroalgal vegetation broke down completely, the decomposition of huge amounts of organic matter resulting in prolonged hypoxia and anoxia, and release of hydrogen sulfide. As a consequence of the massive degradation of *Ulva* which occurred during summer, macroalgae did not accumulate in *Palude della Rosa* in autumn.

Although sediment TOC levels were not the highest at Stns. 3 and 5, they still kept high through sampling periods. When the low temperature occurred in winter, the rapid development of sediment AVS was present at these stations. Apart from the supply of nutrients and factors that control the bioavailability of organic compounds, the chief abiotic factors influencing microbial transformations are temperature, pH, and salinity. An organic pollutant is quickly destroyed in one environment will persist at another one if these factors preclude or retard microbial activity. The prevailing temperature is of paramount importance. When organic compound exists near the surface of soil or water and at the same time immediately preceding and following the winter are typically associated with little or no biodegradation of many organic substrates. Changes in rate of degradation associated with the season are a consequence of the concomitant changes in temperature (ALEXANDER, 1994). KALEJTA and HOCKEY (1991) found the correlation between temperature and production suggested that a lack of extreme temperatures, especially cold temperatures might prolong reproduction of invertebrates and a continuous supply of food for their maintenance at Berg River Estuary, South Africa.

When the beginning of hydrogen sulfide

releasing was observed from August to February 1999, the macrobenthic communities are dominated by *Capitella* sp.I at Stns. 4 and 5 and occurred at Stn 3. Associated with the appearance of species recruited (as is *Capitella* sp.I in my study), the specific richness and diversity (H') decreased and evenness (J') increased. Decrease in diversity is a primary indicator of community response to organic gradients or stresses (PEARSON and ROSENBERG, 1978). Reduce in density of a single dominant species occurred as the changes in macrobenthic composition.

The density of *Capitella* sp.I decreased drastically before the beginning of the environmental deterioration. The observed decline in the *Capitella* sp.I population may be caused by a food shortage, if organic rich sediment containing available food is indispensable for maintaining a large population of *Capitella* sp. I, and if this food supply has already been consumed during high density phase of this species. Present in large number with *Capitella* sp.I were two polychaetes *P. kemberi* and *Rhynchospio* sp.. *P. paucibranchiata* is the second species to re-populate at nutrient-rich particles in the form of unconsumed food particles (YOKOYAMA *et al.*, 1997). Usually peak of abundance in *Capitella* sp. I, *P. kemberi* and *Rhynchospio* sp. occurred in February 1999 and 2000 at Stn. 4 and November 1999 at Stns. 3 and 5. The maximum density values of *Capitella* sp. I (31,000 individuals/m²) was observed at Stn. 4.

At other stations, there were no clear trends in any of the density, biomass, diversity (H') and specific richness. *Heteromatus* sp., *T. fragilis* and *Lumbrineris* sp. were dominant in these stations, and presented throughout the year. *Lumbrineris* and *Heteromatus* are considered as indicator of environmental instability and immaturity such as in early succession stage communities (CREMA *et al.*, 1991; SIMBOURA *et al.*, 1995).

The ABC technique developed the results inconsistent with many of the other biological indices. It was used successfully to identify the areas disturbed by organic enrichment (WARWICK, 1986; AUSTEN *et al.*, 1989; DELVALLS *et al.*, 1998). The ABC method indicated that

only Stn. 5 was grossly disturbed while Stn. 4 and Stns. 1 and 8 were moderately disturbed and Stns. 2, 3, 6 and 7 were undisturbed areas. Stn. 5 was the most organically polluted station, as the most affected one from tidal export from the inner part of the estuary. From the bathymetry of location, Stn. 5 was the deepest. Where the high accumulation of organic matter seasonally enhanced the process of anaerobic decomposition dissolved oxygen concentration depletion and supports the sediment AVS development. Indeed Stn. 4 should be grossly disturbed area as Stn. 5 because the numerical dominance of a single species (*Capitella* sp. I) clearly indicated the area to be typical of gross enrichment. However, Stn. 4 as located in creek where receive running freshwater and particles from rivers. Most of big size particles precipitated at this station. That made bottom sediment particle character was highly percent in sand fraction, which was appropriated for filter feeder as *M. senhousia* (the major biomass contributor). Stns. 1 and 8 showed abundance curve lies above biomass curve at the beginning and change to the opposite pattern. Indicated that inequality in size between the numerical and biomass dominants is reduced and adjusts to stable condition. In consideration of Stns. 1 and 8 location, they was outermost station and surround with seagrass boundary (Stn. 8) which act as sediment trap. Therefore the contents of total organic and AVS in the sediments are much lower. The results of limited food resource at these stations were low macrobenthic density and biomass. ABC curves of Stns. 2, 3, 6 and 7 clearly correspond to stable unpolluted condition. These stations were located in an intermediate zone and better position to sustain a large biomass of the bivalve *M. senhousia*, as food supply was still abundant but not extreme. DRAKE and ARIAS (1997) suggested that the ABC method would lead to an over- or underestimation of disturbance state of the community in short term studies. And the ABC plots are a very good approach for evaluating the organic enrichment (WESTON, 1990; DELVALLS *et al.*, 1998).

In this study, the results show seasonal changes of macrobenthic community fluctua-

tion. They corresponded with the summary of benthic effects for hypoxic systems around the world by DIAZ and ROSENBERG (1995). Which the system levels responding to hypoxia of the Seto Inland Sea were indicated as seasonal hypoxia type, moderate hypoxia level, mortality of response of benthic communities and annual benthic recovery.

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The distribution of picophytoplankton across Kuroshio Current off the Western Pacific Coast of Japan

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Abstract : The distribution of picophytoplankton ($<3\ \mu\text{m}$) across the Kuroshio Current off the Pacific coast of Japan was studied using epifluorescence microscopy. Three groups of picophytoplankton were delineated: *Synechococcus*, *Prochlorococcus* and eukaryotic picophytoplankton. The two prokaryotic picoplankton, *Synechococcus* and *Prochlorococcus*, had a differential pattern as their distribution. The former was dominant in the main body of the Kuroshio Current, while the latter was dominant on the south side of the Kuroshio seaward boundary. The factors that contributed most to their distribution patterns were suggested to be temperature and nutrient levels within the mixed layer. Maximum concentrations of eukaryotic picophytoplankton were found at the depths of the subsurface chlorophyll maximum. *Synechococcus* occurred abundantly in the surface mixed layer of Kuroshio water when nutrients were supplied by frontal eddy pumping or autumn deepening of mixed layer. *Prochlorococcus* (low-light adapted type) distribution was limited in the subsurface depths with higher temperature than 20°C.

1. Introduction

The discovery of the dominance of pico-sized (0.2–2 μm) oxygenic photosynthetic phytoplankton in oligotrophic regions led to a general reconsideration of the structure of marine ecosystems (e.g. Li *et al.*, 1983). The picophytoplankton that tend to dominate these oligotrophic regions are generally known to be prokaryotic genera belonging to *Synechococcus* (JOHNSON and SIEBURTH, 1979; WATERBURY *et al.*, 1979) and *Prochlorococcus* (CHISHOLM *et al.*, 1988). In contrast, the eukaryotic picophytoplankton is much more diverse and evidently composed of organisms that belong to several algal divisions (e.g. SMITH and HOBSON, 1994), including Bolidophyceae (GUILLOU *et al.*, 1999) and Pelagophyceae (ANDERSON *et al.*, 1993) in Chromophyta, and Pedinophyceae (MOESTRUP, 1991) and Prasinophyceae (e.g. EIKREM and THRONDSSEN, 1990; CHERÉTIENNOT-DINET *et al.*, 1995) in Chlorophyta.

Since the study of FURUYA and MARUMO

(1983), there have been many studies aimed at assessing the relative abundance and species composition of the smaller phytoplankton size classes off Japan in the North Pacific. TAKAHASHI *et al.* (1985) found that picophytoplankton distributed anywhere from 20 to 100% of the total chlorophyll *a* (Chl *a*) biomass, off the Sanriku coast of Japan. ODATE *et al.* (1990) compared the distribution of picocyanobacteria and other picophytoplankton along 155°E meridian by epifluorescence microscopy. Shimada *et al.* (1995a) found that picophytoplankton accounted for about 25% of the total Chl *a* biomass in Suruga Bay and measured *Prochlorococcus* abundance of 2.5×10^4 cells ml^{-1} by flow cytometry.

The Pacific coast of Japan is highly influenced by the northward flowing Kuroshio Current. Because the Kuroshio Current is the border between two fairly diverse water masses: eutrophic coastal and oligotrophic offshore waters, it is expected that the phytoplankton composition should also change across the current. This change in the phytoplankton community composition should be most notable in the picophytoplankton size

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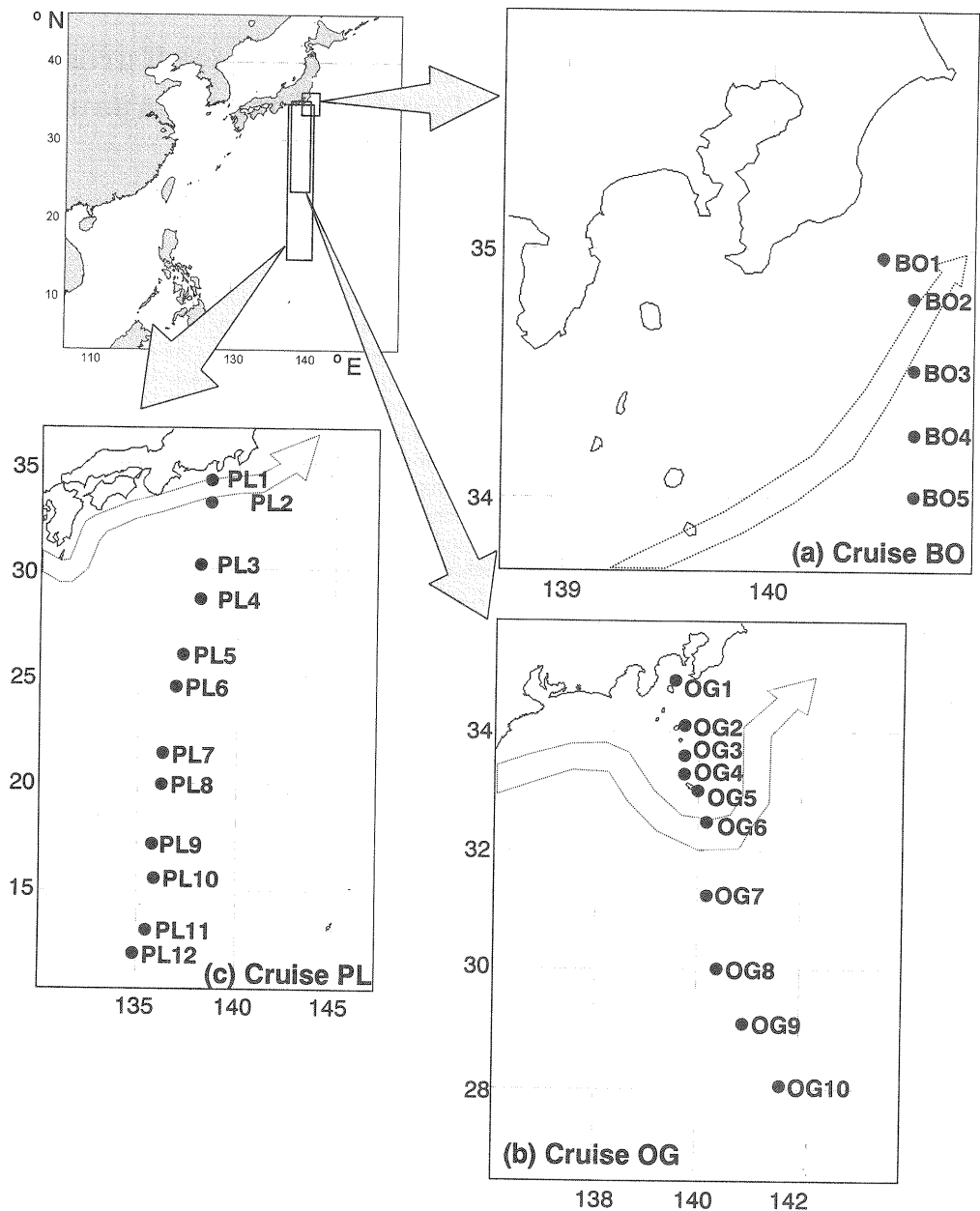


Fig. 1. The stations sampled in the western Pacific Ocean in (a) cruise BO: October 1994, (b) cruise OG: June 1995, and (c) cruise PL: March 1998. A broken line corresponds to Kuroshio Paths measured by the Hydrographic Department of the Japanese Coast Guard.

range, because of their high relative dominance in oligotrophic regions compare to coastal regions. However, there have been no studies conducted to ascertain the biomass and composition of picophytoplankton across the

Kuroshio Current, systematically.

In the present study, we examined the distribution of the two prokaryotic picophytoplankton groups, *Synechococcus* and *Prochlorococcus*, and also the eukaryotic picophyto-

plankton across the Kuroshio Current. Recently, some evidences for niche partitioning has been observed between the prokaryotes, *Synechococcus* and *Prochlorococcus* (OLSON *et al.*, 1990; CAMPBELL *et al.*, 1994; LIU *et al.*, 1998), however, it is still not clear what environmental parameters separate these two groups. Here, we discuss the relationship between the distribution of these groups and the water properties—temperature, salinity, strength of the stratification, and nutrients levels—throughout the Kuroshio Current region.

2. Methods

Study area

Three cruises were carried out on the research and training vessels of the Tokyo University of Fisheries: off the Bouso Peninsula in October 1994 (Cruise BO) on the *Sinyo-maru*, over the Izu Ridge down the south to the Ogasawara Islands during June 1995 (Cruise OG) on the *Seiyo-maru*, and the south of Izu Ridge down the south to Palau Island during March 1998 (Cruise PL) on the *Umitaka-maru*. Station locations for each survey line and the position of the Kuroshio (Hydrographic Department of Japan Coast Guard, 1994, 1995 and 1998) are shown in Fig. 1.

Hydrographic observation

Hydrographic data were taken by OCTOPUS system (OCTO-Parameter Underwater Sensors; ISHIMARU *et al.*, 1984). In order to estimate the water column stability in the surface layer, the Brunt-Väisälä frequency (N), in radians s^{-1} , one of the important descriptors of the oceanic vertical structure (MILLARD *et al.*, 1990), was calculated from vertical profiles of temperature and salinity:

$$N = \sqrt{\left(\frac{g}{\rho}\right) \frac{\Delta\rho}{\Delta z}},$$

where g is the acceleration due to gravity, ρ is density and z is depth. Values of N larger than $0.01 s^{-1}$ roughly corresponded to the position of seasonal thermocline (see Fig. 1 in MILLARD *et al.*, 1990).

Water samples for the analysis of phytoplankton abundance and species composition were taken with 1.7L Niskin bottles attached

on a Rosette Multi-Sampler, which were mounted on the OCTOPUS system. Inorganic nitrate was analyzed using a segmented flow colorimetric auto analyzer (after STRICKLAND and PARSONS, 1972). 200 ml of seawater from each Niskin bottle was filtered onto a 25 mm diameter glass fiber filter (Watmann Co., GF/F) at <150 mm-Hg pressure for later chlorophyll a (Chl a) measurement. Chl a was extracted from the filters by N,N -dimethylformamide for one day at $-20^{\circ}C$ (SUZUKI and ISHIMARU, 1990), and then stored at $-20^{\circ}C$ until measurement. Chl a was determined using a Turner Designs 10R fluorometer following the procedures of STRICKLAND and PARSONS (1972). Relative irradiance within the water column was calculated from an attenuation coefficient using mean water column Chl a concentration after RILEY (1975).

Plankton sampling

For picophytoplankton analysis, 5–25 ml of water was taken from each Niskin bottles. The sample was immediately fixed in glutaraldehyde, with a final concentration of 1.0 %, and stored under cool ($<4^{\circ}C$) and dark conditions for at least 1 day, then filtered onto a 7 mm diameter, $0.2 \mu m$ membrane filter (Millipore Co., JG type). The filter was then embedded between glass cover plates with glycerin-water (3 : 2, v/v) with agar (2% w/v) for preventing the filter from drying out. Reagent grade glycerin (Wako Pure Chem. Ind. Ltd.) and non-fluorescent, low-melting-point-temperature agar (Sigma Chemical Co., type IV) were used to make this agent. All of these processes were conducted under extremely dim light in order to avoid decay of the fluorescence of phytoplankton. Once fully embedded, the samples were stored in a freezer ($<-20^{\circ}C$) for later counting and identification.

Enumeration of picoplankton

Picophytoplankton were enumerated using an epifluorescence microscope (Olympus BH2-RFCA) with an IB (interference blue excitation) cube, that consisted of excitation, dichroic, and absorbance filters: EY495, DM505 and O515, respectively. All cell counting was completed within one month of

collection. Because fluorescence intensity depends on excitation intensity, the mercury lamps of the microscope (Ushio-102D, 100W) were replaced every 100 hours of use. This method was sensitive enough to detect a 0.2 μm fluorescent bead (Polyscience, Inc., cat #09834). All picoplankton within 140 fields per slide, near the centerline of the filter, were counted and identified at a magnification of 1000.

Synechococcus was identified by its vivid yellow to orange fluorescence, a coccid to bacillus shape, and a size between 0.5 and 1.5 μm . We also detected bright yellow cells, individually about 2–3 μm in diameter, that were found both solitary and sometimes in aggregates of up to 20 cells, at 16 to 18°N, 135°W (Stns. PL 9 and PL 10 in cruise PL). Recently, NEVEUX *et al.* (1999) observed some non-motile round cells, about 2–3 μm in size, containing unusual phycoerythrin (fluorescence emission peaks; 494, 564 nm), in the subtropical Pacific Ocean. These yellow cells that we observed, and those observed by NEVEUX *et al.* (1999) are possibly the same organisms as those observed previously by ISHIZAKA *et al.* (1994) and CAMPBELL *et al.* (1997), which were tentatively identified as *Synechocystis* (PARTENSKY *et al.* 1999a). *Prochlorococcus* was identified by its pale red to pale orange fluorescence, a coccid shape with a size of 0.6 to 1 μm . Our method provided not only high contrast, but also low background light, thus *Prochlorococcus*, after the fluorescence was optically bleached, could be detected as a white spot shown in Fig. 2. This method was proved to distinguish a cultured *Prochlorococcus* strain GP2 from the western Pacific (Shimada *et al.*, 1995b). Eukaryotic phytoplankton were identified by the existence of a single red or deep red, cup-like or oval shaped chloroplast with green protoplasm and flagella, with cell size in the range of 1.2 to 3 μm .

3. Results

Water masses

We categorized our study area into three regions: the neritic water on the landward side of the Kuroshio front (LKF), the Kuroshio Current body (KCB) and the water on the south

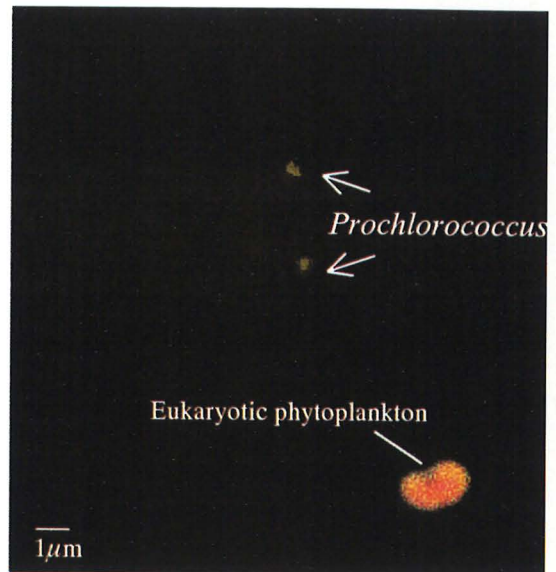


Fig. 2. Bleached *Prochlorococcus* cells recognized under an epifluorescence micrograph.

side of the Kuroshio seaward boundary (WSK). These water masses were determined by examination of vertical structure of temperature for each cruise (Figs. 3A, 4A and 5A). A good indicator of the cross-axis center of the Kuroshio Current body at the surface is the cross-axis position of where the 15°C isotherm intersects a depth of 200 m (*e.g.* KAWABE, 1985). The Kuroshio is also well defined by a sharp southward deepening of isotherms near the northern section in all years (*e.g.* HANAWA and HOSHINO, 1988). Thus, the Kuroshio axis is located between BO2 and BO3 at OG6 and between PL1 and PL2 for the three cruises, respectively. Our determination of the location of the Kuroshio Current axis coincides well with the locations reported in the Bulletin of the Kuroshio (Hydrographic Department of Japan Coast Guard, 1994, 1995 and 1998). During cruises BO and PL, the Kuroshio Current flowed between Miyake-jima and Hachijyo-jima, then passed straight out to the Bousou Peninsula. During cruise OG, the Kuroshio meandered around the Izu Islands and then turned off Aoga-shima. Stations BO1 and BO2 were LKF and stations BO4 and BO5 were WSK during the fall cruise. Stations OG1 to OG5 were LKF, and OG7 to OG10 were WSK in the

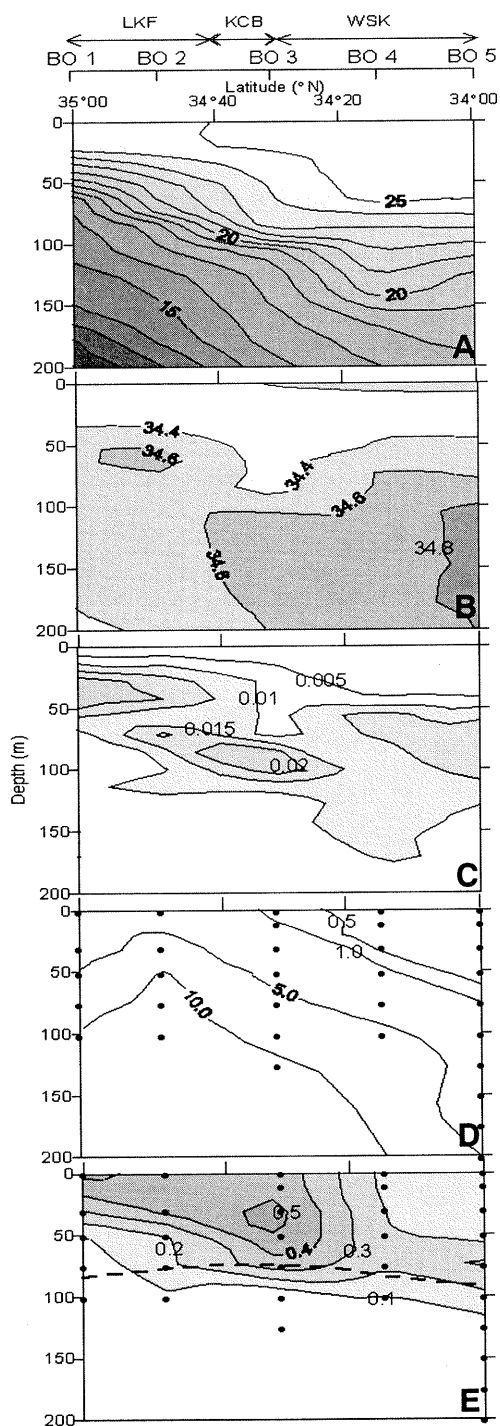


Fig. 3. Vertical sections of A) temperature ($^{\circ}\text{C}$), B) salinity (PSU), C) stability based on Brunt-Väisälä frequency (s^{-1}), D) nitrate (μM), and E) Chl *a* ($\mu\text{g l}^{-1}$) with the depth of the 1% relative light intensity level (dotted line) in the western Pacific Ocean in Cruise BO, October 1994.

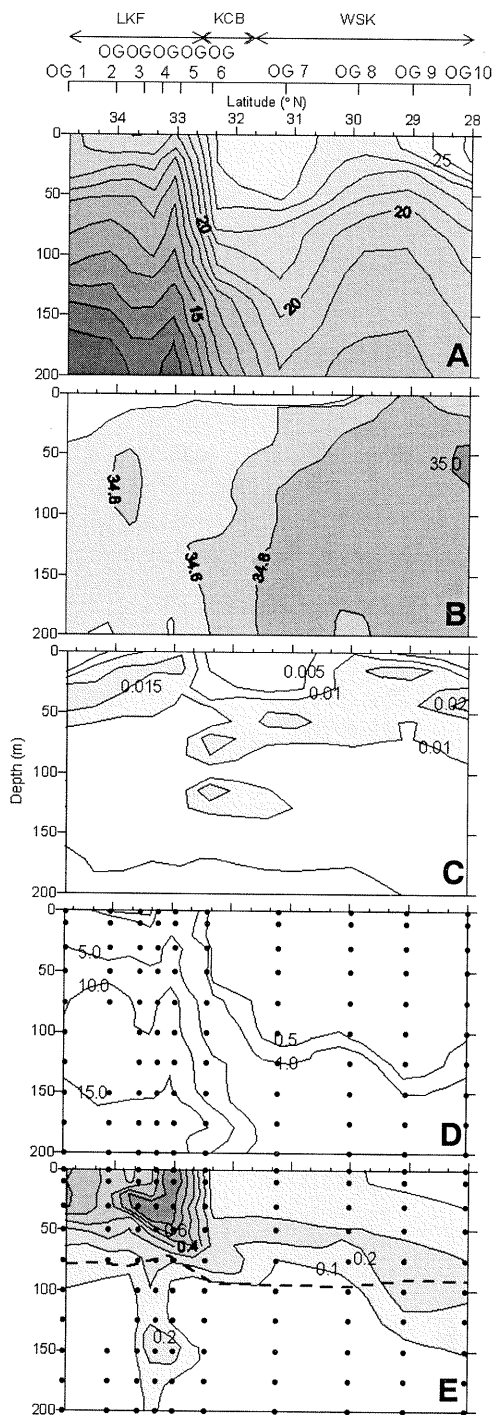


Fig. 4. Vertical sections of A) temperature ($^{\circ}$ C), B) salinity (PSU), C) stability based on Brunt-Väisälä frequency (s^{-1}), D) nitrate (μ M), and E) Chl a (μ g l $^{-1}$) with the depth of the 1% relative light intensity level (dotted line) in the western Pacific Ocean during Cruise OG, June 1995.

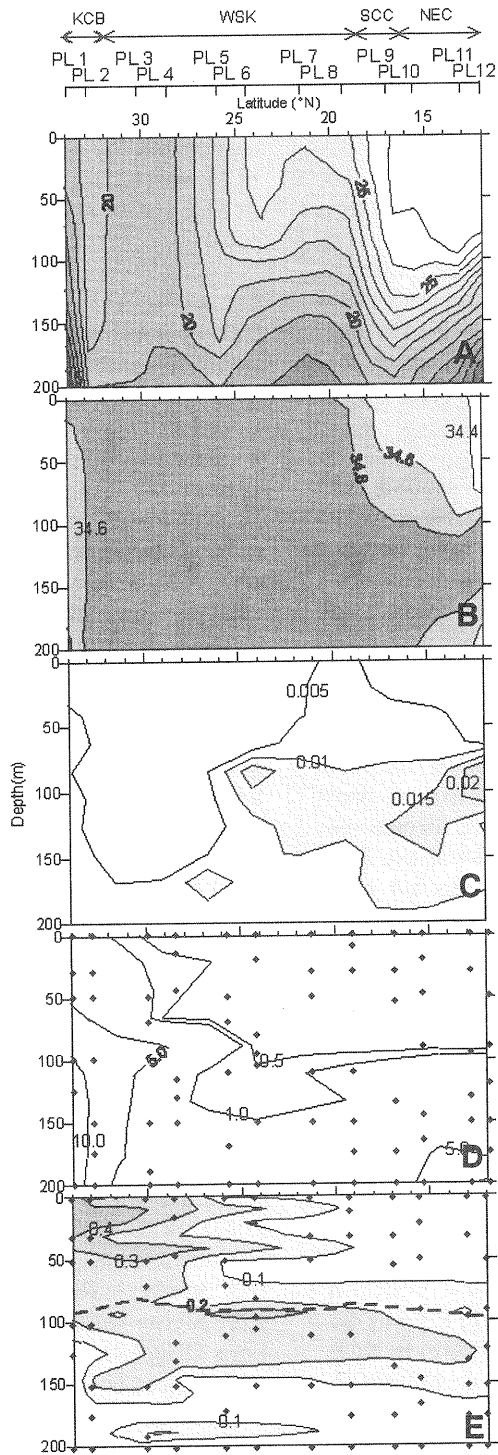


Fig. 5. Vertical sections of A) temperature ($^{\circ}\text{C}$), B) salinity (PSU), C) stability based on Brunt-Väisälä frequency (s^{-1}), D) nitrate (μM), and E) Chl a ($\mu\text{g l}^{-1}$), with the depth of the 1% relative light intensity level (dotted line) in the western Pacific Ocean in Cruise PL, March 1998.

spring cruise. During cruise PL, our stations extended southward, ranging from 12 to 32° N, and therefore transected two other currents, the Subtropical Countercurrent and the North Equatorial Current.

Hydrography, Irradiance, and Nitrate and Chl a concentrations

The distributions of temperature, salinity, Brunt-Väisälä frequency (N), nitrate and Chl a concentrations, and the depth of the 1% relative light intensity at cruise BO, OG, and PL are shown in Figs. 3, 4 and 5, respectively.

Cruise BO

Surface water temperature was around 24°C in LKF and higher than 25°C in KCB and WSK. Deepening of the surface mixing layer had not yet occurred. The strong seasonal thermocline, shown by a value of N greater than 0.02 s^{-1} , was located between 30 and 50 m in LKF, around 80 m in KCB (a high $N \sim 0.015 \text{ s}^{-1}$ here), and between 70 and 100 m in WSK. We found upwelled water with high salinity and high nitrate concentration at 50-m depth at BO2, which was probably caused by frontal eddy pumping such as reported for Gulf Stream meanders (Yoder *et al.*, 1981). However, the high nitrate concentration was not reflected by a high Chl a concentration. Nitrate was not depleted at Sta. BO3 in KCB, probably by the influence of upwelling water around BO2, and Chl a was high ($0.4 \mu\text{g l}^{-1}$) at the surface with a subsurface chlorophyll maximum layer (SCM) above the strong thermocline. In WSK, nitrate was depleted in the surface layer and the SCM with a low Chl a concentration ($<0.2 \mu\text{g l}^{-1}$) was observed just above the thermocline.

Cruise OG

Surface temperature was about 20°C in LKF, and higher than 24°C in KCB and WSK. A thermocline indicated by $N > 0.015 \text{ s}^{-1}$ was between 10 to 30 m in LKF, around 80 m in KCB, and 20 to 60 m in WSK (Fig. 4C). Upwelling occurred in regions shallower than 600 m (data not shown), located at Sta. OG4 and OG5 off the southwest of Hachijyo-jima. Regional upwelling is known to occur near the Izu Islands (*e.g.* FURUYA *et al.*, 1986). Low temperature (18°C)

and high nitrate concentrations ($>5 \mu\text{M}$) were seen at 25-m depth of OG5 with coincident high concentrations of Chl a ($>0.7 \mu\text{g l}^{-1}$). Chl a concentrations higher than $0.4 \mu\text{g l}^{-1}$ were measured from the surface to 50 or 60 m in LKF. A SCM with $0.2 \mu\text{g l}^{-1}$ Chl a was observed at 60 m in KCB (OG6) and deepened to 90 m toward the south.

Cruise PL

Steep southward deepening of isotherms was found around PL9, suggesting eastward flow. This is identified as the Subtropical Countercurrent (SCC), although it is shifted southward compared to its average position (around 25° N at 140° E; see TSUCHIYA, 1982). South of SCC was the North Equatorial Current (NEC) region characterized by low salinity (Fig. 3 in QUI and JOYCE, 1992). The eastward flow around 17° N and low salinity (<34.5 PSU) south of 16° N in 137° E transect were also observed by *Ryofu-maru* cruise during January and March in 1998 (Meteorological Agency of Japan, 1998).

Temperature in the mixing layer was 20°C or lower at stations north of 29° N (PL1 to PL4), where no clear thermocline was present. Strong thermoclines defined by N of $>0.01 \text{ s}^{-1}$ were observed below 80 m at stations south of 25° N (PL6 to PL12), where nitrate was depleted in the mixing layer and a SCM was observed at 100–120 m.

Picophytoplankton Distribution

Cruise BO

Synechococcus was found at high concentrations ($\sim 5 \times 10^4$ cells ml^{-1}) at all the stations from Cruise BO (Fig. 6A), with the maximum concentration ($>3 \times 10^5$ cells ml^{-1}) within KCB at Sta. BO3. Generally, *Synechococcus* concentrations were highest within the mixed layer in this study. *Prochlorococcus* concentrations were higher than 5×10^3 cells ml^{-1} at all the stations (Fig. 6B). Toward the south, maximum abundances occurred at deeper depths. Typically, this subsurface maximum was located within the seasonal thermocline, as defined by a N of $>0.01 \text{ s}^{-1}$, except at Sta. BO5. At Sta. BO5, cell concentration at 150 m was more than 2.5×10^4 cells ml^{-1} , although Chl a was less than

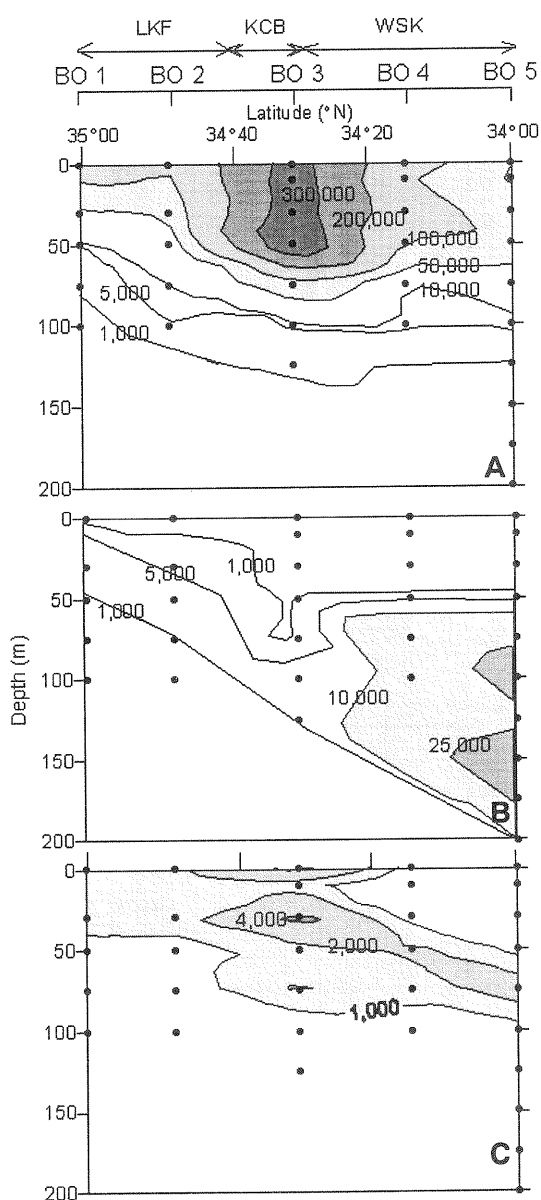


Fig. 6. Vertical sections of A) *Synechococcus* spp., B) *Prochlorococcus* spp., and C) eukaryotic picophytoplankton (cells ml⁻¹) in the western Pacific Ocean during Cruise BO, October 1994.

0.1 $\mu\text{g l}^{-1}$. Eukaryotic picophytoplankton concentration was more than 10^3 cells ml⁻¹ at all stations. Their distribution was similar to the distribution of Chl *a*, with a maximum (4×10^3 cells ml⁻¹) at 25 m in KCB (Fig. 6C).

Cruise OG

Synechococcus was present at all stations, however, high concentrations ($>10^5$ cells ml⁻¹) were only found at shallow depths in LKF and KCB, and concentrations decreased to the south in WSK. The highest concentration ($>2 \times 10^5$ cells ml⁻¹) was found above the seasonal thermocline in KCB (Fig. 7A). *Prochlorococcus* was not detected at LKF, and had only very low concentrations in KCB. High concentrations ($>2.5 \times 10^4$ cells ml⁻¹) were found between 75 and 150 m depths in WSK (Fig. 7B) where the water temperatures were higher than 18°C. Eukaryotic picophytoplankton were abundant ($>6 \times 10^3$ cells ml⁻¹) at around 30-m depth at Stas. OG3 to OG5 in LKF, where upwelling was observed (Fig. 7C). Within KCB and WSK, eukaryotic picophytoplankton concentration at SCM depths decreased ($\sim 2 \times 10^3$ cells ml⁻¹).

Cruise PL

Synechococcus occurred at much lower concentration than in the previous cruise. *Synechococcus* was evenly distributed within the mixed layer, down to 100 m in KCB with high concentrations ($\sim 10^4$ cells ml⁻¹, Fig. 8A). Also, high concentrations were observed at northern stations (PL3 to PL5) in WSK at shallower depths, which corresponded to shallower mixing depth in these stations. Cell concentrations decreased to the south in WSK and *Synechococcus* was not detected in SCC and NEC waters. *Prochlorococcus* was not found within KCB, but within WSK, SCC and NEC were found below the 1% relative light level. Low concentrations ($\sim 10^3$ cells ml⁻¹) of eukaryotic picophytoplankton were found at the surface of KCB, and below the SCM in SCC and NEC.

4. Discussion

Distribution of *Synechococcus*

During Cruise BO (fall) and OG (spring), *Synechococcus* cell concentrations reached their maximum level ($2-3 \times 10^5$ cells ml⁻¹) within the upper mixed layer when the water column was stratified, with a rapid decrease in concentration below the top of the thermocline, which was around the 1% relative light depth.

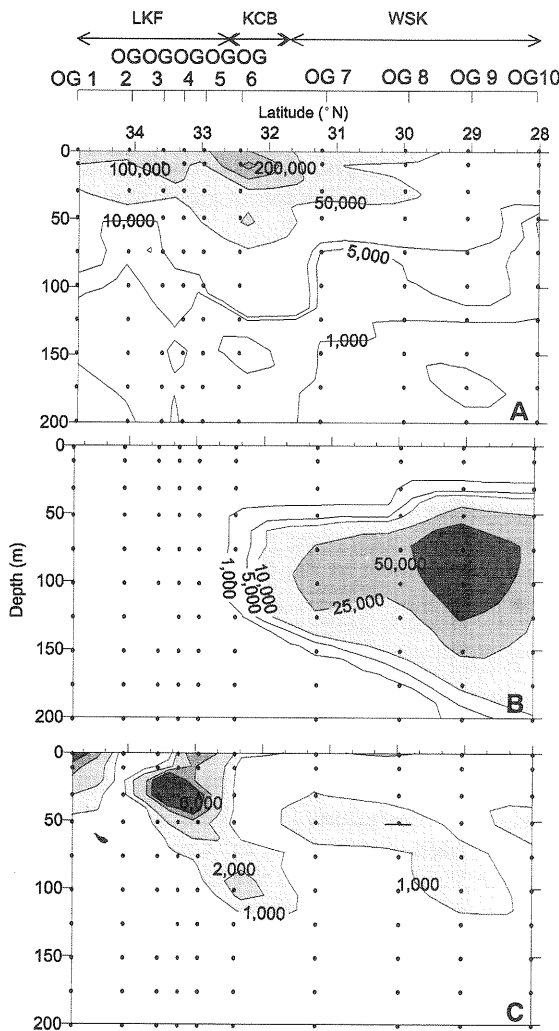


Fig. 7. Vertical sections of A) *Synechococcus* spp., B) *Prochlorococcus* spp., and C) eukaryotic picophytoplankton (cells ml⁻¹) in the western Pacific Ocean during Cruise OG, June 1995.

During Cruise PL (winter), during which the mixed layer extended down to about 100 m or deeper, *Synechococcus* was still distributed throughout the mixed layer in KCB and WSK, although the cell number was thirty times less from the fall and spring levels. In previous works, ODATE *et al.* (1990) observed *Synechococcus* in the western North Pacific Ocean (36.5 to 44°N, 155°E), and noted high concentrations ($\sim 10^5$ cells ml⁻¹) only in the surface of the subtropical water (extension of the Kuroshio

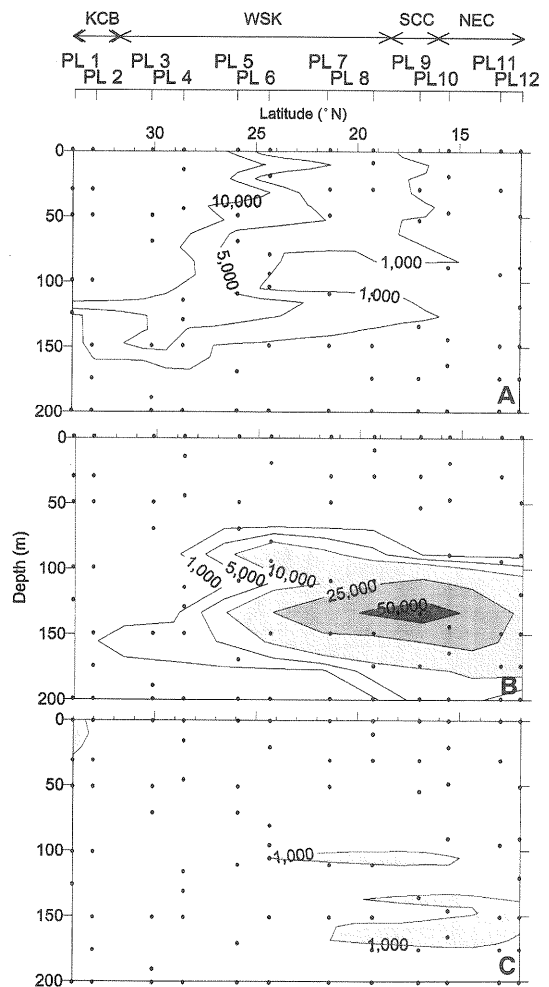


Fig. 8. Vertical sections of A) *Synechococcus* spp., B) *Prochlorococcus* spp., and C) eukaryotic picophytoplankton (cells ml⁻¹) in the western Pacific Ocean during Cruise PL, March 1998.

Current, $>18^{\circ}\text{C}$). This is similar to the maximum cell abundance in oceanic water of 10^5 cells ml⁻¹ as suggested by MURPHY and HAUGEN (1985).

During our study, *Synechococcus* abundance in the Kuroshio Current was always fairly high ($\sim 10^5$ cells ml⁻¹). Previous studies of the near shore coastal areas and certain bays have shown both high and low *Synechococcus* abundances at various times. HAMASAKI *et al.* (1999) found low pico-cyanobacteria concentration ($\sim 10^3$ cells ml⁻¹) during winter when

sea surface temperature was low ($<21^{\circ}\text{C}$) in the inner Sagami Bay, while they found up to 8×10^4 cells ml^{-1} in summer. In Suruga Bay, SHIMADA *et al.* (1995a) found that *Synechococcus* concentrations were low normally, but increased (up to 10^5 cells ml^{-1}) when a branch of the Kuroshio flow into the bay in the summer. High concentrations of *Synechococcus* were also reported off the Izu Peninsula in June (TSUJI *et al.*, 1986) when the Kuroshio Current came very close to the coastal area, judging from its main path at that time (Hydrographic Department of Coast Guard, 1982). The fact that our measurements of *Synechococcus* concentrations within KCB were similar to those reported at particular times within these near shore areas, supports the hypothesis that the Kuroshio Current is responsible for supplying *Synechococcus* to these regions. Therefore, when temperatures are warmer in these areas—an indication of influence by the Kuroshio Current—*Synechococcus* concentrations are typically higher.

The factors which lead to *Synechococcus* dominance are not completely related to the higher temperatures within the Kuroshio waters, but also to nitrate levels. When nitrate levels were low ($<0.5 \mu\text{M}$), *Synechococcus* concentration within WSK waters decreased, such as at Stas. BO4, BO5, OG9 and OG10. At these stations, the *Synechococcus* vertical distribution was strongly influenced by the mixing condition of the water column. During cruises BO and OG, higher *Synechococcus* cell concentrations were observed in KCB than in WSK, when remarkably high nitrate concentrations were observed in KCB (around $1 \mu\text{M}$) compared to previous studies around the Kuroshio Current region (TAKAHASHI *et al.*, 1985). Therefore, the increase of *Synechococcus* cell concentration within KCB in this study could be induced by the start of stratification in spring (spring bloom) or by deepening of mixing depth (autumn bloom). Nutrient supply by upwelling during the stratified season may therefore be an important component of *Synechococcus* blooms in KCB along the Izu Ridge.

Identification of *Prochlorococcus*

Prochlorococcus is difficult to enumerate under the epifluorescence microscopy, especially in surface waters where the fluorescence of the cells is weak and decays very fast (ISHIZAKA *et al.*, 1994). This is in direct contrast to oceanic *Synechococcus*, the majority of which are phycourobilin rich cells with bright orange fluorescence and are easily detected (see PARTENSKY *et al.*, 1999a). SUZUKI *et al.* (1995) measured divinyl Chl *a* (Chl *a*₂) concentration and estimated the *Prochlorococcus* cell concentration. The Chl *a*₂ in the layers above the 10 % isolume depths between the Kuroshio extension and more tropical areas was 0.01 to 0.05 $\mu\text{g l}^{-1}$, which converts to around 4.5×10^4 to 1×10^5 cells ml^{-1} (SUZUKI *et al.*, 1995). However, on the same cruise as this study by SUZUKI *et al.* (1995), ISHIZAKA *et al.* (1994) reported that they could not detect *Prochlorococcus* cells near the surface.

Although we took precise care with our epifluorescence technique described in the methods, we could not detect *Prochlorococcus* from the surface waters covering the subtropical oligotrophic waters where this species has distribution (CAMPBELL *et al.*, 1994, LIU *et al.*, 1997). We did find fairly high concentrations of *Prochlorococcus* cells at 25 to 50-m depth in the coastal water in Cruise BO (Fig. 6A). Because the distribution of *Prochlorococcus* is continuous from off shore subsurface to inshore surface depths along the same isotherms, this may indicate that the cells we sampled all belong to the same population.

Two sub-populations of *Prochlorococcus*—a “dim”, high-light adapted, and a “bright”, low-light adapted strain—have been identified in the past using flow cytometry to measure differential red fluorescence (see PARTENSKY *et al.*, 1999a). The dim subpopulation tends to dominate in the surface depths and the bright population in the subsurface. The high-light adapted form has a low divinyl Chl *b* (Chl *b*₂) /divinyl Chl *a* (Chl *a*₂), and the low-light adapted form has a high divinyl Chl *b*₂/Chl *a*₂ (e.g. MOORE *et al.*, 1998). The cultured strains from both sub-populations keep their pigment ratios after several years of culture (MOORE *et al.*, 1998), and they also fall into two phylogenetic

groups based on 16S RNA sequence analysis (ROCAP *et al.*, 1999).

The fact that the maximal *Prochlorococcus* concentrations found in our study were at or beneath the SCM suggests that the cells we observed belong to the bright fluorescing sub-population. We can count the bright cells by epifluorescence microscope, while it is unlikely that we were able to count the dim cells in this study.

Distribution of Prochlorococcus

In our study, *Prochlorococcus* was detected at relatively high concentrations beneath the mixed layer within WSK, where the temperature was between 22 and 24°C. Its abundance was around 10^3 cells ml⁻¹ at LKF near the surface during fall (Cruise BO), when temperatures were near 24°C. Similar concentrations were found in the KCB beneath the mixed layer where temperatures were around 23 to 24°C in both the fall (Cruise BO) and spring (Cruise OG). *Prochlorococcus* was not observed when temperature in the mixing layer in KCB was below 20°C in the winter. Thus, temperature seems to be an important limiting factor for the distribution of *Prochlorococcus*, which can only extend to the coastal area when water temperature is higher than 20°C. Supporting this hypothesis, SHIMADA *et al.* (1995) observed *Prochlorococcus* in Suruga Bay in the summer when a branch of the Kuroshio came within the bay.

JIAO and YANG (1999) examined samples from the East China Sea during the winter for picophytoplankton using flow cytometry. *Prochlorococcus* abundances were high (maximum 5.6×10^6 cells ml⁻¹) in the Kuroshio Current, but appeared only at low concentrations in waters that were characteristic of a mixture of the shelf water and the Kuroshio Current, with surface temperatures lower than 18°C. FURUYA *et al.* (*in press*), found Chl *a*₂ only in the water south of the Kuroshio seaward boundary in the winter, however, with the development of the summer stratification in East China Sea its distribution extended to the shelf water as indicated by Chl *a*₂ concentration. The temperature at the boundary of its distribution in winter was about 18°C, while during

the summer, temperatures on the shelf were usually higher than 20°C.

Combining these results, the following conclusions are drawn: 1) the Kuroshio Current is the landward boundary of the distribution of *Prochlorococcus* when the temperature within the Kuroshio is higher than that in the coastal water in the East China Sea, 2) The Kuroshio Current transports *Prochlorococcus* northward in winter while the temperature in the mixing layer remains higher than about 20°C, and 3) *Prochlorococcus* spreads into coastal waters when summer stratification is established along the Japanese coast up to the Boso Peninsula area. Our study indicates that *Prochlorococcus* off the Japanese coast require relatively warm water, such as the waters on the south of the Kuroshio Current, which typically results when there is strong stratification.

The Kuroshio Current system is known as a western boundary current, similar to Gulf Stream in the North Atlantic Ocean. OLSON *et al.* (1990), examined the horizontal distribution of phytoplankton across the Gulf Stream, and found that *Prochlorococcus* occurred where the water temperature was higher than 17°C at the surface during September 1986. Thus, the Kuroshio Current, much like the Gulf Stream, acts as a strong barrier to the shoreward distribution of *Prochlorococcus*. The higher temperature limit in the Kuroshio area than in the Gulf Stream suggests the occurrence of different *Prochlorococcus* ecotypes in these waters.

Differential distribution of Prochlorococcus

PARTENSKY *et al.* (1999b) discussed the factors controlling the relative distribution of *Prochlorococcus* versus *Synechococcus*. The two main factors appear to be light and nutrient levels. *Prochlorococcus* appears to be better adapted to low light levels than *Synechococcus*, while there appears to be a positive correlation between *Synechococcus* and nitrogen levels, although this may not always be the case in oligotrophic regions. Our findings within the Kuroshio Current system support these two general mechanisms. We found high *Prochlorococcus* concentrations at deeper depths than *Synechococcus*, and we found the highest *Synechococcus* concentrations in areas where

there may have been nutrient input due to recent mixing or frontal circulation. However, *Synechococcus* was not always found in the regions of highest nitrogen. These two factors, acting in conjunction, lead to an apparent "a differential distribution" of *Prochlorococcus* relative to *Synechococcus*. As suggested by PARTENSKY *et al.* (1999b), the maximum water column integrated concentration of *Prochlorococcus* occurs in a different region from that of *Synechococcus*. In our study, *Prochlorococcus* has maximum integrated abundances in the offshore side of the Kuroshio, while that of *Synechococcus* was usually within the KCB or landward within the LKF. Unfortunately, as mentioned earlier, we probably did not detect any high-light adapted *Prochlorococcus* if they were present, thus, we can not address how their distribution relates to *Synechococcus*.

Distribution of eukaryotic picophytoplankton

The concentrations of the eukaryotic picophytoplankton were much lower than prokaryotic picophytoplankton, and its distribution was fairly different among the different cruises. In general, however, the distribution appears to coincide with chlorophyll distribution. High abundances were found at the surface of coastal stations (PL1 and OG1) and upwelling stations (OG3 to OG5) with high nitrate concentrations (1.0 to 5.0 μM). Eukaryotic picophytoplankton did not occur in nutrient depleted surface waters but occurred in SCM depths off Kuroshio in each cruise. Thus it might require relatively high nutrient. Comparing vertical distribution among three groups of picophytoplankton, eukaryotic picophytoplankton had its maximum concentrations at depths below the maximum of *Synechococcus* and above that of *Prochlorococcus* (typically found at OG7, OG8, BO4, and BO5). Therefore, eukaryotic picophytoplankton might have a light requirement lower than *Synechococcus* and higher than *Prochlorococcus* (low-light adapted type).

In the present study, we found that the Kuroshio, a strong western boundary current, acts as a barrier to the three types of picophytoplankton that we examined. While

we have tried to assess the importance of picophytoplankton – both prokaryotic and eukaryotic – there is still a lot that remains unknown about the distribution and ecology of these groups. One limitation of our study was due to the epifluorescence microscopic method that we used, which cannot detect high-light adapted *Prochlorococcus*. In the future, we are planning to combine this method with high-sensitivity CCD camera, such as shown in SHIMADA *et al.* (1993), which will enable us to observe high-light adapted *Prochlorococcus*, and also give precise information on size and chloroplast shape in eukaryotic picophytoplankton. Fine structure of picophytoplankton using transmission electron microscopy on the same samples collected during the above cruises will be published elsewhere. Another issue is that SHIMADA *et al.* (1995a) reported the appearance of *Prochlorococcus* in winter (14 °C) from Suruga Bay, which has much lower temperature limit than the populations in this and previous reports. So far, only one strain (strain SB, SHIMADA *et al.* 1995b), a high-light and high-temperature type of *Prochlorococcus*, has been isolated from waters directly adjacent to Japan. Therefore, the isolation of new strains and eco-physiological studies on them are also urgently required.

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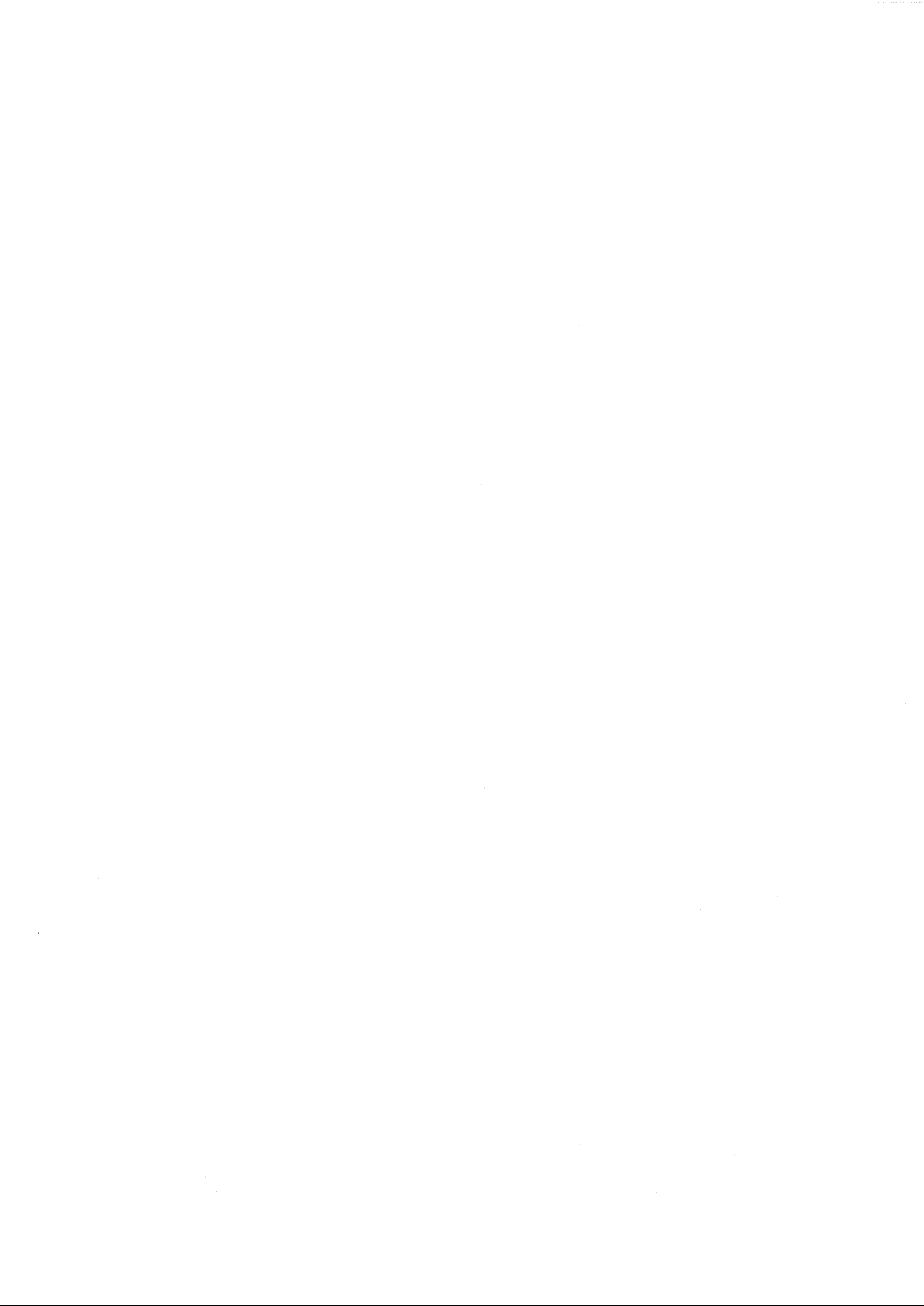
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西部北太平洋における浮遊性軟体動物の鉛直分布

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Vertical distribution of holoplanktonic mollusks in the western North Pacific

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Abstract : The vertical distribution of planktonic gastropods was investigated in the subtropical area of western North Pacific and coastal waters of Japan from 1991 to 1994. Twenty three species of thecosomatous pteropods, nine formae of thecosomatous pteropods and five taxa of planktonic gastropods other than order Thecosomata were identified. No planktonic gastropods were found below 900m. Most species of thecosomatous inhabit 100m during the nighttime and migrate to deeper layer during the daytime. The depth where thecosomatous inhabit during the daytime depends on species and forma. In the case of some species, they distributed in the different depths depending on their growth stage.

Key words : Vertical distribution, Planktonic mollusks, Pteropods.

1. 緒言

浮遊性動物の鉛直移動は、チャレンジャー号探検航海以来知られている。多くは、昼間は深層に夜間には浅層に生活し、明け方と夕方にはその間を移動する、いわゆる日周鉛直移動を行う(村野, 1974)。鉛直分布の様式は、昼間と夜間ではかなり差のある場合があり、したがって、ある海域の浮遊性生物相を調査する際には、この移動を考慮する必要がある。

有殻翼足亜目を含む浮遊性軟体動物は、他のゼラチナス動物プランクトンと同様に、個体数密度が低い。そのため浮遊性生物群集の優占種である甲殻類に比べて注目され難く、鉛直分布についての知見が乏しい。しかしながら、分類学的研究の一環として残されたいくつかの採集報告(MASSY, 1932, TESCH, 1946, 1948)、表層曳採集の出現種と個体数の昼夜による相違から、有殻翼足亜目の昼夜鉛直移動が示唆されていた(奥谷, 1965)。有殻翼足亜目の消化管からは、植物プランクトンや動物プランクトンが見つかり、サイズ選択性の無い雑食性である(LALLI and GILMER, 1989)。糞粒は大きく、多量の珪藻類外殻を含むことから、珪酸塩を速やかに表層から深層へ輸送すると考えられている(SILVER and BRULAND,

1981)。しかしながら、摂餌や排泄の行われる時間帯や深度は不明のままであり、有殻翼足亜目による物質輸送の海洋学的な解明に必須である、鉛直分布と生態の情報が不足しているのが実情である。有殻翼足亜目の遊泳速度は、例えば *Gleba cordata* では一秒間に 45 cm と高い(GILMER and HARBISON, 1986)。そのため、従来の小型ネット採集による調査ではネット逃避の影響があり、定量採集が難しかった。本研究で用いた元田式多層水平ネット(以下MTD: MOTODA, 1971)とMultiple Opening/Closing Net and Environmental Sensing System(多段開閉ネットと環境計測システム, 以下MOCNESS: WIEBE *et al.*, 1976)は、採集能力が大きく短時間に10層以上を定量採集できるという利点を持ち、動物プランクトンの鉛直分布調査に用いられている(広田, 1995)。本研究では、日本沿岸相模湾および西部北太平洋外洋域において、これらの開閉型ネットを用いて浮遊性軟体動物の鉛直分布調査を行った。その結果、出現した翼足目の昼夜鉛直分布を明らかにし、これらの動物群の昼夜鉛直分布について類型化を試みた。さらに翼足目以外の浮遊性軟体動物(5分類群)に関してもデータを付記した。

2. 材料と方法

1991年から1994年にかけて、東京大学海洋研究所研究船白鳳丸のKH91-4次研究航海、同船淡青丸のKT92-11次研究航海、さらに水産庁「北太平洋西部亜熱帯循環系に関する調査」の一環として水産庁開洋丸のKY94

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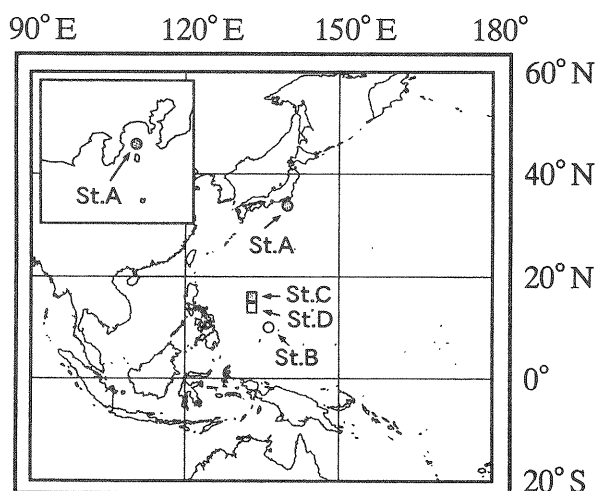


Fig. 1. Location of the sampling stations.

Table 1. Data on net collections.

Research Vessel	'Tansei Maru'		'Hakuho Maru'		'Kaiyo Maru'			
	Cruise KT92-11		Cruise KH91-4		Cruise KY94-1			
Station No.	St.A		St.B		St.C		St.D	
Day or night	Night	Day	Night	Day	Day	Night	Day	Night
Latitude	35-00 N	35-00 N	15-50 N	15-51 N	18-00 N	18-00 N	17-00 N	17-00 N
Longitude	139-20 E	139-20 E	136-54 E	136-52 E	134-00 E	134-00 E	134-00 E	134-00 E
Year	1992	1992	1991	1991	1994	1994	1994	1994
Date	Aug. 3	Aug. 3	July 2	July 2	June 12	June 12	June 13	June 13
Time (Start)	1:05	13:26	0:05	7:37	10:01	19:59	10:55	20:58
Time (Finish)	2:37	15:01	1:26	9:21	16:12	0:58	16:59	1:58
Net type	MTD	MTD	MTD	MTD	MOCNESS	MOCNESS	MOCNESS	MOCNESS
Mesh (mm)	0.33	0.33	0.5	0.5	0.33	0.33	0.33	0.33
Sampling method	Horizontal	Horizontal	Horizontal	Horizontal	Oblique	Oblique	Oblique	Oblique
Sampling depth (m)	0-440	0-450	0-500	0-500	0-1000	0-1000	0-1000	0-1000
Number of sampling layer	11	10	11	11	24	24	24	24
Filtered volume (m ³)	23-417	30-401	610-835	568-1601	180-468	144-460	109-550	125-425

-1次調査航海が行われた。これらの航海は、相模湾および西部北太平洋亜熱帯域を対象としている (Fig. 1)。試料の採集には、口径 80 cm の MTD および口部幅 0.9 m 口部高さ 1.3 m の MOCNESS を用いた。各航海ごとの調査海域と曳網方法は、Table 1 に示した。各ネットによる採集と並行して、CTD (Niel Brown 製) による海洋環境 (水温と塩分) の調査を行った。採集時には各ネットの網口に濾水計と深度計を装着し、濾水量と採集

深度を見積もった。採集した動物プランクトン試料は直ちに 10% 中性ホルマリン海水により固定した。研究室に持ち帰りプランクトン試料から浮遊性軟体動物のみを選別し、殻部の溶解を防ぐため 70% エタノール液で保存した。VAN der SPOEL *et al* (1997) に従って種の同定をした。それぞれの個体数密度 (inds. (10³m³)⁻¹) を算出し、1 を加えた値の対数を図示した。

海洋の鉛直方向の生態学的深度区分の名称は時岡 他

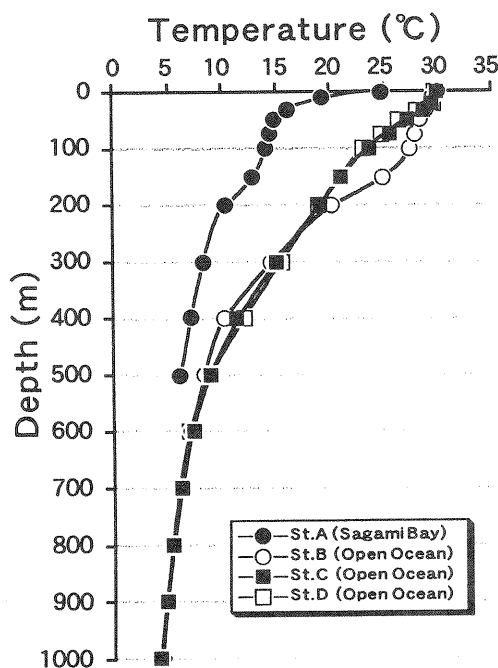


Fig. 2. Vertical profile of water temperature at each sampling station.

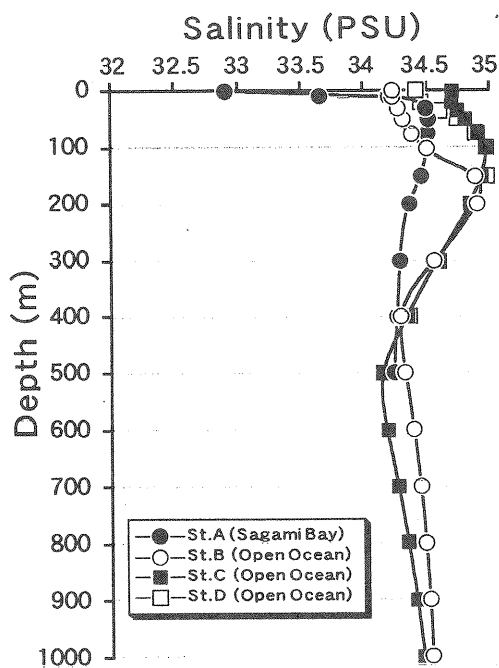


Fig. 3. Vertical profile of salinity at each sampling station.

(1972) に従った。すなわち海表面下から季節躍層の発達する深度 150 m ないし 200 m 付近までを表層、深度 200 m から 500 m もしくは 700 m を中深層、さらに深度 1000 m から 1500 m を上部漸深層とした。表層は海表面を含む深度 1 m 未満を極表層とし、さらに場合によっては深度 20 m から深度 60 m を境に上部表層と下部表層とに区別して表現した。

3. 調査地点の水温と塩分

【KT92-11 次研究航海】調査測点 7-1 および調査測点 7-12 (以下 St. A) は、伊豆大島北方相模湾のほぼ中央に位置する。調査日 4 日前の 1992 年 7 月 29 日には、黒潮は石廊崎の南 90 海里を東に流れ、八丈島の北西 20 海里から北上し、野島崎の南東 30 海里を通り北東に流れており (海上保安庁水路部, 1992), 調査時の観測点は黒潮流軸からは離れていたと判断される。調査時水温の鉛直構造は、極表層から急激に変化し深度 200 m にかけて季節躍層を、さらに 500 m 以深にかけて主躍層を形成していた (Fig. 2)。調査時の塩分の鉛直構造は、極表層から深度 30 m にかけて 34.5 以下の低塩分水が存在していた。調査時は梅雨末期にあたり、陸水に由来する低塩分水 (<33.0) が相模湾の海表面を広く被っていたと考えられる。30 m 以深では塩分の増加はなく、深度 500 m にかけて 34.52 から 34.24 に徐々に減少した (Fig. 3)。

【KH91-4 次研究航海】調査測点 St. C-10 および St. C-16 (以下 St. B) は西部北太平洋北赤道海流域にあたる。海洋環境の調査は St. B に近接する測点 St. A-24 において行った (KIMURA *et al.*, 1994)。調査時水温の鉛直構造は、極表層から急激に変化し深度 150 m にかけて、季節躍層を形成していた (Fig. 2)。さらに深度 400 m にかけては主躍層が形成され、800 m 以深では 5 °C 以下で安定していた。塩分の鉛直構造は、比較的塩分の低い水 (<34.5) が海表面から深度 100 m に存在した (Fig. 3)。深度 125 m から 250 m にかけては 34.7 以上の比較的塩分の高い水が存在し、深度 400 m にかけて顕著な塩分躍層が発達した。塩分極小は深度 400 m で 34.27 を示し、それ以深で塩分は徐々に増加した。

【KY94-1 次研究航海】調査測点 St. 16 および St. 17 (以下 St. C および St. D) は西部北太平洋北赤道海流域にあたる。調査時の水温は、表層から深度 75 m にかけて急激に変化した。さらに深度 500 m にかけては主躍層を形成し、深度 800 m 以深では 5 °C 以下で安定していた (Fig. 2)。これは St. C および St. D で同様であった。塩分の鉛直構造は、St. C では海表面から深度 50 m に 34.5 以下の比較的塩分の低い水が存在したものの、その他の特徴は両調査測点で同様であった。すなわち、深度 125 m から 250 m にかけては 34.7 以上のやや高塩の水が存在し、塩分極小は深度 500 m で 34.15、以深で塩分は徐々に増加した (Fig. 3)。

4. 結果

調査した海域から下記の 12 属 23 種 8 型の翼足目 (Order: Thecosomata) が出現した。さらに翼足目以外の浮遊性軟体動物 (5 分類群) についてもデータを付記した。

Order : Thecosomata Blainville, 1824 翼足目
Suborder : Euthecosomata Meisenheimer, 1905 有殻翼足亜目

Family : Limacinidae Gray, 1847
ミジンウキマイマイ科

- 1 *Limacina bulimoides* (d'Orbigny, 1836)
- 2 *Limacina inflata* (d'Orbigny, 1836)
- 3 *Limacina lesueuri* (d'Orbigny, 1836)
- 4 *Limacina trochiformis* (d'Orbigny, 1836)

Family : Cavoliniidae Fischer, 1883 カメガイ科
Subfamily : Clioinae van der SPOEL, 1967

ウキピンガイ亜科

- 5 *Creseis acicula* Rang, 1828
 - 5-1 *Creseis acicula* forma *acicula* (Rang, 1828)
 - 5-2 *Creseis acicula* forma *clava* (Rang, 1828)
- 6 *Creseis virgula* (Rang, 1828)
 - 6-1 *Creseis virgula* forma *virgula* (Rang, 1828)
 - 6-2 *Creseis virgula* forma *conica* Eschscholtz, 1829

- 7 *Styliola subula* (Quoy and Gaimard, 1827)
- 8 *Hyalocylis striata* (Rang, 1828)
- 9 *Clio pyramidata* (Linnaeus, 1767)

Clio pyramidata forma *lanceolata* (Lesueur, 1813)

- 10 *Clio cuspidata* (Bosc, 1802)

Subfamily : Cuvierininae van der SPOEL, 1967

ウキツツ亜科

- 11 *Cuvierina columnella* (Rang, 1827)
- Cuvierina columnella* forma *urceolaris* (Morch, 1850)

Subfamily : Cavoliniinae van der SPOEL, 1972

カメガイ亜科

- 12 *Diacria costata* (Pfeffer, 1879)
 - 13 *Diacria danae* van der SPOEL, 1968
 - 14 *Diacria maculata* (Bleeker and van der SPOEL, 1988)
 - 15 *Cavolinia inflexa* (Lesueur, 1813)
- Cavolinia inflexa* forma *labiata* (d'Orbigny, 1836)
- 16 *Cavolinia gibbosa* (d'Orbigny, 1836)

Cavolinia gibbosa forma *gibbosa* (d'Orbigny, 1836)

- 17 *Cavolinia globulosa* (Gray, 1850)

- 18 *Diacavolinia angulosa* (Gray, 1850)

- 19 *Diacavolinia longirostris* (de'Blainville, 1821)

- 20 *Diacavolinia vanutrechtii* (van der SPOEL, Bleeker and Kobayasi, 1993)

Suborder : Pseudotheosomata Meisenheimer, 1905 擬殻亜目

Family : Peraclididae TESCH, 1913

アミメウキマイマイ科

- 21 *Peraclis reticulata* (d'Orbigny, 1836)

- 22 *Peraclis apicifulva* Meisenheimer, 1906

Family : Cymbliidae Cantraine, 1841

ヤジリカンテンカメガイ科

- 23 *Cymbulia* spp.

Family : Desmopteridae Chun, 1889

コチョウカメガイ科

- 24 *Desmopterus papilio* Chun, 1889

Order : Gymnosomata De Blainville, 1824

裸殻翼足目

- 25 Gymnosomata spp.

Family : Hydromylidae Pruvot-Fol, 1942

マメツブハダカカメガイ科

- 26 *Hydromyles globulosa* (Rang, 1825)

Order : Mesogastropoda 中腹足目

Superfamily: Atlantacea Philippi, 1853

クチキレウキガイ上科

Family : Atlantidae Wiegmann and Ruthe, 1832

クチキレウキガイ科

- 27 *Atlanta* spp.

Benthic molluscs' planktonic larva

底生性軟体動物の浮遊幼生

- 28 *Gastropods veliger*

- 29 *Bivalves veliger*

Diacria costata, *Diacavolinia longirostris*, *Diacavolinia vanutrechtii* は採集個体が少なかったため、出現の記載のみを行った。

相模湾の St. A において採集個体が多かった *Limacina inflata*, *Limacina trochiformis*, *Clio pyramidata* forma *lanceolata* に関しては、殻長をサイズ分けし、成長段階を区別して鉛直分布を示した。

さらに下記の 5 種については、成体とベリジャー幼生に成長段階を区別して鉛直分布を示した。*Diacria maculata* (成体と幼体), *Cavolinia inflexa* forma *labiata* (成体と幼体), *Cavolinia gibbosa* forma *gibbosa* (幼体のみ), *Cavolinia globulosa* (幼体のみ), *Diacavolinia angulosa* (成体のみ)。

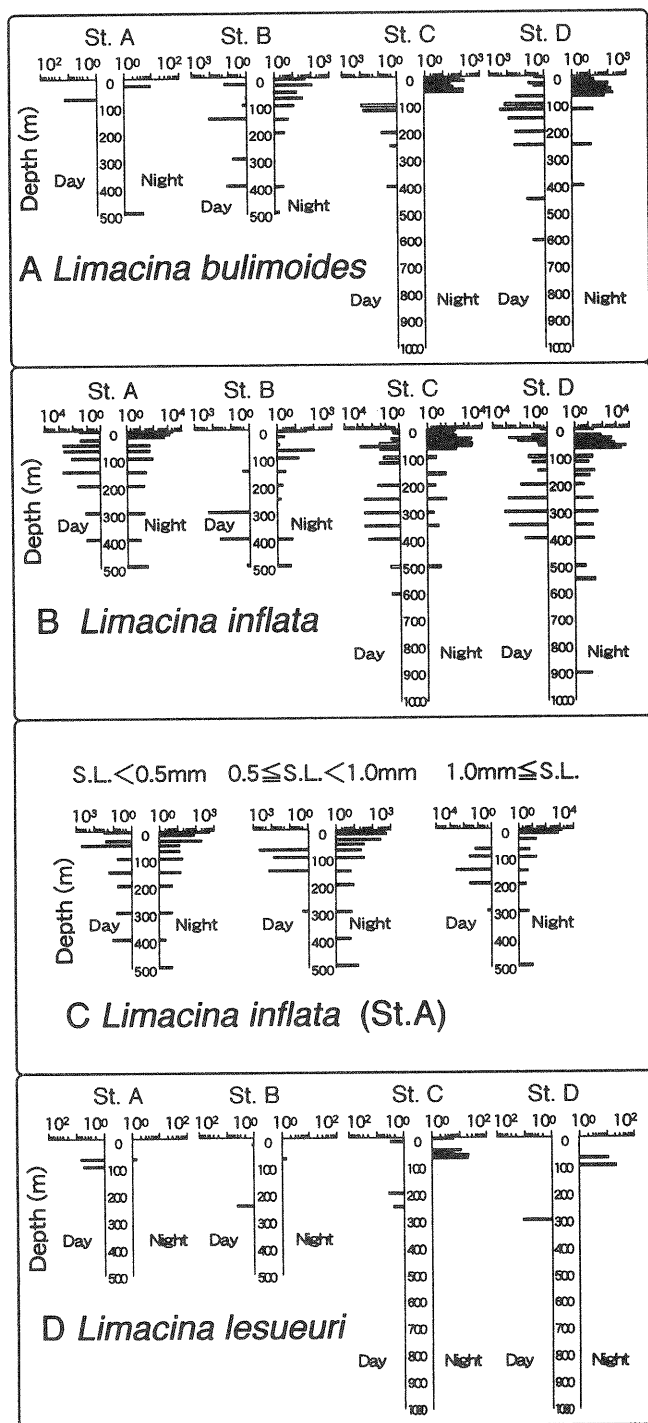


Fig. 4. Vertical distribution of population density (inds. $(10^3\text{m}^3)^{-1}$). (A: *Limacina bulimoides*, B: *L. inflata*, C: for each three size fraction on *L. inflata*, D: *L. lesueuri*)

【翼足目の鉛直分布】

Limacina 属は, *L. bulimoides*, *L. inflata*, *L. lesueuri*, *L. trochiformis* の4種が出現した。*L. bulimoides* は, 極表層から中深層にいたる深度600mに出現したが, 多くの個体は200m以浅の表層内に生息した (Fig. 4-A)。昼間は深度100mから200mの下部表層, 夜間には深度100m以浅の表層に集中することから, 表層内で昼夜鉛直移動を行うと考えられる。*L. inflata* は, 極表層から上部漸深層にいたる深度900mに出現した (Fig. 4-B)。昼間は, 極表層から深度400mに出現し, 表層内の深度100m付近と, 中深層内の350m付近とにそれぞれ出現のピークがあった。夜間は極表層から深度100mに集中して出現した。殻長0.5mm未満, 殻長0.5mm以上1.0mm未満, 殻長1.0mm以上の3つに分類したサイズ別鉛直分布では, 夜間にはどの成長段階においても極表層から深度100mに集中して出現したが, 昼間の鉛直分布は成長段階により異なった (Fig. 4-C)。すなわち, 殻長0.5mm未満の個体が深度50m, 殻長0.5mm以上1.0mm未満のより成長した個体が深度75mから150m, 殻長1.0mm以上のさらに成長した個体が深度150mから200mにそれぞれ集中して出現し, 昼間の生息層は成長が進んだ個体ほど深かった。昼間の鉛直分布に, 表層と中深層にピークがあることを前述したが, それは本種が成長段階によって昼間の生息深度が異なるからと考えられる。これらのことから, 本種は夜間上部表層に出現する昼夜鉛直移動を行い, 昼間の分布は成長段階により異なると考えられる。*L. lesueuri* は, 相模湾の St. A では深度75mから100m, 外洋域 (St. B, St. C および St. D) では深度300m以浅に出現した (Fig. 4-D)。採集個体が少なかったものの, 外洋域では昼間深度300m付近, 夜間には極表層から深度100mに出現することから, 昼夜鉛直移動を行うと考えられる。*L. trochiformis* は, 相模湾の St. A では深度500m以浅, 外洋域の St. B では採集されず, St. C と St. D では深度300m以浅に出現した (Fig. 5-A)。St. B 以外の3測点とも, 昼夜とも深度100m以浅の上部表層内に留まることから, 昼夜鉛直移動はしないと考えられる。3つに分類したサイズ別鉛直分布では, 殻長0.5mm未満の多くの個体は深度75m以浅, 殻長0.5mm以上1.0mm未満の個体は深度500m以浅, 殻長1.0mm以上のより成長した個体では深度30m以浅と深度500mに出現し, 成長段階によって生息深度が異なった (Fig. 5-B)。

Creseis 属は, *C. acicula* と *C. virgula* が出現し, それぞれ *forma acicula* と *forma clava*, *forma conica* と *forma virgula* の2つづつの種内変異型があった。*C. acicula forma acicula* は, 相模湾の St. A では深度500m以浅に出現し, 昼夜とも上部表層内, 特に極表層に多くの個体が集中した (Fig. 5-C)。しかしながら, 外洋域 (St. B, St. C および St. D) での生息深度は150m

以浅の表層内であり相模湾の結果とは異なった。また, 出現の集中する深度は昼間には深度100m付近, 夜間には極表層から50m以浅であった。これらのことから, 表層内で昼夜鉛直移動を行うと考えられる。*C. acicula forma clava* は, 昼間には1個体も採集できず, 昼夜鉛直移動は不明である (Fig. 5-D)。前述の *C. acicula forma acicula* は夜間に多くの個体が極表層に集中したが, *C. acicula forma clava* は極表層には出現せず, 下部表層内の深度50mから100mに出現し, 種内変異型によって互いの生息深度が異なった。*C. virgula forma virgula* は, 相模湾の St. A では500m以浅に出現し生息深度に幅があったものの, 多くの個体は昼夜とも極表層に集中した (Fig. 6-A)。St. B では採集されなかった。外洋域の St. C と St. D では, 深度100m以浅に出現し昼夜とも極表層から上部表層内に生息した。St. A のように極表層にのみ集中して出現する現象はなかったことから, 昼夜鉛直移動は行わないと考えられる。*C. virgula forma conica* は, 昼夜とも深度50m以浅に多くの個体が出現し, 若干の個体が深度400m付近にも出現した (Fig. 6-B)。昼夜とも上部表層内に生息し, 鉛直移動は行わないと考えられる。外洋域 (St. C および St. D) では, 昼間に多くの個体が上部表層内に集中したが, これは前述の *C. virgula forma virgula* の昼間の分布層直上にあたり, 種内変異型によって互いの生息深度が異なった。

Styliola subula は, 極表層から中深層にいたる深度600mに出現した (Fig. 6-C)。昼間は深度25mから500mに出現し, 生息深度に幅があった。外洋域 (St. B, St. C および St. D) では, 夜間に極表層から深度100mに集中したが, 相模湾 (St. A) では生息層に変化がなかった。これらのことから, 昼間は下部表層から中深層に生息し, 外洋域では夜間表層に出現する昼夜鉛直移動を行うと考えられる。

Hyalocylis striata は, 相模湾の St. A では採集されなかった (Fig. 6-D)。外洋域 (St. B, St. C および St. D) では極表層から深度350mに出現し, 昼間は深度100mから350mに, 夜間は極表層から深度100mに出現した。これらのことから本種は, 昼間は下部表層から中深層に, 夜間は上部表層に出現する昼夜鉛直移動を行うと考えられる。

Clio 属は, *Clio pyramidata forma lanceolata* と *Clio cuspidata* が出現した。*C. pyramidata forma lanceolata* は, 相模湾の St. A では表層から深度400mに, 外洋域 (St. B, St. C および St. D) では深度30mから600mに出現し, 海域によって生息深度が異なった (Fig. 7-A)。相模湾では, 昼間の鉛直分布は深度50mから150m, 夜間には極表層から深度100mに多くの個体が出現した。外洋域では, 昼間深度50mから600mと出現層に幅があり, 夜間には深度50mから100mに集中して出現したことから, 昼間は下部表層から中深層に生息

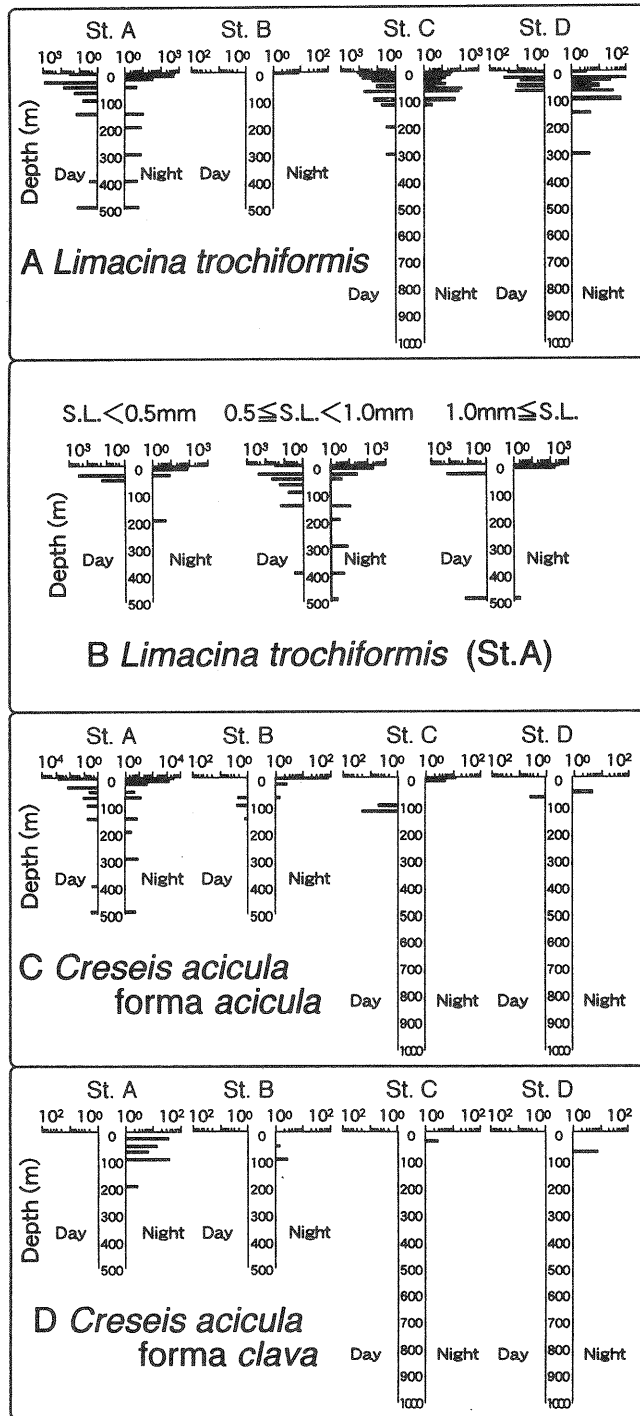


Fig. 5. Vertical distribution of population density (inds. $(10^3\text{m}^3)^{-1}$). (A: *Limacina trochiformis*, B: for each three size fraction on *L. trochiformis*, C: *Creseis acicula* forma acicula, D: *C. acicula* forma clava)

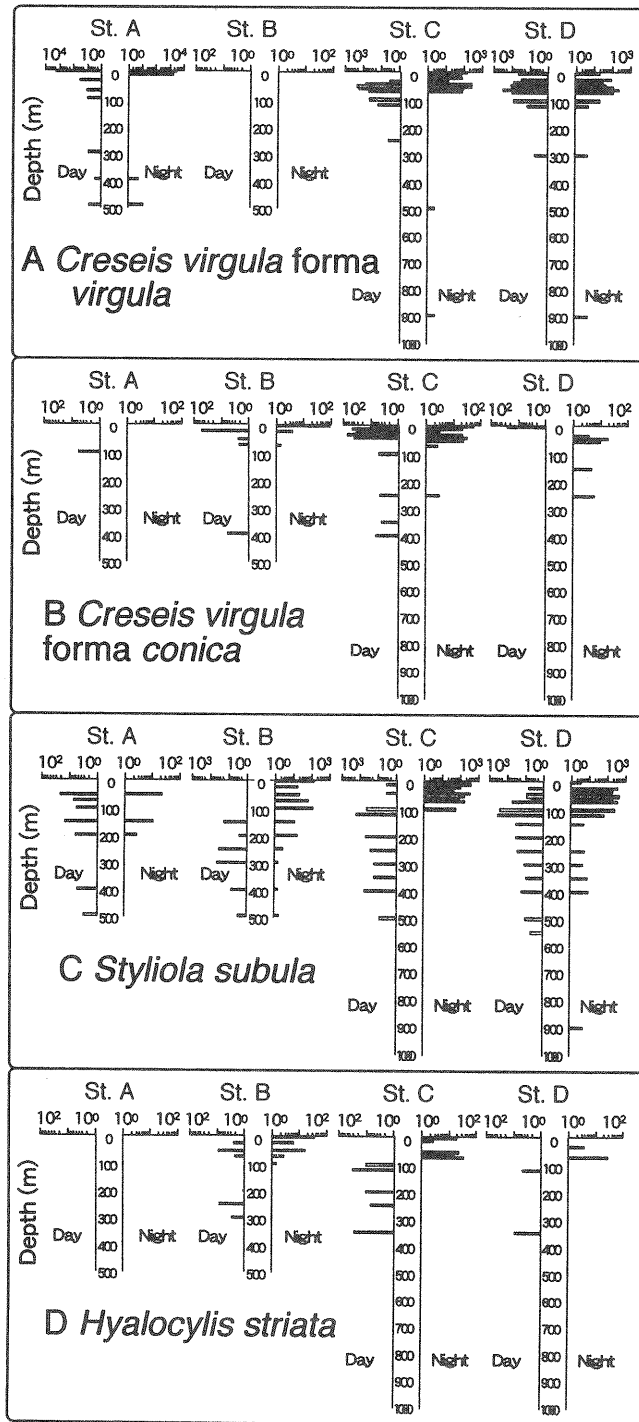


Fig. 6. Vertical distribution of population density (inds. ($10^3 m^3$)⁻¹). (A: *Creseis virgula* forma *virgula*, B: *C. virgula* forma *conica*, C: *Styliola subula*, D: *Hyalocylis striata*)

し、夜間には上部表層へ移動する昼夜鉛直移動を行うと考えられる。5つの区分に分類したサイズ別鉛直分布では、昼間に出現の集中する深度は、殻長 0.5 mm 以下と殻長 0.5 mm 以上 1.0 mm 未満の個体が深度 50 m、殻長 1.0 mm 以上 5.0 mm 未満のさらに成長した個体が深度 50 m から 75 m、殻長 5.0 mm 以上 10.0 mm 未満と殻長 10.0 mm 以上のより成長した個体では深度 150 m であった (Fig. 7-B)。夜間はどの個体も表層から深度 50 m に出現した。つまり、昼間には成長段階の進んだ個体ほどより深層に生息し、夜間にはサイズに関わりなく上部表層に出現した。*C. cuspidata* は、相模湾の St. A では深度 500 m 以浅に、外洋域 (St. B, St. C および St. D) では中深層の深度 300 m から 600 m に出現した。外洋域では昼夜とも深度 400 m 付近の中深層に生息することから、昼夜鉛直移動は行わないと考えられる (Fig. 7-C)。

Cuvierina columnella は、*forma urceolaris* が外洋域の St. C および St. D において採集された。採集個体が少なかったものの、昼間は深度 300 m と 350 m、夜間は深度 150 m 以浅のみにおいて採集されたことから、中深層と表層との間で昼夜鉛直移動を行っていると考えられる。

Diacria 属は、*D. costata*, *D. danae*, *D. maculata* の 3 種が出現した。*D. costata* は、St. B で 2 個体のみを採集した。それぞれの採集深度は、昼間の深度 200 m と夜間の深度 25 m であった。昼夜鉛直移動は不明である。*D. danae* は、相模湾の St. A では採集されなかった (Fig. 7-D)。外洋域の St. B では極表層から深度 500 m に出現し、多くの個体が昼間には深度 150 m、夜間には極表層から深度 25 m に集中した。St. C および St. D では深度 150 m 以浅の表層内に出現し、昼間は極表層から深度 120 m に、夜間には深度 50 m 以浅に集中した。本種は主に表層内に生息し、下部表層と上部表層の間で昼夜鉛直移動を行うと考えられる。*D. maculata* は、深度 550 m 以浅に出現した。成体は採集個体が少なかったものの、昼間は深度 300 m から 400 m、夜間には深度 30 m から 100 m 付近に出現することから、中深層と表層の間で昼夜鉛直移動を行っている可能性がある (Fig. 8-A)。ペリジャー幼生は深度 30 m から 550 m に出現し、成体の生息層よりもより広い深度に出現した (Fig. 8-B)。St. C および St. D では多くの個体が、昼間には深度 50 m から 100 m 付近、夜間には深度 75 m から 175 m に集中して出現した。夜間の出現層は昼間よりも深く、通常とは逆の鉛直移動を行うか、もしくは鉛直移動を行わないと考えられる。

Cavolinia 属は、*C. inflexa*, *C. gibbosa*, *C. globulosa* の 3 種が出現した。*C. inflexa* の成体は、相模湾の St. A では採集されず (Fig. 8-C)、外洋域 (St. B, St. C および St. D) では、極表層から中深層にいたる深度 600 m に出現した。昼間深度 100 m 以浅には出現しないが、

夜間には極表層から深度 75 m に集中して出現することから、中深層と上部表層の間で昼夜鉛直移動を行うと考えられる。ペリジャー幼生の出現深度は、相模湾の St. A では 50 m 以浅、外洋域では極表層から深度 400 m であり、海域によって異なった (Fig. 8-D)。外洋域では、昼間には成体の生息層よりもより浅かったが、成体と同様の昼夜鉛直移動を行うと考えられる。*C. gibbosa* と *C. globulosa* は、外洋域の St. C および St. D において若干の成体を採集したが、多くは幼体であった。*C. gibbosa* の成体は、昼夜とも深度 100 m 付近に出現したが、採集個体が少なく昼夜の鉛直分布に差があるかどうかは不明である。外洋域の St. C および St. D においてペリジャー幼生は、昼間には深度 15 m から 100 m の上部表層に出現し、夜間には深度 50 m から 400 m と出現層が深くなることから、昼間は上部表層に、夜間には下部表層から中深層へ移動する通常とは逆の鉛直移動を行うと考えられる (Fig. 9-A)。*C. globulosa* の成体は極表層から深度 450 m に出現したが、採集個体が少なく鉛直移動は不明である。ペリジャー幼生は外洋域の St. B および St. C において、昼夜とも深度 25 m 以浅に出現し、昼夜鉛直移動はしないとされる (Fig. 9-B)。

Diacavolinia 属は、*D. angulosa*, *D. longirostris*, *D. vanutrechtii* の 3 種が外洋域 (St. B, St. C および St. D) において採集した。*D. angulosa* は 200 m 以浅、*D. longirostris* の成体は 50 m 以浅、*D. vanutrechtii* の成体は 20 m 以浅で採集した。*D. angulosa* は、St. C および St. D において昼間多くの個体が深度 100 m 付近に集中して出現したが、夜間には極表層から深度 75 m に出現したことから、表層内を昼夜鉛直移動すると考えられる (Fig. 9-C)。

Peraclis 属は、*P. reticulata* と *P. apicifulva* が出現した。*P. reticulata* は、深度 500 m 以浅に出現し生息層に幅があった。多くの個体は昼夜とも表層内に生息し、昼夜鉛直移動はしないとされる (Fig. 9-D)。*P. apicifulva* は、相模湾の St. A では深度 30 m から 500 m に出現した (Fig. 10-A)。外洋域 (St. B, St. C および St. D) では多くの個体が、下部表層から中深層にあたる深度 100 m から 400 m に出現した。昼夜で生息層に変化がないことから、昼夜鉛直移動は行わないと考えられる。

Cymbulia spp. は、外洋域の St. B では採集されなかった。多くの個体は深度 150 m 以浅に出現し、昼夜とも表層内に出現した (Fig. 10-B)。

Desmopterus papilio は、極表層から深度 800 m に出現したが、多くの個体は極表層から深度 100 m に集中して出現した (Fig. 10-C)。昼間は極表層に出現しないが、夜間には極表層にも出現した。表層内において昼夜鉛直移動を行うと考えられる。

【翼足目以外の鉛直分布】

Gymnosomata spp. は、外洋域の St. B では採集され

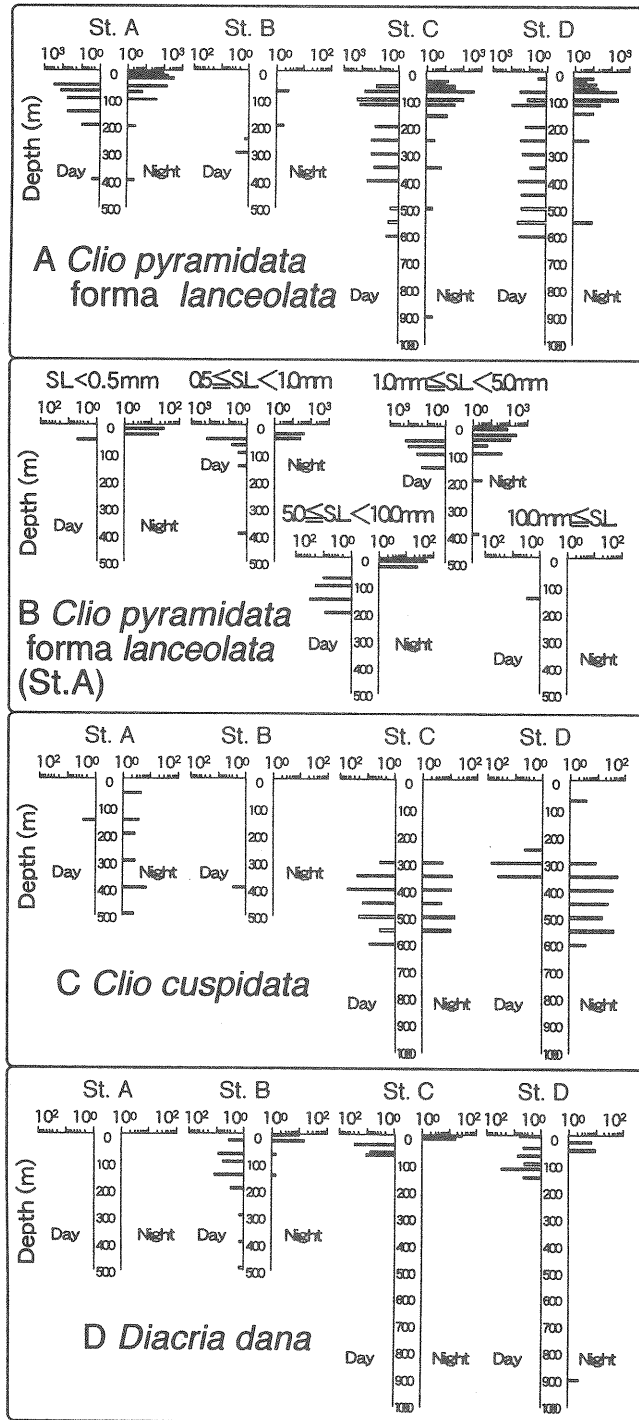


Fig. 7. Vertical distribution of population density (inds. (10³m³)⁻¹). (A: *Clio pyramidata* forma *lanceolata*, B: for each five size fraction on *C. pyramidata* forma *lanceolata*, C: *C. cuspidata*, D: *Diacria dana*)

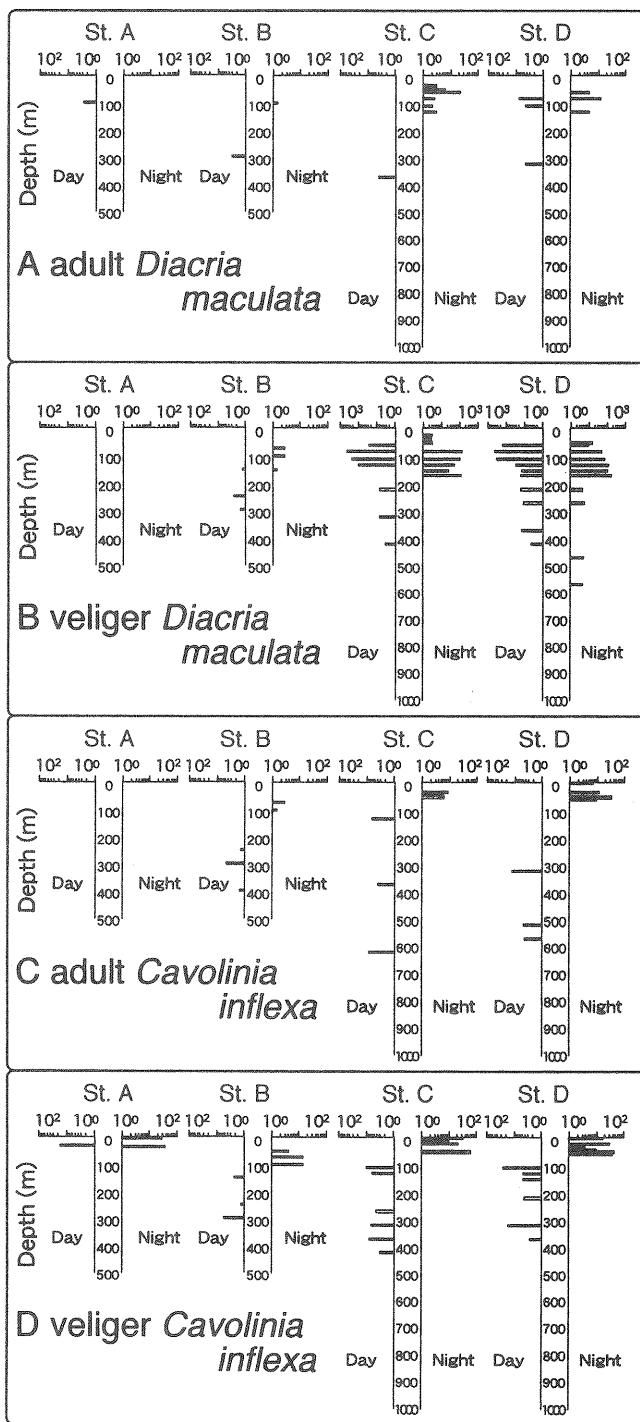


Fig. 8. Vertical distribution of population density (inds. (10^3 m^3)⁻¹). (A: adult *Diacria maculata*, B: veliger *D. maculata*, C: adult *Cavolinia inflexa*, D: veliger *C. inflexa*)

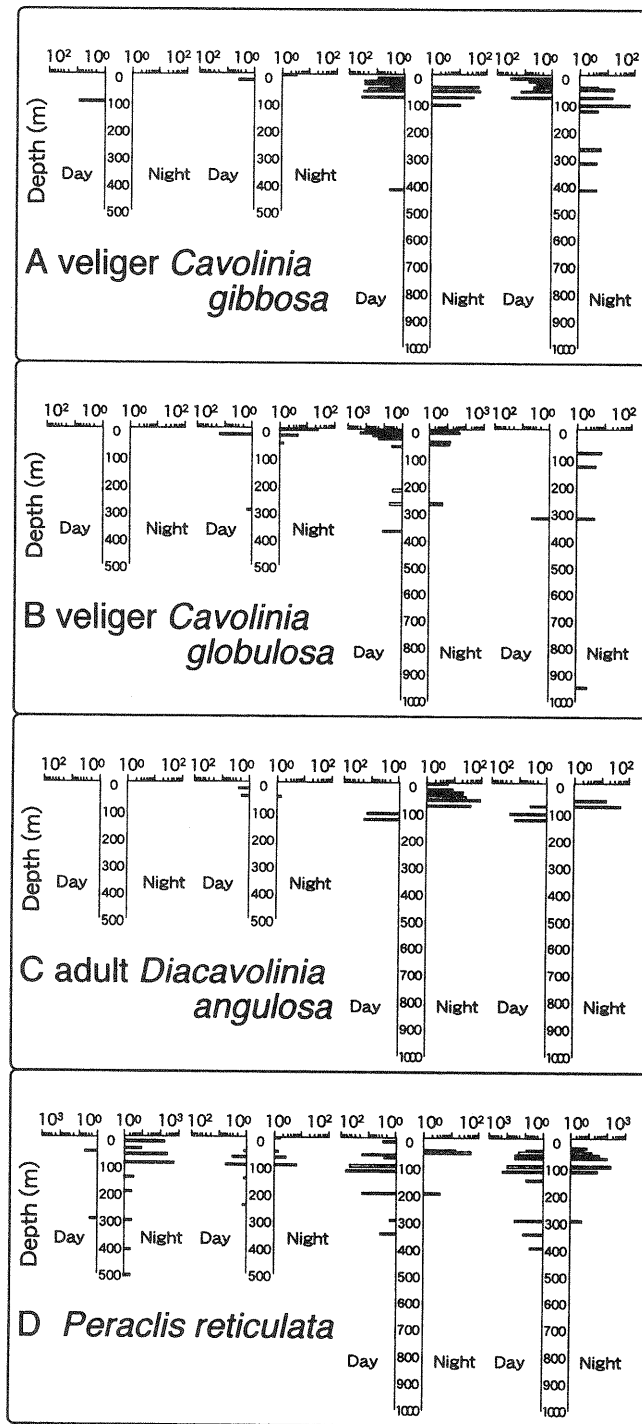


Fig. 9. Vertical distribution of population density (inds. (10³m³)⁻¹). (A: veliger *Cavolinia gibbosa*, B: veliger *C. globulosa*, C: adult *Diacavolinia angulosa*, E: *Peraclis reticulata*)

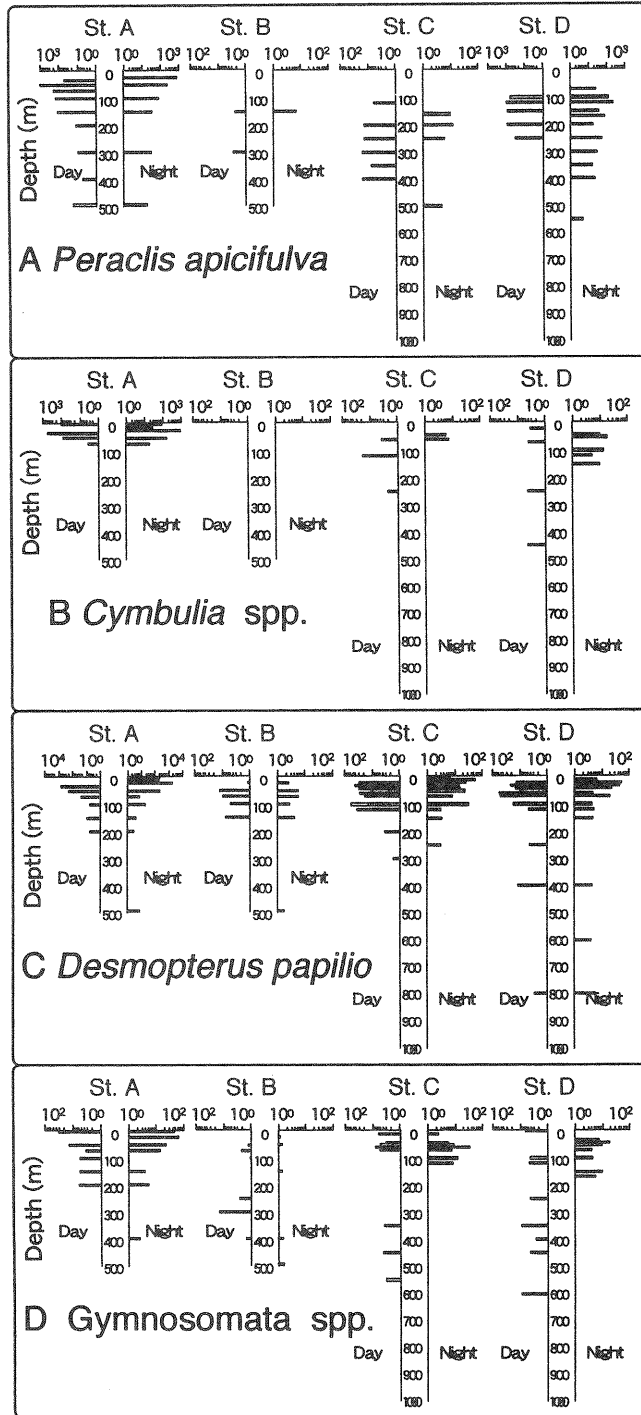


Fig. 10. Vertical distribution of population density (inds. $(10^3 \text{ m}^3)^{-1}$) . (A: *Peraclis apicifulva*, B: *Cymbulia* spp, C: *Desmopterus papilio*, D: *Gymnosomata* spp.)

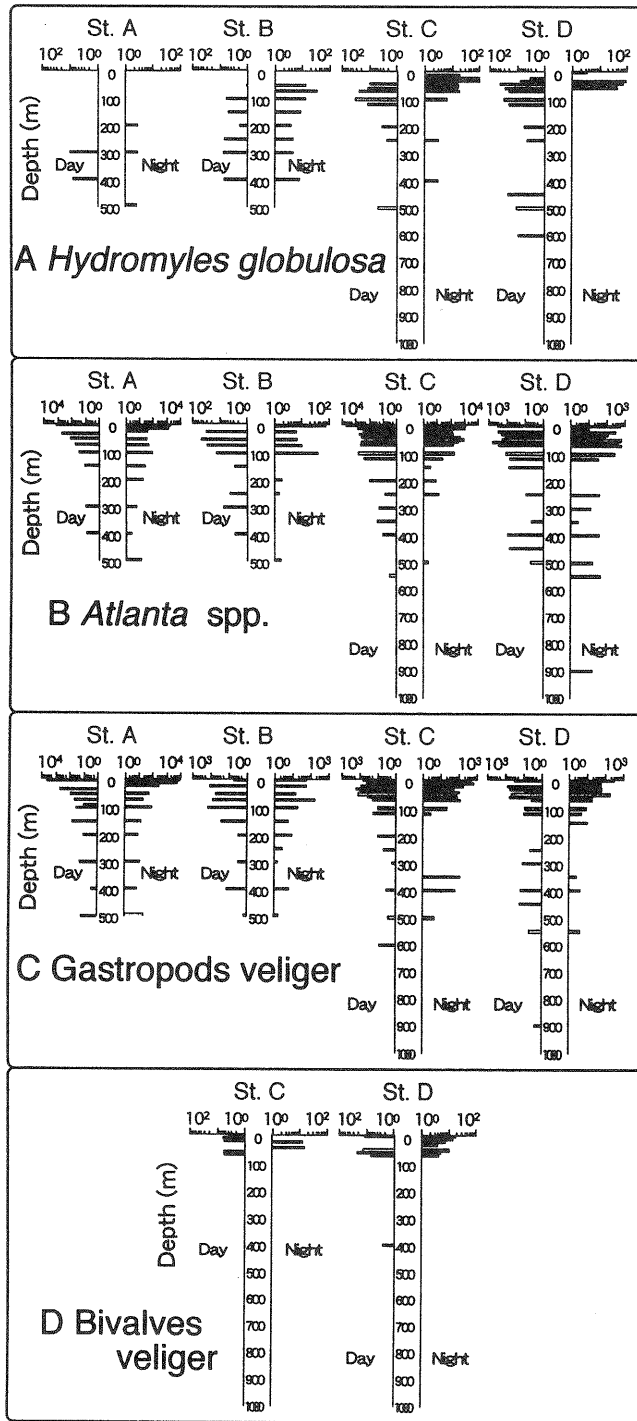


Fig. 11. Vertical distribution of population density (inds. (10³m³)⁻¹) . (A: *Hydromyces globulosa*, B: *Atlanta* spp., C: Gastropods veliger, D: Bivalves veliger)

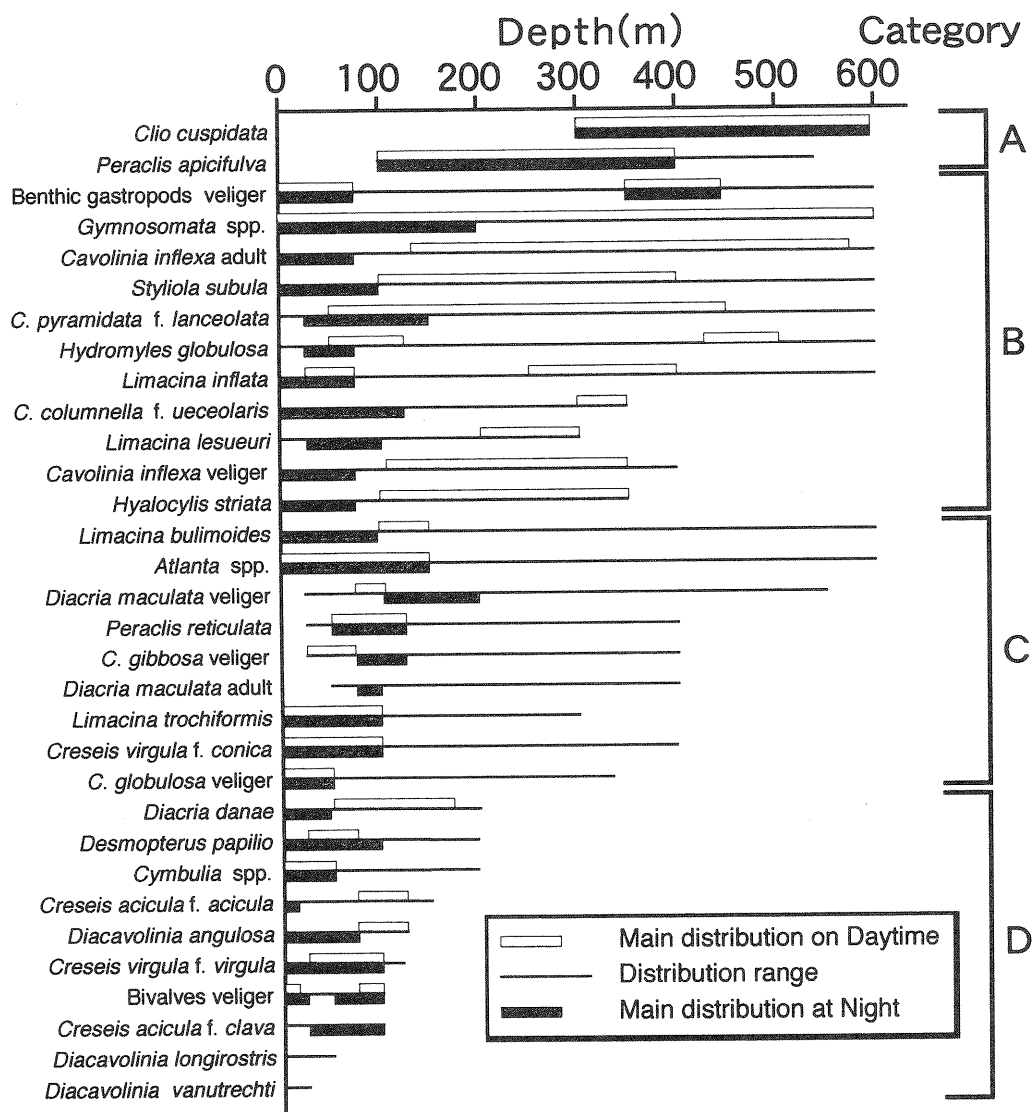


Fig. 12. Diagram of vertical distribution of planktonic mollusks and their category of distribution pattern.

なかった。昼間には極表層から深度 600 m と中深層にまで出現するが、夜間には極表層から深度 150 m の表層内に集中した (Fig. 10-D)。

Hydromyles globulosa は、相模湾では採集個体が少なく、深度 200 m から 500 m に出現した (Fig. 11-A)。外洋域 (St. B, St. C および St. D) では極表層から中深層にいたる深度 600 m に出現した。昼間には深度 25 m から 600 m と広い深度に出現し、深度 100 m 付近と深度 500 m 付近にそれぞれピークがあった。夜間には深度 100 m 以浅に集中して出現した。海域によって生

息深度が異なり、表層内もしくは表層と中深層との間で昼夜鉛直移動を行うと考えられる。

Atlanta spp. は、極表層から上部漸深層にいたる深度 900 m に出現した (Fig. 11-B)。広い深度に出現したが、多くの個体は極表層から深度 150 m の上部表層内に集中して出現し、昼夜で変化がなかった。

底生性腹足類のベリジャー幼生は、極表層から上部漸深層にいたる深度 900 m に出現した (Fig. 11-C)。深度 100 m 以浅の上部表層と深度 400 m 付近にピークがあったが、それらの由来は不明である。底生性斧足類の

ベリジャー幼生は、外洋域の St. C および St. D において採集された。極表層から深度 400 m に出現したが、多くの個体は 75 m 以浅の上部表層に出現した (Fig. 11-D)。

浮遊性軟体動物の多くは、夜間は深度 100 m 以浅の表層に出現するが、昼間の出現層は種により異なった。また 300 m 以深に出現が限られる中深層性種や、昼間に上層に出現し夜間に最も深くまで下降する「nocturnal migration」を行う種があった。*D. maculata* のように、成長段階によって昼夜の出現層が異なる種もあり、鉛直分布生態は多様であった。

外洋域 (St. B, St. C および St. D) に出現した有殻翼足亜目 20 種 8 型とその他の浮遊性軟体動物に関して鉛直分布模式を図示し (Fig. 12)、鉛直分布について以下の 4 つに類型化した。

- A 表層下縁から中深層に生息する。昼夜鉛直移動を行わない中深層性種である。*Clio cuspidata* と *Peracris apicifilva* である。
- B 表層から中深層に生息する。昼夜で主な生息層が異なり、昼間は中深層に生息し、夜間は表層へと広範囲な移動を行う。
代表種は、*Limacina inflata* である。
- C 表層から中深層に生息するが、主な生息層は表層である。
代表種は、*Limacina bulimoides* である。
- D 生息層が昼夜とも表層内に限られる。
代表種は、*Diacria danae* である。

上記カテゴリー A に含まれる *Clio cuspidata* は、昼夜移動をしない中深層種であるが、大型ネットによる表層採集によって大型の個体が希に採集されることもあり (小林, 未発表)、本調査では知り得なかった生態を持ち得る可能性がある。BEAND GILMER (1977) は、本研究では出現しなかった *Limacina helicoides*, *Clio polita*, *Clio chaptali* を深層性種 (Bathypelagic species) とし、他の浮遊性軟体動物は異なる鉛直分布生態を持つものとして区分している。これらは深度 500 m から 2000 m に出現し、*Clio cuspidata* の出現した深度 300 m から 600 m よりもさらに深層に分布する。

B および C は翼足目の鉛直分布で最も多い。これらは躍層を通過することから、水温と塩分の変化に対し広範囲に適応していると考えられる。

D は表層内に分布し、躍層以深には分布しない表層性種である。*Diacavolinia* 属は、採集個体が少なかったものの、出現した 3 種ともにこのタイプであった。

5. 考察

本研究で出現した有殻翼足亜目は、相模湾では 12 種、外洋域では 20 種であった。特に、カメガイ亜科に含まれる *Diacria* 属、*Cavolinia* 属および *Diacavolinia* 属は、相模湾ではほとんど採集されなかった。これらカメガイ

亜科に含まれる 3 属は、外洋域を主たる生息場とする。本来の分布域から離れた相模湾での出現は、海流による輸送の影響を大きく受ける。調査時の黒潮流軸は相模湾から離れており、黒潮による輸送個体の減少と密度低下、さらに湾内の水温および塩分の低下に示される生息環境の変化によって、出現種が減少したと考えられる。

浮遊性軟体動物の多くは、昼間表層から中深層に生息し夜間表層に出現する昼夜鉛直移動を活発に行っていると考えられる。夜間の生息層は深度 100 m 以浅に集中するが、昼間の生息層は種によって異なった。それら以外に、昼間に上層に生息し夜間に最も深くまで下降する「nocturnal migration」を行う種、深度 300 m から 500 m に生息層が限られる中深層性種が確認された。

昼間と夜間を過ごすための好適な深度は種ごとに異なり、さらに生活戦略や性によっても異なるであろう。一般に、動物プランクトンの鉛直分布は、水中照度、水温、塩分、溶存酸素濃度、水圧などの環境条件によって大きな影響を受け、上層から供給される餌料の量やその沈降速度、分解速度とも密接な関係を有する。本研究で取り上げた浮遊性軟体動物においても、生息層の幅や分布の中心といった鉛直分布が、水域ごとの海洋環境の特徴に対応し、相異していた。昼間の生息層は、相模湾では深度 100 m 付近に集中したが、外洋域では多くの種がさらに下層、すなわち下部表層から深度 400 m の中深層に集まり、水域によって鉛直分布が異なった。相模湾 St. A におけるこれらの深度 150 m から 100 m では、水温は 12.8 °C から 13.8 °C、塩分は 34.47 から 34.49 であり、低温低塩分な沿岸水の影響を大きく受けた表層水である。一方、外洋域 St. C における深度 400 m から 350 m では、水温は 11.9 °C から 13.8 °C、塩分は 34.33 から 34.49 で、西部北太平洋中層水である (KIMRA *et al.*, 1994)。浮遊性軟体動物の昼間の生息層は特定の範囲の水温と塩分によく一致し、異なる水域であればその海洋構造に応じて変化すると考えられる。

フロリダ海流域では *Limacina* 属に含まれる 4 種の昼間の生息層は、*L. bulimoides* が深度 80 m 付近、*L. inflata* が深度 236 m から 300 m 付近、*L. lesueurii* が深度 100 m 付近、*L. trochiformis* が深度 165 m 付近である (van der SPOEL, 1997)。本研究の外洋域におけるそれら 4 種の昼間の分布は、*L. bulimoides* が深度 150 m 付近、*L. inflata* が深度 200 m から 400 m、*L. lesueurii* が深度 200 m から 300 m、*L. trochiformis* が深度 100 m 以浅であった。*L. trochiformis* 以外の 3 種は、太平洋外洋域でより深層くに生息し、種毎の生息層の順番が異なった。鉛直分布、特に昼間の主な生息層が同属種間で互いに異なる傾向は、上述の *Limacina* 属以外、*Creseis* 属、*Clio* 属、*Diacria* 属、*Cavolinia* 属、*Peracris* 属にも見られた。種内変異型が認められた *Creseis aciculata* と *Creseis virgura* は、それぞれで鉛直分布が異なり、両者の生態的差異を裏付ける結果となった。有殻翼足亜

目は、雄性先熟の雌雄同体である。カメガイ科の場合、雄性個体同士が交接し精包を交換し合うことにより、有性生殖が行われる。精子は精包から伸びた軸を通して輸送され、体内に蓄えられる。雄性生殖器官が消滅し雌性生殖器官が完全に成熟して雌相に移ると、貯め込まれていた精子を用いて受精が行われる (LALLI and GILMER, 1989)。このように生活史の早い時期に配偶子の交換が行われるので、成長段階の同じ個体がある特定の水深に集中することは、他の動物プランクトンに比べて個体数密度が低い有殻翼足亜目には、繁殖の機会を高める有効な手段であると考えられる。さらに種内変異型間もしくは同属種間といった近縁種間で生息層を違えることにより、同じ種内変異型のみが集中し、生殖的隔離を強める効果があると考えられる。

生活環もしくは個体発生に伴って生息空間が変化する現象は、動物プランクトンのみならず動物界一般によく見られる現象である。底生性軟体動物においては、イシダミ (*Monodonta*) 属をはじめとして多くの腹足綱において個体の成長に伴う生息場所の変化が報告されている (IJIMA and FUROTA, 1996)。浮遊性被囊類のウミタル (*Doliolujm*) 類では、無性生殖個体 (oozoid) と有性生殖個体 (gonozoid) とではそれぞれの生息層が異なり、一生を通して鉛直分布が変化する (西川, 1995)。また、個体の日周鉛直移動幅や生息深度がその成長に伴って変化し、一般に若い個体ほど上層に見られる現象は、表層性ヤムシ類の *Sagitta elegans* (TERAZAKI, 1993, TERAZAKI and MARUMO, 1982)、オキアミ類や遊泳性エビ類等の浮遊性甲殻類 (根本, 1974, 大森, 1974) といった、遊泳力の大きい大型の動物プランクトンにおいて知られている。サイズもしくは成長段階を区別した有殻翼足亜目 *Limacina inflata*, *Creseis virgula* forma *conica*, *Clio pyramidata* forma *lanceolata*, *Diacria maculata*, *Cavolinia inflexa* は、5種とも成長段階の進んだものがより深い深度に生息し、幼体とは異なる鉛直分布であった。さらに *D. maculata* のベリジャー幼生は、昼間の分布深度が夜間よりも浅い「nocturnal migration」を行った。このような通常とは逆向きの昼夜鉛直移動は、*Limacina retroversa* においても報告がある (WORMUTH, 1985)。

SMITH and TEAL (1973) は、昼夜鉛直移動を行う表層性種と鉛直移動を行わない深層性種について、その生息深度幅における水温、水圧と呼吸との関係を調べた。その結果、生息深度範囲での水温の変化に伴って、表層性種では呼吸速度に変化が生じたが、深層性種では変化しなかった。さらに水圧に関しては、表層性種では 50 atm 以上の条件で死に至り、深層性種では 50 atm から 150 atm で通常の酸素取り込みが行われた。これらの結果から表層性種は昼間は水温の低い中深層で過ごすことにより、呼吸によるエネルギー消費を最小にし代謝効率を増大させると考えられている。本研究で出現した翼足

目の多くは、表層から中深層と生息深度幅が広く、水温や塩分の躍層を通過して活発に昼夜鉛直移動を行っていた。その移動に要するエネルギーを上回る利点の一つとして、代謝効率の増大があると考えられる。

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資 料

第 39 卷第 4 号掲載欧文論文要旨

Nittaya CHAIYANATE*・門谷 茂* : 瀬戸内海の河口干潟域潮下帯における堆積物環境の季節変化と底生生物群集の応答

瀬戸内海の東部備讃瀬戸に面する河口干潟において、その潮下帯に 8 定点を設け、1998 年 11 月から 2000 年 2 月にかけて、合計 6 回にわたって海洋観測を行うとともに、底生生物を採取し、優占種の特定と生物量等を定量した。また、堆積物中の各種化学パラメーターの分析定量を行った。その結果、二枚貝の *Teora fragilis* と多毛類の *Kumbrineris* が優占していた。埋め立て地の直立護岸に近い定点では、種組成、生物量とも極めて変動が大きく、冬季に優占したのは、日和見種である小型多毛類の *Capitella* sp. 1 であった。底生動物の群集組成から、水質データなどからは区別ができなかった 8 定点を、4 つのクラスターに明確に分けることができた。(*香川大学農学部生命機能科学科 〒761-0795 香川県木田郡三木町池戸)

堀本奈穂*・山口征矢*・石丸 隆* : 黒潮を横切る西部太平洋海域におけるピコ植物プランクトンの分布

黒潮を横切る西部太平洋海域において、ピコ植物プランクトン (3 μm 以下) の分布を蛍光顕微鏡を用いて調査した。ピコ植物プランクトンは *Synechococcus* (単細胞性ラン藻) および *Prochlorococcus* (原核緑藻) と少数種の鞭毛藻からなる真核ピコ植物プランクトンで構成されていた。*Synechococcus* は黒潮流軸において優占したが、*Prochlorococcus* は黒潮よりも南側の海域に卓越した。これらの分布パターンの違いは、混合層内の水温と栄養塩濃度に起因すると考えられた。一方、真核ピコ植物プランクトンの細胞数は、海域間における変化が小さかったが、クロロフィル極大水深付近に多く見られた。高濃度の *Synechococcus* が黒潮流軸に出現したのは、黒潮フロント渦や秋季に成層が崩れることによって混合層内に栄養塩が供給されたためと考えられた。弱光適応型の *Prochlorococcus* は、水温が 20 $^{\circ}\text{C}$ 以上の亜表層にのみ分布していた。(*東京水産大学海洋環境学科 〒108-8477 東京都港区港南 4-5-7)

学 会 記 事

1. 2001年9月12日(水) 東京水産大学において幹事会(第3回)が開催された。主な議事は下記の通り。

(1) 報告事項

- 10月1日付けで会計幹事を松山優治会員から山崎秀勝会員へ交代する。
- 10月1日~10月5日に開催される日本水産学会創立70周年記念国際シンポジウムで、日仏海洋学会の概要の紹介を行うパネル展示に参加することを水産学研連へ回答した。
- 学会の英文表記を Japanese-French Oceanographic Society とすることとした。
- その他

(2) 審議事項

- 日仏海洋学会論文賞規定の原案が提案され、文言修正の上承認された。
- 日本水産学会創立70周年記念国際シンポジウムにおける日仏海洋学会の概要の紹介を行うパネル展示(案)が示され、審議の結果承認された。
- 本学会のホームページを開設することを検討していくこととなった。
- 学会誌 La mer 第38巻第4号(第10回 JECSS/PAMS ワークショップ特集号)の一般配布価格は通常号と同じ1600円とすることとした。

2. 2001年11月19日(月) 東京水産大学において幹事会(第4回)が開催された。主な議事は下記の通り。

(1) 報告事項

- 9月24日、清水市で開催された日本海洋学会創立60周年記念祝賀会において、今協副会長が学会を代表して祝辞を述べた。
- 10月3日、4日の両日、横浜市で開催された日本水産学会創立70周年記念国際シンポジウムにおいて、日仏海洋学会の紹介パネルの展示、学会誌、記念出版物等の展示を行った。
- 10月26日に日仏会館で開催された学会協会に佐伯和昭会員が出席、12月1日開催予定のシンポジウムの内容について協議が行われた。
- 日本学術会議から学会のホームページがあれば相互にリンクして欲しいとの依頼があった。

(2) 審議事項

- 学会のホームページを至急立ち上げることとした。
- 12月1日開催予定の日仏会館シンポジウム時の座長は会長が対応することとした。
- 平成14年・15年度の学会役員の選出日程を以下次のように決定した。

公示、投票期間:

平成13年11月26日~平成14年1月5日

開票:平成14年1月15日(火)

3. 2001年11月19日(月) 東京水産大学において学会賞等選考委員会(第1回)が開催され、選考委員長に関文威会員を選出し、選考の方法等を審議した。

4. 新入会員(正会員・学生会員*)

氏名	所属・住所等	紹介者
森重輝政	(株)東京久栄	森永 勤
	〒333-0866 埼玉県川口市芝鶴丸6906-10	

5. 退会

小菅 晋(逝去)、堀越増興、中村幸雄、安達六郎、中村 泉

6. 受贈図書(受付順)

農業工学研究所ニュース 19
養殖研究所研究報告 30
なつしま 187, 188, 189
NTT R&D 50 (9, 10)
NII News 6, 7
農業工学研究所年報 13
ОКЕАНОПОТИЯ 41 (2, 3, 4)
Journal of the Korean Society of Oceanography 36 (3, 4)
Travaux de la Station Biologique de Roscoff 38
Ocean and Polar Research 23 (3, 4)

La mer (Bulletin de la
Société franco-japonaise
d'océanographie)
Tome 38 (2000)

Sommaire

Numéro 1

Notes originals

- Short-time scale phytoplankton variability and ambient conditions highly dynamic marine basin
.....Wagdy LABIB 1-9
- Research on providing habitable environment for bivalves by use of artificial reefs
.....Hirokazu SUMI and Akira WADA 11-25

Conférence à la remise du Prix de la Société franco-japonaise d'océanographie

- Original achievements reading inductivity towards quantitative evaluation of detritus food chains in the marine food webHumitake SEKI 27-37

Faits divers

- Interannual variations of coastal sea levels and annual tides spectra neighbor Kuroshio flow (in Japanese)
.....Shigehisa NAKAMURA 39-43
- Abstracts of the papers presented in annual meeting (in Japanese) 44-49

- Procès-verbaux 51-56

Numéro 2

Notes originales

- Quantification of microphytobenthos in intertidal sediments: layer dependent variation of chlorophyll *a* content determined by spectrophotometric and HPLC methodsPaolo MAGNI, Nao ABE and Shigeru MONTANI 57-63
- Seasonal variation in sea surface temperature around Java derived from NOAA AVHRR
.....Suhendar I SACHOEMAR and Tesuo YANAGI 65-75
- Ontogenetic intervals based on the development of swimming- and feeding-related characters in the hexagrammid, *Hexagrammos agrammus*, larvae and juveniles (in Japanese)

うみ (日仏海洋学会誌)

第38巻 (2000年)

総目次

第1号

原著

- 変動の激しい海域における植物プランクトンの短期間変動とその周辺の条件 (英文)
.....Wagdy LABIB 1-9
- 人工リーフによる二枚貝生息場の好適化に関する研究 (英文)
.....鷺見浩一・和田 明 11-25

日仏海洋学会賞受賞記念講演

- 海洋食物網における腐食連鎖の卓越性に関する主導的研究 (英文)関 文威 27-37

資料

- 黒潮流域の沿岸潮位および年周潮スペクトルの長期変動中村重久 39-43
- 平成12年度日仏海洋学会学術研究発表会講演要旨 44-49
- 第38巻第1号掲載欧文論文の和文要旨 50
- 学会記事 51-56

第2号

原著

- 表層堆積物中の底生微細藻類生物量の定量: 分光光度法と HPLC 法で測定したクロロフィル *a* 量の比較 (英文)
.....Paolo MAGNI・門谷 茂 57-63
- NOAA 熱赤外画像によるジャワ島周辺の海面水温の季節変動特性 (英文)
.....Suhendar I SACHOEMAR・柳 哲雄 65-75
- 遊泳と摂餌に関する形質の発達に基づいたクジメ仔稚魚の発育段階
.....河野 博・栗田 豊・青海忠久 77-86
- 紀伊半島に接近する東に直進する黒潮から切離した暖水の構造 (英文)

…Hiroshi KOHNO, Yutaka KURITA and Tadahisa SEIKAI	77-86
Warm water structure that approaches to Kii Peninsula, separated from the straight zonal Kuroshio Path …Yoshihiko SEKINE and Takayuki OKUBO	87-93
Résumé	
Pigment composition of <i>Pedinomonas noctilucae</i> (Pedinophyceae), an endo- symbiont of green <i>Noctiluca</i> (Dino- phyceae) …Ken FURUYA and Thaithaworn LIRDWITAYAPRAST	95-97
Faits divers ………………	99
Procés-verbaux ………………	101-102

Numéro 3

Sommaire complet, Tomes 19-37 (1981- 1999)	
Edition special pour la commémoration du quarantieme anniversaire	103-164

Numéro 4

The Proceedings of the 5th Interna- tional Marine Science Symposium on the Physical, Biological, Chemical and Geological Processes in the Pacific Ocean and Asian Marginal Seas (The tenth PAMSS/JECSS Workshop)	
Preface ………………Akio MAEDA and Hiroshi ICHIKAWA	165
Introduction: the physical, biological, chemical and geological processes in the Pacific Ocean and asian marginal seas …Hiroshi ICHIKAWA and Akio MAEDA	167-172
The Kuroshio east of Taiwan and in the East China Sea in July 1997 …Yaochu YUAN, Yonggang LIU, Huiqun WANG, Jilan SU and Arata KANEKO	173-178
Variation of the currents east of the Ryukyu Islands in 1998 …Yonggang LIU and Yaochu YUAN	179-184
Study on the free oscillations in the Yel- low Sea ………………Chengchun QIAN	185-188
Circulation patterns of the Japan Sea …Vladimie PONPMAREV and Olga TRUSENKOVA	189-198
The SeaSonde HF radars for coastal cur- rent mapping with recent oceanog- raphic applications …Donald E. BARRICK,	

…関根義彦・大久保孝之	87-93
短 報	
グリーンノクチルカに細胞共生する緑色鞭 毛藻類 <i>Pedinomonas noctilucae</i> の色素 組成 (英文) …古谷 研・Thaithaworn LIRDWITAYAPRASIT	95-97
資 料	
第38巻第2号掲載欧文論文の和文要旨 …	99
学会記事……………	101-102

第 3 号

創立 40 周年記念号 論文総目次集 第 19 巻 ～第 37 巻 (1981-1999)	103-164
--	---------

第 4 号

第 5 回 太平洋およびアジア縁辺海域の物 理, 生物, 化学および地学過程に関する国 際海洋科学シンポジウムプロシーディン グス (第 10 回 JECSS/PAMS ワークショッ プ)	
はじめに……………前田明夫・市川 洋	165
序論: 太平洋およびアジア縁辺海域の物理, 生物, 化学および地学過程 (英文) …市川 洋・前田明夫	167-172
1997 年 7 月の台湾東方および東シナ海にお ける黒潮 (英文) …Yaochu YUAN・Yongganng LIU・ Huiqun WANG・Jilan SU・金子 新	173-178
1998 年の琉球列島東方の流れの変動 (英文) …Yonggang LIU・Yaochu YUAN	179-184
黄海の自由振動 (英文) …Chengchun QIAN	185-188
日本海の循環パターン (英文) …Vladimie PONPMAREV and Olga TRUSENKOVA	189-198
沿岸流の流動分布測定のためのシーズンデ短 波海洋レーダーとその最近の海洋学的応用 (英文) ………………Donald E. BARRICK, Laura A. PEDERSON and	

Laura A. PEDERSON and Steven R. RAMP Seasonal changes of circulation in North Pacific by a MOM2 simulationDongfeng XU, Yaochu YUAN, Noriya YOSHIOKA and Tasushi YOSHIKAWA	199-203 205-210	Steven R. RAMP MOM2 数値モデルによる北太平洋循環の季 節変動 (英文)Dongfeng XU, Yaochu YUAN, Noriya YOSHIOKA and Tasushi YOSHIKAWA	199-203 205-210
Water, heat and salt transports from diag- nostic world ocean and north Pacific cir- culation modelsZexun WEI, Byung-Ho CHOI and Guohong FANG	211-218	全球と北太平洋の海水循環に関する診断型モ デルから求めた水と熱と塩分の輸送料 (英 文) ...Zexun WEI, Byung-Ho CHOI and Guohong FANG	211-218
Coastal impacts of offshore meso-scale ed- dies through the Kuroshio variationKaoru ICHIKAWA and Atsushi KANEDA	219-226	外洋中規模渦の黒潮変動を通じた沿岸への影 響 (英文)市川 香・金田 篤 高潮の数値計算における抵抗係数の影響 (英 文)Xiuqin WANG, Chengchun QIAN and Wei WANG	219-226 227-231
The influence of the drag coefficient on the simulation of storm surges ...Xiuqin WANG, Chengchun Qian and Wei WANG	227-231	シベリア寒気の吹き出しによる大規模大気攪 乱への日本海 (東海) の応答についての数 値計算結果 (英文)Christopher N. K. MOOERS, HeeSook KANG and Shuyi S. CHEN	227-231 233-243
Several aspects of the simulated response of the Japan (East) Sea to synoptic at- mospheric forcing due to siberian cold air outbreaksChristopher N. K. MOOERS, HeeSook KANG and Shuyi S. CHEN	233-243		

La mer (Bulletin de la
Société franco-japonaise
d'océanographie)
Tome 39 (2001)

うみ (日仏海洋学会誌)

第39巻 (2001年)

総目次

Sommaire

Numéro 1

Notes originals

Microscale processes in the ocean: why are they so important for ecosystem functioning?Laurent SEURONT	1-8
Size-fractionated chlorophyll <i>a</i> and primary productivity in the offshore Oyashio waters in July 1992Akihiko SHIOMOTO and Shinji HASHIMOTO	9-18
Recent trends of nutrients in Tokyo Bay (1989-1998) (in Japanese)Tsuyoshi MATSUMURA, Naho HORIMOTO and Takashi ISHIMARU	19-32
Prof. Luigi Sanzo: a bibliographic revision with ichthyological noteKazunori TAKAGI	33-58
Faits divers	59
Procès-verbaux	60-62

Numéro 2

Notes originales

Numerical modeling of density-driven current in Tokyo BayIvonne M. RADJAWANE, Masaji MATSUYAMA, Yuji KITADE and Toru SUZUKI	63-75
Seasonal variation of water characteristics in the northern coastal area of JavaSuhendar I. SACHOEMAR and Tetsuo YANAGI	77-85
Automated identification of larval bivalbs utilizing an image processor (in Japanese)Makoto TERAZAKI, Masami HAMAGUCHI, Hironori USUKI and Hiroko ISHIOKA	87-93
Oceanic structure in the vicinity of Komahashi Daini Kaizan, a seamount in the Kyushu-Palau Ridge. Part I. Temperature and salinity fieldsYoshihiko SEKINE	95-106
Oceanic structure in the vicinity of Komahashi Daini Kaizan, a seamount in the Kyushu-Palau Ridge. Part II.	

第1号

原 著

海洋の微細構造: 生態系にとってなぜ重要なのか? (英文)Laurent SEURONT	1-8
1992年7月の沖合域の親潮水域におけるサイズ分画したクロロフィル <i>a</i> と基礎生産力 (英文)塩本明弘・橋本慎治	9-18
東京湾における栄養塩の動向 (1989-1998)松村 剛・堀本奈穂・石丸 隆	19-32
寄 稿	
ルイジ・サンツォ教授業績目録の校訂と校註 (英文)高木和徳	33-58
資 料	
第39巻第1号掲載欧文論文の要旨	59
学会記事	60-62

第2号

原 著

東京湾の密度流に関する数値実験 (英文)Ivonne M. RADJAWANE・松山優治・北出裕二郎・鈴木 亨	63-75
ジャワ北岸海洋の水質の季節変化 (英文)Suhendar I. SACHOEMAR・柳 哲雄	77-85
画像解析システムを用いた二枚貝幼生の自動識別法の試み寺崎 誠・浜口正巳・薄 浩則・石岡宏子	87-93
九州パラウ海嶺にある駒橋第二海山近辺の海洋構造	
第1部 水温および塩分分布 (英文)関根義彦	95-106
九州パラウ海嶺にある駒橋第二海山近辺の海洋構造	
第2部 流速場 (英文)関根義彦	107-112

Velocity fields	Yoshihiko SEKINE	107-112
Faits divers		113
Procès-verbaux		114-119

Numéro 3

Notes originales

Reconstruction of the feeding activity of marine top-predators foraging at sea	Yan Ropert-COUDERT, Akiko KATO and yasuhiko NAITO	121-132
Allozyme determination of genetic diversity in Japanese and Thai populations of Oval Squid (<i>Sepioteuthis lessoniana</i> Lesson, 1830)	Boonyarath PRATOOMCHAT, Yutaka NATSUKARI, Ikuko MIKI and Kashane CHALERMWAT	133-139
Seasonal variations of the oceanic condition along the southern coastal area of Java to Sumbawa, Indonesia	Suhendar I SACHOEMAR and Tetsuo YANAGI	141-154
Conférence à la remise du Prix de la Société franco-japonaise d'océanographie		
Ecological studies on carnivorous plankton, Chaetognatha (in Japanese)	Makoto TERAZAKI	155-160
Faits divers		161
Proces-verbaux		162-166

Numéro 4

Notes originales

Response of macrobenthic community to seasonal sediment environmental parameter changes in a tidal estuary of the Seto Inland Sea, Japan	Nittaya CHAIYANATE and Shigeru MONTANI	167-180
The distribution of picophytoplankton across Kuroshio Current off the Western Pacific Coast of Japan	Naho HORIMOTO, Yukuya YAMAGUCHI and Takashi ISHIMARU	181-195
Vertical distribution of holoplanktonic mollusks in the western North Pacific (in Japanese)	Harumi KOBAYASHI and Makoto TERAZAKI	197-214
Faits divers		215
Proces-verbaux		216
Sommaire du Tome 38		(1)-(3)
Sommaire du Tome 39		(4)-(5)

資料		
第 39 卷第 2 号掲載欧文論文の要旨		113
学会記事		114-119

第 3 号

原 著

海洋高次捕食者の採餌行動の再構築 (英文)	Yan Ropert-COUDERT・加藤明子・内藤靖彦	121-132
日本産およびタイ産アオリイカの遺伝的多様性のアロザイム分析 (英文)	Boonyarath PRATOOMCHAT・夏 莉 豊・三木育子・Kashane CHALERMWAT	133-139
インドネシア, ジャワースンバワ南岸沿いにおける海況の季節変動 (英文)	Suhendar I SACHOEMAR・柳 哲雄	141-154
日仏海洋学会賞受賞記念講演		
肉食プランクトン毛顎動物の生態学的研究	寺崎 誠	155-160
資料		
第 39 卷第 3 号掲載欧文論文の和文要旨		161
学会記事		162-166

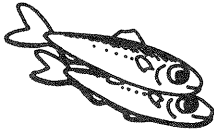
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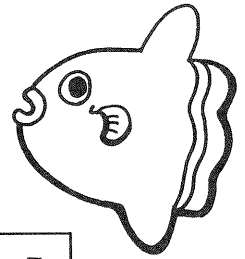
瀬戸内海の河口干潟域潮下帯における堆積物環境の季節変化と底生生物群集の応答 (英文)	Nittaya CHAIYANATE・門谷 茂	167-180
黒潮を横切る西部太平洋海域におけるピコ植物プランクトンの分布 (英文)	堀本奈穂・山口征矢・石丸 隆	181-195
西部北太平洋における浮遊性軟体動物の鉛直分布	小林晴美・寺崎 誠	197-214
資料		
第 39 卷第 4 号掲載欧文論文の和文要旨		215
学会記事		216
第 38 卷総目次		(1)-(3)
第 39 卷総目次		(4)-(5)

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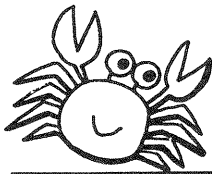


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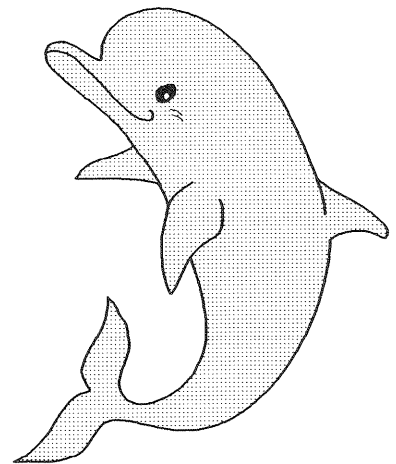
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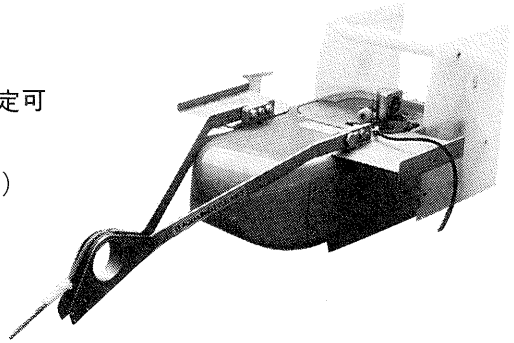
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第 39 卷 第 4 号

Notes originales

- Response of macrobenthic community to seasonal sediment environmental parameter changes in a tidal estuary of the Seto Inland Sea, Japan
.....Nittaya CHAIYANATE and Shigeru MONTANI 167
- The distribution of picophytoplankton across Kuroshio Current off the Western Pacific Coast of Japan
.....Naho HORIMOTO, Yukuya YAMAGUCHI and Takashi ISHIMARU 181
- Vertical distribution of holoplanktonic mollusks in the western North Pacific (in Japanese)Harumi KOBAYASHI and Makoto TERAZAKI 197

Faits divers215

Procès-verbaux 216

Sommaire du Tome 38 (1)

Sommaire du Tome 39 (4)

原 著

- 瀬戸内海の河口干潟域潮下帯における堆積物環境の季節変化と底生生物群集の応答 (英文)Nittaya CHAIYANATE・門谷 茂 167
- 黒潮を横切る西部太平洋海域におけるピコ植物プランクトンの分布 (英文)堀本奈穂・山口征矢・石丸 隆 181
- 西部北太平洋における浮遊性軟体動物の鉛直分布.....小林晴美・寺崎 誠 197

資 料

- 第 39 卷第 4 号掲載欧文論文の和文要旨215
- 学会記事.....216
- 第 38 巻総目次(1)
- 第 39 巻総目次(4)

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