PRODUCTION ECOLOGY WITHIN THE LOWER TROPHIC LEVELS IN MARINE ECOSYSTEMS

By

Tsuneo ODATE*

Division of Marine Biochemical Science, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041, Japan

Contents

The present work was submitted as a partial fulfillment of the requirements for Doctor's degree in Fisheries Science at Hokkaido University in 1989.

* Present address: Faculty of Bioresources, Mie University, Tsu, Mie 514, Japan.

I. Introduction

Steele (1974) has given a lucid and clear statement on the marine food chain. "The phytoplankton of the open sea is eaten nearly as fast as it is produced, so that effectively all plant production goes through the herbivores. The animals living on the sea bottom depend on herbivore feces, rather than on a direct fallout of plants, for their food supply. One of the main technical problems in plankton studies has been to demonstrate experimentally that the herbivorous zooplankton can get enough to eat from the densities of phytoplankton found normally in the sea. All indications suggest that herbivores in the sea *are* resource-limited. On the other hand, there is evidence that these herbivores are highly efficient at transferring energy through the food chain from plants to primary carnivores." The consideration that the main fate of phytoplankton is to be eaten seems to have originated from Hervey (1945) who provided us with the generalization but little supporting evidence. Now, we have to study quantitatively the transportation from phytoplankton to zooplankton or productive zone to non-productive zone.

Since the cycling of organic matter is a fundamental concept in biological oceanography, attention should be devoted initially to primary production as the starting-point in the cycle. Although the contribution of benthic plants can be significant in inshore waters, the overwhelming importance of the planktonic algae in global primary production justifies a substantial study of phytoplankton production (Raymont, 1980).

It is well known that the size composition of the phytoplankton community shows considerable variations with season (Larsson and Hagström, 1982) and region (Furuya and Marumo, 1983). Such variations may be large in the northern sea areas, considering the large seasonal variation of environmental conditions (e.g. light, temperature, and nutrient concentrations) (Taniguchi, 1981). Hence, it is necessary for investigators studying trophodynamics in the northern sea areas to recognize the seasonal changes in plankton community structures. There is no

doubt that the first step of the food chain is phytoplankton production and herbivores grazing. In classical concepts of the food chain, diatoms and copepods were considered to be the major primary producers and primary herbivores, respectively (Steele, 1974). Recent studies have shown that picoplankton, which is defined as smaller than 2 μm by Sieburth *et al.* (1978), accounts for the majority of the total primary production and chlorophyll *a* concentrations in coastal waters during summer (Larsson and Hagström, 1982) and in the open ocean (Berman, 1975; Sieburth *et al.*, 1978; Furuya and Marumo, 1983; Joint and Pomroy, 1983; Li *et al.*, 1983; Platt *et al.*, 1983; Takahashi and Bienfang, 1983; Takahashi and Hori, 1984; Takahashi *et al.*, 1985; Glover *et al.*, 1985a, b; Smith *et al.*, 1985; Stockner, 1988). It has been considered that the microzooplankton, including protozoa, can feed directly on such small primary producers as picophytoplankton, on which large zooplankton can not graze. In turn, they may be preyed upon by omnivorous and carnivorous zooplankton (Beers and Stewart, 1967; Parsons and LeBrasseur, 1970; Heinbokel and Beers, 1979; Burkill *et al.*, 1987; Sanders, 1987). In order to fully understand the dynamics of the lower trophic levels in marine ecosystems, it is essential to know the biomass and feeding rates of zooplankton, including microzooplankton.

The major factors affecting phytoplankton standing stock in the euphotic zone are grazing by zooplankton and sinking (Laws *et al.*, 1988). If loss due to sinking is known, total grazing by zooplankton can be calculated. In recent studies, vertical transport of organic matter was estimated using samples collected with sediment traps. From this, phytoplankton sinking loss can be easily estimated.

Although ^{14}C methods (Steemann Nielsen, 1952) have provided accurate data for the estimation of organic carbon production rate by phytoplankton, there is no conventional method to estimate the production or grazing rates of zooplankton communities. In order to do so several assumptions have to be made. One of the methods to estimate the zooplankton community production is by adopting the Ikeda-Motoda method (Ikeda and Motoda, 1978), which is based on the respiration rate of the animal (Ikeda, 1974).

Ikeda (1974), using various zooplankton collected from tropical, subtropical, temperate and boreal waters, measured the rates of respiration and ammonia-nitrogen excretion. He observed that these rates were correlated to body weight and habitat temperature. Based on the observed relationships, Ikeda and Motoda (1978) formulated an equation to estimate the food requirement and production by herbivorous zooplankton. Although the weight specific metabolic rate of protozoans has been considered to be one order of magnitude lower than that of the metazoans, Taniguchi (1985) asserted that the equation of Ikeda and Motoda can be applied to estimate protozooplankton production. This has resulted from recent studies (Klekowski, 1981; Fenchel and Finlay, 1983; Kawakami *et al.*, 1985) which revealed substantially high respiration rates by protozoans. Using this method, zooplankton production rate was estimated in several sea areas (Taniguchi, 1977a; Ikeda and Motoda, 1978; Joh and Uno, 1983; Uye *et al.*, 1986). However, there is no study to identify the organic carbon flow from primary to secondary producers.

The purpose of this study is to investigate the transport of organic matter from

primary to secondary producers and from the productive to the non-productive zones. In the following chapters, seasonal changes in the size compositions of the phyto- and zooplankton communities, and the phytoplankton sedimentation in the temperate neritic waters of Funka Bay, southern Hokkaido, Japan, will be discussed. With these results, problems in estimating the grazing rates of the zooplankton communities will be pointed out (Chapter III). Considering the problems, methods to estimate the actual grazing rates on phytoplankton will be examined (Chapter IV). Regional variations of phytoplankton communities and zooplankton communities will be investigated (Chapter V). Using a realistic method, seasonal and regional variations in grazing rate will be estimated in Funka Bay and in the western North Pacific Ocean, respectively (Chapter VI). If phytoplankton is grazed as fast as it is produced as mentioned by Steele (1974), we have to evaluate the contribution of copepods, microzooplankton, and others to the total grazing activity. In this study, flow of organic carbon through the lower trophic levels in marine ecosystems will be dealt with temporally and spatially. I believe that these results will provide the necessary information for both marine oceanographers and fisheries scientists in their quest to understand the food dynamics not only of lower trophic levels but also of higher trophic levels.

II. Materials and Methods

II-1. Samplings

II-1-i. Temporal investigations in Funka Bay

Funka Bay is located in the southwestern region of Hokkaido, Japan. The entrance of the bay opens onto the North Pacific Ocean (Fig. 1). Oceanographic observations and plankton samplings were carried out during day light hours (11 : 00 to 15 : 00) at two stations in Funka Bay, from April 1984 to May 1985. Station 9 (water depth of 56m) was located at the west of the port of Muroran and Station 30 (water depth of 92 m) was in the central part of the bay. During the spring phytoplankton bloom of 1986 (from February 27 to April 30), further samplings were done at two or three week intervals, at Station 30. Moreover, a year round survey was conducted at Station 30, in 1988. In addition to these, a few samples which had been collected at this station in November and December of 1986 and March 1987 were also dealt with. Water samples were collected using a Van Dorn sampler at about 10m intervals between the surface and bottom. Vertical towing of a NORPAC standard net (mesh aperture 0.33 mm) was conducted from 30 m and 74 m depth to the surface. In the samplings of 1986, a calibrated flowmeter was used. In all other cases, as a flowmeter was not used, filtering efficiency was assumed to be 100%.

A sediment trap system [as described by Maita *et al.* (1986)] was moored at a depth of 74 m at Station 30, for two week intervals, during the summer season (August 21-October 1, 1984) and winter season (November 15-December 3, 1984 and February 1-March 15, and May 10-23, 1985). During the spring phytoplankton bloom period of 1986, the sediment traps were also deployed at 30 m and 74 m depths at Station 30. This system was composed of eight cylindrical traps, of which four were covered with screen while the remaining four were left open. Antiseptic

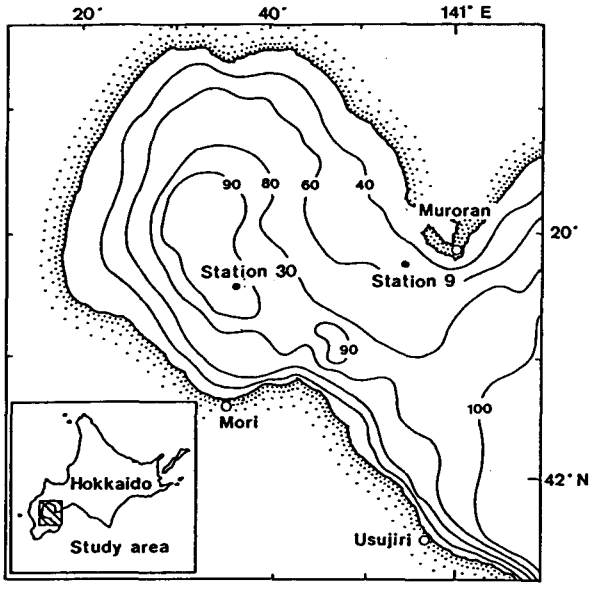


Fig. 1. Location of the sampling Stations in Funka Bay, southwestern Hokkaido, Japan. Station 9: 42°17.6'N, 140°54.0'E. Station 30: 42°16.2'N, 140°36.0'E.

treatment of 1.5 M NaCl with 1% formalin was applied to the screened traps and the open traps. In this study, subsamples from one of the treated open cylinders were used.

II-1-ii. Spatial investigations in the western North Pacific Ocean

Plankton samples were collected from the western North Pacific Ocean during the Cruise KH-85-2 of the R/V Hakuho Maru from April 12 to May 15, 1985. Fig. 2 shows the sampling stations. At Stations B, C, D, E, and F (open circles), water samples were taken from 10 different depths between the surface and 200 m depth, and zooplankton were collected by vertical towing of a NORPAC standard net (mesh aperture 0.33 mm) from 200 m depth to the surface. Because a flowmeter was not used, filtering efficiency was assumed to be 100%. At Stations 1-64 (closed circles), surface water samples were collected from a sea water outlet on the deck every 4 h during the cruise. The first and second leg of the cruise was from Tokyo to Kushiro and from Kushiro to Tokyo, respectively. Duplicate samplings were conducted in the area surrounded by a rectangle.

II-2. Environmental parameters

In 1984, 1985, and 1986, seawater temperature was measured using a reversing thermometer equipped on Nansen sampler. Salinity was determined with an inductive salinometer (Model 601 MKIII). While vertical profiles of water temperature and salinity of 1988 were obtained using a CTD system. Hydrographic data of the western North Pacific Ocean was used from the Preliminary Report of the Hakuho Maru Cruises KH-83-3 and KH-85-2 (Hattori and Nakai, 1986).

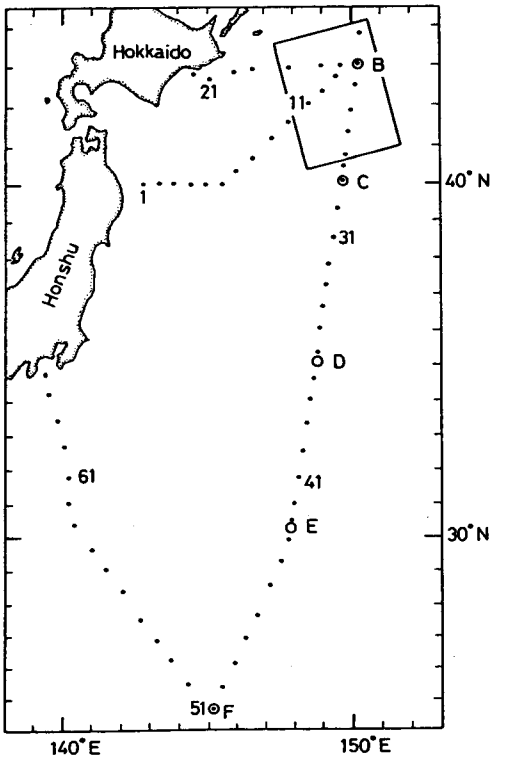


Fig. 2. Sampling stations in the western North Pacific Ocean during the Cruise KH-85-2 of the R/V Hakuho Maru. At Stations B, C, D, E, and F (open circles), vertical series of seawater was collected. At Stations 1–64 (closed circles), only surface seawater was taken. At some stations surrounded by a rectangular duplicate sampling was carried out in the cruise of the first leg (April 16–24) and the second leg (May 1–2).

The seawater samples (100 mL) were frozen and later analyzed for nutrient concentration using an autoanalyzer (Technicon II) following the methods of Strickland and Parsons (1972).

The total amount of particulate organic carbon (POC) in one liter of seawater sample was determined using a Hitachi 026 CHN analyzer (Parsons *et al.*, 1984).

II-3. Autotrophic organisms

II-3-i. Enumeration of phytoplankton

One liter of seawater sample was fixed with Lugol's solution (3%, v/v) for microscopic observations. After three days of settling, these samples were reduced to 20 mL by removal of excess water by careful use of a siphon. An aliquot of 1/200 of the concentrate was examined using a light microscope. Phytoplankters were identified at the species level when possible, otherwise they were grouped. It should be noted that cell densities of small sized phytoplankters ($<10\,\mu$m) may have been underestimated using this present procedure, because of an outflow or overlooking of cells.

Aliquots of water samples (5–100 mL) were filtered through Millipore HA filters (pore size, 0.45 μm; diameter, 25 mm) under low vacuum. The filters were observed immediately under a Nikon Optiphot XF microscope equipped with an epifluorescent illuminator system (Nikon EDF, 100 W super pressure mercury lamp)

and a Nikon filter cassette B (blue excitation; excitor 420-490 nm, dichroic mirror 510 nm, barrier 520 nm).

According to Murphy and Haugen (1985), phycoerythrin-rich cyanobacteria (PEC) fluoresce bright yellow and the other picophytoplankton (OPP) fluoresce deep red when observed under an American Optical Fluorcluster No. 2072 (blue excitation; excitor KV418+BG12, dichroic mirror 500 nm, barrier OG515). Hence, bright yellow cells were considered as PEC, while red ones were counted as OPP. In principle, members of other phycoerythrin containing organisms (e.g. Rhodophyta and Cryptophyta) might interfere when attempting to count PEC, but in practice differences in size, form and chloroplast morphology permit the unambiguous identification and enumeration of PEC (Waterbury *et al.*, 1986).

Cells were counted at a magnification of 200× or 400× after their presence were confirmed at 1,000× magnification. About 200-500 cells occurring in more than ten random fields were counted per filter for the samples in the upper 30 m. Only cells smaller than 5 μm were counted.

II-3-ii. Primary production

Phytoplankton organic carbon production was estimated based on the ^{14}C uptake rate measurement (Steemann Nielsen, 1952), using sea water from 100, 30, 15, and 2% light depths calculated from the Secchi disk transparency (Idso and Gilbert, 1974). These sea water samples (100 mL) were prefiltered through an 0.33 mm mesh sized screen and were incubated with 5 μCi of radio isotope ($NaH\ ^{14}CO_3$) in a tank at the laboratory. Three light and aluminum foil covered dark two bottles were exposed to light intensities (regulated using neutral filters) similar to that in the sampling depth. After three hours incubation at the *in situ* surface water temperature under a light intensity of ($240\pm10\ \mu E \cdot m^{-2} \cdot s^{-1}$), the phytoplankton were filtered onto a Millipore HA filter (pore size, 0.45 μm). All the filters were fumed with HCl vapor and stored in a vacuum desiccator until measurement of radioactivity using a liquid scintillation counter (Aloka Model LSC 673). Daily primary production was estimated based on the hourly ^{14}C uptake rates at each light level and the length of day light (from dawn till dusk) during a sampling date.

Seawater samples from the 100% and 60% light depth were used to determine the size-fractionated primary productivity. One light bottle and one dark bottle were prepared for the determinations. The 600 ml of water sample was poured into each glass bottle. Incubation was done in the same method described above. After incubation, each of the two subsamples (250 mL) was sequentially filtered through a 10 μm pore size Nuclepore filter, and through filters of 2, 0.45, and 0.2 μm pore size. The 0.2-0.45 μm fraction was subsequently combined into the 0.2-2 μm fraction due to low radioactivity of that fraction.

Between April and August of 1984, primary production per water column was estimated from the data of a size-fractionated ^{14}C uptake rate for the surface water with the assumption that the surface ^{14}C uptake rate decreases linearly with depth, becoming negligible at the 2% light depth (Idso and Gilbert, 1974).

II-3-iii. Chlorophyll *a* concentration

Seawater (0.5 or 1.0 L) was filtered with a Whatman GF/C glass fiber filter. Chlorophyll *a* pigment was extracted using 90% acetone and determined by fluorometry (Parsons *et al.*, 1984).

Using the water samples from 100% and 60% light depths in Funka Bay, chlorophyll *a* concentrations were size-fractionated using the same procedures used for the size-fractionated primary production. On the other hand, all water samples collected from the western North Pacific Ocean were filtered using 10, 2 and 0.2 μm Nuclepore filters on ship. These were kept in the freezer (-20°C) until the determination of chlorophyll *a* concentration.

II-4. Heterotrophic organisms

II-4-i. Zooplankton communities

Zooplankton collected by a NORPAC net were fixed with neutral formalin (5%, v/v) and from here will be referred to as net plankton. The wet weight of net plankton was measured. Copepods smaller than 200 μm in body width were excluded from this classification. Among the net plankton, copepods (adult and copepodite stage) larger than 200 μm in body width were classified as large copepods.

Seawater (10 or 20 L) was filtered through a screen with a mesh aperture of 40 μm. The zooplankton collected on this screen and in 1.0 L of filtrate were fixed with Lugol's solution (3–5%, v/v). Among these zooplankton, copepods smaller than 200 μm in body width were defined as small copepods, and others were classified as microzooplankton.

Zooplankton biomass was estimated based on 1/2–1/20 subsamples. Sizes of the major body parts were measured using an ocular micrometer fitted into a light microscope. Since intraspecific size variation of abundant species was small, the average size (based on 20 organisms) was used for the succeeding calculations. For rare species, body length and width of all individuals counted were measured.

The volume of zooplankton other than copepods was calculated based on the assumption that the body shape conforms to an ellipsoid. It was converted into dry weight under the most commonly used assumptions for zooplankton, that is, 1.0 for specific gravity and 0.1 for the dry to wet weight ratio. For tintinnids, the animal volume was assumed to be equal to half the lorica volume with a specific gravity of 1.0 and the dry weight was 20% of the wet weight (Capriulo and Carpenter, 1983). The conversion factor for lorica volume to dry weight (0.1) was the same as that of the body volume to dry weight of other zooplankton. Dry weight of copepods was calculated using the equation of dry weight against length for total copepods provided by Uye (1982). The zooplankton dry weight was further converted to organic carbon, assuming that the carbon content per dry weight is 40% (Ikeda, 1974; Uye, 1982).

II-4-ii. Phagotrophic dinoflagellates

Using 1/10–1/20 subsamples from the same seawater samples used in the enumeration of phytoplankton, phagotrophic dinoflagellate density was estimated following the same procedure as in the phytoplankton cell enumeration.

II-5. Vertical flux of organic matters

Organic carbon fluxes of intact phytoplankton cells, intact zooplankton bodies and zooplankton fecal pellets were estimated using the sediment trap samples.

Diatoms with visible protoplasm were counted as intact cells in 1/200 subsam-

ples using a light microscope. Considering the negligible sinking velocity of small cells less than 2 or 10 μm (Takahashi and Bienfang, 1983), vertical flux of diatoms well represents the total phytoplankton flux, because the phytoplankton community larger than 10 μm is accounted for by diatoms as shown later. The volume of zooplankton, excluding large-size organisms which are considered as swimmers (e.g. Knauer *et al.*, 1979), was calculated based on measurements of body length and width observed in 1/20-1/200 subsamples. Organic carbon was estimated as described earlier for zooplankton biomass.

Volume of fecal pellets was also estimated based on length and width measurements. Total volume of fecal pellets was calculated using the mean volume of more than 100 pellets and the total number. Pellet volume was converted to organic carbon; assuming specific gravity of 1.22 (Wiebe *et al.*, 1976), dry weight to wet weight ratio of 0.11 and carbon content of 0.2 (Johannes and Satomi, 1966).

II-6. Calculations

II-6-i. Food requirement

Respiration rates were calculated based on body weight and water temperature using Ikeda's formula (Ikeda, 1974):

$$R = aBW^b, \quad 1$$

where R is respiration rate (μL $O_2 \cdot animal^{-1} \cdot h^{-1}$), BW is body dry weight (mg$\cdot$animal^{-1}). Constants, a and b, are given as a function of habitat temperature (°C):

$$\log_{10} a = 0.02538T - 0.1259, \quad 2$$
$$b = -0.01089T + 0.8918. \quad 3$$

The amount of oxygen respired was converted to carbon (R′), adopting a respiratory quotient of 0.8 (protein metabolism). Assuming an assimilation efficiency of 70% and a gross growth efficiency of 30% (Ikeda and Motoda, 1978), food requirement (FR, $gC \cdot m^{-2} \cdot day^{-1}$) and production rates (ZP, $gC \cdot m^{-2} \cdot day^{-1}$) were estimated using the formula of Ikeda and Motoda (1978):

$$FR = 100R'/(70-30) = 2.5R', \quad 4$$
$$ZP = 30R'/(70-30) = 0.75R'. \quad 5$$

II-6-ii. Food consumption

Phytoplankton carbon consumed by zooplankton (FC) can be estimated by the following equation (Huntley and Boyd, 1984; Frost, 1987);

$$FC = PB \cdot CR, \quad 6$$

where PB is the amount of available phytoplankton carbon (=phytoplankton biomass) and CR is the clearance rate of a zooplankter. If CR for each animal is known, the total zooplankton food consumption can be calculated by summing up the FC of each zooplankter.

Huntley and Boyd (1984) demonstrated that a positive significant relationship exists between BW (=body weight) and CR of zooplankters. Their analyses, however, were conducted only for net zooplankton. The relationship between BW and CR of zooplankters including microzooplankton from published data (Table 1)

Table 1. Summary of clearance rate data.

Species	Temperature (°C)	Reference
Protozoa		
Favella taraikaensis	17	Taniguchi & Kawakami 1985
Favella sp.	15	Stoecker 1984
Helicostomella subulata	17.5-22	Capriulo 1982
Stenosemella oliva	22	Capriulo 1982
Stenosemella ventricosa	12	Rassoulzadegan & Etienne 1981
Tintinnidium fluvatile	16.9-19	Capriulo 1982
Tintinnopsis acuminata	19	Capriulo 1982
Tintinnopsis acuminata	15-25	Verity 1985
Tintinnopsis cf. *acuminata*	18	Heinbokel 1978a
Tintinnopsis parva	17.5	Capriulo 1982
Tintinnopsis vasculum	2	Capriulo 1982
Tintinnopsis vasculum	5-15	Verity 1985
Metazoa		
Acartia clausi	2-15	Anraku 1964
Acartia tonsa	8	Anraku 1964
Neocalanus plumchrus	11.5	Frost et al. 1983
Calanus finmarchicus	2-15	Anraku 1964
Calanus helgolandicus		
nauplius IV-VI	15	Paffenhöfer 1971
copepodite I-V	15	Paffenhöfer 1971
adults	15	Paffenhöfer 1971
Calanus pacificus	12	Runge 1980
Pseudocalanus minutus	2-15	Anraku 1964
Pseudocalanus sp.	12	Frost 1980

is analyzed. The CR values are normalized assuming $Q_{10}=2$ (e.g. Gilbert and Bogdan, 1984) and plotted in Fig. 3, since the original experiments were conducted under various water temperature conditions (2-25°C) (Table 1). The slope and intercept of the regression line calculated (Table 2) are comparable with the range by Huntley and Boyd (1984), who obtained 0.734-1.092 for slope and 0.561-2.589 for intercept. The 95% confidence limits of the slope and intercept of the regression line were used for upper and lower limits of CR calculation. The same Q_{10} value was further assumed to calculate the CR values applicable to the field temperature conditions. Ikeda (1974) established similar Q_{10} values for the zooplankton respiration and ammonia-nitrogen excretion rates. The relationship between BW and CR showed a positive correlation with a slope of less than 1.0 ($p<0.01$), that is, the clearance rate per unit body weight decreases with an increase in body weight

Table 2. Summary of regression statistics for analysis of relationship of Log CR (clearance rate, mL•animal^{-1}•h^{-1}) on Log BW (dry weight, mg dry weight•animal^{-1}).

Equation of the regression line $\log CR = n \log BW + \log b$	Number of data	r^2	95% confidence limit on slope	95% confidence limit on intercept
$\log CR = 0.738 \log BW + 1.534$	87	0.901	± 0.050	± 0.077

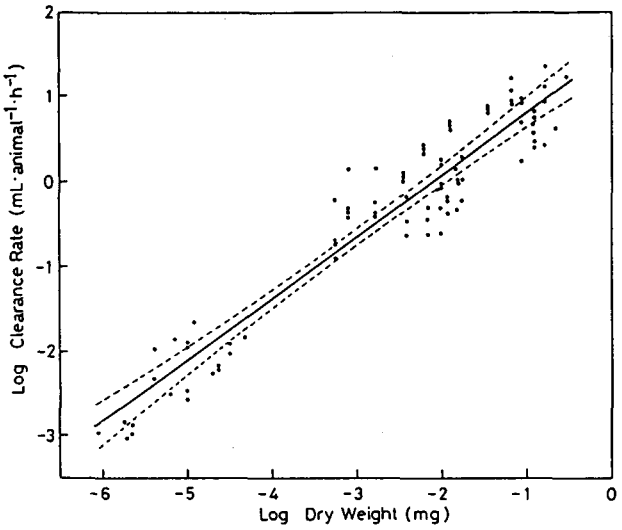


Fig. 3. Relationship between body weight and clearance rate of several zooplankters. Broken lines indicate 95% confidence limits of the regression equation. Species, temperature of experiment, and source of measurement are given in Table 1. Results of the regression analysis are shown in Table 2.

(Capriulo, 1982; Huntley and Boyd, 1984). This trend is consistent with the results of Ikeda (1974) which shows that the weight specific respiration rate decreases with increasing body weight.

Heinbokel (1978a) observed that the ingestion rate of tintinnids remains constant at a food concentration of ca. 100 μg C•L^{-1} and decreases thereafter. Hence, we considered that the CR of ciliates (tintinnids and naked ciliates) decreases at phytoplankton carbon concentrations of higher than 100 μg C•L^{-1}.

Grazing activity of phagotrophic dinoflagellates was estimated using equation 6. Clearance rates of armored dinoflagellates were used, i.e., 0.5–28.3 μL•cell•h^{-1} (Lessard and Swift, 1985). Because the clearance rate range is wide, we used the 95% confidence interval around the mean clearance rate (3.3 ± 1.1 μL•cell^{-1}•h^{-1}) for the minimum and maximum estimations.

II-6-iii. Fecal matter production

Fecal matter production rates were estimated based on both food requirement

(FR) and consumption (FC) assuming an assimilation efficiency of 70% (Ikeda and Motoda, 1978), i.e., the fecal matter production rate (FPP) was obtained by multiplying food requirement or consumption rate by 0.3 (=1−0.7) as follows (Sasaki *et al.*, 1988),

$$FPP = 0.3 \cdot FR \text{ or } FC. \qquad 7$$

III. Seasonal Changes in Plankton Community Structure in Funka Bay

It is known that the bay water is exchanged seasonally between the Oyashio Water originating from the subarctic waters and the Tsugaru Warm Water orginating from the subtropical waters (Ohtani and Kido, 1980). Such changes in water masses affects the plankton community structure in the bay (Nakata, 1982; Hirakawa, 1983; Dohi, 1982). This chapter aims to reveal the major primary producer and grazer, and to show the fate of primary production.

III-1. *Results*

III-1-i. Physical and chemical conditions

Temporal temperature profiles from April 1984 to May 1985 at Stations 9 and 30 of Funka Bay are shown in Fig. 4. Surface water temperature increased from April. The water column thermally stratified between April and September at both stations. A rapid increase in water temperature in the 20–60 m layer from August to September was clearly observed at Station 30. This can be attributed to the inflow of the Tsugaru warm water. Vertical mixing began in November with the onset of cool winds, and a thermally homogeneous water was observed from the surface to bottom until February.

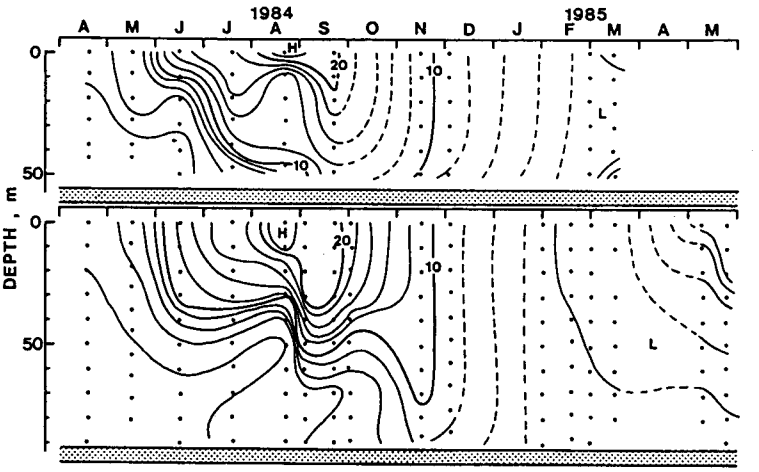


Fig. 4. Vertical profiles of water temperature (°C) at Station 9 (top) and Station 30 (bottom) observed from April 1984 to May 1985.

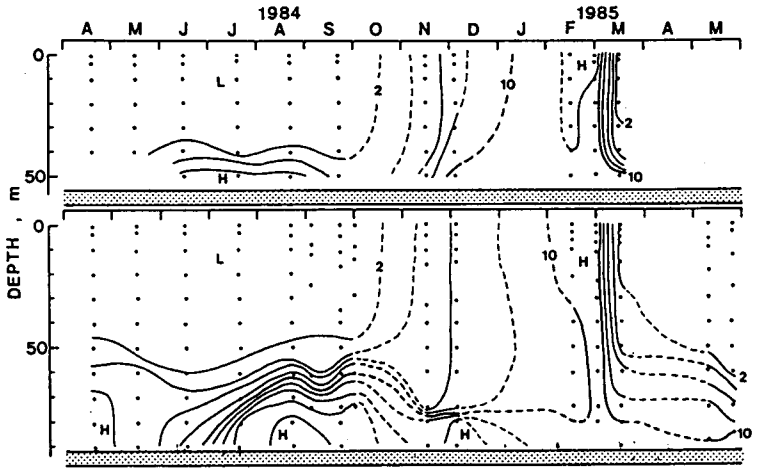


Fig. 5. Vertical profiles of nitrate concentration (μM) at Station 9 (top) and Station 30 (bottom) from April 1984 to May 1985.

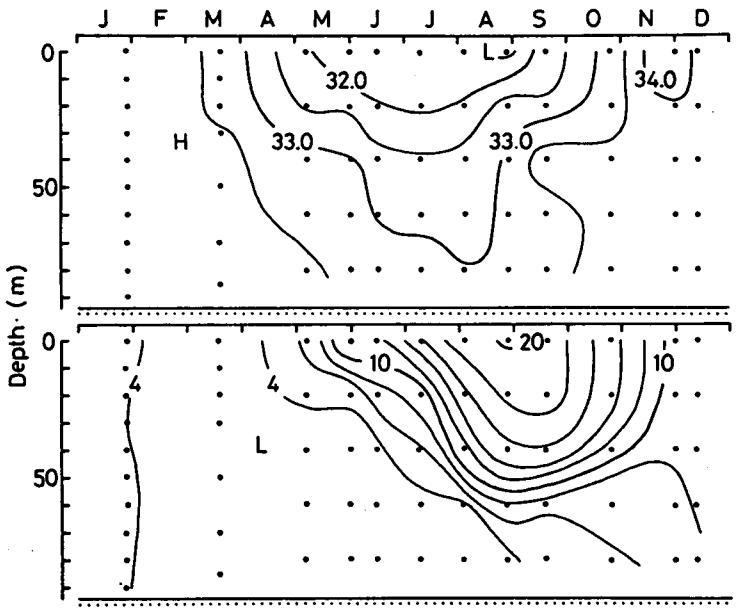


Fig. 6. Vertical profiles of salinity (top) and water temperature (C) (bottom) observed at Station 30 in 1988.

Corresponding to the seasonal changes in the physical structure of water column, nitrate concentration varied seasonally (Fig. 5). During the period from April to September, nitrate concentrations in the upper layer at Stations 9 (40 m) and 30 (50 m) were less than 2 μM and were nearly zero above 30 m, resulting from the thermal stratification of the water column. The concentration increased from 2 to 10 μM during October to January, reflecting the vertical mixing of the water column, and decreased rapidly by mid March, suggesting a spring phytoplankton bloom.

Seasonal vertical profiles of salinity and temperature in 1988 are shown in Fig. 6. Salinity was higher than 33.3 throughout the water column in March and those in the upper 20 m became lower than 32.5 in May, implying that subarctic coastal Oyashio water flows into the bay between March and May. On the other hand, high salinity water of 33.8 was observed again at 40 m in September, indicating the inflow of subtropical Tsugaru warm water. Water column was thermally stratified between May and October, and the stratification was disturbed by the end of November. A thermally homogenous water column was observed between January and March, and during December.

Such seasonal changes in the water masses and physical structure of the water column in 1984, 1985, and 1988 are a regular phenomenon of Funka Bay as shown by Ohtani and Kido (1980).

III-1-ii. Phytoplankton communities

Seasonal changes of total chlorophyll *a* standing stock in the upper 30 m in 1984 and 1985 are shown in Fig. 7. Chlorophyll *a* standing stock in the upper 30 m at

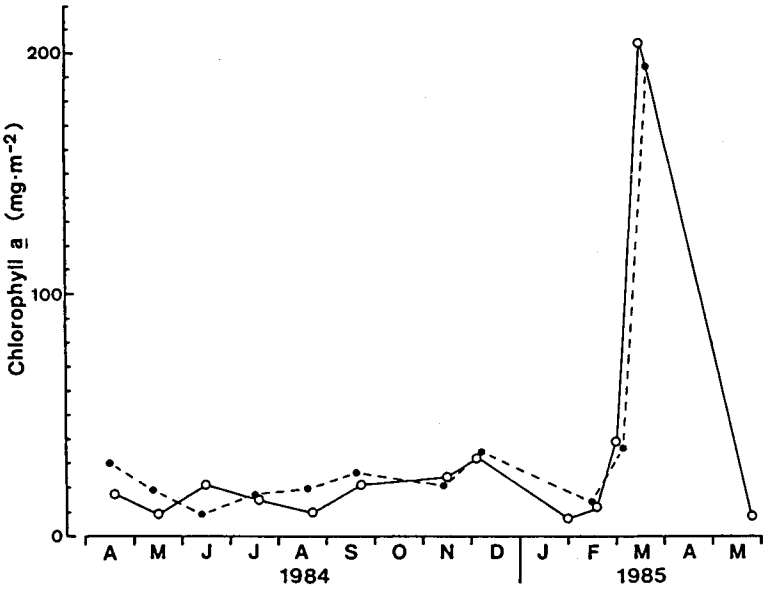


Fig. 7. Monthly changes in chlorophyll *a* integrated over the upper 30 m from April 1984 to May 1985. Closed circles: Station 9, open circles: Station 30.

both stations fluctuated from 9 to 30 $mg \cdot m^{-2}$ between April and November. The standing stock slightly increased in December, and decreased until the middle of February. It reached approximately 200 $mg \cdot m^{-2}$, the annual maximum, in mid-March. The large increase in chlorophyll *a* standing stock clearly indicates the spring phytoplankton bloom.

Seasonal change of chlorophyll *a* concentrations in 1988 is shown vertically in Fig. 8. The maximum concentration of 4.3 $\mu g \cdot L^{-1}$ was obtained at 10 m depth in mid March, which indicates the spring outburst of phytoplankton during this year. The concentration (mean+SD) in the upper 30 m at this time (3.76 ± 0.39 $\mu g \cdot L^{-1}$, $n=4$) was significantly higher than that in the upper 40 m observed between May and November (0.65 ± 0.36 $\mu g \cdot L^{-1}$, $n=27$) ($p<0.001$). During the latter period, the mean concentration below 60 m (0.11 ± 0.09 $\mu g \cdot L^{-1}$, $n=18$) was significantly lower than that of the upper 30 m ($p<0.001$). Low concentration in the deep layer may result from insufficient light intensity. Then, it was considered that the variations of chlorophyll *a* concentration in the upper 30 m well represented those of live phytoplankton biomass in the water column.

Total chlorophyll *a* standing stock showed considerable seasonal change, which was attributed to variations of different size fractions (Fig. 9). The high chlorophyll *a* concentrations were observed from late February to mid March, 1985, at both stations. During the blooming period, nearly 90% of the total chlorophyll *a* was accounted for by the greater than 10 μm fraction. On the other hand, the total chlorophyll *a* concentrations were low during summer in 1984, and the percentage contribution of the greater than 10 μm size fraction was also considerably lower than that during the spring bloom period. The percentage contribution of the less than 2 μm size fraction was 28-57% at Station 30. Chlorophyll *a* concentrations in the greater than 10 μm and 2-10 μm size fractions showed some differences between stations, whereas that of the less than 2 μm fraction showed minor local differences.

As well as chlorophyll *a* concentration, at Station 30, a very large total uptake rate was found on March 15, 1985 (Fig. 10). This indicated that the phytoplankton bloom had begun. However, the same trend was not observed at Station 9, even though nitrate concentration decreased sharply from March 1 to 16, 1985 along with

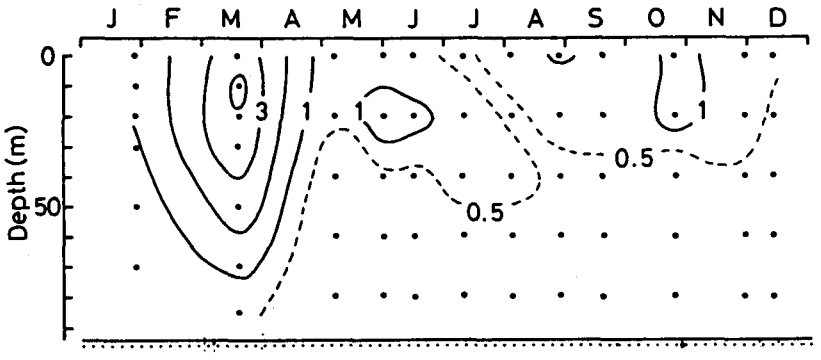


Fig. 8. Vertical profile of chlorophyll *a* concentration ($\mu g \cdot L^{-1}$) observed at Station 30 in 1988.

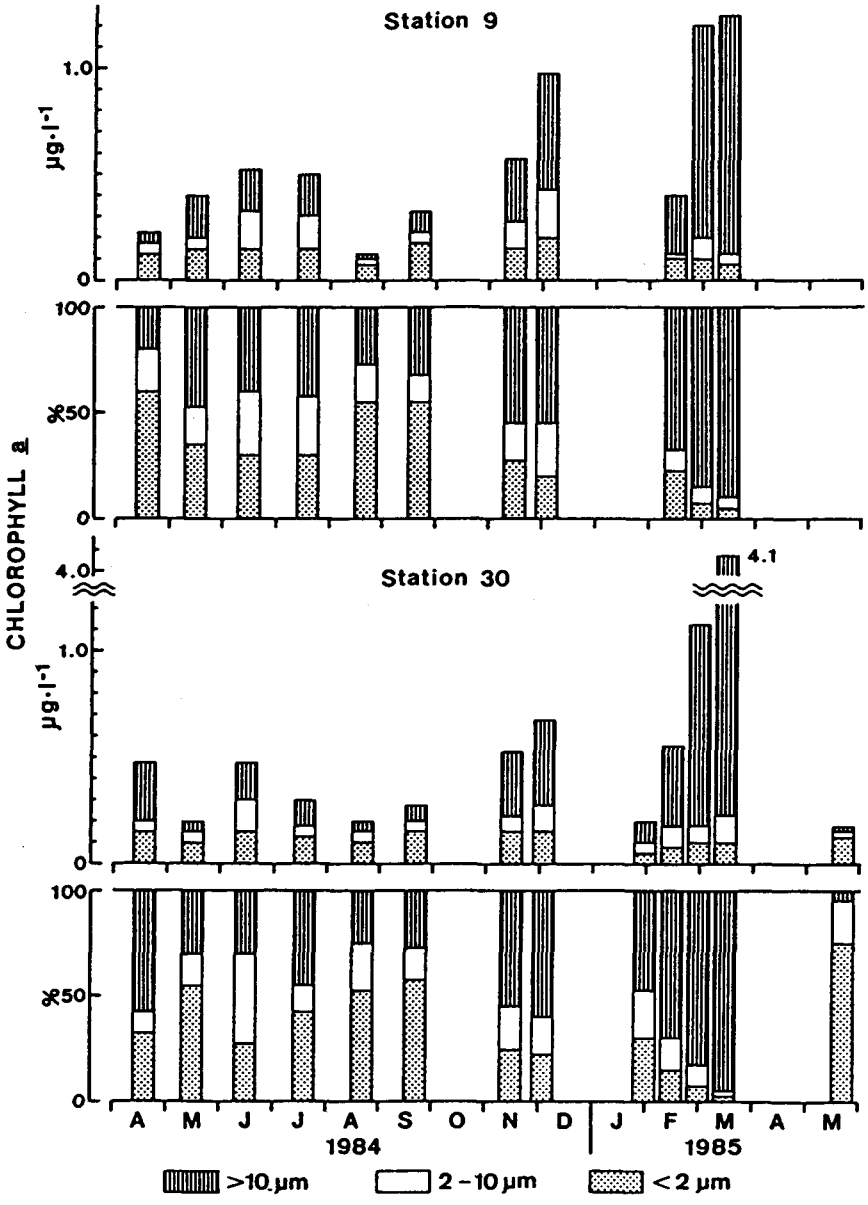


Fig. 9. Monthly changes in chlorophyll *a* concentrations of different size fractions and the relative composition at Station 9 (top) and Station 30 (bottom) from April 1984 to May 1985. Data are simple average of 100% and 60% light depth.

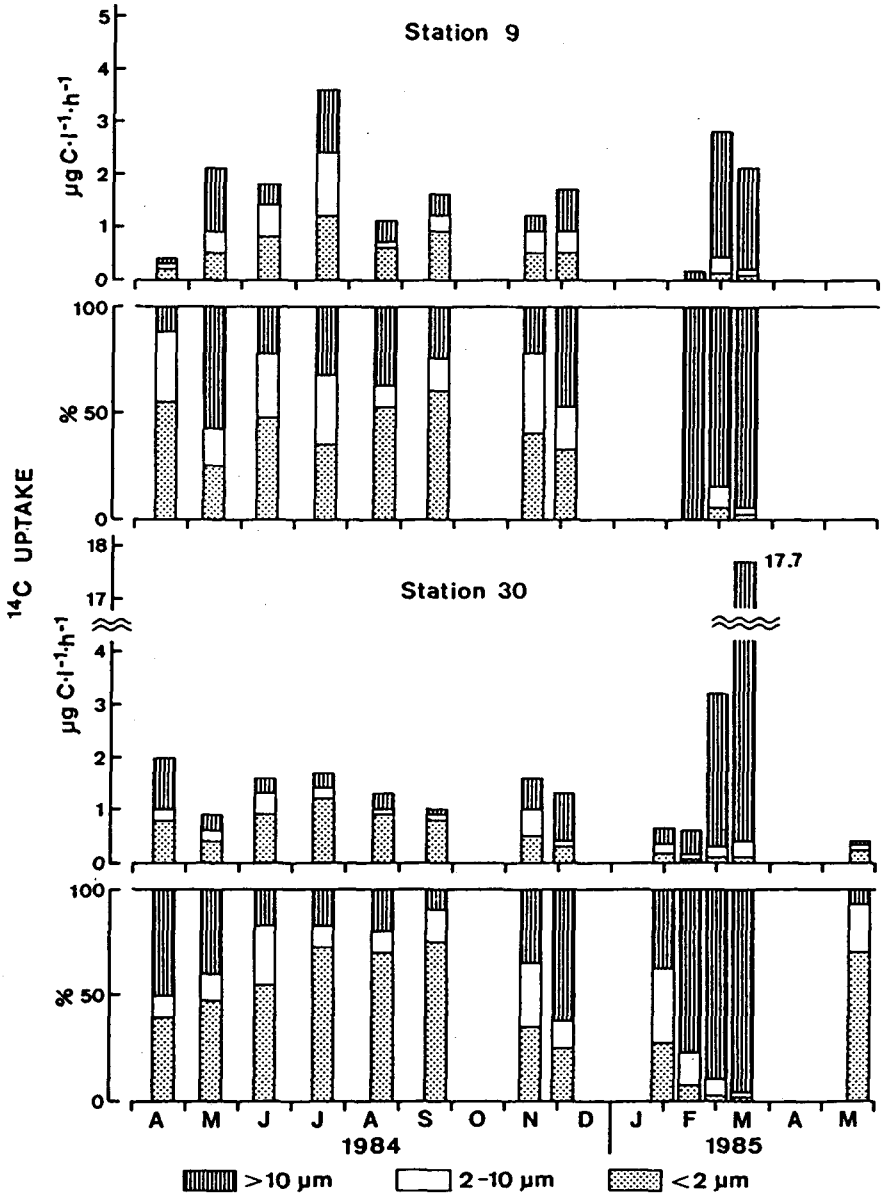


Fig. 10. Monthly changes in ^{14}C uptake rates of different size fractions and the relative composition at Station 9 (top) and Station 30 (bottom) from April 1984 to May 1985. Data are simple average of 100% and 60% light depth.

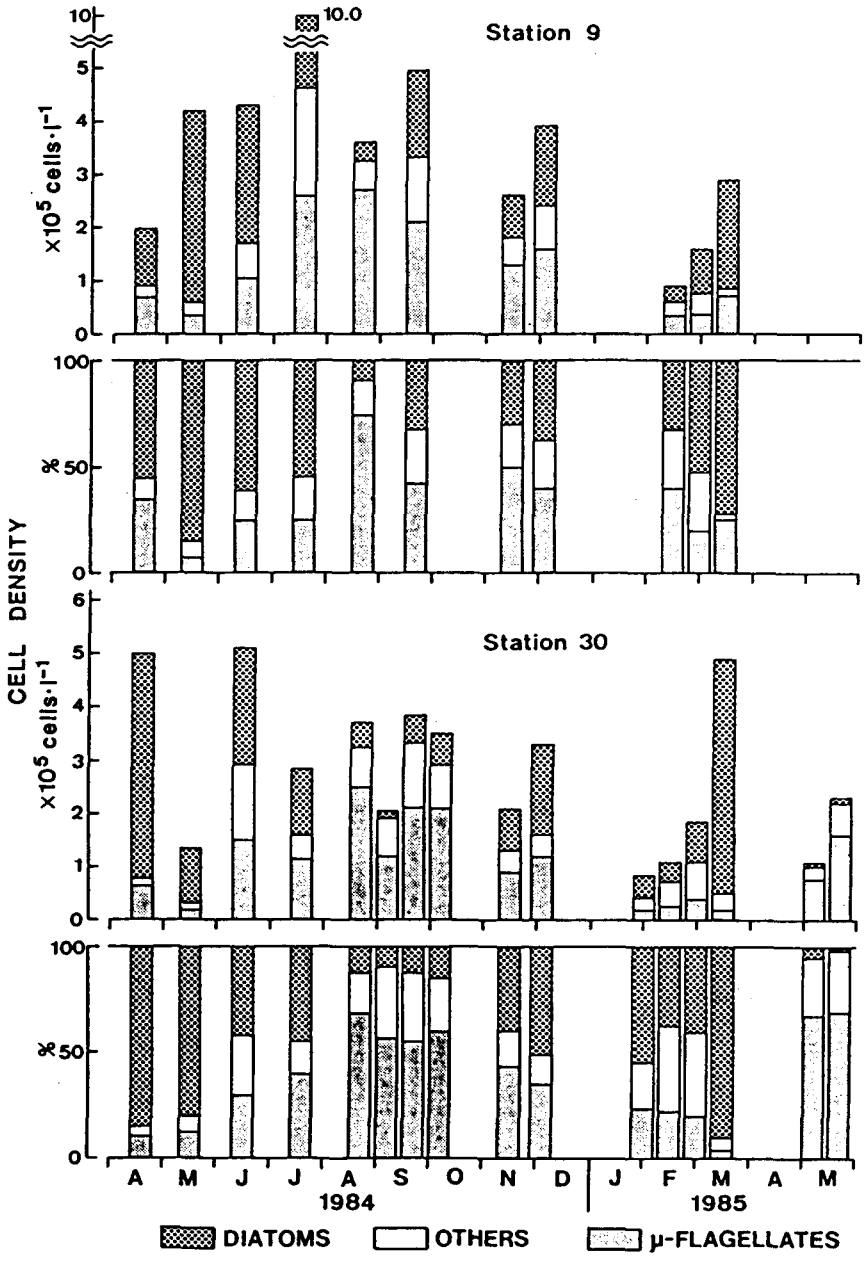


Fig. 11. Monthly changes in phytoplankton cell density and the relative abundance at Station 9 (top) and Station 30 (bottom) from April 1984 to May 1985. Data are simple average of 100% and 60% light depth.

an indication of a phytoplankton bloom occurring in the integrated chlorophyll *a* data. During the blooming period at both stations, the size fraction greater than 10 μm accounted for more than 80% of the total ^{14}C uptake (Fig. 10). The dominance of this large size fraction started in November, when vertical mixing of the water column began and nutrient concentrations increased. When the water column was stratified during the summer, the ^{14}C uptake rate for the size fraction of less than 2 μm increased to 25–59% (45% average) at Station 9 and 40–75% (60% average) at Station 30. Some differences in the ^{14}C uptake rate were observed between the stations. At Station 9, the large size fraction still had high uptake rates during May and July, however no corresponding trend was observed at Station 30. It became obvious that the major difference in the total ^{14}C uptake rate between the stations was not due to differences in uptake of the smallest fraction, but was due to that of the large fraction as same as the size-fractionated chlorophyll *a* concentration.

During the spring phytoplankton bloom, diatoms were abundant (2.1×10^5 cells$\cdot L^{-1}$ at Station 9; 4.4×10^5 cells$\cdot L^{-1}$ at Station 30) (Fig. 11). The dominant species during the blooming period was the large diatom, *Thalassiosira angustelineata*, having a frustle diameter of greater than 10 μm. Total cell density at Station 9 was about four times greater than that at Station 30 during May and July when some differences between stations were noted in size-fractionated chlorophyll *a* concentration and ^{14}C uptake rate. This was due to the abundance of *Chaetoceros compressum* during May, and *Skeletonema costatum* and *Leptocylindrus minimus* in July.

Although micro-flagellates were dominant during summer being most abundant in August (2.7×10^5 cells$\cdot L^{-1}$ at Station 9; 2.5×10^5 cells$\cdot L^{-1}$ at Station 30) (Fig. 11), these densities may be underestimated for picophytoplankton as mentioned in the Materials and Methods section. Indeed, three orders of magnitudes with higher densities than microflagellate densities were obtained, with the use of a epifluorescence microscope (Fig. 12). At Station 30 in 1988, phycoerythrin-rich cyanobacteria (PEC) cell density was high in the upper 20 m from July to October ($>10^8$ cells$\cdot L^{-1}$), and other picophytoplankton (OPP) were abundant in the upper 20 or 40 m from May to October ($>10^7$ cells$\cdot L^{-1}$) except at the beginning of August. In spring and winter when the water column was vertically homogenous, the picophytoplankton populations were distributed uniformly throughout the water column. In the upper 30 m, the PEC density varied from 2×10^4 to 4×10^8 cells$\cdot L^{-1}$ with an annual maximum in September, while the OPP density varied from 1×10^6 to 6×10^7 cells$\cdot L^{-1}$, with an annual maximum in August. From May 30 to July 7, a large increment in PEC cell density (ca. three orders of magnitude) was observed in the surface water. In a temporal scale, the picophytoplankton populations were predominated by OPP during winter to early summer (November to June) and by PEC during late summer (July to October). Abundance of cyanobacteria had been originally reported to reach 10^7–10^8 cells$\cdot L^{-1}$ in the surface waters of the Sargasso Sea (Johnson and Sieburth, 1979) and in the Arabian Sea (Waterbury *et al.*, 1979). The present results show that abundance of PEC in Funka Bay reaches 4×10^8 cells$\cdot L^{-1}$. The densities with the same orders of magnitude were observed commonly in neritic waters (e.g. Murphy and Haugen, 1985; Waterbury *et al.*, 1986; Shapiro and Haugen, 1988).

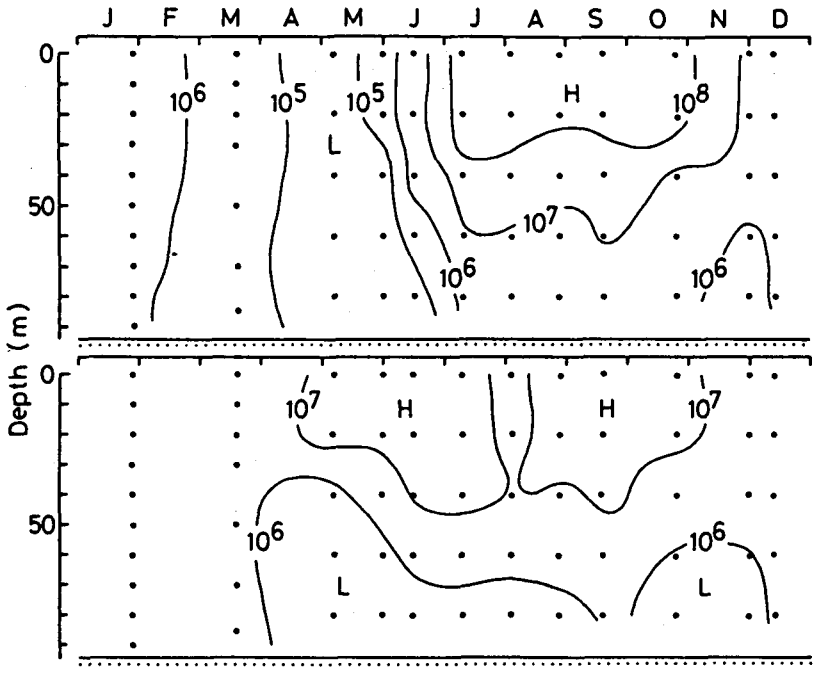


Fig. 12. Vertical profiles of cell density of the phycoerythrin-rich cyanobacteria (PEC, top) and other picophytoplankton (OPP, bottom) enumerated with a epifluorescence microscope at Station 30 in 1988 (cells•L^{-1}).

Both densities of PEC and OPP were low on March 17 when total chlorophyll *a* concentration reached the annual maximum (=spring phytoplankton bloom). Then, most of the total chlorophyll *a* concentration during spring bloom is accounted for by phytoplankters other than picophytoplankton. Cell density of PEC was high in summer, but low in winter and spring. This trend is similar to those reported for temperate waters (Murphy and Haugen, 1985; El Hag and Fogg, 1986; Joint *et al.*, 1986; Waterbury *et al.*, 1986). Density of PEC further decreased from 3×10^5–7×10^5 cells•L^{-1} on March 17 to 2×10^4 cells•L^{-1} on May 6, although water temperature increased. It is known that the exchange of water masses in Funka Bay from the stagnant subtropical water (so called winter Funka Bay water) to cold subarctic water (Oyashio Water) occurs in early spring (Ohtani and Kido, 1980). In 1988, the inflow of Oyashio water occurred between March 17 and May 6. According to Murphy and Haugen (1985), the cyanobacteria density decreases along a northerly directed latitude gradient, suggesting positive correlation to temperature. The low PEC density temporally observed in May in Funka Bay, therefore, was possibly affected by the intrusion of the cold Oyashio water.

Annual production in the surface water (simple average of the 100 and 60% light depths over the year) is summarized in Table 3. Since the ^{14}C uptake rate was not measured during the peak of the spring phytoplankton bloom at Station 9, the

annual average at this station may be underestimated. Hence, based on the data at Station 30, about half of the annual primary production in Funka Bay was accounted for by the larger than 10 μm size phytoplankters during the spring bloom. During this period, the major phytoplankton consisted of diatoms (e.g. *Thalassiosira anguste-lineata*). Since earlier studies (Nakata, 1982; Odate, 1987) have also shown that the phytoplankton bloom is basically an outburst of diatoms, it appears that the annual primary production in the bay is strongly affected by the spring bloom of diatoms.

During summer, when nutrients were low due to a fairly stable water column, the major primary producers were very small phytoplankters (<2 μm), and the percent contribution of picoplankton to the total primary production was 59% at Station 30, and 40% at Station 9 (Table 3). However, from November to April, during which nutrients in the top 30 m increased due to vertical mixing, chlorophyll *a* concentration or ^{14}C uptake rate of the less than 2 μm fraction decreased and that of the larger size fraction increased. This tendency for the smaller size fractions to

Table 3. Seasonal changes in size-fractionated primary production (g C·m^{-3}·season^{-1}) in the surface water at Stations 9 and 30 in Funka Bay. Percentages of the total production are shown in parentheses.

Season	Station	Primary production			
		0.2-2 μm	2-10 μm	>10 μm	Total
Summer					
Apr.-Nov. 212 days	9	2.1 (40%)	1.4 (26%)	1.8 (34%)	5.3
	30	2.3 (59%)	0.7 (18%)	0.9 (23%)	3.9
Winter					
Nov.-Feb. 104 days	9	0.3 (27%)	0.2 (18%)	0.6 (55%)	1.1
	30	0.2 (18%)	0.2 (18%)	0.7 (64%)	1.1
Spring bloom					
Mar.-Apr.[a] 49 days	9	0.1 (10%)	0.1 (10%)	0.8 (80%)	1.0[b]
	30	0.2 (3%)	0.1 (2%)	5.5 (95%)	5.8
Annual production					
365 days	9	2.5 (34%)	1.7 (23%)	3.2 (48%)	7.4[b]
	30	2.7 (25%)	1.0 (9%)	7.1 (66%)	10.8

[a] Production during April, 1984 was used for April, 1985.

[b] Values might be underestimated due to missing data of the spring phytoplankton bloom.

dominate the primary production during summer and the larger ones in winter has also been observed by Larsson and Hagström (1982). It is generally considered that the low ambient nutrient concentrations and frequent but small inputs of nutrients favor assimilation by minute phytoplankton having a high surface to volume ratio (Takahashi and Bienfang, 1983). Recently, Glover *et al.* (1988) demonstrated that transient increases in nitrate concentration at the nanomolar level occurs in the surface layer of stratified oceanic water columns resulting in a rapid increase in cyanobacteria cell density. High densities of PEC and OPP in summer may be correlated to low nutrient conditions caused by the thermal stratification of water column. On the other hand, the dominance of the $>10\ \mu$m size fraction started in November, when vertical mixing of water column began and nutrient concentrations increased. Occurrence of large-sized phytoplankters as competitors for nutrients may also affect the abundance of picophytoplankton.

These results on size and species composition of the phytoplankton community suggests that primary production may be linked to microzooplankton in summer and to net zooplankton in winter and spring, since it is generally considered that the larger zooplankton require larger particles as food and *vice versa* (Parsons and LeBrasseur, 1970; Taniguchi, 1977a, b).

III-1-iii. Flux of organic matters

Most of the sinking particles were of irregular shape (Plate Ia) and were composed of fine grains (Plate Ib). These were classified as residual fraction, because of the difficulty of microscopic measurement. Aside from these unidentified particles, cylindrical fecal pellets (Plate Ic), intact bodies of zooplankton (Plate Id), fragments of zooplankton (e.g. lorica of tintinnids; Plate Ie), and intact phytoplankton cells (Plate If) were observed. The examples shown in Plate Ic were typical small sized fecal pellets found in the stratified water column. Fecal pellets larger than 500 μm in length were rarely observed, but their contribution in terms of carbon amount was significant.

Biogenic fluxes from August 21 to October 1, 1984 are shown in Table 4. Daily

Table 4. Fluxes of zoogenic and phytogenic matter (mg C$\cdot$m$^{-2}\cdot$d^{-1}) and the percent contribution to the total organic carbon flux in the stratified water column in Funka Bay.

Period	Zoogenic matter			Phytogenic matter		sum (A)	Total* (B)	Unidentified (B)−(A)
	intact	frag-ments	fecal pellets	intact	frag-ments			
I	10	2	8	1	1	22	224	202
Aug. 21-Sep. 3	4%	1%	4%	ng	ng	10%	100%	90%
II	39	3	5	1	1	49	258	209
Sep. 3-Sep. 20	15%	1%	2%	ng	ng	19%	100%	81%
III	35	1	5	4	10	55	238	183
Sep. 20-Oct. 1	15%	ng	2%	2%	4%	23%	100%	77%

ng; negligible (less than 0.5%).

* Total organic carbon flux by Maita *et al.* (1986).

carbon flux of the identified components ranged from 22 to 55 mg $C \cdot m^{-2}$ while the total organic carbon fluxes during the same period were 224 to 258 mg $C \cdot m^{-2} \cdot d^{-1}$ (Maita *et al.*, 1986). This shows that only 10 to 23% of the total organic carbon flux could be classified. About 75 to 96% of the identified biogenic matter in the sinking particles originated from zoogenic matter. Intact organisms accounted for 45 to 80% of the calculated fluxes, whereas 2 to 7% was intact phytoplankton (less than 1% of primary production).

Table 5 shows the fluxes during the early mixing period (November 15 to December 3, 1984), the late mixing period (February 1 to March 15, 1985), and after the mixing period (May 10 to May 23, 1985). During the early mixing period, the identified fraction of biogenic organic carbon (corresponding to 10% of the total carbon flux) was composed of fecal pellets (79%) and intact phytoplankton (21%).

In the late mixing period, a greater fraction of sinking particles could be identified. For example, the contribution of the identified matter to the total organic carbon flux increased to 28% in February and 70% in March. Intact organisms were the major component, comprising 50 to 72% of the identified matter or 63 to 78 mg $C \cdot m^{-2} \cdot d^{-1}$. The contribution by phytogenic matter to the total carbon flux also increased. This increment corresponded to the spring bloom of phytoplankton, which was dominated by diatoms. From February 28 to March 15, intact phytoplankton flux was 2% of primary production.

The flux of identified particles after the mixing period 545 mg $C \cdot m^{-2} \cdot d^{-1}$) comprised 84% of the total organic carbon flux (645 mg $C \cdot m^{-2} \cdot d^{-1}$; Yanada, personal communication). Ninety-three percent of that was composed from the intact zooplankton, mostly copepods (*Calanus plumchrus*). The flux of phytogenic

Table 5. Fluxes of zoogenic and phytogenic matter (mg $C \cdot m^{-2} \cdot d^{-1}$) and the percent contribution to the total organic carbon flux in the mixed water column in Funka Bay.

Period	Zoogenic matter			Phytogenic matter		sum (A)	Total* (B)	Unidentified (B)−(A)
	intact	fragments	fecal pellets	intact	fragments			
IV	tr	tr	15	4	tr	19	189	170
Nov. 15-Dec. 3	ng	ng	8%	2%	ng	10%	100%	90%
V	65	tr	41	8	2	116	413	297
Feb. 1-Feb. 18	16%	ng	10%	2%	ng	28%	100%	72%
VI	78	tr	16	12	2	108	329	221
Feb. 18-Feb. 28	24%	ng	2%	4%	1%	33%	100%	67%
VII	63	1	40	20	1	125	157	32
Feb. 28-Mar. 15	40%	1%	25%	13%	1%	80%	100%	20%
VIII	507	tr	36	1	1	545	645	100
May 10-May 23	79%	ng	6%	ng	ng	84%	100%	16%

tr; trace (less than 0.5 mg $C \cdot m^{-2} \cdot d^{-1}$).

ng; negligible (less than 0.5%).

* Total organic carbon flux by Yanada (unpublished results).

matter was only 2 mg C•m^{-2}•d^{-1}, being comparable to the rate during the summer period.

III-1-iv. Zooplankton communities

Seasonal variations were noted in the abundance of net zooplankton (=large copepods), small copepods, and microzooplankton (=copepod nauplii and ciliates) found in the upper 30 m, from April 1984 to May 1985. The highest total number and volume of large copepods occurred in April and May (Fig. 13A and B). Another small peak can also be seen in December. The mean individual volume of the large copepod began to increase in November and reached a maximum in May (Fig. 13C). Here, in terms of volume, large species such as *Calanus plumchrus*, *Eucalanus bungii bungii* and *Metridia pacifica* were predominant in the large copepod community. Seasonal changes in small copepods number and volume (Fig. 14) differed from those of large copepods. The maximum abundance of the small copepods at Stations 9 and 30 occurred in August and July, respectively (Fig. 14A). The highest total volume at these stations was observed in June and July (Fig. 14B). The dominant genera found during the summer maximum were *Microsetella* and

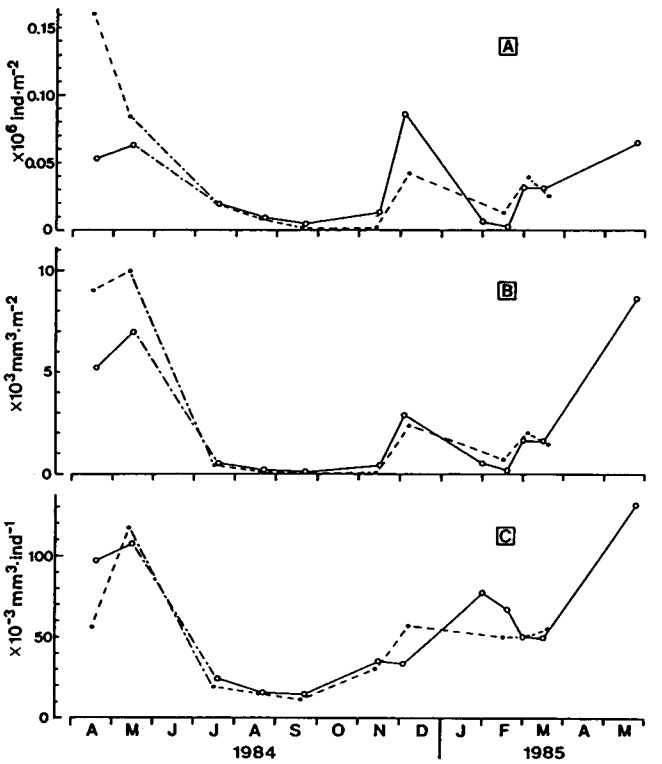


Fig. 13. Monthly changes in the total number (A), volume (B), and the mean individual volume (C) of large copepods integrated over the upper 30 m. Closed circles: Station 9, open circles: Station 30.

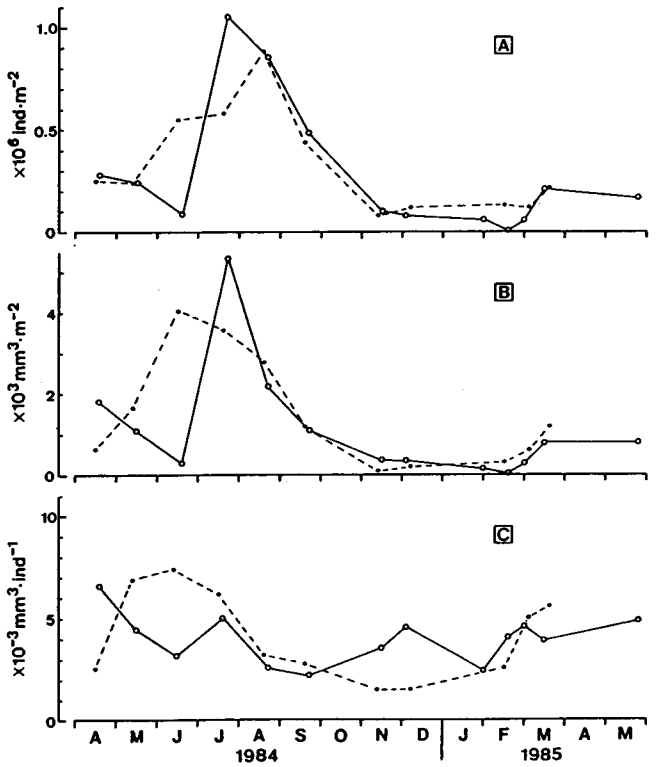


Fig. 14. Monthly changes in the total number (A), volume (B), and the mean individual volume (C) of small copepods integrated over the upper 30 m. Closed circles: Station 9, open circles: Station 30.

Oithona. The mean volume got smaller by September at Station 30, and by November at Station 9, and larger in spring (Fig. 14C). The mean volumes at Station 9 were larger than that of Station 30. Seasonal variations in the number of copepod nauplii seem to be divided into three peaks, i.e., in summer, autumn, and spring (Fig. 15A). Their total volume increased during spring with a slight increase also noted in the summer and autumn (Fig. 15B). The mean individual volume of nauplii clearly got smaller in the summer but larger during the spring phytoplankton bloom (Fig. 15C). Ciliate biomass was highest during April (Fig. 16B). The total number and volume were also large in September (Fig. 16A and B), however the mean individual volume was small (Fig. 16C). This occurs when the Tsugaru warm water flows into the bay (Ohtani and Kido, 1980). Dominance of small-size tintinnids in September has also been observed by Dohi (1982).

The dominant group in the zooplankton community was ciliates, in terms of number. The maximum individual number of ciliates was obtained at Station 9 in September (ca. 20×10^6 ind$\cdot$m^{-2}), which was one to three orders of magnitude higher than other groups. In terms of volume, however, large copepods were the dominant

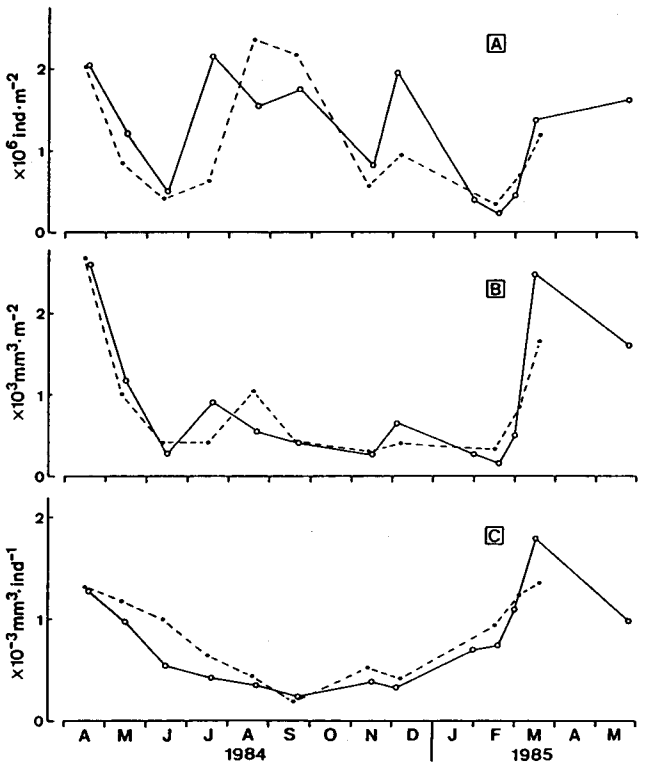


Fig. 15. Monthly changes in the total number (A), volume (B), and the mean individual volume (C) of copepod nauplii integrated over the upper 30 m. Closed circles: Station 9, open circles: Station 30.

groups in the zooplankton community during April, May, and December, and small copepods from June to September. In mid-March, copepod nauplii predominated in volume in the zooplankton community.

The annual peak of the large copepods volume had about one and two month lag from the period of the phytoplankton bloom. However, seasonal variations of small copepods volume were not consistent with that of phytoplankton biomass. The increment in volume of copepod nauplii coincided with the spring phytoplankton bloom. Ciliates volume may also coincide with the spring increase of phytoplankton biomass, since a high volume was obtained at both stations during April, 1984.

Zooplankton communities were dominated by larger individuals in and after the phytoplankton bloom but by smaller ones during the summer. This trend clearly shows a strong positive correlation in size between food particles and the consumers. This supports the general assumption that the larger zooplankton require larger food particles and *vice versa* (Parsons and LeBrasseur, 1970; Taniguchi, 1977a, b).

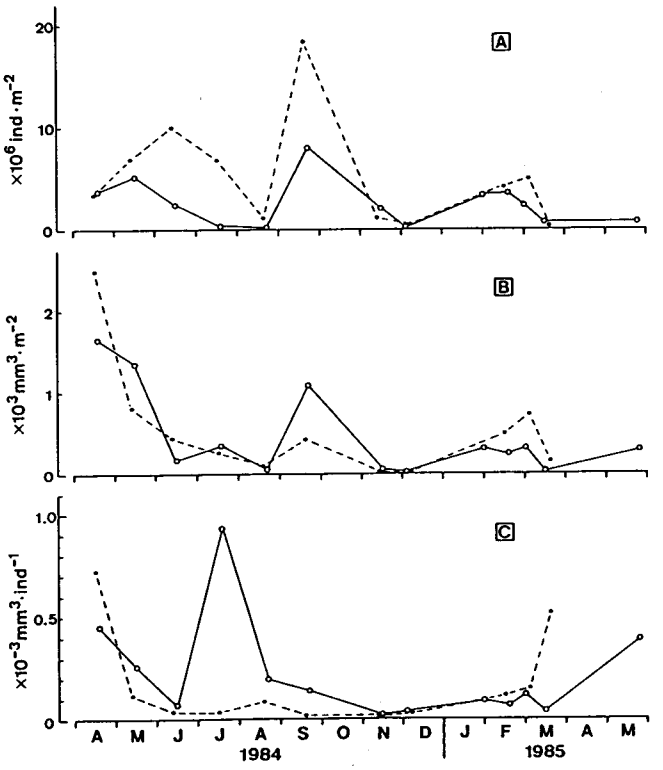


Fig. 16. Monthly changes in the total number (A), volume (B), and the mean individual volume (C) of ciliates integrated over the upper 30 m. Closed circles: Station 9, open circles: Station 30.

In the samples of the spring bloom in 1985, phagotrophic dinoflagellates were accidentally observed (Plate IIa-f). The normal form of one species of dinoflagellate (*Gyrodinium* sp.) is shown in Plate IIa. In Plate IIb, the hypocone of the flagellate has enveloped three quarters of the diatom, *Thalassiosira* sp. A completely engulfed diatom cell is shown in Plate IIc and d; the valve sculpture of the diatom in the latter can be clearly seen. Sometimes, two diatom cells can be observed inside a dinoflagellate (Plate IIe and f). Another species of unarmored dinoflagellate, *Gymnodinium* sp., also grazes on diatoms (Plate IIf). About 10% of these gymnodiniid flagellates contained diatoms and many had small food globules. In all cases, we have observed that the diatom engulfed by dinoflagellates is *Thalassiosira* sp., the dominant species during the 1985 spring phytoplankton bloom.

III-1-v. Zooplankton food requirement

The food requirement of zooplankton except phagotrophic dinofagellates was calculated separately for each of the 4 class sizes in the zooplankton community described above and summed up to give a total (Fig. 17). From July to September, the food requirement varied from 46% to 161% of the primary production. Since

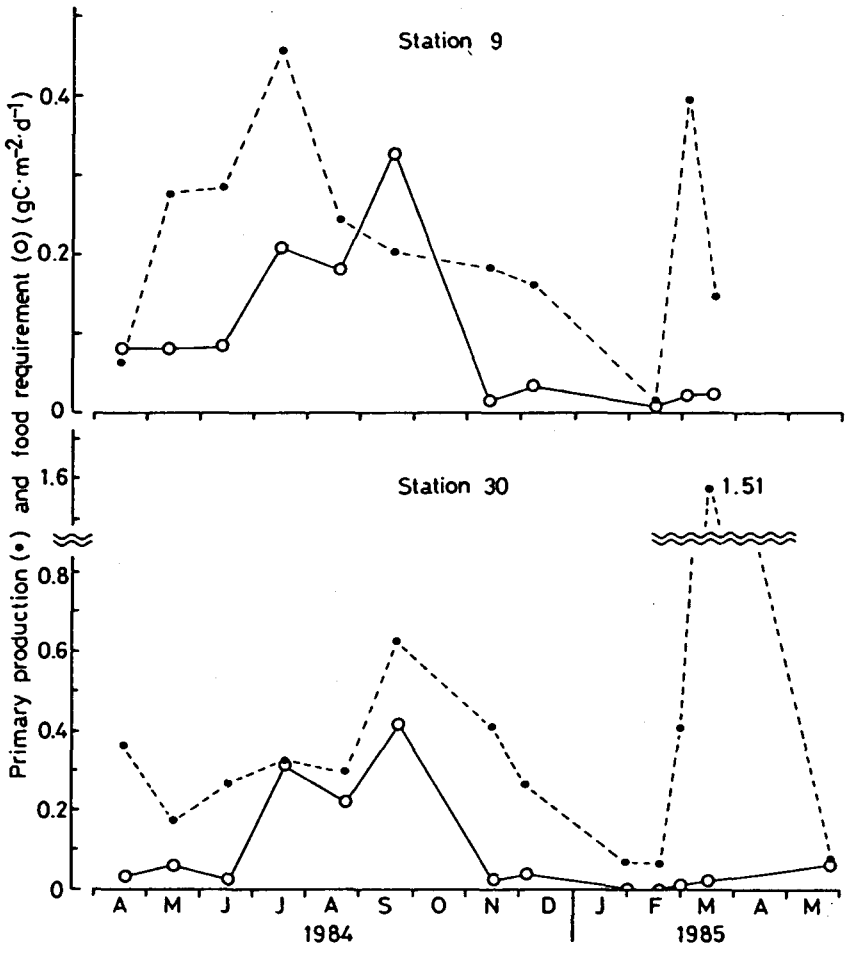


Fig. 17. Monthly changes in estimated food requirement of the total zooplankton assembly (open circle) in the upper 30 m at Stations 9 (above) and 30 (below). Primary production are also shown (closed circles).

herbivorous plankton other than copepods and ciliates were not considered here, the present estimate for the carbon requirement may be minimal as the total herbivores. Then, a stronger grazing impact should be expected in the summer. Of the highest food requirement observed in September, 70 and 76% was attributed to microzooplankton at Stations 9 and 30, respectively.

Table 6 summarizes the food requirement of each zooplankton group. The total food requirement from April to November corresponded to about 63 to 53% of the primary production. During this period, microzooplankton accounted for about half of the requirement, while small and large copepods accounted for about 40 and 10%, respectively. From November to April, however, the large copepods consumed approximately half of the total requirement. The food requirement for the

total zooplankton community was lower than the primary production throughout the year, with the exception of September at Station 9. During the spring phytoplankton bloom, the requirement was especially small at 3% of the primary production for Station 30 (Table 6). Integrated annual carbon requirement of the total zooplankton community was 39 g C·m^{-2}, equivalent to 52% of the primary production at Station 9; 45 g C·m^{-2} or 32% of the primary production at Station 30.

Estimated fecal pellet production of large copepods and observed pellet flux are shown in Table 7. Flux of the pellets was low in the stratified period and high in the mixed period. This trend is consistent with the results of Knauer *et al.* (1979). During the stratified period, the observed pellets in the trap accounted for 96–126% of the estimated fecal pellet production of large copepods based on food requirement by Ikeda-Motoda's method. The observed pellet flux surpassed the pellet production rate during the late mixing period. This suggests a significant contribution by larger zooplankton and micro-necton other than copepods (e.g. euphausiids, amphipods, fish larvae) and/or underestimation of the fecal pellet production rate based on food requirement during this period.

Table 6. Carbon requirement of different zooplankton groups in the top 30 m with the percentage of zooplankton carbon requirement to primary production.

Season	Station	Carbon requirement					Primary production
		LC[1]	SC[2]	NP[3]	CL[4]	Total	
		(g C·m^{-2}·season^{-1})					(g C·m^{-2}·season^{-1})
Summer	9	3.9	13.5	7.5	9.6	34.5	55.0
Apr.-Nov.		(7%)	(25%)	(14%)	(17%)	(63%)	(100%)
212 days	30	3.3	16.1	9.0	12.4	40.8	76.9
		(4%)	(21%)	(12%)	(16%)	(53%)	(100%)
Winter	9	1.2	0.3	0.7	0.3	2.5	12.9
Nov.-Feb.		(9%)	(2%)	(5%)	(2%)	(19%)	(100%)
104 days	30	1.3	0.3	0.8	0.2	2.6	19.1
		(7%)	2%)	(4%)	(1%)	(14%)	(100%)
Spring	9	0.9	0.2	0.5	0.3	1.9	7.4[5]
Mar.-Apr.		(12%)	(3%)	(7%)	(4%)	(26%)	(100%)
49 days	30	0.6	0.2	0.5	0.1	1.4	46.3
		(1%)	(0%)	(1%)	(0%)	(3%)	(100%)
		(g C·m^{-2}·yr^{-1})					(g C·m^{-2}·yr^{-1})
Year	9	6.0	14.0	8.7	10.2	38.9	75.3
365 days		(8%)	(19%)	(12%)	(14%)	(52%)	(100%)
	30	5.2	16.6	10.3	12.7	44.8	142.3
		(4%)	(12%)	(7%)	(9%)	(31%)	(100%)

[1] Large copepods.
[2] Small copepods.
[3] Copepod nauplii.
[4] Ciliates.
[5] Peak of spring bloom was missed.

Table 7. Estimated fecal pellet production by large copepods based on food requirement and observed fecal pellet flux (mg C•m^{-2}•d^{-1}).

Period	Fecal pellet production	Fecal pellet flux
Aug. 21 - Sep. 3	7.3	7.8
Sep. 3 - Sep. 22	4.3	5.4
Sep. 21 - Oct. 1	5.2	5.0
Nov. 15 - Dec. 3	12.3	14.5
Feb. 1 - Feb. 18	1.1	40.7
Feb. 18 - Feb. 28	2.7	15.6
Feb. 28 - Mar. 15	4.8	40.0
May 10 - May 23	57.3	35.5

III-2. *Discussion*

During the summer period, biomass of phytoplankton did not accumulate with time (Fig. 7), although a somewhat large primary production was observed (Fig. 17), suggesting that some removal factors acting on the phytoplankton biomass may exist during this period. At Station 30 from August to September, 1984, sinking loss of intact phytoplankton from the 0-74 m water column was 1 mg C•m^{-2}•d^{-1} (Table 4), which was less than 1% of primary production, suggesting that most of the primary production may be grazed upon by zooplankton. A high food requirement supports this consideration. Since, during this period, the major primary producer was cyanobacteria, and most of the food was required by microzooplankton, it is considered that the primary organic carbon flows from cyanobacteria to microzooplankton.

On the other hand, during winter and spring when phytoplankton size got larger, the percent contribution of large copepods to the total food requirement increased. This might suggest that the primary production flowed from diatom to net zooplankton. Total food requirement, however, was only 3% of primary production and sinking loss of phytoplankton at 74 m was 2% of phytoplankton production in spring phytoplankton bloom. If zooplankton graze on only phytoplankton to meet their requirement, a large portion of the fate of primary production in spring cannot be identified. However, since herbivorous plankton other than copepods and ciliates were not dealt with here, these result may imply that the contributions of other heterotrophic organisms are large during this period. For example, phagotrophic dinoflagellates were observed in the samples of the spring bloom in 1985 (cf. Plate IIa-f).

It is well known that the ingestion rate of zooplankton increases with prey concentration (Frost, 1975 ; Mullin *et al.*, 1975 ; Heinbokel, 1978a). The method of Ikeda and Motoda (1978) does not take into consideration phytoplankton density, although a large increment in phytoplankton biomass was observed during the

spring phytoplankton bloom. This may result in an underestimation of the grazing rate by the Ikeda-Motoda method. The fact that a larger amount of fecal pellets than the expectation based on food requirement was caught with the sediment trap suggests this speculation. Therefore, it is necessary to examine the actual grazing rate during the spring phytoplankton bloom, considering the above problems.

IV. Organic Carbon Flow within the Lower Trophic Levels during the Spring Phytoplankton Bloom in Funka Bay

The purpose of this chapter is to estimate the actual grazing rate of zooplankton including microzooplankton and phagotrophic dinoflagellates during the spring phytoplankton bloom in Funka Bay, and to show the fate of phytoplankton produced within the productive zone of the water column. Moreover, we attempt to reveal the percent contribution of heterotrophic organisms to the total grazing activity during this period.

IV-1. *Results*

IV-1-i. Calculated grazing rate based on phytoplankton mass dynamics

Figure 18a shows temporal changes in primary production at Station 30 in Funka Bay, from February 27 to April 30 1986. This was integrated from the surface to 2% light depth (Fig. 18b). The maximum production was obtained on March 26, indicating a peak of the spring phytoplankton bloom of this year. The total primary production within this period (62 d) was estimated to be 58.8 g C$\cdot$m^{-2}, which was almost the same daily production as that at this station during the previous year's spring (46.3 g C$\cdot$m$^{-2}\cdot$49 d^{-1}) (cf. Table 6). On February 27, the less saline Oyashio water mass ($<$33.0; Ohtani and Kido, 1980) was observed in the upper 10 m, while saline water ($>$33.4) which was considered to be the winter Funka Bay water (Ohtani and Kido, 1980) was in the deeper 30 m (Fig. 18b). After that, the less saline water occupied between the surface and 60–70 m depth. The more saline water was observed only in the deeper layers ($>$80 m). Salinity distribution showed that most of the results except on February 27 were obtained in the Oyashio water mass. The water temperature range was observed to be 1.3–4.9 °C. Lower temperature was observed in March, after which it increased, reaching the highest value by the end of April.

Both the chlorophyll *a* concentration and diatom cell density increased from February 27 to March 26, 1986, suggesting that the spring phytoplankton bloom was in progress (Fig. 19). The maximum chlorophyll *a* concentration of 8.4 mg$\cdot$m^{-3} was observed at 5 m depth on March 26. Almost the same concentration was recorded at this station during the spring bloom in 1985. A significant relationship was obtained ($r=0.965$, $n=46$, $p<0.001$) between the diatom cell density and chlorophyll *a* concentration, reflecting that the diatom was the most dominant group in the phytoplankton community during this period as shown also by Odate (1987). Increment in phytoplankton biomass in the 0–74 m water column was two times higher than that in the 0–30m during the first sampling interval. The larger increment may be attributed to the change in water masses.

In the following estimations, phytoplankton carbon was calculated using the

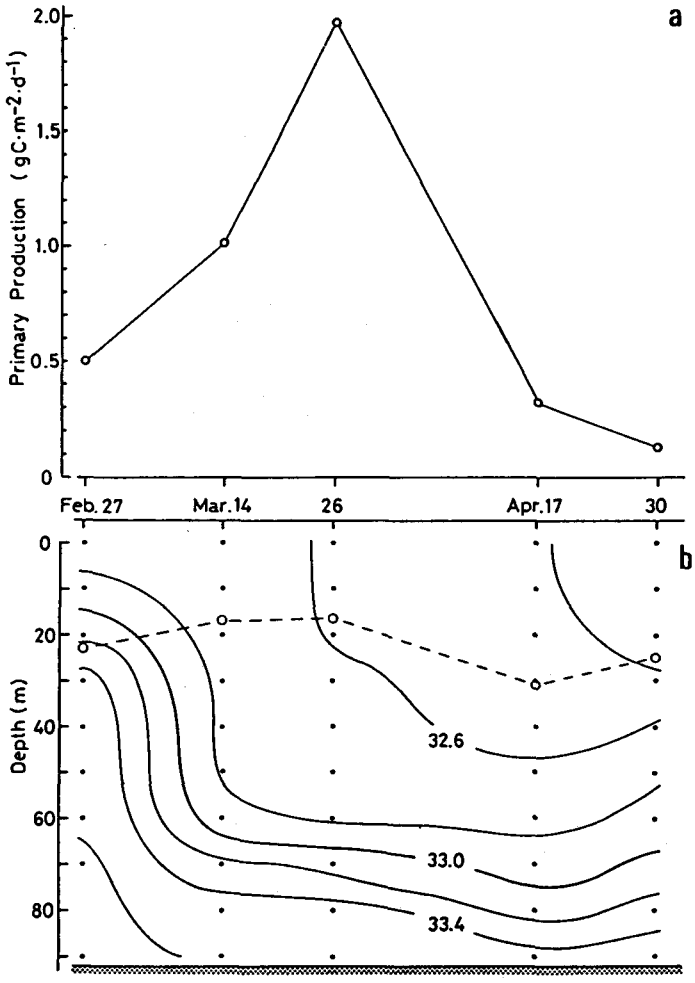


Fig. 18. Temporal changes in primary production integrated from the surface to the 2% light depth (a). Vertical distribution of salinity from February 27 to April 30, 1986. Open circles denote the 2% light depth (b).

carbon to chlorophyll *a* ratio determined by Antia *et al* (1963), i.e., 25 for actively growing cells in NO_3 sufficient water and 60 for cells grown in NO_3 depleted water. It is well known that a rapid decrease of NO_3 concentration was observed after the peak of spring phytoplankton bloom (e.g. Fig. 5). Then, the former ratio was applied during the bloom (February 27, March 14, and March 26) and the latter was used during the subsequent periods (April 17 and 30). Since these ratios are the lower values reported by Antia *et al.* (1963), the calculations were done using two times higher carbon to chlorophyll ratios, i.e., 50 for the bloom periods and 120 for the latter ones.

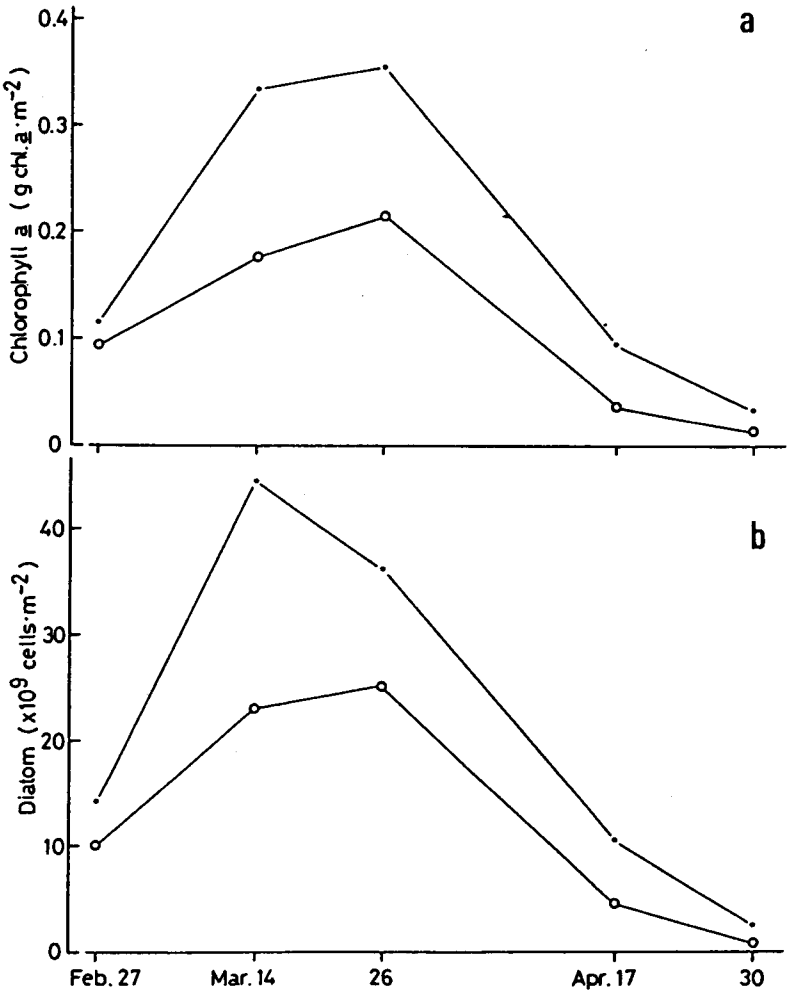


Fig. 19. Temporl changes in chlorophyll *a* standing stock (a) and abundance of diatom (b) within the water column (0-30 m, open circles; 0-74 m, closed circles).

The vertical flux of intact phytoplankton cells is shown in Fig. 20. Temporal changes in the flux coincided approximately with phytoplankton biomass, except for the high flux of intact phytoplankton cells which was observed between February 27 and March 14 at 30 m depth (0.2×10^9 cells$\cdot$m$^{-2}\cdot$d^{-1}). The phytoplankton fluxes at 30 m in each period were equivalent to 1.4, 0.9, 0.5, and 1.3% of the average diatom standing stock in the top 30 m. Between March 14 and 26, a high flux of 0.2×10^9 cells$\cdot$m$^{-2}\cdot$d^{-1} occurred at 74 m depth. The flux at 74 m depth were 0.4, 0.6, 0.4, and 0.7% of the average diatom standing stock.

Phytoplankton biomass is governed by its production rate (PP), flux (PF) and

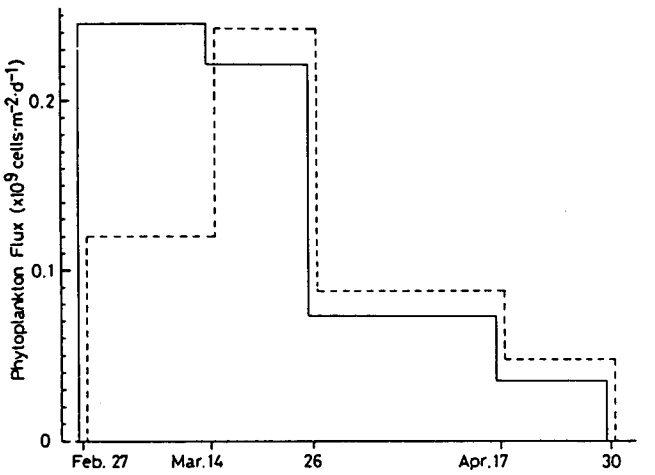


Fig. 20. Temporal changes in the phytoplankton vertical flux at 30 m (solid line) and 74 m (broken line).

Table 8. Grazed carbon (g C·m^{-2}·period^{-1}) within the top 30 m calculated by equation 8. Phytoplankton carbon was converted from chlorophyll standing stock using carbon to chlorophyll ratio, i.e., (a), 50 during February, March and 120 during April. (b) 25 during the former and 60 during the latter. (c) 44 (February 27), 39 (March 14), 54 (March 26), 74 (April 17), and 97 (April 30) (see text).

Period	C : Chl	PB_t-PB_0	Production	Flux	Grazed carbon
Feb. 27-Mar. 14	(a)	4.2	12.1	1.4	6.6
15 days	(b)	2.1	12.1	0.7	9.3
	(c)	2.8	12.1	1.1	8.2
Mar. 14-Mar. 26	(a)	1.8	18.6	1.1	15.7
12 days	(b)	0.9	18.5	0.5	17.1
	(c)	4.6	18.5	1.0	13.0
Mar. 26-Apr. 17	(a)	−6.3	25.2	0.8	30.7
22 days	(b)	−3.1	25.2	0.4	28.0
	(c)	−8.8	25.2	0.8	33.2
Apr. 17-Apr. 30	(a)	−2.8	2.9	0.5	5.2
13 days	(b)	−1.4	2.9	0.3	4.0
	(c)	−1.4	2.9	0.3	4.0
Whole period	(a)	−3.1	58.8	3.8	58.1
62 days		(−5%)	(100%)	(6%)	(99%)
	(b)	−1.5	58.8	1.9	58.5
		(−3%)	(100%)	(3%)	(99%)
	(c)	−2.8	58.8	3.2	58.4
		(−5%)	(100%)	(6%)	(99%)

zooplankton grazing rate (G) (Welschmeyer and Lorenzen, 1985; Laws *et al.*, 1988). A temporal change of phytoplankton biomass can be expressed as follows;

$$PB_t - PB_0 = PP - PF - G, \qquad 8$$

where PB_0 is the phytoplankton biomass on the initial day, and PB_t is that on t days after. PP can be estimated from the primary production data. PF is calculated from the phytoplankton flux expressed as a percentage of the standing stock mentioned earlier. Since the species composition of the standing stock and flux

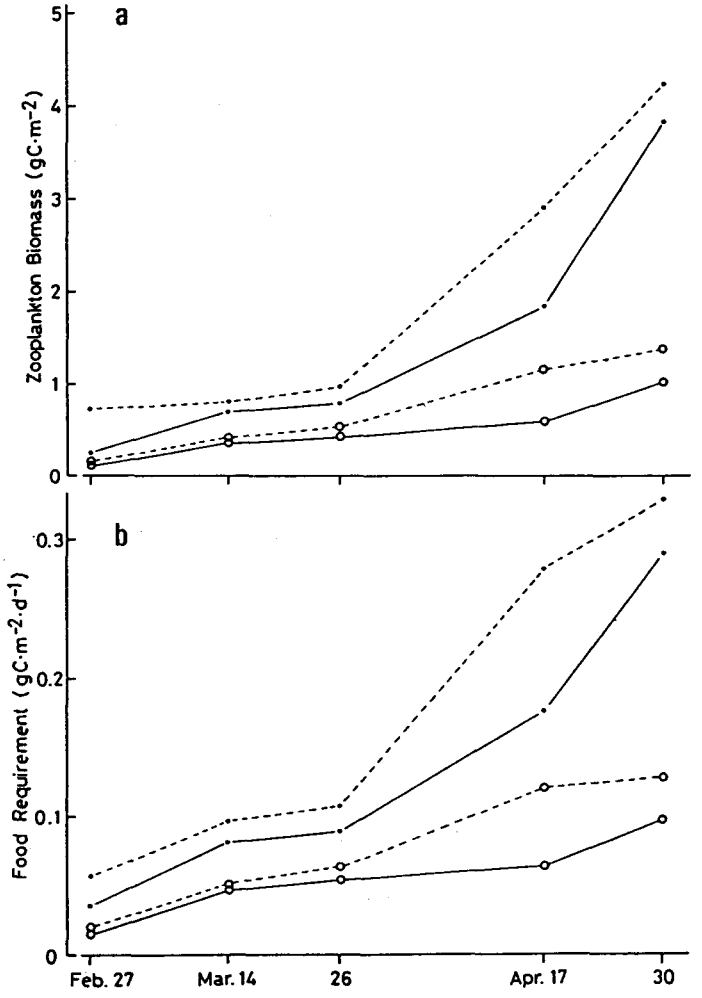


Fig. 21. Temporal changes in the biomass (a) and food requirement (b) of the total zooplankton (broken lines) and of four major groups (large and small copepods, copepod nauplii, and ciliates; solid lines) within the water column (0-30 m, open circles; 0-74 m, closed circles).

were almost the same, the flux can be converted to chlorophyll units and to carbon units using the carbon to chlorophyll ratio.

Grazed carbon (G in equation 8) within the upper 30 m is shown in Table 8. From the phytoplankton mass dynamics, it is apparent that, of the spring phytoplankton production, 3-6% was lost from the water column because of sinking and 99% was grazed upon by zooplankton. The surplus removal by grazing was attributed to the decrease of phytoplankton biomass from the same water column from February 27 to April 30. Although the calculation was carried out using the two times higher carbon to chlorophyll ratio, the largest difference in grazed carbon was a factor of 1.5 (February 27 to March 14). In particular, grazed carbon during the whole period was almost the same.

IV-1-ii. Grazing rate based on food requirement and food consumption

Temporal changes in total zooplankton biomass (large and small copepods, copepod nauplii, ciliates, and others except dinoflagellates) expressed as organic carbon units and their food requirement are shown in Fig. 21. The changes were quite different from those in phytoplankton. A distinct increase in zooplankton biomass was observed after the peak of the bloom (March 26), reaching the highest values on April 30 (Fig. 21a). In particular, a large increase in the zooplankton biomass was observed in the deeper layer (>30 m), and was attributed mainly to large copepods as shown by Hirakawa (1983). Food requirement is shown in Fig. 21b and detail data are listed in Table 9. Temporal changes in the food requirement were similar to those in the biomass. The highest food requirement was obtained on April 30, reflecting the highest biomass of zooplankton. On March 26,

Table 9. Estimated food requirement (g C·m^{-2}·period^{-1}) within the top 30 and 74 m calculated following the Ikada and Motoda's methods.

Period	Layer	Food requirement					
		Large copepods	Small copepods	Microzooplankton Nauplii	Microzooplankton Ciliates	Others	Total
Feb. 27-Mar. 14	0-30 m	0.1	tr	0.1	0.2	0.1	0.5
15 days	0-74 m	0.3	0.1	0.2	0.3	0.3	1.1
Mar. 14-Mar. 26	0-30 m	0.1	0.1	0.2	0.2	0.1	0.7
12 days	0-74 m	0.3	0.2	0.3	0.2	0.2	1.2
Mar. 26-Apr. 17	0-30 m	0.2	0.5	0.5	0.2	0.7	1.0
22 days	0-74 m	1.2	0.7	0.8	0.2	1.3	4.2
Apr. 17-Apr. 30	0-30 m	0.4	0.3	0.3	0.1	0.6	1.6
13 days	0-74 m	1.9	0.6	0.5	0.1	0.9	3.9
Whole period	0-30 m	0.8	0.9	1.1	0.7	1.5	4.8
62 days		(16%)	(18%)	(22%)	(13%)	(30%)	(100%)
	0-74 m	3.6	1.6	1.8	0.8	2.7	10.5
		(34%)	(15%)	(17%)	(8%)	(26%)	(100%)

tr, less than 0.05 g C·m^{-2}·period^{-1}.

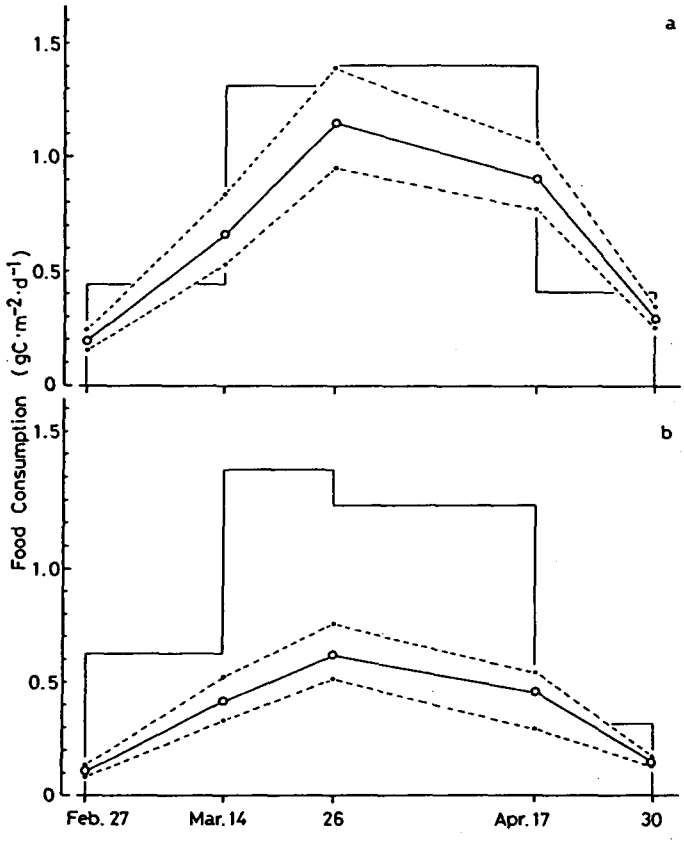


Fig. 22. Temporal changes in the food consumption by the total zooplankton except phagotrophic dinoflagellates within the upper 30 m (open circles and solid lines). Different sets of carbon to chlorophyll *a* ratio are used, i.e., (a) 50 during February and March, 120 during April, (b) 25 during the former period and 60 during the latter. Calculation are also conducted using 95% confidence limits of the regression equation (closed circles and broken lines) (see Table 2). Histogram denotes the grazed carbon calculated by equation 8.

the food requirement was only 3% (0-30 m) and 5% (0-74 m) of the primary production. Total food requirement throughout the sampling period was 4.8 g C·m^{-2} (0-30 m) and 10.5 g C·m^{-2} (0-74 m), which was equivalent to 8 and 18% of the grazed carbon, respectively (Table 9). Only a small fraction of the total primary production was required by the zooplankton in the previous year (cf. Fig. 17).

Food consumption of the zooplankton as above in the water column (0-30 m) is shown in Fig. 22. The consumed carbon was quite different from the food requirement, but similar to the phytoplankton biomass and production. The food consumed was considerably higher than the requirement, especially during the peak of the spring phytoplankton bloom. Using the higher carbon to chlorophyll ratio (50 and 120), food consumption was a little less than the grazed carbon denoted by the

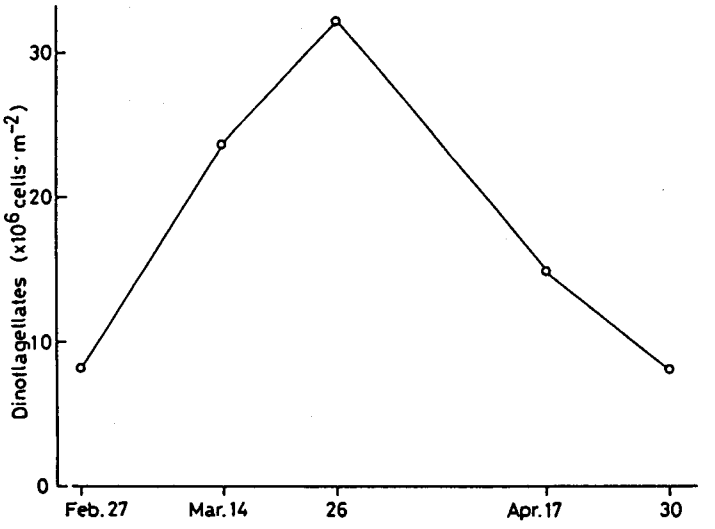


Fig. 23. Temporal changes in the abundance of phagotrophic dinoflagellates within the upper 30 m.

histogram (Fig. 22a). The food consumption during the whole period was 68-98% of the grazed carbon. If the lower carbon to chlorophyll ratio (25 and 60) was used, the food consumption became lower than the grazed carbon (Fig. 22b). It would be 36-53% of the grazed carbon during the whole period.

Temporal variation in cell density of phagotrophic dinoflagellates, mostly *Gyrodinium* spp. and *Gymnodinium* spp. is shown in Fig. 23. It can be seen that it varies with phytoplankton biomass and primary production. The maximum density of flagellates was 1,073 cells$\cdot L^{-1}$ on March 26 (average throughout the water column, 0-30 m).

The grazing rate of phagotrophic dinoflagellates is given in Fig. 24. Temporal variations in their food consumption were similar to those of phytoplankton biomass and production. The stippled area in the figure indicates the amount of carbon grazed upon in excess of estimated food consumption except phagotrophic dinoflagellates. In the case of higher carbon to chlorophyll ratio, their food consumption during this period was 31-62% of grazed carbon, and the difference could be easily explained by phagotrophic dinoflagellates consumption (Fig. 24a). In the lower carbon to chlorophyll ratio, the food consumption became 16-31% of the grazed carbon, and the dinoflagellates could not account for the difference (Fig. 24b). The total food consumption by the zooplankton and phagotrophic dinoflagellates during the whole period was 99-161% (using high carbon to chlorophyll ratio) and 52-85% (using low carbon to chlorophyll ratio) of the grazed carbon. Then, if actual carbon to chlorophyll ratios are between 25-50 and 60-120 in each period, the total grazed carbon may be explained by the zooplankton and phagotrophic dinoflagellates food consumption.

To estimate the carbon to chlorophyll ratio on each sampling date, regression

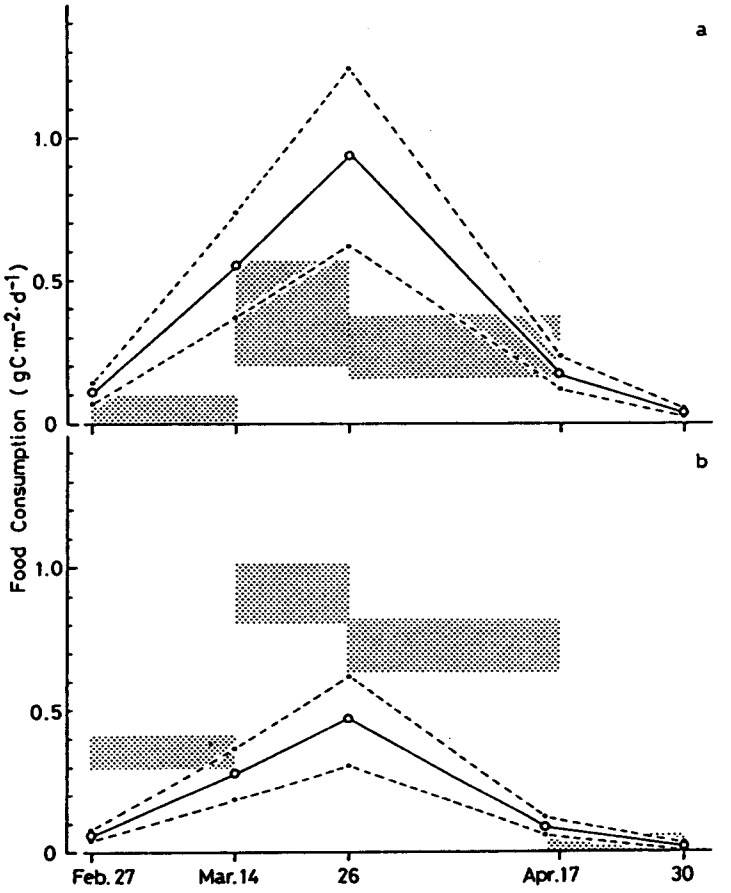


Fig. 24. Temporal changes in the food consumption by phagotrophic dinoflagellates within the upper 30 m. Calculation are conducted using the mean clearance rate (Lessard and Swift, 1985) (open circles and solid lines). 95% confidence limits of clearance rate are also used (closed circles and broken lines). Different sets of carbon to chlorophyll *a* ratio are used, i.e., (a) 50 during February and March, 120 during April, (b) 25 during the former period and 60 during the latter. Dotted area denotes the shortage in food consumption by the total zooplankters except phagotrophic dinoflagellates to grazed carbon calculated by equation 8.

analyses of particulate organic carbon on chlorophyll were conducted (Eppley *et al.* 1977). The relationships are shown in Fig. 25. Slope and intercept of the regression line (Table 10) give carbon to chlorophyll ratio and amount of detritus carbon, respectively (Banse, 1977). Most of these relationships were not significant largely because of the limited data available. However, the carbon to chlorophyll ratios obtained were within the range of published values (Antia *et al.*, 1963; Caperon and Meyer, 1972; Eppley and Renger, 1974; Strickland, 1965; Welschmeyer and Lorenzen, 1985). Moreover, the changes in the carbon to chlorophyll ratio with

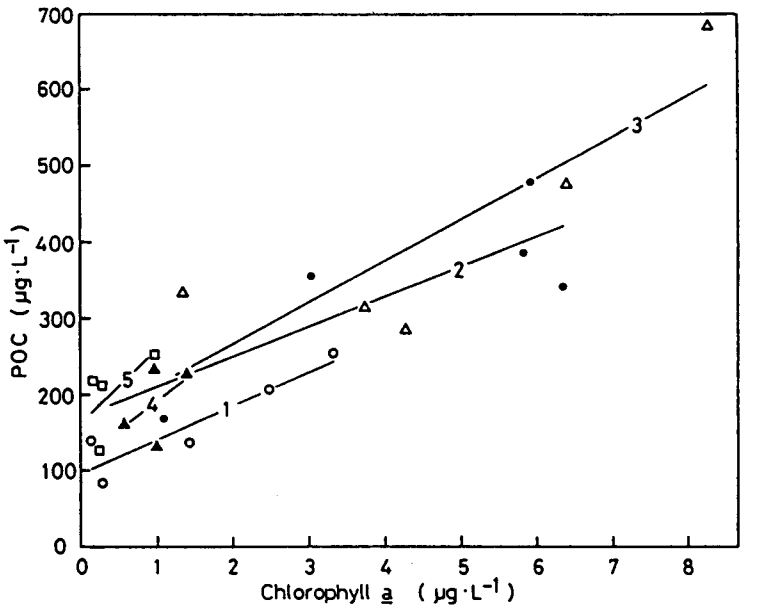


Fig. 25. Relationship between chlorophyll *a* concentration and particulate organic carbon concentration (POC). February 27, open circles (1); March 14, closed circles (2); March 26, open triangles (3); April 17, closed triangles (4); April 30, open squares (5). Results of the regression analyses are listed in Table 10.

Table 10. Summary of regression statistics for analysis of relationship of POC (particulate organic carbon, $\mu g\ C \cdot L^{-1}$) on CHL (chlorophyll *a*, $\mu g \cdot L^{-1}$).

Date of sampling	Equation of the regression line	Number of data	r
Feb. 27	POC=44CHL+98	5	0.93[1)]
Mar. 14	POC=39CHL+172	5	0.79[2)]
Mar. 26	POC=54CHL+158	5	0.85[2)]
Apr. 17	POC=74CHL+115	4	0.52[2)]
Apr. 30	POC=97CHL+164	4	0.62[2)]

[1)] Relationship is significant ($p<0.05$).
[2)] Relationship is not significant ($p>0.05$).

time was consistent with the trend observed by Antia *et al.* (1963). Then, the slopes were used as the carbon to chlorophyll ratio for each sampling day.

Food consumption of zooplankton groups and phagotrophic dinoflagellates was estimated based on the above carbon to chlorophyll ratios. The results are summarized in Table 11. The estimated food consumption of total heterotrophs corresponded to 98-159% of grazed carbon during each period (see Table 8c). Total food

Table 11. Estimated food consumption (g C•m^{-2}•period^{-1}) within the top 30 m calculated by equation 6 with carbon to chlorophyll ratio of 44 (February 27), 39 (March 14), 54 (March 26), 74 (April 17), and 97 (April 30).

Period	Food consumption							
	Large		Small	Microzooplankton			Phagotrophic	Total
	Copepod	Others	Copepods	Nauplii	Ciliates	Others	dinoflagellates	
Feb. 27-Mar. 14 15 days	0.9	0.1	0.2	1.8	1.5	0.8	3.9	9.3
Mar. 14-Mar. 26 12 days	1.5	0.4	2.3	3.7	1.5	1.2	8.6	19.3
Mar. 26-Apr. 17 22 days	1.9	1.4	5.3	6.5	1.3	4.0	12.2	32.4
Apr. 17-Apr. 30 13 days	0.5	0.5	1.1	1.4	0.3	1.6	0.9	6.3
Whole period 62 days	4.8 (9%)	2.4 (4%)	8.9 (13%)	13.3 (20%)	4.6 (7%)	7.7 (11%)	25.7 (38%)	67.3 (100%)

Table 12. Organic carbon flux at the depths of 30 and 74 m in Funka Bay (g C•m^{-2}•period^{-1}). Phytoplankton carbon flux was estimated with carbon to chlorophyll ratio of 44 (February 27), 39 (March 14), 54 (March 26), 74 (April 17), and 97 (April 30) (see text).

Period	Depth	POC[1] (a)	Phytoplankton (b)	Zooplankton (c)	Fecal pellet (d)	Detritus (a-b-c-d)
Feb. 27-Mar. 14	30 m	2.3	1.1	0.2	0.2	0.7
15 days	74 m	2.5	0.6	tr	0.7	1.2
Mar. 14-Mar. 26	30 m	3.7	1.0	0.4	0.2	2.1
12 days	74 m	2.2	1.2	0.1	0.7	0.3
Mar. 26-Apr. 17	30 m	10.5	0.8	0.7	0.4	8.6
22 days	74 m	17.6	1.1	0.1	0.7	15.7
Apr. 17-Apr. 30	30 m	13.5	0.3	10.0	0.3	2.8
13 days	74 m	13.1	0.5	0.3	1.2	11.1

[1] Data from Yanada (unpublished results).
tr, less than 0.05 g C•m^{-2}•period^{-1}.

consumption during the whole sampling period was 115% of grazed carbon. The relative contribution of each group to the total food consumption was 7% for large copepods, 4% for other large-size zooplankters, 13% for small copepods, 20% for copepod nauplii, 7% for ciliates, 11% for other microzooplankters, and 38% for phagotrophic dinoflagellates.

IV-1-iii. Flux of organic matters

The composition of flux of organic matter is summarized in Table 12. A large

Table 13. Comparison of fecal pellet flux and fecal pellet production rate of large copepods (g C•m^{-2}•period^{-1}) based on the food requirement (a) and on the food consumption (b) within the top 30 and 74 m.

Period	Layer	Flux	Fecal pellet Production (a)	Fecal pellet Production (b)
Feb. 27-Mar. 14	0-30 m	0.2	tr	0.3
15 days	0-74 m	0.7	0.1	0.4
Mar. 14-Mar. 26	0-30 m	0.2	tr	0.5
12 days	0-74 m	0.7	0.1	0.6
Mar. 26-Apr. 17	0-30 m	0.4	0.1	0.6
22 days	0-74 m	0.7	0.3	1.2
Apr. 17-Apr. 30	0-30 m	0.3	0.1	0.1
13 days	0-74 m	1.2	0.6	0.8

tr. less than 0.05 g C•m^{-2}•period^{-1}.

total POC flux was observed at both depths after the peak of spring bloom (March 26-April 30, 1986). During this period, more than 80% of the POC flux was detritus, excluding the flux from April 17 to 30 at 30 m, where 74% was due to the flux of intact zooplankton bodies. Such a high contribution by intact zooplankters was also observed in 1985.

Table 13 shows the rate of fecal pellet production by large copepods, because

Table 14. Temporal changes in standing stock of total particulate organic carbon (POC, a), phytoplankton carbon (PPC, b), and detrital carbon (DTC, a-b) within the top 30 m (g C•m^{-2}). Temporal changes in detritus based on the difference of intercepts of regression lines between chlorophyll *a* and POC (c) is also shown (see Table 10). Feces production based on food consumption (FPP, g C•m^{-2}•period^{-1}) by microzooplankton and phagotrophic dinoflagellates as detritus production obtained from equation 7 is shown (e).

Period	Difference of POC (a)	PPC (b)	DTC (a-b)	DTC (c)	Flux (d)	Detritus Production [(a−b)+d]	Detritus Production (c+d)	FPP (e)
Feb. 27-Mar. 14 15 days	5.9	2.8	3.2	2.2	0.7	3.8	2.9	2.4
Mar. 14-Mar. 26 12 days	3.5	4.6	−1.1	−0.4	2.1	0.9	1.6	4.5
Mar. 26-Apr. 17 22 days	−13.6	−8.8	−4.8	−1.3	8.6	3.8	7.3	7.2
Apr. 17-Apr. 30 13 days	− 1.2	−1.4	0.2	1.5	2.8	3.0	4.3	1.3

their fecal pellets are large and sink so fast such that they are caught with a sediment trap (Paffenhöfer and Knowles, 1979; Small *et al.*, 1979). Observed fecal pellet flux was much higher than the fecal pellet production rate estimated from the food requirement, but close to the estimate based on the food consumption. The latter estimation represents 43-188% of the observed pellet flux. Although the observed fecal pellet flux should not be considered as the fecal pellet production because coprophagy or decomposition of fecal pellets must take place to some extent (Paffenhöfer and Knowles, 1979; Lorenzen *et al.*, 1983; Emerson and Roff, 1987; Sasaki *et al.*, 1988), similarity between the observed pellet flux and the pellet production rate based on food consumption suggests that the food consumption for grazing rate is reasonable for large copepods.

Grazing by microzooplankton can not be reflected by fecal pellet sedimentation, since their small feces are fragile and do not sink so fast (Paffenhöfer and Knowles, 1979; Small *et al.*, 1979; Stoecker, 1984). Grazing rate of such small heterotrophs may be revealed by detrital carbon dynamics in water column. Table 14 shows the temporal changes in detrital carbon which was obtained by the difference between POC and phytoplankton carbon. On the other hand, intercept of the regression line POC on chlorophyll gives the amount of detrital carbon (Banse, 1977). Temporal changes in detrital carbon are also estimated based on the intercept (see Fig. 25 and Table 10). Because most of the relationships were insignificant, the differences of both methods were large. However, the tendency to increase and decrease was the same.

Detritus mass dynamics can be treated in the same manner as equation 8

$$DB_t - DB_0 = DP - DF - RD, \qquad 8'$$

where DB_0 is detritus biomass on the an initial day, and DB_t is that on t days after. DP is detritus production rate and DF is detritus flux. If decomposition or ingestion for detritus (RD) were neglected, detritus production is equal to temporal difference plus detritus flux. From February 27 to March 14, detritus production based on the mass detritus mass dynamics in the water column was almost the same as the feces production by microzooplankton and phagotrophic dinoflagellates food consumption (Table 14). From March 26 to April 17, the estimated detritus production using the intercepts was similar to the feces production. From April 17 to 30 they were of the same order of magnitude. However, less detritus than feces productions were estimated during the mid bloom (March 14 to 26), suggesting either decomposition or ingestion. Excluding the mid bloom, detritus production was generally consistent with feces production based on the food consumption. These trends (Table 14) may support the food consumption as grazing rate of small organisms.

IV-2. *Discussion*

Grazed carbon based on the phytoplankton mass dynamics was much higher than the food requirement even if the whole water column (0-74 m) was considered (Table 9). If zooplankters grazed on phytoplankton only to meet their requirement, the change in phytoplankton biomass observed in this bay could not be explained, since sinking loss of phytoplankton was only 3-6% of primary production. This

suggests that zooplankters must sweep up phytoplankton in excess of their requirement, being consistent with the results of Anraku (1964). He showed that organic carbon consumed by copepods is larger than those calculated from respiratory rates such as the Ikeda-Motoda's method.

Many studies (Frost, 1972, 1975; Mullin *et al.*, 1975; Heinbokel, 1978a; Ayukai and Nishisawa, 1986; Tsuda and Nemoto, 1987) have shown that most zooplankton ingestion rates increase with food density because of their constant clearance rate and high saturation point which is seldom observed *in situ*. Estimation of Ikeda and Motoda's food requirement, however, does not include the phytoplankton biomass as a factor (see equations 1-5).

An alternative estimation of grazing rates, i.e., food consumption by heterotrophs communities including phagotrophic dinoflagellates varied between 98-159% of the grazed carbon, if the calculated carbon to chlorophyll ratios are used (Table 10). The food consumption during the whole period was 115% of the grazed carbon. It is considered that the grazed carbon can be explained by the food consumption by total heterotrophs. In this estimation, maximum food consumption per day (daily ration) was on the average about 230% of body weight. Smaller organisms showed a high daily ration and large ones low, reflecting a slope of less than one for clearance rate versus body weight. Such a trend has also been noted by Ikeda (1977). The average daily ration is not especially high, considering the reported values of 240-1,800% (Heinbokel, 1978a) and max. 1,300% (Taniguchi and Kawakami, 1985) for tintinnids, 292-481% for nauplii and 28-85% for adult copepods (Paffenhöfer, 1971), and max. 700% for adult copepods (Ikeda, 1977). The high zooplankton grazing rates during the spring phytoplankton bloom may be reflected in the high zooplankton production rate. This should provide a comfortable condition for walleye pollock larvae, which are abundant during this period in Funka Bay (Kamba, 1977; Nakatani, 1988).

My estimate of food consumption is more realistic than the food requirement calculated by the Ikeda-Motoda method (1978) and easily explains both the phytoplankton and detritus dynamics during the spring phytoplankton bloom. The latter method may give a much lower estimation for this period. This may result from the fact that their equations consider the effects of water temperature but not of phytoplankton biomass (see equations 1-5). Since a phytoplankton spring bloom regularly occurs in the subarctic waters (Raymont, 1980) usually under the low water temperature conditions, it appears that the annual food consumption by zooplankters or their production cannot be estimated using the Ikeda-Motoda method.

The present results show that grazing largely took place in the upper 30 m, where phytoplankton production is very active (=productive zone) and that almost all of the organic carbon produced by phytoplankton during the spring bloom in Funka Bay was immediately consumed by heterotrophs. Although it has been considered that phytoplankton production during the spring phytoplankton bloom may be grazed upon by large-sized copepods (Cushing, 1959; Heinrich, 1962; Steele, 1974), their contribution to the total grazing pressure was only 7%. Low contribution of large-sized copepods during spring phytoplankton bloom has been suggested by previous studies (Taguchi and Fukuchi, 1975; Dagg *et al.*, 1982;

Table 15. Comparison of the fate of primary production during the spring bloom in Funka Bay, Hokkaido and Auke Bay, Alaska.

	Funka Bay (this study)	Auke Bay (Laws *et al.* 1988)
Duration (day)	62	56
Depth (m)	94	60
Temperature (°C)	1–5	4–8
Phytoplankton		
Maximum stock (mg chl. $a \cdot m^{-3}$)	8	75
Production ($g\,C \cdot m^{-2}$)	58.8 (100%)	144 (100%)
Flux	3.2 (6%)	45.6 (40%)
Change in biomass ($g\,C \cdot m^{-2}$)	−2.8 (−5%)	2.3 (2%)
Consumption ($g\,C \cdot m^{-2}$)	58.3 (99%)	66.1 (58%)
Relative contribution (%)		
Net zooplankton	11[1)]	55
Microzooplankton	89[2)]	45

[1)] Large copepods and other large-size zooplankters collected with a Norpac net (mesh aperture, 0.33 mm).

[2)] Small copepods, copepod nauplii, ciliates, other small-size zooplankters, and phagotrophic dinoflagellates collected with Van Dorn sampler.

Frost *et al.* 1983; Frost, 1987). From my estimation, it becomes clear that, even during the bloom, about 90% of phytoplankton production flowed into the small organisms other than net zooplankton, and that the major grazer was phagotrophic dinoflagellates.

The large total POC flux observed after the bloom may be due to the detritus produced by the grazing activities of microzooplankton and phagotrophic dinoflagellates. Kido and Ohtani (1981) observed large amounts of particulate organic matter, called *Nuta* in Japanese, after the spring phytoplankton bloom in the sediment of this bay. My results suggest that *Nuta* may be derived from the feces of microzooplankton and phagotrophic dinoflagellates.

The fate of carbon produced by phytoplankton during spring in Auke Bay, which was estimated by Laws *et al.* (1988) using the modified Welschmeyer-Lorenzen model (Welschmeyer and Lorenzen, 1985), is shown in Table 15 together with that of Funka Bay. Maximum phytoplankton biomass in Auke Bay is one order of magnitude higher than that in Funka Bay, and the primary production is two times higher than in Funka Bay. Although there is little difference in the total carbon consumption by zooplankton in both bays, a large difference is noted in the phytoplankton flux. This suggests that ingestion rates of grasers may be saturated

in Auke Bay, since phytoplankton biomass is considerably higher there. Hence, grasers could not sweep up the phytoplankton present, which may be lost only through sinking. In fact, phytoplankton loss due to sinking is much higher than that in Funka Bay. Contribution of microzooplankton (including small copepods here) to grazing in Funka Bay is higher than that in Auke Bay and is the same as that in the open subarctic Pacific Ocean (Station P in the Gulf of Alaska) (Frost, 1987). From these results, it may be considered that the contribution of microzooplankton to the total grazing on phytoplankton may be more important in a phytoplankton poor region. This consideration is consistent with the general idea that the biomass ratio of microzooplankton to net sooplankton will increase in an oligotrophic water, such as the subtropical water (Endo *et al.*, 1983; Taniguchi, 1984, 1985).

V. Regional Changes in Plankton Community Structure in the Western North Pacific Ocean

There are two distinct water masses east of Honshu; the Oyashio water mass in

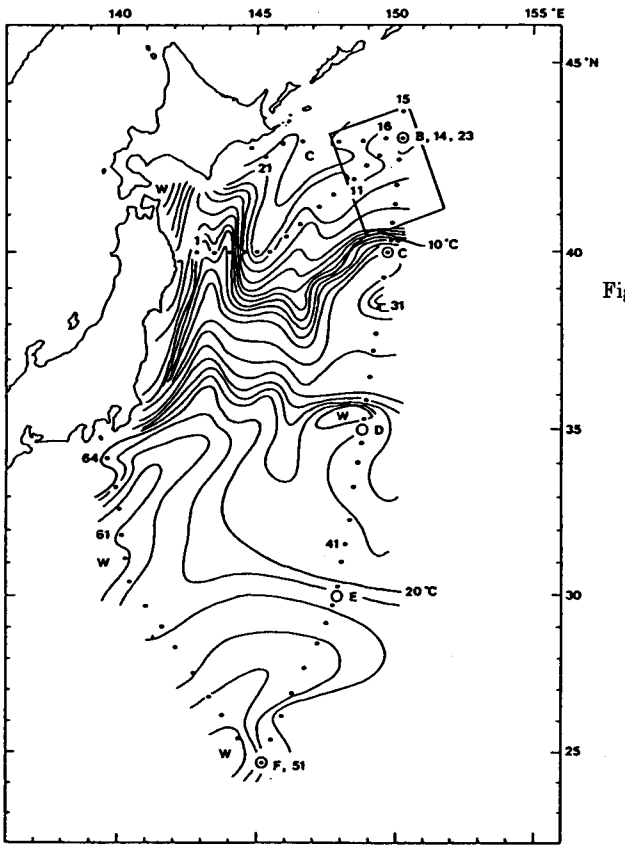


Fig. 26. Horizontal distribution of temperature during the Cruise KH-85-2 from April to May, 1985. Data were cited from the results of Hattori and Nakai (1986) based on the drift data of NNSS and the satellite images of NOAA-6 and 7.

the subarctic region and the Kuroshio water mass in the subtropical region. Little study to demonstrate the size composition of the phytoplankton community of the subarctic open water has been done. Since the composition of the phytoplankton communities varies from north to south (e.g. Marumo, 1967), chlorophyll *a* contribution by the different size fractions would definitely differ in the two water masses. But until now, the actual contribution by the different size fractions to the total phytoplankton biomass which is usually estimated by the chlorophyll *a* concentration is not yet known.

It is hypothesized that relative abundance of microzooplankton biomass to net zooplankton biomass is generally high in the subtropical water and low in the subarctic water (Taniguchi, 1984, 1985), because the percent contribution of large sized phytoplankters is high in the latter (Furuya and Marumo, 1983), and the size of available food affects the size distribution of the zooplankton (Marshall and Orr, 1956; Taniguchi, 1977a, b, 1984).

In this chapter, the contribution of the different size fractions to the total chlorophyll *a* concentration and abundance of microzooplankton and net zooplankton in the subarctic, transition, and subtropical waters of the western North Pacific Ocean were compared.

V-1. *Results*

V-I-i. Discrimination of water masses

Figure 26 shows the surface distribution of water temperature based on the satellite image taken during this sampling period (Hattori and Nakai, 1986). The presence of a southward flow of the Oyashio Current along 145°E meridian was

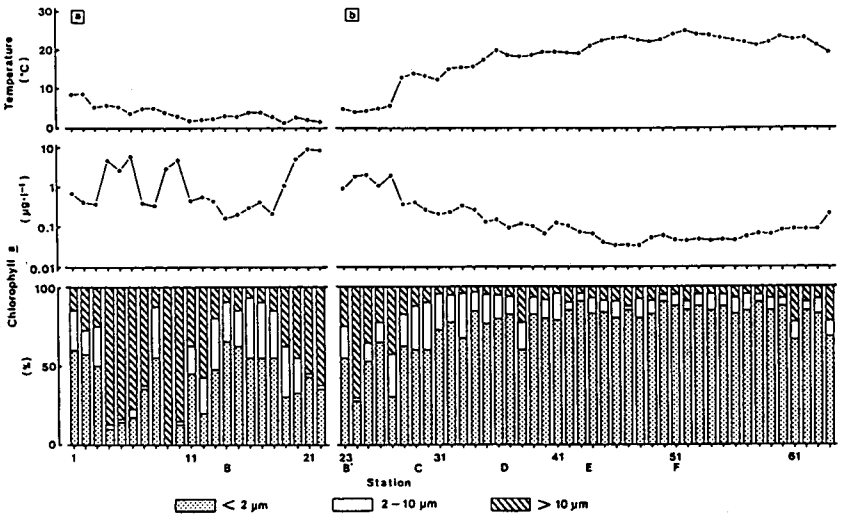


Fig. 27. Horizontal distribution of surface water temprature, chlorophyll *a* concentration, and its size composition along the first leg (a) and the second leg (b) of the Cruise KH-85-2 from April to May, 1985.

apparent. Considering this distribution pattern and the horizontal surface temperature records of the R/V Hakuho Maru Cruise KH-85-2, three water masses were discriminated, i.e., the subarctic water (<10°C), transition water (10–20°C), and subtropical water (>20°C) (as in Kawai, 1955).

VII-ii. Phytoplankton communities

Figure 27a shows the surface temperature profile, chlorophyll *a* concentration, and its size composition during the first leg of the cruise (April 12–25). The water temperatures at the first two stations off Sanriku Coast were slightly higher (ca. 8°C) than those at the other stations wherein the water temperatures were between 1.0–5.4°C. This implies that all of the stations sampled during the first leg were in the subarctic water mass. Chlorophyll *a* concentrations at the surface varied irregularly. Concentrations of more than 1.0 $\mu g \cdot L^{-1}$ were observed at Stations 4–6, 9–10 and 19–22. At these stations, the percent contributions of the >10 μm size fraction were large (71%, on the average). During the second leg of the cruise (April 30-May 15) (Fig. 27b), an increase of 7.2°C in the water temperature between Stations 27 and 28 was observed implying that a front, the Oyashio Front, lies between these stations. The temperature change coincided with the horizontal isopleth based on the satellite images shown in Fig. 26. In the subarctic area, north of the front (Stations 24–27), the concentrations of chlorophyll *a* were more than 1.0 $\mu g \cdot L^{-1}$, and the contributions of the >10 μm size fraction to the total chlorophyll *a* concentrations were high (22–70%). Within the subarctic waters, the coefficient of variation of the chlorophyll *a* concentrations in the total, >10 μm, 2–10 μm, and <2 μm size fraction was 281%, 222%, 30%, and 116%, respectively (n=27), reflecting a considerable horizontal variation of phytoplankton standing stock in this region. Remarkable differences in both concentration and size composition of chlorophyll *a* were observed at Stations 27 to 28 (Fig. 27b), near the Oyashio Front. Towards the

Table 16. Chlorophyll *a* concentration ($\mu g \cdot l^{-1}$, mean±1 SD) in each size fraction in the surface water of the subarctic, transition and subtropical areas of the western North Pacific Ocean. Number of samples (n) are also shown. Subarctic water is divided into two cases; total chlorophyll *a* concentration more (I) and less (II) than 1.0 $\mu g \cdot l^{-1}$. Data in parentheses are persent contribution (%, mean± 1 SD).

Sea area	n	Size fractions >10 μm	2–10 μm	<2 μm	Total
Subarctic (I)	13	2.55 ±1.75	0.22 ±0.31	1.10 ±1.09	3.86 ±2.5
		(61±24)	(9±11)	(29±18)	
Subarctic (II)	14	0.11 ±0.09	0.09 ±0.05	0.20 ±0.11	0.40 ±0.19
		(25±17)	(24±10)	(51±11)	
Transition	17	0.02 ±0.02	0.04 ±0.03	0.13 ±0.06	0.19 ±0.10
		(9± 6)	(17± 8)	(75±10)	
Subtropical	20	0.005±0.003	0.004±0.002	0.046±0.014	0.054±0.017
		(9± 4)	(7± 3)	(84± 5)	

Table 17. Comparison of mean chlorophyll *a* concentration and percent contribution to total chlorophyll *a* concentration in each size fraction between the surface water of the subarctic, transition (TR) subtropical areas (ST) of the western North Pacific Ocean using Student's t-test or Cochran-Coxtest. Subarctic water is divided into two cases; total chlorophyll *a* concentration more (SAI) and less (SAII) than 1.0 $\mu g \cdot l^{-1}$.

Concentration					Size fraction							
		>10 μm			2-10 μm			<2 μm			Total	
Sea area	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST
SAI	>>>	>>>	>>>	ns	ns	>	>	>>	>>	>>>	>>>	>>>
SAII		>>	>>		>>	>>>		ns	>>>		>>	>>>
TR			>			>>			>>>			>>>
Percent contribution												
		>10 μm			2-10 μm			<2 μm				
Sea area	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST			
SAI	>>>	>>>	>>>	<<	ns	ns	<<	<<<	<<<			
SAII		>>	>>		>	>>>		<<<	<<<			
TSR			ns			>>>			<<			

ns, difference is not significant.
>, >>, and >>> denote that sea area in the row is larger than in the column at $p<0.05$, 0.01, and 0.001, respectively.
<< and <<< denote that sea area in the row is smaller than in the column at $p<0.01$ and 0.001, respectively.

southern region, the concentration of chlorophyll *a* decreased from 2.01 $\mu g \cdot L^{-1}$ to 0.37 $\mu g \cdot L^{-1}$ as the contribution of the >10 μm size fraction decreased from 43% to 18% and the contribution of the <2 μm size fraction increased from 31% to 63%. The percent contribution of the <2 μm size fraction gradually increased to 80–90% at Station F, which was considered to be in the subtropical area. The coefficient of variation of the chlorophyll *a* concentration in the total, >10 μm, 2–10 μm, and <2 μm of the subtropical waters was less than 0.5% (n=20), suggesting that over this area, phytoplankton were relatively uniformly distributed (Fig. 27b).

Mean chlorophyll *a* concentrations in each size fraction within the subarctic, transition, and subtropical waters are summarized in Table 16. These mean values are statistically analyzed (Table 17). In both tables, the subarctic water is divided based on the total chlorophyll *a* concentration; higher (=SAI) and lower (=SAII) than 1.0 $\mu g \cdot L^{-1}$. The total concentration in SAI (range 1.03–8.96 $\mu g \cdot L^{-1}$) was about 10, 20, and 70 times as high as that in SAII, the transition water (=TR), and the subtropical water (=ST), respectively. The mean value of the total chlorophyll

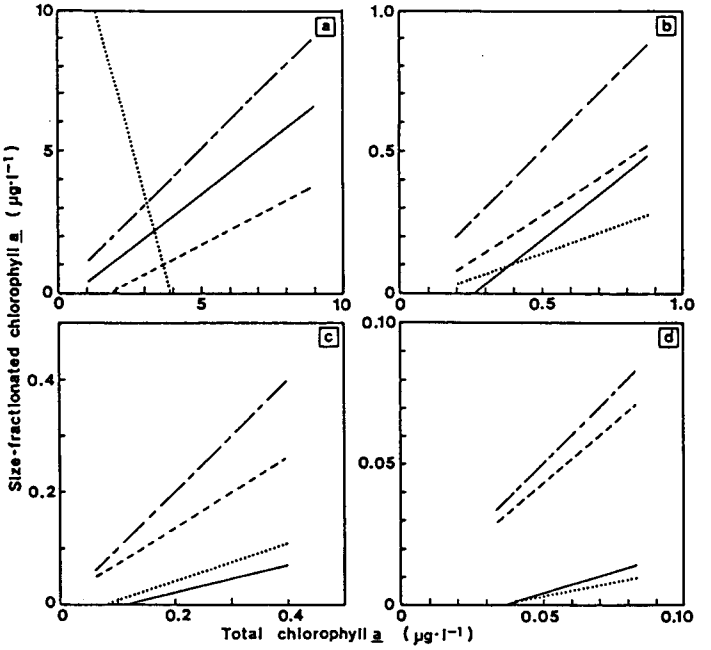


Fig. 28. Relationship between the total and size fractionated chlorophyll *a* concentration in the subarctic, transition (c), and subtropical waters (d) in the western North Pacific Ocean. The subarctic waters are divided based on the total chlorophyll *a* concentration; >0.1 $\mu g \cdot L^{-1}$ (a) and <1.0 $\mu g \cdot L^{-1}$ (b). The >10 μm size fraction, solid line; the 2–10 μm size fraction, dotted line; the <2 μm size fraction, broken line. Dotted and broken lines indicate the line with slope of 1. Relationships between the total and the 2–10 μm size fraction in the case I of the subarctic waters (a) is not significant ($p>0.5$). Others are significant ($p<0.02$). Only the range of total chlorophyll *a* concentration observed is shown.

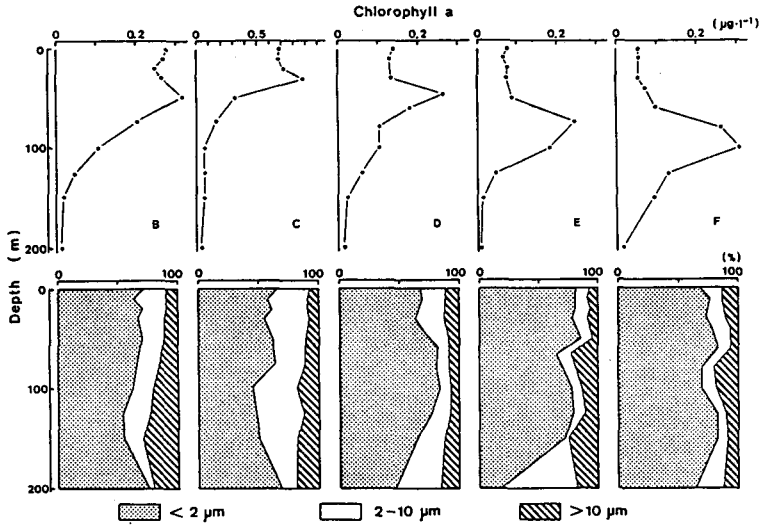


Fig. 29. Vertical distribution of chlorophyll *a* concentration and its size composition. The results of Station B were obtained in the first leg of the Cruise KH-85-2.

a concentration was significantly different ($p<0.001$). A large portion (ca. 71%) of the difference in the total chlorophyll *a* concentration between SAI and SAII could be attributed to the $>10\ \mu$m size fraction. Moreover, the percent contribution of the $<2\ \mu$m size fraction was low in SAI and high in SAII, TR, and ST, although the concentration of this size fraction was significantly high in SAI.

Relationships between the total and size fractionated chlorophyll *a* concentration in each water are illustrated in Fig. 28. In SAI, the total concentration was attributed to the $>10\ \mu$m size fraction ($n=13$, $r^2=83\%$, $p<0.001$). While variations of the total concentration were due to the $<2\ \mu$m size fraction in SAII ($n=14$, $r^2=74\%$, $p<0.001$), TR ($n=17$, $r^2=94\%$, $p<0.001$), and ST ($n=20$, $r^2=92\%$, $p<0.001$).

Vertical profiles of the concentration and size composition of chlorophyll *a* at Stations B, C, D, E, and F are shown in Fig. 29. In all stations, the chlorophyll *a* maximum layer was below the surface, which tended to be deeper towards the south. In the subarctic (Station B) and transition (Station D) waters the contribution of the $>10\ \mu$m size fraction was uniformly distributed throughout the water column, whereas in the subtropical region (Station F) the contribution of the $>10\ \mu$m size fraction increased at the chlorophyll maximum layer.

Table 18 shows temporal changes in the chlorophyll *a* concentration and the percentage contribution of the $>10\ \mu$m size fraction in the surface water surrounded by the rectangle in Fig. 28. The total chlorophyll *a* concentration increased significantly ($p<0.01$) from April ($0.31\ \mu g \cdot L^{-1}$) to May ($1.54\ \mu g \cdot L^{-1}$). Increment of the concentrations in the $>10\ \mu$m and $<2\ \mu$m size fraction were also significant ($p<0.05$). However, difference of the percent contribution in the $<2\ \mu$m size fraction was not significant. From April to May, the total phytoplankton cell

Table 18. Temporal changes in chlorophyll *a* concentration and percent contribution of each size fraction obtained in the surrounded area by rectangular in Fig. 26. Data are mean±1 SD. Results of comparison of mean value between April and May using Student's t-test or Cochran-Cox test are also shown.

Date	Size fraction >10 μm	2-10 μm	<2 μm	Total
Apr. 16-24 (μg•l^{-1}) (n=11) (%)	0.07±0.09 19±15	0.08±0.04 26±8	0.16±0.05 55±15	0.31±0.12
May 1-2 (μg•l^{-1}) (n=5) (%)	0.65±0.44 39±19	0.22±0.18 15±9	0.67±0.25 46±17	1.54±0.55
Comparison				
Concentration	i	ns	i	ii
Percent contribution	i	i	ns	

ns, difference is not singificant.
i, difference is significant ($p<0.05$).
ii, difference is significant ($p<0.01$).

Table 19. Temporal changes in cell density of each phytoplankton groups in the surrounded area by rectaugular in Fig. 26 (×10^3 cells•l^{-1}, mean±1 SD). Results of comparison of mean value between April and May using Student's t-test or Cochran-Cox test are also show.

Date	Diatoms	Dino-flagellates	Micro-flagellates	Others	Total
Apr. 16-24	20.2±21.8	60.0±12.2	105.4±27.8	22.5± 7.0	208.1± 35.4
May 1-2 (n=5)	238.2±138.7	73.9±21.6	140.2±24.3	75.8±36.7	528.1±133.0
Comparison	i	ns	i	i	ii

ns, difference is not singificant.
i, difference is significant ($p<0.05$).
ii, difference is significant ($p<0.01$).

density increased significantly ($p<0.01$) (Table 19). Among the phytoplankton groups examined, the large increment in the total cell density was attributed to growth diatoms bigger than 10 μm (e.g. *Chaetoceros convolutum*, *Chaetoceros* spp. *Thalassiosira* spp. *Denticulopsis seminae*, and *Fragilaria oceanica*).

Large variations in the concentration and size distribution of chlorophyll *a* were observed in the subarctic region (1-27). The relationship between the concentration in the >10 μm size fraction and the cell density of phytoplankton larger than 10 μm collected at Stations 1-36 is shown in Fig. 30. A linear relationship between the cell density and the chlorophyll *a* concentration in the >10 μm size fraction, composed mainly of diatoms, was observed ($n=36$, $r^2=90\%$, $p<0.001$). A

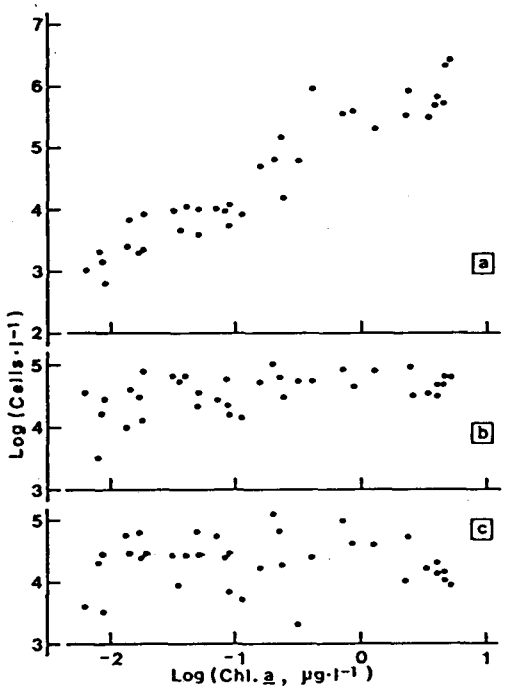


Fig. 30. Relationships between chlorophyll *a* concentration in $>10\,\mu$m size fraction and cell density of phytoplankton larger than $10\,\mu$m. Diatoms (a), dinoflagellates (b), other phytoplankton (c).

weak but significant positive correlation coefficient was obtained for the cell density of dinoflagellates ($n=36$, $r^2=22\%$, $p<0.01$). On the other hand, the relationships between the cell density of other phytoplankters and chlorophyll *a* concentration were insignificant ($n=36$, $r^2=0\%$, $p>0.5$). Variation in the chlorophyll *a* in the $>10\,\mu$m size fraction was due to diatoms.

V-I-iii. Zooplankton communities

Latitudinal distributions of total number, volume, and average body size (=total volume/total number) of naked ciliates, tintinnids, copepod nauplii, and small copepodites observed in the surface water samples are shown in Figs. 31–34, respectively. Their mean values in the subarctic water I (SAI), where water temperature was <10°C and chlorophyll *a* concentration was $>1.0\,\mu g\cdot L^{-1}$, subarctic water II (SAII), where water temperature was <10°C and chlorophyll *a* concentration was $<1.0\,\mu g\cdot L^{-1}$ transition water (TR), where water temperature was 10–20°C, subtropical water (ST), where water temperature was >20°C are listed in Table 20. Results of statistical comparisons of the regional mean values of microzooplankton communities are also shown in Table 21. Although other microzooplankters, such as radiolarians, foraminifera, and appendicularia frequently occurred, their total number and volume were small. Moreover, phagotrophic dinoflagellates observed in the samples of Funka Bay (Plate II) were seldom observed.

The most abundant total number (4,439 ind$\cdot L^{-1}$) and volume ($15\times10^6\,\mu m^3\cdot L^{-1}$) of naked ciliates (e.g. genera *Laboea*, *Strobilidium*, and *Strombidium*) were observed in SAII (Station 16), decreasing towards the south (Fig. 31a and b).

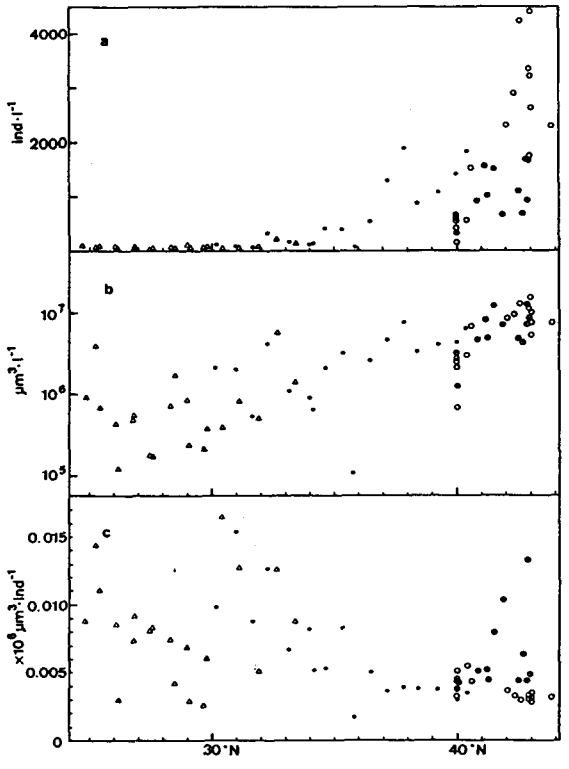


Fig. 31. Latitudinal variations in the total number (a), volume (b), and average size (c) of naked ciliates in the surface water. Symbols denote the sea area, i.e., Subarctic water I, total chlorophyll *a* concentration of more than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles and dots); Subarctic water II, total chlorophyll *a* concentration of less than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles); transition waters, water temperature between 10 and 20°C (closed circles); subtropical waters, water terperature higher than 20°C (open triangles).

Regional rank order of the total number of naked ciliates was SAII>SAI=TR (between which difference is not significant) >ST (Table 21). While, the rank order of volume was SAI=SAII>TR>ST. Large average body size as in SAI is also observed in TR and ST (Fig. 31c). Average body size in SAII was significantly smaller than that in the other waters.

The highest number and volume of tintinnids (928 ind$\cdot L^{-1}$ and 34×10^6 $\mu m^3 \cdot L^{-1}$, respectively) were observed in SAI (Station 10), while those in TR and ST were almost the same (Fig. 32a and b). Regional rank orders of tintinnids number and volume were SAI=SAII>TR=ST and SAI>SAII>TR=ST, respectively. Large average body sizes around 40°N in SAII and TR were due to *Parafavella ventricosa* and *P. gigantea*. Small average body sizes in the subarctic water especially in SAII (Fig. 32c) were attributed to the predominance of *Codonellonsis frigida* and *Achanthostomella norvegica*, of which oral diameters were ca. 20 and 25 μm, respectively. While, large average body size in SAI resulted from the predominance of *Ptychocylis obtusa* (oral diameter, ca. 50 μm). Large species of tintinnids (e.g. *Rhabdonella inflata*) sometimes caused the average body size in ST to be bigger. Regional differences in average body size was not significant, if analyses were conducted using all data obtained. Eliminating the two high data of average size collected along 40N of SAII (269×10^3 $\mu m^3 \cdot ind^{-1}$ at Station 1 and 440×10^3 $\mu m^3 \cdot ind^{-1}$ at Station 2) and the two high data near 40°N of TR (424×10^3 $\mu m^3 \cdot ind^{-1}$ at Station 28 and 551×

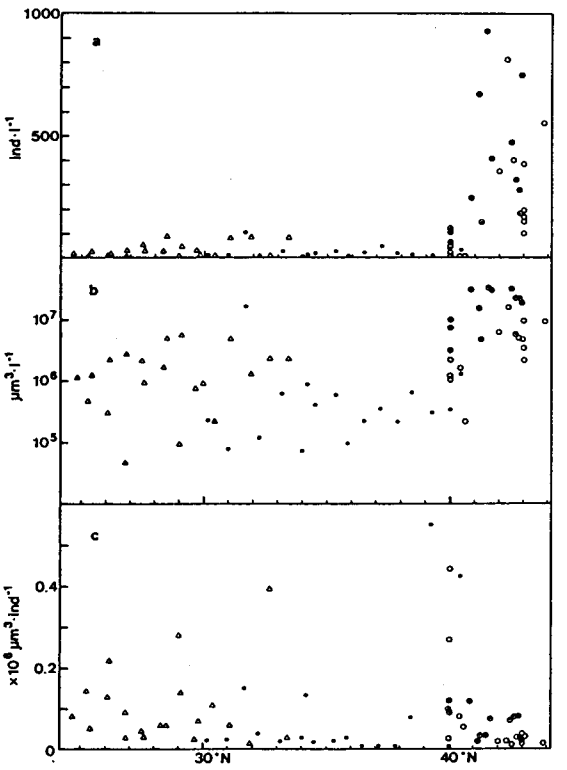


Fig. 32. Latitudinal variations in the total number (a), volume (b), and average size (c) of tintinnids in the surface water. Symbols denote the sea area, i.e., Subarctic water I, total chlorophyll *a* concentration of more than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles and dots); Subarctic water II, total chlorophyll *a* concentration of less than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles); transition waters, water temperature between 10 and 20°C (closed circles); subtropical waters, water temperature higher than 20°C (open triangles).

10^3 $\mu m^3 \cdot ind^{-1}$ at Station 30) (Fig. 32c), average body size in SAI was significantly greater than that in SAII. Average body size in SAII was significantly smaller than that in ST.

The maximum total number and volume of copepod nauplii (124 $ind \cdot L^{-1}$ and 221×10^6 $\mu m^3 \cdot L^{-1}$, respectively) were observed in SAI near the Oyashio Front (Station 27), decreasing towards the south (Fig. 33a and b). Total number of nauplii in SAI was significantly higher than that in other waters. Regional rank order of total volume was SAI>SAII>TR>ST. The average body size of this group apparently became smaller from north to south (Fig. 33c). Rank order of average body size was SAI=SAII>TR>ST.

Total microzooplankton number and volume were largely affected by naked ciliates and nauplii, respectively, as shown by Taniguchi (1984). Total microzooplankton biomass expressed as volume was 107, 35, 13, and 6×10^3 $\mu m^3 \cdot L^{-1}$ in SAI, SAII, TR, and ST, respectively. The biomass ratio of SAI : SAII : TR : ST was 16 : 5 : 2 : 1.

Total number of small copepods higher than 25 $ind \cdot L^{-1}$ was observed only in SAI and SAII (Fig. 34a). The rank order of total number was SAI>SAII=TR>ST. The total volume of this group in SAI was significantly higher than that in other waters, among which differences were not significant. Average body size in

Table 20. Mean abundance and size of microzooplankton communities in the surface waters of the subarctic I ($>1.0\,\mu$g chl. $a \cdot l^{-1}$) (SAI), subarctic II($<1.0\,\mu$g chl. $a \cdot l^{-1}$) (SAII), transition (TR), and subtropical waters (ST) in the western North Pacific Ocean. Number, ind$\cdot l^{-1}$; volume, $\times 10^6\,\mu m^3 \cdot l^{-1}$; size, $\times 10^3\,\mu m^3 \cdot ind^{-1}$. Data are mean$\pm$1 SD.

Sea area	Naked ciliates	Tintinnids	Copepod nauplii	Small copepods
SAI (n=13)				
Number	1020±459	359±275	56±30	22±13
Volume	6±3	20±11	81±52	106±74
Size	6±3	69±33	1435±352	4868±2337
SAII (n=14)				
Number	2173±1397	228±243	18±16	8±10
Volume	7±4	5±4	23±18	32±48
Size	4±1	30±19[1)]	1484±741	3648±1502
TR (n=17)				
Number	629±641	20±25	19±13	8±5
Volume	3±2	1±4	9±7	41±45
Size	6±3	41±45[1)]	491±250	4707±3852
ST (n=20)				
Number	78±49	30±31	12±16	4±4
Volume	1±1	2±2	3±5	28±43
Size	10±8	103±97	274±106	6447±4640

[1)], entremely high values obtained around 40°N are eliminated.

ST was sometimes larger than that in the other waters (Fig. 34c). Although average body size between SAII and ST was significantly different, the differences among others were not significant.

Vertical distributions of the three major microzooplankton groups and small copepods are shown in Fig. 35. The data on Station B was taken in the early half of the cruise. Microzooplankters were distributed in the upper 150 m, while small copepodites were sometimes abundant in the deeper layer (e.g. 150 m at Station E and 200 m at Station F). Naked ciliates were always abundant in the top 50 or 60 m at Stations B, C and D. The highest density of naked ciliates occurred in the 20 m layer at Station B, 7,505 ind$\cdot L^{-1}$. The largest number and volume of nauplii were almost always observed in the chlorophyll maximum layer indicated by hatches (cf. Fig. 29), although this was not the case for tintinnids and small copepods.

Table 22 gives the integrated biomass of the total microzooplankton and net zooplankton communities. As with the surface microzooplankton communities (Table 20), the vertically integrated biomass of microzooplankton were abundant in the northern sea areas. The mean biomass in the northern two stations (B and C)

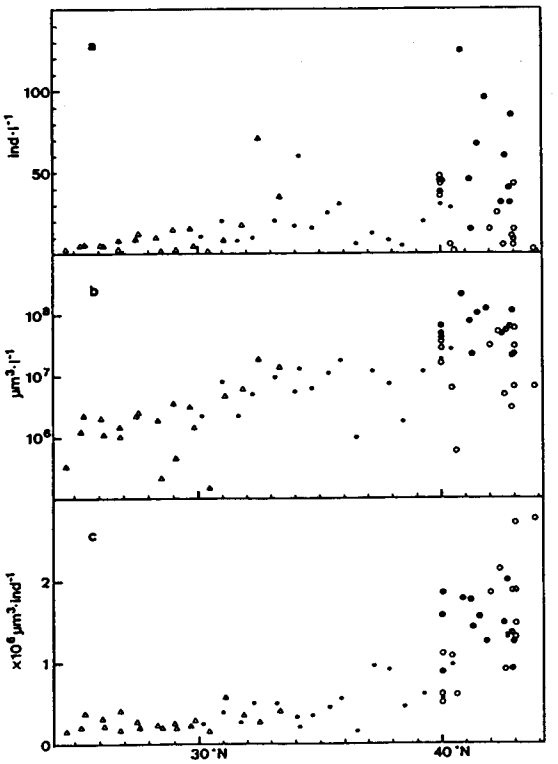


Fig. 33. Latitudinal variations in the total number (a), volume (b), and average size (c) of copepod nauplii in the surface water. Symbols denote the sea area, i.e., Subarctic water I, total chlorophyll *a* concentration of more than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles and dots); Subarctic water II, total chlorophyll *a* concentration of less than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles); transition waters, water temperature between 10 and 20°C (closed circles); subtropical waters, water temperature higher than 20°C (open triangles).

was significantly higher than that in the southern three stations (D, E, and F) ($p < 0.05$). The highest and lowest total microzooplankton biomass were observed at Stations C and E, respectively. The difference between the two stations was 5.3 g wet wt$\cdot m^{-2}$ or factor of ca. 5. On the other hand, the highest biomass of net zooplankton was observed at Station C, being one order of magnitude higher than the lowest one at Station E. The difference of these two values was 72.8 g wet wt$\cdot m^{-2}$. Net zooplankton in the northern two stations (B and C) was higher than that in the southern three stations (D, E, and F). However, the difference between their mean values was insignificant ($p > 0.05$). This may result from the large variation in the former area (30.4–80.3 g wet wt$\cdot m^{-2}$). Relative abundance of microzooplankton to net zooplankton varied between 8.3–30.4%. Difference between the northern (Stations B and C) and southern (Stations D, E, and F) sea areas was not significant ($p > 0.05$). A clear trend suggesting the relative abundance of microzooplankton to net zooplankton is low in the former and high in the latter was not obtained.

V-2. *Discussion*

From the results of this part, it is shown that phytoplankton biomass is high in the northern region and that percent contribution of large size phytoplankters is high in the subarctic region while the phytoplankton communities were predominat-

Table 21. Regional comparisons of mean values of number, volume, and average size of naked ciliates, tintinnids, copepod nauplii, and small copepods between the surface water of the subarctic, transition (TR) subtropical areas (ST) of the western North Pacific Ocean using Student's t-test or Cochran-Cox test. Subarctic water is divided into two cases ; total chlorophyll *a* concentration more (SAI) and less (SAII) than 1.0 $\mu g \cdot l^{-1}$.

Number

	Nakaed ciliates			Tintinnids			Nauplii			Copepodites		
Sea area	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST
SAI	<	ns	>>>	ns	>>>	>>	>>	>>	>>>	>>	>>	>>>
SAII		>>	>>>		>>	>		ns	ns		ns	
TR			>>			ns			ns			>

Volume

	Naked ciliates			Tintinnids			Nauplii			Copepodites		
Sea area	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST
SAI	ns	>>	>>>	>>>	>>>	>>>	>>	>>>	>>>	>>	>	>>
SAII		>>	>>>		>	>		>	>>		ns	ns
TR			>>			ns			>			ns

Average size

	Naked ciliates			Tintinnids[1)]			Nauplii			Copepodites		
Sea area	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST	SAII	TR	ST
SAI	>	ns	ns	>>	ns	ns	ns	>>>	>>>	ns	ns	ns
SAII		>	>>		ns	<<		>>>	>>>		ns	<
TR			ns			<			>>			ns

ns, difference is not significant.

>, >>, and >>> denote that sea area in the row is larger than in the column at $p<0.05$, 0.01, and 0.001, respectively.

< and << denote that sea area in the row is smaller than in the column at $p<0.05$ and 0.01, respectively.

[1)], extremely high values obtained around 40°N in SAII and TR are eliminated.

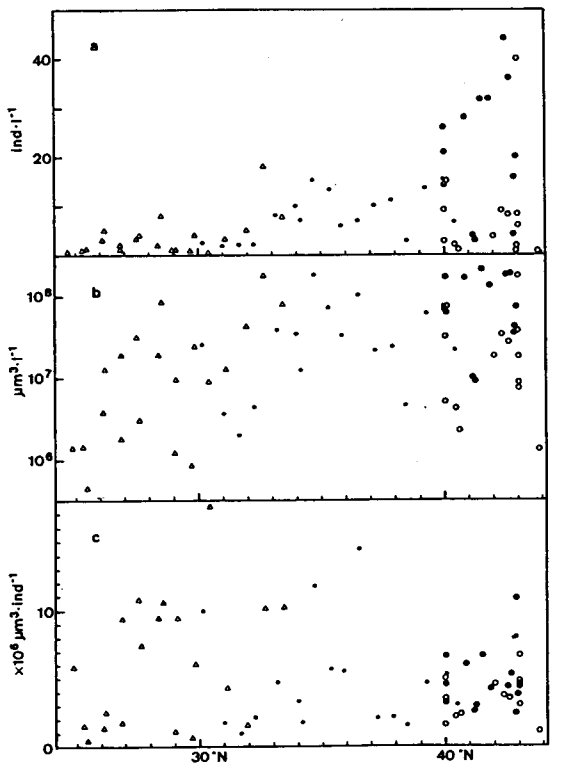


Fig. 34. Latitudinal variations in the total number (a), volume (b), and average size (c) of small copepods in the surface water. Symbols denote the sea area, i.e., Subarctic water I, total chlorophyll *a* concentration of more than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles and dots); Subarctic water II, total chlorophyll *a* concentration of less than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles); transition waters, water temperature between 10 and 20°C (closed circles); subtropical waters, water temperature higher than 20°C (open triangles).

ed by small size phytoplankters in the subtropical region (Table 16), as shown by Furuya and Marumo (1983). As expected, the transition water mass showed characteristics intermediate to the other two water masses.

In the subtropical and transition regions, the phytoplankton community is mainly composed of the picoplankton fraction ($<2\ \mu m$) (84% and 75%, respectively), while the contribution of $>10\ \mu m$ size fraction to the total chlorophyll *a* concentration is very small in these water masses (Table 16). The percent contributions of picoplankton are comparable to the results in the subtropical Hawaiian waters (80%; Takahashi and Bienfang, 1983), in the western North Pacific Ocean and China Sea (>70%; Takahashi and Hori, 1984) and in the Gulf of Maine (70–80%; Glover *et al.*, 1985b). Their importance in the estimation of primary production in oligotrophic subtropical waters has been documented (e.g. Stockner, 1988).

In subtropical waters, the coefficient of variation of the chlorophyll *a* concentration in the surface was very low (less than 0.5%) implying a homogeneous system (e.g. Hayward *et al.*, 1983). However, the vertical profile of chlorophyll *a* concentration showed subsurface biomass peaks (e.g. 100 m at Station F) (Fig. 29). Slight differences in the size composition of phytoplankters were observed between the surface and subsurface chlorophyll maximum layer. This is in contrast to that observed in the subarctic, where variation in the total concentration and size composition of chlorophyll *a* is pronounced horizontally rather than vertically.

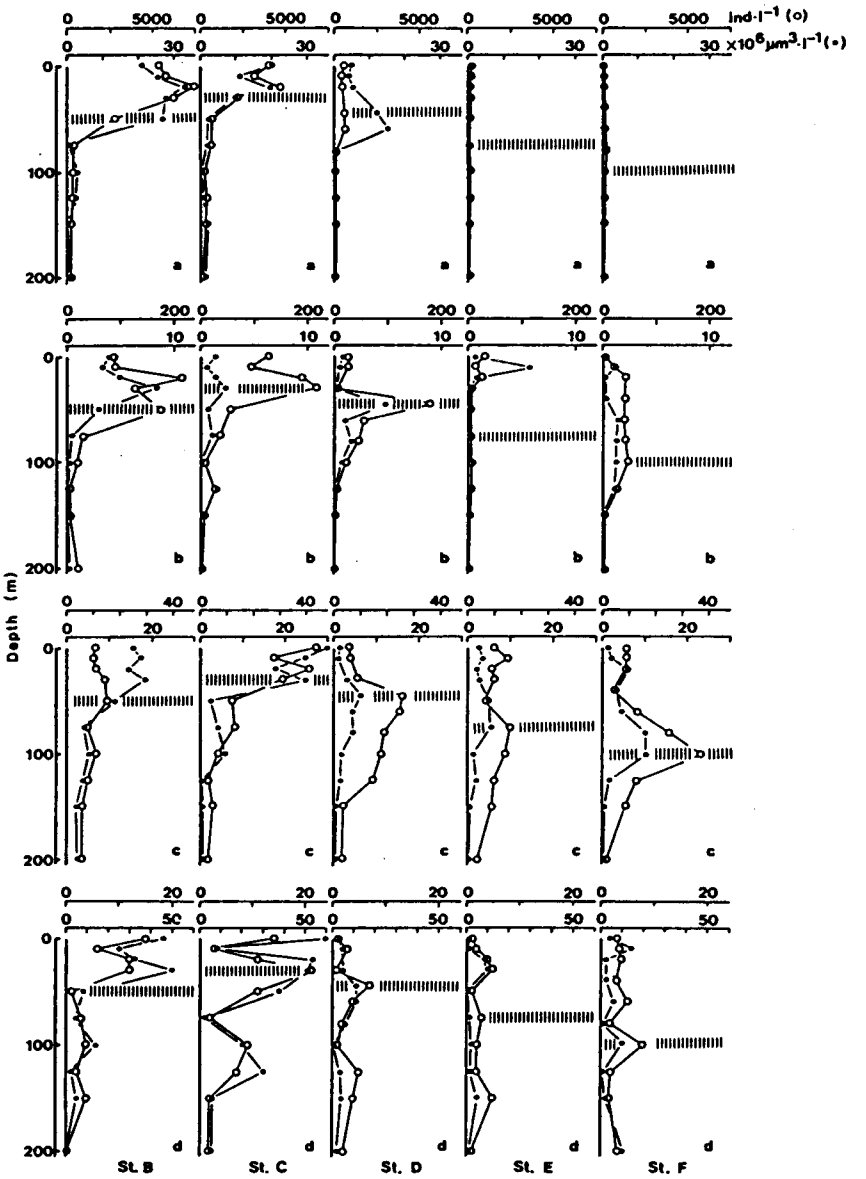


Fig. 35. Vertical distribution of the total number (open circles) and volume (closed circles) of naked ciliates (a), tintinnids (b), copepod nauplii (c) and small copepods (d) at Stations B, C, D, E, and F. Hatched layers indicate chlorophyll maximum layers.

Table 22. Biomass (g wet wt•m^{-2}) of net zooplankton and microzooplankton and their ratio (%) througout the water column (0-200 m) in the western North Pacific Ocean.

Station	Net zooplankton (A)	Micro-zooplankton (B)	Ratio (B/A)
B	30.4	6.6	21.8
C	80.3	6.7	8.3
D	7.6	2.3	30.4
E	7.5	1.4	18.9
F	7.9	2.1	26.0

In the subarctic waters, differences both in the total concentration and the size composition of chlorophyll *a* among the stations were large (cf. Fig. 27a). At the stations where the total chlorophyll *a* concentration was less than 1.0 μg•L^{-1} in the subarctic waters (=SAII), about half of the total chlorophyll *a* concentration was composed of picoplankton. On the other hand, it is shown that the high phytoplankton biomass within the subarctic waters (=SAI) is mainly attributed to the large size fraction (>10 μm) (Table 16). Since the size composition of chlorophyll *a* varies with the stages of phytoplankton bloom (Fig. 9), it is assumed that Stations 1-27 are in different stages; SAI was in the progressed stage of the bloom, SAII was before (or after) the bloom. This suggests that phytoplankton blooms occur at different times resulting in the horizontal variation in the phytoplankton community structure within the same water mass. Moreover, this implies that in the subarctic water contribution of picoplankton is large if phytoplankton bloom does not occur.

Temporal changes in the total concentration and size composition of chlorophyll *a* were mainly caused by phytoplankters larger than 10 μm (Table 18), primarily diatoms (Table 19). From these it is apparent that the total biomass as well as the percentage contribution by the different size fractions are strongly affected by the bloom of diatoms. Primary production in the subarctic waters varies with season and is characterized by a high annual production (Taniguchi, 1981). It has been shown that about half of the annual primary organic carbon in Funka Bay water is produced during the spring bloom wherein diatoms larger than 10 μm dominate. This may be the typical case in the subarctic oceanic waters dealt with in this study.

Booth (1988), however, showed that in the eastern North Pacific Ocean (50-53°N, 145°W) the nanoplankton fraction dominated by flagellates and coccoids, not diatoms, is associated with high chlorophyll *a* concentrations. This may result from the fact that Booth's data was obtained from waters in which the total chlorophyll *a* concentration was less than 1.0 μg•L^{-1}. My data collected in the low chlorophyll *a* concentration waters (case II) also showed the importance of small size phytoplankton (Table 16, Figs. 27b and 28b). It is well known that, in the eastern North Pacific Ocean, phytoplankton biomass is low through the year (McAllister *et al.*, 1960). The highest chlorophyll *a* concentration recorded from the surface

waters at Station P (50°N, 145°W) between 1958 and 1974 was 2.08 $\mu g \cdot L^{-1}$ [Anderson *et al.*, 1977 ; cited from Booth (1988)]. This concentration is about half of the mean value in the western North Pacific Ocean (Table 16). Kawarada and Sano (1972) also reported high chlorophyll *a* concentration (14.21 $\mu g \cdot L^{-1}$), which was due to the outburst of diatom (*Thalassiosira nordenskioeldii*) [this species is larger than 10 μm (e.g. Taylor and Waters, 1982)], in the western North Pacific Ocean (48°N, 155°E). Then, it may be concluded that phytoplankton biomass characterized by diatoms larger than 10 μm in the western North Pacific Ocean is higher than that in the eastern part, where the outburst of diatom is seldom observed.

Recent studies show that the major component of the picoplankton community is cyanobacteria (Johnson and Sieburth, 1979 ; Waterbury *et al.*, 1979). It is also known that the density of cyanobacteria does not tend to be very abundant at water temperature <10°C (Murphy and Haugen, 1985). However, chlorophyll *a* concentration in the picoplankton fraction was high (Table 16) in the subarctic water where water temperature was below 10°C (Fig. 26). Hence, it may be considered that the higher chlorophyll *a* concentration of this size fraction in the subarctic waters is due to picophytoplankton other than cyanobacteria. Indeed, the picophytoplankton community is characterized by cyanobacteria in the southern water (36.5-41.0°N, 155.0°E) but by picophytoplankton other than cyanobacteria in the northern water (42.5-44.0°N, 155.0°E) of the western North Pacific Ocean (Odate *et al.*, 1990).

The dominant group in the microzooplankton assembly, in terms of number, was naked ciliates (Table 20), coinciding with earlier studies (Beers and Stewart, 1971 ; Endo *et al.*, 1983 ; Taniguchi, 1984). Regional distribution of naked ciliates (Fig. 31a and Table 20) tended to be more in the subarctic waters (Taniguchi, 1984) and less in the subtropical waters (Endo *et al.*, 1983). Within the subarctic waters, however, the density in SAI, where spring phytoplankton bloom had progressed as mentioned before, was significantly lower than that in SAII (Table 21). This implies that naked ciliate density became lower during the spring phytoplankton bloom. The insignificant difference in the total volume of naked ciliates between SAI and SAII results from the predominance of large-sized ones in SAI (Table 21). Considering the small size of naked ciliates (Fig. 31c) and the dominance of large-sized phytoplankton during the spring phytoplankton bloom (Fig. 27), the decrease of density due to the reason that relatively smaller naked ciliates could not graze upon the large-sized phytoplankton.

Tintinnids were more abundant in the subarctic waters than that in TR and ST (Table 20). Although difference of tintinnids densities was insignificant, that of total volume was significant between SAI and SAII. This suggests that the body size increased during phytoplankton bloom. In fact, average body size in SAI was significantly higher than that in SAII except for two high values in SAII. It is generally considered that oral diameter of tintinnid restricts the upper limit of available food size, and that this organisms effectively utilizes the particles smaller than half of their oral diameter (Heinbokel, 1978b). Present results showed that large species of tintinnids predominated during the phytoplankton bloom. This change in dominant species of tintinnids may be affected by food availability in size,

since large-sized phytoplankton ($>10\ \mu$m) predominated during the phytoplankton bloom (Fig. 27a). These changes in body size of naked ciliates and tintinnids may be survival of the fittest for food size.

There was no change in the average body sizes of nauplii and small copepodites between during and not during the phytoplankton bloom period. This can be interpreted to mean these groups were not affected by the drastic change in phytoplankton size composition, being different from the former two microzooplankton groups.

Microzooplankton and net zooplankton abundance was high in the northern sea area, being consistent with earlier studies (Endo *et al.*, 1983; K. Odate, 1986; Taniguchi, 1977a, b, 1984). This may result from the fact that the available phytoplankton biomass is much in the northern sea area and less in the southern one (Kawarada and Sano, 1972; Fig. 27). It is hypothesized that relative abundance of microzooplankton biomass to net zooplankton biomass is generally high in the subtropical waters and low in the subarctic waters (Endo *et al.*, 1983; Taniguchi, 1984, 1985), because percent contribution of large size phytoplankters is high in the latter (Furuya and Marumo, 1983; Fig. 27), and the size of available food affects the size distribution of the zooplankton (Marshall and Orr, 1956; Nival and Nival, 1976; Parsons and LeBrasseur, 1970; Taniguchi, 1977a, b, 1984). In this study, the relative abundance except for at Station C was almost the same as that previously reported for the western North Pacific Ocean, 9.9–18.1% (Endo *et al.*, 1983). The low percentage was attributed to the large biomass of net zooplankton, which was about two times higher than the annual maximum biomass of net zooplankton observed in the subarctic water (K. Odate, 1986). In high latitude sea areas, the maximum biomass of net zooplankton in a year is observed after the spring phytoplankton bloom (Cushing, 1959; Heinrich, 1962; K. Odate, 1986). Hence, it may be expected that the percentage at Station C would increase to some extent. It can be said that the relative abundance of microzooplankton to net zooplankton temporarily becomes lower after the spring phytoplankton bloom in the northern sea area. However, we can not say that the relative abundance of microzooplankton in the northern sea area is always lower than that in the southern one. This may result from temporally different variations in microzooplankton biomass and net zooplankton biomass, that is, microzooplankton biomass is large during the spring phytoplankton bloom, but net zooplankton biomass becomes high after the bloom. These results do not always support the hypothesis provided by Endo *et al.* (1983) and Taniguchi (1984, 1985).

Regional biomass ratios of microzooplankton and net zooplankton in subarctic, transition and subtropical waters in the western North Pacific Ocean in spring were 5–16 : 2 : 1 (Table 20) and 3.7 : 1.3 : 1 (K. Odate, 1986), respectively. These give the ratio of relative abundance of microzooplankton to net zooplankton in these water masses as 1.4–4.3 : 1.5 : 1, which implies that the relative abundance in subarctic waters may not be lower than that in subtropical waters. This suggests that herbivory of larger zooplankton may be weaker than that of smaller ones. This point will be considered in the next chapter.

VI. Practical Applications of Grazing Rate Estimation

Using the phytoplankton biomass and zooplankton biomass data, which has been obtained in Funka Bay (Station 30, from April 1984 to May 1985) and in the western North Pacific Ocean, the grazing rate can be estimated based on food consumption by equation 6.

VI-1. Estimation of annual grazing rate in Funka Bay

Phytoplankton biomass (data source is Fig. 7), which was converted from the chlorophyll standing stocks using different carbon to chlorophyll ratios for each size fraction (data source is Fig. 9). Antia *et al.* (1963) determined the carbon to chlorophyll ratio of 25 for the total phytoplankton community in the blooming period. The carbon to chlorophyll ratio of 25 was adopted for the $>10\,\mu$m size fraction, since this size fraction was dominant during the spring phytoplankton bloom. It is known that the slope of the regression lines of cellular carbon on cellular volume is significantly lower than that of cellular chlorophyll *a* on volume (Mullin *et al.*, 1966; Strathmann, 1967), except for in case of cyanobacteria. This means that carbon to chlorophyll ratios of smaller cells is lower than that of larger ones. Then, it is assumed that the carbon to chlorophyll ratio is 10 for the 2–10 μm size fraction. Such a trend is not the case for cyanobacteria, which is the major component of the $<2\,\mu$m size fraction. Since most of the phytoplankton community is composed of picophytoplankters smaller than 2 or 3 μm (Li *et al.*, 1983; Takahashi and Bienfang, 1983; Glover *et al.*, 1985a, b), the carbon to chlorophyll ratio of 100, which is generally used for the various sea areas (Holm-Hansen, 1969),

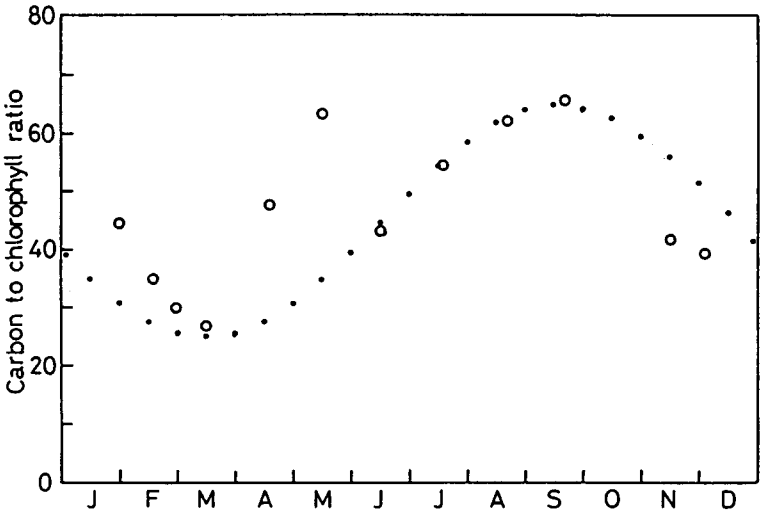


Fig. 36. Seasonal variations in the calculated total carbon to chlorophyll ratios (open circles). Seasonal fluctuation in the carbon to chlorophyll ratio proposed by McAllister (1969) is modified and shown by closed circles, i.e., $F=45-20\cos[2\pi(T-75)/365]$, where F is the carbon to chlorophyll ratio and T is the day of the year.

is assumed for the $<2\,\mu$m size fraction.

Seasonal fluctuations in calculated total carbon to chlorophyll ratio is shown in Fig. 36. The ratio should be between 10 and 100, since used carbon to chlorophyll ratios were 25, 10, and 100, for the $>10\,\mu$m 2-10 μm, and $<2\,\mu$m size fraction, respectively. The total carbon to chlorophyll ratio became high in summer and low in winter, reflecting the dominant size fraction (Fig. 9). This trend is, however, consistent with the results of McAllister (1969), who proposed that the ratio varies along the cosine curve with time, i.e., $F=30-15\cos[2\pi(T-15)/365]$, where F is the carbon to chlorophyll ratio and T is the day of the year. The calculated ratios were almost all distributed on the cosine curve, i.e. $F=45-20\cos[2\pi(T-75)/365]$. Moreover, the calculated total carbon to chlorophyll ratio of March 15 was 26.4. On that day, the relationship between concentrations of chlorophyll and particulate organic carbon was significant ($r=0.93$, $n=8$, $p<0.001$), while the slope of the regression line, which gives the carbon to chlorophyll ratio (Eppley *et al.*, 1977), was 26.6. These results may suggest the validity of the assumed carbon to chlorophyll ratios.

Seasonal variations in abundance of large copepods, small copepods, copepod nauplii, and ciliates observed from April 1984 to May 1985 have been described (Figs. 13-17). The phagotrophic dinoflagellates cell density during this period was high only during the spring phytoplankton bloom (March to April), with the maximum cell density of 991 cells$\cdot$L^{-1} (Fig. 37). During the other seasons their densities were extremely low.

The total grazing rate based on the food consumptions were much higher than primary production almost through the year (55-463% of daily primary production) (Fig. 38). The annual grazing rate by all heterotrophs was 308 g C$\cdot$m$^{-2}\cdot$yr^{-1}, which

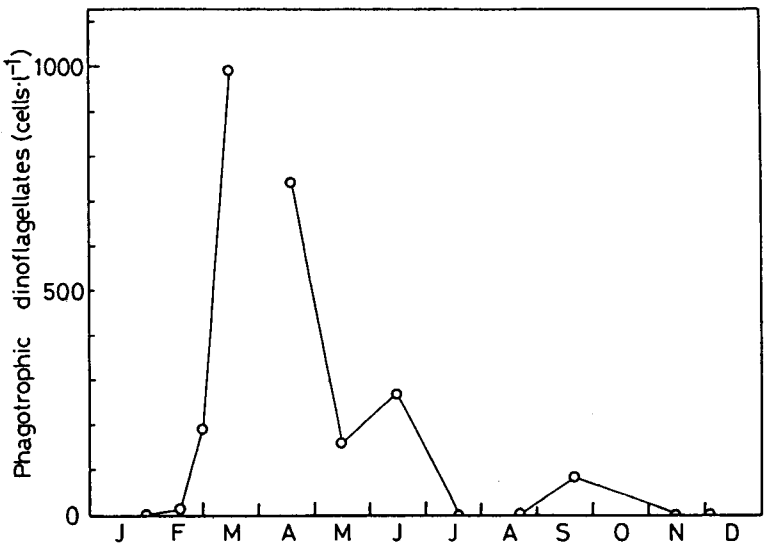


Fig. 37. Monthly changes in the averaged cell density of phagotrophic dinoflagellates throughout the water column (0-30 m).

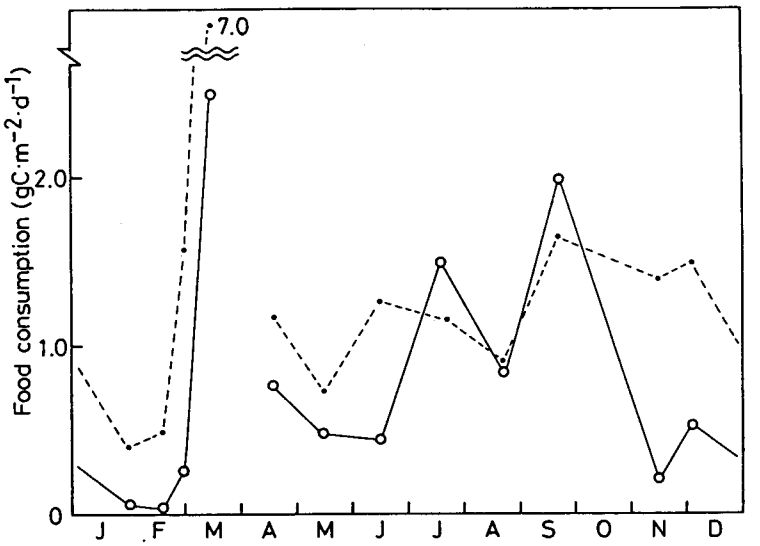


Fig. 38. Monthly changes in grazing rate based on food consumption without consideration to the size-selectivity (open circles). The maximum available food amount (phytoplankton biomass + daily production) is also shown (closed circles and broken line). The food consumption can not exceed the maximum available food amount.

reached to 216% of the yearly primary production. However, this estimation may be far from realistic, because the total daily grazing rates exceeded the total amount of phytoplankton biomass and production during July and September. If such a high grazing activity did occur, the phytoplankton community would perish. Thus, in this estimation it can be considered that the upper limits would be impossible to accomplish.

There is a general consideration that large zooplankters require large food particles and *vice versa* (Parsons and LeBrasseur, 1970; Taniguchi, 1977a, b). Table 23 shows the assumed size selectivity of each heterotrophs considered here. That is, it is assumed that large copepods could not graze upon phytoplankton of smaller than 10 μm throughout the year (e.g. Marshall and Orr, 1956) and that small copepods graze upon the 2-10 μm size fraction, when they are small, and eat on the >10 μm size fraction, when they are large (Nival and Nival, 1976). It is considered that microzooplankters would like to graze upon particles smaller than 10 μm (e.g. Burkill *et al.*, 1987). The mean weight of ciliates was considerably small among the total zooplankton assembly. Then, it is assumed that they eat upon the <2 μm size fraction. Since the size of nauplii showed a large seasonal variation, they eat particles larger than 10 μm, when they are large, while they eat the 2-10 μm size fraction when they are small. For phagotrophic dinoflagellates, it is assumed that their prey size is larger than 10 μm, because they selectively graze upon diatoms larger than 10 μm (e.g. Plate II).

Estimations of grazing rate based on the size-selective assumption are given in Fig. 39. Grazing rates in this version were well consistent with primary production.

Table 23. Assumed size-selective grazing of heterotrophic organisms dealt with in the present study.

Heterotrophs groups	Period	Prey size
Large copepods	(always)	>10 μm
Small copepods	(larger than their mean size)	>10 μm
	(smaller than their mean size)	2-10 μm
Copepod nauplii	(larger than their mean size)	>10 μm
	(smaller than their mean size)	2-10 μm
Ciliates	(always)	<2 μm
Phagotrophic dinoflagellates	(always)	>10 μm

It has been shown that, from August to September, vertical flux of intact phytoplankton cell at the 74 m layer was 0.001 g C$\cdot$m$^{-2}\cdot$d^{-1} (Table 5). Accepting this value to the 30 m layer, grazed phytoplankton carbon, i.e., primary production−(difference of phytoplankton biomass + phytoplankton flux), during this period was calculated as 13.7 g C$\cdot$m^{-2} which is almost the same level as the grazing rates based on food consumption of 15.7 g C$\cdot$m^{-2} (Table 24).

The grazing rates of each organisms are summarized in Table 25. During summer (from April to November), 76% of the total grazing was accounted for by ciliates, suggesting the organic carbon flow from picoplankton (mostly cyanobacter-

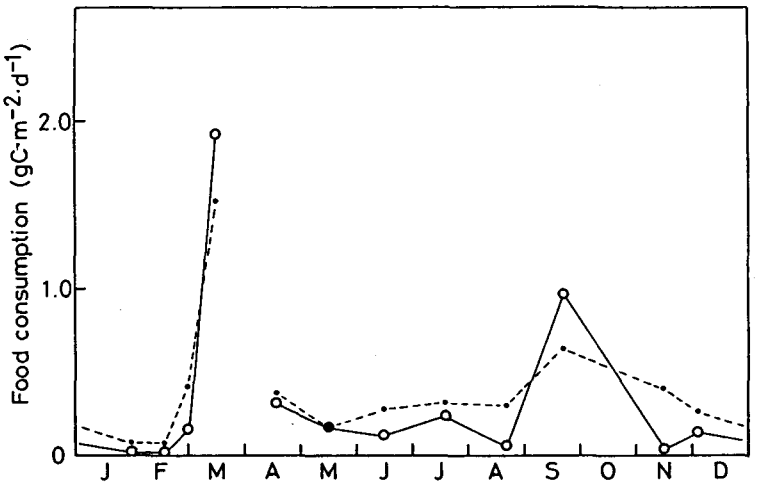


Fig. 39. Monthly changes in grazing rate based on food consumption with consideration to the size-selectivity (open circles). Daily primary production is also shown with closed circles and broken line.

Table 24. Grazed carbon ($g\,C \cdot m^{-2} \cdot period^{-1}$) within the top 30 m at Station 30. Food consumption is also shown.

Period	B_t-B_0	Primary production	Flux	Grazed carbon	Food consumption
Aug. 21-Sep. 21 31 days	0.7	14.4	0.03	13.7	15.7

Table 25. Food consumption ($g\,C \cdot m^{-2} \cdot period^{-1}$) and relative contribution to the total grazing (%) within the top 30 m at the central part of Funka Bay, Japan. Primary production ($g\,C \cdot m^{-2} \cdot period^{-1}$) is also shown.

Season	Food consumption						Primary production
	Large copepods	Small copepods	Copepod nauplii	Ciliates	Dino-flagellate	Total	
Summer Apr.-Nov. 212 days	3.4 (5%)	9.1 (14%)	2.5 (4%)	49.2 (76%)	0.4 (1%)	64.6	76.9
Winter Nov.-Feb. 104 days	4.4 (5%)	1.0 (14%)	0.1 (48%)	1.2 (16%)	0.2 (1%)	7.3	19.1
Spring Mar.-Apr. 49 days	9.1 (17%)	0.8 (1%)	31.0 (58%)	2.7 (5%)	9.8 (18%)	53.4	46.3
Year Apr.-Apr. 365 days	16.9 (13%)	10.9 (9%)	34.1 (27%)	53.1 (42%)	10.3 (8%)	125.4	142.3

ia, see Fig. 12) to ciliates. Large copepods were the major grazer in winter (from November to February). On the other hand, 58% and 18% of grazing during the spring was due to copepod nauplii and phagotrophic dinoflagellates, respectively. The rank order of them was different from that of 1986. This might result from yearly variations. On an yearly basis, the annual grazing was 125 $g\,C \cdot m^{-2} \cdot yr^{1}$ (=88% of primary production).

VI-2. Estimation of grazing rate in the western North Pacific Ocean

Phytoplankton carbon were converted from chlorophyll *a* concentration with carbon to chlorophyll ratios of 50, 20, and 200 for $>10\,\mu m$, 2-10 μm, and $<2\,\mu m$ size fraction, respectively. These were two times higher than those used in Funka Bay (25, 10, and 100). However, the relationship between chlorophyll concentration and particulate organic carbon concentration showed a two times higher slope. Then, I chose those high carbon to chlorophyll ratios. As with the estimation in Funka Bay, size-selectivities were considered (Table 23).

The total zooplankton grazing rate with equation 6 and food requirement by

Table 26. Grazing rate (GR) and food requirement (FR) of net zooplankton, small copepods, microzooplankton (copepod nauplii and ciliates), and others within the water column (0–200 m) in the western North Pacific Ocean (mg C·m^{-2}·d^{-1}).

Station		Net zooplankton	Small copepods	Micro-zooplankton	others	Total
B	GR	2.9	2.2	144.3	3.0	152.4
	FR	92.9	14.5	39.5	1.7	148.6
	GR/FR (%)	3.1	15.2	36.5.3	17.65	102.6
C	GR	18.3	51.3	333.2	6.5	409.3
	FR	544.1	94.8	167.0	4.5	810.4
	GR/FR (%)	3.4	54.1	199.5	141.4	50.5
D	GR	1.3	1.4	118.1	1.0	121.8
	FR	122.6	72.3	296.5	3.5	494.9
	GR/FR (%)	1.1	1.9	39.8	28.6	24.6
E	GR	1.8	0.7	31.0	1.2	34.7
	FR	123.0	63.7	133.4	6.8	326.9
	GR/FR (%)	1.5	1.1	23.2	17.6	10.6
F	GR	2.8	1.9	75.6	3.5	83.8
	FR	165.6	116.3	254.6	10.1	546.6
	GR/FR (%)	1.7	1.6	29.7	14.7	15.3

Ikeda and Motoda's methods are as shown in Table 26. At all stations, the contributions of net zooplankton to the total grazing was less than 10%. More than 70% was accounted for by microzooplankton. Such a trend coincides with the results of Frost (1987), who speculated that more than 75% of the total phytoplankton grazing may be attributed to microzooplankton in the open subarctic waters.

Regional changes in the grazing rate by the zooplankton community, except net zooplankton, observed in the surface water are shown in Fig. 40, together with the food requirement. Higher grazing rates were estimated in northern waters. While the food requirements were high in southern waters, this being consistent with the results of Ikeda and Motoda (1978). The high grazing rates were attributed to the high phytoplankton biomass, while the low food requirements were due to the low water temperature of the subarctic waters. Regional variations in the grazing rate was larger than that of the food requirement. The grazing rate, which was much lower than the food requirement in ST, surpassed the food requirements in SAI and SAII.

Table 27 summarizes the grazing rate and food requirement by zooplankters in the surface waters of each sea area. In SAI, the grazing rate was about one order of magnitude higher than the food requirement (700–2,941%). A high grazing rate was also obtained in SAII, where the grazing rate was 47–431% of the food require-

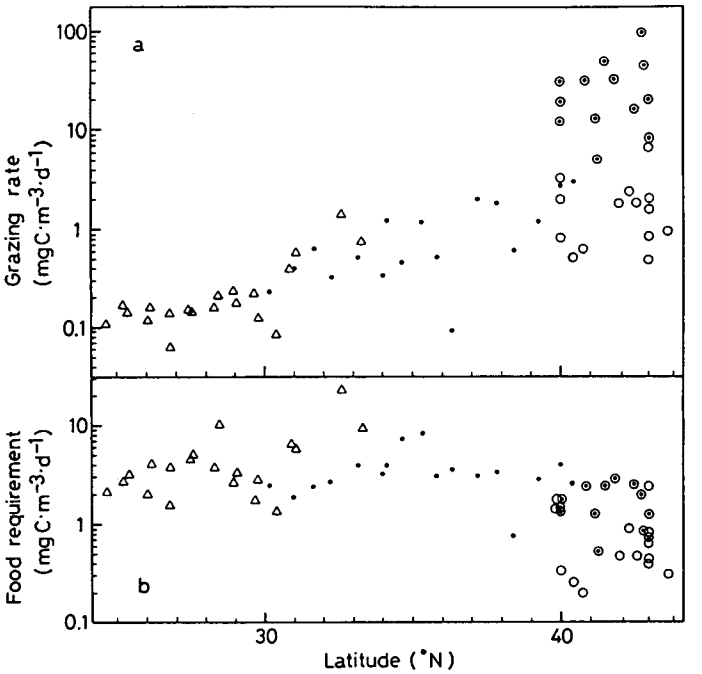


Fig. 40. Latitudinal variations in grazing rate (a) and food requirement (b). Symbols denote the sea area, i.e., Subarctic water I, total chlorophyll *a* concentration of more than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles and dots); Subarctic water II, total chlorophyll *a* concentration of less than 1.0 $\mu g \cdot L^{-1}$ and water temperature lower than 10°C (open circles); transition waters, water temperature between 10 and 20°C (closed circles); subtropical waters, water temperature higher than 20°C (open triangles).

ment. In TR and ST, however, the grazing rate was only 3-57% and 1-12% of the food requirement, respectively.

Figure 41 shows the factor of the total grazing rate within water column (0-200 m) to the grazing rate of the zooplankton community observed in surface waters at the same station. Between them a significant correlation was obtained ($\log Y = -0.657 \log X + 2.11$; $r = -0.947$, $p < 0.02$, $n = 5$). The factor is high when the grazing rate in the surface is low. This results from the fact that the high grazing layer was deep in the southern sea area, since the maximum layer of chlorophyll *a* and microzooplankton biomass deepened going the southward.

Using this correlation, the surface grazing rate (Fig. 40a) can be converted to the total grazing rate in water column and is summarized in Table 28. In the subarctic waters in which the grazing rate was 98-593 mg $C \cdot m^{-2} \cdot d^{-1}$ and primary production was 205-500 mg $C \cdot m^{-2} \cdot d^{-1}$ (Takahashi and Ichimura, 1972). In ST, primary production was 120-380 mg $C \cdot m^{-2} \cdot d^{-1}$ (Takahashi and Ichimura, 1972), which is two to three times higher than the grazing rate.

Table 27. Averaged grazing rate (GR) and food requirement (FR) by zooplankters observed in the surface waters of the subarctic, transition, and subtropical waters in the western North Pacific Ocean (mg C·m^{-3}·d^{-1}). Subarctic water is divided into two cases; total chlorophyll *a* concentration more (Subarctic I) and less (Subarctic II) than 1.0 μg·l^{-1}.

Sea area	Naked ciliates	Tintinnids	Copepod nauplii	Copepod small	Other	Total
Subarctic I (n=13)						
GR	2.681	7.471	13.117	5.167	0.214	28.650
FR	0.103	0.254	0.669	0.737	0.013	1.776
FR/FR (%)	2,603	2,914	1,961	701	1,646	1,613
Subarctic II (n=14)						
GR	0.634	0.297	0.736	0.139	0.033	1.839
FR	0.147	0.071	0.239	0.293	0.009	0.759
GR/FR (%)	431	418	308	47	367	242
Transition (n=17)						
GR	0.447	0.060	0.409	0.053	0.036	1.004
FR	0.786	0.166	0.771	1.652	0.083	3.458
GR/FR (%)	57	36	53	3	43	31
Subtropical (n=20)						
GR	0.058	0.065	0.107	0.014	0.031	0.275
FR	0.740	0.782	0.887	2.259	0.345	5.013
FR/FR (%)	8	8	12	1	9	6

VI-3. *Discussion*

The results obtained in Funka Bay may support the opinion that the grazing rate based on food consumption (=equation 6) gave a reasonable value to explain the phytoplankton dynamics not only for the spring ecosystem as mentioned before, but also for the summer one. These results imply that phytoplankton production are immediately grazed upon by heterotrophic micro-organisms within the productive zone of the top 30 m. The results also showed that ca. 80% of annual phytoplankton production is linked to microheterotrophs, i.e., copepod nauplii, ciliates, and phagotrophic dinoflagellates.

Food requirement calculated by the Ikeda-Motoda method gives enough carbon for routine digestion, respiration, and production (Ikeda and Motoda, 1978). Table 26 indicates that net zooplankton predominated by copepods depend on phytoplankton carbon for less than 10% of their food requirement at every station. This means that, in TR and ST, zooplankton were not supplied only with phytoplankton. In particular in ST, they depend upon phytoplankton for only 5% of the require-

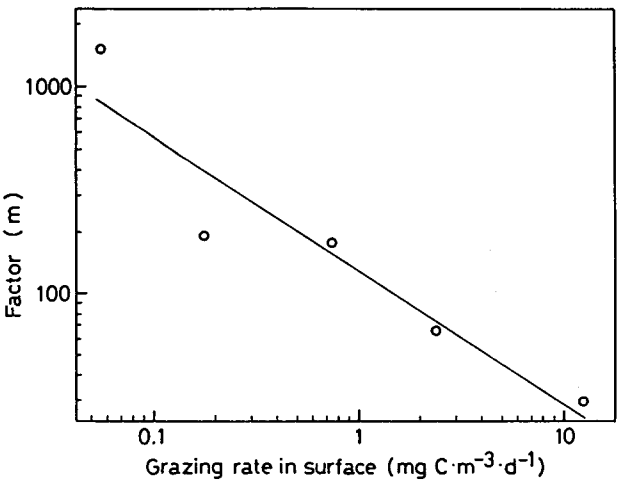


Fig. 41. Factor of the total zooplankton grazing rate within water column (Station B-F) to the grazing rate of zooplankton community observed in surface water at the same station. Regression line was obtained by the least square method was significant.

Table 28. Estimated grazing rate by total zooplankters within water column (0-200 m) in the subarctic, transition, and subtropical waters in the western North Pacific Ocean (mg C·m^{-2}·d^{-1}). Primary production are also listed. Subarctic water is divided into two cases; total chlorophyll *a* concentration more (Subarctic I) and less (Subarctic II) than 1.0 μg·l^{-1}.

Sea area	Grazing rate		Primary production*	
	Range	Mean	Range	Mean
Subarctic I	214-593	370	205-500	358
Subarctic II	98-186	145		
Transition	55-183	116	—	280
Subtropical	49-142	75	120-380	260

*, Takahashi and Ichimura (1972).

ment on the average. To meet their requirement, they have to eat organic matter other than phytoplankton (e.g. organic detritus, bacteria, heterotrophic flagellates or microzooplankton). As suggested in the former chapter, weak herbivory of large zooplankton is expected from the present calculations, then relative abundance of microzooplankton to net zooplankton is not always high in the southern sea area. That is, net zooplankton maintain their metabolic activity by eating organic carbon from sources other than phytoplankton.

In the subarctic waters, the grazing rate was almost the same level as primary production. In the southern sea areas, however, the former was less than the latter. It is known that dominant phytoplankton size in the subtropical open waters is of

the picoplankton size (e.g. $<2\,\mu$m) (Stockner, 1988). The present study also revealed that the dominant size of phytoplankton in the transition water was <2 μm, too. Takahashi and Bienfang (1983) demonstrated that the sinking velocity of picoplankton was negligible. Hence, sinking loss of phytoplankton biomass within water column could not be expected and most phytoplankton production may be considered to be grazed upon by heterotrophs. Less portion of the grazing rate to primary production in the southern sea areas may suggest that the large portion of primary production is grazed upon by other heterotrophs (e.g. heterotrophic flagellates), suggesting the importance of the microbial loop (Azam *et al.*, 1983).

It is possible to consider that most of the daily primary production is consumed by heterotrophs in the open waters of the western North Pacific Ocean as well as the neritic waters of Funka Bay. The key heterotrophic group was microzooplankton in all sea areas. This is different from the classical concept on the energy flow from primary to secondary producers as suggested by Steele (1974).

VII. General Consideration

Steele (1974) has provided the scheme of a food web in the North Sea (Fig. 42). Present results show that phytoplankton sedimentation (process 2 in Fig. 42) is low in proportion to primary production even during the spring phytoplankton bloom in the neritic waters of Funka Bay. Because phytoplankton in the open waters except during spring phytoplankton bloom is small in cell-size, their sinking velocity is low. It could not be expected that the large portion of primary production was lost from the euphotic zone by sedimentation. This study further revealed that most phyto-

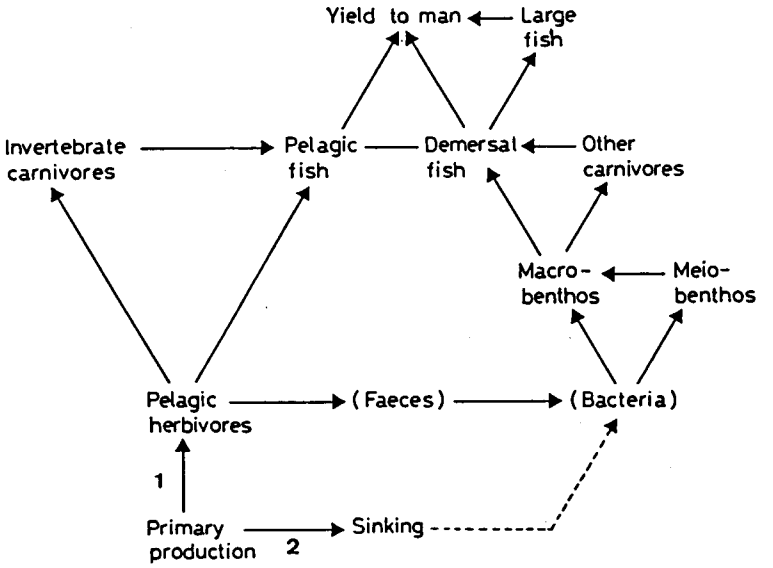


Fig. 42. A food web in North Sea (modified from Steele, 1974).

plankton production is immediately consumed by heterotrophs within the productive zone as speculated by Steele (1974). In the classical food chain concept, primary producers and primary grazers (process 1 in Fig. 42) are considered to be diatoms and copepods, respectively. My results, however, reveal that the former is picoplankton (mostly cyanobacteria) and the latter is microzooplankton (mostly ciliates) during the summer period. Although large-sized diatoms predominate during the spring phytoplankton bloom, large copepods alone can not consume all the phytoplankton production and the major grazers are microzooplankton and phagotrophic dinoflagellates.

If gross growth efficiency of 30% is used (Ikeda and Motoda, 1978), the estimated annual food consumption will be equivalent to the annual secondary production of 38 g C•m^{-2} in Funka Bay. About 76% of the secondary production is accounted for by microzooplankton and phagotrophic dinoflagellates (Table 25). This value implies a transfer efficiency of 27%. Generally, the transfer efficiency varies between 10 and 30% (Cushing, 1971; McAllister, 1972). However, these previously reported values are based on only the net zooplankton collected from 100 or 200 m to the surface. Excluding microheterotrophs, yearly secondary production within the top 30 m is 5.1 g C•m^{-2}, which is equivalent to 4% of the transfer efficiency. The difference in the transfer efficiency of net zooplankton partly resulted from the depth of net towing. Recent studies show that copepods, the major component of the net zooplankton community, are not herbivore-type feeders but omnivore-types, and the dominant grazers are microzooplankton (Frost, 1987). According to Frost (1987), the proportion of total diet of the large calanoid copepods (*Neocalanus* spp.) contributed by phytoplankton is about 25%. He concluded that the major grazers were microzooplankton and the net zooplankton were omnivorous feeders. If the net zooplankton production depends upon organic carbon other than phytoplankton, their production based on the food requirement should not be called secondary production. Moreover, it is considered that the previously reported transfer efficiencies which are based only on net zooplankton data do not represent the true transfer efficiency from primary production to secondary production. Actual secondary production can not be discussed without considering microzooplankton activity.

Since almost all primary production may be consumed by heterotrophs and gross growth efficiency is 30%, transfer efficiency should be 30%. On the other hand, gross growth efficiencies of higher than 50% are established for microheterotrophs (e.g. Heinbokel, 1978a). This suggests that the transfer efficiency of microheterotrophs-dominated communities may be higher than that of net zooplankton dominated ones. It is known that a negative correlation exists between the transfer efficiency and primary production (Blackburn, 1973; Taniguchi, 1973). This may be attributed to the difference in the zooplankton community structure.

It is thought that, in stratified water columns, the nitrogen source of primary producers is mostly ammonia which is excreted by zooplankters. Such primary production is called regenerated production (Dugdale and Goering, 1967). Zooplankton production which depends on regenerated primary production and organic detritus may also be regarded as regenerated secondary production. In the subarctic waters, zooplankters can eat more phytoplankton than their requirements,

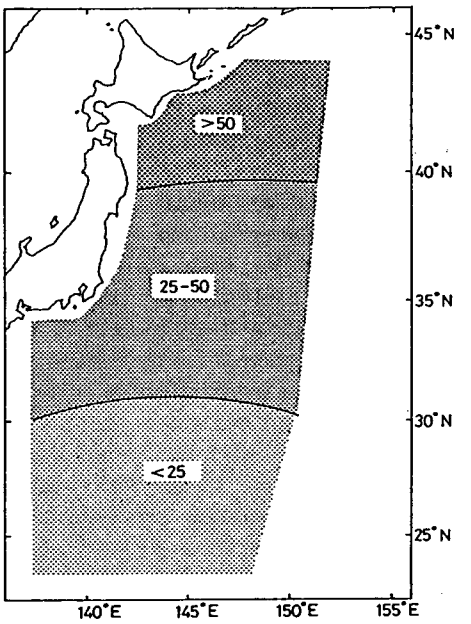


Fig. 43. Shematic distribution of secondary production (mg C•m^{-2}•d^{-1}) estimated in present study.

reflecting a high phytoplankton biomass. This suggests a direct link between primary production and zooplankters. Now, this process may be referred to as new secondary production as opposed to regenerated secondary production.

Secondary production in the western North Pacific Ocean can be also calculated from the grazing rate data (Table 28), assuming gross growth efficiency of 30%. The mean secondary production is 111 mg C•m^{-2}•d^{-1} in the subarctic waters during a spring phytoplankton bloom, 44 mg C•m^{-2}•d^{-1} in the subarctic waters during no bloom, 35 mg C•m^{-2}•d^{-1} in the transition waters, and 22 mg C•m^{-2}•d^{-1} in the subtropical water. Secondary production during phytoplankton bloom in the subarctic waters in four times higher than that in the subtropical waters. Even though during no bloom, secondary production in the former is two times larger than that in the latter. In general, secondary production is high (>50 mg C•m^{-2}•d^{-1}) in the subarctic waters, but low (<25 mg C•m^{-2}•d^{-1}) in the subtropical waters (Fig. 43). This trend that secondary production is high in the northern sea areas and low in the southern sea areas is quite different from the scheme proposed by Ikeda and Motoda (1978). Ikeda and Motoda (1978) estimated secondary production in the western North Pacific Ocean using their methods (=Ikeda and Motoda's methods) and pointed out that the difference of secondary production between water masses may be small. This may result from the fact that their methods do not take into consideraion to phytoplankton biomass as mentioned former. Fig. 43 is different from the previously scheme (i.e. Ikeda and Motoda, 1978) but very reasonable, if fish production is considered. High secondary production in the northern sea areas may supply the feeding needs of migratory fishes (e.g. Pacific saury) in this area.

VIII. Summary

I investigated the temporal and spatial variations in phyto- and zooplankton community structures, considering an aspect of size. Production and sedimentation of phytoplankton and food requirement, consumption, and production of zooplankton were estimated.

1. It is shown that the phytoplankton community is accounted for by species larger than 10 μm during the spring phytoplankton bloom in the subarctic open waters as well as in Funka Bay, while by minute algae less than 2 μm (picophytoplankton) during summer and in the open waters of the western North Pacific Ocean. Phytoplankton species larger than 10 μm are represented by diatoms, and those less than 2 μm are represented by cyanobacteria under a high water temperature condition but by other picophytoplankton under a low water temperature condition.

2. Using the Ikeda and Motoda's methods, food requirements of zooplankton (large copepods, small copepods, copepod nauplii, and ciliates) in Funka Bay, are estimated to be 39-45 g C$\cdot$m$^{-2}\cdot$yr^{-1}. These are 46-161% of the daily primary production in summer, but are considerably less than primary production (3%) during the spring phytoplankton bloom period. Because phytoplankton flux is 2% of the primary production, the fate of the primary production in spring can not be identified with the estimation by the Ikeda and Motoda's methods. An alternative estimation of grazing rate based on the Huntley and Boyd's methods (=food consumption) well explains the mass dynamics not only in the phytoplankton bloom, but also in summer. It has been revealed that grazing activity of phagotrophic dinoflagellates is large (38% of total grazing) even though during the spring bloom, large copepods' grazing activity is not as high as previously thought.

3. Considering the seasonal size variations of phytoplankton and zooplankton, an annual grazing rate of the total heterotrophs including phagotrophic dinoflagellates in Funka Bay is estimated to be 125 g C$\cdot$m$^{-2}\cdot$yr^{-1} (88% of the annual primary production), of which 77% is accounted for by microheterotrophs (copepod nauplii, ciliates, and phagotrophic dinoflogellates). The estimated grazing rates imply that phytoplankton production is immediately eaten by heterotrophs within the productive zone.

4. In subarctic waters, the grazing rate is 47-2,941% of the food requirement. In the transition and subtropical waters, however, the grazing rate is 3-57% and 1-12% of the food requirement, respectively. This means that, in the latter sea areas, zooplankton are not supplied only with phytoplankton. Such a trend is severe for larger zooplankton. It is considered that they have to eat organic matter other than phytoplankton (e.g. organic detritus, bacteria, heterotrophic flagellates and microzooplankton), to meet their food requirements.

5. Although it has been hypothesized that relative abundance of microzooplankton biomass to net zooplankton biomass is generally high in the subtropical waters and low in the subarctic waters, the present results do not support such the idea. It is considered that this may result from weaker herbivory of net zooplankton, that is, net zooplankton maintain their metabolic activity eating on organic carbon other than phytoplankton, in the southern sea areas.

6. Secondary production in Funka Bay is 38 g C$\cdot$m$^{-2}\cdot$yr^{-1}, which is equiva-

lent to 27% of primary production (=transfer efficiency). On the other hand, secondary production in the western North Pacific Ocean is estimated to be 111, 44, 35, and 22 mg $C \cdot m^{-2} \cdot d^{-1}$ in the subarctic water during phytoplankton bloom, not bloom, transition, and subtropical water, respectively. This scheme that secondary production is high in the northern sea areas and low in the southern sea areas is quite different from the former scheme, but reasonable when we consider the fish production in the western North Pacific Ocean.

IX. Acknowledgements

I would like to express my sincere thanks to Professor Yoshiaki Maita, Division of Marine Biochemical Science, Research Institute of North Pacific Fisheries, Hokkaido University, for his encouragement given during the present study and his critical reading of this manuscript. I am very grateful to Professors Takashi Minoda and Shizuo Tsunogai for their kind criticisms and valuable suggestions. Thanks are extend to Dr. T.R. Parsons, University of British Columbia, Drs H. Maske and K.-G. Barthel, Institut für Meereskunde, an der Universität Kiel, Dr. M. Takahashi, University of Tokyo, Dr. A. Taniguchi, Tohoku University, Dr. T. Ikeda, Japan Sea Regional Fisheries Research Laboratory, Dr. S. Taguchi, University of Hawaii, for their helpful suggestions, critical comments, and warm encouragements through this study. I wish to thank Dr. M. Yanada for his kind permission to use his unpublished data. I thank Captain K. Matsushima, and crew of the T/S Ushio Maru, Faculty of Fisheries, Hokkaido University, for their helpful assistance in sampling and excellent performance in setting up and collecting of the sediment trap system. I also thank Dr. A. Hattori, Chief scientist, other scientists of R/V Hakuho Maru Cruise KH-85-2, captain, and crew member of R/V Hakuho Maru, Ocean Research Institute, University of Tokyo for their kind assistance in sampling. Gratitude is extended to Ms. L.V. Castillo for her reading of this manuscript.

References

Anderson, G.C., Lam, R.L., Booth, B.C. and Glass, J.M. (1977). A description and numerical analysis of the factors affecting the processes of production in the Gulf of Alaska. p. 477-798. In National Oceanic and Atmospheric Administration, U.S. Department of Interior (ed.), *Environmental Assessment of the Alaska Continental Shelf, Annual Reports of Principal Investigators for the Year Ending March 1977, Volume 7. Receptors — Fish. Littoral. Benthos.*, Washington, D.C.

Anraku, M. (1964). Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. Respiration and feeding. *Limnol. Oceanogr.* **9**, 195-206.

Antia, N.J., McAllister, C.D., Parsons, T.R., Stephens, K. and Strickland, J.D.H. (1963). Further measurements of primary production using a large-volume plastic sphere. *Ibid.* **8**, 166-183.

Ayukai, T. and Nishizawa, S. (1986). Defecation rate as a possible measure of ingestion rate of *Calanus pacificus pacificus* (Copepoda: Calanoida). *Bull. Plankton Soc. Japan* **33**, 3-10.

Azam, F, Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A. and Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* **10**, 257-263.

Banse, K. (1977). Determining the carbon-to-chlorophyll ratio of natural phytoplankton. *Mar. Biol.* **41**, 199-212.

Beers, J.R. and Stewart, G.L. (1967). Micro-zooplankton in the euphotic zone at five locations across

the California Current. *J. Fish. Res. Bd. Can.* **24**, 2053-2068.
Beers, J.R. and Stewart, G.L. (1971). Micro-zooplankters in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep-Sea Res.* **18**, 861-883.
Berman, T. (1975). Size fractionation of natural aquatic populations associated with autotrophic and heterotrophic carbon uptake. *Mar. Biol.* **33**, 215-220.
Blackburn, M. (1973). Regressions between biological oceanographic measurements in the eastern tropical pacific and their significance to ecological efficiency. *Limnol. Oceanogr.* **18**, 552-563.
Booth, B.C. (1988). Size classes and major taxonomic groups of phytoplankton at two locations in the subarctic Pacific Ocean in May and August, 1984. *Mar. Biol.* **97**, 275-286.
Burkill, P.H., Mantoura, R.F.C., Llewellyn, C.A. and Owens, N.J.P. (1987). Microzooplankton grazing and selectivity of phytoplankton in coastal waters. *Ibid.* **93**, 581-590.
Caperon, J. and Meyer, J. (1972). Nitrogen-limited growth of marine phytoplankton-I. Changes in population characteristics with steady-state growth rate. *Deep-Sea Res.* **19**, 601-618.
Capriulo, G.M. (1982). Feeding of field collected tintinnid microzooplankton on natural food. *Mar. Biol.* **71**, 73-86.
Capriulo, G.M. and Carpenter, E.J. (1983). Abundance, species composition and feeding impact of tintinnid micro-zooplankton in central Long Island Sound. *Mar. Ecol. Prog. Ser.* **10**, 277-288.
Cushing, D.H. (1959). The seasonal variation in oceanic production as a problem in population dynamics. *J. Cons. int. Explor. Mer* **24**, 455-464.
Cushing, D.H. (1971). Upwelling and the production of fish. *Adv. mar. Biol.* **9**, 255-334.
Dagg, M.J., Vidal, J., Whitledge, T.E., Iverson, R.L. and Goering, J.J. (1982). The feeding, respiration, and excretion of zooplankton in the Bering Sea during a spring bloom. *Deep-Sea Res.* **29**, 45-63.
Dohi, K. (1982). Seasonal change of tintinnid community in Funka Bay. *Bull. Plankton Soc. Japan* **29**, 77-87. (In Japanese with English abstract).
Dugdale, R.C. and Goering, J.J. (1967). Uptake of new and regenerated forms of nitrogen in primary production. *Limnol. Oceanogr.* **12**, 196-206.
El Hag, A.G. and Fogg, G.E. (1986). The distribution of coccoid blue-green algae (Cyanobacteria) in the Menai Straits and the Irish Sea. *British Phycology Journal* **21**, 45-54.
Emerson, C.W. and Roff, J.C. (1987). Implications of fecal pellet size and zooplankton behaviour to estimates of pelagic-benthic carbon flux. *Mar. Ecol. Prog. Ser.* **35**, 251-257.
Endo, Y., Hasumoto, H. and Taniguchi, A. (1983). Microzooplankton standing crop in the western subtropical Pacific off the Bonin Islands in winter, 1980. *J. Oceanogr. Soc. Japan* **39**, 185-191.
Eppley, R.W. and Renger, E.H. (1974). Nitrogen assimilation of an oceanic diatom in nitrogen-limited continuous culture. *J. Phycol.* **10**, 15-23.
Eppley, R.W., Harrison, W.G., Chisholm, S.W. and Stewart, E. (1977). Particulate organic matter in surface waters off Southern California and its relationship to phytoplankton. *J. Mar. Res.* **35**, 671-696.
Fenchel, T. and Finlay, B.J. (1983). Respiration rate in heterotrophic, free-living Protozoa. *Microb. Ecol.* **9**, 99-122.
Frost, B.W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* **17**, 805-815.
Frost, B.W. (1975). A threshold feeding behavior in *Calanus pacificus*. *Ibid.* **20**, 263-266.
Frost, B.W. (1980). The inadequacy of body size as an indicator of niches in the zooplankton. p. 742-753. In Kerfoot, W.C. (ed.). *The Evolution and Ecology of Zooplankton Population.* American Society of Limnology and Oceanography Special Symposium III.
Frost, B.W. (1987). Grazing control of phytoplankton stock in the open subarctic Pacific Ocean : a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Mar. Ecol. Prog. Ser.* **39**, 49-68.
Frost, B.W., Landry, M.R. and Hassett, R.P. (1983). Feeding of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific Ocean. *Deep-Sea Res.* **30**, 1-13.
Furuya, K. and Marumo, R. (1983). Size distribution of phytoplankton in the western Pacific Ocean and adjacent waters in summer. *Bull. Plankton Soc. Japan* **30**, 21-32.
Gilbert, J.J. and Bogdan, K.G. (1984). Rotifer grazing: *in situ* studies on selectivity and rates. p. 97-133. In Meyers, D.G. and Stricker, J.R. (eds.) *Trophic Interactions within Aquatic*

Ecosystems. Westview Press, Boulder.
Glover, H.E., Phinney, D.A. and Yentsch, C.S. (1985a). Photosynthetic characteristics of picoplankton compared with those of larger phytoplankton populations, in various water masses in the Gulf of Maine. *Biol. Oceanogr.* **3**, 223-248.
Glover, H.E., Smith, A.E. and Shapiro, L. (1985b). Diurnal variation in photosynthetic rates: comparisons of ultraphytoplankton with a larger phytoplankton size fraction. *J. Plankton Res.* **7**, 519-535.
Glover, H.E., Prézelin, B.B., Campbell, L., Wyman, M. and Garside, C. (1988). A nitrate-dependent *Synechococcus* bloom in surface Sargasso Sea water. *Nature* **331**, 161-163.
Hattori, A., and Nakai, T. (eds.) (1986). *Preliminary Report of The Hakuho Maru Cruise KH-83-3 and KH-85-2.* Ocean Research Institute, University of Tokyo.
Hayward, T.L., Venrick, E.L. and McGowan, J.A. (1983). Environmental heterogeneity and plankton community structure in the central North Pacific. *J. Mar. Res.* **41**, 711-729.
Heinbokel, J.F. (1978a). Studies on the functional role of tintinnids in the southern California Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.* **47**, 177-189.
Heinbokel, J.F. (1978b). *Ditto* II. Grazing rates of field populations. *Ibid.* **47**, 191-197.
Heinbokel, J.F. and Beers, J.R. (1979). *Ditto* III. Grazing impact of natural assemblages. *Ibid.* **52**, 23-32.
Heinrich, A.K. (1962). The life histories of plankton animals and seasonal cycles of plankton communities in the ocean. *J. Cons. int. Explor. Mer* **27**, 15-24.
Hervey, H.W. (1945). *The Chemistry and Biology of Seawater.* Cambridge Univ. Press, Cambridge.
Hirakawa, K. (1983). Seasonal distribution of the planktonic copepods, and life history of *Calanus pacificus. Calanus plumchrus* and *Eucalanus bungii bungii* in the waters of Funka Bay. southern Hokkaido, Japan. Ph. D. Thesis, Hokkaido Univ. (In Japanese with English summary).
Holm-Hansen, O. (1969). Determination of microbial biomass in the ocean profiles. *Limnol. Oceanogr.* **14**, 740-747.
Huntley, M. and Boyd, C. (1984). Food-limited growth of marine zooplankton. *Am. Nat.* **124**, 455-478.
Idso, S.B. and Gilbert, R.G. (1974). On the universality of the Poole and Atkins Secchi disk-light extinction equation. *J. Appl. Ecol.* **11**, 399-401.
Ikeda, T. (1974). Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido Univ.* **22**, 1-97.
Ikeda, T. (1977). Feeding rates of planktonic copepods from a tropical sea. *J. Exp. Mar. Biol. Ecol.* **29**, 263-277.
Ikeda, T. and Motoda, S. (1978). Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. *Fish. Bull.* **76**, 357-367.
Joh, H. and Uno, S. (1983). Zooplankton standing stock and their estimated production in Osaka Bay. *Bull. Plankton Soc. Japan* **30**, 41-51. (In Japanese with English abstract).
Johannes, R.E. and Satomi, M. (1966). Composition and nutritive value of fecal pellets of a marine crustacean. *Limnol. Oceanogr.* **11**, 191-197.
Johnson, P.W. and Sieburth, J. McN. (1979). Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. *Ibid.* **24**, 928-935.
Joint, I.R. and Pomroy, A.J. (1983). Production of picoplankton and small nanoplankton in the Celtic Sea. *Mar. Biol.* **77**, 19-27.
Joint, I.R., Owens, N.J.P. and Pomroy, A.J. (1986). Seasonal production of photosynthetic picoplankton and nanoplankton in the Celtic Sea. *Mar. Ecol. Prog. Ser.* **28**, 251-258.
Kamba, M. (1977). Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (PALLAS), in early life stage in Uchiura Bay, Hokkaido. *Res. Inst. N. Pac. Fish.. Hokkaido Univ. Spec. Vol.* 175-197.
Kawai, H. (1955). On the polar frontal zone and its fluctuation in the waters to the northeast of Japan (I). *Bull. Tohoku Reg. Fish. Res. Lab.* No. **4**, 1-46. (In Japanese with English abstract).
Kawakami, R., Ayukai, T. and Taniguchi, A. (1985). A preliminary report on respiration rates of two tintinnid species (Ciliata). *Bull. Plankton Soc. Japan* **32**, 171-172.
Kawarada, Y. and Sano, A. (1972). Distribution of chlorophyll *a* and phaeopigments in the

northwestern North Pacific in relation to the hydrographic conditions. p. 125-133. In Takenouti, A.Y. *et al.* (eds.) *Biological Oceanography of the Northern North Pacific Ocean.* Idemitsu Shoten, Tokyo.

Kido, K. and Ohtani, K. (1981). Preservation of particulate organic matter in the cold basin water in Funka Bay after the vernal phytoplankton bloom. *Bull. Fac. Fish. Hokkaido Univ.* **32**, 357-375.

Klekowski, R.Z. (1981). Size dependence of metabolism in protozoans. *Verh. Internat. Verein. Limnol.* **21**, 1498-1502.

Knauer, G.A., Martin, J.H. and Bruland, K.W. (1979). Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. *Deep-Sea Res.* **26**, 97-108.

Larsson, U. and Hagström, A. (1982). Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. *Mar. Biol.* **67**, 57-70.

Laws, E.A., Bienfang, P.K., Ziemann, D.A. and Conquest, L.D. (1988). Phytoplankton population dynamics and the fate of production during the spring bloom in Auke Bay, Alaska. *Limnol. Oceanogr.* **33**, 57-65.

Lessard, E.J. and Swift, E. (1985). Species-specific grazing rates of heterotrophic dinoflagellates in ocean waters, measured with a dual-label radioisotope technique. *Mar. Biol.* **87**, 289-296.

Li, W.K.W., Subba Rao, D.V., Harrison, W.G., Smith, J.C., Cullen, J.J., Irwin, B. and Platt, T. (1983). Autotrophic picoplankton in the tropical ocean. *Science* **219**, 292-295.

Lorenzen, C.J., Welschmeyer, N.A., Copping, A.E. and Vernet, M. (1983). Sinking rates of organic particles. *Limnol. Oceanogr.* **28**, 766-769.

Maita, Y., Yanada, M. and Shiomoto, A. (1986). Fluxes of particulate organic carbon and nitrogen in Funka Bay in autumn. *Bull. Fac. Fish. Hokkaido Univ.* **37**, 124-133. (In Japanese with English abstract).

Marshall, S.M. and Orr, A.P. (1956). On the biology of *Calanus finmarchicus* IX. Feeding and digestion in the young stages. *J. mar. biol. Ass. U.K.* **35**, 587-603.

Marumo, R. (1967). General features of diatom communities in the Northpacific Ocean in summer. *Information Bulletin on Planktology in Japan* Commemoration Number of Dr. Y. Matsue, 115-122.

McAllister, C.D. (1969). Aspect of estimating zooplankton production from phytoplankton production. *J. Fish. Res. Bd. Can.* **26**, 199-220.

McAllister, C.D. (1972). Estimates of the transfer of primary production to secondary production at ocean station. p. 575-579. In Takenouti, A.Y. *et al.* (eds.) *Biological Oceanography of the Northern North Pacific Ocean*, Idemitsu Shoten, Tokyo.

McAllister, C.D., Taylor, T.R. and Strickland, J.D.H. (1960). Primary productivity in station "P" in the northeast Pacific Ocean. *J. Cons. int. Explor. Mer* **25**, 240-259.

Mullin, M.M., Sloan, P.R. and Eppley, R.W. (1966). Relationship between carbon content, cell volume and area in phytoplankton. *Limnol. Oceanogr.* **11**, 307-311.

Mullin, M.M., Stewart, E.F. and Fuglister, F.J. (1975). Ingestion by planktonic grazers as a function of concentration of food. *Ibid.* **20**, 259-262.

Murphy, L.S. and Haugen, E.M. (1985). The distribution and abundance of phototrophic ultraplankton in the North Atlantic. *Ibid.* **30**, 47-58.

Nakata, K. (1982). Species composition of phytoplankton community of Funka Bay in the spring bloom, 1981. *Bull. Japan. Soc. Fish.* **41**, 27-32. (In Japanese with English abstract).

Nakatani, T. (1988). Studies on the early life history of walleye pollock *Theragra chalcogramma* in Funka Bay and vicinity, Hokkaido. *Mem. Fac. Fish. Hokkaido Univ.* **35**, 1-46.

Nival, P. and Nival, S. (1976). Particle retention efficiencies of a herbivorous copepod, *Acartia clausi* (adult and copepodite stages): Effects on grazing. *Limnol. Oceanogr.* **21**, 24-38.

Odate, K. (1986). Automatic data processing for estimation of abundance of zooplankton in the waters off northeastern Honshu, Japan, 1951-1976. Bull. *Tohoku Reg. Fish. Res. Lab.* No. **48**, 31-47. (In Japanese with English abstract).

Odate, T. (1987). Temporal and horizontal distribution of the diatom community during the spring bloom in Funka Bay, southern Hokkaido. *Bull. Plankton. Soc. Japan* **34**, 33-42.

Odate, T., Yanada, M, Castillo, L.V. and Maita, Y. (1990). Distribution of cyanobacteria and other picophytoplankton in the western North Pacific Ocean, summer 1989. *J. Oceanogr. Soc. Japan* **46**, 184-189.

Ohtani, K. and Kido, K. (1980). Oceanographic structure in Funka Bay. *Bull. Fac. Fish. Hokkaido Univ.* **31**, 84-114. (In Japanese with English abstract).

Paffenhöfer, G.-A. (1971). Grazing ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. *Mar. Biol.* **11**, 286-298.

Paffenhöfer, G.-A. and Knowles, S.C. (1979). Ecological implications of fecal pellet size, production and consumption by copepods. *J. Mar. Res.* **37**, 35-49.

Parsons, T.R. and LeBrasseur, R.J. (1970). The availability of food to different trophic levels in the marine food chain. p. 325-343. In Steele, J.H. (ed.) *Marine Food Chains*. Oliver & Boyd, Edinburgh.

Parsons, T.R., Maita, Y. and Lalli, C.M. (1984). *A Manual of Chemical and Biological Methods for Seawater Analysis*. 173 p. Pergamon Press, Oxford.

Platt, T., Subba Rao, D.V. and Irwin, B. (1983). Photosynthesis of picoplankton in the oligotrophic ocean. *Nature* **301**, 702-704.

Rassoulzadegan, F. and Etienne, M. (1981). Grazing rate of the tintinnid *Stenosemella ventricosa* (Clap. & Lachm.) Jorg. on the spectrum of the naturally occurring particulate matter from a Mediterranean neritic area. *Limnol. Oceanogr.* **26**, 258-270.

Raymont, J.E.G. (1980). *Phytoplankton and Productivity in the Oceans. 2nd ed., Vol. 1. Phytoplankton*. 489 p. Pergamon Press, Oxford.

Runge, J.A. (1980). Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnol. Oceanogr.* **25**, 134-145.

Sanders, R.W. (1987). Tintinnids and other microzooplankton-seasonal distributions and relationships to resources and hydrography in a Maine estuary. *J. Plankton Res.* **9**, 65-77.

Sasaki, H., Hattori, H. and Nishizawa, S. (1988). Downward flux of particulate organic matter and vertical distribution of calanoid copepods in the Oyashio Water in summer. *Deep-Sea Res.* **35**, 505-515.

Shapiro, L.P. and Haugen, E.M. (1988). Seasonal distribution and temperature tolerance of *Synechococcus* in Boothbay Harbor, Maine. *Estuar. Coast. Shelf Sci.* **26**, 517-525.

Sieburth, J. McN., Smetacek, V. and Lenz, J. (1978). Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol. Oceanogr.* **23**, 1256-1263.

Small, L.F., Fowler, S.W. and Unlu, M.Y. (1979). Sinking rates of natural copepod fecal pellets. *Mar. Biol.* **51**, 233-241.

Smith, J.C., Platt, T., Li, W.K.W., Horne, E.P.W., Harrison, W. G., Subba Rao, D.V. and Irwin, B.D. (1985). Arctic marine photoautotrophic picoplankton. *Mar. Ecol. Prog. Ser.* **20**, 207-220.

Steele, J.H. (1974). *The Structure of Marine Ecosystems*. 128 p. Harvard Univ. Press, Camb., Mass.

Steemann Nielsen, E. (1952). The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J. Cons. int Explor. Mer* **18**, 117-140.

Stockner, J.G. (1988). Phototrophic picoplankton: An overview from marine and freshwater ecosystems. *Limnol. Oceanogr.* **33**, 765-775.

Stoecker, D.K. (1984). Particle production by planktonic ciliates. *Ibid.* **29**, 930-940.

Strathmann, R.R. (1967). Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Ibid.* **12**, 411-418.

Strickland, J.D.H. (1965). Production of organic matter in the primary stages of the marine food chain. p. 477-610. In Riley, J.P. and Skirrow, G. (eds.) *Chemical Oceanography*. Academic Press, London.

Strickland, J.D.H. and Parsons, T.R. (1972). *A Practical Handbook of Seawater Analysis. 2nd ed. Fish. Res. Bd. Canada Bull.* **167**, Ottawa, 311 pp

Takahashi, M. and Bienfang, P.K. (1983). Size structure of phytoplankton biomass and photosynthesis in subtropical Hawaiian waters. *Mar. Biol.* **76**, 203-211.

Takahashi, M. and Hori, T. (1984). Abundance of picophytoplankton in the subsurface chlorophyll maximum layer in subtropical and tropical waters. *Ibid* **79**, 177-186.

Takahashi, M. and Ichimura, S. (1972). Some aspects of primary production in the northwestern Pacific Ocean. p. 217-229. In Takanouti, A.Y. *et al.* (eds.) *Biological Oceanography of the Northern North Pacific Ocean*. Idemitsu Shoten, Tokyo.

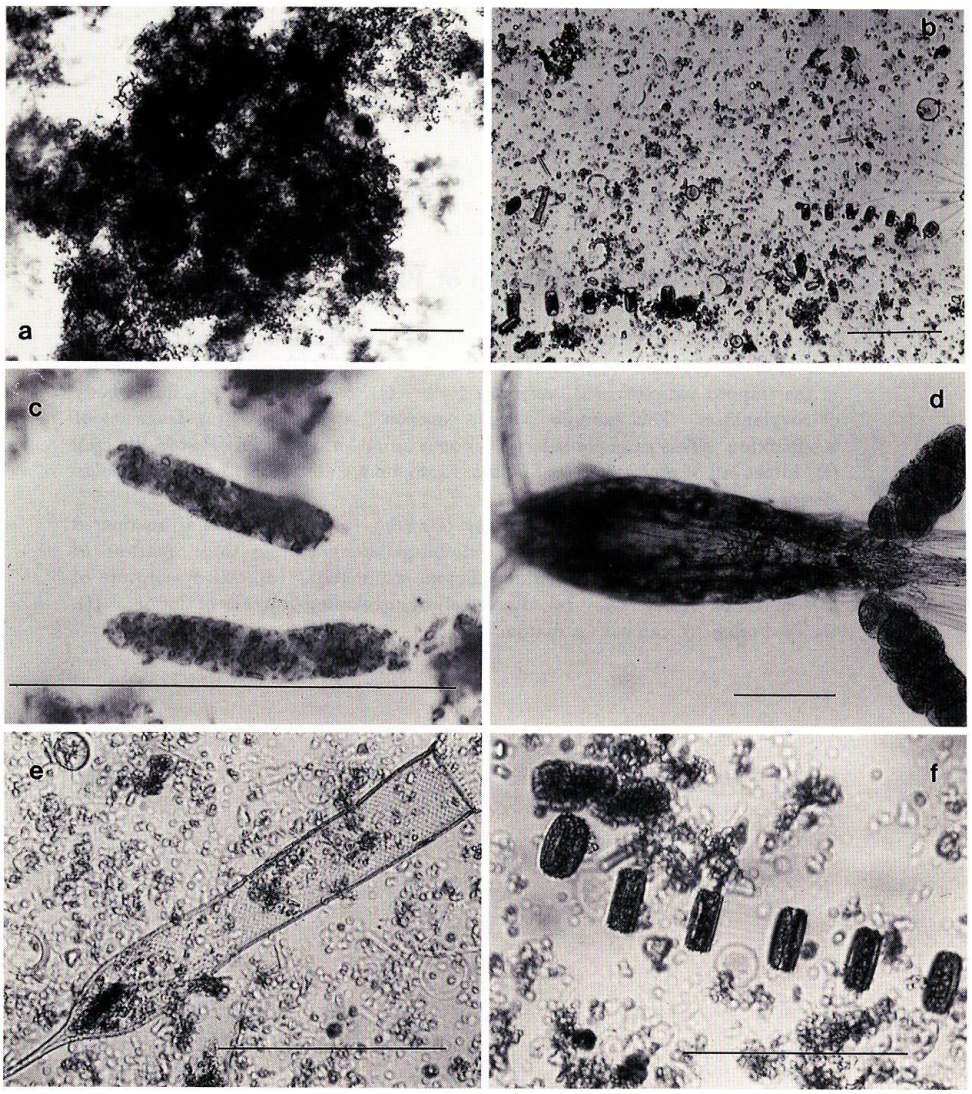
Takahashi, M., Kikuchi, K. and Hara, Y. (1985). Importance of picocyanobacteria biomass (unicellular blue-green algae) in the phytoplankton population of the coastal waters off Japan. *Mar.*

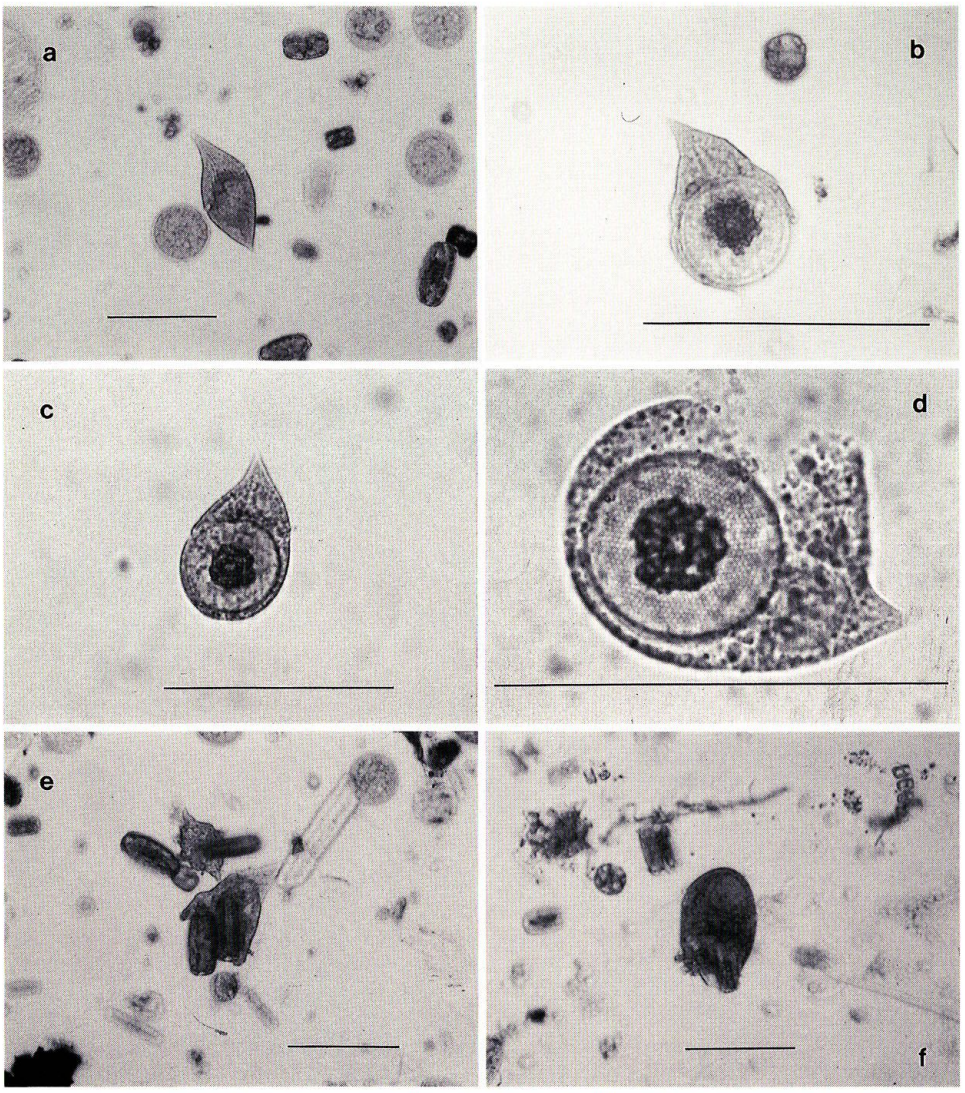
Biol. **89**, 63-69.
Taguchi, S. and Fukuchi, M. (1975). Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. *J. Exp. Mar. Biol. Ecol.* **19**, 145-164.
Taniguchi, A. (1973). Phytoplankton-zooplankton relationships in the western Pacific Ocean and adjacent seas. *Mar. Biol.* **21**, 115-121.
Taniguchi, A. (1977a). Biomass and size composition of copepod nauplii and tintinnids in the Philippine Sea and the Celebes Sea, summer 1972. *Bull. Plankton Soc. Japan* **24**, 1-10.
Taniguchi, A. (1977b). Distribution of microzooplankton in the Philippine Sea and Celebes Sea in summer, 1972. *J. Oceanogr. Soc. Japan* **33**, 82-89.
Taniguchi, A. (1981). Plankton productivities in the Pacific subarctic boundary zone: food condition of the migrating pelagic fishes. *Res. Inst. North Pac. Fish. Fac. Fish. Hokkaido Univ. Special Volume 1981*, 23-35. (In Japanese with English abstract).
Taniguchi, A. (1984). Microzooplankton biomass in the Arctic and subarctic Pacific Ocean in summer. *Mem. Nat. Inst. Polar Res. Spec. Issue* No. **32**, 63-76.
Taniguchi, A. (1985). Plankton research in Japan with special reference to microzooplankton studies. *Bull. Mar. Sci.* **37**, 411-413.
Taniguchi, A. and Kawakami, R. (1985). Feeding activity of a tintinnid ciliate *Favella taraikaensis* and it variability observed in laboratory cultures. *Mar. Microb. Food Webs* **1**, 17-34.
Taylor, F.J.R. and Waters, R.E. (1982). Spring phytoplankton in the subarctic North Pacific Ocean. *Mar. Biol.* **67**, 323-335.
Tsuda, A. and Nemoto, T. (1987). The effect of food concentration on the gut clearance time of *Pseudocalanus minutus* Krøyer (Calanoida: Copepoda). *J. Exp. Mar. Biol. Ecol.* **107**, 121-130.
Uye, S. (1982). Length-weight relationship of important zooplankton from the Inland Sea of Japan. *J. Oceanogr. Soc. Japan* **38**, 149-158.
Uye, S., Kuwata, H. and Endo, T. (1986). Standing stock and production rates of phytoplankton and planktonic copepods in the Inland Sea of Japan. *Ibid.* **42**, 421-434.
Verity, P.G. (1985). Grazing, respiration, excretion, and growth rates of tintinnids. *Limnol. Oceanogr*, **30**, 1268-1282.
Waterbury, J.B., Watson, S.W., Guillard, R.R. and Brand, L.E. (1979). Widespread occurrence of a unicellular marine planktonic cyanobacterium. *Nature* **277**, 239-294.
Waterbury, J.B., Watson, S.W., Valois, F.W. and Franks, D.G. (1986). Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*. p. 71-120. In Platt, T. and Li, W.K.W. (eds.) *Photosynthetic Picoplankton. Can. Bull. Fish. Aquat. Sci.* **214**. Ottawa.
Welschmeyer, N.A. and Lorenzen, C.J. (1985). Chlorophyll budgets: Zooplankton growth in a temperate fjord and the Central Pacific gyre. *Limnol. Oceanogr.* **30**, 1-21.
Wiebe, P.H., Boyd, S.H., and Winget, C. (1976). Particulate matter sinking to the deep-sea floor at 2,000 m in the Tongue of the Ocean, Bahamas with a description of a new sedimentation trap. *J. Mar. Res.* **34**, 341-354.

Explanation of Plates

Plate I. Examples of sinking particles. The volume of items a and b was not evaluated. Bars indicate 100 μm. (a), unidentified amorphous, which were the most abundant in the trapped samples. (b), very fine grain. (c), fecal pellets. (d), intact body of zooplankton. This example is alive copepod (*Oithona* sp.). (e), fragment of zooplankton. This example is lorica without animal of tintinnid (*Parafavella* sp.). (f), intact cell of phytoplankton. These examples are alive cells of diatom (*Thalassiosira anguste-lineata*).

Plate II. Phagotrophic dinoflagellates. Bars = 100 μm. (a), normal form of unarmored disoflagellate (*Gyrodinium* sp.). (b), dinoflagellate engulfing three quarters of diatom. (c), dinoflagellate engulfing diatom completely. (d), valve sculpture of diatom can be clearly seen. (e), dinoflagellate enveloping two cells of diatom. (f), *Gymnodinium* sp. can eat on diatom.


a
b
c
d
e
f



ODATE : Plankton dynamics in marine ecosystems