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# Development of benthic microalgal assemblages on an intertidal flat in the Seto Inland Sea, Japan: effects of environmental variability

Paolo MAGNI* and Shigeru MONTANI*

**Abstract** : A bi-weekly survey lasting 13 months was carried out at low-tide on an intertidal flat in the Seto Inland Sea, Japan. We monitored the environmental conditions at a river and a low-tide shore-line stations and examined the factors affecting the development of benthic microalgal assemblages. At the two stations, the physico-chemical parameters of both emerged sediment (*i.e.* nutrient concentrations of the pore water) and the nearby low-tide water (*i. e.* salinity and dissolved oxygen concentration) showed strong but similar short- (days) and long-term (interannual) variability. However, the benthic microalgal standing stock was significantly higher at the river station (240.5±121.1mg $m^{-2}$, n=107) than at the low-tide shore line station (121.9±41.4 mg $m^{-2}$, n=108). Accordingly, estimated annual primary production was 634 g C $m^{-2}yr^{-1}$(1.74±0.65 g C $m^{-2}day^{-1}$) and 259 g C $m^{-2}$ $yr^{-1}$ (0.71±0.27g C $m^{-2}$ $day^{-1}$), respectively. At the river station, more elevated than the low-tide shore-line station, the development of benthic microalgal assemblages was significantly limited by the washout caused by rainfall, but greatly enhanced during calm and fine weather. At the low-tide shore-line station, the reduced emersion of the surface sediment and the hydrodynamic energy (tidal currents, waves) were major factors responsible for keeping lower and less fluctuating microalgal biomass. Comparable primary production by intertidal microalgae (447gC $m^{-2}$ $yr^{-1}$) and phytoplankton in the Seto Inland Sea (285gC $m^{-2}$ $yr^{-1}$) is discussed as evidence of the high primary productivity of the intertidal zone, most likely underestimated in light of the grazing pressure by the macro-zoobenthos which is similarly abundant on this intertidal flat.

## 1. Introduction

The occurrence and the development of intertidal communities of the microphyto benthos, commonly represented by epipelic and epipsammic diatoms (COLIJN and DIJKEMA, 1981; COLIJN and DE JONGE, 1984; DE JONGE, 1985), are regulated numerous physico-chemical parameters. Such parameters include : temperature (COLIJN and BURT, 1975; ADMIRAAL, 1977a; ADMIRAAL and PELETIER, 1980; BLANCHARD *et al.*, 1996), salinity (ADMIRAAL, 1977b), gas diffusion and nutrient fluxes (ADMIRAAL *et al.*, 1982; WHILSHIRE, 1992), and organic enrichment (PELETIER, 1996).

Along a tidal estuary, noticeable differences in the benthic microalgal standing stock may also depend on the elevation of the station, which relates to the extent of the solar radiation available for the photosynthesis (ADMIRAAL and PELETIER, 1980; COLIJN and DE JONGE, 1984; DE JONG and DE JONGE, 1995) and the influence of the atmospheric condition on dessication and/or freezing of the emerged sediment (ADMIRAAL *et al.*, 1982) and flushing away of epipelic diatoms with the rainfall.

Further variability is related to the tidal currents and waves which influence the immigration rate (STEVENSON, 1983) and cause resu spension and transport of the microphytobenthos (MOSS and ROUND, 1967; CADÉE and HEGEMAN, 1974; DE JONGE and VAN DEN BERG,

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1987; Grant *et al.*, 1988). Accordingly, physical sorting and grain-size composition of the sediment have been demonstrated important factors controlling the dynamics of the species composition of benthic diatoms (De Jonge, 1985) and the microalgal biomass (Colijn and Dijkema, 1981; De Jong and De Jonge, 1995), respectively.

All these physico-chemical and abiotic variables, along with the grazing pressure by the macro-zoobenthos (Nicotri, 1977; Lopez and Levinton, 1987; Bianchi and Rice, 1988; Smith *et al.*, 1996), are likely to affect the benthic microalgal biomass independently from expected seasonal patterns which may justify an estimation of the annual microphytobenthic production on the basis of relatively few Chl *a* samples distributed over the year (Cadée and Hegeman, 1977; Colijn and De Jonge, 1984). MacIntyre and Cullen (1996) recently suggested that the optimal use of resources to quantify the microalgal productivity would focus on between-day rather than within-day (Pinckney *et al.*, 1994) variability.

In light of such a variability, during the present study we made an intensive sampling effort (two times per week for 13 months) in order to assess the short-time (days) and seasonal environmental variability of an intertidal flat during low-tide in the Seto Inland Sea, and to examine the factors affecting the development of the microphytobenthos. A total of more than a hundred samples were collected at two stations, which allowed a more reliable estimation of the annual primary production. Values of annual primary production by the microphytobenthos reported from other intertidal flats and by the phytophankton in the Seto Inland Sea are compared and discussed within the frame of an integrated project which aims at quantifying the dynamics of biophilic elements (i.e. carbon, nitrogen and phosphorus) in this estuary and to assess the roles played by producers (microphyto benthos) and consumers (macrobenthos) on the processes.

## 2. Study area

The investigations were carried out at a river station (Stn.A) and a low-tide shore-line station (Stn. B4) of an intertidal flat in the Seto Inland Sea, south-western Japan (Fig. 1). The mean tidal range is *ca.* 2 m.

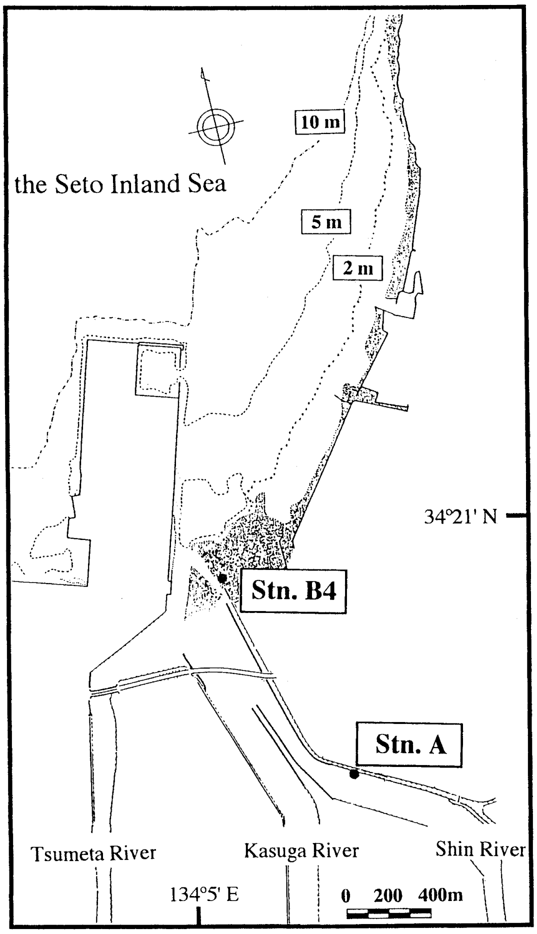


Fig. 1. Study area and location of the sampling stations.

The backwards Stn. A was more elevated and sheltered than Stn. B4, and was located about 1.1 km from the low-tide shore-line. The surface sediment emerged at a tidal level of about +140 cm. Stn. B4 was located near the low-tide shore-line, between the LWL (low water level) and the ELWL (extreme low water level), and therefore more exposed to the hydrodynamic energy of tidal currents and waves. The surface sediment emerged at a tidal level of about +70 cm.

Both stations were few ten meters away from the Shin River, which formed, during the low tide, a shallow pool (20 to 50 cm in depth) at

Stn. A and a reduced stream (20 to 50 cm in depth) at Stn. B4. The stream was flowing directly toward the low-tide shore-line and progressively mixing with intertidal and subtidal waters.

## 3. Materials and methods

### 3-1 *Sampling procedure and meteorological parameters*

Sampling activities always started from Stn. B 4. We monitored salinity (YSI portable salinometer), temperature and dissolved oxygen concentration (UK 2000 portable D.O. meter) of low-tide water close to the two stations. Emerged sediment samples were randomly taken at 7-8 spots of each station using acrylic core tubes (3 cm *i.d.*) gently pushed by hand into the sediment. Surface (0-0.5 cm) and sub-surface (0.5-2 cm) layers were carefully sliced off the sediment. Sediment samples from the same layer were pooled together and brought to the laboratory within 2 hours for chemical analysis. Sampling was carried out at low-tide twice a week from July 1993 to July 1994.

Data of daily rainfall and solar radiation were obtained from the Takamatsu Meteorological Agency Station, located near the intertidal flat under investigation.

### 3-2 *Sediment treatment*

In the laboratory, pigments were extracted from duplicate subsamples of wet sediment (*ca.* 1 g) using 90% acetone. After 24 hrs of darkness at 4℃, extracts were analyzed for Chl *a* and pheo-pigments by spectrophotometer, before and after acidification with 1N HCl, respectively, according to LORENZEN's (1967) method, as described in PARSONS *et al.* (1984), where the volume of water is substituted by the dry weight of the sediment, expressed in grams. From the same pool of fresh sediment, acid-volatile sulfide (AVS) content was determined in duplicate subsamples (*ca.* 1g) with an AVS test column (Gastec, Model 201L and 201H). Values were expressed as $\mu g\ g^{-1}$ and $mg\ g^{-1}$, respectively, and corrected for porosity, as measured by the water content (obtained after drying sediment subsamples at 105℃ for 20 hours). The remaining sediment was then centrifuged at 3,000 rpm for 20 min. The extracted pore water was filtered on small filters (0.45 μm) fitted to a 10 ml syringe and the obtained dissolved phase was stored at −20℃ for later analysis of $NH_4^+$-N and $(NO_3^- + NO_2^-)$-N. Nutrients were determined with a Technicon autoanalyzer II, according to STRICKLAND and PARSONS (1972). Not all the samples collected for pigment analysis were analyzed for nutrients due to the insufficient amount of extracted pore water.

For the particle-size determination of the sediment, 0 to 10 cm in depth core samples were collected at each station. They were freeze-dried and sieved on 2 mm, 1 mm, 500 μm, 250 μm, 125 μm and 63 μm mesh-size sieves. Particle-size composition was expressed as a percentage of the dry weight of each fraction.

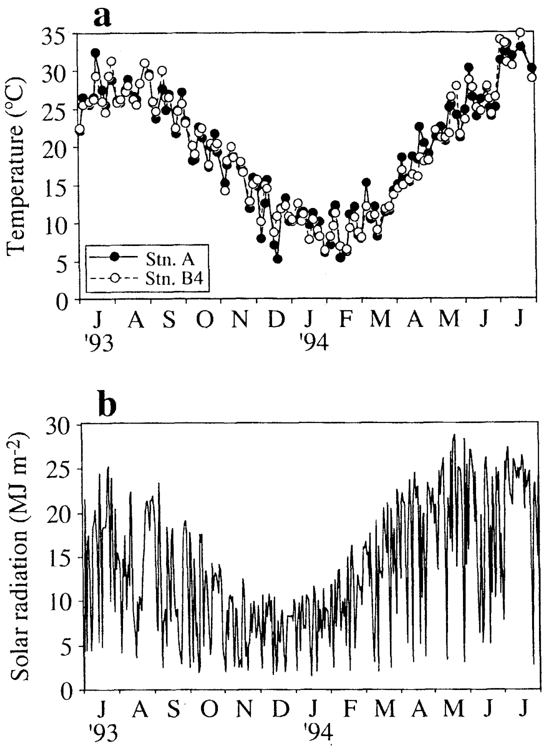
## 4. Results

### 4.1 *Physico-chemical parameters*

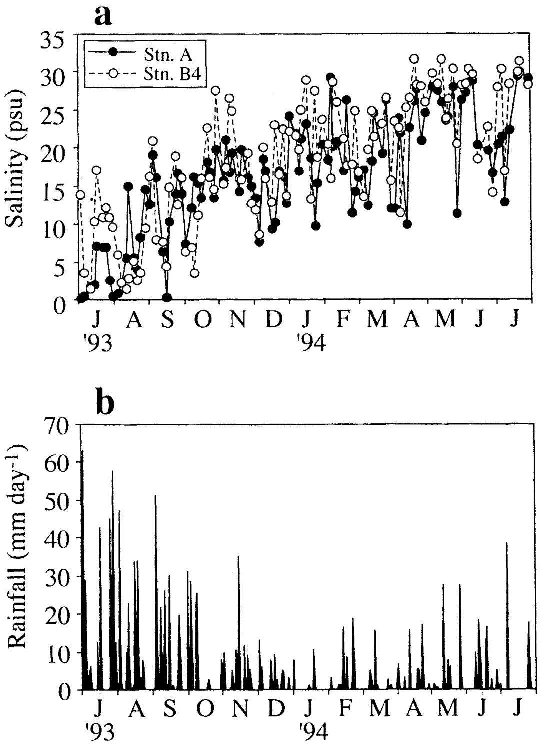
Low-tide water temperature (Fig. 2a) varied from 5.2℃ (December 18, 1993) to 34.8℃ (July 20, 1994) recorded at Stn. A and Stn. B4, respectively. It highly correlated with the temperature of emerged surface sediment ($r^2 = 0.973$ at Stn. A and $r^2 = 0.980$ at Stn. B4, data not shown; annual mean, ± S.D., in Table 1). Noticeable interannual differences were found, which corresponded to solar radiation higher in July 1994 than in July 1993 (Fig. 2b).

Low-tide water salinity (Fig. 3a) strongly fluctuated over both few days and the long period. The significant increase of salinity from the summer 1993 to the summer 1994 was caused by the progressive decrease of the rainfall, highest between July and early October 1993 (Fig. 3b). Values ranged from 0.1 psu (Stn. A, July 2, 1993) to 31.6 psu (Stn. B4, April 20 and May 14, 1994) and were slightly lower at Stn. A than at Stn. B4 (Fig. 3a, Table 1).

Low-tide water dissolved oxygen (D.O.) concentration (Fig. 4a) widely fluctuated. At Stn. A, it varied from 2.0 mg $l^{-1}$ (22.0% saturation, December) to 16.7mg $l^{-1}$ (232.5% saturation, May 18). At both stations, D.O. concentration showed a decreasing trend from mid-summer to autumn, but progressively increased from late-winter to early-spring, often resulting



Figs. 2a and b. Low-tide water temperature (a) recorded during each sampling occasion at Stns. A and B4 and daily solar radiation (b) obtained from the Takamatsu Meteorological Agency station where the intertidal flat is located.



Figs. 3a and b. Low-tide water salinity (a) recorded during each sampling occasion at Stns. A and B4 and daily rainfall (b) obtained from the Takamatsu Meteorological Agency Station where the intertidal flat is located.

oversaturated. D.O. concentration appeared to some extent influenced by the seasonal fluctuations of temperature (Fig. 2a) and solar radiation (Fig. 2b). A significant difference between Stns A and B4 was found in July 1994 (Fig. 4a), with a mean of 6.0±1.8 mg $l^{-1}$ and 10.2±2.3 mg $l^{-1}$, respectively.

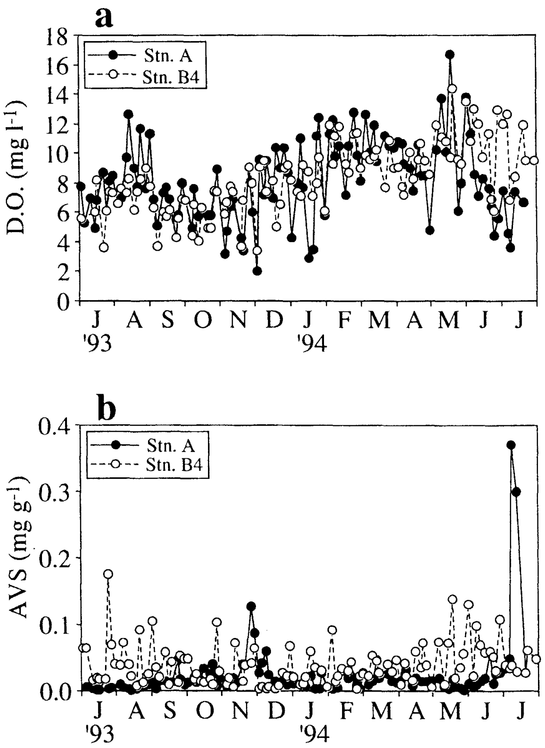
At the surface sediment (0–0.5 cm), acid volatile sulfide (AVS) level (Fig. 4b) was complexively lower at Stn. A (mean of 0.025±0.047 mg $g^{-1}$) than at Stn. B4 (mean of 0.039±0.031 mg $g^{-1}$). At Stn. A, it ranged from 0.001 mg $g^{-1}$ (July 16, 1993) to 0.371 mg $g^{-1}$ (July 8, 1994). At Stn. B4, it varied from 0.003 mg $g^{-1}$ (February 23, 1994) to 0.176 mg $g^{-1}$ (July 24, 1993). At both stations, no clear seasonal pattern was found. However, AVS level was less fluctuating at Stn. A, in spite of a sharp peak in July 1994 (Fig. 4b), while it varied the most at the less emerged Stn. B4 (Fig. 4b).

Fig. 5 shows the grain size composition of the sediment layer 0–10 cm at Stns A and B4. At both stations the sediment was sandy. However at Stn. A, the percentage of the fine (250–0.063 mm) and mud (<0.063 mm) fraction was significantly higher than that at Stn. B4 (37.4%–3.2% at Stn. A and 8.4%–1.5% at Stn. B4, respectively). The higher percentage of small-particle fraction at Stn. A went together with a higher water content (Table 1).

Table 1 reports the mean concentrations (±S.D.) of dissolved inorganic nitrogen (DIN) [$NH_4^+$-N and $(NO_3^-+NO_2^-)$-N] in the pore water of the surface layer (0–0.5 cm) of the sediment. $(NO_3^-+NO_2^-)$-N concentration was slightly higher at Stn. A, but overall, no significant difference in DIN concentration between the two stations was found.

Table 1. Average (±S.D.) of the physico-chemical parameters of low-tide water and the surface (0–0.5cm) sediment of Stns. A and B4.

| | Water | | | Sediment | | | |
|---|---|---|---|---|---|---|---|
| | Temp. (℃) | Sal. (psu) | D.O. (mg/l) | Temp. (℃) | W.C. (%) | Amm. ($\mu$M) | Nitr. ($\mu$M) |
| Stn. A | 19.6 | 16.4 | 8.1 | 19.2 | 33.4 | 116.6 | 8.6 |
| S.D. | (±7.7) | (±7.8) | (±2.8) | (±8.2) | (±11.2) | (±65.8) | (±8.7) |
| n. | 109 | 107 | 109 | 107 | 107 | 71 | 66 |
| Stn. B4 | 19.5 | 18.4 | 8.3 | 19.1 | 25.5 | 99.1 | 5.3 |
| S.D. | (±7.6) | (±8.3) | (±2.4) | (±7.8) | (±7.6) | (±50.3) | (±2.8) |
| n. | 109 | 107 | 109 | 107 | 108 | 50 | 41 |



Figs. 4a and b. Low-tide water dissolved oxygen concentration (a) and emerged surface sediment-volatile sulfide level (b) recorded during each sampling occasion at Stns. A and B4.

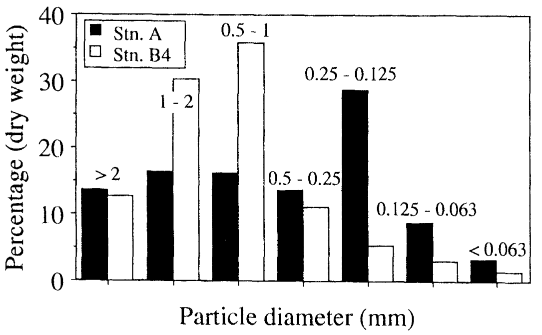


Fig. 5. Grain size composition of the 0–10 cm layer of the sediment at Stns. A and B4.

### *4-2 Photosynthetic pigment contents*

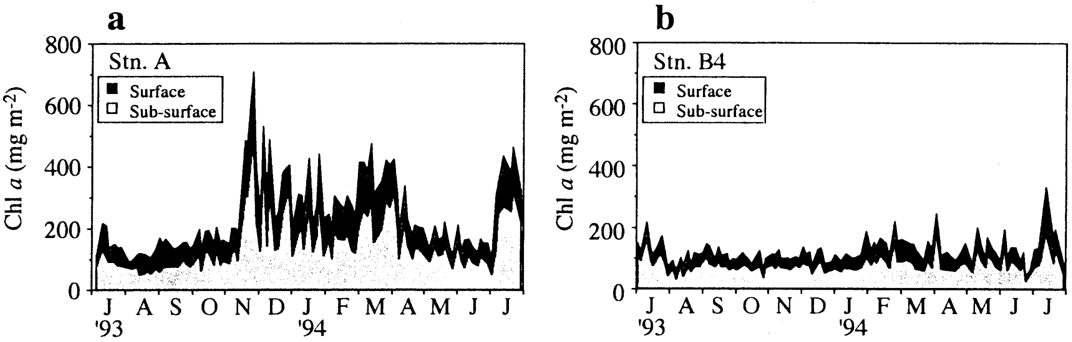
Chlorophyll *a* and pheo-pigment contents were obtained as a $\mu g\ g^{-1}$ of dry sediment. They were then converted $\mu g\ g^{-1}$ to mg $m^{-2}$ by accounting the bulk-density of the sediment particle as 2.5 g $cm^{-3}$ (MONTANI and OCHAICHI, 1984). A factor *f* was obtained from the ratio between the sediment particle bulk density and the total vulume, where the maximum value of 1 is for an hypothetical sediment with 0% of pore water. Thus, this ratio changed depending on the different water content of each sample, not corrected for salinity, and varied from 0.14 (water content 70.9%) to 0.69 (water content 15.3%).

The conversion equation was :

1. surface (0–0.5 cm) : $\mathrm{mg\ m^{-2}\ Chl}\,a = 5000\mathrm{cm^3 m^{-2}} * 2.5\ \mathrm{g\ cm^{-3}} * f * \mathrm{mg\ g^{-1}\ Chl}\,a$ (or pheo-pigments)
2. sub-surface (0.5–2 cm) : $\mathrm{mg\ m^{-2}\ Chl}\,a = 15000\ \mathrm{cm^3\ m^{-2}} * 2.5\ \mathrm{g\ cm^{-3}} * f * \mathrm{mg\ g^{-1}\ Chl}\,a$ (or pheo-pigments)

Square regression lines of Chlorophyll *a* plots were :

for Stn. A : $y(\mathrm{mg\,m^{-2}}) = 2.5x(\mu\ \mathrm{g\,g^{-1}}) + 45.4$ ($r^2 = 0.696$, $n = 107$) at the surface and $y = 12.4x + 35.6$ ($r^2 = 0.917$, $n = 105$) at the sub-surface; for Stn. B4 : $y = 5.4x + 8.1$ ($r^2 = 0.793$, $n = 108$) at the surface and $y = 16.8x + 16.1$ ($r^2 = 0.736$, $n = 108$) at the sub-surface (plots not shown).



Figs. 6a and b. Chlorophyll *a* content (expressed as mg m$^{-2}$ of dry sediment) of the surface (0 0.5 cm) and the sub-surface (0.5–2 cm) at Stns. A(a) and B4 (b).

Square regression lines of pheo–pigment plots were :

for Stn. A : y (mg m$^{-2}$) = 2.3x ($\mu$g g$^{-1}$) + 62.4 ($r^2 = 0.842$, n = 107) at the surface and y = 12.6x + 67.4 ($r^2 = 0.868$, n = 105) at the sub–surface; for Stn. B4 : y = 5.8x + 7.1 ($r^2 = 0.762$) at the surface and y = 15.8x + 48.5 ($r^2 = 0.708$, n = 108) at the sub - surface (plots not shown).

*4–3 Chlorophyll a and pheo–pigment distributional patterns*

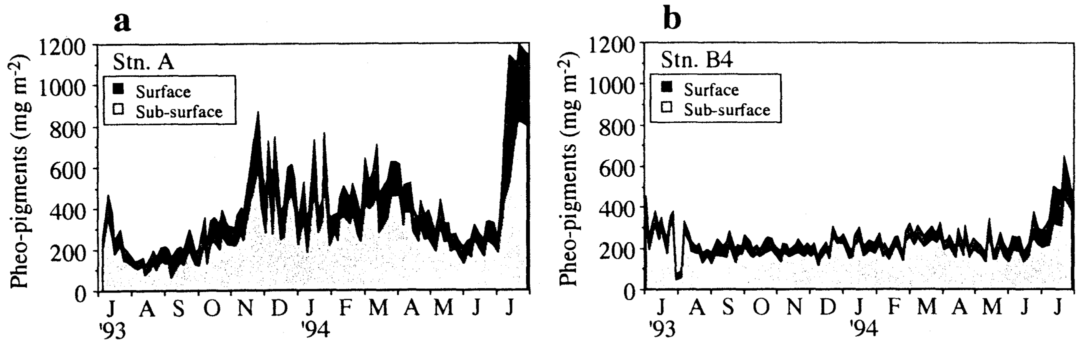
Chlorophyll *a* content of both surface (0–0.5 cm) and sub–surface (0.5–2 cm) sediment was complexively higher at Stn. A than at Stn. B4 (Figs. 6a and b). Mean Chl *a* content (as a sum of the two layers) was 241 ± 121 mg m$^{-2}$ and 122 ± 41.4 mg m$^{-2}$ at Stns A and B4, respectively.

At Stn. A, strong temporal (rather than seasonal) variability was found. Chl *a* content varied from 91.2 mg m$^{-2}$ (August 3, 1993) to 708 mg m$^{-2}$ (November 24, 1993) (Fig. 6a). From July to early October, the period of maximum precipitation rate (Fig. 3b), Chl *a* content was low and comparable to that of Stn. B4 (Fig. 6b). In mid–November, in spite of decreasing temperature (Fig. 2a) and solar radiation (Fig. 2b), but in coincidence with a reduced rainfall (Fig. 3b), a sharp peak occurred (Fig. 6a). From December to mid–February, Chl *a* content tended to decrease again, showed wide short - term (days) fluctuations, but remained constantly higher than that at Stn. B4 (Fig. 6a and b). From late February to March, at still low temperature (Fig. 2a) but with a progressive increase of solar radiation (Fig. 2b) and little rain (Fig. 3b), Chl *a* content significantly increased again. From April to the end of June, a new decrease occurred, which coincided with a more intensive rainfall (Fig. 2c) as also revealed by a rapid decrease of low–tide water salinity (Fig. 2d). During this period, as in summer 1993, Chl *a* content was similar to that found at Stn. B4 (Figs. 6a and b). In July 1994, atmospheric conditions were the most favourable for the development of the microphytobenthos. Indeed, during warm (Fig. 2a) and irradiated (Fig. 2a) days with no rain (Fig. 3b), a new sharp increase occurred (463 mg m$^{-2}$ in July 22). However, the Chl *a* content at this time was not as high as that found in late-autumn and early spring (Fig. 6a).

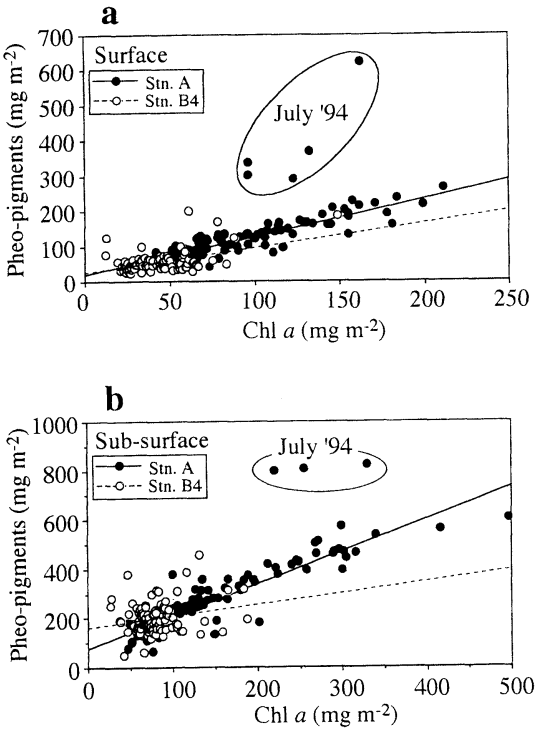
At Stn. B4, Chl *a* content ranged between 39.3 mg m$^{-2}$ (June 24, 1994) and 333 mg m$^{-2}$ (July 12, 1994)(Fig. 6b). The microalgal biomass remained constantly lower tha at Stn. A, and was rather uniform in spite of the strong changes of the environmental conditions which significantly affected the microalgal development at Stn. A. A slight increase occurred between February and March, at the surface sediment. In mid–July 1994, with the significant improvement of the meteorological conditions (Figs. 2b and 3b), a remarkable peak was found. However within few days, Chl *a* content was again as low as during the whole investigated period.

Pheo–pigment content (Figs. 7a and b) was generally higher than Chl *a* content. It averaged 414 ± 218 mg m$^{-2}$ and 251 ± 84.1 mg m$^{-2}$ (as a sum of the surface and sub–surface layers) at Stns A and B4, respectively.

Wide temporal fluctuations were found at



Figs. 7a and b. Pheo-pigment content (expressed as mg $m^{-2}$ of dry sediment) of the surface (0–0.5 cm) and the sub-surface (0.5–2 cm) at Stns. A(a) and B4 (b).



Figs. 8a and b Correlation between Chlorophyll *a* and pheo-pigment content at the surface (0–0.5 cm) (a) and the sub-surface (0.5–2 cm) (b) sediment of Stns. A and B4. Square regression lines were significant at Stn. A ($r^2 = 0.816$ at the surface and $r^2 = 0.843$ at the sub surface), but not at Stn. B4 ($r^2 = 0.210$ at the surface and $r^2 = 0.045$ at the sub-surface). At Stn. A, some samples of July 1994 (delimited in the circle) were rather deviating from the linear correlation and excluded from the plots. See Discussion.

both stations. Pheo-pigment content varied from 143 mg $m^{-2}$ (August 3, 1993) to 1192 mg $m^{-2}$ (July 22, 1994) at Stn. A and from 84.8 mg $m^{-2}$ (August 3, 1993) to 655 mg $m^{-2}$ (July 22, 1994) at Stn. B4. Plots of Chl *a* against pheo-pigment at both the surface (Fig. 8a) and the sub-surface (Fig. 8b) indicated that the temporal variations of Chl *a* and pheo-pigment content (Figs. 6 and 7) were rather parallel at Stn. A ($r^2 = 0.816$ and $r^2 = 0.843$ at the surface and the sub-surface, respectively), but not at Stn. B4 ($r^2 = 0.210$ and $r^2 = 0.045$ at the surface and the sub-surface, respectively). At Stn. A, some samples collected in July 1994 were also deviating from a significant correlation (Figs. 8a and b) due to an exceptionally high content of pheo-pigments in respect to that of Chl *a* (Figs. 6a and 7a).

### *4-4 Primary production*

Primary production by the microphytobenthos was estimated on the basis of the mean (±S.D.) monthly content of Chl *a*, assuming that the top 0–0.5 cm layer (surface sediment) was photo-syntetically competent. Monthly averaged light intensity incident on the sediment surface and photosynthetically available for the microphytobenthos was calculated as the sum of that fully available during the emersion period of the surface sediment and that partly available during the submerged period. For the submerged period we used an attenuation coeffcient of 0.6 Due to the differences in elevation between the two stations, the mean hours per day photosyntetically-available (including both periods of sediment emersion and submersion) varied from 6.9 to 9.1 hours and from 6.1 to 8.0 hours, at Stn. A and Stn. B4, respectively. On the basis of the production rate values reported by previous studies on microphyto-benthos (COLIJN and DE JONGE, 1984) and phy-toplankton (HARRISON and PLATT, 1980), factors of 2 (December to February), 2.5 (September to November and March to May) and 3 (June to August) were used as a minimum production rate per unit of Chl *a* (mg C mg Chl $a^{-1}$ $h^{-1}$) in attempt not to overestimate of the annual primary production by the micro-phytobenthos of this intertidal flat.

At Stn. A, microalgal primary production varied from 1.21±0.27 g C $m^{-2}$ $day^{-1}$ (May 1994) to 3.27±1.49 g C $m^{-2}$ $day^{-1}$(July 1994). Annual primary production was 634 g C $m^{-2}$ $yr^{-1}$. At Stn. B4, on the other hand, it varied from 0.46±0.14 g C $m^{-2}$ $day^{-1}$ (December 1993) to 1.71±0.91 g C $m^{-2}$ $day^{-1}$ (July 1994). Annual primary production was 259 g C $m^{-2}$ $yr^{-1}$.

## 5. Discussion

### 5-1 Environmental variability and development of benthic microalgal assemblages

The intensive and prolonged sampling effort enabled us to assess the short-time (days) and interannual variability of the physico-chemical parameters of low-tide water and emerged sediment and to examine possible differences between two stations as related to the development of the microphytobenthos. The constant low-tide status of samplings minimized possible misunderstanding of the results due to the high daily variability related to a complete tidal cycle (MONTANI *et al.*, 1998).

Plots of water and sediment temperature against Chl *a* (not shown) showed a broad distribution, with neither significative seasonal patterns nor differences between the stations (Table 1). On the other hand, temperature and solar radiation played an important role in determining a remarkable interannual variability (between July 1993 and July 1994, Figs. 2a and b) in the microphytoventhic development (Figs. 6a and b) at both stations. Temperature and solar radiation also affected the degradation rate of the primary products. It was particularly evident at Stn. A where the pheo pigment content, relative to that of Chl *a*, was higher during the warm and irradiated July 1994 than during the microphytobenthic blooms of autumn and spring (Figs. 6a and 7a). This fact resulted in values exceptionally deviating from the significant correlation found at this station between Chl *a* and pheo-pigments (Fig. 8a and b).

Salinity of low-tide water nearby the two stations (Fig. 3a) was rapidly influenced by the rainfall (Fig. 3b). Due to vicinity of the spots where sediment samples were collected, we infer that such variations were also representative of the temporal variations of the salinity of the pore water during low-tide, a factor possibly affecting the development and species composition of the microphytobenthos (ADMIRAAL, 1977b). Salinity was slightly but not significantly lower at Stn. A (Table 1), as it was more distant from the low-tide shore-line and relatively less affected by high-salinity water. Besides the strong short-term (days) fluctuations, a significant increasing trend of salinity from the summer 1993 to the summer 1994 was found, which indicated that interannual differences were more marked than seasonal ones, as strongly related to the rainfall (Figs. 3a and b).

Dissolved oxygen concentration (Fig. 4a) was enhanced by high solar radiation (Fig. 2b) and limited by the deterioration of atmospheric condition (*i.e.* rainfall, Fig. 3b) at both stations (average and S.D. in Table 1). A more distictive decline of D.O. concentration occurred at Stn. A in November 1993 and July 1994 (Fig. 4a) in coincidence with an increase of AVS (Fig. 4b) and pigment (Figs. 6a and 7a) content. We assume that the shallow low-tide water we monitored nearby the emerged sediment was rapidly influenced by the *in situ* benthic processes of oxygen production by the microphytobenthos and oxygen uptake due to the decay of plant material, respectively.

At the sediment level, ($NO_3^-$+$NO_2^-$)-N concentration was only slightly higher at the backward of Stn. A (Table 1), as relatively more affected by the river runoff which has been found a major source of nitrate+nitrite nitrogen to this tidal estuary (MONTANI *et al.*, 1998; MAGNI and MONTANI, submitted to J. Oceanogr.). However, dissolved inorganic nitrogen concentration was com-plexively similar at the two stations (Table 1), indicating no nutrient limitation for the development of the microphytobenthos at Stn. B4.

Overall, the above mentioned physico-chemical parameters were not significantly different at the two stations as to explain the differences in development of the benthic microalgal assemblages.

Within the abiotic sphere, two factors resulted more distictive. Firstly, the different elevation between the two stations. Stns A and B4 emerged at a tidal level of *ca.*+140 and+70cm, respectively. This fact was also indicated by a generally lower AVS level at Stn. A than at Stn. B4 (Fig. 4b and Table 1), as an evidence of a longer exposure of the surface sediment to the atmosphere. Assuming that photo-inibition is almost absent in benthic microalgae (ADMIRAAL and PELETIER, 1980; PELETIER *et al.*, 1996), the higher elevation of Stn. A, and thus a better availability of solar radiation for the photosynthesis, favoured a higher microphytobenthic production. Our results support previous studies which showed higher standing stock of the microphytobenthos at higher elevation (ADMIRAAL and PELETIER, 1980; COLIJN and DE JONGE, 1984; DE JONG and DE JONGE, 1995). On the other hand, the higher elevation of Stn. A also resulted in a faster degradation of Chl *a* into pheo-pigments during warm and irradiated days, such as in July 1994 (Figs. 8a and b). Such a high pheo-pigment content coincided with a significant and unusual increase of AVS level as a result of the enhancement of anaerobic decomposition processes due to decaying microphytobenthos.

As related to the station elevation, the rainfall more strongly influenced the microphytobenthos standing stock at Stn. A. Rather than causing differences in salinity between the two stations, it appeared to be a major factor in limiting the blooming and/or precluding the existence of a stable microalgal vegetation (COLIJN and DE JONGE, 1984) during the summer 1993 and the late spring 1994 (Fig. 8a), as a possible result of a continuous washout (COLIJN and DIJKEMA, 1981). Indeed at Stn. A, the Chl *a* peaks of November, early spring and July 1994 occurred after minor rain and in coincidence or following days of fine weather. Neither dessication nor freezing of the sediment was observed during the course of this investigation.

A second abiotic factor significantly divergent between the two stations was the grain size composition of the sediment. As stated by DE JONG and DE JONGE (1995) the clay content is generally used to define the hydrodynamic energy (tidal currents and waves) of a location, a parameter difficult to measure. An area with low hydrodynamic energy will result in a smaller grain-size composition due to an easier settlement of the silt-clay particles. Accordingly, the sediment at Stn. A had a higher silt clay content than that Stn. B4 (Fig. 5), as it was more distant from the low-tide shore-line and less affected by the tidal currents and waves. A better water retention by smaller particles at Stn. A resulted indeed in a higher water content (Table 1). Differently, the bigger particle size of the sediment of Stn. B4 indicated an area with higher hydrodynamic energy. Thus, the processes of resuspension more strongly limited the primary production of the microphytobenthos at this station (DE JONGE, 1985; DE JONGE and VAN DEN BERGS, 1987). The different impact of the tidal currents on the physical sorting of the sediment (COLIJN and DIJKEMA, 1981; DE JONG, 1985) further contributed to determine the differences in Chl *a* content between the two stations, according to previous studies which found a good positive correlation between silt-clay percentage and pigment contents (COLIJN and DIJKEMA, 1981; DE JONG and DE JONGE, 1995).

### *5-2 Benthic microalgal standing stock, primary production and consumers*

Both the surface (0-0.5 cm) and the sub-surface (0.5-2 cm) layers of the sediment were used to calculate the standing stock of the microphytobenthos, according to DE JONGE and COLIJN (1994) who showed that only 35% to 60% of the total biomass of the microphytobenthos is taken into account, if only the top 0.5 cm are used. In this study, Chl *a* content of the sub-surface (0.5-2 cm) sediment was reduced to 54.8±19.6% and to 67.4±21.1%, at Stn A and B4 respectively. We agree with DE JONGE and COLIJN (1994) that accounting the

0–2 cm layer, rather than the 0–0.5 cm layer, will result in a more accurate estimation of the microphytobenthic standing stock, a certain food resource for the macro-zoobenthos (NICOTRI, 1977; LOPEZ and LEVINTON, 1987; BIANCHI and RICE, 1988; SMITH *et al.*, 1996). At Stn. A, also pheo-pigment content was lower at the sub-surface (78.2±20.6%). Differently, at Stn. B4 it was higher (132.4±39.3%). This facts may be related to the hydrodynamic energy and the particle size of the sediment which allows a faster penetration of microalgal material into the sediment at Stn. B4.

Primary production by the microphytobenthos was estimated assuming the top 0–0.5 cm layer of the sediment as photo-synthetically competent (DE JONGE and COLIJN, 1994) in spite of a deeper presence of vital cells due to physical factors, migration (PINCKNEY *et al.*, 1994) and bioturbation (BRANCH and PRINGLE, 1987).

Both Chl *a* standing stock and annual primary production were generally higher than those reported for the Ems-Dollard estuary, Dutch Wadden Sea (CADÉE and HEGEMAN, 1977; ES VAN, 1982; COLIJN and DE JONGE, 1984), and the Western Scheldt estuary, SW Netherlands (DE JONG and DE JONGE, 1995). On the Western Scheldt estuary, the contribution of the microphytobenthos on the total primary production was estimated at least as 17% (DE JONGE and DE JONGE, 1995). In our study, annual primary production by the microphytobenthos (634 gC $m^{-2}$ $yr^{-1}$ and 259 gC $m^{-2}$ $yr^{-1}$, at Stns. A and B4 respectively) was higher or similar to that reported by the phytoplankton in the Seto Inland Sea (285 gC $m^{-2}$ $yr^{-1}$, mean euphotic depth 27.2 m) (TADA, 1997). The present study indicated the high productivity of the intertidal zone, most likely underestimated on the light of the grazing pressure by the macro-zoobenthos which is similarly abundant on the intertidal flat under invenstigation.

Besides the differentiated development of the benthic microalgal assemblages along the estuary, as related to abiotic factors (*i.e.* station elevation and sediment gran-size composition), further studies are in progresses to quantify the effects of the grazing pressure by the macro-zoobenthos on the microphytobenthic standing stock and primary production. Since April 1994, we extended the investigations on the seasonal changes of abundance and faunal composition of the benthic communities quantitatively. Stn. A is inhabited by brachyuran feeding on the surface sediment, while at Stn. B 4 the filter feeder bivalves *Ruditapes philippinarum* and *Musculista senhousia* are dominant (MAGNI *et al.*, in preparation). It is likely that an important food source for the filter feeders is represented not only by organic materials from the water column, but also by epipelic and epipsammic microphytobenthos resuspended with sediment particles (NUMAGUCHI, 1990). We suggest that not accounting the *potential* primary production of the microphytobenthos, as that masked by the grazing effect of the consumers, would lead to a significant underestimation of the autotrophic benthic processes of this intertidal flat.

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# Size of suspended particles caught by Manila clam, *Ruditapes philippinarum*

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**Abstract:** The sizes of suspended particles caught by common Manila clam and the shell-length variations in the selection of particle sizes were investigated using a Coulter Counter. A total of 450 samples were examined under 4 different shell lengths, viz. 5, 10, 20, and 30mm. The simulated feed suspensions were either the phytoplankton *Pavlova lutheri* (average size 3.5 $\mu$m) or pulverized pellet powder (average size 3.7 $\mu$m), which is used as artificial feed for abalone. The percent catch rate was based on the proportion of particles reduced from the initial number. The particle sizes examined were in the range 2.2 to 45.2 $\mu$m.

The catch-rates of adult clam (shell length of 30mm) under vigorous filtration indicated nearly constant particle size selection when they were maintained for 60 minutes in the sea water containing $3\times10^5$ pellet particles/ml. When the particle concentration increased to $6\times10^5$/ml, however, the catch rates of sizes less than 15 $\mu$m decreased to almost a third of the above mentioned concentration. A similar reduction was noted when the exposure was for 180 minutes. Furthermore, the catch rates for particle sizes more than 5 $\mu$m increased by almost 20% when pellet was replaced with phytoplankton.

When Manila clam of different shell lengths were kept for 60 minutes in the sea water containing $3\times10^5$ particles/ml, the catch rates of 5 mm clams for the entire range of particle sizes were almost uniform, showing an average value of $0.68\%\cdot h^{-1}$. When their shell lengths increased to 10 mm or 20mm, the catch rates for the larger sizes appeared to increase. Thus the larger clams, among the sizes examined, seeks intentionally larger suspended particles to meet their growth requirements.

## 1. Introduction

The bivalve Manila clam, *Ruditapes philippinarum*, is found abundantly in the coastal waters all around Japan. Since it feeds on suspended particles, it is considered as one of the important benthos from the view-point of cleaning or purifying sea water (AKIYAMA, 1985; AOYAMA and SUZUKI, 1997). The growth of the clam's natural larvae as well as the artificially introduced seed-shells is influenced by not only such environmental factors as coastal water properties, bottom materials, and predators but also their feeding itself. Particularly, the latter is considered to exert the most serious influence on the clam's growth in their early stages.

A great deal of information exists on the feed and filtration of bivalves. For instance, those of oyster reported by LOOSANOFF and ENGLE (1947), KUSUNOKI (1977 a, b, c) and RIISGÅRD (1988). Information on sea mussel has been provided by JØRGENSEN (1949), UMEZU *et al.* (1967) and LUCAS *et al.* (1987) and others. These authors investigated the quantities of suspended particles caught by oyster and mussel according to particle sizes.

With regard to studies on Hard clam and Manila clam, there are the reports of CHIBA and OHSHIMA (1957), FURUKAWA (1961), NUMAGUCHI

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(1990), Toba and Miyama(1993) and Mukai (1993). Chiba and Ohshima(1957) investigated the influence of muddy water on the filtration process of several bivalves including Manila clam, and reported that their rates did not go down even in the water suspended thickly with bentonite particles. Recently, Numaguchi (1990) investigated the distributions of Manila clam and the properties of suspended particles around the river month in the Bay of Ariake, and suggested that the particles selected as feed were in the size range from 1.2 to 50 $\mu$m and richly pigmented.

Apart from the work of Toba and Miyama (1993), there is very little information on the size-preferences in selection of suspended particles by Manila clam, let alone the shell length based selection. Therefore this study broadly attempts to examine (1) the change of particle catch-rates with time, (2) the quantity and quality of those particles depending on filtration performance, and (3) to find out the sizes of captured-particles in relation to the different shell-lengths of the clam.

## 2. Materials and methods

### *2-1. Samples and materials*

Artificial seed-shells (shell length : 5 and 10 mm) produced at Futtsu Branch of Chiba Prefectural Fisheries Experimental Station, as well as natural clams (shell length : 20 and 30 mm) collected from the Tokyo Bay were used as the samples. A total of 450 clams were used for the experiments and the observational error in shell length was restricted to be less than ±0.1 mm. Each sample was kept from one to three months in basin with filtered sea water maintained at 21℃.

The feed particle suspensions were either artificial feed or phytoplankton. The artificial feed employed in this experiment was a commercial pellet manufactured by Halios Japan Combination Feed Co. Ltd, for abalone. The pellet was finely ground and the resulting powder, was mixed with sea water filtered through millipore CP15 (pore-size 1 $\mu$m), and later filtering the suspension itself through a net of mesh size 50 $\mu$m, the average size of the resulting particle suspension being 3.7 $\mu$m. On the other hand, the phytoplankton *Pavlova lutheri* was monocultured in a constant temperature room, and was allowed to emigrate into the sea water of the experimental basin, at the average size of 3.5 $\mu$m. The phytoplankton culture was considered to include both clastic cells and agglutinative forms. The particle size distributions of pulverized pellet and phytoplankton are shown in Fig. 1.

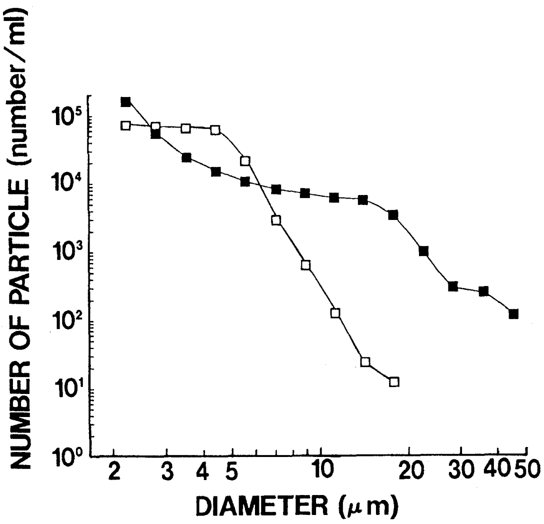

Fig. 1. The particle size distributions of the pellet and phytoplankton offered to the Manila clam.

Symbols ■ and □ denote the particle sizes of artificial feed (pellet) and phytoplankton *Pavlova lutheri*, respectively.

### *2-2. Experimental methods*

The experimental apparatus is illustrated in Fig. 2. The experimental tank was cylindrical in shape, and had a diameter of 15 cm and depth of 10 cm. This tank contained yet another cylindrical-shaped inner container, 4 cm both in dia. and depth, which held the bivalves. A stirrer was provided to facilitate water circulation.

The animals were deprived of food for 24 hours prior to the start of a series of experiments. The number of samples under the shell-lengths of 5 and 10 mm were forty and twenty respectively, whereas for the 20 and 30 mm size only individual clams were used. Artificial feed particles were added to one liter of filtered sea water so that it produced suspensions with concentration of $1 \times 10^5$, $3 \times 10^5$, and $6 \times 10^5$ part-

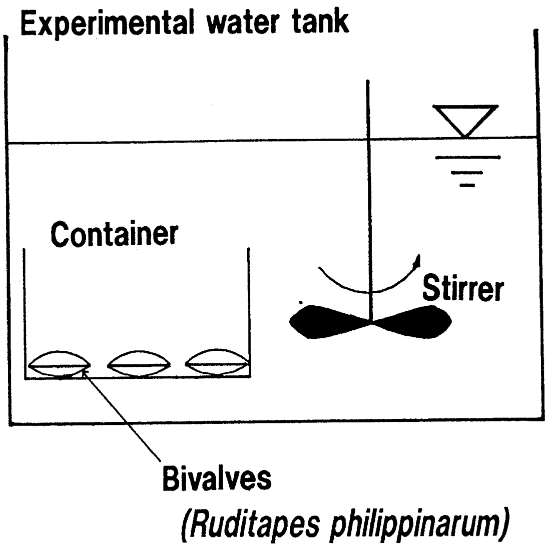

Fig. 2. Diagrammatic representation of the experimental set up.

icles/ml while the test phytoplankton concentration was $3\times10^5$ cells/ml. After leaving the sample clam for 30, 60 or 180 minutes in the sea water at the particle concentrations mentioned above, the clam's retainer on the bottom of the vessel was taken out in order to avoid a possible contamination of the water with the clam's excrement.

The number of particles in the vessel was measured with Coulter Counter Model ZM (aperture size of 100 $\mu$m). The objective particles for the study were those in the range from 2.2 to 45.2 $\mu$m. A control was employed simultaneously using the vessel without the experimental animals, and then the number of particles were counted.

Almost soon after each clam was let into the experimental container, it extended its incurrent siphon and started vigorous filtration. The clam used in the present experiment performed active filtration with the end of the incurrent siphon opened (Mukai, 1993).

The catch rate, $Cr_{(i)}$, is obtained using the following formula :

$$Cr_{(i)} = \frac{1}{n\cdot t}\,\frac{Cc_{(i)}-Ce_{(i)}}{Cc_{(i)}}\cdot 100 \qquad (1)$$

where, $Cc_{(i)}$ is the concentration of particles without the clam, $Ce_{(i)}$ denotes the concentration of particles (diameter at i-class : $di$) contained in the water with the clam, $t$(hour) stands for the experimental period, and n is the number of clams. Besides, the average diameter of captured particle ($\bar{D}$) is based on the following formula :

$$\bar{D} = \frac{\Sigma\, di\cdot Ndi}{\Sigma\, Ndi} \qquad (2)$$

Where, $di$ stands for the diameter of particle-size at i-class, and $Ndi$ stands for the number of particles at the diameter $di$.

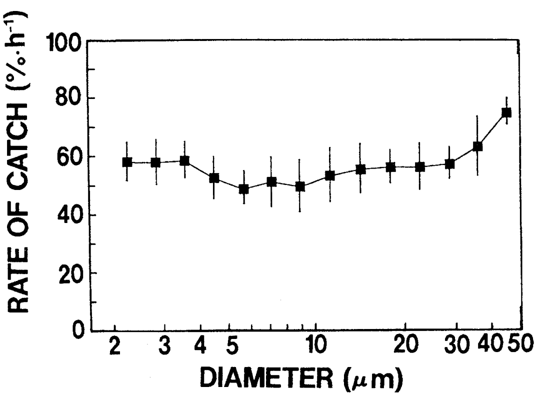

Fig. 3. Particle catch rates of adult Manila clam. The solid squares are average values from 11 clams, along with standard deviations.

## 3. Results

### *3-1. Particle Catch-Rates of Adult Clam*

### *3-1-1. Changes with time*

Figure 3 depicts the particle catch rate of the clam in a state of motion, when it was kept for 60 minutes in sea water containing $3\times10^5$ pellet particles/ml. The catch rates were 57.8%$\cdot$h$^{-1}$ corresponding to the particle size of 2.8 $\mu$m, 53.1%$\cdot$h$^{-1}$ for 11.3 $\mu$m size, and 63.2%$\cdot$h$^{-1}$ for 35.9 $\mu$m. Speaking generally, they exhibited catch rates within the range 50 to 60%$\cdot$h$^{-1}$ for particle size less than 25 $\mu$m, but slightly higher for those larger than that. Besides, the total volume of particles caught by adult was 0.031 mm$^3$. From these results it could be concluded that when the clam is in a state of motion, the particle catch rate distributions are almost uniform over a wide range of particle sizes, the median value being approximately 60%$\cdot$h$^{-1}$.

Figure 4 depicts the change catch rates in relation to the particle sizes, and the length of

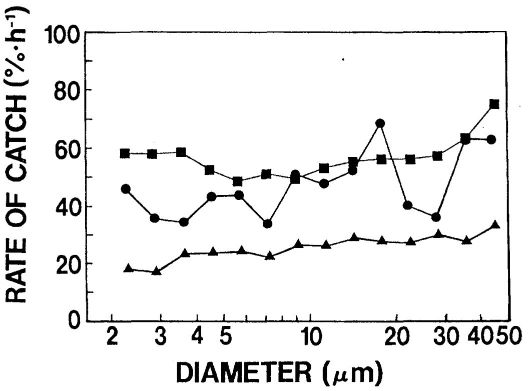

Fig. 4. Changes in the catch rates of adult clams under varying experimental periods.

Symbols ●, ■, and ▲ represent the rates for periods of 30, 60, and 180 minutes, respectively. Values are means of 6, 11, and 2 observations for periods of 30, 60, and 180 minutes.

exposure time. The experimental clams were introduced into the sea water of $3\times10^5$ particles/ml, for durations of 30, 60, and 180 minutes. The data for 60 minutes exposure is the same as that in Fig. 3. The particle catch rates measured after being submerged for 30 minutes were 35.6%•h$^{-1}$, 47.0%•h$^{-1}$, and 62.6%•h$^{-1}$ corresponding to particle sizes of 2.8 μm, 11.3 μm, and 35.9 μm, respectively. These rates after being left for 60 minutes were 57.8%•h$^{-1}$, 53.1 %•h$^{-1}$ and 63.2%•h$^{-1}$, respectively; and after 180 minutes of submergence the values were 17.0%•h$^{-1}$, 25.3%•h$^{-1}$, and 26.7%•h$^{-1}$, respectively. Thus, the average particle catch-rate to the whole range of the particle sizes varied widely when the clam was submerged for only 30 minutes. However there was uniformity in the capture rates for the different size groups when the clams were submerged for 60 minutes (about 60%•h$^{-1}$), and 180 minutes (only around 20%•h$^{-1}$). The variation in the catch-rates for the group exposed for the shortest duration lacks a proper explanation.

### *3-1-2. Changes with particle quality and quantity*

In order to investigate the influence of particle concentration on catch rates, adult clams were treated as in the earlier description. Fig. 5 shows the particle catch rates classified by different particle concentrations. The results under the conditions of $3\times10^5$ particles/ml exhibited in Fig. 5 are the same as those introduced in Fig. 3. The catch rates for the range of particle-sizes tested were approximately 40 to 50%•h$^{-1}$ for the particle concentration of $1\times10^5$ particles/ml, and around 60%•h$^{-1}$ for the higher concentration of $3\times10^5$ particles/ml. However, at the highest particle concentration of $6\times10^5$ particles/ml, the catch rates were greater for the large size particles. The values were 21.2%•h$^{-1}$ and 42.0%•h$^{-1}$ for the particle-sizes 14.2 μm and 45.2 μm, respectively. On the other hand, when the particle assimilation was expressed on a volume basis, the ratios were 1.0 : 4.4 : 5.0 for the corresponding concentrations of $1\times10^5$, $3\times10^5$, and $6\times10^5$ particles/ml. This is a clear indication that the sample clam prefers larger particles.

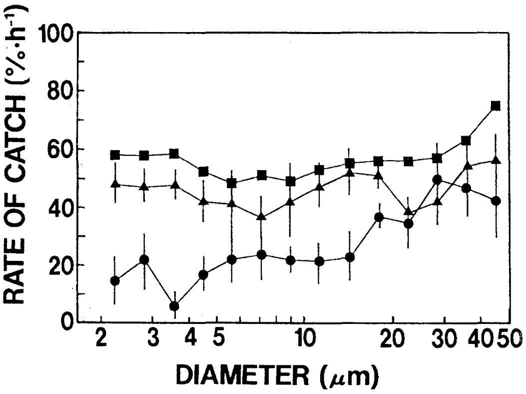

Fig. 5. Changes in the catch rates of adult clams under different concentrations of the suspended particles.

Symbols ▲, ■, and ● denote concentrations of $1\times10^5$, $3\times10^5$, and $6\times10^5$ particles/ml, respectively. Values are means of 3, 11, and 5 observations for the concentrations $1\times10^5$, $3\times10^5$, and $6\times10^5$ particles/ml, along with their standard deviations.

Figure 6 shows the phytoplankton catch-rates corresponding to the different cell-sizes after allowing for 60 minutes in the test medium. The results were compared with the identical data of the pellet particle catch-rates exhibited in Fig. 3. As mentioned earlier, the catch-retes of the pellets was approximately 60%•h$^{-1}$, irrespective of the particle sizes. The phytoplankton cell catch rates, however, was

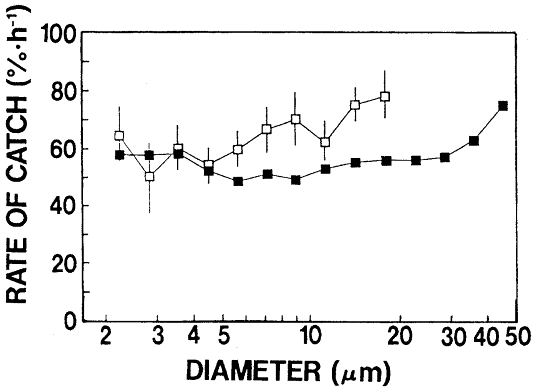

Fig. 6. Changes in the catch rates of adult clams when offered two different foods.

Symbols ■ and □ represent pellet and phytoplankton, respectively.

The corresponding sample numbers were 11 and 3 for pellet and phytoplankton. Standard deviations of the values are also indicated.

50.3%•h$^{-1}$ for the cell-size of 2.8 μm and 62.3%•h$^{-1}$ for 11.3 μm size, indicating increased rates for larger cells. It was noted that for both phytoplankton and feed pellets, the catch rates were uniform for particle sizes less than 5 μm, but above this size the catch rates of phytoplankton increased by approximately 20%. This result suggests that the mollusc tends to discriminate the particle quality when the particles are larger than 5 μm.

*3-2. Changes based on shell lengths of clam*

The particle catch rates of the adult clam for the particle-size range from 2.2 to 45.2 μm were more or less 60%•h$^{-1}$, and the average size of the particles was 3.87 μ m. We further examined the influence of different shell lengths, on the particle catch-rates and their average diameters. Fig. 7 shows the catch distribution rates for clams of shell lengths 5, 10, 20, and 30 mm. The data for the 30 mm shell length shown in Fig. 7 has been adopted from Fig. 3. In case of the shell length of 5 mm, the particle catch rate was 0.80%•h$^{-1}$ corresponding to 2.8 μm particle-size, 0.66%•h$^{-1}$ to 11.3 μm, and 1.1%•h$^{-1}$ to 35.9 μm, respectively. Generally the catch rates were almost uniform for particle sizes less than 30 μm, and the average value was 0.68%•h$^{-1}$. In case of the 10 mm shell size, the catch rate for the particle size of 2.8 μm was 1.51%•h$^{-1}$, that for 11.3 μm was 1.28%•h$^{-1}$, and that for 35.9 μm was 2.33%•h$^{-1}$ ; and in case of the 20mm, the catch rate for 2.8 μm was 24%•h$^{-1}$, that for 11.3 μm was 20%•h$^{-1}$, and that for 35.9 μm was 54%•h$^{-1}$. The general tendency was that the rate increased for the larger particle size. However, for the 30mm shell length group, the catch rates were again uniform, being around 60%•h$^{-1}$, irrespective of the particle size. The average size of particles caught by clams of shell lengths 5, 10, 20, and 30 mm was 3.76, 3.80, 3.92, and 3.87 μm, respectively. Therefore, considering the average particle sizes, it is evident that the young clam tend to catch larger sizes of suspended particles in accordance with their growth.

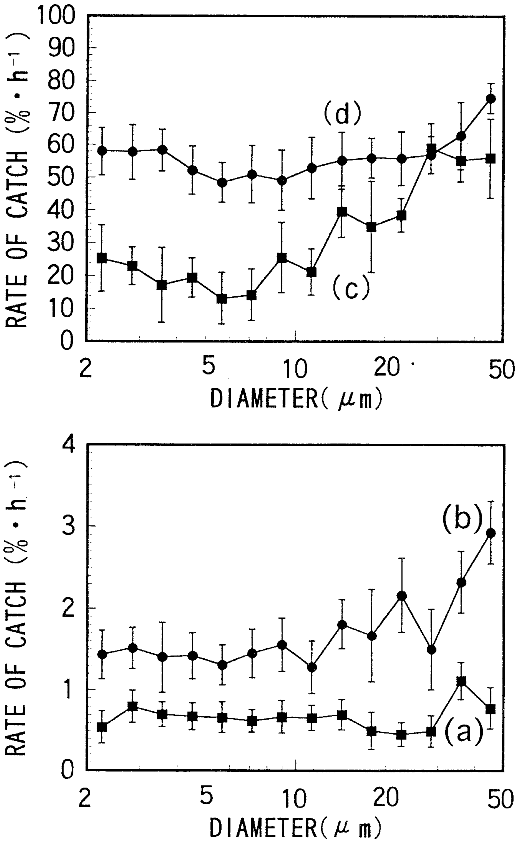

Fig. 7. Changes in the catch rates of clams dependent on their shell lengths.

The graph for the shell lengths of 5, 10, 20, and 30 mm are indicated as (a), (b), (c), and (d) in the figure. Values (±SD) are means of several repetitions : a=8, b=9, c=4, d=11.

## 4. Discussion

Mukai (1993) investigated the relationship between the volume of water filtered by Manila clam and their shell length when they were either performing active filtration or not. He reported that the clam in a state of motion could filter more water as the shell length increased, while the volume of water filtered in a state of rest did not vary with shell length and the amount was only a tenth of that in a state of motion. Though the present observations are based on clam in a state of motion, we have also made observations when they were in a state of rest, and found that the filtered volumes varied remarkably with time and particle size.

Most reports till date on the intake of particles by bivalves have based the filtration rate calculations on the equation provided by Jørgensen (1966) and Coughlan (1969) which is as indicated below :

$$r = \frac{M}{n \cdot t} Ln \frac{C_0}{C_t} \qquad (3)$$

where, $r$ is the filtration rate, $M$ is the suspension volume, $n$ is the number of samples, $t$ is the time lapsed, $C_0$, $C_t$ are the initial and final particle concentrations.

In our study, the particle catch rates are expressed as a percentage reduced from the initial quantity, since the range of particle size measured is broad and the sedimentation may influence the actual availability of the particles.

Akiyama (1985), and Aoyama and Suzuki (1977) investigated the filtration rate of Manila clam. They reported that the rate indicated the value of 33.8 and 33.5 $\ell \cdot gN^{-1} \cdot h^{-1}$, respectively. In this study, we calculated the filtration rate of adult clam by equation (3) mentioned above. The result based of the total volume of particle caught by Adult is 37.0 $\ell \cdot gN^{-1} \cdot h^{-1}$. This value is similar to afore-mentioned two results. However, we found out that the filtration rate had a great variation on quality, quantity, and size of particle. It can not be compared with both values easily.

The particle catch rates of adult clam (shell-length : 30 mm) were more or less $60\% \cdot h^{-1}$ corresponding to the particle size range of 2.0 to 25 $\mu$m; above which, it tended to increase slightly.

Kusunoki (1965) studied the ingestion mechanism of pearl oyster, using the carbon particles of diameter 2.5 to 30 $\mu$m, and reported that the ingestion rates were greater for the smaller particles. This is quite different from the present observations on Manila clam.

In a related study on North-East American bivalves, Riisgård (1988) reported that when the particle sizes less than 4 $\mu$m were considered, the larger among them had higher catch-rates, whereas no such difference in catch rate was noted for the size group 5 to 10 $\mu$m. An earlier study by Jørgensen and Goldberg (1953) on the filtration activity of *Crassostrea virginica* found that particle-sizes of 1 to 2 $\mu$m were hardly captured, but those from 2 to 3 $\mu$m was filtered aplenty. Thus in comparison to *Crassostrea virginica*, the clam seem to seize the smaller suspended particles ($<2\,\mu$m).

In the present study we also noted the changes in catch rates with time, higher values being recorded after 60 minutes, in comparison to a third of that value when they were exposed for 180 minutes. But the catch rates for larger particles increased. Mukai (1993) also made time based observations on the active filtration performances and found continuous alternations between a state of motion and that of rest, at different intervals from about some minutes to several hours. In our experiments, we visually inspected the samples to judge if they were in a state of rest, and if found so, the values were discarded for making necessary corrections in the catch rate calculation. It is therefore assumed that the filtration activity continued through the experiments, and the clam catch intentionally the larger suspended particles with the lapse of time.

In a study on the relation between the concentration of suspended particles and the catch rate, Kusunoki (1977c) disclosed that oysters mainly captured suspended particles which were more than 3 $\mu$m in dia. when there was an abundance of the particles, but the capture size dropped to 2 $\mu$m when there was only fewer number of suspended particles. This is similar to the observations on Manila clam.

Chiba and Oshima (1957) reported that the Manila clam caught both organic and inorganic the suspended particles irrespective of their quality, provided the particle-size ranged from 3 to 4 μm. In the current investigation employing both pellet and phytoplankton, there were no differences in catch rates corresponding to particle sizes less than 5 μm, though it increased remarkably above that size. Judging from these results, it is considered that the Manila clam tend to catch indiscriminately the particles less than 5 μm in size, and above that size they exhibit some preference. A study probing the relation between the captured particle size and the shell length, by Furukawa (1961), revealed that hard clam with the shell-length of 39.7 to 48.8 mm had a higher ability to catch suspended particles than those of the group 50.0 to 65.2 mm. However, the Manila clam could catch intentionally the larger suspended particles in accordance with their growth.

In the present study, when the Manila clam with the shell lengths of 5 to 20mm were exposed to a particle concentration of $3\times10^5$ pellets/ml, the larger particles were found to be captured by clams of greater shell-lengths. This size preference by the clam noted in this study could either be due the changes in the gill characteristics or the experimental particle concentration. This has to be examined further.

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# Photosynthetic characteristics and primary productivity of phytoplankton in the Arabian Sea and the Indian Ocean during the NE monsoon season

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**Abstract:** Chlorophyll *a* distribution, photosynthetic characteristics and primary productivity of phytoplankton were investigated in the Arabian Sea and eastern part of the Indian Ocean during the NE monsoon season (January 1994). Concentration of chlorophyll *a* at surface waters varied from 0.05 mg $m^{-3}$ in the South Equatorial Current region to 0.71 mg $m^{-3}$ in the Somali Current region. Standing stock of chlorophyll *a* within the euphotic zone ranged from 7.0 to 20.5 mg $m^{-2}$. A clear subsurface chlorophyll maximum (SCM) was observed in the layer at depth of 15 to 120 m that was 2–3 % penetration of the incident light. Depth of the SCM varied according to depths of the euphotic zone and mixed layer. The amounts of chlorophyll *a* in the SCM occupied more than 60% of the chlorophyll *a* standing stock within the euphotic zone. Photosynthesis–Irradiance curves illustrated clear differences of photosynthetic characteristics. Initial slope of the curve ($\alpha$) varied from 0.009 to 0.034 mgC(mg chl. *a*)$^{-1}$h$^{-1}$($\mu$mol quanta $m^{-2}$ $s^{-1}$)$^{-1}$ at the surface and from 0.002 to 0.208 mgC(mg chl. *a*)$^{-1}$h$^{-1}$($\mu$mol quanta $m^{-2}$ $s^{-1}$)$^{-1}$ at the SCM. The maximum value of $\alpha$ (0.208) indicaties the evidence of the dark adaptation of phytoplankton at the most southern site. Both $\alpha$ and maximal photosynthetic rate ($P_{max}$) were very low at the SCM in the Equatorial Countercurrent region ($P_{max}$=2.1 mgC (mg chl. *a*)$^{-1}$ h$^{-1}$) and the South Equatorial Current($P_{max}$=1.2 mgC(mg chl. *a*)$^{-1}$ h$^{-1}$). These low values suggested that phytoplankton at the SCM had lost their activity. Primary production varied largely from 0.08 to 0.76 gC $m^{-2}$ day$^{-1}$. The maximum production was estimated in the Somali Current region, that was attributed to the high ability of photosynthesis as shown on the P–I curve. Light utilization index ($\Psi$) also indicated the large variance of water column quantum yield within our studied area and high ability of production in the Somali Current region.

## 1. Introduction

The Arabian Sea and the Indian Ocean were under the influence of monsoons. The monsoons, SW during June–August and NE during December – February, and currents play a very important role in determining the variability of phytoplankton productivity and biomass (KREY, 1973; YENTSCH and PHINNEY, 1993) . Primary productivity and biomass of phytoplankton in these area were measured concentrically during the International Indian Ocean Expedition (IIOE; 1959–1965) by numerous research vessels. The level of primary production as the results of the IIOE were reported by RYTHER *et al.* (1966) in the western part of this region and by SAIJO (1965) in the eastern part, and summarized by KREY (1973) and ARUGA (1973).

After the days of the IIOE, some investigations of photosynthetic characteristics, primary production and chlorophyll *a* standing stocks in the Arabian Sea has been carried out by ship or satellite (e.g. BANSE and MCCLAIN, 1986; BANSE, 1987; YENTSCH and PHINNEY, 1993; GOES *et al.*, 1993; PANT, 1993; BROCK *et al.*, 1993) focused on the interested phenomena such as upwelling and phytoplankton bloom.

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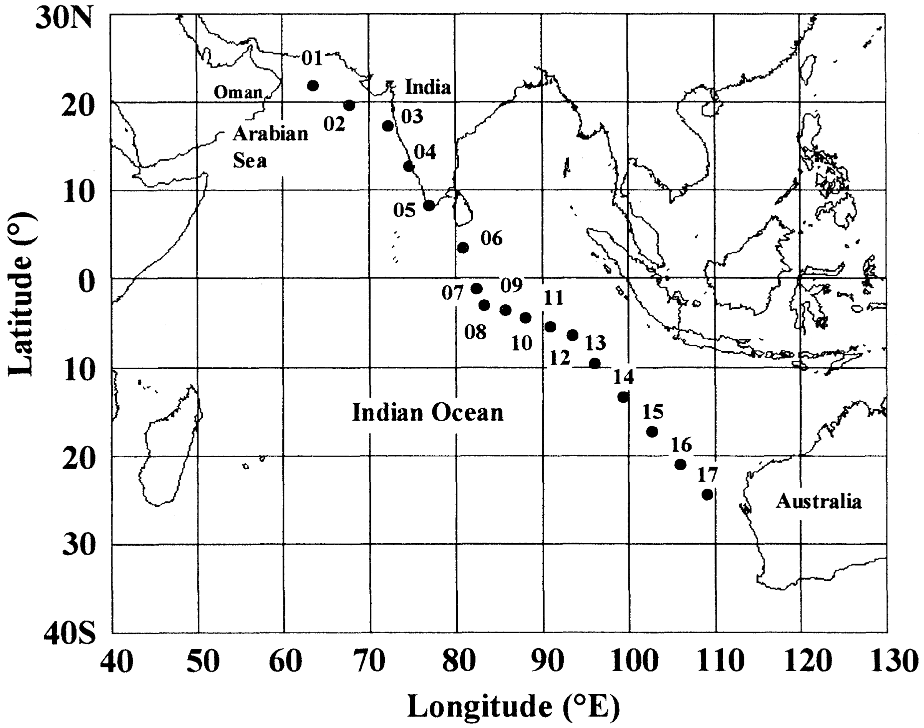

Fig. 1. Map showing the position of sampling stations (●) in the Arabian Sea (Stns. 01–05) and eastern part of the Indian Ocean (Stns. 06–17).

Photosynthetic characteristics shown by Photosynthesis–Irradiance curve (P–I curve) are important factors controlling the photosynthetic activity of phytoplankton in their natural environment (CÔTÉ and PLATT, 1984) and the parameters are being used in models for estimating primary production from remotely sensed data (e.g. PLATT *et al.*, 1988). In the Indian Ocean, however, these parameters have apparently not reported to date. New ocean color sensors such as SeaWIFS and OCTS must need the parameters that are not interpolated.

During the cruise of the T/V Umitaka-Maru III of Tokyo University of Fisheries in January 1994, we made a measurements of primary productivity of phytoplankton in the Indian Ocean included the Arabian Sea. In this paper, the authors present the photosynthetic characteristics and primary productivity of phytoplankton during the NE monsoon season.

## 2. Material and Methods

A series of investigation was carried out on the cruise from the Gulf of Oman to Fremantle, Australia (Fig. 1).

Water temperature and salinity were measured with a CTD (ICTD, FSI) : OCTOPUS system (OCTO-Parameter Underwater Sensor; ISHIMARU *et al.*, 1984) at 17 stations. The sensor of salinity was calibrated with salinometer.

Primary productivity of phytoplankton was measured at 14 stations except Stns. 05, 06 and 08. Seawater samples for primary productivity were collected using Van Dorn bottles from the sea surface and from the depth of subsurface chlorophyll maximum (SCM) recognized by the data of *in situ* fluorometer equipped with an OCTOPUS system. Additional water samples were collected using a Rossete Multi Water Sampler equipped with an OCTOPUS System for measurement of chlorophyll *a* standing stock of phytoplankton.

For measurement of phytoplankton chlorophyll *a*, 200 ml of water sample was filtered through glass fiber filter (Whatman GF/F, $\phi$ 25 mm). The filter was immediately soaked in

N, N-Dimethylformamide (DMF) and extracted pigments in the dark (SUZUKI and ISHIMARU, 1990). Concentration of chlorophyll *a* was determined fluorometrically with Turner Designs 10-005R fluorometer within a few days after the soaking (PARSONS *et al.*, 1984).

Photosynthetic activity of phytoplankton was measured by the stable $^{13}$C isotope method (HAMA *et al.*, 1983). Water samples were transferred into 2000 ml clear poly carbonate bottles. After adding $NaH^{13}CO_3$ (approximately 10% of total carbonate, ISOTEC Inc.), the samples were incubated for 4 hours in water bath controlled at surface water temperature under natural light (full sunlight, 46, 21, 11, 6% and dark). After the incubation, the water samples were filtered through glass fiber filters (Whatman GF/F, $\phi$ 47mm) precombusted at 450℃ for 4 hours. The filters were treated with fume of HCl to remove traces of inorganic carbon, and the isotope ratios of $^{12}$C and $^{13}$C were determined by infrared absorption spectrometry (SATOH *et al.*, 1985) with a $^{13}$C analyzer (EX 130, JASCO). The photosynthetic activity was calculated by the equation of HAMA *et al.* (1983), and the rate at each depth was calculated on the basis of P-I curve fit to the model of EILERS and PEETERS (1988) with a nonlinear curve-fitting minimization that uses a Gauss-Newton method. The equation of the model takes the form :

$$p = I/(aI^2 + bI + c)$$

where $p$ is photosynthetic rate, $I$ is irradiance, and $a$, $b$, and $c$ are the fitted parameters. Photosynthetic characteristics were calculated with the formulas : initial slope $(\alpha) = 1/c$, optimal intensity $(I_m) = (c/a)^{0.5}$, maximal photosynthetic rate $(P_{max}) = [b + 2(ac)^{0.5}]^{-1}$, and intensity of onset of light saturation $(I_k) = P_{max}/\alpha$.

Photosynthetically available radiation (PAR) was measured with a LI-190SB air quantum sensor and a LI-192SB underwater quantum sensor (LI-COR inc.), and recorded with an LI 1000 (LI-COR inc.) quantum meter.

Primary production in water column was estimated by integrating the value multiplied the photosynthetic rate by chlorophyll *a* concentration at each depth over the entire euphotic zone. Daily value of production was calculated on the basis of integrated PAR during the incubation period and during the whole day (WETZEL and LIKENS, 1991).

## 3. Results

### *Hydrographic condition*

Based on the surface currents (e.g. MOLINARI *et al.*, 1990), studied area was distinguished into total of four regions : Somali Current region (SC, Stns. 01-05); Equatorial Countercurrent region (ECC, Stns. 07-13); South Equatorial Current region (SEC, Stns. 14-16); and West Australian Current region (WAC, Stn. 17).

Spatial distributions of water temperature, salinity and $\sigma$-t in the upper 200 m of water column are shown in Fig. 2a, Fig. 2b and Fig. 2c, respectively. Although the salinity was homogeneous vertically, physical features indicated the stratification between 50 and 130 m except in the SC region. Especially, thermocline was developed in the ECC region as illustrated in Fig. 2a. The thermocline weakened at 10 °S where ECC and SEC formed a front. Low salinity band (<35 PSU) was observed at 10 °S (Fig. 2b) and separated the high salinity water mass. In the SC region, water mass was well mixed. In contrast with low temperature (<26 ℃) and high salinity (>36 PSU) near the Gulf of Oman, warm (>28 ℃) and low saline (<34 PSU) water mass was observed along the west coast of India.

### *Chlorophyll a distribution and photosynthetic characteristics*

Spatial distribution of chlorophyll *a* concentration in the upper 200m of water column is shown in Fig. 2d, and the surface values and standing stock of chlorophyll *a* for each region are listed in Table 1. Chlorophyll *a* concentration at the sea surface was low (0.05-0.71 mg m$^{-3}$). The surface water from the SCC to WAC regions had extremely low (0.05-0.09 mg m$^{-3}$) chlorophyll *a* concentrations. Although the highest surface value (0.71 mg m$^{-3}$) was observed at Stn. 01 in the Somali Current region, shallower station of the same region had relatively low values.

Chlorophyll *a* standeng stock within the euphotic zone ranged from 7.0 mg m$^{-2}$ at Stn. 15 in the SEC region to 20.5 mg m$^{-2}$ at Stn. 01 in

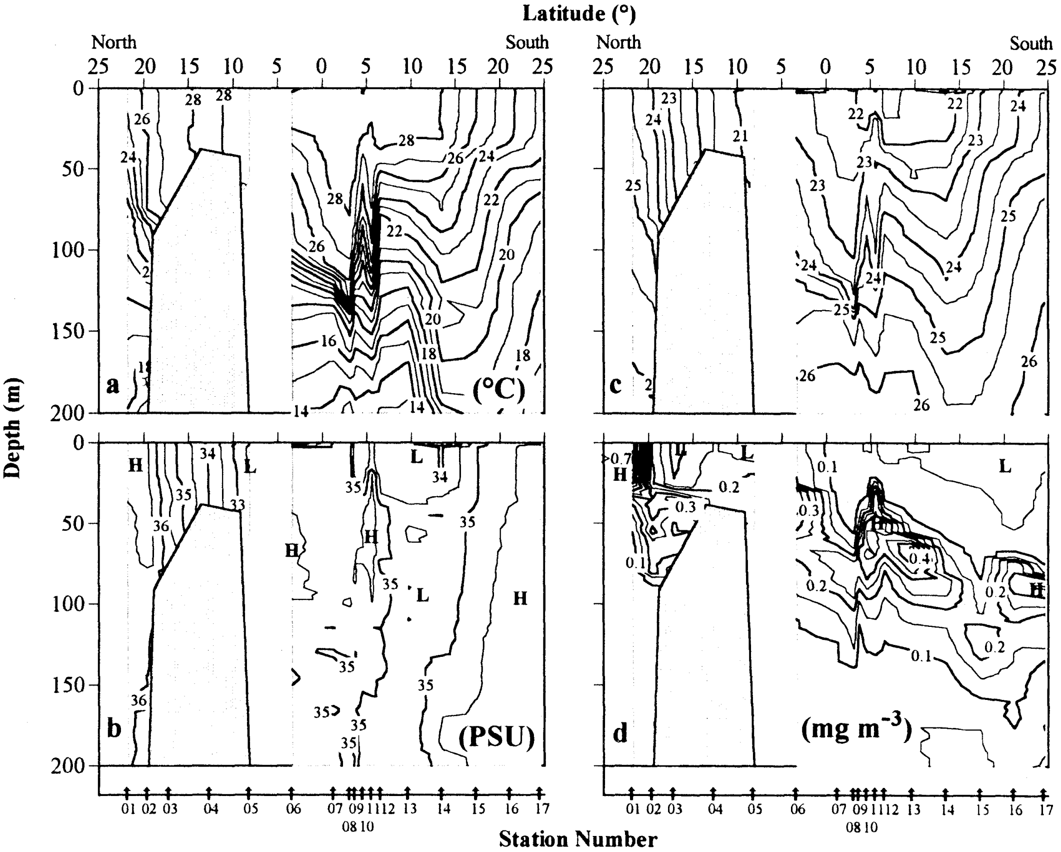

Fig. 2. Vertical sections of (a) water temperature, (b) salinity, (c) σ-t, and (d) chlorophyll *a* concentration in the Arabian Sea and the Indian ocean. Blank area denotes no data.

Table 1. Surface concentration and standing stock within euphotic zone of chlorophyll *a*, primary production, solar radiation incident upon surface, and light utilization index in the different regions showing range and mean. Values in parentheses are mean.

| Region | Station | Chlorophyll *a* | | Primary production (gC m$^{-2}$ day$^{-1}$) | Solar Radiation (mol quanta m$^{-2}$ day$^{-1}$) | Ψ * |
|---|---|---|---|---|---|---|
| | | Surface (mg m$^{-3}$) | Standing Stocks (mg m$^{-2}$) | | | |
| Somali Current | 01–05 | 0.19–0.71(0.40) | 8.5–20.5(12.7) | 0.28–0.76(0.45) | 28.0–34.2(30.4) | 0.88–1.27(1.06) |
| Equatorial Countercurrent | 07–13 | 0.09–0.14(0.12) | 8.7–15.2(12.4) | 0.09–0.20(0.14) | 23.9–43.3(35.1) | 0.22–0.63(0.36) |
| South Equatorial Current | 14–16 | 0.05–0.09(0.08) | 7.0–13.0(10.1) | 0.08–0.11(0.10) | 43.1–50.6(45.8) | 0.18–0.29(0.22) |
| West Australian Current | 17 | 0.08 | 11.8 | 0.29 | 35.7 | 0.69 |
| | Average | 0.19 | 12.0 | 0.23 | 36.1 | 0.55 |
| | C.V.(%) | 89.7 | 27.3 | 80.8 | 21.1 | 67.6 |

*light utilization index(gC(gchl.*a*)$^{-1}$(mol quanta m$^{-2}$)$^{-1}$)

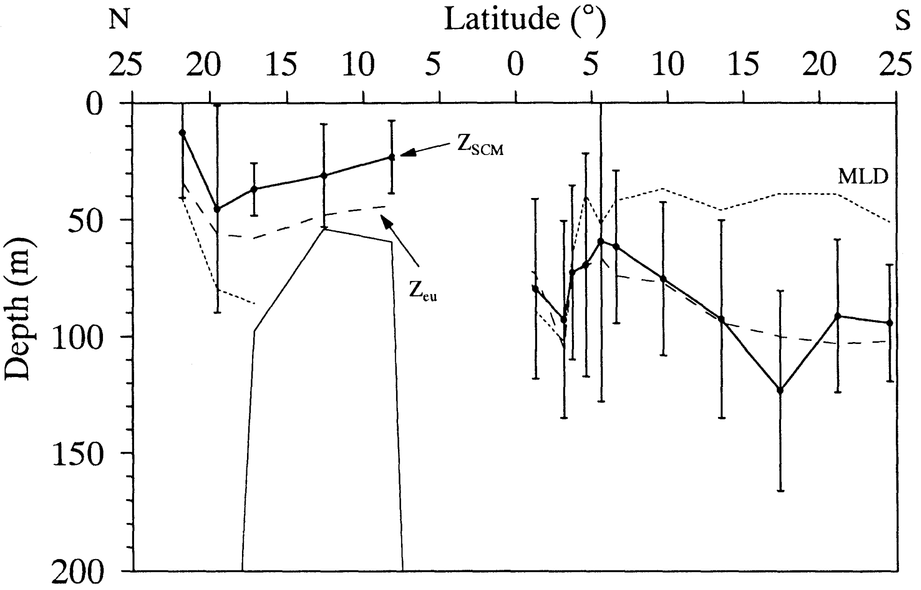

Fig. 3. Depth of subsurface chlorophyll maximum, ($Z_{SCM}$; —●—), euphotic zone defined as 1% penetration of incident light ($Z_{eu}$; — —), and mixed layer (MLD; ···). Error bar shows a range of the maximum. Blank area denotes no data.

the SC region. The averaged value in the SC region was relatiely higher (12.7 mg $m^{-2}$) than those in the other regions. Although surface chlorophyll *a* concentrations had a wide range within the studied area (89.7% C.V.), variation of standing stocks with region was small (27.3% C.V.).

In the layer at depths of 15 to 40 m in the SC region and at 50 to 120 m in the other regions, distinct subsurface chlorophyll maximum (SCM) was observed (Fig. 2d). Maximal concentations at the SCM layer ranged 0.27–0.99 mg $m^{-3}$ in the SC region and 0.25–0.50 mg $m^{-3}$ in the other regons. The SCM occupied more than 60% of the chlorophyll *a* standing stock (Table 1) within the euphotic zone. Comparison of peak depth and range of the SCM, depth where PAR is reduced to 1% of the surface ($Z_{eu}$ : euphotic zone depth), and mixed layer depth (MLD) is shown in Fig. 3. In the present study, range of the SCM is determined on the basis of Gaussian Curve fit (LEWIS *et al.*, 1983; PLATT *et al.*, 1988) modified by MATSUMURA and SHIOMOTO (1993), and MLD is defined as the first depth at which the temperature is 1.0 ℃ less than that at 10 m (RAO *et al.*, 1989). Peaks of the SCM were lower part of the euphotic zone, that were 2–3 % penetration of the surface light except Stn. 15. The SCM changed its vertical distribution according to a relative position of MLD and $Z_{eu}$. In the SC region, mixed layer (41–86 m) included whole of euphotic zone (34–58 m) and the SCM was approximately within the MLD and/or euphotic zone. MLD in the ECC region was close to $Z_{eu}$ and turned upside-down where top and bottom of the SCM (except Stn. 13 at about 10 °S where is a front as mentioned above) were positioned at above and at below of both depths, respectively. In the SEC and the WAC regions more southern than the front of 10 °S, $Z_{eu}$ was completely lower than MLD. The SCM in these regions was distributed lower than MLD and expanded up to extremely weak light layer deeper than $Z_{eu}$.

P-I curves at sea surface and SCM in the each region and the parameters of photosynthetic characteristics were shown in Fig. 4 and listed in Table 2, respectively. P-I curves illustrated a clear difference of photosynthetic characteristics between the surface and SCM, and between the regions. All curves at the sea surface show a weak photoinhibition, though, $P_{max}$ of the surface were 1.3–5.4 times as high as for the SCM.

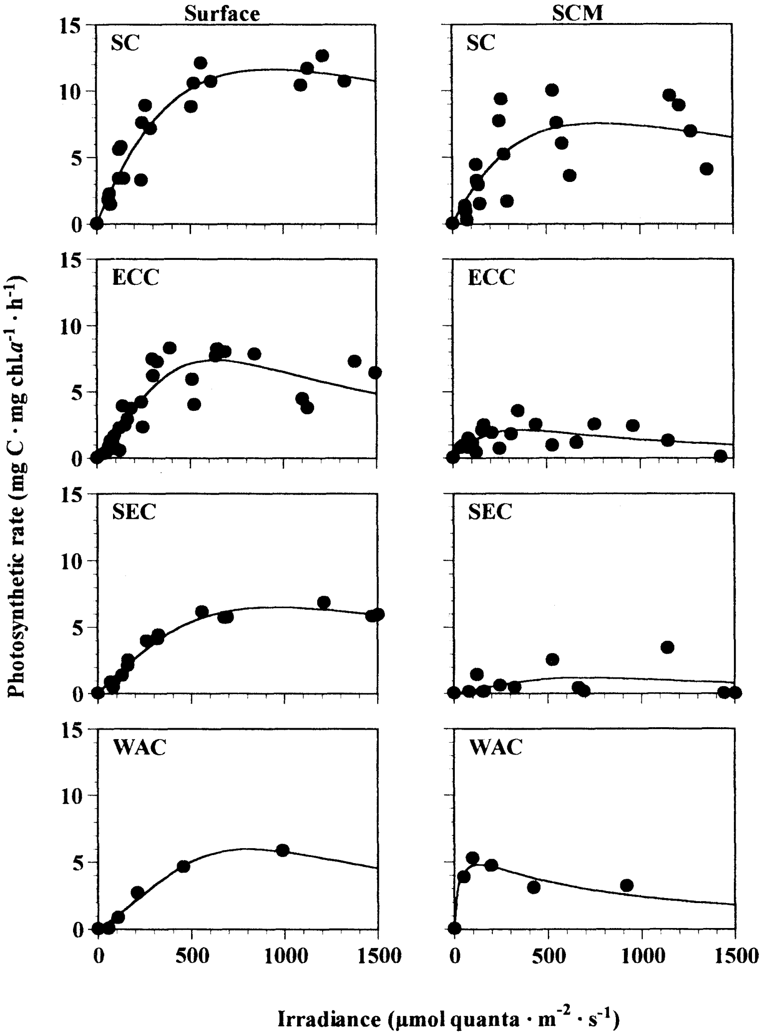

Fig. 4. Photosynthesis–Irradiance curves at surface and SCM fitted to all data in the (SC) Somali Current region, (ECC) Equatorial Countercurrent region, (SEC) South Eauatorial Current region, and (WAC) West Australian Current region.

Table 2. Parameters showing photosynthetic characteristics of phytoplankton in different regions.

| Region | Surface | | | | | SCM | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Station | $\alpha$ * | $P_{max}$ ** | $I_m$ † | $I_k$ ‡ | $\alpha$ * | $P_{max}$ ** | $I_m$ † | $I_k$ ‡ |
| Somali Current | 01–05 | 0.034 | 11.6 | 938 | 338 | 0.027 | 7.5 | 780 | 281 |
| Equatorial Countercurrent | 07–13 | 0.018 | 7.4 | 634 | 412 | 0.014 | 2.1 | 356 | 156 |
| South Equatorial Current | 14–16 | 0.014 | 6.5 | 954 | 458 | 0.002 | 1.2 | 693 | 496 |
| West Australian Current | 17 | 0.009 | 6.0 | 810 | 660 | 0.208 | 4.8 | 132 | 23 |

*initial slope (mgC(mg chl. $a)^{-1}h^{-1}$ (μmol quanta $m^{-2}$ $s^{-1})^{-1}$)

**maximal photosynthetic rate (mgC(mg chl. $a)^{-1}h^{-1}$)

†optimal intensity (μmol quanta $m^{-2}$ $s^{-1}$)

‡intensity of onset of light saturation (μmol quanta $m^{-2}$ $s^{-1}$)

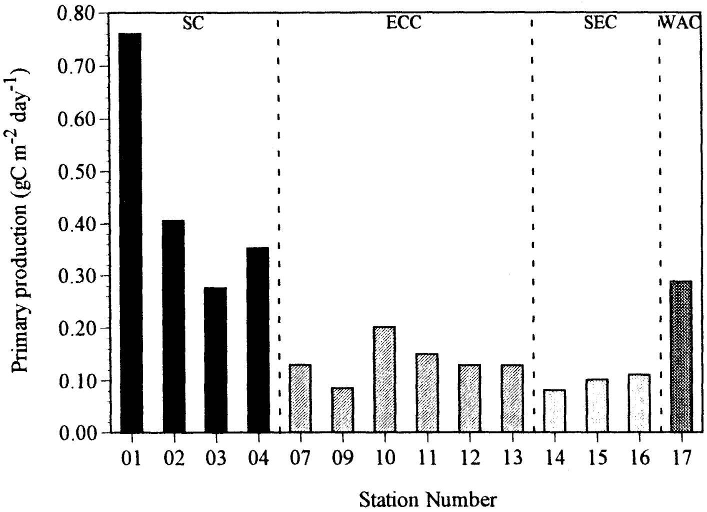

Fig. 5. Primary production at each sampling station. Dashed lines separates the stations into four current regions.

$P_{max}$ was especially high in the SC region that was 1.6–1.9 times at the surface (11.6 mgC (mg chl. $a$)$^{-1}$ h$^{-1}$) and 1.6–6.3 times at the SCM (7.5 mgC (mg chl. $a$)$^{-1}$ h$^{-1}$) as high as for the others. $\alpha$ of the surface (0.034 mgC (mg chl. $a$)$^{-1}$ h$^{-1}$ ($\mu$mol quanta m$^{-2}$ s$^{-1}$)$^{-1}$) in the SC region is also highest value, that shows most productive surface water. As shown by the values of $I_m$ (634–954 $\mu$mol quanta m$^{-2}$ s$^{-1}$) and $I_k$ (338–660 $\mu$mol quanta m$^{-2}$ s$^{-1}$) of the surface, phytoplankton at the surface was adapted to strong insolation. While at the SCM, photoadaptation to dark was not observed except the WAC region. The SCM in the WAC had high value of an $\alpha$ (0.208 mgC (mg chl. $a$)$^{-1}$h$^{-1}$ ($\mu$mol quanta m$^{-2}$ s$^{-1}$)$^{-1}$) showing high activity at low light intensity. Although $I_k$ at the SCM in the ECC region was relatively low (156 $\mu$mol quanta m$^{-2}$ s$^{-1}$), low $P_{max}$ (2.1 mgC (mg chl. $a$)$^{-1}$ h$^{-1}$) denies a dark adaptation. Phytoplankton at the SCM of the SEC was reduced its activity more than those in the ECC. It appears that high $I_m$ and $I_k$ in this region indicate light adaptation. But this is only a lost of activity because of the remarkably low $\alpha$ (0.002 mgC(mg chl. $a$)$^{-1}$h$^{-1}$ ($\mu$mol quanta m$^{-2}$ s$^{-1}$)$^{-1}$) and $P_{max}$ (1.2 mgC (mg chl. $a$)$^{-1}$ h$^{-1}$).

*Primary production and light utilization index*

Distribution of daily primary production was shown in Fig. 5, and the values for the each region were shown in Table 1. The studied regions had a widely one order range of primary production (0.08–0.76 gC m$^{-2}$ day$^{-1}$). The highest value of production was obtained in Stn. 01 in the SC region. Production in the SC region, of which mean production was 0.45 gC m$^{-2}$ day$^{-1}$ with the range of 0.28–0.76 gC m$^{-2}$ day$^{-1}$, was 1.5–4.5 times in mean value as high as the others. The waters in the ECC region were low productive (0.09–0.20 gC m$^{-2}$ day$^{-1}$), and more oligotorophic water was observed in the SEC region as shown in the value of primary production (0.08–0.11 gC m$^{-2}$ day$^{-1}$). Although the WAC region keep close to the SEC region, that had relatively high value (0.29 gC m$^{-2}$ day$^{-1}$) because of the high photosynthetic activity of phytoplankton in the SCM layer.

Total water column light utilization index ($\Psi$ : FALKOWSKI, 1981) for each region was shown in Table 1. $\Psi$ was estimated from the expression :

$$\Psi = P/(B \cdot I_0)$$

where $P$ is the daily primary production of water column in gC m$^{-2}$ day$^{-1}$, $B$ is the chlorophyll $a$ standing stock in g chl. $a$ m$^{-2}$, and $I_0$ is solar radiation at the sea surface (Table 1) in mol quanta m$^{-2}$ day$^{-1}$. Averaged value of $\Psi$ for all regions was 0.55 gC (gchl.$a$)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$ with 67.6% (C.V.) of variation. In the SC region, mean value of $\Psi$ was 1.06 gC (g chl. *a*)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$ with the narrow range (0.88–1.27 gC (g chl. *a*)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$) that is 15% in C.V., and the value was the highest within the all studied regions. The index $\Psi$ was fallen into the averaged value of 0.22 gC (g chl. *a*)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$ in the SEC region (26% C.V.), and relatively high in the WAC region (0.69 gC (g chl. *a*)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$). In the ECC region, the highest variance of $\Psi$ was observed (50% C.V.).

## 4. Discussion

Distinct physical features in the studied are the front and the low salinity band which had observed also during the IIOE (WYRTKI, 1971; 1973). WYRTKI (1973) suggested that the low salinity band is characteristic of the front formed at 10 °S and separates the high salinity water mass of the northern Indian Ocean from the subtropical high salinity water of the subtropical gyre. Low saline water along the west coast of India is also typical of the SC region. This water mass marks the northward flowing equatorial surface waters (ESW; GOES *et al.*, 1993) from the southwestern Bay of Bengal (BRUCE *et al.*, 1994). Surface salinity maps demonstrated by WYRTKI (1971) also showed the intrusion of low–salinity water from the Bay of Bengal into the Arabian Sea. Moreover, low chlorophyll water mass observed in this region was originated from the Bay of Bengal associated with the ESW (GOES *et al.*, 1993).

Clear differences in chlorophyll distribution, photosynthetic characteristics and primary production were observed, that is according to four regions distinguished by surface currents. In the SC region of the Arabian Sea, these values were distinctly higher than those in the other regions. Moreover $\alpha$ and $P_{max}$ in this region ($\alpha$ =0.034, $P_{max}$ =11.6 at Surface; $\alpha$ = 0.027, $P_{max}$ =7.5 at SCM) was higher than values : $\alpha$ =0.017 mgC (mg chl. *a*)$^{-1}$h$^{-1}$ ($\mu$mol quanta m$^{-2}$ s$^{-1}$)$^{-1}$ (convert watts to mols of quanta assuming 1W=4.6 $\mu$mol quanta s$^{-1}$) and $P_{max}$=5.37 mgC (mg chl. *a*)$^{-1}$h$^{-1}$ published by SATHYENDRANATH *et al.* (1996) in the Somali Basin (southwest of Stn. 01). Similar to the conditions in the Somali Basin during the NE monsoon (January 1993) reported by VELDHUIS *et al.* (1997), the MLD exceeded the $Z_{eu}$. So that, it is considered that the nutrients is supplied enough to keep a high activity compared with it in the other regions. The SC region in this study is including the shallow waters, that is also a reason of high $\alpha$ and $P_{max}$. However, primary production at the shallow stations (0.28–0.41 gC m$^{-2}$ day$^{-1}$) was lower than the result of Somali Basin (VELDHUIS *et al.*, 1997) because of the low standing stocks.

In the ECC region, the MLD was closed to the $Z_{eu}$ and almost of the SCM was distributed along the $Z_{eu}$ at depth more than 50m. The SCM in the SEC and the WAC region were also along the $Z_{eu}$ and entirely beneath the MLD situated at approximately 50m. AS long as seen in these results, the SCM was depended on light intensity, but the dark adaptation was observed only in the WAC and activity of phytoplankton were very low as shown in the values of $\alpha$ and $P_{max}$ in the ECC ($\alpha$ =0.014, $P_{max}$=2.1) and SEC ($\alpha$ =0.002, $P_{max}$=1.2). The results of JITTS (1965) also illustrated that productivity along the 110° E was infinitesimal at the depth more than about 50m. SAIJO (1965) suggested from the results of the tank experiments that the chlorophyll at the depth of the SCM had almost lost their photosynthetic ability. He more implied that the SCM is not the result of the passive accumulation of senescent phytoplankton but represents an accumulation of actively growing phytoplankton (SAIJO, 1973). The SCM in the ECC and the SEC appeared in our study might avoid the nutrients impoverished surface water mass and strong solar radiation.

Distinct difference and variability in water column light utilization index ($\Psi$) were appeared in like manners of productivity and P–I curve parameters. The index means water column averaged quantum yield for photosynthesis and has been used as important factor of productivity model estimate the depth-integrated primary production (FALKOWSKI, 1981; PLATT, 1986; MOREL, 1991). The value of $\Psi$ changes with a variety of environments (PLATT, 1986) such as the values of FALKOWSKI (1981)($\Psi$ =0.43), YODER *et al.* (1985)($\Psi$ =1.5), CAMPBELL and O'REILLY(1988)($\Psi$ =1.47), and BALCH *et al.* (1989)($\Psi$ =0.27). The averaged value obtained of our study ( $\Psi = 0.55$) was lower than the world-wide averaged value of 0.96 gC (g chl. $a$)$^{-1}$ (mol quanta m$^{-2}$)$^{-1}$ (BALCH and BYRNE, 1994). However the value in the SC region ($\Psi = 0.88$–$1.27$) is relatively high within values of the world oceanic waters (e.g. FALKOWSKI, 1981), and same level as much as the values by $^{14}C$ based experiments in the Somali Basin ($\Psi = 0.84$–$1.59$; VELDHUIS *et al.*, 1997) in spite of the difference in the technique and method that induces large error (BALCH and BYRNE, 1994). In contrast with the SC region, $\Psi$ in the SEC region ($\Psi = 0.18$–$0.29$) was one of the lowest value in the world oceans. In case we try to estimate the primary production of water column from satellite derived data, it is difficult to regard our studied regions as only one area where has constant value of $\Psi$, due to its large variance. In other words, it was appropriate that a variable $\Psi$ and photosynthetic characteristics ($\alpha$, $P_{max}$, $I_k$, $I_m$) were ramified into four region based on the surface currents.

Although we presented chlorophyll distribution, productivity and photosynthetic characteristics of phytoplankton in the Arabian Sea and the eastern Indian Ocean related to the hydrographic condition and the light penetration, the obtained primary production data are only shipboard estimates that are "point" or "line". It is hoped that the primary production in this area will estimated in more broad-scale from satellite to resolve the global carbon cycle.

It is ideal that simple mathematical model is utilized to estimate the integrate primary production from remotely sensed data. The simplest productivity models estimate primary production as a function of sea surface chlorophyll (e.g. EPPLEY *et al.*, 1985). This simplest relationship for the Arabian Sea and the Indian Ocean (HIRAWAKE *et al.*, 1996) has a strong correlation ($r^2 = 0.90$ for the same dataset as this study), but the model induced a large error in the sites where primary production depends on the standing stock within the SCM layer or chlorophyll concentration was high. It is expected that a more complicated model is attempted for such regions. Although the complex approach also need information on the photosynthetic characteristics, there was very little about these parameters in our studied area, especially from the ECC to WAC region. It is clear that the photosynthetic characteristics presented in this study are very precious data on the next step in the primary producton model.

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# 日仏海洋学会誌　うみ（La mer）第35巻掲載欧文論文和文要旨

［35巻1号］

**A.Z. Segatto*, E. Granéli*・C. Haraldsson**：2種の植物プランクトンの成長に対するコバルトとビタミン$B_{12}$の影響**

珪藻 *Ditylum brightwellii* と渦鞭毛藻 *Prorocentrum minimum* の成長に対するコバルトとビタミン$B_{12}$の影響を調べた．実験は培地として，栄養塩を添加し滅菌した大西洋亜表層水を26％に希釈した海水を用い，実験室条件下で行った．コバルトはKattegat海峡やSkagerrak海峡の沿岸水や，貧栄養の外洋水で測定される濃度に相当する0.5-3nMの濃度で添加した．実験期間を通して毎日細胞密度とクロロフィル*a*濃度を測定した．*P. minimum*の成長率と生物量はコバルトの添加によって影響を受けなかったが，*D. brightwellii*の成長率と生物量の増加は著しく抑制された．（*Department of Marine Ecology, University of Lund, 223 62 Lund, Sweden, **Department of Analitical and Marine Chemistry, University of Gothenburg, 412 96, Gothenburg, Sweden）

**D-V. Manh*・柳　哲雄*：Tongking湾の潮汐と潮汐流の三次元数値モデル**

三次元数値モデルによりTongking湾の潮流，潮汐残差流の研究を行った．モデルでは，鉛直方向に引伸したいわゆる$\sigma$-座標系を用い，差分法により計算した．$K_1$, $O_1$, $M_2$, $S_2$の潮汐主要4成分についての計算結果は，各地検潮所で得られた潮位観測結果とよく一致した．つぎに，$K_1$, $M_2$分潮に起因する潮汐残差流をそれぞれ計算した．$K_1$分潮の潮汐残差流は海南島の南西海岸域で最も強く，10cm/sに達した．（*〒790-77松山市文京町3番　愛媛大学工学部）

［35巻2号］

**東谷知範*・磯田　豊*：東部ベーリング海陸棚上における潮流とその混合エネルギーの空間分布**

東部Bering海陸棚域における半日及び日周期の潮汐・潮流の空間分布をf平面水平2次元数値モデルを用いて調べた．Alaska沿岸に位置するBristol湾とNorton Soundとでは潮汐・潮流の応答が異なっている．すなわち，Bristol湾では半日周潮流が卓越し，Norton Soundでは日周潮流が卓越している．数値モデルの計算結果は，各湾で卓越する分潮の違いは強制振動の周期に関係し，共振潮汐によって説明ができることがわかった．さらに，モデル結果は，陸棚斜面に捕捉された地形性ロスビー波の励起が，陸棚斜面に沿った日周潮流の振幅を増大させていること示唆している．次に，モデルで予測された潮流データを用いて空間的な潮流エネルギー分布を計算し，夏季東部Bering海の成層分布にどの程度影響を及ぼしているかを調べた．1963年～1992年の海洋観測資料を用いて計算したポテンシャルエネルギーアノマリーの分布はAlaska沿岸に沿った密度フロントの存在を示す．このフロントが形成されている位置がほぼ潮汐混合パラメータ$\log(H/U^3)=2.5\sim3.0$に対応していることから，主に潮流の鉛直混合エネルギーがフロント形成に寄与し，潮汐フロントの存在が推測される．しかし，Anadyr Currentが陸棚を横切るSt. Lawrence島の北部の海域の成層分布は潮汐混合パラメータ$\log(H/U^3)$分布とは一致せず，潮汐の鉛直混合だけでは説明できない．（*〒041函館市港町3-1-1　北海道大学水産学部）

**S.Y. Maestrini*・M. Balode**・C. Bechemin*・I. Purina**・C. Verite*：東部バルト海のリガ湾における，1996年春から初夏の藻類の潜在成長力を制限する栄養潮類**

1996年5月，6月および7月に，リガ湾において河川流入の影響を強く受けた東側の測線沿い，影響の比較的少ない西側の測線沿い，主要流入河川のダニューブ川河口の1測点，湾中央部の1側点および西側の沿岸沿いの数点から採水を行った．植物プランクトンの成長力を制限する栄養要素を知るために，バイオアッセイ法による実験を行うとともに，現場の溶存無機窒素，リン酸および珪酸の測定を行った．溶存無機窒素（DIN）：溶存無機リン（DIP）比とRedfield比との比較によっても，またバイオアッセイによっても同様の結果が得られた．無機リンは，河川流入の影響を強く受けた湾南部－東部域の表層に春中期に出現する窒素分に富んだ水域からの試供種の潜在成長を最も抑制する要因であった．晩春には，貯留DINの減少にともなって窒素とリンは制限要素として同様の効果を示した．この海域のより深い層や河

ロプラム外の海域（湾の西側や中央海域）では，窒素が制限因子であった．河川流入の最も少ない夏季には，1つを除き全てのDIN濃度は1.6-2.6μMであり，全ての海域で藍藻類や試供藻類に対して窒素が制限因子であった．窒素が制限要因となっている試料の74％では，リンが第2の制限要因であった．対照的に，珪素は*Microcystis aeruginosa*や*Phaeodactylum tricornutum*の成長に対して制限要因となることはなかった．すなわちDIN：$SiO_3$＞1（5月）の季節にはリンが，DIN：$SiO_3$＜1（6月および7月）の季節には窒素が制限要因であった．近年報告されている珪素負荷の減少や，そのことによって有毒種の発生をもたらすような種間競争を引き起こすような事態はリガ湾では起こっていないと考えられた．鉄は栄養因子試験の12％で潜在成長を制限した．また*M. aeruginosa*が利用した窒素の注目すべき割合（～4 μg-atom N $l^{-1}$）が有機態窒素の形であることがわかった．すなわち，リガ湾における今後の研究を進める場合には，これらの栄養因子により注意を払う必要がある．

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［35巻3号］

**柳　哲雄*・高尾敏幸*・森本昭彦*：衛星高度計データより得られた南シナ海の同時潮図と等潮差図**

TOPEXの高度計データにより得られた海面高度データを調和解析して，南シナ海の$M_2$，$S_2$，$K_1$，$O_1$，$P_1$，Sa分潮の同時潮図と等潮差図を描いた．得られた$M_2$，$K_1$分潮の図は，過去沿岸の潮位計データをもとに描かれた図とよく一致した．また，$S_2$分潮の図は$M_2$分潮の図と，$O_1$，$P_1$分潮の図は$K_1$分潮の図と，それぞれよく似ている．Sa分潮の振幅は北東部と南西部で大きく，位相は両地域で180度ずれている．さらにSa分潮の無潮点がふたつベトナム沖に存在する．

（*〒790-77松山市文京町3番　愛媛大学工学部）

［35巻4号］

**パオロ　マーニ*・門谷　茂*：瀬戸内海の干潟域における底生微細藻類の消長：環境因子の影響について**

瀬戸内海のある河口干潟において，底生微細藻類の消長と環境因子の関係を明らかにするために，河口域に2定点を設定して1週間に2回以上の詳細な環境調査を13ケ月に渡って実施した．互いに約1キロメートルほど離れている2定点において観測された様々な環境因子の内，栄養塩濃度や塩分，溶存酸素濃度など，ほとんどの物理・化学項目は良く似ていた．しかしながら，底生微細藻類の現存量は標高の高い，河口から遠い定点で得られたもの（240.9＋121.1 mg $m^{-2}$,n＝107）の方が，低潮位線近くの定点で得られた値（121.9＋41.4 mg $m^{-2}$, n＝108）と比べて有意に高く，見積もられた年間基礎生産量も（それぞれ634 gC $m^{-2}yr^{-1}$ と 259 gC $m^{-2}yr^{-1}$）同様であった．このように，低潮位線近くの定点に比べて河口から遠い定点の方が，底生微細藻類の現存量が大きい理由は，流体力学的なエネルギーが小さいことによる環境の安定性が高いためと考えられた．また，瀬戸内海で得られている水柱の年平均基礎生産量（285 gC $m^{-2}yr^{-1}$）に比べて，今回得られた干潟の堆積物表層部における年平均基礎生産量（447 gC $m^{-2}yr^{-1}$）が極めて高いことなども議論した．（*〒761-07香川県木田郡三木町池戸2393　香川大学農学部）

**荒川久幸*・矢尾板俊秀**・小池　隆**・森永　勤*：二枚貝アサリ*Ruditapes philippinarum*の懸濁粒子の捕捉サイズ**

アサリの懸濁粒子の捕捉サイズや殻長別の捕捉サイズの変化をコールタ・カウンタにより調べた．アサリの殻長は5，10，20および30mm，使用総数は約450個体である．懸濁粒子はアワビ用人工飼料（ペレット）の粉砕粒子（平均粒径；3.7μm）および植物プランクトン*Pavlova lutheri*（3.5μm）を，濾過海水にそれぞれ懸濁させ，用いた．その濃度は前者で$1\times10^5$，$3\times10^5$，および$6\times10^5$個／ml，後者で$3\times10^5$cell／mlである．粒子捕捉率は懸濁水中の粒子が一定時間が減少する割合とした．殻長30mm，濾過活動の活発なアサリ成員の捕捉率は，ペレット粒子濃度　$3\times10^5$個/mlの懸濁海水中に60分間静置した場合，全粒径（2.2～45.2μm）において60％・$h^{-1}$でほぼ均一であった．その濃度が$6\times10^5$個/mlに増大すると捕捉率は15μm以下の粒径で約1/3に低下した．また，180分間での捕捉率は全粒径において約1/3に低下した．さらに，懸濁粒子の種類をペレットから植物プランクトンへ取り替えると，捕捉率はペレットの場合より5μm以上の粒径で約20％高くなった．殻長の異なるアサリをそれぞれ，ペレット粒子濃度$3\times10^5$個/mlの懸濁海水中に60分間静置したとき，殻長5mmの捕捉率は全粒径範囲で平均0.68％・$h^{-1}$とほぼ均一であるが，殻長が10，20mmと増大するに従い，捕捉率は大きな粒径でより高くなる傾向を示した．このことは，殻長20mmまでの稚貝では成長するにともない，よ

り大きな粒子を選択的に捕捉していることを示唆している．

（*〒108港区港南4-5-7　東京水産大学海洋環境学科，
〒514三重県津市上浜町1515　三重大学生物資源学部）

**平譯　享*・石丸　隆*・佐藤博雄*：北東季節風期のアラビア海，インド洋における植物プランクトンの光合成特性と基礎生産力**

北東季節風期（1994年1月）のアラビア海，東部インド洋において，クロロフィル*a*，光合成特性および基礎生産力について調査を実施した．表層のクロロフィル*a*濃度は0.05mg $m^{-3}$（南赤道海流域）から0.71mg $m^{-3}$（ソマリ海流域）の範囲であった．有光層内のクロロフィル現存量は7.0-20.5mg $m^{-2}$であった．明瞭な亜表層クロロフィル極大が15-120m 層に観測された．海面入射光の2-3%である層に極大は分布し，極大の深度は有光層深度および混合層深度にしたがって変化した．また，クロロフィル現存量の60%はこの亜表層クロロフィル極大中に存在した．光合成-光曲線は光合成特性の明確な違いを示した．初期勾配$\alpha$は表層において0.009-0.034 mgC $(\mathrm{mgchl.}a)^{-1}\mathrm{h}^{-1}(\mu\mathrm{mol\ quantam}^{-2}\mathrm{s}^{-1})^{-1}$，亜表層クロロフィル極大において0.002-0.208mgC $(\mathrm{mg\ chl.}a)^{-1}\mathrm{h}^{-1}(\mu\mathrm{mol\ quanta\ m}^{-2}\mathrm{s}^{-1})^{-1}$であった．$\alpha$の最高値（0.208）が最も南の測点において測定され，この海域の植物プランクトンの弱光適応を示している．赤道反流域と南赤道流域の亜表層クロロフィル極大における$\alpha$と最大光合成活性$P_{max}$は共に低く，$P_{max}$の値はそれぞれ2.1mgC$(\mathrm{mg\ chl.}a)^{-1}\mathrm{h}^{-1}$および1.2mgC$(\mathrm{mg\ chl.}a)^{-1}\mathrm{h}^{-1}$であった．これらの低い値から，クロロフィル極大の植物プランクトンが活性を失っていることが示唆された．基礎生産量は海域により大きく変化し，0.08-0.76gC $\mathrm{m}^{-2}\mathrm{day}^{-1}$であり，ソマリ海流域において最も高かった．これは光合成-光曲線に示された高い光合成活性に起因する．光利用指数$\Psi$もまた，調査海域内における水柱量子収率の大きな変動とソマリ海流域における生産力の高さを示した．

（*〒108港区港南4-5-7　東京水産大学海洋環境学科）

La mer 35: 172, 1997
Société franco-japonaise d'océanographie, Tokyo

# 学　会　記　事

1. 1997年11月14日（金）　東京水産大学において平成9年度学会賞受賞候補者推薦委員会（第1回）が開かれ，委員長に関根義彦氏を選出し，推薦の方法および次回の日程を決めた．

2. 1997年11月14日（金）　東京水産大学において平成9年度第2回幹事会が開かれた．主要な議事は下記の通り．

報告事項

1) 平成9年10月末日段階の学会の会計状況が報告された．
2) 学会誌 La mer の編集状況が報告された．

協議事項

1) 平成10～11年度評議員選挙の日程について審議した．投票用紙発送は11月中，投票締切は平成10年1月10日（土），開票は平成10年1月19日（月）と決定した．
2) 次期会長選挙の日程について審議した．投票用紙発送は平成10年2月10日までに，投票締切は平成10年2月28日（土），開票は平成10年3月9日（月）と決定した．

3. 新入会員（正会員）

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4. 住所・所属機関等変更（正会員・受付順）

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5. 退会（正会員）

山路　勇

6. 受贈図書

NTT R&D　46
なつしま　150
国立科学博物館研究報告　23(3)
養殖研ニュース　35
Biodiversity and Aquaculture for Sustaineble Development
東海大学紀要　44
Journal of the Korean Society of Oceanography 31 (1-4)
The Sea　2(1)
海洋与湖沼　26(1-6), 27(1-5)

### 日仏海洋学会役員・評議員
（1996～1997年度）

顧　　問：ユーベル・ブロシェ　ジャン・デルサルト　ジャック・ローベル　アレクシス・ドランデール　ミシェル・ルサージュ　ローベル・ゲルムール　ジャック・マゴー　レオン・ヴァンデルメルシュ　オーギュスタン・ベルク　ユーベル・セカルディ　オリビエ・アンサール
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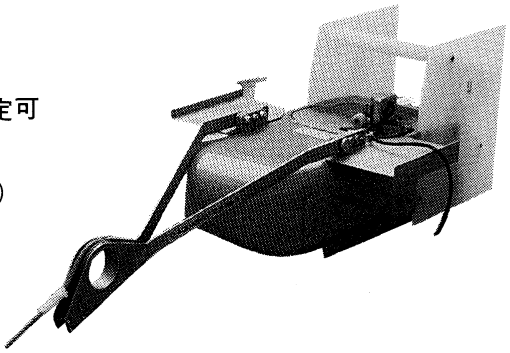

# 日仏海洋学会入会申込書

（正会員・学生会員）

| | | |
|---|---|---|
| | 年度より入会 | 年　月　日申込 |
| 氏　名<br>ローマ字 | | 年　月　日　生 |
| 勤務先 | 住　所　〒<br>機関名<br>電　話 | |
| 自　宅 | 住　所　〒<br>電　話 | |
| 紹介会員氏名 | | |
| 送付金額　円 | 送金方法 | |
| 会誌の送り先（希望する方に○をつける） | 勤務先　自　宅 | |

（以下は学会事務局用）

| | | | | |
|---|---|---|---|---|
| 受付 | 名簿<br>原簿 | 会費<br>原簿 | あて名<br>カード | 学会<br>記事 |

入会申込書送付先：〒150　東京都渋谷区恵比寿3-9-25
（財）日仏会館内
日仏海洋学会

郵便振替番号：00150-7-96503

## 日仏海洋学会編集委員会（1996-1997）

## 投稿の手引

1.「うみ」（日仏海洋学会機関誌；欧文誌名 **La mer**）は，日仏海洋学会正会員およびそれに準ずる非会員からの投稿（依頼稿を含む）を，委員会の審査により掲載する。
2．原稿は海洋学および水産学両分野の原著論文，原著短報，総説，書評，資料などとする。すべての投稿は，本文，原図とも正副2通とする。副本は複写でよい。本文原稿用紙はすべてA4判とし，400字詰原稿用紙（和文）に，または厚手白紙にダブル・スペース（和文ワープロでは相当間隔）で記入する。表原稿および図説明原稿は，それぞれ本文原稿とは別紙とする。
3．用語は日，仏，英3カ国語の何れかとする。ただし，表および図説明の用語は仏文または英文に限る。原著論文（前項）には約200語の英文または仏文の要旨を，別紙として必ず添える。なお，欧文論文には，上記要旨の外に，約500字の和文要旨をも添える。ただし，日本語圏外からの投稿の和文要旨については編集委員会の責任とする。
4．投稿原稿の体裁形式は最近号掲載記事のそれに従う。著者名は略記しない。記号略号の表記は委員会の基準に従う。引用文献の提示形式は，雑誌論文，単行本分載論文（単行本の一部引用を含む），単行本などの別による基準に従う。
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9．原稿の送り先は下記の通り。

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