

Biomass, production and trophic roles of micro- and net-zooplankton in Dokai Inlet, a heavily eutrophic inlet, in summer

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Abstract: We measured the abundance, biomass and production rate of micro- and net-zooplankton in Dokai Inlet, a heavily eutrophic and polluted embayment in northern Kyushu, in August 1996. This inlet nourished a much higher biomass of net-zooplankton (mean: $53.2 \mu\text{g C l}^{-1}$) than microzooplankton ($10.1 \mu\text{g C l}^{-1}$). Mean contribution of tintinnid ciliates to the total microzooplankton biomass was largest (75%), followed, in order, by copepod nauplii (20%) and naked ciliates (5%). For net-zooplankton, the mean biomass of copepods (i.e. *Acartia*, *Euterpina*, *Oithona* and *Paracalanus*) was lower (43% of the total net-zooplankton biomass) than non-copepod taxa, such as chaetognaths and the larvae of bivalves and polychaetes. Mean secondary production rates of micro- and net-zooplankton in the inlet were 14.4 and $38.3 \text{ mg C m}^{-3} \text{ d}^{-1}$, respectively, and the mean tertiary production rate of net-zooplankton was $4.20 \text{ mg C m}^{-3} \text{ d}^{-1}$. The transfer efficiency from phytoplankton primary production to zooplankton secondary production was 28%, and the efficiency from secondary production to tertiary production was 7.9%. The amount of food required to support zooplankton secondary production was equivalent to 87% of the phytoplankton primary production, indicating that zooplankton, particularly net-zooplankton, are the major phytoplankton grazers in this extremely eutrophic inlet.

Key words: biomass, production, microzooplankton, net-zooplankton, Dokai Inlet

Introduction

Dokai Inlet (Fig. 1), located in northern Kyushu, is a waterway-like inlet opening to the Japan Sea, with an approximately 13 km NE–SW axis, an area of 10 km^2 and an average depth of 7 m (Kita-Kyushu City Inst. Environ. Sci. 1990). This inlet was extremely polluted in the 1950s and 1960s, due to the introduction of non-treated wastes from nearby heavy/chemical industries and was often reported as a “dead sea area”. After the 1970s, as a result of a decline of industrial activity and acts to regulate industrial effluents, the water quality of Dokai Inlet has gradually improved. However, this inlet is still one of the most heavily eutrophicated and polluted embayments in Japan, as evidenced by the extraordinarily high total N and P concentrations (annual average: 476 and $4.4 \mu\text{M l}^{-1}$, respectively) and frequent outbreaks of red tides

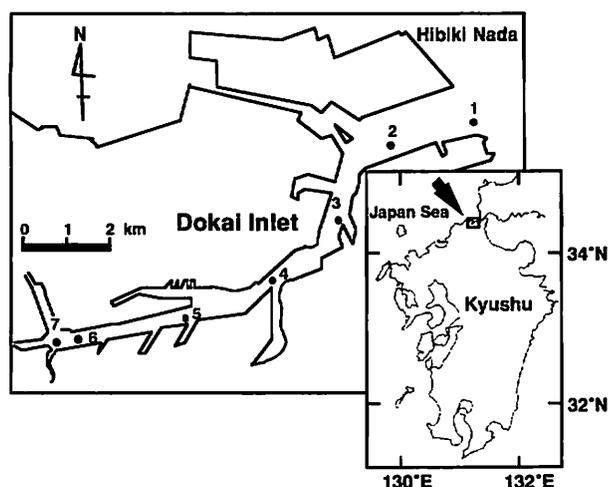


Fig. 1. Map showing the location of sampling stations in Dokai Inlet.

(Kita-Kyushu City Inst. Environ. Sci. 1994).

In order to improve the water quality of Dokai Inlet, a considerable reduction in N and P loads from land runoff is important. One of the approaches used to estimate the necessary cut-backs is ecological modeling (Yanagi 1995; Yanagi et al. 1997). For modeling to be effective, it is necessary to measure the phytoplankton primary production rate and its consumption by zooplankton. Macrozooplankton, particularly copepods, have traditionally been thought to be the major consumers of phytoplankton in the sea. However, there is now increasing evidence that microzooplankton play a more important role than previously thought in biological production and material cycling in the sea (Capriulo 1990; Pierce & Turner 1992). Further, the importance of microzooplankton relative to macrozooplankton is particularly emphasized in eutrophic areas (Revelante et al. 1985; Sasaki 1991). Hence, it is important to survey both micro- and macrozooplankton simultaneously to evaluate the roles of the zooplankton community in the trophodynamics of coastal marine waters. Previous studies on the zooplankton fauna of Dokai Inlet were confined to reports on the seasonal occurrence of the major taxonomic groups (Tsuruta & Yamada 1978), and no comprehensive surveys to assess the trophodynamic roles of zooplankton had been undertaken.

The objective of this study is to evaluate the roles of micro- and macrozooplankton (we employ the term "net-zooplankton") in biological production and carbon flux in Dokai Inlet. We determined the composition of major taxonomic groups, abundance, biomass and production rates in summer. Combining the results from this study with those from collaborative work to determine the biomass and production rates of phytoplankton and bacteria (Tada et al., unpublished data) enabled us to determine the carbon flow in the lower trophic levels of this extremely eutrophic embayment.

Materials and Methods

Field investigation

Zooplankton samples were collected at 7 stations in Dokai Inlet (Fig. 1) on 21 August 1996. At each station, vertical profiles of temperature and salinity were obtained with an Alec CTD. Water samples were collected with a Van-Dorn bottle at 3 depths (i.e. 0.5, 4 and 8 m),

and used to determine the concentrations of dissolved oxygen (through Winkler titration) and GF/F retained Chl *a* (through spectrophotometric determination). Microzooplankton samples (500 ml) were taken and immediately fixed with glutaraldehyde to a final concentration of 1%. These were kept refrigerated at ca. 3°C in darkness until examination. Net-zooplankton were collected using a plankton net (0.225-m mouth diameter, 100- μm mesh size, fitted with a Rigosha flowmeter) towed vertically from the bottom to the surface, and preserved in 5–10% formalin-seawater solution.

Microzooplankton analyses

Each microzooplankton sample was subsampled, and concentrated by settling to a final volume of ca. 10 ml, and was transferred to a settling chamber for examination under an inverted microscope. Microzooplankton were classified into 3 major groups, i.e. tintinnid ciliates, naked ciliates (including mixotrophic ones) and copepod nauplii. Further, tintinnids were identified to species according to Kofoed & Campbell (1929) and Marshall (1969) based on the morphology of their lorica, and naked ciliates were identified to genus level according to Maeda (1986) and Maeda & Carey (1985). They were enumerated and their appropriate body dimensions were measured to determine lorica volume of tintinnids and cell volume of naked ciliates according to their geometric configurations. Carbon weight of a tintinnid (C_t , pg) was converted from lorica volume (LV , μm^3) using the regression equation: $C_t = 444.5 + 0.053LV$ (Verity & Langdon 1984), and that of a naked ciliate was converted from cell volume using a factor of $0.14 \text{ pg } \mu\text{m}^{-3}$ (Putt & Stoecker 1989). Carbon content of a nauplius (C_c , ng) was calculated from body length (BL , μm) with the regression equation: $C_c = 1.51 \times 10^{-5} BL^{2.94}$ (Uye, unpublished).

The production rate of each taxonomic group (P , $\text{mg C m}^{-3} \text{ d}^{-1}$) was estimated from biomass (B , mg C m^{-3}) and empirically-determined specific growth rate (g , d^{-1}): $P = B \times g$. For copepod nauplii, we employed the regression equation used to describe the composite relationship between specific growth rate and temperature (T , °C) for 8 copepod species from the Inland Sea of Japan (Uye et al. 1996): $g = 0.057e^{0.0697T}$. For ciliated protozoans, the following multiple regression equation, proposed by Müller & Geller (1993), was used: $\ln g = 1.52 \ln T - 0.27 \ln CV - 1.44$, where CV is cell volume (μm^3). The cell volume of tintinnids was back-calculated from their body carbon content using the conversion factor of $0.14 \text{ pg } \mu\text{m}^{-3}$ used for naked ciliates. Because the growth data used in the above regressions were maximal or were derived from food-satiated laboratory conditions, the computed production rates are considered to be close to potential ones.

Net-zooplankton analyses

From 1/2 subsamples, large zooplankters such as cnidarians, chaetognaths, malacostracans and fish larvae were counted and sorted onto pre-combusted and pre-weighed glassfiber filters. Their dry weights were determined after drying in an electric oven (60°C) for 48 h, and were converted to carbon weights. Remaining subsamples were further split into 1/32 to 1/64 of the original samples, from which small zooplankters such as copepods (adults and copepodites), cladocerans, appendicularians, polychaete larvae, gastropod larvae and bivalve larvae were enumerated, and their body dimensions measured using a video micrometer (Olympus, VM-10) attached to a stereoscopic microscope. The size dimension information was automatically converted, using a personal computer, to carbon weights using pre-determined length-carbon weight regressions (see Uye & Shimazu 1997 for detail).

The method employed to estimate the production rate of net-zooplankton was basically the same as for microzooplankton. Detailed procedures that enabled the determination of growth rates for each taxonomic group are described in Uye & Shimazu (1997). Secondary and tertiary production was calculated separately, based on the feeding habits (i.e. herbivores, omnivores and carnivores) of each taxon (see Uye & Shimazu 1997). The production by typical herbivores and carnivores was assigned to secondary and tertiary production, respectively, and the production by omnivores was halved and added to each production value.

Results

Environmental variables

The temperature profile showed slight stratification; the water-column average varied from 27.0 to 27.8°C (Fig. 2). Salinity was vertically homogeneous at the mouth of the inlet, but stratification was evident inside the inlet (Fig. 2). Dissolved oxygen concentration decreased with depth and it was $<2 \text{ ml l}^{-1}$ near the bottom at Stn 6 (Fig. 2). Chlorophyll-*a* concentrations were highest at the surface and gradually decreased with depth (Fig. 2). The average

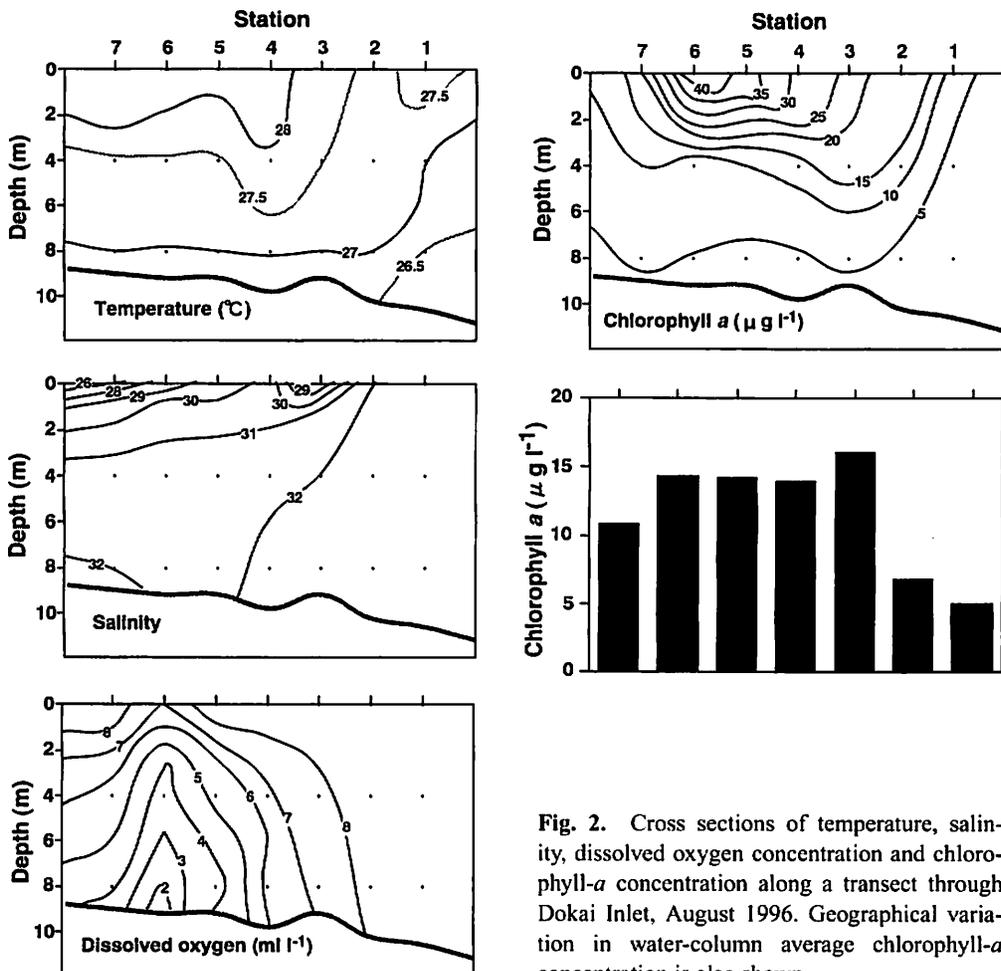


Fig. 2. Cross sections of temperature, salinity, dissolved oxygen concentration and chlorophyll-*a* concentration along a transect through Dokai Inlet, August 1996. Geographical variation in water-column average chlorophyll-*a* concentration is also shown.

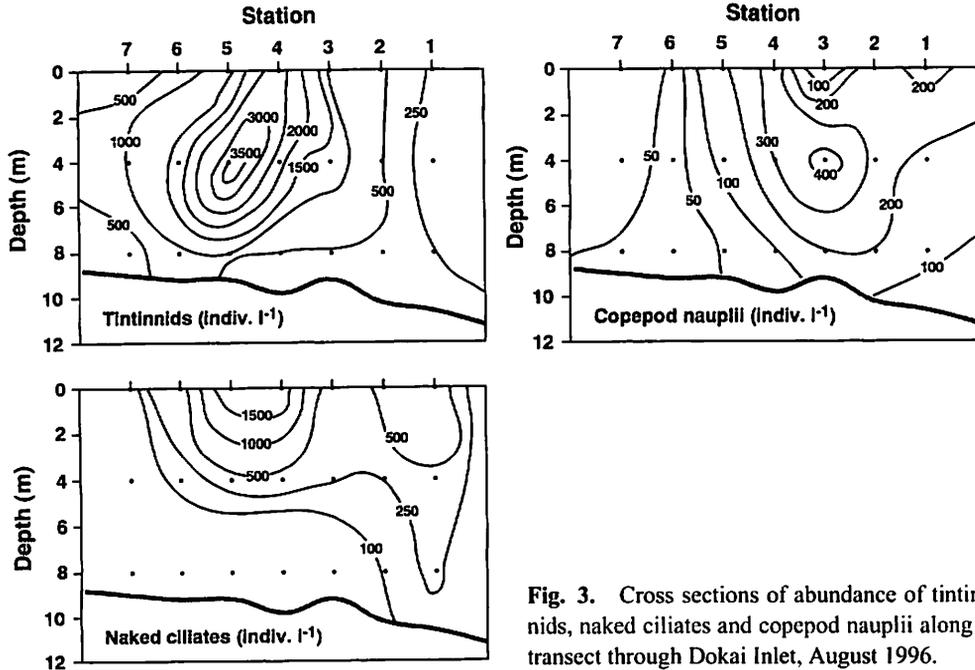


Fig. 3. Cross sections of abundance of tintinnids, naked ciliates and copepod nauplii along a transect through Dokai Inlet, August 1996.

Chl-*a* concentration throughout the water-column at each station varied from $4.94 \mu\text{g l}^{-1}$ at Stn 1 to $15.94 \mu\text{g l}^{-1}$ at Stn 3 with an integrated mean of $11.5 \mu\text{g l}^{-1}$ over the inlet.

Microzooplankton

Cross-sectional distribution maps along the transect (Fig. 3) show that tintinnids, naked ciliates and copepod nauplii tended to aggregate at shallow or intermediate depths at stations in the middle part of the inlet. The average abundance of total microzooplankton in the water column varied from 760 to 2674 indiv. l^{-1} (Fig. 4) with a mean of 1473 indiv. l^{-1} . Tintinnid ciliates were most numerous (68%) and copepod nauplii were least numerous (12%).

Twelve tintinnid species representing 7 genera were identified: *Amphorellopsis acuta*, *Eutintinnus lususundae*, *Favella ehrenbergii*, *Helicostomella longa*, *Leprotintinnus* sp., *Tintinnidium mucicola*, *Tintinnopsis beroidea*, *T. cylindrica*, *T. directa*, *T. radix*, *T. tocaninensis* and *T. tubulosa*. Amongst them, *Tintinnopsis beroidea* and *T. tocaninensis* were the most abundant species. Populations of these 2 species were separated geographically (Fig. 4).

Of the naked ciliates, 3 genera, i.e. *Strobilidium*, *Strombidium* and *Tiarina*, were identified in addition to an unidentified genus. The genus *Strobilidium* occurred throughout the entire inlet and dominated in the inner part of the inlet, while the unidentified genus was relatively abundant near the mouth of the inlet (Fig. 4).

The average biomass of microzooplankton in the water column varied from $2.92 \mu\text{g C l}^{-1}$ at Stn 7 to $22.42 \mu\text{g C l}^{-1}$ at Stn 3 with a mean of $10.10 \mu\text{g C l}^{-1}$ (Fig. 5). The contribution made by tintinnids, naked ciliates and copepod nauplii was 75, 5 and 20%, respectively.

The average production rate of microzooplankton in the water column varied from 5.50 to $25.57 \mu\text{g C l}^{-1} \text{d}^{-1}$ with a mean of $14.40 \mu\text{g C l}^{-1} \text{d}^{-1}$ (Fig. 5), of which tintinnids, naked ciliates and copepod nauplii contributed 83, 12 and 5%, respectively.

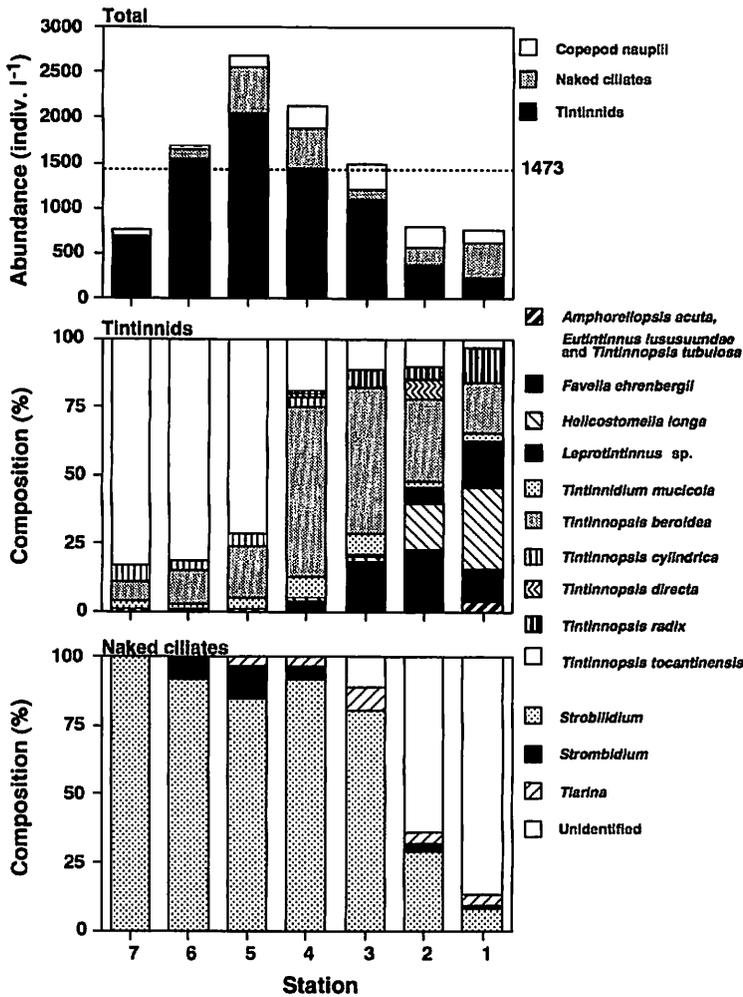


Fig. 4. Geographical variations in abundance of microzooplankton and taxonomic composition of tintinnids and naked ciliates along a transect through Dokai Inlet, August 1996. A dotted horizontal line denotes the mean.

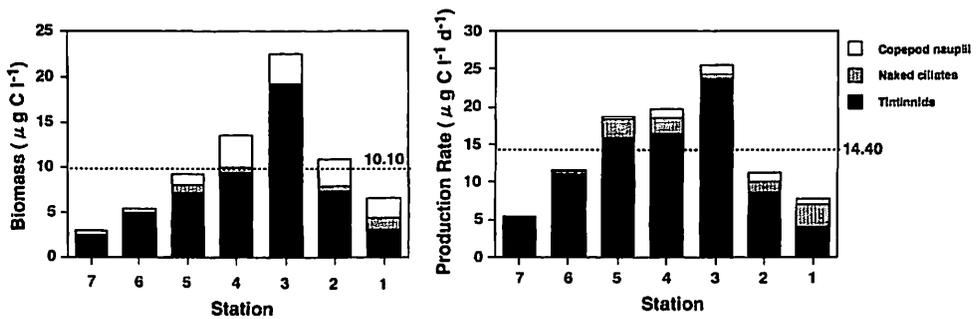


Fig. 5. Geographical variation in biomass and production rate of microzooplankton along a transect through Dokai Inlet, August 1996. Dotted horizontal lines denote the mean.

Net-zooplankton

The geographical variations in abundance and biomass of net-zooplankton are shown in Fig. 6. They were more abundant in the inner part of the inlet than near the mouth, ranging from 39.3×10^3 to 153×10^3 indiv. m^{-3} with a mean of 106×10^3 indiv. m^{-3} . Copepods (the major genera: *Oithona*, *Acartia*, *Euterpina* and *Paracalanus*) barely outnumbered (53%) non-copepod zooplankters. Bivalve larvae were the most abundant of the non-copepod zooplankters, accounting for 64% by numbers.

Net-zooplankton biomass varied from 20.6 to 73.1 mg C m^{-3} with a mean of 53.2 mg C m^{-3} . Based on biomass data, copepods were relatively less important (43%) than the non-copepod group. The dominant copepod genera shifted from *Euterpina* (49–65% of the total copepod biomass at Stns 1 and 2), *Oithona* (64% at Stn 3) to *Acartia* (36–61% at Stns 4 to 7) along the transect. Bivalve larvae again dominated (mean contribution: 68%) the non-copepod net-zooplankton biomass.

The secondary production rate of net-zooplankton ranged from 13.9 to $56.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ with a mean of $38.3 \text{ mg C m}^{-3} \text{ d}^{-1}$ (Fig. 7). The secondary production of copepods was low, only accounting for 15% of the total secondary production of net-zooplankton. The tertiary production rate ranged from 0.52 to $7.26 \text{ mg C m}^{-3} \text{ d}^{-1}$ with a mean of $4.20 \text{ mg C m}^{-3} \text{ d}^{-1}$

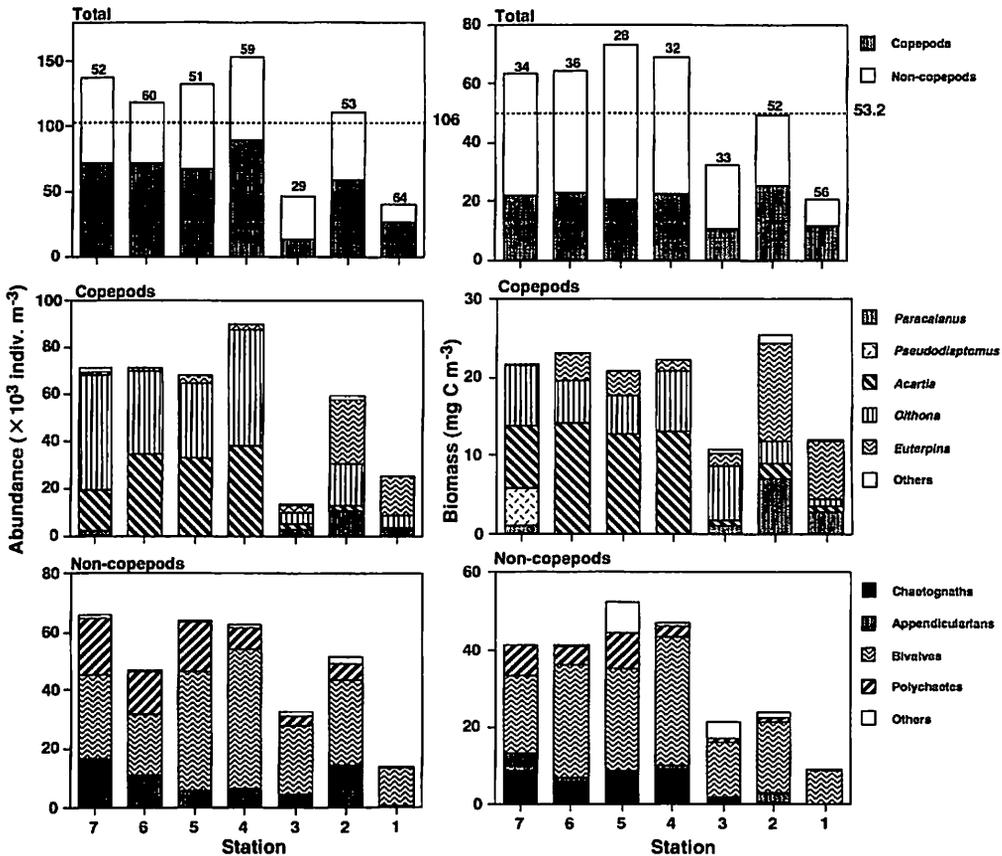


Fig. 6. Geographical variation in abundance and biomass of net-zooplankton along a transect through Dokai Inlet, August 1996. Numerals above the columns indicate % composition of copepods. Dotted horizontal lines denote the mean.

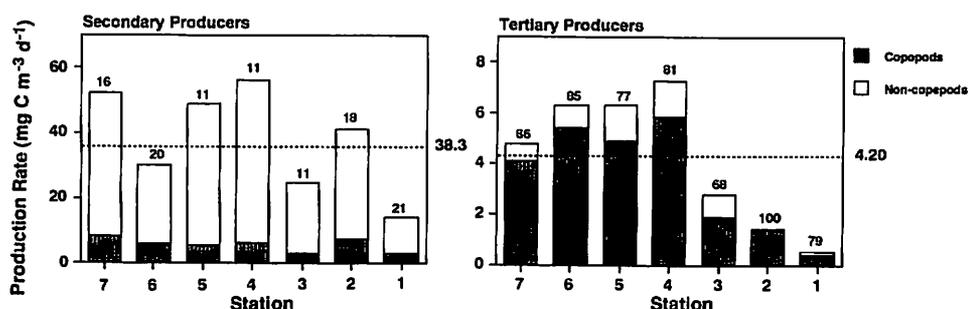


Fig. 7. Geographical variation in secondary and tertiary production rates of net-zooplankton along a transect through Dokai Inlet, August 1996. Numerals above the columns indicate % composition of copepods. Dotted horizontal lines denote the mean.

(Fig. 7), 82% of which was attributed to copepods.

Discussion

Microzooplankton

In coastal marine waters, along the nutrient gradient created by the input of nutrients from terrestrial human activities, there is a trend that microzooplankton, particularly ciliated protozoans, occur more abundantly in inshore eutrophic waters (Revelante et al. 1985). The degree of eutrophication is judged to be much higher in Dokai Inlet than in Tokyo Bay and the Inland Sea of Japan, as, for example, the average concentration of dissolved inorganic nitrogen (DIN) is 1 to 2 orders of magnitude higher in Dokai Inlet (average DIN concentration on our sampling date: $>100 \mu\text{M l}^{-1}$, S. Montani, Kagawa Univ., pers. comm.) than in Tokyo Bay or the Inland Sea of Japan (Oceanogr. Soc. Japan 1985). Nomura et al. (1992) investigated seasonal variations in the abundance of microzooplankton in the central part of Tokyo Bay, and found that they rarely declined to less than $1000 \text{ indiv. l}^{-1}$ and the population maximum of $21,656 \text{ indiv. l}^{-1}$ was reached in early summer. Uye et al. (1996) studied the abundance of microzooplankton at 21 stations in the Inland Sea of Japan once per season, and found that their average abundances in the water column ranged from 30 to $2190 \text{ indiv. l}^{-1}$. Although information on the numerical abundances of microzooplankton over an extended period is lacking in Dokai Inlet, the abundance of microzooplankton is apparently less in Dokai Inlet (mean: $1473 \text{ indiv. l}^{-1}$) than in Tokyo Bay (annual mean: ca. $4000 \text{ indiv. l}^{-1}$), but more numerous than the Inland Sea of Japan (regional mean in each season: $239\text{--}400 \text{ indiv. l}^{-1}$).

The spatial distribution of microzooplankton was contiguous as shown in Fig. 3. Figure 8 shows the relationship between microzooplankton biomass and the concentration of Chl *a* in the $<20 \mu\text{m}$, which may represent the food supply of many of the microzooplankton, for 21 water samples. Chlorophyll-*a* concentration of the $<20 \mu\text{m}$ fraction was determined only for the samples from Stn 6 (mean contribution to the total chlorophyll: 70%), and the contribution of the $<20 \mu\text{m}$ fraction was assumed to be the same for the remaining water samples. No significant correlations were evident between Chl-*a* concentration and microzooplankton biomass. A chain-forming diatom *Skeletonema costatum*, which is thought to be a poor food source for tintinnids (Verity & Villareal 1986), occurred at densities $>10^3 \text{ cells ml}^{-1}$ at the surface at Stns 3 to 7 (M. Yamada & T. Higashi, Kita-Kyushu City Inst. Environ. Sci., pers.

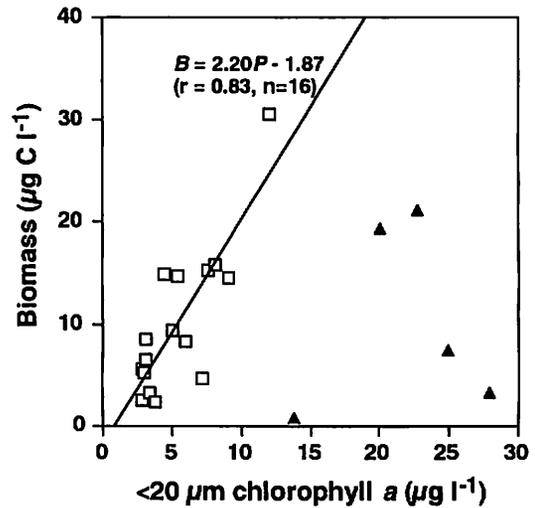


Fig. 8. Relationship between biomass of microzooplankton and chlorophyll-*a* concentration of the <20 µm fraction in water samples. Data from the surface layer of Stns 3 to 7 (▲) were omitted from the calculation (see text).

comm.). When data from these samples were excluded, a significant ($p < 0.01$) positive correlation was obtained, indicating that food supply is the prime factor underlying the spatial distribution of microzooplankton.

One of the difficulties associated with microzooplankton research concerns the preservation of delicate forms (Dale & Burkill 1982; Leakey et al. 1992). We used glutaraldehyde (final concentration: 1%) as a preservative, and consequently non-loricated ciliates are likely to be underestimated to an extent. In Dokai Inlet, tintinnids contributed to 68 and 75% to the abundance and biomass, respectively, of the total microzooplankton, a finding similar to that of previous studies in other coastal waters (Revelante & Gilmartin 1983; Nomura et al. 1992; Buskey 1993; Kamiyama 1994). All tintinnid species found in Dokai Inlet are contained in the species list compiled for the northern area of Hiroshima Bay (Kamiyama & Tsujino 1996).

Net-zooplankton

The mean biomass of net-zooplankton was much higher in Dokai Inlet (53.2 mg C m^{-3}) than in the Inland Sea of Japan ($13.2\text{--}35.5 \text{ mg C m}^{-3}$, Uye & Shimazu 1997). Net-zooplankton comprised 84% of the total zooplankton biomass, a value similar to that found in the Inland Sea of Japan (80–87%, Uye et al. 1996; Uye & Shimazu 1997). Such a high contribution by net-zooplankton was unexpected, since the relative importance of fraction in the zooplankton community tends to shift from larger zooplankters to smaller (i.e. microzooplankton) zooplankters with eutrophication (Revelante et al. 1985; Mathes & Arndt 1994; Uye 1994). The contribution of merozooplankton, particularly bivalve larvae, was important, as predicted from the dense populations of adults (major species: *Mytilus galloprovincialis* and *Limnoperna fortunei kikuchii*) attached to the quay wall throughout the inlet (Kajiwara & Yamada 1997).

In heavily eutrophic embayments like Tokyo Bay (Uye 1994) and the northern portion of Hiroshima Bay (Uye et al. 1992), copepod communities shift towards monopolization by the small cyclopoid, *Oithona davisae*. In the inner part of Dokai Inlet, however, *O. davisae* was ranked as the second most important species following *Acartia pulmosa*. Why *O. davisae* did not predominate in this extremely eutrophic inlet might be a result of the dominance of di-

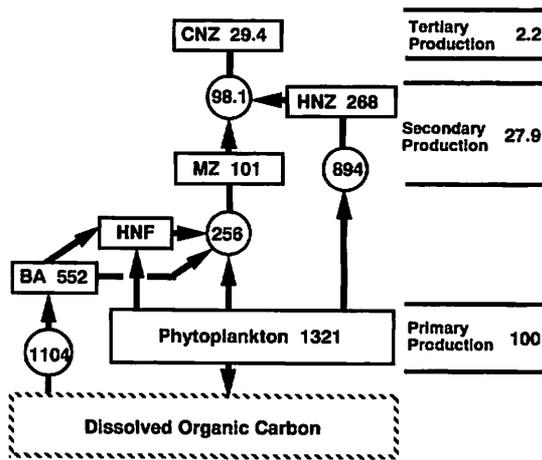


Fig. 9. Daily carbon flow ($\text{mg C m}^{-2} \text{d}^{-1}$) through components of the plankton community in Dokai Inlet, August 1996. Values in boxes denote daily production rates and those in circles are daily requirements by the components above them. BA: bacteria, HNF: heterotrophic nanoflagellates, MZ: microzooplankton, HNZ: herbivorous net-zooplankton, CNZ: carnivorous net-zooplankton.

atoms, which are not ingested by this species (Uchima 1988), in the phytoplankton (Yamada & Higashi, pers. comm.) and reduced levels of benthic anoxia during this study.

Trophic dynamics

In order to assess the roles played by micro- and net-zooplankton in the trophodynamics of Dokai Inlet, we drafted a diagram describing carbon flow through the major components of the food web (Fig. 9). Phytoplankton primary production rates and bacterial production rates were determined by Tada et al. (unpublished data). Primary production rates were determined using the ^{13}C -technique at 2 locations (near Stn 3 and at Stn 6). We averaged 5 measurements of primary production taken in August 1996 ($1321 \text{ mg C m}^{-2} \text{d}^{-1}$) and used this value as the average primary production rate in Dokai Inlet during our sampling period. The bacterial production rates were determined by means of an incubation technique using surface water from the above-mentioned stations. The mean bacterial production rate was $552 \text{ mg C m}^{-2} \text{d}^{-1}$ during the sampling period. To determine the potential carbon flow from prey organisms to predators, the amount of carbon required by the consumers to support their estimated production rates was calculated. In the calculation, we used a gross growth efficiency of 0.3 for metazoans (Ikeda & Motoda 1978), 0.4 for protozoan microzooplankton (Fenchel 1987) and 0.5 for bacteria (Cole et al. 1988).

If both microzooplankton and herbivorous net-zooplankton depended entirely on phytoplankton for food, their carbon requirement ($256 \text{ plus } 894 \text{ mg C m}^{-2} \text{d}^{-1}$) was equal to 87% of the primary production. This requirement also corresponded to 36% of the phytoplankton carbon biomass, which was converted from mean Chl-*a* concentration using a carbon:chlorophyll ratio of 40 (Parsons et al. 1984). The transfer efficiency from primary production to secondary production was 28%, which is close to the potential value derived from the results of laboratory rearing experiments using herbivorous copepods (ca. 30%, Ikeda & Motoda 1978). Phytoplankton were also grazed by heterotrophic nanoflagellates and filter-feeding molluscs attached to the quay. Although microbial food chains are beyond the scope of our study, the amount of dissolved organic carbon required for bacterial production was equal to 85% of the primary production. Such a high level of bacterial production might not be attained unless terrestrially produced organic carbon were available. This study shows that, even in this heavily eutrophic inlet, phytoplankton primary production is not always sufficient to support the po-

tential production rates of heterotrophic organisms and instead terrestrially produced carbon contributes significantly to fueling the microbial food chain. Allochthonous organic carbon is thus cascaded through the food chain, and thereby the observed transfer efficiency from primary production to secondary production is higher than when only autochthonous organic carbon is available.

The transfer efficiency from secondary production to tertiary production was 8%. The amount of carbon required by tertiary producers may have been met by the high level of secondary production evident in the inlet.

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