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Spatial distributions and mixing energies of tidal currents over the eastern Bering Sea shelf

Tomonori AZUMAYA* and Yutaka ISODA*

Abstract: The spatial semidiurnal and diurnal tides and their tidal currents over the eastern Bering Sea shelf were investigated by use of a two-dimensional barotropic model on f -plane. There is a different tidal response between the two main bays along the Alaska coast. The semidiurnal tidal current predominates in Bristol Bay, while the diurnal tidal current predominates in Norton Sound. The results of our model attribute this difference to that between the forcing periods of the respective co-oscillating tides. Furthermore, the model results suggest that the larger amplitudes of diurnal tidal current along the slope relative to those of the shelf area are caused by the topographic Rossby wave manner with energy trapping on the shelf slope. To spatially investigate the effect of the tidal energy on the mixing of water column, the potential energy anomaly was calculated using hydrographic data taken between 1963 and 1992. The tidal front forms along the coast of Alaska, where the potential energy anomaly is relatively small, and its location well corresponds to the spatial contour-lines of the critical parameter of $\log(H/U^3) = 2.5 \sim 3.0$ for the tidal mixing energy. It is inferred that the vertical mixing energy of tidal currents plays an important role in the formation of this coastal front there. However, the spatial configuration of the potential energy anomaly cannot be explained by the $\log(H/U^3)$ in the north of St. Lawrence Island, where the Anadyr Current flows across the shelf.

1. Introduction

The eastern Bering Sea shelf extends about 1,000 km from Unimak Pass in the southeast to Cape Navarin in the northwest. It is bounded by lands on three sides: the Alaskan Peninsula in the southeast, the Alaskan mainland in the northeast, and Siberia in the northwest (Fig. 1). With its surface area of $1.2 \times 10^6 \text{ km}^2$, it is one of the widest ocean shelves known, and also boasts one of the world's most productive ocean ecosystems.

Current-meter records over the eastern Bering Sea shelf have shown that 60–95% of the variance in the current's horizontal kinetic energy was the result of tidal components (SCHUMACHER and KINDER, 1983). The mean vector speeds of the shelf's current ($< 2 \text{ cm} \cdot \text{s}^{-1}$) were one order of magnitude lower than the speeds of the tidal current ($20 \text{ cm} \cdot \text{s}^{-1}$). Hence, the shelf has become notorious for strong tidal

currents.

Tidal waves enter the Bering Sea as free waves from the North Pacific Ocean, mainly through the central and western passages of the Aleutian–Komandorski Islands. The Arctic Ocean is a secondary source of tides which propagate southward into the north Bering Sea. PEARSON *et al.* (1991) used long-term direct current measurements to determine that the predominant semidiurnal tides, such as the M_2 and N_2 constituents, are seen throughout most of the shelf, while diurnal tides, such as the K_1 and O_1 constituents, predominate in the Norton Sound. Diurnal tides also predominate over the shelfbreak at the northeastern Bering Sea shelf (MOFJELD, 1986). Recently, SCHUMACHER and REED (1992) showed that the amplitudes of the K_1 tidal current ($19.8 \text{ cm} \cdot \text{s}^{-1}$) are larger than that of the M_2 tidal current ($6.9 \text{ cm} \cdot \text{s}^{-1}$) based on direct current measurements on the shelf slope.

A numerical model by SÜNDERMAN (1977) predicted the distribution of the M_2 constituent

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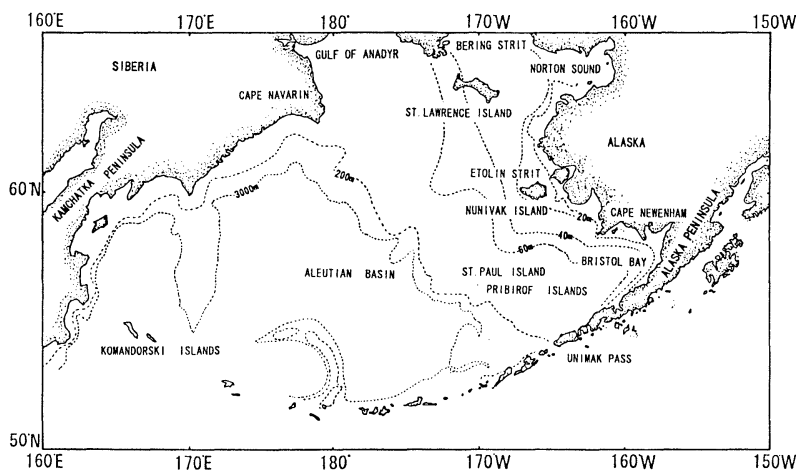


Fig. 1. Bottom topography of the Bering Sea.

in the Bering Sea, as well as the M_2 tidal current ellipses and tidal dissipation. The model resulted in a good quantitative agreement for the M_2 constituent. The three-dimensional model by LIU and LEENDERTSE (1982, 1986) also predicted the M_2 and K_1 constituents in the Bering and the Chuckchi Sea, though it did not predict either the diurnal tidal current of the whole shelf to add to the shelf slope or the spatial distributions of tidal mixing energy.

SCHUMACHER and KINDER (1979) investigated the structure of the tidal front along the coast of Alaska and its frontogenesis. This tidal front, the boundary between the mixed water of the coastal shallow region and the stratified water of the middle region, is about 20 km wide along the 50 m depth contour. Another tidal front, discovered in the vicinity of the British Isles, has been discussed by SIMPSON (1971, 1978), SIMPSON and HUNTER (1974), PINGREE *et al.* (1974), FEARNHEAD (1975) and JAMES (1977). These authors proposed that the tidal front might have been generated by an energy balance between tidally generated mixing and buoyancy input. SIMPSON and HUNTER (1974) suggested that the location of frontogenesis depends on a critical parameter $\log(H/U^3)$ for the mixing energy (H is the water depth in m and U the amplitude of tidal current in $m \cdot s^{-1}$). However, numerous aspects of the tidal current, including its spatial distributions and the relationship between the parameter $\log(H/U^3)$ and potential energy anomaly, have yet to be

determined for most of the eastern Bering Sea shelf.

Accordingly, the purpose of the present study is to describe, using a numerical model, the characteristics of the distribution of the tide and tidal currents over the Bering Sea shelf and to examine how the distributions of $\log(H/U^3)$ correspond to the distributions of the potential energy anomaly over the shelf.

2. Mean field of temperature, salinity and density

Hydrographic data for the eastern Bering Sea shelf were obtained by T.S. Oshoromaru (Faculty of Fisheries, Hokkaido Univ., 1964-1993). The data were collected using Nansen bottles until 1983, and by CTD since 1984. Figure 2 shows the number of hydrographic stations of inside $1^\circ \times 1^\circ$ quadrangles for 1963-1992 to describe the spatial mean distributions of temperature and salinity.

Figures 3(a), (b) and (c) show the averaged vertical section of temperature, salinity and density from 180° meridian to $159^\circ W$ at along $59^\circ N$ over the eastern Bering Sea shelf based on long-term successive observations over the summers of 1963-1992 (see Fig. 2 for its location). Thermocline lies at the depth of 20 m-30 m on the shelf edge. Cold water of less than $2^\circ C$ occupies the region from the shelfbreak to the middle shelf during the spring and summer (OHTANI, 1973; COACHMAN and CHARNELL, 1979). In the coastal shallow region of Alaska,

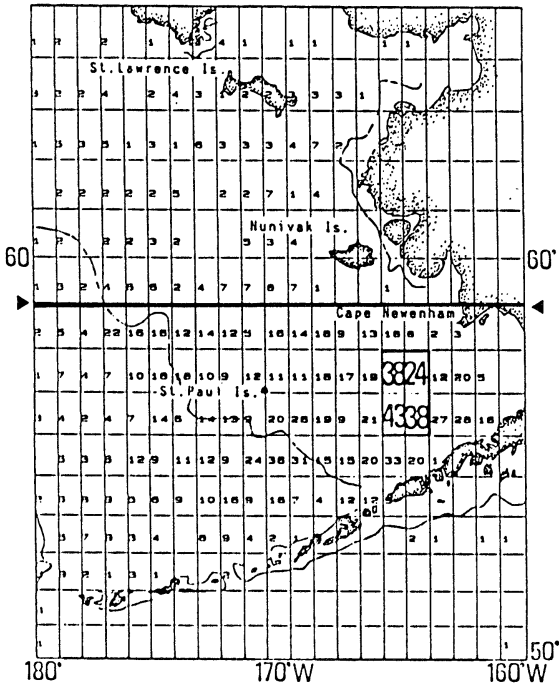


Fig. 2. Number of hydrocast and CTD in each quadrangle.

where the surface water temperature rises to 8°C, the water column is well-mixed and the water temperature near the bottom higher than 6°C. The water near the coast of Alaska has a salinity of less than 31 PSU and is fresher than offshore waters. The density structure almost depends on the salinity over the shelf region. Between the middle shelf and coastal region, there is a narrow transition separating the two-layered middle shelf region from the well-mixed coastal region. Therefore, the tidal front is a common feature in long term aver-

aged vertical sections of water temperature, salinity and density.

3. Numerical simulations of tide

3.1 Model description

To obtain the spatial distributions of tides and tidal currents, we use the vertically integrated equation of motion and continuity in a Cartesian coordinate system :

$$\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} + f \mathbf{k} \times \mathbf{u} = -g \nabla \zeta - \frac{\gamma_b^2 |\mathbf{u}| \mathbf{u}}{H + \zeta} + A_h \nabla^2 \mathbf{u} \quad (1)$$

$$\frac{\partial \zeta}{\partial t} + \nabla \cdot \{(H + \zeta) \mathbf{u}\} = 0 \quad (2)$$

where \mathbf{u} is the depth-averaged velocity, t the time, ∇ the horizontal differential operator, \mathbf{k} the vertical unit vector, g ($=980 \text{ cm} \cdot \text{s}^{-2}$) the gravitational acceleration, ζ the sea surface elevation above the mean sea surface, γ_b^2 ($=0.0026$) the bottom frictional coefficient, A_h ($=10^7 \text{ cm}^2 \cdot \text{s}^{-1}$) the coefficient of horizontal eddy viscosity, H the water depth and the f the Coriolis parameter at 60° N ($f=1.25 \times 10^{-4} \text{ s}^{-1}$). Here, the validity of the f model for a simulation in this region may be checked by estimating planetary-beta $\beta_p=1 \times 10^{-13} \text{ cm}^{-1} \cdot \text{s}^{-1}$ (the meridional gradient of f) and topographic-beta $\beta_t=5 \times 10^{-12} \text{ cm}^{-1} \cdot \text{s}^{-1}$ ($=\frac{f}{H} \cdot \frac{dH}{dx}$). Thus,

the topographic β_t is dominant by at least one order, and β_p may be ignored relative to β_t .

This model sea is covered by a quadratical grid of 50 km \times 50 km. As shown in Fig. 4, the model incorporates the actual bathymetry of the eastern Bering Sea region, taking its bathymetric data from a chart published by

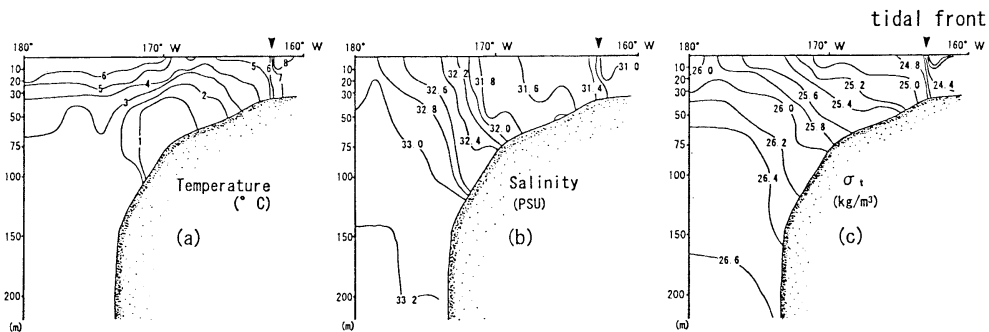


Fig. 3. Mean vertical distributions of temperature (a), salinity (b) and density (c) at latitude of 59° N (line in Fig. 2).

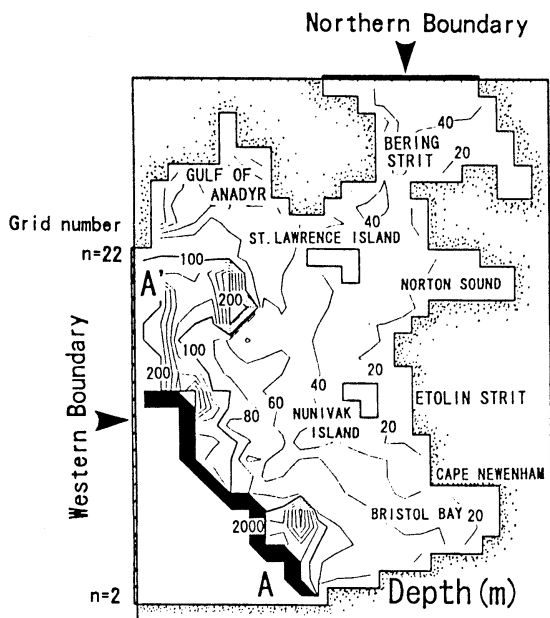


Fig. 4. Bottom topography of the eastern Bering Sea shelf (contours are in m). The model basin with a depth of more than 2000 m is assumed to be 2000 m constant.

the Japan Maritime Safety Agency. This results in two distinct domains : a deep basin and relatively shallow shelf.

The M_2 and K_1 constituents are dominant over the eastern Bering Sea shelf. These two tidal constituents are the only ones included in the computations, both because their amplitudes are larger than those of N_2 and O_1 , respectively, and because their cotidal and corange charts are very similar to those for N_2 and O_1 tides (PEARSON *et al.*, 1981). Here, the M_2 and K_1 constituents are generally representative of the semidiurnal and diurnal tides. The observed tidal amplitude and phase lag (Fig. 4) are given along two open boundaries to the west of the eastern Bering Sea shelf and the Bering Strait as located using cotidal charts by SÜNDERMAN (1977) and PEARSON *et al.* (1981). Table 1 shows the harmonic constants in two open boundaries. The tidal elevations across the two open boundaries are specified as cosines :

$$\zeta = A \cdot \cos(\omega t - G) \quad (3)$$

where A is the amplitudes, G the Greenwich phase lags, and ω the angular frequency. The

Table 1 Harmonic constants in boundaries.

	M_2		K_1	
	a (cm)	G	a (cm)	G
West boundary	20	$70-0.8n$	30	330
North boundary	7	231	20	310

a : amplitude (cm) G : phase (degree)
n : grid number

harmonic constants of the tidal currents are determined by harmonic analyses of the current records of SÜNDERMAN (1977), PEARSON *et al.* (1981), MOFJELD (1986), and SCHUMACHER and REED (1992). Equations (1) and (2) were approximated by the finite-differences and solved by the primitive method. The tidal model ran for a simulation time of 10 days until the solution showed no significant changes from cycle to cycle. The sea surface elevation and velocity were sampled every hour. These data were then used to perform the harmonic analysis to determine the tidal constants and current ellipse parameters.

3.2 Model results

Semidiurnal and diurnal tides

Spatial distributions of observed cotide and corange lines for the M_2 constituent are shown in Fig. 5(a). The three amphidromic points of the M_2 tide located near Cape Newenham, in Norton Sound, and southeast of St. Lawrence Island. The amplitudes of M_2 tide varied from 40 cm off the mouth of Bristol Bay to 120 cm along the coast of the Alaskan mainland. On the other hand, in Norton Sound the amplitudes were less than 10 cm, smaller than those in Bristol Bay. Figure 5(b) shows the spatial distributions of the calculated cotide and corange lines for the M_2 constituent. The calculated amphidromic points locate at the same positions as the observed ones. In addition to these three points, the model predicts the existence of an amphidromic point off the Gulf of Anadyr and one in the Bering Strait. The calculated amplitude in Bristol Bay is 120 cm, larger than that in Norton Sound. The calculated phase lines in the Etolin Strait change abruptly

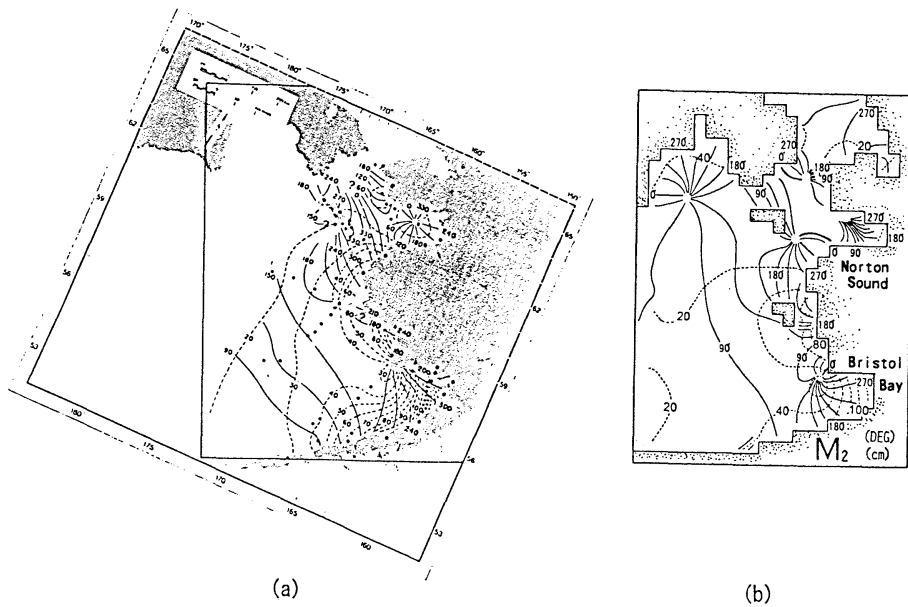


Fig. 5. (a) Observed cotidal map for M_2 tide (PEARSON *et al.*, 1981). (b) Model-predicted cotidal map for the M_2 tide. Solid lines are cotide lines referenced to Greenwich in degrees. Broken lines are corange lines in cm.

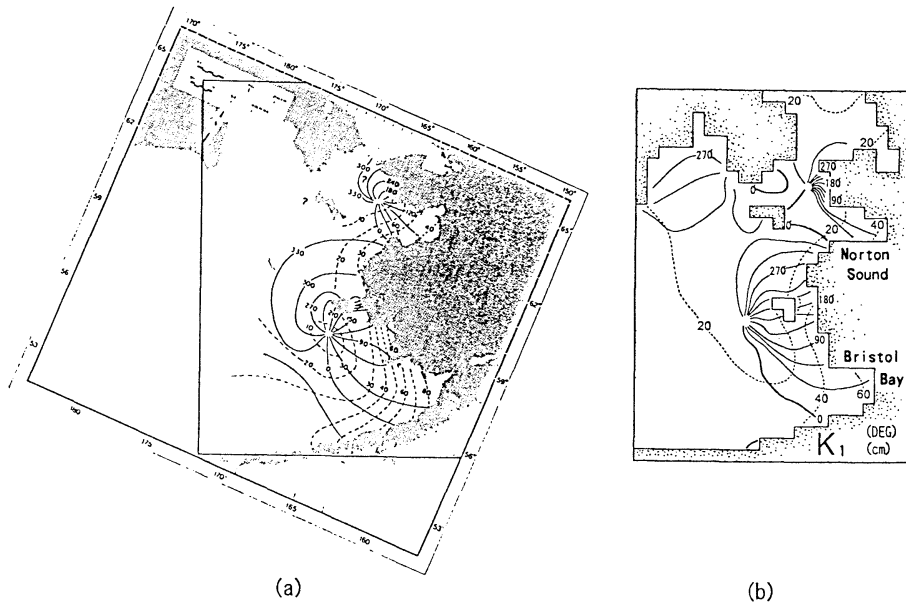


Fig. 6. (a) Same as Fig. 5(a) but for K_1 . (b) Same as Fig. 5(b) but for K_1 .

between the north and south ends.

Spatial distributions of the observed cotide and corange lines for the K_1 constituent are shown in Fig. 6(a). One of the two amphidromic points of the K_1 tide located west

of Norton Sound, and other point in the area between Nunivak Island and the Pribilof Islands. The maximum amplitude of the K_1 tide in Bristol Bay was about 60 cm, and in Norton Sound was about 40 cm. Figure 6(b) shows the

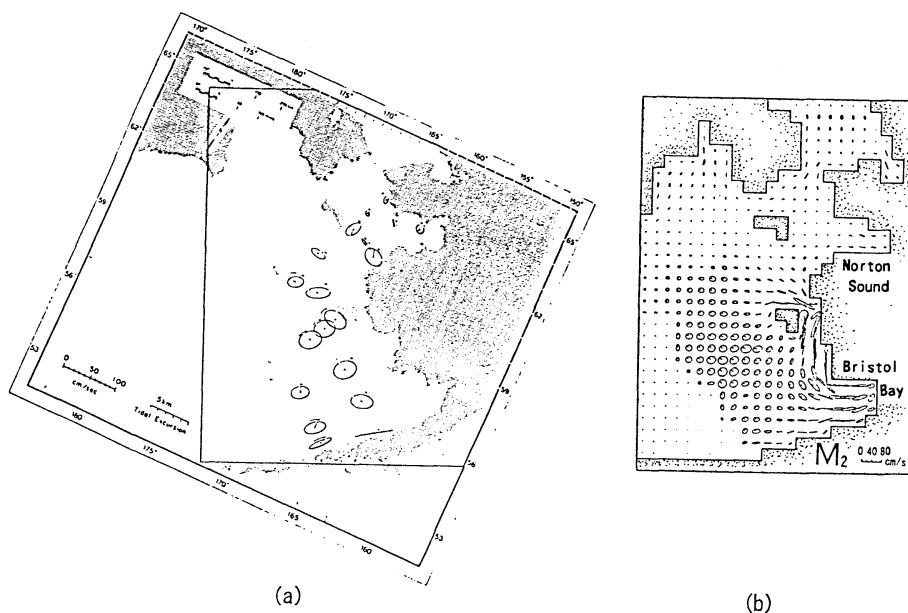


Fig. 7. (a) Observed tidal current ellipses for M_2 (PEARSON *et al.*, 1981). (b) Model-predicted tidal current ellipses for M_2 .

spatial distributions of the calculated cotide and corange lines for the K_1 tide. The amphidromic points locate at the same area in the observed cotide lines. The phase and amplitude distributions of the calculated diurnal tide are highly similar to the observed ones.

Semidiurnal and diurnal tidal currents

Figure 7(a) shows the spatial distributions of observed tidal current ellipses for the M_2 constituent. The observed M_2 tidal current ellipses over the shelf were almost circular, and exhibited a clockwise rotation. However, there were two exceptions, one near the Alaskan Peninsula, where the ellipses had a nearly rectilinear motion, and the other in Bristol Bay, where the rotation was anticlockwise. Figure 7(b) shows the distributions of calculated tidal current ellipses for the M_2 constituent. They are almost identical to those of the observed ones. The rotation of the observed tidal current ellipses is well reproduced by the numerical model. At the mouth of Bristol Bay, the major axes of these predicted ellipses have a maximum speed of $30\sim 40\text{ cm}\cdot\text{s}^{-1}$, while in Norton Sound the maximum speed of tidal current is less than $20\text{ cm}\cdot\text{s}^{-1}$. The model predicts tidal-

current amplitudes of more than $40\text{ cm}\cdot\text{s}^{-1}$ in the Etolin Strait, where the predicted amplitudes is largest in the whole region.

Figure 8(a) shows the observed tidal current ellipses for the K_1 constituent. They rotate nearly clockwise and are elongated to form a straight line, unlike the nearly circular tidal ellipses of M_2 . The observed amplitudes of K_1 over the shelf are $10\sim 15\text{ cm}\cdot\text{s}^{-1}$ and almost smaller than the tidal ellipses of M_2 with the exception of those in Norton Sound. The amplitudes of the K_1 tidal current in Bristol Bay are as large as those over the shelf. On the other hand, the amplitudes of the tidal current in Norton Sound are larger than $30\text{ cm}\cdot\text{s}^{-1}$. The calculated K_1 tidal-current ellipses distribute like the observed ones, as shown in Fig. 8(b). Our model also reproduces these differences of predominant tidal current in each bay. The ellipses along the shelf slope become circular and their maximum amplitudes are over $40\text{ cm}\cdot\text{s}^{-1}$, although the calculated phase and amplitudes of K_1 tidal currents vary widely.

4. Discussions

4.1 Tidal currents in Bristol Bay and Norton Sound

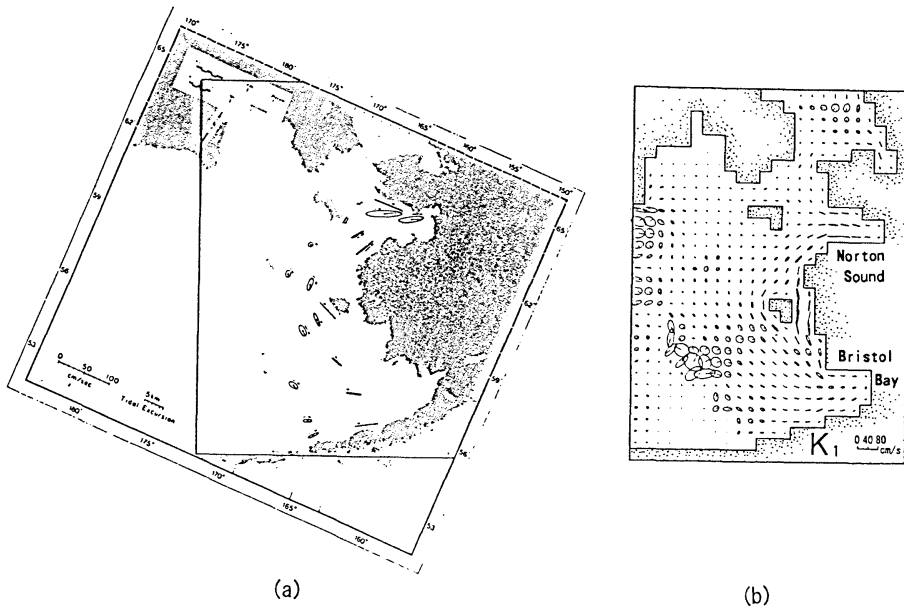


Fig. 8. (a) Same as Fig. 7(a) but for K_1 . (b) Same as Fig. 7(b) but for K_1 .

PEARSON *et al.* (1981) proposed that the small semidiurnal tidal current in Norton Sound might have been the result of bottom friction across the broad Bering Sea shelf, and that the diurnal tidal current in Norton Sound was larger than that in Bristol Bay because of the shallower depth. However, if bottom friction dissipated tidal current, then the amplitude of not only the semidiurnal tidal current but also the diurnal tidal current must be small in Norton Sound than in Bristol Bay. Since PEARSON *et al.* (1981) also reported that the diurnal tide /tidal current phase relationship indicated predominantly standing wave characteristics in Norton Sound, we suspected that the co-oscillating tide was associated with the position of amphidromic points in both Bristol Bay and Norton Sound. To examine the cause of the different behaviors of tidal current in both locations, we used the simple one-dimensional co-oscillating tidal models shown in Figs. 9(a) and (b). The length l of both Bristol Bay and Norton Sound is 250 km (the mouth of the bay is $x=0$), where x is the coordinate defined along the longitudinal axis of the bay. The depth h of Norton Sound is 20 m. On the other hand, in the case of Bristol Bay, with its constant bottom slope and a water depth determined as

$h=2h_m(1-x/l)$, the mean water depth is $h_m=40$ m. The tide is assumed to oscillate by the elevation a_m at the mouth of the bay for each forcing period. Here, a_m is the observed amplitude of the tide, and the given a_m at the mouth of Bristol Bay and Norton Sound are 40 cm and 10 cm, respectively. These a_m are constant for each forcing period. The case for Norton Sound is given by Eqs. (4) and (5), below.

$$\eta(x) = a_m \cdot \frac{\cos(k(l-x))}{\cos(kl)} \quad (4)$$

$$u(x) = a_m \cdot \frac{C}{h} \cdot \frac{\sin(k(l-x))}{\cos(kl)} \quad (5)$$

The standing oscillation in the linear case for Bristol Bay is given by Eqs. (6) and (7) (UNOKI and ISOZAKI, 1965) :

$$\eta(x) = a_m \cdot \frac{J_0(\sqrt{2}kl\sqrt{1-x/l})}{J_0(\sqrt{2}kl)} \quad (6)$$

$$u(x) = \frac{a_m \cdot C}{\sqrt{2}h_m\sqrt{1-x/l}} \cdot \frac{J_1(\sqrt{2}kl\sqrt{1-x/l})}{J_0(\sqrt{2}kl)} \quad (7)$$

where J_0 and J_1 the zero- and the first-order Bessel functions, $\eta(x)$ the elevation, $u(x)$ the velocity, g the gravitational acceleration, C the propagation speed of phase for gravity wave (\sqrt{gh}), k the wave number ($2\pi/C \times T$), and T the forcing period.

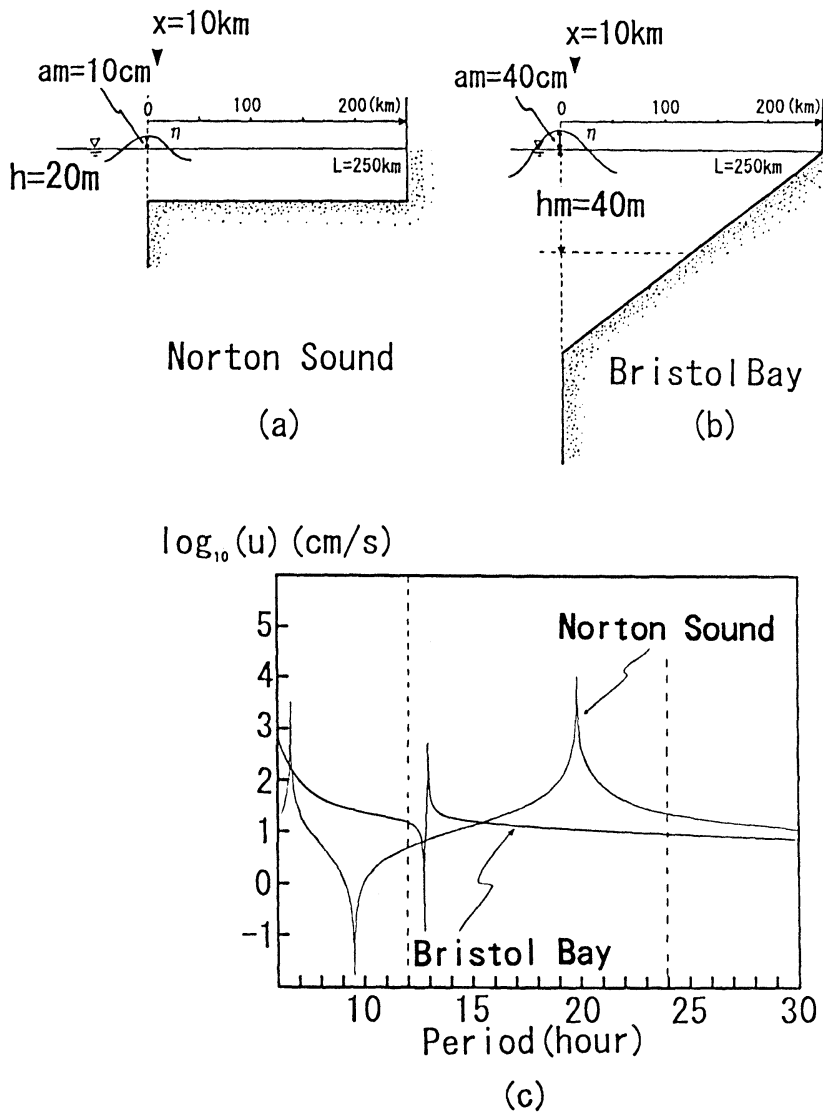


Fig. 9. (a) Depth profile for Norton Sound. (b) Depth profile for Bristol Bay. (c) Theoretical amplitudes of $u(x=10\text{ km})$ for each forcing period of Norton Sound and Bristol Bay.

Figure 9 (c) shows the distributions of u ($x=10\text{ km}$) for the the forcing period in the simple model of each bay. The peak of the theoretical amplitudes of $u(x=10\text{ km})$ is seen at about hour 13 of the forcing period in Bristol Bay. This result indicates that the semidiurnal tidal period is equal to that of the fundamental oscillation in Bristol Bay. Thus, the standing oscillation is generated due to the resonance, and consequently, gives rise to the large amplitudes of u ($x=10\text{ km}$). On the other hand, in

Norton Sound the peaks of the theoretical amplitudes of u ($x=10\text{ km}$) are found at hours 7 and 20 of the forcing period. Since the period of fundamental oscillation is near the diurnal tidal period, the resonance also occurs in the bay over the diurnal forcing period. The resulting theoretical amplitudes are thus larger than those in Bristol Bay, as shown in Fig. 9(c). These calculated amplitudes of tidal current can be brought into close agreement with those of our realistic model quantitatively.

Collectively, these results from the simple one-dimensional model suggest that the difference between the predominant tidal currents for each forcing period in Bristol Bay and the comparable currents in Norton Sound may be attribute not to bottom friction but to the co-oscillations of the tides in each bay.

4.2 The predominant diurnal tidal currents along the shelf slope area

The calculated amplitudes, as shown in Fig. 8(b), of the diurnal tidal current along the shelf slope are substantially larger than those on the shelf, even though there is only a small change in sea level. In addition, since the inertial period of 13.9 hours at the latitude of this study area is shorter than a diurnal period, no inertial-gravity waves can be considered to propagate along the shelf slope. We believe that this fluctuation in tidal current is driven by a topographic Rossby wave. Thus, it is would also seen that the energy of the tidal current is trapped in the area of the steep shelf slope. Using a theoretical model by BUCHWALD and ADAMS (1968), we next examine the dispersion relation of the topographic Rossby wave trapped on the shelf edge. The topography consists of an exponential shelf slope connecting to the shelf and open ocean of constant depth of 2000 m (Fig. 10(a)). We assume an infinite, straight shelf edge and a depth dependent on offshore distance only. Figure 10(b) shows the theoretical dispersion curves for the 1st mode, and Fig. 10(c) shows this model's phase speed and group velocity. Since the group velocity is much lower than the phase speed at period = 24 hours ($\omega/f = 0.6$), it follows that the energy of the diurnal tidal current is trapped along the shelf slope. The theoretical wavelength of the diurnal tide has a value of about 400 km as determined from the dispersion curve (Fig. 10(b)), and the phase speed for the period of 24 hours is about $4 \text{ m} \cdot \text{s}^{-1}$ (Fig. 10(c)). We estimate the relative vorticity ($V_x - U_y$) for the transect A-A' (Fig. 4) along the shelfbreak in order to investigate the temporal and spatial variabilities. The space-time diagram of the relative vorticity is illustrated in Fig. 11. The contour lines for the relative vorticity suggest a northwestward propagation along the shelf

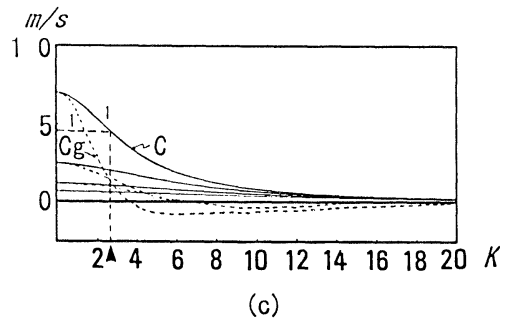
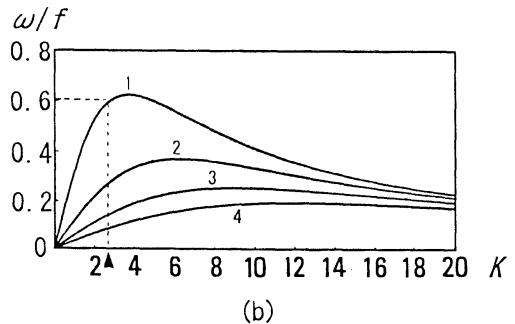
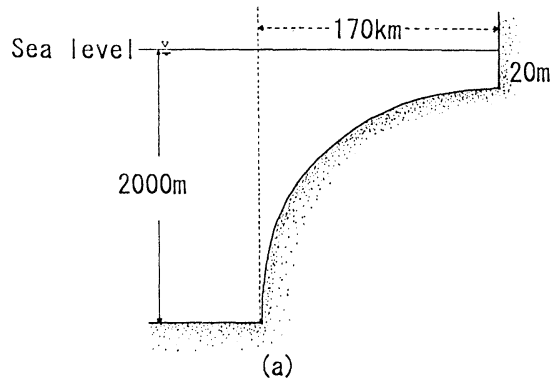


Fig. 10. The x-axis is taken along the bay.

(a) The form of the depth profile. (b) Dispersion curves. K is a nondimensional wave number based on width of shelf ($L=170$ km). The y-axis is a nondimensional frequency based on the Coriolis parameter (f), (c) Phase velocity (C) and group velocity (C_g)

break at a speed of about $4 \text{ m} \cdot \text{s}^{-1}$ and a wavelength of about 350 km. This theoretical phase speed of the 1st mode topographic Rossby wave model is consistent with that of the diurnal tidal current fluctuations at the shelf slope.

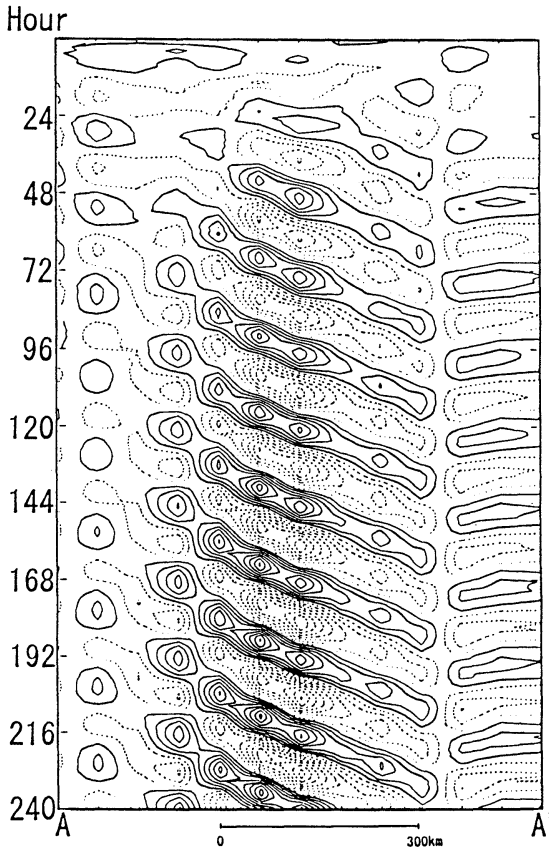


Fig. 11. Space-time diagram along the shelf slope (line A-A' in Fig. 4) for the vorticity of the period of 24 hour. Positive (negative) vorticities are shown by solid (broken) lines.

These calculated characteristics of the diurnal tidal current on the shelf slope well reproduce those actual characteristics observed by SCHUMACHER and REED (1992). Therefore, this feature suggests one evidence that the predominant diurnal tidal current fluctuations may cause the topographic Rossby wave.

4.3 Spatial distributions of potential energy anomaly and parameter $\log(H/U^3)$

The tidal front along the coast of Alaska separates a well-mixed coastal region from a stratified middle region. MUENCH (1976) first suggested that the tidal front exists only near Bristol Bay over the shelf. SCHUMACHER and KINDER (1979) confirmed the existence of such

a front along the coast of Alaska, and calculated the parameter $\log(H/U^3)=3.5$ at the front near Nunivak Island. As shown in Figs. 3 (a), (b) and (c), the tidal front is also seen in the averaged vertical sections of temperature, salinity, and density.

Here, we calculate the parameter $\log(H/U^3)$ using our model results over the whole shelf for purpose of comparison with the spatial distributions of the potential energy anomaly. This potential energy anomaly for a density stratification relative to its well-mixed state is defined by the following equations :

$$\bar{\rho} = \frac{g}{H} \int_{-H}^0 \rho(z) dz \quad (8)$$

$$V = \frac{g}{H} \int_{-H}^0 (\rho(z) - \bar{\rho}) z dz \quad (9)$$

where V is the potential energy anomaly, $\rho(z)$ the density in each layer, $\bar{\rho}$ the averaged density for the water column, g the acceleration of gravity, and H the water depth.

Figure 12 shows the spatial distribution of potential energy anomaly over the eastern Bering Sea shelf based on hydrographic data gathered over a period of 30 years (1963-1992). The potential energy anomaly is less than 1.0 near the coast of Alaska and around the Nunivak Islands. These regions are well-mixed states, as shown in the vertical sections of Fig. 3. The value of the potential energy anomaly gradually increases from the coast of Alaska toward the shelf break. The potential energy anomaly corresponding to the tidal front has a value of 1.0~1.5, which is distributed parallel to about 60 m isobath over the shelf (cf. Fig. 4).

We used the calculated current amplitudes (U) of the semidiurnal and diurnal tides and the depth (H) to estimate the spatial distributions of $\log(H/U^3)$. Since the amplitudes of the M_2 and O_1 tidal currents are, respectively, 31% of the M_2 tidal current and 61% of the K_1 tidal current (see PEARSON *et al.*, 1981, table 8-1), the sum of the tidal current amplitudes (U) at each grid can be estimated as

$$U = 1.31 \cdot U_{M_2} + 1.61 \cdot U_{K_1} \quad (10)$$

where U_{M_2} and U_{K_1} are the principal tidal current amplitudes of the M_2 and K_1 tides.

Figure 13 shows the spatial distribution of

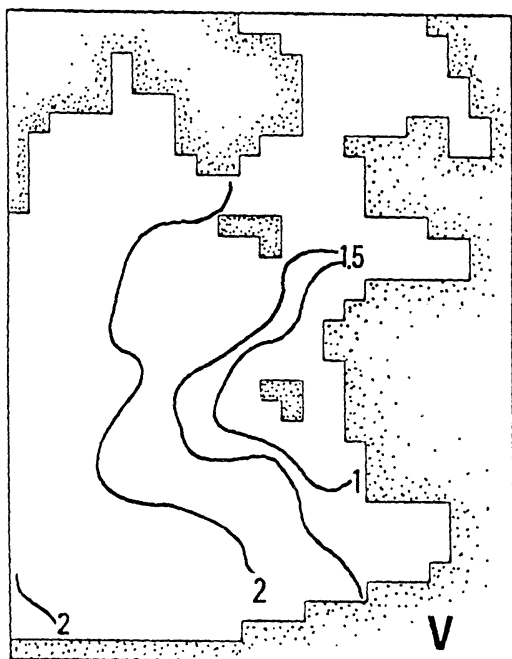


Fig. 12. Spatial distribution of the potential energy anomaly.

$\log(H/U^3)$ over the eastern Bering Sea shelf as derived from the model. A value smaller than $\log(H/U^3)=3.0$ spreads from the south-west area of Nunivak Island to the shelfbreak, and is also found in Bristol Bay and Norton Sound. The value for the Etolin Strait is smaller still, less than $\log(H/U^3)=1.0$, while that around St. Lawrence Island is greater than $\log(H/U^3)=4.0$.

SCHUMACHER and KINDER (1979) showed that a front having the value of $\log(H/U^3)=3.5$ was restricted along the 50 m isobath. However, these authors used the observed value of $25 \text{ cm} \cdot \text{s}^{-1}$ around the front in their calculation, for our estimation of $\log(H/U^3)$ we used the calculated amplitudes of the semidiurnal and diurnal tidal currents, values which were greater than $35 \text{ cm} \cdot \text{s}^{-1}$. Consequently, the relatively small value of $\log(H/U^3)=2.5\sim 3.0$ appears from the coast of Alaska to the shelf slope. Because the parameter $\log(H/U^3)$ is highly sensitive to the choice of tidal current amplitudes, the difference in amplitude may have caused that between the SCHUMACHER and KINDER's observed and our estimated distribution of

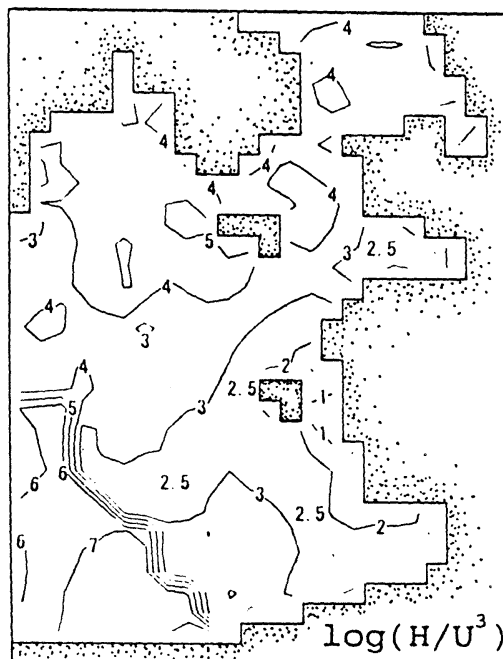


Fig. 13. Spatial distribution of $\log(H/U^3)$ calculated from the model ocean.

$\log(H/U^3)$.

A comparison between the spatial distributions of $\log(H/U^3)$ (Fig. 13) and those of the potential energy anomaly (Fig. 12) reveals the following. The contour lines of $\log(H/U^3)=2.5\sim 3.0$ along the coast of Alaska and Bristol Bay, where the tidal front is seen, run parallel to those of the potential energy anomaly. These distributions suggest that the tidal current may control the mixing process in these regions. Although the small potential energy anomaly 1.6 north of St. Lawrence indicates very weak stratification, the tidal mixing energy is relatively small here. This result would suggest that the density structure north of St. Lawrence Island cannot be explained by tidal mixing. As COACHMAN and SHIGAEV (1988) noted, the Bering Slope Current comes into this region, and the Anadyr Current flows through the Bering Strait (KINDER *et al.*, 1986) and generates the turbulent energy north of St. Lawrence Island. Thus, the stratification downstream from the Anadyr Strait may be weak.

2.5 Conclusions

The calculated cotide, corange distributions, and tidal current ellipses for the semidiurnal and diurnal constituents agreed well with the observed ones. The finding obtained in the present study can be summarized as follows :

(1) The semidiurnal tidal current dominates in Bristol Bay, while the diurnal tidal current is predominant in Norton Sound. In both cases, the co-oscillating tide varies according to tidal period. The difference in predominant tidal current between Norton Sound and Bristol Bay can be attributed to the different forcing periods of the respective co-oscillating tides.

(2) Our model shows a relatively large diurnal tidal current rather than a semidiurnal tidal current along the shelf slope, and predicts large tidal current fluctuations propagating northwestward. These results are similar to the observed features for this area. Because the inertial period in this area is shorter than a diurnal-period, the energy of the diurnal tidal current is trapped at the shelf slope. We suggest that these large fluctuations of the diurnal tidal current behave like a 1st mode topographic Rossby wave.

(3) The parameter $\log(H/U^3)$ along the coast of Alaska and Bristol Bay gradually increases with offshore, as does the potential energy anomaly. This indicates that stratification near the coast of the Alaskan mainland is dependent on tidal current mixing. On the other hand, the strength of the stratification cannot be explained by the dissipation of tidal energy at the north Bering Sea shelf. Although the parameter $\log(H/U^3)$ is relatively large north of St. Lawrence Island, the water column seems to have weak stratification. In this area, the Anadyr current may break down the density stratification.

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Nutrients limiting the Algal Growth Potential (AGP) in the Gulf of Riga, eastern Baltic Sea, in spring and early summer 1996

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Abstract: In May, June and July 1996, samples were collected along one transect greatly influenced by river discharge (eastern side of the gulf), along one transect slightly influence by river discharge (western side), at one station located in the mouth of the main river (River Daugava), at one station located in the center of the Gulf and at several nearshore locations of the western side. Ratios of molecular concentrations of *in situ* dissolved inorganic nitrogen, phosphorus and silicon, as well as enrichment bioassays were used to determine which nutrient (s) limited the potential biomass of phytoplankton. Both comparison of $(\text{NO}_3 + \text{NO}_2 + \text{NH}_4) : \text{PO}_4$ (DIN : DIP) values with Redfield's ratio and bioassay inspection led to the same conclusions. Phosphorus was clearly the nutrient most limiting for the potential biomass of test species in nitrogen-rich waters, which occurred in mid spring, in the upper layer of the southern-eastern part of the Gulf which is greatly influenced by river discharge. In late spring, with the decrease of the total DIN reserve, nitrogen and phosphorus showed an equal limiting role. In deeper layers of this area and out of the river plume (western side and central part of the gulf), nitrogen was the limiting nutrient. In summer, when river discharge was the lowest, all DIN concentrations but one ranged between 1.6 and 2.6 μM , and the whole area was nitrogen-limited for both the cyanobacterial and the algal test strains. In 74% of the samples for which nitrogen was the limiting nutrient, phosphorus was recorded to be the second potentially limiting nutrient. In contrast, silicon never appeared as limiting the growth potential of either *Microcystis aeruginosa* or *Phaeodactylum tricorutum*; phosphorus was the limiting nutrient when DIN : SiO₃ values were >1 (in May), but DIN : SiO₃ was <1 when nitrogen was limiting (June and July). The authors conclude that the recently reported decrease of silicon loading in coastal waters and its subsequent enhanced importance in pushing the outcome of species competition towards harmful species may not yet be the most important factor for the Gulf of Riga. Iron appeared for 12% of the tests in the list of nutrients limiting the potential biomass. Tentative results also indicated that a significant fraction of the nitrogen ($\sim 4 \mu\text{g-atom N l}^{-1}$) taken up by *Microcystis aeruginosa* may have been in the form of dissolved organic nitrogen (DON). It is thus also suggested tentatively that more attention be paid to these nutrients during further research in the Gulf of Riga.

1. Introduction

In recent decades, noxious algal events have emerged as a major environmental problem in the Baltic Sea (HORSTMANN, 1975; NIEMI, 1979; NEHRING, 1992), as well as in many other coastal waters (NIXON, 1990; DEDEREN, 1992; HALLEGRAEFF, 1995). Increase in nutrient con-

centration resulting from river discharges and varied loadings has been suggested as responsible for both macroalgal and phytoplankton biomass increases (BOIKOVA, 1986; ROSENBERG *et al.*, 1990; ANDRUCHAITIS *et al.*, 1993, 1995; PITKÄNEN *et al.*, 1993; YURKOVSKIS *et al.*, 1993). Bottom-water oxygen deficiencies and subsequent faunal mortality have been the most commonly observable consequences of excess in algal biomass in summer (BADEN *et al.*, 1990; RICHARDSON, 1990). Changes in phytoplankton population structure have been also marked (SCHULZ and KAISER 1986, WULFF *et al.*, 1986;

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CEDERWALL and ELMGREN, 1990; BALODE, 1996).

Nitrogen has been invoked most as the principal nutrient limiting algal growth potential in seawater when light and temperature are adequate and losses do not prevail (RYTHER and DUNSTAN, 1971; HCKY and KILHAM, 1988; HOWARTH, 1988; GRANÉLI *et al.*, 1990). Accordingly, one might expect that the more nitrogen were present, the more algal biomass would develop (RUDEK *et al.*, 1991). Several authors, however, have reported either co-occurring or successive limiting nutrients (SMAYDA, 1974; BERLAND *et al.*, 1978; LEVASSEUR *et al.*, 1990; FISHER *et al.*, 1992). In addition, the growth potentials of different species in the same assemblage may be limited by different nutrients (MAESTRINI and BONIN, 1981).

Human activities have significantly increased the input of algal nitrogenous and phosphorus nutrients to estuarine and coastal waters. In contrast, the silicon concentration has remained constant or has even decreased in river loadings, as a result of its absence in human wastewater and the secondary effect of eutrophication in freshwater, which leads to larger blooms of diatoms and subsequent exhaustion of the silicate content before discharge into the sea (SCHELSCKE and STOERMER, 1972; EGGE and AKNES, 1992). Hence, altogether, along with increased eutrophication in coastal water, N:Si and P:Si nutrient ratios have increased (RAHM *et al.*, 1996), and silicon limitation has become potentially more likely (OFFICER and RYTHER, 1980; Conley *et al.*, 1993; RAGUENEAU *et al.*, 1994).

Cyanobacteria have been the taxon most frequently cited as giving harmful blooms in the Baltic Sea in summer (EDLER *et al.*, 1985; KONONEN, 1992; BALODE, 1993; HEISKANEN and KONONEN, 1994; LEPPÄNEN *et al.*, 1995; TENSON, 1995). Moreover, their presence seems to have increased in the past decades both in space and time (KAHRU *et al.*, 1994). Toxin-producing dinoflagellates, which develop in waters of low nutrient concentrations, and which can be harmful at low biomass levels, have also been recently reported in the same area (WILLÉN *et al.*, 1990; CARPENTER *et al.*, 1995; BALODE and PURINA, 1996). Thus, the present situation might concur with the above-mentioned

assumption that the continuous relative depletion of silicon in freshwater would lead to diatoms being replaced by non-siliceous forms such as cyanobacteria and green algae (SCHELSCKE and STOERMER, 1972).

On this basis, we have endeavored to investigate whether uptake of dissolved organic compounds might favor the growth potential of toxic cyanobacteria and dinoflagellates in the same assemblage. Here we report an investigation of the nutrients limiting the growth potential in one cyanobacterium and one diatom, both grown in water collected from spring to summer in the Gulf of Riga. Data provided by bioassays have also been tentatively used to estimate the fraction of nitrogen taken up by these strains which might have been provided by dissolved organic matter

2. Material and methods

Samples were collected following two different strategies: (i) In early May, early June and early July 1996, seawater was taken at varied depths along two transects (Fig. 1); the first transect started from Saulkrasti, on the south-eastern coast of the gulf, while the second one started from Melluzi, on the south-western coast. In addition, one sample was collected in the mouth of the river Daugava, and another in the central part of the gulf. Seawater was sampled with Niskin bottles, filtered on glass-fiber filters (GF/C, 0.8 μm pore equivalent), and stored deep-frozen until use on 10 July. (ii) On 19 July 1996, nearshore surface water was collected with a bucket at various stations on the southern coast. Samples were filtered on glass-fiber filters (GF/C, 0.8 μm pore equivalent), then kept overnight at 4°C and used for experiment on 20 July.

Ammonium (KOROLEFF, 1969) and phosphate (MURPHY and RILEY, 1962) concentrations were immediately measured by using manual protocols. Other nutrients were analysed later on deep-frozen subsamples by using a Skalar autoanalyzer: nitrate (reduction to nitrite according to protocols of STRICKLAND and PARSONS, 1972), nitrite (BENDSCHNEIDER and ROBINSON, 1952), silicate (MULLIN and RILEY, 1965), urea (KOROLEFF, 1976). Total nitrogen and total phosphorus were obtained after

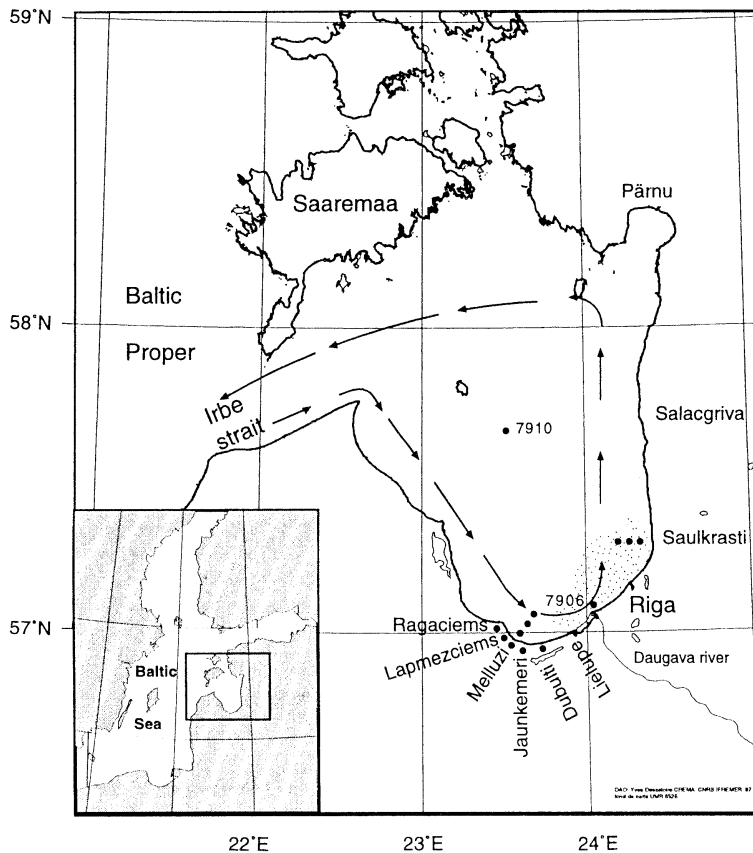


Fig. 1. Study area and positions of sampling stations.

ultraviolet oxidation under successive acid and alkaline conditions (COLLOS and MORNET, 1993), and then treated as for soluble reactive nitrogen and phosphorus.

Bioassays for nutrient (s) limiting growth potential.

Aliquots (30 ml) of either unfrozen or subsequently thawed samples were placed in 33-ml polycarbonate tubes, and the respective enrichment mixtures (Table 1) were added in volumes of 1 ml. Initial nutrient concentrations in the spike-enriched media were assumed to be low enough not to change the ecophysiological adaptation of the test algae and to be high enough to sustain an algal biomass significantly higher than that sustained by the unenriched control, thereby making clear which nutrients, if any, were present *in situ* at concentrations sufficiently high to sustain

growth and which were not (for detailed discussion, see MAESTRINI *et al.*, 1984). Two cultured strains were used as test organisms: *Microcystis aeruginosa* (strain: Station Marine d'Endoume, France, courtesy of Dr B. BERLAND) was chosen for being a dominant summer component of local planktonic communities (BALODE and PURINA, 1996); *Phaeodactylum tricorutum* (strain: Plymouth Marine Biological Laboratory, England, courtesy of Dr. M. PARKE) was chosen for its capability to take up nutrients at extremely low concentrations (BONIN *et al.*, 1986). Test cells were inoculated in maximum volumes of 250 μ l, in numbers to give an initial cell density of 136×10^6 cells. l^{-1} (experiment of 10 July) or 557×10^6 cells. l^{-1} (experiment of 20 July) of *Microcystis aeruginosa*, and 6.9×10^6 cells. l^{-1} (experiment of 10 July) or 9.2×10^6 cells. l^{-1} (experiment of 20 July) of *Phaeodactylum tricorutum*; these cells

Table 1. List and composition of spike enrichments used to bioassay the nutrient (s) limiting the growth potential of *Microcystis aeruginosa* and *Phaeodactylum tricorutum*; initial nutrient concentrations in the test cultures (equivalent to the enrichments alone) are indicated within parentheses.

1	Nothing	12	All-N
2	Nothing	13	All-P
3	Nothing	14	All-P
4	Nothing	15	All-Si
5	Nothing	16	All-Si
6	All	17	All-(Fe-EDTA)
7	All	18	All-(Fe-EDTA)
8	All-N	19	All-vitamin mix(Vit)
9	All-N	20	All-vitamin mix
10	All-N	21	All+metal mix(M)
11	All-N	22	All+metal mix

All=N (50 μ M) + P (3.4 μ M) + Si (60 μ M) + Fe (200 nM) + EDTA (1.2 μ M) + Metal mix = Co (5 nM) + Mn (100 nM) + Mo (100nM) + Vitamin mix = biotin (410 pM) + cyanocobalamin (135 pM) + thiamin (150 nM)

had been previously nutrient-depleted by culture for 2-3 days in nutrient-poor water. Incubation of the test cultures was carried out by placing the tubes before a north-facing window; light period was roughly 14 hours' light and 10 hours dark, at circa 100 μ mole. m^{-2} . s^{-1} ; temperature varied between 18°C and 22°C within a circadian period. *In vivo* fluorescence was monitored daily, during 6-10 days, with a R10 Turner Fluorometer (BRAND *et al.*, 1981), up to the respective maximum growth. Respective fluorescence values were then used to produce bar diagrams, with the value obtained after all-nutrient enrichment defined as 100%.

Data sets were first inspected by comparing the different enriched-culture fluorescence values to those of the unenriched and all-nutrient enriched controls. For each set (one water sample-one test species), it resulted in a number and a rank for each limiting nutrient. Then, in order to quantify the limiting role of each nutrient, the ratio of fluorescence in the "All minus one nutrient" enriched aliquots to the fluorescence in the unenriched control (abridged "All-X/control") was also calculated. In other words, for each particular nutrient missing in the spike and therefore present in the culture medium at its *in situ* concentration, this ratio is the increase in the coefficient of the natural AGP sustained by that nutrient. Hence, the lower the coefficient, the greater limiting

effect, and vice versa. All included, 35 bioassay sets were done with 28 water samples and two test strains. All test cultures but four grew well, thus indicating no adverse chemical condition.

Bioassays for indirect estimation of the uptake of dissolved organic nitrogen.

Aliquots (30 ml) of unfrozen or thawed samples were distributed in 33-ml polycarbonate tubes. For *Microcystis aeruginosa*, five aliquots were left unenriched, and five others were enriched with the "All - N" mixture. With *Phaeodactylum tricorutum* only, five unenriched aliquots were grown. Growth and maximal biomass were estimated as for the differentially enriched bioassays. Mean values and standard deviations were calculated for each set of five biomass values; samples which differed by more than 50% of the standard deviation were discarded; others were pooled and used for analysis of DIN (NO_3 , NO_2 , NH_4). Nitrogen uptake was calculated as being the difference between concentration at time zero and the respective concentration at the time of maximum biomass. The biomass was estimated after filtration on glassfiber filters (nominally 0.45 μ m), by analysis of the content of protein (PETTY *et al.*, 1982) for *M. aeruginosa*, or chlorophyll *a* (JESPERSEN and CHRISTOFFERSEN, 1987) for *P. tricorutum*.

Table 2. Nutrient concentrations (μM) in samples collected at different depths along transects on 1-5 May, 4 June and 3-4 July, as well as samples collected on 19 July at different nearshore stations. SA: transect from Saulkrasti, ME: transect from Melluzi.

Stations	Z (m)	S %	NO ₃ (μM)	NO ₂ (μM)	NH ₄ (μM)	Urea (μM)	DIN (μM)	PO ₄ (μM)	DIN : P	SiO ₃ (μM)	DIN : Si
Sampling of 1-5 May											
SA-03	0	3.64	35.8	0.7	0.5	3.6	36.9	0.22	167.8	10.1	3.7
SA-10	0	4.16	26.4	0.7	0.3	2.8	27.4	0.26	105.4	9.6	2.9
SA-30	5	3.70	37.5	0.6	1.0	4.3	39.1	0.34	115.1	12.6	3.2
SA-30	30	5.93	14.1	0.2	2.7	5.6	17.0	1.11	15.3	27.4	0.6
ME-10	0	5.38	8.7	0.2	0.6	1.3	9.5	0.45	21.7	2.2	4.3
ME-30	0	3.88	43.4	0.5	0.6	1.6	44.3	0.59	75.0	5.1	8.7
ME-30	10	5.17	4.7	0.7	0.6	1.9	6.0	0.73	8.1	0.4	15.0
ME-30	20	5.58	10.6	0.6	1.1	1.6	12.2	0.82	14.9	7.6	1.6
ME-30	30	6.00	12.5	0.4	1.7	3.3	14.7	1.20	12.3	20.9	0.7
7906	5	1.97	108.3	0.9	2.1	-	111.3	0.75	148.4	4.5	24.7
7910	0	5.42	5.5	0.7	0.2	1.7	6.4	0.33	19.5	3.0	2.1
Sampling of 4 June											
SA-10	0	4.01	5.6	0.5	0.7	0	6.8	0.05	135.4	1.3	5.2
SA-30	0	4.50	1.4	0.2	0.4	3.8	2.0	0.40	49.0	2.2	0.9
SA-30	5	4.95	0.4	0.1	0.4	2.8	0.9	0.03	0.5	1.8	0.5
SA-30	10	5.00	1.1	0.1	0.4	1.9	1.6	0.003	1.0	1.6	1.0
SA-30	30	5.94	11.4	0.2	1.9	7.0	13.4	0.18	103.4	19.5	0.7
Sampling of 3-4 July											
SA-05	0		1.0	0.4	1.0	4.5	2.4	0.23	10.4	3.3	0.7
SA-10	0		0.9	0.3	0.8	4.4	2.0	0.17	11.6	3.2	0.6
SA-20	0		0.7	0.3	1.0	4.2	1.9	0.15	12.8	3.1	0.6
SA-30	2.5		0.6	0.3	1.6	2.4	2.5	0.20	12.4	3.1	0.8
SA-30	5		0.5	0.2	1.7	2.9	2.4	0.15	16.2	2.6	1.0
SA-30	10		0.5	0.1	1.0	3.3	1.6	0.25	6.2	2.0	0.8
Sampling of 19 July											
Dubulti	0	4.14	0.7	0.7	0.4	5.6	2.3	0.38	6.1	6.3	0.4
Jaunkemeri	0	4.57	0.3	0.6	0.4	1.7	1.6	0.23	7.0	3.4	0.5
Lapmezciems	0	2.28	0.7	0.6	0.5	2.9	2.3	0.42	5.4	6.8	0.3
Lielupe	0	3.36	8.1	1.7	0.3	5.5	10.4	1.14	9.1	8.4	1.2
Melluzi	0	3.97	0.9	0.8	0.5	4.1	2.6	0.39	6.5	6.6	0.4
Ragciems	0	4.90	0.3	0.6	0.6	2.1	2.1	0.28	7.5	5.4	0.4

3. Results

An important decrease in the nutrient concentration occurred between spring and summer. In early May, waters were nitrogen-rich; most values of total dissolved inorganic nitrogen concentration ($\text{DIN} = \text{NO}_3 + \text{NO}_2 + \text{NH}_4$) ranged between 4.7 μM and 43.4 μM (Table 2), and the mean value was 19.9 μM ($s=14.5$, $N=10$). There was also an exceptional value of 108.3 μM recorded with water (station 7906)

sampled in the plume of River Daugava. Although the absolute values were rather high (concentrations ranged between 0.22 and 1.20 μM ; mean value was 0.62 μM ; $s=0.34$; $N=11$), the phosphorus content was relatively not as high; most values of the ratio $\text{DIN} : \text{PO}_4$ ($\text{DIN} : \text{DIP}$) were greater than 16. The silicon content was also low relative to that of inorganic nitrogen. Only two values of the $\text{DIN} : \text{SiO}_3$ ratio were lower than 1; the others ranged between 1.6 and 15.

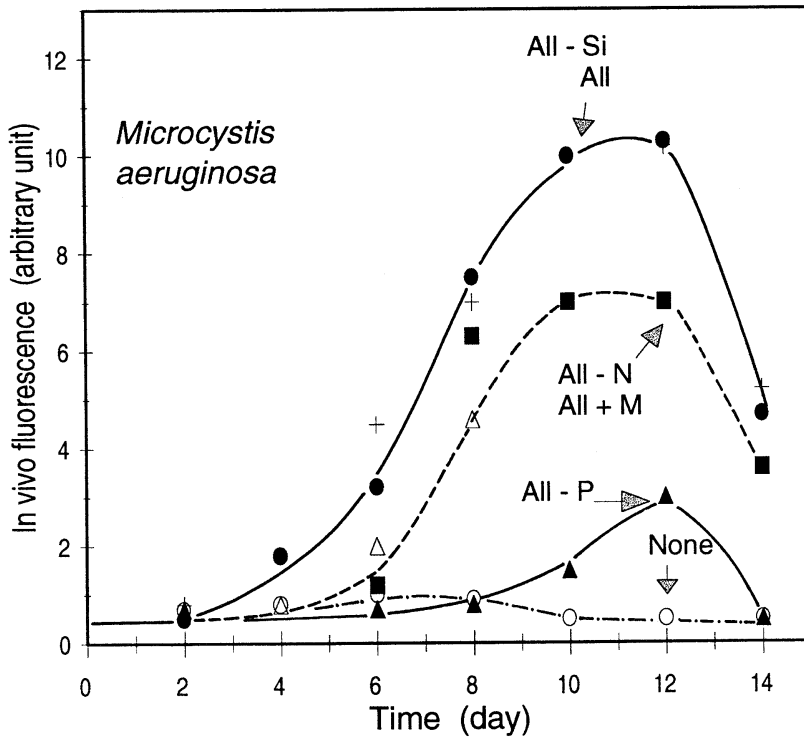


Fig. 2. *In vivo* fluorescence (arbitrary units) versus time, in differentially-enriched aliquot cultures of *Microcystis aeruginosa* (to allow the software to draw the figure, few missing data have been replaced by the mean of preceding and following values). Example of sample collected in early May 1996, at surface, at station 30 meters of the Melluzi transect.

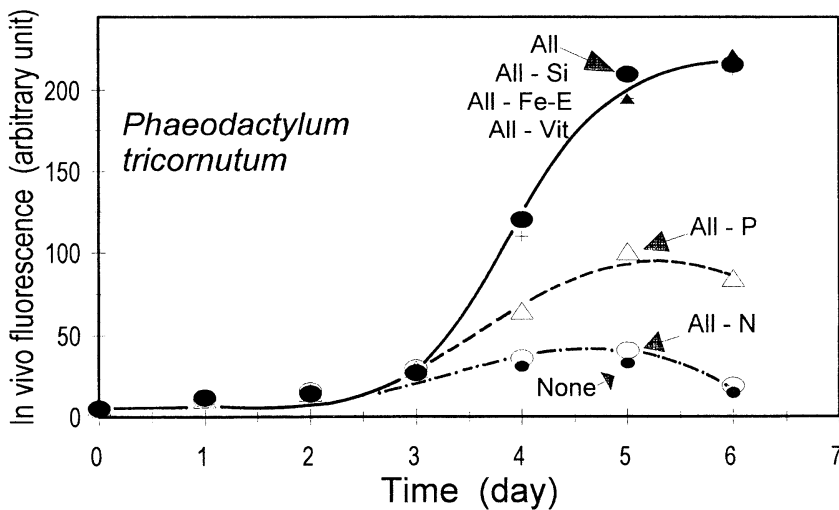


Fig. 3. *In vivo* fluorescence (arbitrary units) versus time, in differentially-enriched aliquot cultures of *Phaeodactylum tricornutum* (to allow the software to draw the figure, few missing data have been replaced by the mean of preceding and following values). Example of sample collected on 19 July 1996, at Lielupe station.

Table 3. Mean relative growth in unenriched seawater expressed as a percentage of that in the best nutrient enrichment, of *Microcystis aeruginosa* and *Phaeodactylum tricornutum* cultured in water sampled from early May to early July 1996 along Saulkrasti and Melluzi transects, and/or water collected nearshore on 19 July at different locations.

	Transect May–July	Sampling of 19 July	
	<i>M. aeruginosa</i>	<i>M. aeruginosa</i>	<i>P. tricornutum</i>
Mean	20.4	6.6	6.7
Standard deviation	16.8	2.8	4.8
N	20	6	6

In early June, the nutrient content had already decreased significantly. Values of DIN concentration for the upper waters ranged between 0.9 and 6.8 μM ($\bar{x}=2.8$; $s=2.7$; $N=4$), and those for phosphorus ranged between 0.03 and 0.40 μM ($\bar{x}=0.13$; $s=0.18$). A sharp decrease in silicon concentration ($\bar{x}=1.7 \mu\text{M}$; $s=0.4$) was also observed. Near the bottom (30-m depth) the ammonium and nitrate concentrations were much higher than in near-surface waters: 1.9 and 11.4 μM , respectively. Most values of DIN:DIP were still greater than 16, however. The silicon concentration was also high (19.5 μM).

In summer, (early July), all the coastal stations along the Saulkrasti transect, and all nearshore stations visited on 19 July (except one) were nitrogen-poor: the mean concentration of DIN was 2.2 μM ($s=0.3$; $N=11$). The Lielupe station (near the mouth of the river Lielupe and also close to the mouth of Daugava River), however, showed high DIN, 10.4 μM (Table 2). In contrast, concentrations of phosphorus and silicon had not decreased as much: mean values recorded were 0.26 μM ($s=0.10$) and 4.2 μM ($s=1.7$), respectively; at the Lielupe station, recorded values were 1.14 μM PO_4 and 8.4 μM SiO_3 . Accordingly, all values of the DIN: PO_4 ratio were <16 and those of the DIN: SiO_3 ratio were <1 , again except at Lielupe.

For reasons not apparent, water from two samples did not support growth and water from a further two samples supported only weak growth. Water from all the other samples, however, supported good growth. In growth trials started on 10 July, there was a two-day lag phase which prompted us to increase the initial cell density for trials started on 20 July. Overall, growth rate of *Phaeodactylum*

tricornutum, as reflected by the increase of *in vivo* fluorescence, was higher than that of *Microcystis aeruginosa*.

Except for a single sample in which nutrient concentrations were extremely high (i.e. 108 μM NO_3 , 1 May at station 7906), nutrient-spiked test cultures showed a significant increase in the final biomass compared with unspiked cultures (Fig. 2 and 3). With surface samples collected on 19 July, the maximum biomass in the unspiked controls averaged no more than 6.6% for *M. aeruginosa* and 6.7% for *P. tricornutum*, of the spiked culture giving the best growth. With waters taken during transects in early May, June and July, the unenriched aliquots sustained a biomass in *M. aeruginosa* averaging 20.4% of that in the best enrichments (Table 3). Growth was only slightly enhanced, however, when nitrogen or phosphorus were absent in the enrichments (Fig. 4). Omission of phosphorus alone (All-N) usually gave a smaller biomass than did omission of nitrogen alone (All-P), however. The absence of chelated iron had similar consequences in only four cases. Omission of silicon and vitamins from the enriching mixtures did not decrease the yield of either the cyanobacterium and the diatom. On the other hand, the addition of Co, Mn and Mo clearly did not promote growth, and even slightly inhibited growth in both test species (Fig. 4).

Inspection of the bioassay sets showed that in all cases but a few, the AGP was limited by at least two nutrients; in only 4 samples was nitrogen the single limiting nutrient, although there was also one sample for which no nutrient was limiting (Table 4). Over the 31 sets of bioassays which led to clear results, three simultaneous limiting factors were found in only

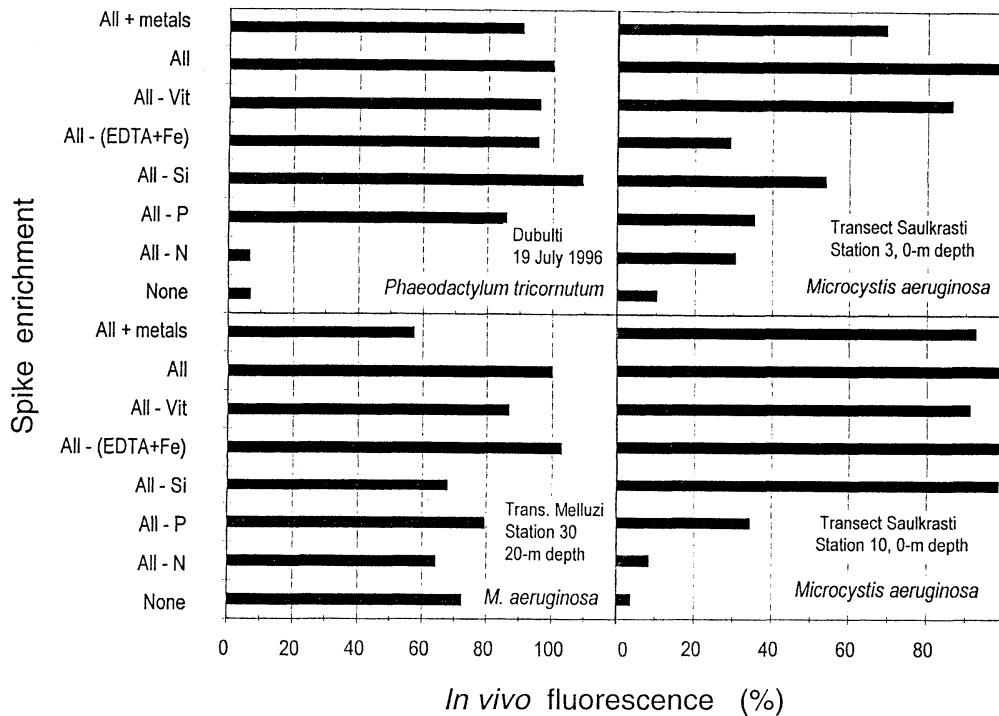


Fig. 4. Relative maximum algal biomass (%) versus spike enrichment; typical sets of data used for empirical analysis of nutrient limitation of AGP. *Phaeodactylum tricornutum* (top, left): N only is limiting; *Microcystis aeruginosa*: (top, right): N and Fe-EDTA are equally limiting, P is the third limiting nutrient; (bottom, left): inconclusive data; (bottom, right): N is first limiting, P is the second limiting nutrient.

6 samples. For both test species, nitrogen was found to be the primary limiting nutrient in 68% samples, but phosphorus in only 13%, colimitation by N and P in 19% (all for *M. aeruginosa*), and one case for which Fe-EDTA was equally as limiting as N and P. When nitrogen or phosphorus was not the first limiting nutrient, it was the second, except for one case of co-limitation at the second rank by nitrogen and iron. Equal third as the most limiting nutrient were iron and the vitamins, each in two samples over the 31 sets of bioassays. Silicon never appeared to limit the growth potential of the test species.

The nature of nutrients limiting the growth potential of test species changed from spring to summer. In early May, over nine samples (Table 4), phosphorus was the first limiting nutrient for *M. aeruginosa* growth in three samples and was co-limiting with nitrogen in a further four. In one sample, phosphorus was also

first limiting for *P. tricornutum*. In contrast, nitrogen was the first limiting nutrient in all samples collected on 19 July, for both *M. aeruginosa* and *P. tricornutum*.

Mean values of the coefficient reflecting the limiting effect of each nutrient ranged between 0.2 and 2.2 for nitrogen (Table 5), between 2.2 and 6.3 for phosphorus, between 7.7 and 34.8 for silicon, between 7.1 and 25.6 for iron and Fe+EDTA, and between 3.3 and 32.4 for the vitamin pool. Addition of trace metals decreased the growth potential, however, values of the index varying between 3.8 and 32.8, while those related to the mixture containing all nutrients but metals ranged between 8.1 and 35.0.

Biomass formed in control cultures was low, especially in July water (Table 3). Accordingly, plots of biomass formation versus DIN uptake were scattered. In contrast, sample aliquots which were nutrient-enriched with all nutrients but nitrogen led to more homogene-

Table 4. Nutrients limiting the potential biomass of the cyanobacterium *Microcystis aeruginosa* and the diatom *Phaeodactylum tricornutum* in seawater sampled in the Gulf of Riga, from early May to 19 July 1996, with indication of respective DIN : PO₄. Growth : as increase of biomass in best promoting mixtures versus: +++ : 15–20 fold increase or more; ++ : 10–15 fold; + : 5–10 fold.

Station	Depth(m)	Growth	Limiting nutrient			DIN : PO ₄
			1 st	2 nd	3 rd	
1 May - <i>P. tricornutum</i>						
7910	0	+++	P	N		19.5
1 May - <i>M. aeruginosa</i>						
7906	0	+++		Inconclusive		148.4
7910	0	0		Inconclusive		19.5
Transect Melluzi, 1–5 May - <i>M. aeruginosa</i>						
10	0	++	N	P		21.7
30	0	++	P	(N, Fe-EDTA)		75.0
30	10	+++	N	P		8.0
30	20	++	None			14.9
30	30	++	N			12.3
Transect Saulkrasti, 3–4 May - <i>M. aeruginosa</i>						
03	0	+++	(N, Fe-EDTA, P)			167.8
10	0	+++	P	N		105.4
30	5	+++	P	N		115.1
30	30	++	N			15.3
Transect Saulkrasti, 4 June - <i>M. aeruginosa</i>						
10	0	++	N	P		135.4
30	0	+++	N			49.0
30	5	++	(N, P)			0.5
30	5	+	(N, P)		Fe-EDTA	1.0
30	30	++	(N, P)			103.4
Transect Saulkrasti, 3–4 July - <i>M. aeruginosa</i>						
05	0	++	(N, P)			
10	0	++	N	P		
20	0	++	N	P		
30	2.5	++	N	P		
30	5	+	Inconclusive			
30	10	++	N	P		
Nearshore stations, 19 July - <i>M. aeruginosa</i>						
Dubulti	0	+++	N	P		6.1
Jaunkemeri	0	+++	N	P	Vit	7.0
Lapmezciems	0	+++	N	P	Vit	5.4
Lielupe	0	++	N			9.1
Melluzi	0	+++	N	P		6.5
Ragciems	0	0	Inconclusive			7.5
Nearshore stations, 19 July - <i>P. tricornutum</i>						
Dubulti	0	+++	N			6.1
Jaunkemeri	0	+++	N	P	Fe-EDTA	7.0
Lapmezciems	0	+++	N	P		5.4
Lielupe	0	+++	N	P		9.1
Melluzi	0	+++	N	P		6.5
Ragciems	0	+++	N	P		7.5

Table 5. Mean growth (relative to that in unenriched water) when enriched with the following substances: All; All+metals; All except the component marked, in *Microcystis aeruginosa* and *Phaeodactylum tricornutum*. In water sampled from early May to early July 1996 along Saulkrasti and Melluzi transects, and water collected nearshore on 19 July at different locations. Parentheses indicate standard deviation.

Presence of	Absence of	Transects of May-early July	Nearshore samples of 19 July	
		<i>M. aeruginosa</i> (N=21)	<i>M. aeruginosa</i> (N=6)	<i>P. tricornutum</i> (N=7)
All		8.1 (2.5)	12.4 (16.7)	35.0 (30.1)
All+metals		7.2 (2.1)	3.8 (02.5)	32.8 (29.0)
	N	2.2 (0.8)	0.2 (00.5)	1.5 (00.7)
	P	3.2 (1.3)	2.2 (03.5)	6.3 (04.8)
	Si	7.7 (2.3)	9.9 (10.9)	34.8 (29.9)
	Fe-EDTA	7.1 (2.1)	8.2 (07.5)	25.6 (25.8)
	Vitamins	8.0 (1.6)	3.3 (02.4)	32.4 (28.2)

ous plots. All nutrients out of nitrogen being present in excess in these samples, the mean biomass formation was higher than that in the control (Table 5). The overall plot of data obtained with *M. aeruginosa* grown in transect samples cuts the X axis at roughly -4 (Fig. 5), thus suggesting that an average amount of $\sim 4 \mu\text{g}$ atom nitrogen per liter was taken up by the cells under a chemical form other than NO_3 , NO_2 and NH_4 (DIN). Since in most samples the available volume of water was insufficient, similar plots for *P. tricornutum* are unavailable.

4. Discussion

REDFIELD (1934) observed that N- NO_3 and P- PO_4 are taken up by phytoplankton at a constant atomic ratio of 16:1, and FLEMING (1940) pointed out that this value is also that of the elemental composition of phytoplankton. It has since been agreed that ratios lower than 16:1 in the natural nutrient reservoir indicates nitrogen limitation, while a value higher than 16 reflects limitation by phosphorus. This concept must be used with care, because it applies to algal growth as crop, not as growth rate. On the other hand, differential enrichments (bioassays) apply to the potential maximum biomass, not to the actual biomass which can be first limited by the rate of losses. Nevertheless, determining the nutrient(s) limiting the potential biomass greatly helps to focus on the proper nutrient(s) and mechanisms leading to the situation of interest.

According to the respective nutrient contents of the water samples collected, it might be expected that at the time of the spring bloom (early May) the first limiting nutrient would be phosphorus in upper waters of the eastern eutrophicated part of the gulf, and nitrogen near the bottom. DIN:DIP values were indeed greatly >16 for samples taken at the surface and at a depth of 5 m depth, and <16 for the water collected at 30 m (Saulkrasti transect). Results given by the bioassays indicated exactly the same order of importance for the two main limiting nutrients (Table 4). At the same time, on the western side of the gulf, free from river discharge (Melluzi transect), the situation was different. Here nitrogen was the overall limiting nutrient, while phosphorus was limiting in only one sample for which DIN:DIP=75; Redfield's ratio and the bioassays furthermore led to exactly the same conclusions for all waters collected near the shore in July: DIN:DIP values ranged between 5.4 and 16.2 ($\bar{x}=9.3$; $s=3.4$; $N=12$), thus indicating that nitrogen was the first limiting nutrient, which was confirmed by bioassay.

Overall, it is clear that phosphorus was the most limiting nutrient for cyanobacterial growth potential in the nitrogen-rich waters. These conditions prevailed in spring, in the upper layer of the southern-eastern part of the Gulf, which is greatly influenced by river discharge. In late spring, with the decrease of the total DIN reserve, from $>17 \mu\text{M}$ to $<13 \mu\text{M}$

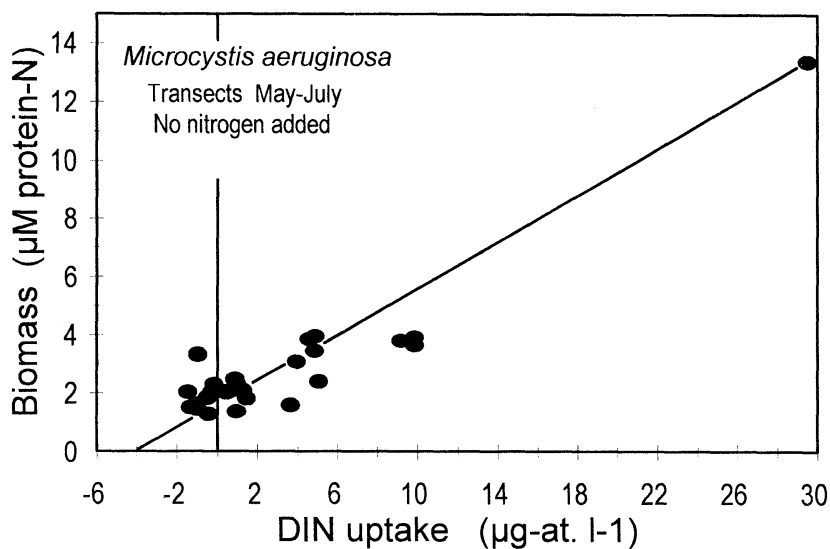


Fig. 5. Biomass (protein N) formed versus dissolved inorganic nitrogen taken up by the cyanobacterium *Microcystis aeruginosa* grown in waters collected in the Gulf of Riga, from early May to mid July, and nutrient-enriched with all nutrients but nitrogen.

(Table 2), nitrogen and phosphorus then played a similar role. In deeper layers of this area and out of the river plume, nitrogen was the limiting nutrient. It is likely that these differences are related to the circulation regime; although there are both cyclonic and anticyclonic currents and turnovers, the general trend of the circulation is that saline water of high salinity from the Baltic Proper enters into the gulf through the Strait of Irbe and flows south eastwards along the western coast (Fig. 1), while water of low-salinity having received fresh water from the River Daugava is flowing northwards along the eastern coast (BERZINSH, 1995). In summer, when the river discharge is the lowest, all DIN concentrations but one ranged between 1.6 and 2.6 μM , and the whole area was nitrogen-limited for both the cyanobacterium and the diatom test strains.

YURKOVSKIS *et al.* (1993), who sampled along the 20-m isobath and at greater depths from February to October 1989, reported mean monthly DIN:DIP values from 19 to 56. On this basis, they inferred that the phytoplankton of the whole gulf was phosphorus-limited. In contrast, at one station located in the Baltic Proper, mean DIN:DIP values for the same period ranged between 2.9 and 7.1, leading to the

conclusion that nitrogen was the limiting nutrient. From these results as well as from those showing that the open-sea waters on the Baltic are presently nitrogen-limited (GRANÉLI *et al.*, 1990; KIVI *et al.*, 1993), PÖDER and JAANUS (1995) hypothesized that the shift from DIN:DIP values >16 to those <16 should be observed in the Irbe Strait area which separates the Gulf of Riga and the Baltic Proper. Samples they collected in summer 1993–94, along transects from the strait towards the gulf and the open sea, showed that most DIN:DIP values were <3 ; only for August waters, a few ranged between 5 and 10. Accordingly, the authors concluded there was no shift from phosphorus to nitrogen limitation from the gulf to the open sea, and concluded that nitrogen was the limiting nutrient in both the Baltic Proper and the Gulf of Riga. Further records on nutrient concentrations and comparison with previous long-term data led YURKOVSKIS *et al.* (1996) to show that drastic changes have occurred in the Gulf of Riga in the 90s. Since late 80s–early 90s, nitrate concentration has continuously decreased: from $\sim 18 \mu\text{M}$ in 1991 to $\sim 10 \mu\text{M}$ in 1993, in the upper (0–10 m) layer, in February; and from $\sim 3.5 \mu\text{M}$ in 1989 to $\sim 0.5 \mu\text{M}$ in 1994, in the same layer, in August, while in deeper (20–50 m)

waters in August, they have decreased from $\sim 22 \mu\text{M}$ in 1991 to $\sim 5 \mu\text{M}$ in 1994. During the same period, concentrations of phosphorus have risen, leading to a situation of nitrogen limitation. Hence, all results agree. Most of the Gulf of Riga is now clearly nitrogen-limited in late spring and summer. In contrast, for small and shallow areas, whether nitrogen or phosphorus is limiting is an open question, because river discharges significantly influence salinity and nutrient concentrations, particularly in surface waters.

Important changes in nutrient reserves, nutrient ratios and the species composition of natural phytoplankton assemblages occur along salinity gradients from river mouths to the open sea. SAKSHAUG and MYKLESTAD (1973) and SAKSHAUG *et al.* (1983) found a permanent phosphorus limitation of phytoplankton biomass in the inner section of the Trondheim Fjord, but a clear nitrogen limitation in high-salinity waters; with DIN:DIP values falling from 50 to 10–12. In ponds and coastal waters of Massachusetts, bioassays showed that in low-salinity ponds (0–6.5 psu) phytoplankton biomass was phosphorus limited, while nitrogen addition stimulated phytoplankton growth only in the most saline ponds (31 psu) and the open sea; in ponds of intermediate salinity, phytoplankton biomass was limited both by nitrogen and phosphorus (CARACO *et al.*, 1987; CARACO, 1988).

Similar features have been reported for the Baltic Sea. LIGNELL *et al.* (1992) observed that phytoplankton carbon uptake rate and biomass were P-limited in a fjord-like inlet with low salinity on the south-west coast of Finland, whereas in the open sea both nitrogen and phosphorus were limiting. PITKÄNEN and TAMMINEN (1995) have shown that, in summer, from the river Neva to the open part of the Gulf of Finland, there was an associated gradient for salinity, nutrient concentrations and DIN:DIP. Both DIN:DIP values and bioassays indicated that phosphorus was limiting the potential biomass of phytoplankton in the river; then, phosphorus was first limiting and nitrogen was the second limiting nutrient in the estuary, and nitrogen was first limiting and phosphorus was the second limiting nutrient in the transition

zone, whilst nitrogen was the single limiting nutrient in the open gulf.

Although technical limitations did not allow us to take more than two samples on the transect from the river Daugava to the open sea, our results as a whole agree with the scheme of gradual changes from river water to the open sea. Accordingly, the shift between DIN:DIP values >16 (freshwater-influenced waters) and those <16 (typical marine waters) that PÖDER and JAANUS (1995) endeavored to observe in the Strait of Irbe should be searched inside the Gulf of Riga, at the limit of the river plume. Controlled by the river discharge regime, the transition area would not have a fixed area and limits, however, and important seasonal variations are likely, as already observed for other areas. In the Patuxent River estuary (Chesapeake Bay), D'ELIA *et al.* (1986) reported great seasonal variability in river flow, nutrient regimes, and the response of natural phytoplankton assemblages to nutrient addition. During the high-flow season, in late winter, DIN:DIP typically exceeded 90, and addition of phosphorus stimulated growth. In late summer, DIN:DIP in nutrient standing stocks was characteristically <5 ; so when nitrogen was added the growth response was very rapid, reflecting nitrogen limitation. In the southern Baltic, GRANÉLI *et al.* (1988) have compared different coastal waters sampled outside Warnemünde, Rostock, Sopot and Falsterbo. Although the nutrient levels of their samples were different, there were no significant differences between the different locations for nutrients limiting the potential biomass. During winter, before the spring phytoplankton bloom had started, phosphorus was the most limiting nutrient for phytoplankton biomass formation; after the bloom, nitrogen appeared to be the most limiting nutrient.

Whether in nutrient-poor or in nutrient-rich waters, important variations in the nature of the limiting nutrient have been also observed with species. In oligotrophic coastal Mediterranean water, BERLAND *et al.* (1978) reported that the diatom *Skeletonema costatum* was phosphorus-limited, especially from February to June, whereas *Cylindrotheca closterium* was limited according to a complex succession invol-

ving nitrogen, phosphorus, silicon, and vitamins. In the Trondheim Fjord, (SAKSHAUG, 1987; GRANÉLI *et al.*, 1988) showed that phosphorus was the limiting nutrient for *Skeletonema costatum* when DIN:DIP=12, and for most of the other species only when DIN:DIP=18–25.

In the Helsinki archipelago, RINNE and TARKIAINEN (1978) reported a nitrogen limitation for potential phytoplankton biomass, except for the nitrogen-fixing cyanobacterium *Nodularia spumigena* which showed phosphorus limitation. Similar findings were reported by TAMMINEN *et al.* (1985) who ran *in situ* mesocosm experiments at the entrance to the Gulf of Finland, in an area not directly influenced by large sewage discharge; addition of ammonium significantly increased the total phytoplankton biomass, while phosphate addition stimulated the growth of nitrogen-fixing cyanobacteria. Other authors have also reported that addition of phosphorus stimulated the growth of *Nodularia spumigena* (HUBER, 1986; LUKATELICH and McCOMB, 1986), thus supporting HORSTMANN'S (1975) contention that blooms of this species are a consequence of phosphorus loading. Furthermore, KONONEN *et al.* (1996) have inferred that *N. spumigena* blooms in a frontal region at the entrance of the Gulf of Finland benefited from the low DIN:DIP value which prevailed in surface water at the onset of the bloom. Blooms of *Aphanizomenon flos-aquae* and *N. spumigena* in the Gulf of Gdansk have been also related to low values of DIN:DIP (PLINSKI and JOZWIAK, 1996).

Since the 90s, blooms of the nitrogen-fixing species *Aphanizomenon flos-aquae* and *Nodularia spumigena* have also occurred in the Gulf of Riga, in summer (BALODE and PURINA, 1996). Their appearance was related to the decrease of the DIN:DIP ratio (YURKOVSKIS *et al.*, 1996). This is in agreement with the overall nitrogen limitation we observed; species such as diatoms or non-nitrogen-fixing cyanobacterium such as *Microcystis aeruginosa* that we used as test species were nitrogen-limited. In contrast, *N. spumigena* were not nitrogen-limited, and therefore may take the upper hand in the assemblage, although diatoms appear not to be silicon-limited.

Silicon never appeared to be limiting for

either of the two strains we used for bioassays. This might be a consequence of the absence of silicon requirement for *M. aeruginosa* and the very low needs of *Phaeodactylum tricornutum* (BONIN *et al.*, 1986). On the other hand, DIN:SiO₂ was <1 in June and July, and phosphorus was the limiting nutrient when DIN:SiO₂ values were >1 (Table 2); hence silicon could never be more limiting than nitrogen or phosphorus. YURKOVSKIS *et al.* (1993) found no silicate limitation in the Gulf of Riga in the 80s, but recent data have shown silicon acting as a limiting nutrient during the spring bloom (YURKOVSKIS, personal communication). Nevertheless, it is likely that altogether the recently reported decrease of silicon loading in coastal waters and its subsequent enhanced importance in pushing the outcome of species competition towards summer harmful species (SMAYDA, 1990; SOMMER, 1996) may not yet be critically important for the Gulf of Riga.

In four cases, iron appeared to be in the list of nutrients limiting potential biomass (Table 2). This appears to be the first report indicating finding iron to limit Baltic phytoplankton. Although role of iron has been stressed mostly for low-chlorophyll-high-nutrient regions (JENNINGS *et al.*, 1984; MARTIN and FITZWATER, 1988; ZETTLER *et al.*, 1996), it has also been found to be limiting on occasion in coastal waters; namely, in the Gulf of Maine (GRAN, 1933; GLOVER, 1978; WALLS *et al.*, 1991), the coast of Oregon (GLOOSCHENKO and CURL, 1971), and the north-west Australian coast (Tranter and Newel, 1963). Moreover, iron is required for N₂ fixation by diazotrophic cyanobacteria (RUETER *et al.*, 1998; PAERL *et al.*, 1994), whereas it has been reported that at least 40–90% of the iron transported by freshwater aggregated and sedimented when salinity reaches 4–5 psu in the estuary of the Öve River, western Baltic (FORSGREN *et al.*, 1996). More research on the role of iron as a nutrient in the Gulf of Riga may thus be desirable.

Our results suggest that a significant fraction of the nitrogen taken up by the two test species may have been as dissolved organic nitrogen (DON). It is estimated that an average of ~4 µg-atom N l⁻¹ was taken up by *Microcystis aeruginosa*. This amount is close to the

mean concentration of urea we recorded (\bar{x} = 3.3; s = 1.5; N = 26; range 1.3 to 7.0 μM). Similar estimations have been made in oyster ponds of the French Atlantic coast (MAESTRINI and ROBERT, 1981), where diatom test species were found to take up 0.6 to 30.7 $\mu\text{g-atom l}^{-1}$ of DON, and which, results suggested, had the capacity to take up six times more DON than DIN. These findings agree with current knowledge on nutritional capabilities of phytoplankton.

Several algae have been reported to grow in culture with organic compounds as the sole source of nitrogen and phosphorus (TERNETZ, 1912; DROOP, 1961; KUENTZLER and PERRAS, 1965; FLYNN and BUTLER, 1986; BERMAN *et al.*, 1991). Field research also shown that half-saturation values (K) for urea falls within natural urea concentrations (McCARTHY, 1972); accordingly, urea has been considered as an important potential nitrogen source for phytoplankton in various coastal waters (KRISTIANSEN, 1983; IGNATIADES, 1986; KOKKINAKIS and WHEELER, 1988; PRICE and HARRISON, 1988; FERNANDEZ *et al.*, 1996). In mesocosm experiment carried out *in situ*, in water of the western coast of the Baltic Sea, SÖRENSSON *et al.* (1989) reported an uptake rate for urea up to five times faster than that for nitrate. TAMMINEN and IRMISCH (1996) showed that urea uptake dominated that of total nitrogen in an incubation experiment with size-fractionated assemblages collected in summer at the entrance of the Gulf of Finland; urea appeared to be a particularly important nitrogen source during the regenerated phase of plankton succession. Also, dissolved free amino-acids have been reported to sustain a significant part of algal growth in the Chesapeake Bay (GLIBERT *et al.*, 1991). Moreover, PALENIK *et al.* (1988-89) have shown that some phytoplankters are able to use various forms of DON without initial transport into the cell, by using cell-surface enzymes to degrade these forms of nitrogen to NH_4 , and TRANVIK *et al.*, (1993) observed the ingestion of proteins such as ferritin, casein and albumin by heterotrophic flagellates.

Suggestion has also been made that organic compounds from land-drainage origin, such as humic acids, have favored harmful dinoflagellate growth versus that of harmless species

(CARLSSON and GRANÉLI, 1993; CARLSSON *et al.*, 1995; LARA *et al.*, 1993; MORAN and HODSON, 1994). Some results are conflicting, however. For instance, during a drogue experiment in the Baltic proper, SÖRENSSON and SAHLSTEN (1987) recorded no uptake of DOM whose molar C:N was >20 , which they inferred was refractive. These results led them to believe the nitrogen fixers, mostly *N. spumigena*, relied mainly on N_2 for their nitrogen demand.

The cyanobacterium we used as test species, *Microcystis aeruginosa*, is not a N_2 -fixing species. Accordingly, whether or not DOM is a significant factor in triggering the onset of toxic blooms in the Gulf of Riga is still an open question and should be a focus for further research.

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Résumé—Nutriment (s) limitant la biomasse potentielle («AGP») dans le Golfe de Riga, est Mer Baltique : bioessais conduits avec la cyanobactérie *Microcystis aeruginosa* et la diatomée *Phaeodactylum tricornutum*.

Des échantillons ont été recueillis début mai, juin et juillet 1996, le long de deux radiales situées, l'une dans la partie sud-est du golfe fortement influencée par les eaux fluviales, l'autre dans la partie sud ouest recevant peu d'eau douce, à une station située dans le panache de la principale rivière (Daugava), au milieu du golfe ; mi-juillet, des eaux proches du rivage ont été prélevées à différentes stations de la côte ouest. Les valeurs relatives des concentrations ioniques *in situ* en azote, phosphore et silicium et des bioessais (enrichissements différentiels) conduits en laboratoire ont été utilisées pour déterminer les nutriments limitant la biomasse potentielle. Les deux méthodes ont montré que le phosphore était le nutriment limitant pour les deux espèces tests dans les eaux de surface riches en azote minéral recueillies en début mai dans la partie sud-est du golfe ; en fin de printemps, l'azote et le phosphore avaient un rôle équivalent. Dans les couches plus profondes de la partie est et dans toute les autres parties du golfe peu influencées par les eaux fluviales, l'azote était le nutriment limitant. En été au moment du plus faible débit des rivières, pour toutes les stations échantillonnées, la concentration en azote minéral était comprise entre 1,6 et 2,6 μM et l'azote était le nutriment limitant. Pour 74% des échantillons où l'azote était le nutriment limitant, le phosphore est apparu comme étant potentiellement le nutriment limitant venant en second. En revanche, le silicium n'est jamais apparu comme pouvant limiter la biomasse, aussi bien pour la cyanobactérie que pour la diatomée tests ; le phosphore était limitant quand le rapport $\text{NO}_3 + \text{NO}_2 + \text{NH}_4 : \text{SiO}_2$ était >1 , en mai, et <1 en juin et juillet quand l'azote était limitant. Les auteurs estiment que l'accroissement en importance du rôle silicium pour la compétition interspécifique au sein du phytoplancton au bénéfice des espèces toxiques non silicifiées récemment mis en exergue pour d'autres eaux côtières n'est pas encore significatif pour le golfe de Riga. Le fer est apparu dans la liste des nutriments limitants pour 12% des test. En outre, bien que les valeurs absolues soient entachées d'imprécision, certains résultats indiquent qu'une fraction non négligeable de l'azote prélevé ($\sim 4 \mu\text{g-atom N l}^{-1}$) pourrait l'avoir été sous une forme organique. Les auteurs suggèrent de prêter attention à ces deux facteurs pour les recherches à venir.

Биогены лимитирующие потенциал роста водорослей в Рижском заливе, Восточной части Балтийского моря (весна-лето, 1996).

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Резюме: Пробы воды были собраны в мае, июне, июле 1996 года на трёх разрезах: первом- с сильным воздействием речного стока (восточное побережье), втором- без речного воздействия (западное побережье), третьем- против устья реки Даугава (на станциях у самого устья реки и в открытой части залива); а также на нескольких литоральных станциях западного побережья. Для выявления элемента, лимитирующего потенциальный рост фитопланктона, были использованы отношения растворимого азота, фосфора и кремния *in situ* и тесты биогенного лимитирования. Сравнение отношений растворимого неорганического азота к растворимому неорганическому фосфору (DIN/DIP) с отношением Редфилда и результаты экспериментов биогенного лимитирования привели к идентичным выводам. Фосфор выявлен как главный элемент лимитирующий потенциальный рост фитопланктона весной в богатых азотом поверхностных слоях вод юго-восточной части Рижского залива, где наблюдается сильное воздействие речного стока. В конце весны- начале лета наблюдается уменьшение резервов DIN. В это время как фосфор, так и азот становятся лимитирующими элементами. В более глубоких водных слоях этого района и в западной части залива, где не наблюдается воздействие речного стока, лимитирующим элементом был азот. Летом, когда наблюдается наименьшее воздействие пресных вод, концентрации DIN достигали 1.6-2.6µM, что обуславливало азотное лимитирование исследуемого района на что указывает также биотесты проведенные цианобактериями и диатомовыми. В 74% проб, где азот был лимитирующим элементом, фосфор выявлен как второй более значимый элемент. В то же время кремний не ограничивал рост *Microcystis aeruginosa* и *Phaeodactylum tricornutum* ни при отношении DIN к SiO₃ >1 (в мае), когда фосфор был лимитирующим элементом, ни при отношении DIN к SiO₃ <1 (в июне, июле), когда лимитирующим был азот. Железо в 12% проб лимитировало потенциал роста фитопланктона. Результаты исследований показывают, что тестовые культуры могут ассимилировать некоторое количество азота (~4µg-atomN/l) в форме растворимого органического вещества. Этому факту следует уделить больше внимания в последующих исследованиях фитопланктона Рижского залива.

1993年7月鹿島灘に形成された暖水舌と 微小プランクトンの分布

石垣 哲治*・西川 淳*・津田 敦**・寺崎 誠*

Distribution of nanoplankton around a warm water tongue in the Kashima-Nada Sea in July 1993

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Abstract: The abundances and distribution of nanoplankton were investigated within a warm water tongue and its adjacent waters in the Kashima-Nada Sea from 6 to 8 July 1993. Nanoplankton abundances in the upper 50m ranged from $3.1 \times 10^2 - 5.9 \times 10^3$ cells/ml for heterotrophic nano-flagellates (HNF), $3.8 \times 10^2 - 4.9 \times 10^3$ cells/ml for autotrophic nano-flagellates (ANF), $7.0 \times 10^2 - 8.1 \times 10^4$ cells/ml for cyanobacteria and $2.5 \times 10^5 - 1.3 \times 10^6$ cells/ml for bacteria, respectively. A tendency for abundances to decrease below the thermocline layer, which was between 50m and 100m, was seen. The depth of the maximum abundance layers for both HNF and bacteria were the same and there was also a strong correlation between the maximum abundance layers of ANF and chlorophyll *a*. However, the stations at which the maximum abundances of HNF and bacteria occurred were different from those where ANF and chlorophyll *a* maximum occurred. The HNF maximum abundance layer (10 m) occurred in the layers above the maximum abundance layer of ANFs (30 m). Although the biomass of macrozooplankton varied with different water masses, total cell numbers of nanoplankton in the water column did not.

1. 緒言

従属栄養性微小鞭毛虫類 (Heterotrophic Nano-Flagellates: HNF) は葉緑素を持たない無色の非光合成鞭毛藻類としてその存在が古くから知られ、植物プランクトンとして位置づけられていた。しかし栄養形態は当初より従属栄養を行うものと認識されていた (BEERS, 1982)。

1970年代後半、蛍光顕微鏡によって水界の総細菌数 (HOBIE *et al.*, 1977) が大きく、また [³H] (チミジン) の取り込み実験 (HOLLIBAUGH *et al.*, 1980) により細菌が早い増殖速度を示すことがそれぞれわかった。その後、Microbial loop (AZAM *et al.*, 1983) 説が提唱され、

HNF は、細菌や微小藻類等の捕食者 (FENCHEL, 1975; JOHNSON *et al.*, 1982; GOLDMAN and CARON, 1985) として、水圏生態系の物質循環に果たす役割と存在が重要視されるようになった。以後、現在に至るまで、細胞数密度の測定 (FENCHEL, 1982; DAVIS and SIEBURTH, 1982; LEINIKKI and KOUSA, 1990; HAAS, 1982; SHERR and SHERR, 1983 a, b; CARON, 1983)、捕食速度の測定 (SHERR *et al.*, 1987; NYGAARD *et al.*, 1988; NYGAARD and HESSEN, 1990) などが行われてきた。

HNF は全世界の海域に普遍的に存在することが知られている (FENCHEL, 1982; ANDERSEN nad FENCHEL, 1985)。太平洋側日本近海では、黒潮および親潮が流れる非常に変化に富んだ海洋環境を有しているが、微小プランクトン、特に HNF や独立栄養性微小鞭毛虫類 (Autotrophic Nano-Flagellates: ANF) の細胞数密度、現存量などの報告例は周防灘 (今井・伊藤, 1984)、広島湾 (岩本ら, 1993) などの沿岸での水平分布に限られている。

鹿島灘は、黒潮、親潮系水、沿岸水等が流れ込む複雑

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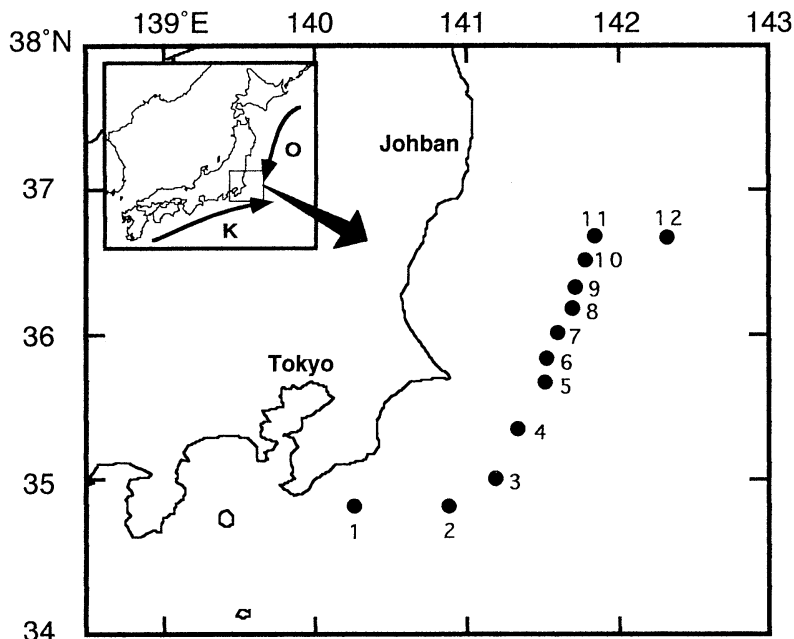


Fig. 1. Location of sampling stations during the Cruise KT 93-10 in July, 1993. Numbers denote stations. Stations 1 and 11 were not sampled. O: Oyashio current, K; Kuroshio current.

な海洋環境を形成し、ネット動物プランクトン群集は水塊やフロントに対応して種組成が変化し、現存量も変動することが知られている (NISHIKAWA *et al.*, 1995)。本研究は、鹿島灘におけるHNF, ANF, 細菌およびラン藻類 (主に *Synechococcus*) などの微小プランクトンの細胞数密度の測定を行い、その分布構造を明らかにすることを目的とした。

2. 材料と方法

1) 採集地点と流速の測定

東京大学海洋研究所研究船淡青丸 KT93-10 次航海において、1993年7月6～8日に鹿島灘の黒潮フロント域をはさむ黒潮から親潮分枝を縦断する形で設けた、計10測点 (測点2から10までと測点12) において微小プランクトンの採集を行った (Fig. 1)。また、航行中、船に搭載された ADCP (Acoustic Doppler Current Profiler: 船用超音波ドップラー流速プロファイラー) により、水深0, 20, 100 および 200 m の計4層の流速を測定した。尚、船速が10ノット以上の時に測定された ADCP の値を使用した。

2) 採集と分布測定

採集は、CTD を装着したロゼット型採水器 (RMS:

以後 CTD-RMS と示す) で行った。ただし、表面のみはバケツで採水した。採水層は0, 10, 30, 50, 100, 150, 200 および 250 m の計8層とした。採水後直ちに採水器より 80 ml を取り、グルタルアルデヒドを用いて、最終濃度が1% になるように固定した。細菌と藻類は DAPI (PORTER and FEIG, 1980) で染色後、イルガランブラックで染色した孔径 0.2 μm スクレポアフィルターでろ過を行い、HNF および ANF は DAPI と Primulin (CARON, 1983) の二重染色 (SHERR and SHERR, 1983a) を行った後、イルガランブラックで染色した孔径 0.8 μm スクレポアフィルターでろ過を行い、それぞれプレパラートを船上にて作成した。プレパラートは作成までの処理を採集後3日以内に行った後、計数直前まで凍結保存 (-20°C) した。計数は航海終了後1ヶ月以内に研究室にて落射型蛍光顕微鏡 (Zeiss 社製 Axioplan) 下で行った。励起光に紫外線を用い、細菌については倍率1000倍で300細胞以上、HNF については倍率400倍で50細胞以上を計数した。ラン藻類および ANF の計数は、青色励起光による自家蛍光が橙色および赤色を発したものを、それぞれ倍率400倍にて50細胞以上に達するまで行った。なお、各プランクトンの鉛直分布図の作成には作図用ソフト Spyglass Transform 2.1 (Spyglass 社製) を使用し、内挿法を用いて求めた。また、各測点の水柱

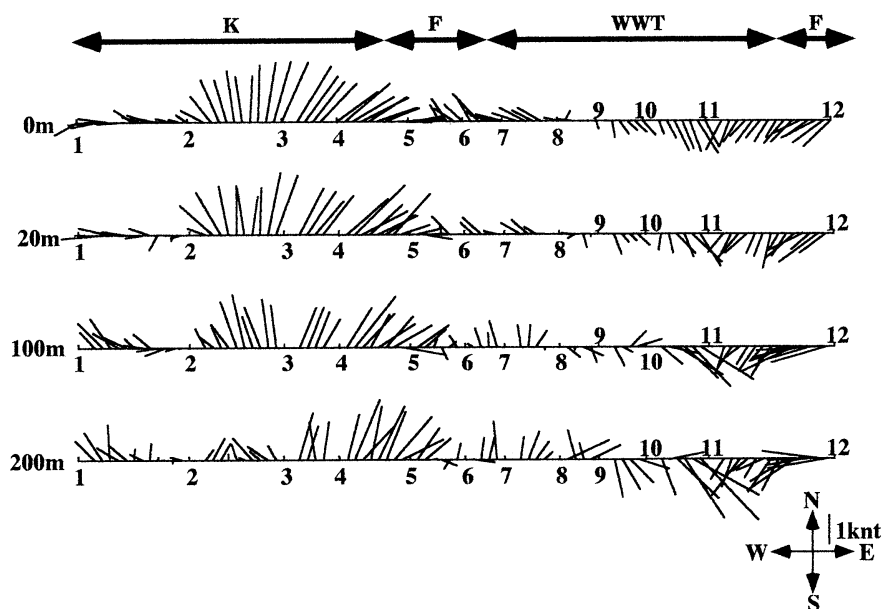


Fig. 2. Stick diagram of water flow at four depth layers recorded by the ADCP. Vectors were plotted at 5 minutes intervals. Data taken while the ship was cruising at speeds less than 10 knots were not included. K: Kuroshio, WWT: Warm Water Tongue, F: Front.

積算細胞数は内挿法によって得られた鉛直分布から1 m 間隔の細胞数密度を0 m から250 m まで積算することにより求めた。

3) 栄養塩およびクロロフィル *a* 測定

採水は10測点の0, 10, 20, 30, 50, 75, 100, 125, 150, 175, 200 および250 m の計12層についてCTD-RMS により行った。栄養塩(硝酸・亜硝酸態窒素: $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$, 以後 NO_3 と示す。リン酸態リン: $\text{PO}_4\text{-P}$, 以後 PO_4 と示す)濃度とクロロフィル *a* 量の測定は航海終了後研究室に持ち帰って行った。栄養塩濃度については、船上にて試水10ml を0.45 μm ミリポアフィルターでろ過後、凍結保存(-20°C)し、研究室にて室温で解凍し、オートアナライザー(BRAN+LUBBE 社製)を用いて測定した。クロロフィル *a* 量は、船上にて試水200 ml をWhatman GF/F フィルター(直径2.5 mm)でろ過し、N, N-Dimethylformamide(凝固点-61°C)によりクロロフィル *a* を抽出し(SUZUKI and ISHIMARU, 1990)、低温保存(-20°C)した試料を、研究室にて蛍光光度計(TURNER MODEL 111)により計測した。

3. 結果

1) 海洋環境

調査海域の海洋環境の概要(詳細は NISHIKAWA *et al.*, 1995)は以下の通りである。調査海域の全測点において0, 20, 100 および200 m の4層の流向および流速は、ほぼ同一方向かつ同速度であった(Fig. 2)。測点5, 6 および12には、フロントが形成され、親潮系水と考えられる低水温、低塩分水(6°C, 34.0 PSU 以下)が200 m 以深に認められた(Fig. 3)。測点2から4までは、全層にわたり比較的高水温、高塩分(18°C, 34.5 PSU 以上)の黒潮系水が存在し、北東方向の強い流れが観測された。測点7から10までは、250 m 以深に低塩分水(34.0 PSU 以下)が存在し、100 m 付近に黒潮系水と考えられる比較的高塩分(34.5 PSU)の暖水が流れ込むように存在する、暖水舌が形成され、特に測点7から10に向かって北西方向の流れが南向きの流れに変化する複雑な流向を示した。

なお、上記の NISHIKAWA *et al.*, (1995) の区分に従い、本調査海域は、測点2から4までを黒潮域、測点7から10までを暖水舌域、そして測点5, 6 および12をフロント域と定義した。水温躍層は、黒潮域の50~100 m 層、フロント、暖水舌域の50~60 m 層にそれぞれ存在した。

栄養塩濃度の鉛直分布は測点5を除く全測点の0~30 m までは、 NO_3 , PO_4 ともに枯渇していた。しかし、測

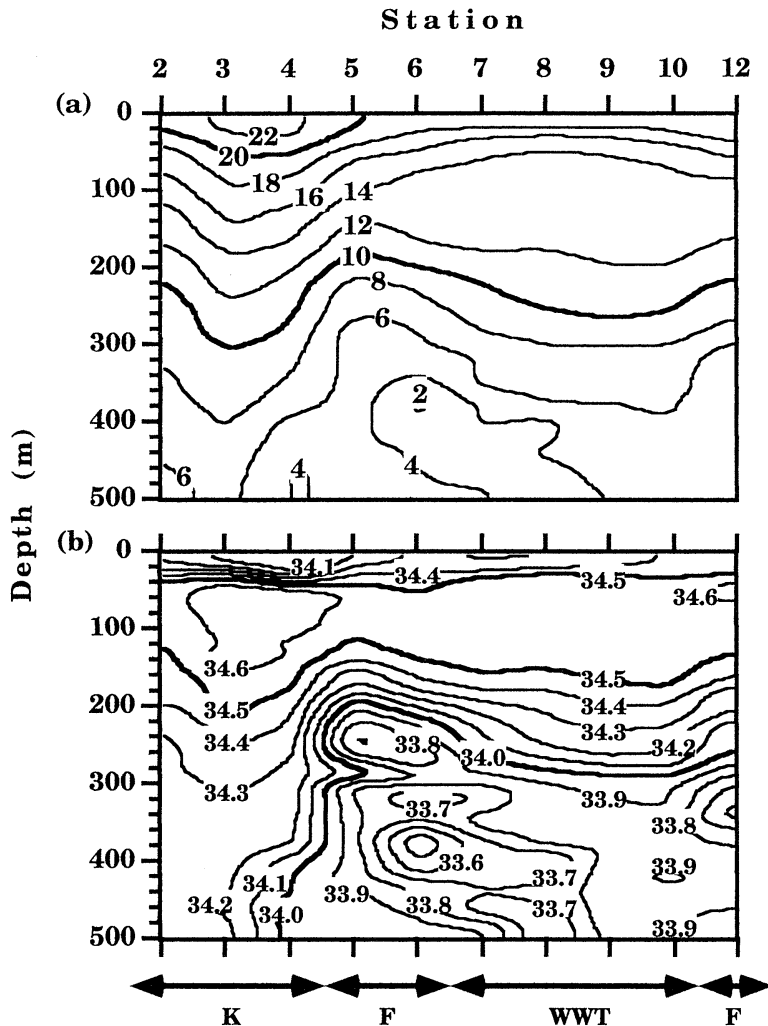


Fig. 3. Vertical profiles of (a) temperature ($^{\circ}\text{C}$) and (b) salinity (PSU) at Kashima-Nada Sea, off the Pacific coast of central Japan. Abbreviations follow Fig. 2.

点5の表面では、 $0.98\ \mu\text{M}$ (NO_3), $0.1\ \mu\text{M}$ (PO_4) と比較的高い値が観測された (Fig. 4)。

2) 微小プランクトンの細胞数密度と鉛直分布

HNF, 細菌, ラン藻類およびANFの調査海域における0~250mまでの水柱積算細胞数の平均値はそれぞれ、 1.7×10^{11} , 7.0×10^{13} , 2.1×10^{12} , 1.5×10^{11} cell/mlであった。黒潮域, フロント域および暖水舌域それぞれの間で各生物の水柱積算個体数の関係は以下の通りであった。細菌およびラン藻類では、黒潮域に比べフロント域の方が有意に多かったが ($p < 0.05$: Mann-WhitneyのU検定), 他の海域間には有意差が認められなかった。HNF

およびANFでは3海域それぞれの間で有意差が認められなかった。また、ラン藻類とANFでは、水温躍層上層(50m)の上側に分布の中心があったが、細菌とHNFでは水温躍層の上側と下側でほぼ等しい水柱積算細胞数を示した (Fig. 5)。

クロロフィルaは30mにおいて極大層を示した。測点5の30mにおいて最大値 $4.28\ \mu\text{g/l}$ が観測された (Fig. 6)。

ラン藻類の分布極大層はSCM (Subsurface chlorophyll maximum layer: 亜表層クロロフィル極大層) より上の10mに存在した。細胞数密度は 10^4 cell/ml 台に達し、水温躍層の下層では水深とともに急激に減少し、

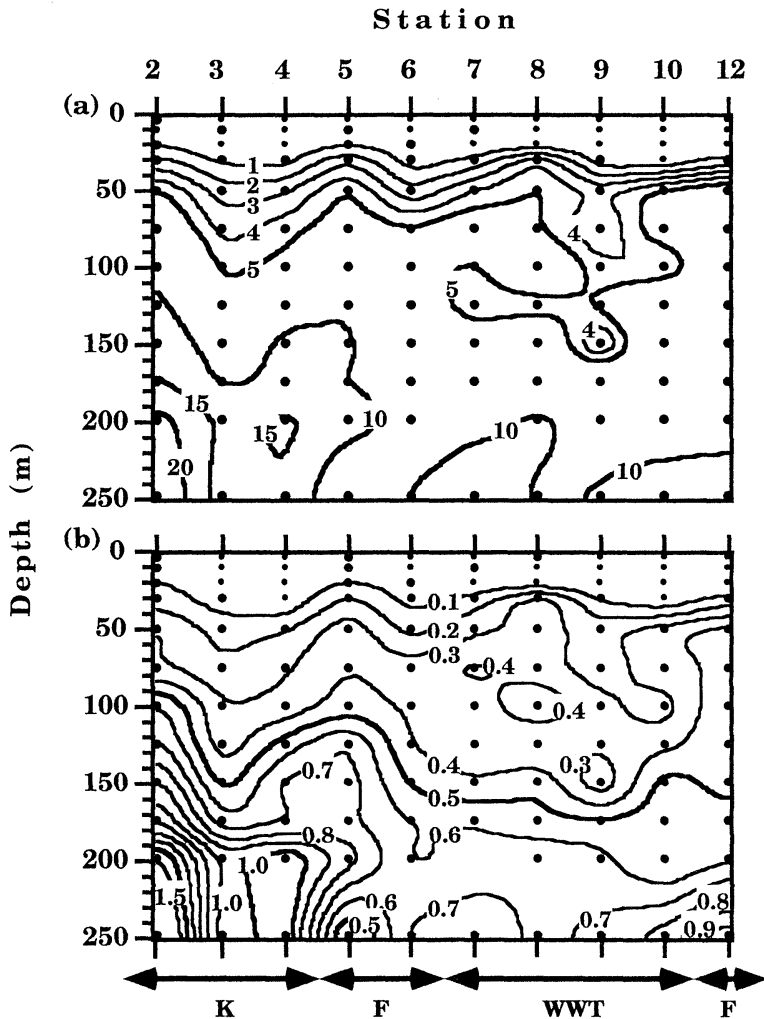


Fig. 4. Vertical profiles of nutrients in the Kashima-Nada Sea, off the Pacific coast of central Japan. (a) NO₃ (μM) and (b) PO₄ (μM). Small dots at sampling depths indicate undetectable concentrations of the nutrients. Other abbreviations follow Fig. 2.

100 m 以深では 10^2 cells/ml 以下であった。測点 5 の 10 m において最大細胞数密度 8.1×10^4 cells/ml が観測された (Fig. 6)。

細菌は、測点 2 の 10 m において 1.3×10^6 cells/ml であったことを除き、調査海域全水柱において 10^5 cells/ml 台であった。分布極大層は 30 m に存在し、100 m 以深では 3.0×10^5 cells/ml 以下であった (Fig. 7)。

ANF と HNF は、50 m 以浅では 10^3 cells/ml 台であったが、50 m 以深では急激に減少し、 10^2 cells/ml 以下となる傾向が見られた。ANF の分布極大層は 30 m に存在し、SCM と一致した。しかし、現存量の大小では常にクロロフィル *a* とは一致せず、ANF の最大細胞数

密度はクロロフィル *a* が最大値を示した測点 5 ではなく測点 8 の 30 m (4.9×10^3 cells/ml) に存在した。測点 5 の 30 m における ANF の細胞数密度は 3.3×10^3 cells/ml であった。100 m 以深では ANF はほとんど検出されなかった。一方、HNF の分布極大層は ANF の極大層に比べて浅く、10 m に存在した。測点 4 の 10 m において最大細胞数密度 5.9×10^3 cells/ml が観測され、この値は他の測点より 2~3 倍高い値であった。100 m 以深では HNF は測点 5、6 の 150 m においてそれぞれ 1.7×10^3 、 1.1×10^3 cells/ml であったが、通常 10^2 cells/ml 台であった (Fig. 6, 7)。

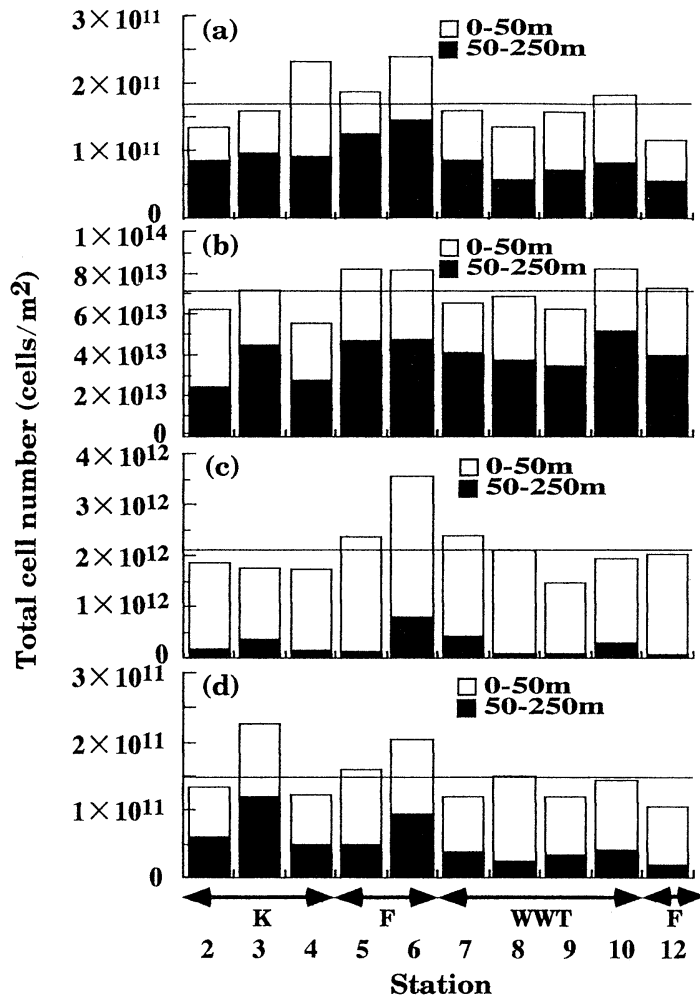


Fig. 5. Total cell number (cells/ml) of (a) HNF, (b) bacteria, (c) cyanobacteria, and (d) ANF in the 0-50 m and 50-250 m water columns at each station. Solid lines indicate mean values over all stations. Abbreviations follow Fig. 2.

4. 考察

大西洋の沿岸および外洋における HNF の細胞数密度は、 $1.0 \times 10^2 \sim 3.7 \times 10^4$ cells/ml (PORTER *et al.*, 1985; SANDERS *et al.*, 1992) であり、沿岸において高い値を示し最大 10^4 cells/ml 台であったが、沿岸から外洋に向かって減少し外洋において平均 10^2 cells/ml 台、最大 10^3 cells/ml 台であると報告されている。また、DAVIS *et al.*, (1985) によると北大西洋において海域の水深の増加(沖合に向かう)とともに表層の HNF の細胞数密度は減少していき、水深 200 m までの沿岸海域では $3.1 \times 10^3 \sim 9.0 \times 10^4$ cells/ml、水深 200 m 以上の沖合海域では $6.6 \times 10 \sim 1.6 \times 10^2$ cells/ml であった。また、DAVIS and

SIEBURTH (1982) によると ANF の細胞数密度は北大西洋において沿岸から外洋に向かって減少し $5.0 \times 10^2 \sim 9.0 \times 10^3$ cells/ml であると報告されている。DAVIS *et al.*, (1985) の区分では、本調査海域(水深 1000~2000 m) は大陸斜面に属し、大陸斜面表層での HNF の細胞数密度は $7.1 \times 10^2 \sim 1.5 \times 10^3$ cells/ml であると報告している。事実、本調査の結果は 50 m 以浅における HNF と ANF の細胞数密度が $3.1 \times 10^2 \sim 5.9 \times 10^3$ HNF/ml および $3.8 \times 10^2 \sim 4.9 \times 10^3$ ANF/ml であることを示したので (Fig. 6, 7), 太平洋側日本近海の大陸斜面表層 50 m における HNF と ANF の細胞数密度は北大西洋のそれとほぼ同程度であることが明らかとなった。

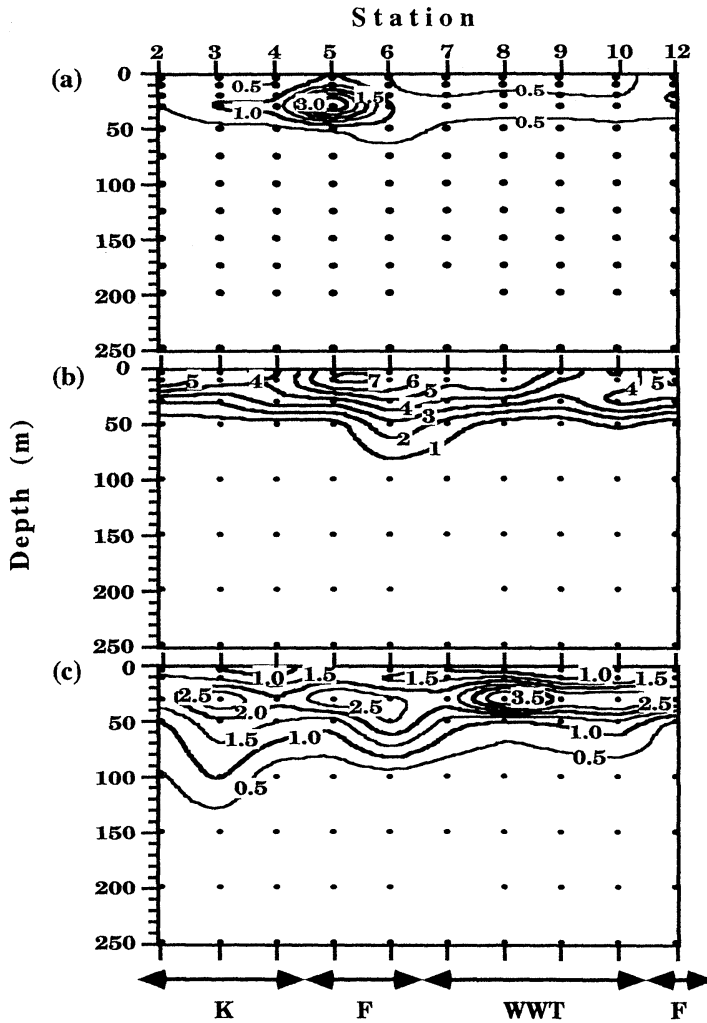


Fig. 6. Vertical profiles of (a) chlorophyll *a* ($\mu\text{g/l}$), (b) cyanobacteria ($\times 10^4$ cells/ml), and (c) ANF ($\times 10^3$ cells/ml) in the Kashima-Nada Sea, off the Pacific coast of central Japan. Abbreviations follow Fig. 2.

TOWNSEND and CAMMEN (1985)によれば、Maine湾では夏季にSCMが20~30 m層に存在し、35 μm 以上の原生生物の現存量はSCMと75~100 m層との2層で分布極大を示したと報告している。これは深いところの流れのシャー (shear: 流れを横切る方向に流速が変化すること) や表面の暖水等と下層の低水温低塩分水との境界である75~100 m層に密度躍層などが生じたことによって、原生生物の栄養源となる生物死骸などのデトリタス粒子や生物生産にともなって排出される有機物などが表層から沈降して75~100 m層に集積したためであると考察した (TOWNSEND and CAMMEN, 1985)。また、大陸棚のフロント域では、ナノサイズとマイクロサ

イズのプランクトンの細胞数密度がSCM付近で増加するということが知られている (LONGHURST and HARRISON, 1989)。本調査海域ではフロント域を除きHNFおよび細菌の分布極大は10 mにあり、SCM (30 m)と一致しなかったが、フロント域の測点5と6ではHNFと細菌の分布極大は10 mと150 mの2層に存在した (Fig. 7)。フロント域において流向が測点5から6に向かって東向きから北西方向へと変化する複雑な流れにあり、また150 m付近に親潮系の低水温低塩分水が存在し、150 m以浅に黒潮系の暖水が存在していたため (Fig. 3)、シャーが150 m付近に生じていたものと考えられる。したがって、この海域のフロント域では表層が

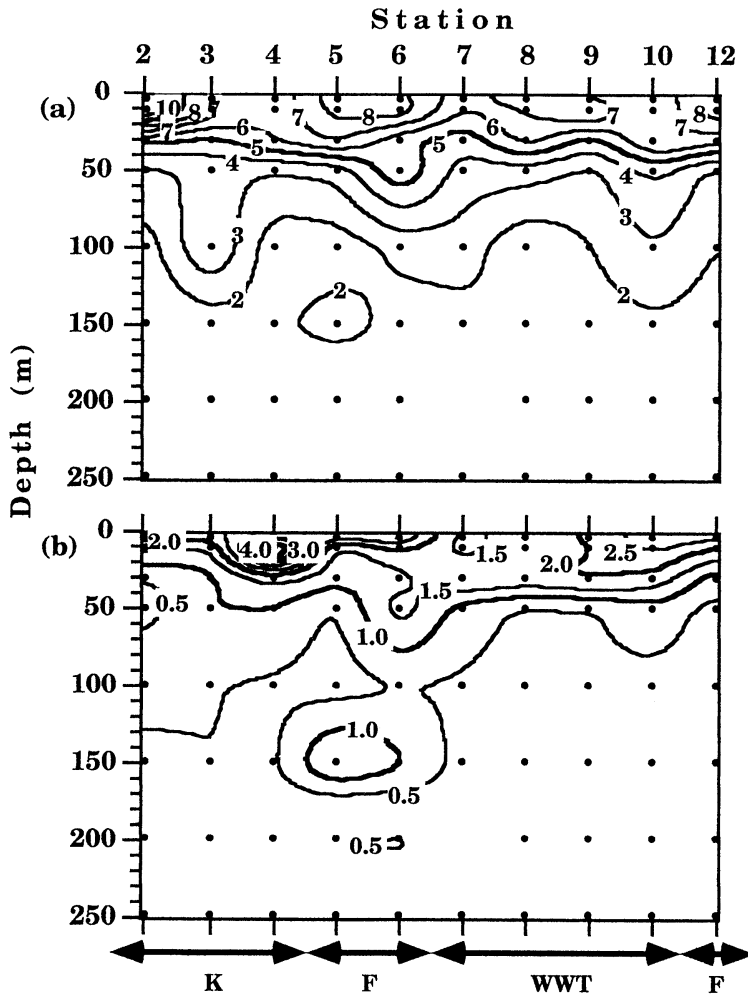


Fig. 7. Vertical profiles of (a) bacteria ($\times 10^5$ cells/ml), and (b) HNF ($\times 10^3$ cells/ml) abundances in the Kashima-Nada Sea, off the Pacific coast of central Japan. Abbreviations follow Fig. 2.

ら沈降する生物死骸などのデトリタス粒子や生物生産にともなって排出される有機物などが150m付近に集積したため、2層分布極大が形成されたと考えられる。

本調査海域は暖水舌を形成する複雑な海況を呈していた。大型動物プランクトンの総生物量には水塊により顕著な差が認められ、黒潮域ではフロント域および暖水舌域に比較して有意に小さかった(NISHIKAWA *et al.*, 1995)。一方、微小プランクトンの水柱積算細胞数は、細菌とラン藻類において黒潮域とフロント域の間で有意差が認められた以外、水域による顕著な差が認められなかった。この理由として、第1には、種レベルでは各微小プランクトンの水柱積算細胞数について水域による差の可能性

は考えられるが、微小プランクトンの種の同定が困難であるため本調査では微小プランクトンを高次分類群レベルで計数したことが考えられる。第2には、微小プランクトンの水柱積算細胞数は水塊変化、すなわち水温および塩分の変化に規定されるものではなく、水柱内に溶存する各微小プランクトンの増殖に寄与する有機物や微量元素の量などの化学的な要因に規定されるからであると考えられる。

HNFは細菌(HAAS and WEBB, 1979; FENCHEL, 1982)やラン藻類(JOHNSON *et al.*, 1982; ITURRIAGA and MITCHELL, 1986)を捕食することが知られている。SHERR *et al.* (1984)は定点季節変化について調査した結

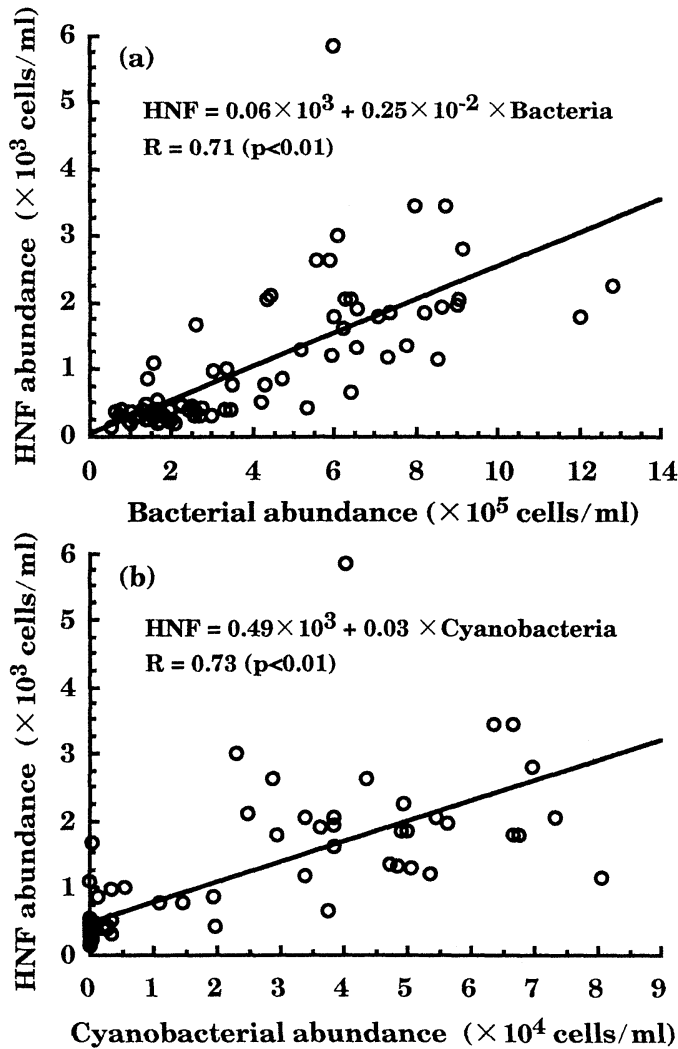


Fig. 8. Relationships in abundance between (a) bacteria and HNF, and (b) cyanobacteria and HNF in the 0-250 m water from of the Kashima-Nada Sea, off the Pacific coast of central Japan.

果、HNF と細菌の細胞数密度の間に正の相関が見られる時、両者が捕食被捕食関係にあることを報告した。また、沿岸、外洋および陸水における HNF に対する細菌の細胞数密度比はほぼ 1000 であるとされている (FENCHEL, 1986; SANDERS *et al.*, 1992)。さて、本調査海域の全水柱について、HNF と細菌、HNF とラン藻類それぞれ細胞数密度の間には (Fig. 8), $R=0.71$, $R=0.73$ の危険率 1% で正の相関がみられたが、HNF に対する細菌の細胞数密度比は平均 482 (Fig. 9) であり、上記の値より高かった。また、各微小プランクトンの細胞数密度は水温躍層以深において急激に減少し、ラン藻と

ANF は約 70% が 50 m より浅層に分布していたのに対し、細菌と HNF は、50 m を境界とした上下でほぼ同程度分布していた (Fig. 5)。50 m 以浅と 50 m 以深での HNF と細菌、HNF とラン藻類それぞれの細胞数密度の関係は次の通りであった。50 m 以浅では、HNF と細菌、HNF とラン藻類 ($R=0.44$, $R=0.50$) には、ともに危険率 1% で正の相関が認められたが、50 m 以深では、HNF と細菌、HNF とラン藻類 ($R=0.28$, $R=0.21$) ともに危険率 5% で正の相関を示さなかったものの、HNF と細菌の相関では $p=0.08$ であり、かなりの相関があるものと考えられる (Fig. 10)。以上から

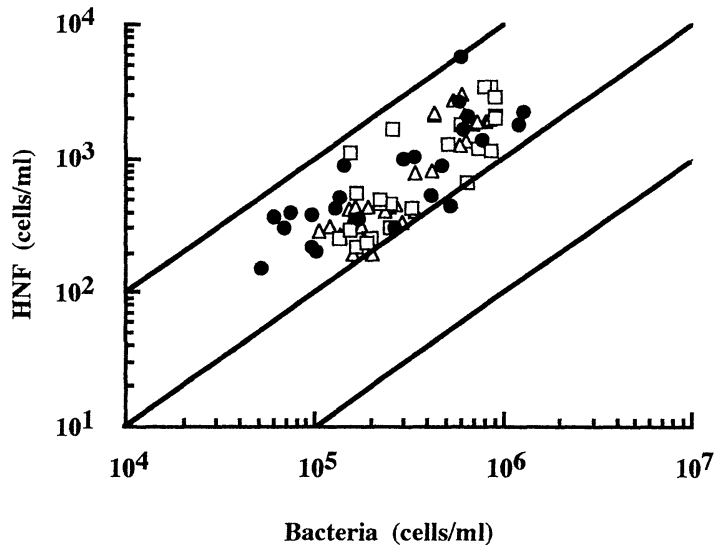


Fig. 9. Relationship in abundances of bacteria and HNF observed during the Cruise KT 93-10. The three lines represent bacteria/HNF ratios of 100, 1000 and 10000. Mean ratio in the Kuroshio area (black circle) was 423.4, at the Front area (white triangle) was 527.1 and in a warm water tongue area (white square) was 493.6. The overall mean was 481.6.

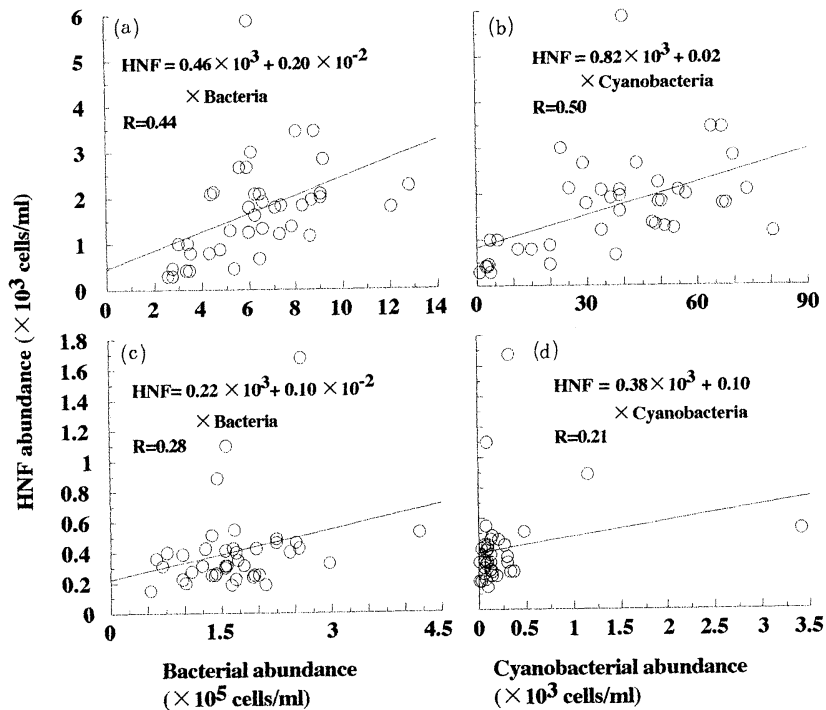


Fig. 10. Relationships in abundance of bacteria and HNF (a, c) and cyanobacteria and HNF (b, d) in the 0-50 m (a, b) and 50-250 m (c, d) water columns in the Kashima-Nada Sea, off the Pacific coast of central Japan.

HNF は水温躍層の上側でラン藻と細菌の両方を捕食し、水温躍層の下側では主に細菌を捕食しているのではないかと推測される。

さて、ANF にも従属栄養を行う種が知られ (ESTEP *et al.*, 1986; BENNET *et al.*, 1988; ANDERSSON *et al.*, 1989), 今回の計数値にはこれらの種も含まれていたものと推察される。また, ANDERSSON *et al.* (1989) によれば, 従属栄養を行う ANF は増殖のために従属栄養を行い, 貧栄養条件下で生き残る戦略として光合成による独立栄養を行う。しかし, 本研究は短期間の観測であったため, 観測中に現場海域の時系列変動を明らかにできなかった。従って, 空間的分布からは HNF と細菌, HNF とラン藻類それぞれの間に捕食被捕食関係があると推察されるが, 時系列的に現場海域において HNF と細菌, HNF とラン藻類それぞれの細胞数密度の変動周期が同調していた状態にあったか否か, また従属栄養を行う ANF が増殖する状態か個体群保存を行う状態であったか, それぞれについて判断することは現時点では難しい。

今回の調査結果から太平洋側日本近海の微小プランクトン (主に HNF と ANF) の細胞数密度は水温躍層以深において急激に減少するが, 水温躍層以浅においては 10^3 cells/ml であり, 従来の報告値とほぼ同程度であることが明らかとなった。今後は, 微小プランクトンの海洋生態系内における動態を明らかにするために, 捕食者である大型動物プランクトンとの関係を明らかにする必要がある。さらに微小プランクトンの種の同定法の簡便化により詳細な種組成の調査を行っていきたい。

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学 会 記 事

1. 1997年3月31日(月)東京水産大学において平成8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8年度活動状況が報告された。
- 2) 学会誌 La mer の編集状況が報告された。
- 3) 平成8年度収支決算が報告された。
- 4) 平成9年度学会賞受賞候補者選考経過および結果が報告された。
- 5) 日本学術会議第17期会員候補者として有賀祐勝会長、推薦人として山口征矢会員、推薦予備人として森永 勤会員を届け出た事が報告された。

協議事項

- 1) 平成9年度事業計画(案)について審議した。
- 2) 平成9年度予算(案)について審議した。
- 3) 平成9年度の学術研究発表会・総会を5月31日(土)に開催、会場は日仏会館とすることとした。
- 4) 学会誌の Regional editor として、Paul H. LeBLOND 博士の推薦があり、編集委員会で検討することとした。
- 5) 1997年度日仏学者交換公募に関する案内を評議員に送付することとした。
- 6) 国際シンポジウム「日本の海洋科学に何が期待されているか;太平洋社会との望ましい海洋科学の接点を求めて」(4月21日、つくば市)を協賛することとした。
- 7) 総会に向けて、次回幹事会・評議会を5月24日(土)に開催することとした。

2. 1997年5月24日(土)東京水産大学において平成9年度第1回幹事会及び評議会が開かれた。主要な議事は下記の通り。

報告事項

- 1) 平成8年度事業が報告された。
- 2) 学会誌 La mer の編集状況が報告された。34巻1号から4号を刊行。第3号は第8回 JECSS-PAMS ワークショップのプロシーディスグス(特集号)。
- 3) 平成9年度学会賞受賞候補者選考経過が報告された。

- 4) 日本学術会議第17期会員候補者として有賀祐勝会長、推薦人として山口征矢会員、推薦予備人として森永 勤会員を届け出た事が報告された。
- 5) 平成8年度収支決算の報告および監査報告が行われた。

協議事項

- 1) 平成9年度事業計画(案)について審議した。
 - ① 総会1回、学術研究発表会1回、幹事会4回
 - ② シンポジウムおよび講演会の開催および後援
 - ③ 学会誌 La mer の刊行
 - ④ 平成9年度学会賞授与および平成10年度学会賞受賞候補者の推薦
 - ⑤ その他
- 2) 平成9年度予算(案)について審議した。
- 3) 平成9年度学会賞受賞候補者推薦委員会委員として次の会員を推薦することとした。

青木三郎 今脇資郎 落合正宏 鎌谷明善
岸野元彰 小池勳夫 小池 隆 関根義彦
竹松 伸 谷口 旭 中村重久 松山優治
門谷 茂 柳 哲雄 山口征矢

3. 新入会員(正会員)

氏名	所属・住所	紹介者
長島 秀樹	東京水産大学海洋環境学科 〒108 港区港南4-5-7 TEL: 03-5463-0465	松山 優治

4. 住所・所属機関等変更(正会員・受付順)

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6. 逝去

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7. 受贈図書 (受領順)

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本学会員・編集委員 半沢正男氏は去る 1997 年
 3 月 24 日逝去されました。ここに謹んで哀悼の意
 を表します。 日仏海洋学会

Dr. Masao HANZAWA, a member of the Society,
 passed away on 24 March 1997. The Society
 presents sincere condolence to his death.

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” SPOT アプリケーションシンポジウム” が開催されます

(財)リモートセンシング技術センターと SPOTIMAGE 社(フランス)の共催、(株)CRC 総合研究所およびテクノコンサルタンツ(株)の協力により、標記のシンポジウムが開催されます。このシンポジウムはフランス大使館および宇宙開発事業団の後援が予定されています。

開催日：1997年11月26日(水)

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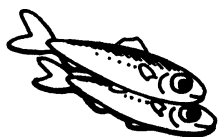
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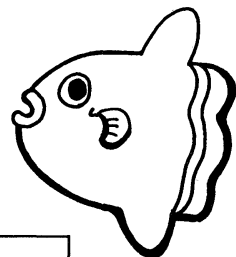
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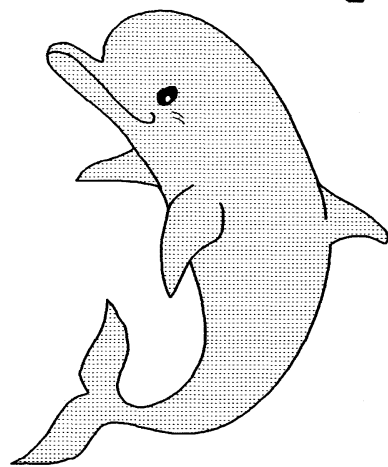
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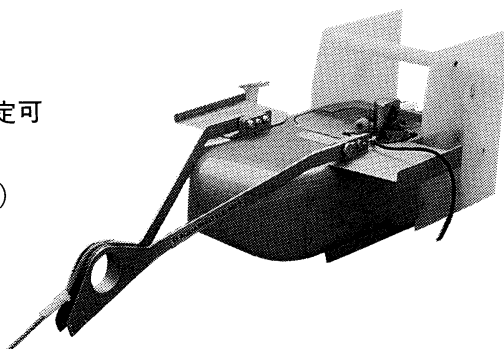
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