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Geographical variations in abundance, biomass and trophodynamic role of microzooplankton across an inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean

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Abstract: The geographical variations in taxonomic composition, abundance, biomass and trophodynamic role of microzooplankton were investigated across a eutrophic and oligotrophic gradient from Hiroshima Bay, the Inland Sea of Japan, to the Pacific Ocean in summer and winter. The overall mean abundance and biomass of total microzooplankton, excluding the 3 most offshore stations in summer, were higher 2.4 and 2.8 times, respectively, in summer than in winter. Both in summer and winter, ciliated protozoans (i.e. naked ciliates and tintinnids) were numerically overwhelming (81 and 83%, respectively), but in terms of biomass, copepod nauplii were comparable (i.e. 47 and 55% in summer and winter, respectively) to ciliated protozoans. The average production rate of microzooplankton was also higher (3.3 times) in summer than in winter, and the majority (>83%) of the production was attributed to ciliated protozoans. Geographically there were marked declines in their abundance, biomass and production rate from inshore to offshore stations in summer, but these geographical variations were less pronounced in winter. The grazing impact of microzooplankton as expressed by daily removal of phytoplankton biomass was relatively small over the transect; the overall mean was 7.2% (excluding a very high value at the most offshore station) in summer and 2.6% in winter. These facts indicate that microzooplankton play a minor role as phytoplankton grazers over inshore and offshore stations (except the most offshore one) in spite of a remarkable trophic gradient.

Key words: Microzooplankton, biomass, production, inshore–offshore gradient, Inland Sea of Japan

Introduction

In recent years, there has been an upsurge of interest in research on microzooplankton (body dimensions between 20 and 200 μm) in the marine ecosystem, owing to the recognition of their importance in trophic dynamics. They are ubiquitous and comprise a substantial portion of the marine zooplankton community, even though their biomass is usually less than the biomass of meso- and macrozooplankton (Beers & Stewart 1969, 1971). However, due to small body size, microzooplankton, particularly ciliated protozoans, have higher weight-specific physiological rates such as feeding, respiration, excretion and growth (Fenchel 1987; Verity 1985) than large metazoans, and they are capable of exploiting pico- and nanoplankton, which are inefficiently utilized by large metazoans such as copepods (Nival & Nival 1976). They also act as a significant food source for a variety of invertebrate and vertebrate predators (Robertson 1983; Stoecker & Egloff 1987; Stoecker & Capuzzo 1990; Fukami et al. 1999). Thus, microzooplankton are an important link in transferring pico- and nanoplankton production to higher trophic levels (Gifford 1991).

Despite the evident importance of microzooplankton in the marine pelagic food web, little has been studied of their taxonomic composition, spatio-temporal distribution and

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actual trophodynamic roles in the Inland Sea of Japan (Kamiyama 1994; Kamiyama & Tsujino 1996; Uye et al. 1996). In the western part of the Inland Sea of Japan, water exchange is primarily through the Bungo Channel, and the water from the Bungo Channel intrudes into the inner part of the Inland Sea of Japan through mixing with inshore water. Hiroshima Bay is one of the most eutrophic embayments in the Inland Sea of Japan, since large amounts of nutrients are supplied, mainly from the Ohta River (annual load of total nitrogen and phosphorus: 3700 and 290 t respectively; Yamamoto et al. 1996) and municipal sewage plants from densely populated cities like Hiroshima city. Therefore, a remarkable eutrophic and oligotrophic gradient is formed from Hiroshima Bay to the Pacific Ocean. Across a eutrophic and oligotrophic gradient formed in the eastern part of the Inland Sea of Japan, from Osaka Bay through Kii Channel to the Pacific Ocean, Uye et al. (1998) surveyed the geographical variations in plankton community structure and found that microzooplankton were most abundant in heavily eutrophic Osaka Bay and declined towards the offshore oligotrophic area. It is of interest to investigate the microzooplankton community in relation to different degrees of eutrophication, since the response of microzooplankton to eutrophication is not well documented in the marine environment (Revelante et al. 1985).

The purpose of our study was to examine the geographical, summer and winter variations in taxonomic composition, abundance and biomass of microzooplankton and to assess the production rate and grazing impact along a transect from Hiroshima Bay to the Pacific Ocean. The seasonal variations in taxonomic composition, abundance and the grazing impact of microzooplankton were investigated in the inner part of Hiroshima Bay (Kamiyama 1994: Kamiyama & Tsujino 1996). At 21 stations scattered in the Inland Sea of Japan, the abundance, biomass and production rate of microzooplankton were determined once per season (Uye et al. 1996). This is the first study characterizing the microzooplankton community across the trophic gradient formed in the western part of the Inland Sea of Japan through the Bungo Channel.

Materials and Methods

Cruises were made by the R/V *Toyoshio Maru*, Hiroshima University, in June 1998 and February–March 1999 to cover 9 and 8 stations, respectively, along a transect from Hiroshima Bay through the Bungo Channel to the Pacific Ocean off Kyushu (Fig. 1). In the latter cruise, however, we could not navigate offshore beyond Stn 8 due to limited ship time. Bottom depth was shallowest (28 m) at Stn 2 beyond which it declined gradually to 110 m at Stn 8, and then steeply declined to >2000 m at Stn 11. At each station, vertical profiles of temperature and salinity were obtained by a cast of a Sea-Bird STD. Water samples were collected with a pair of 10-liter Van Dorn bottles at 3 to 5 different depths shallower than 100 m. For chlorophyll-*a* concentration, 20–200 ml of water were filtered through glassfiber (Whatman GF/C) filters, which were then transferred to plastic vials containing 6 ml of N,N-dimethylformamide and kept in darkness at ca. −20°C until measurement with a fluorometer (Turner Designs, Model 10).

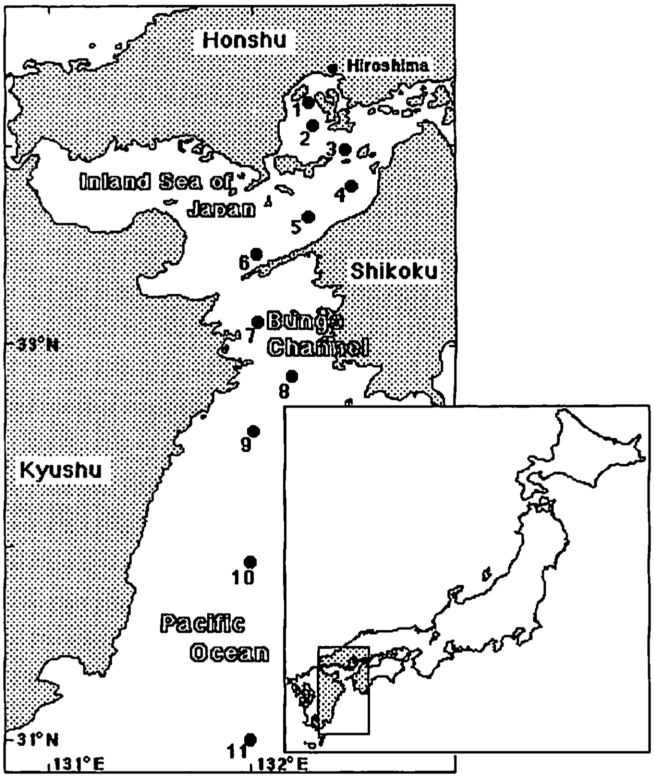

Fig. 1. Map of study area with the locations of sampling stations.

For microzooplankton analysis, 500 or 1000 ml of water from each depth was fixed with 1% glutaraldehyde and was kept refrigerated at ca. 3°C in darkness until microscopic examination. The preserved samples were concentrated by settling to a final volume of 25 ml, which was transferred to settling chambers for counting, according to the method of Utermöhl (1958), under an inverted microscope. In this study, we assigned tintinnid ciliates, naked ciliates and copepod nauplii to the microzooplankton. Heterotrophic dinoflagellates, which often comprise an important component of the microzooplankton (Lessard 1991), were not included. Counting was made on the species level for tintinnids according to the lorica morphology described by Kofoid & Campbell (1929), Marshall (1969) and Taniguchi (1997). Naked ciliates were counted on the genus level, according to Maeda (1997). Copepod nauplii were treated as a single group. Lengths of their appropriate body dimensions, e.g. length and diameter of lorica for tintinnids, short and long diameters for naked ciliates and body length for copepod nauplii, were measured to the nearest 1 μm using an eye-piece micrometer. For tintinnids, lorica volume (LV, μm^3) was converted to body carbon weight (Ct, pg) using the regression equation: Ct=444.5+0.053LV (Verity &

Langdon 1984). Lorica occupancy was assumed to be 100%. Differences between fixation by formalin and glutaraldehyde in estimating the mean population volume are generally low (Leakey et al. 1994), hence, a factor of 0.14 pg C μm^{-3} was used to convert cell volume of naked ciliates to carbon weight (Putt & Stoecker 1989). Carbon content of a copepod nauplius (Ct, ng) was calculated from body length (BL, μm) with the regression equation: $Ct = 1.51 \times 10^{-5}\ BL^{2.94}$ (Uye et al. 1996).

For each taxonomic group, the production rate (P, μg C $l^{-1} d^{-1}$) was estimated from biomass (B, μg C l^{-1}) and the empirically-determined specific growth rate (g, d^{-1}): $P = B \times g$. For copepod nauplii, the regression equation that describes 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) was used: $g = 0.057e^{0.069T}$. For ciliates, the multiple regression: $\ln g = 1.52 \ln T - 0.27 \ln CV - 1.44$, where T is temperature (°C) and CV is cell volume (μm^3), proposed by Müller & Geller (1993) was used. The cell volume of tintinnids was back-calculated from their body carbon weight using the conversion factor of 0.14 pg C μm^{-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.

Results

In summer

There were distinct horizontal and vertical variations in temperature, salinity and chlorophyll-*a* concentration (Fig. 2). The surface temperature was lowest (17.5°C) at Stn 3 and increased inshore to 20.2°C at Stn 1 as well as offshore to 25.7°C at Stn 10. The average temperature through the water column (<100 m) ranged from 16.4°C at Stn 5 to 20.9°C at Stn 10. Salinity was lowest (31.4) at the surface at Stn 1 and gradually increased offshore, with average water-column salinity ranging from 33.2 to 34.8. Chlorophyll-*a* concentration was highest (4.8 μg l^{-1}) at the surface at Stn 1 and decreased with depth as well as with station offshore. The lowest concentration (0.11 μg l^{-1}) was recorded at 100-m depth at Stn 11. The average total water-column chlorophyll-*a* concentration decreased from 2.56 μg l^{-1} at Stn 1 to 0.18 μg l^{-1} at Stn 11.

Usually microzooplankton were most abundant at the surface, decreasing with depth (Fig. 3). They were most abundant (2190 indiv. l^{-1}) at the surface at Stn 3, where naked ciliates were overwhelming. At Stns 1–5, tintinnids tended to be more abundant near the bottom. Their water-column-averaged abundances were much higher (416–496 indiv. l^{-1}) at Stns 1–3 than at Stns 9–11 (110–135 indiv. l^{-1}, Fig. 4). Throughout the stations, naked ciliates numerically

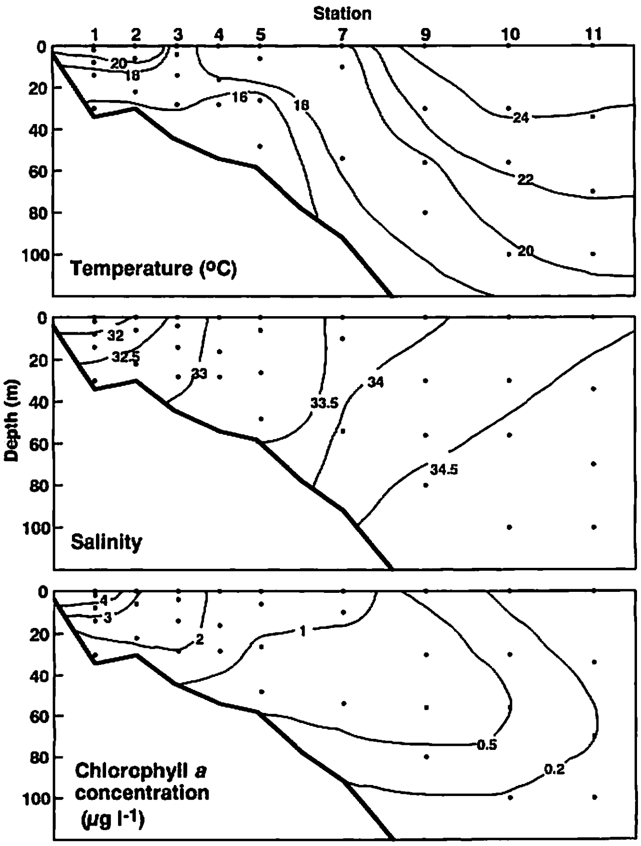

Fig. 2. Vertical distribution of temperature, salinity and chlorophyll-*a* concentration across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in June 1998.

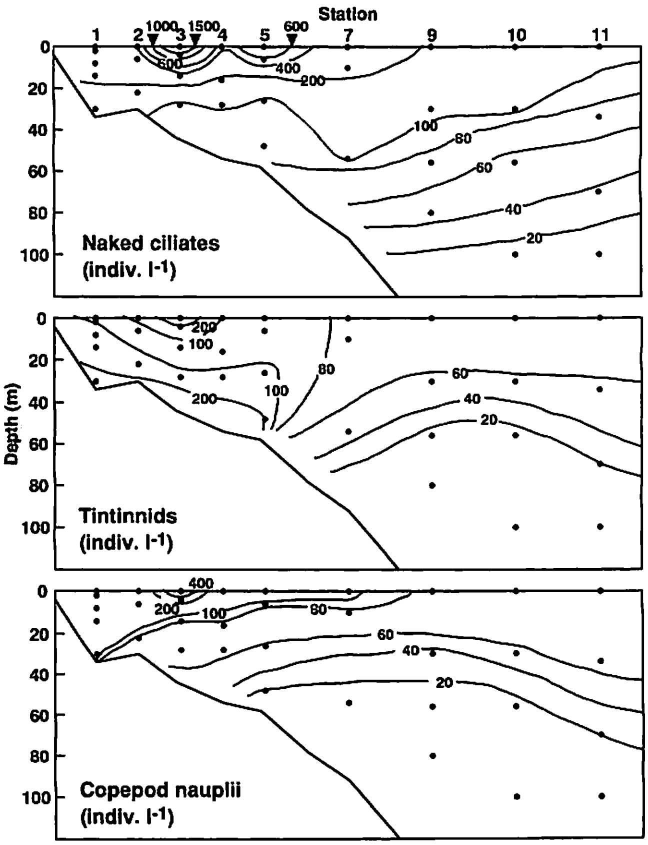

Fig. 3. Vertical variation in abundance of naked ciliates, tintinnids and copepod nauplii across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in June 1998.

dominated the microzooplankton community (overall mean: 57%), followed, in order, by tintinnids (24%) and copepod nauplii (19%).

A total of 42 species of tintinnids belonging to 8 genera were identified, although their detailed distribution pattern will be reported elsewhere (Godhantaraman & Uye, in preparation). Of these, 23 species belonged to the genus *Tintinnopsis*. *Tintinnopsis beroidea*, *T. brevicollis*, *T. nana* and *Stenosemella nivalis* were most common at all stations and they accounted for ca. 40–60% of total tintinnid abundance. Tintinnid species diversity decreased from inshore to offshore stations. Of naked ciliates, only 2 genera, i.e. *Strombidium* and *Strobilidium* were identified, the former comprising 55% on average of the numerical total.

The water-column-averaged biomass of microzooplankton showed a similar inshore-to-offshore pattern (Fig. 4), being highest (4.24 μg C l^{-1}) at Stn 1 and lowest (0. 39 μg C l^{-1}) at Stn 10. In terms of biomass, the contribution of copepod nauplii was largest (overall mean: 47%), due to their heavier individual body weight compared to naked ciliates and tintinnids, which comprised 28 and 25%, respectively.

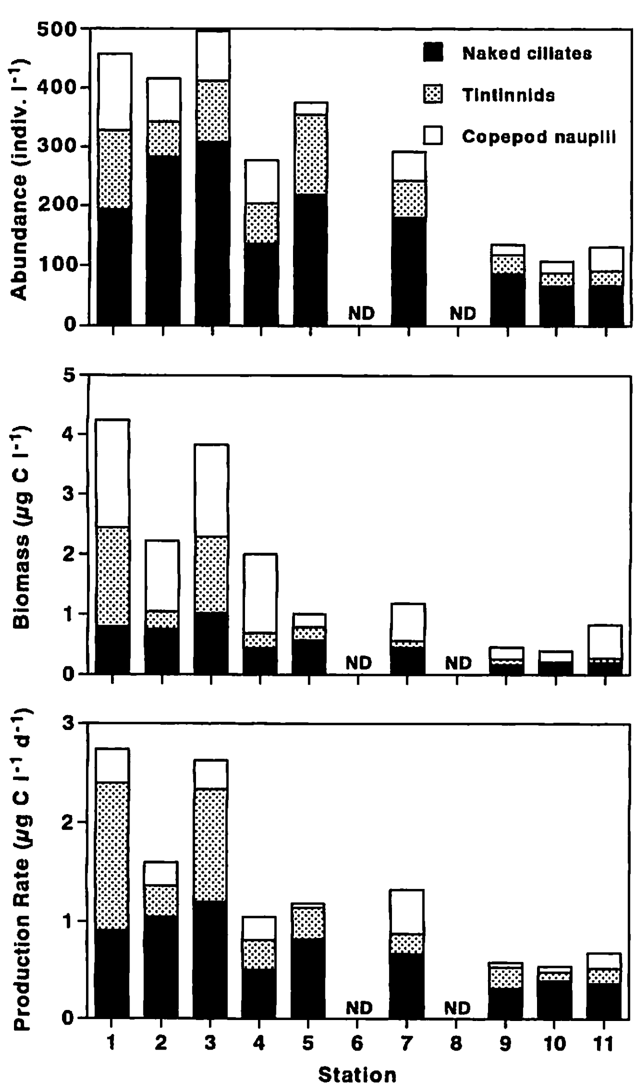

Fig. 4. Geographical variations in abundance, biomass and estimated production rate of microzooplankton across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in June 1998. Values are depth-weighted water-column averages. ND indicates no data.

The estimated production rate of microzooplankton also showed a similar geographical pattern (Fig. 4) to that noted above. The water-column-averaged production rate was highest (2.74 μg C l^{-1} d^{-1}) at Stn 1 and lowest (0.54 μg C l^{-1} d^{-1}) at Stn 10. The contribution by ciliate protozoans was remarkable: on average 50% by naked ciliates and 35% by tintinnids.

In winter

Temperature, salinity and chlorophyll-*a* concentrations were more or less vertically homogenous (Fig. 5). The water-column-averaged temperature was lowest (11.3°C) at Stn 1 and increased to 16.7°C at Stn 8. Average salinity varied from 32.8 to 34.6. Average chlorophyll-*a* concentration was highest (2.14 μg l^{-1}) at Stn 1 and decreased to 0.75 μg l^{-1} at Stn 5, beyond which it increased to 1.57 μg l^{-1} at Stn 8.

Each taxonomic group exhibited its own specific distribution pattern (Fig. 6). Naked ciliates were distributed homogeneously near the surface at all stations and their density decreased gradually with depth. Tintinnids were aggregated at the surface at Stn 3 and near the bottom at Stn 1. Their abundance declined to <40 indiv. l^{-1} at Stn 4 and offshore. Copepod nauplii were most abundant near the bottom at Stn 1 and decreased offshore. The average abundance of total microzooplankton throughout the water-column was highest (260 indiv. l^{-1}) at Stn 1 and declined gradually offshore to 105 indiv. l^{-1} at Stn 8 (Fig. 7). Over the transect, tintinnids were numerically overwhelming (overall mean: 46%), followed, in order, by naked ciliates (37%) and copepod nauplii (17%). Tintinnids were particularly important at Stns 1–3, where they accounted for >50%, while naked ciliates were more important at Stns 6–8, where they comprised >45%.

In winter, the total number of tintinnid species identified decreased to 20, representing 3 genera. Of numerical importance were *Stenosemella nivalis* and *Tintinnopsis beroidea*, which were also common in summer. There was a clear decline in species diversity from inshore to offshore stations. Of the naked ciliates, only the genus *Strombidium* was identified.

The geographical variation in biomass was different from the pattern observed for numerical abundance, the highest value (1.19 μg C l^{-1}) being recorded at Stn 4 (Fig. 7). This was due to the relatively large contribution of copepod nauplii to the microzooplankton biomass, with an overall mean of 55%. Tintinnids and naked ciliates accounted for 29 and 16%, respectively.

The production rate was relatively high (i.e. >0.4 μg C

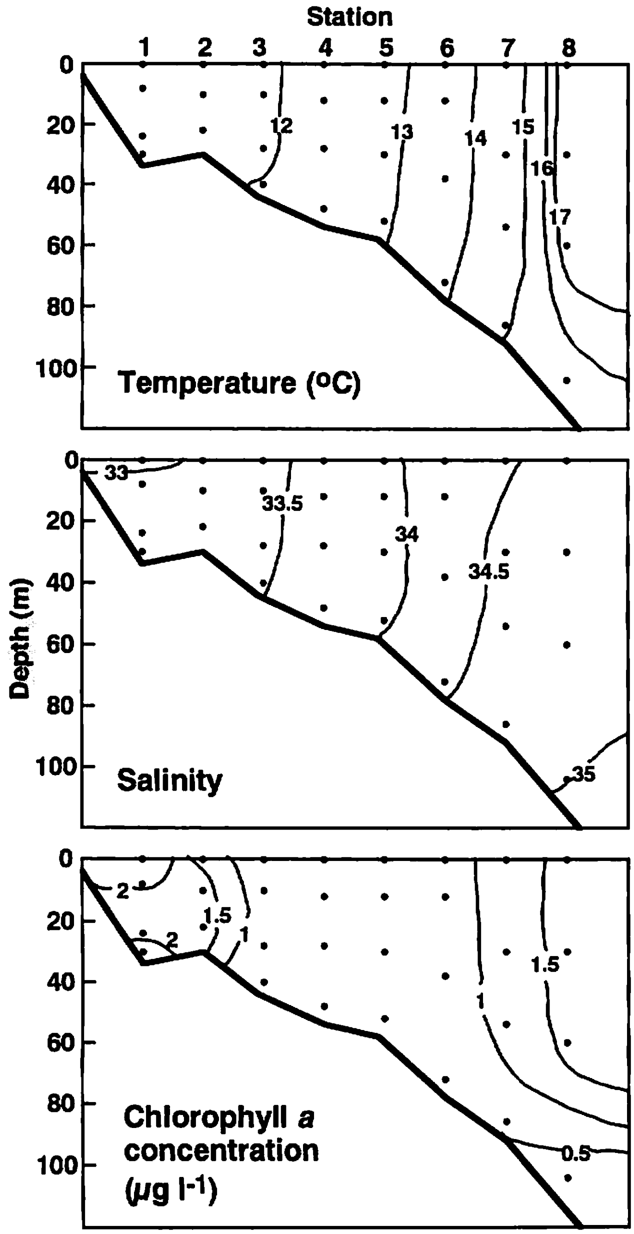

Fig. 5. Vertical distribution of temperature, salinity and chlorophyll-*a* concentration across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in February–March 1999.

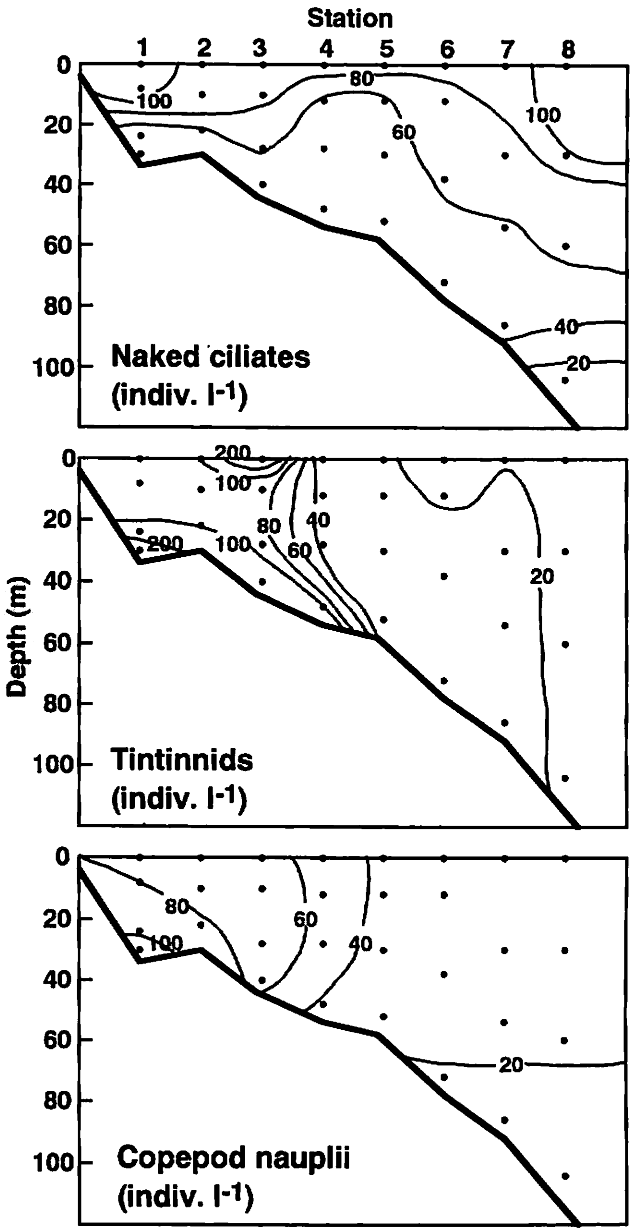

Fig. 6. Vertical variation in abundance of naked ciliates, tintinnids and copepod nauplii across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in February–March 1999.

l^{-1} d^{-1}) at Stns 1–3 and 8, and was lowest (0.27 μg C l^{-1} d^{-1}) at Stn 5 (Fig. 7). The overall mean was 0.40 μg C l^{-1} d^{-1}. The production rate of ciliated protozoans contributed, on average, 83% of the total production rate.

Discussion

Abundance and biomass

In general, temperate waters, and eutrophic waters in particular, are known to show remarkable seasonal changes in taxonomic composition, abundance and biomass of microzooplankton, and these parameters are usually highest in summer and lowest in winter (Burkill et al. 1987; Dolan & Coats 1990; Leakey et al. 1992; Edwards & Burkill 1995). Such seasonal variations have also been demonstrated in the innermost part of Hiroshima Bay by Kamiyama (1994) and Kamiyama & Tsujino (1996). Our surveys were conducted only in June and February–March, and hence represent the microzooplankton community in summer culminating and winter depressing conditions. Excluding the data obtained from the most offshore 3 stations (i.e. Stns 9–11) in summer, the overall mean abundances and biomasses of total microzooplankton were comparable; they were 386

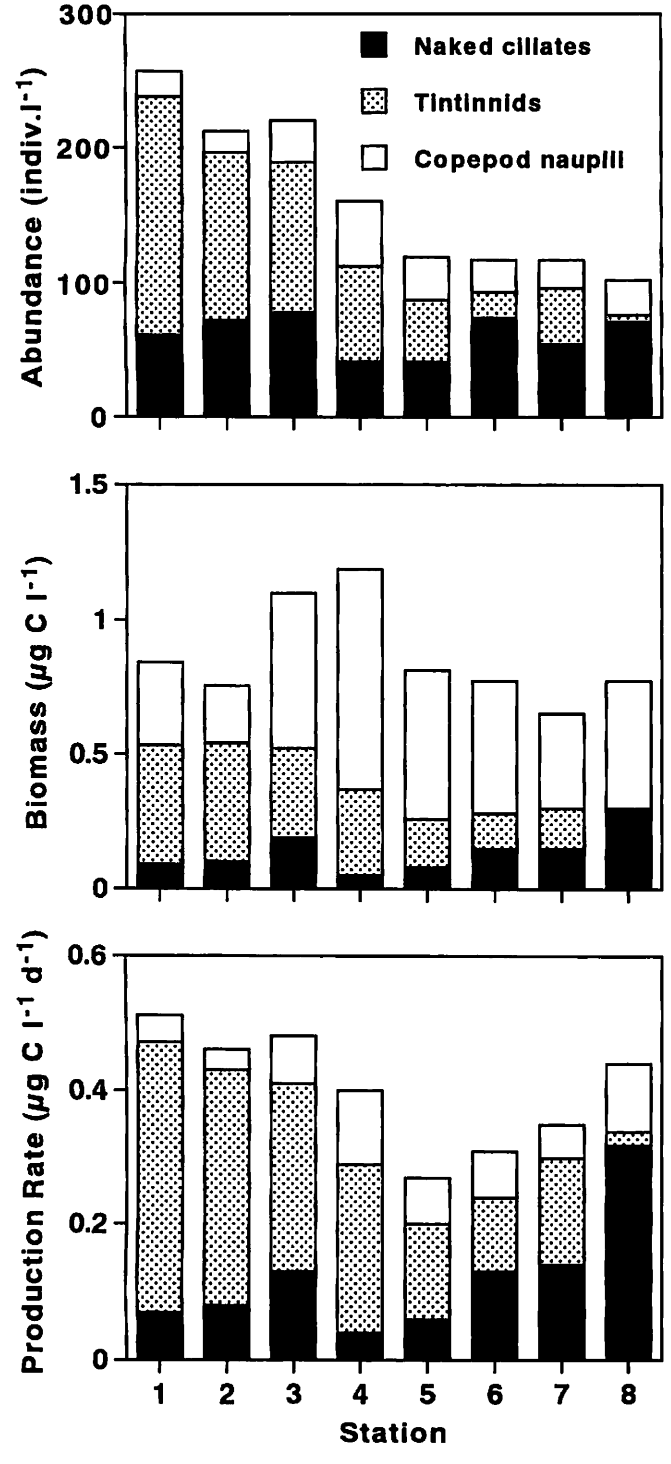

Fig. 7. Geographical variations in abundance, biomass and estimated production rate of microzooplankton across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean in February–March 1999. Values are depth-weighted water-column averages.

indiv. l^{-1} and 2.41 μg C l^{-1} in summer and 162 indiv. l^{-1} and 0.86 μg C l^{-1} in winter, respectively. Compared to the large, i.e. one to two orders of magnitude, difference in numerical abundance observed by Kamiyama (1994), our summer and winter variance was only 2.4 fold. Mean chlorophyll-*a* concentration, an indicator of the potential phytoplanktonic food supply for microzooplankton, was only slightly higher in summer (2.56 μg l^{-1}) than in winter (2.14 μg l^{-1}). Hence, the higher proliferation of microzooplankton in summer may be attributed mainly to higher temperatures rather than higher food concentrations; both factors have been reported as the most important factors affecting the growth rates of microzooplankton (Heinbokel 1978; Taniguchi & Kawakami 1983; Verity 1986).

However, there was a shift in numerical dominance with season; between loricated ciliates and aloricated ones, the former group was more abundant in winter while the latter dominated in summer. A similar seasonal shift between these two protozoan groups was also observed by Kamiyama (1994) in Hiroshima Bay, indicating that the reproductive response of these groups to the seasonal environmental factors may not be the same.

In both seasons, there were marked decreases in microzooplankton abundance from inshore to offshore stations. The highest water-column-averaged abundance observed in our survey was 496 indiv. l^{-1} at Stn 3. This was higher than the value (212 indiv. l^{-1}) observed in June by Uye et al. (1996) at a station near Stn 1. Kamiyama (1994) investigated the seasonal change in microzooplankton abundance in the more eutrophic part of Hiroshima Bay shorewards of our Stn 1, and his numerical data from 2-m depth in June were much greater (ca. 5000 to 10000 indiv. l^{-1}) than the maximum density we observed at the surface at Stn 3 (2190 indiv. l^{-1}). At. Stns 4–7, where the water is less eutrophic (water-column-averaged dissolved total phosphorous and nitrogen ranged from 0.17 to 0.48 μg-at l^{-1} and from 4.8 to 13. 1 μg-at l^{-1}, respectively) compared to Hiroshima Bay (ranges 0.3 to 0.58 μg-at l^{-1} and 3.03 to 14.7 μg-at l^{-1}, respectively, Hashimoto et al. 1996), the densities were 116–375 indiv. l^{-1}, almost comparable to those (128–238 indiv. l^{-1}) reported by Uye et al. (1996) at stations near Stns 5 and 7. At Stns 9–11, where the water is largely of oceanic origin, because of intrusion by the highly oligotrophic Kuroshio-associated water, microzooplankton densities were lowest (110–135 indiv. l^{-1}). A similar inshore-high and offshore-low gradient of microzooplankton density was demonstrated along a eutrophic and oligotrophic transect drawn in the eastern part of the Inland Sea of Japan through the Kii Channel (Uye et al. 1998). To combine results from these previous works (Kamiyama 1994; Uye et al. 1996, 1998) and those from the present study, the geographical distribution of microzooplankton in the Inland Sea of Japan and adjacent waters can be roughly summarized as follows. They are always most abundant in heavily eutrophic embayments like Osaka Bay and Hiroshima Bay and gradually decrease towards the Pacific Ocean through Kii Channel and Bungo Channel.

In addition to the geographical distribution pattern, microzooplankton also showed clear trends in their vertical distribution. In summer, the distribution of 3 taxonomic

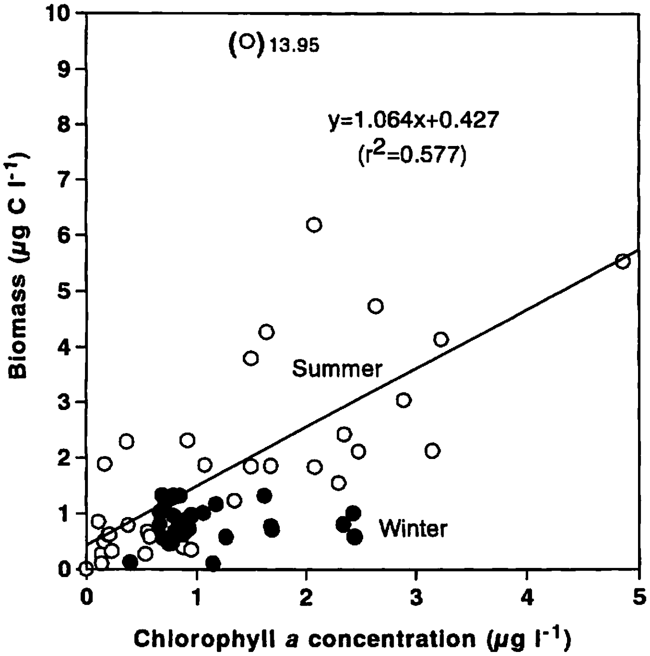

Fig. 8. Relationship between biomass of microzooplankton and chlorophyll-*a* concentration in summer (open circles) and winter (filled circles). An extremely high value (in parenthesis) was omitted for the calculation of the regression line in summer. Note no significant relationship in winter.

groups exhibited more or less similar cross-sectional patterns (Fig. 3), indicating that the factors affecting their distribution were the same. Many previous studies (Revelante & Gilmartin 1983; Revelante et al. 1985; Sanders 1987; Kamiyama 1994; Uye et al. 1996) have demonstrated that food supply is the primary factor influencing the spatial distribution of microzooplankton. We examined the relationship between microzooplankton biomass and chlorophyll-*a* concentration for all water samples ($n=34$), although our chlorophyll values represented all size categories of phytoplankton. As shown in Fig. 8, a significantly ($p<0.05$) positive correlation was obtained, supporting the previous findings on the importance of food supply. In winter, the cross-sectional distribution pattern differed among taxonomic groups; the difference between the protozoan groups was particularly striking (Fig. 6). There was no significant relationship between microzooplankton biomass and chlorophyll-*a* concentration (Fig. 8). In addition, there was no significant relationship between the biomass of each taxonomic group and chlorophyll-*a* concentration. This may be due to lower growth rates of microzooplankton at the lower winter temperatures, even when the same amount of phytoplankton food is available as in summer. The differences in phytoplankton quality and predator abundance may also be important regulators of the tightness of trophic coupling (Verity & Villareal 1986; Verity 1987; Sanders 1987; Stoecker & Capuzzo 1990).

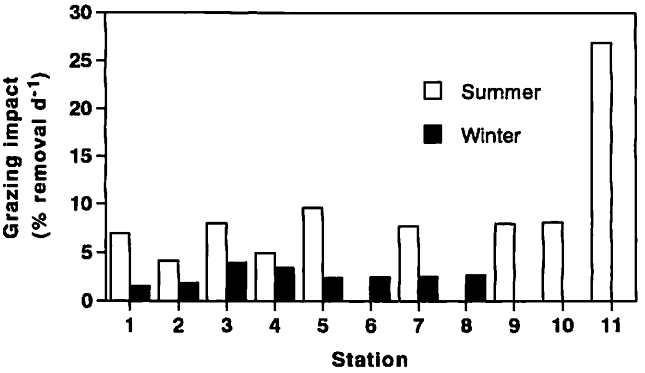

Fig. 9. Geographical variations in grazing impact of microzooplankton as expressed by percent (%) removal of phytoplankton biomass per day across the inshore–offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean during summer and winter.

Trophodynamic roles

The average production rate of microzooplankton over Stns 1 to 8 was 3.3 times higher in summer than in winter, due to the combined effects of higher biomass and temperatures in summer. In both seasons, the majority (>83%) of the production was attributed to ciliated protozoans. In contrast to the remarkable inshore-offshore gradient in production rate observed in summer, the geographical variation was moderate in winter, reflecting the relatively homogenous distribution of microzooplankton, particularly ciliated protozoans.

The trophodynamic roles of microzooplankton, particularly as phytoplankton grazers, across the inshore and offshore trophic gradient were assessed by estimating their daily removal rate of phytoplankton biomass. For this, phytoplankton carbon biomass was estimated from chlorophyll-*a* concentration using a carbon : chlorophyll ratio of 40 (Parsons et al. 1984). The amount of phytoplankton food required to meet the production rate was estimated assuming that the gross growth efficiency is 0.4 for ciliated protozoans (Fenchel 1987) and 0.3 for copepod nauplii (Ikeda & Motoda 1978). As shown in Fig. 9, the potential percentage of the initial phytoplankton biomass removed by grazing by microzooplankton was relatively constant over the transect except at Stn 11 in summer. In summer, it varied from 4.1 to 9.6% with mean of 7.2%, except at Stn 11 where it was 27%. In winter, the daily grazing impact varied from 1.5 to 3.9% with a mean of 2.6%. Kamiyama (1994) reported on the seasonal variation in grazing rate of the microzooplankton community determined by the dilution technique (Landry & Hassett 1982); it was high in summer and low in winter with an annual mean of 19.1 and 11.6% at 2 stations in Hiroshima Bay. Compared to his data, our results, particularly in winter, were considerably lower. Hence, over the extended study area, microzooplankton might play a relatively minor role as phytoplankton grazers, and their minor importance held over the significant trophic gradient. The high removal rate found at Stn 11 in summer suggested that the trophodynamic role of microzooplankton might be more important in the offshore oligotrophic waters beyond this station.

In conclusion, in summer, although microzooplankton showed marked geographical variations in terms of numerical abundance, biomass and estimated production rates across the inshore to offshore gradient, their trophodynamic role as phytoplankton grazers was relatively small and constant except at the most offshore station. In winter, microzooplankton were much fewer in number and exhibited less geographical variation compared to summer. Their grazing impact upon the phytoplankton was much less than in summer and showed little geographical variation across the trophic gradient.

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Literature Cited

Beers, J. R. & G. L. Stewart 1969. Microzooplankton and its abundance relative to the larger zooplankton and other seston components. *Mar. Biol.* 4: 182–189.

Beers, J. R. & G. L. Stewart 1971. Microzooplankton in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep-Sea Res.* **18**: 861–883.

Burkill, P. H., R. F. C. Mantoura., C. A. Llewellyn & N. J. P. Owens 1987. Microzooplankton grazing and selectivity of phytoplankton in coastal waters. *Mar. Biol.* **93**: 581–590.

Dolan, J. R. & D. W. Coats 1990. Seasonal abundance of planktonic ciliates and microflagellates in mesohaline Chesapeake Bay waters. *Estuar. Coast. Shelf Sci.* **31**: 157–175.

Edwards, E. S. & P. H. Burkill 1995. Abundance, biomass and distribution of microzooplankton in the Irish Sea. *J. Plankton Res.* **17**: 771–782.

Fenchel, T. 1987. *Ecology of Protozoa-The Biology of Free-Living Phagotrophic Protists.* Springer-Verlag, Berlin, 197 pp.

Fukami, K., A. Watanabe., S. Fujita., K. Yamaoka & T. Nishijima 1999. Predation on naked protozoan microzooplankton by fish larvae. *Mar. Ecol. Prog. Ser.* **185**: 285–291.

Gifford, D. J. 1991. The protozoan-metazoan trophic link in pelagic ecosystems. *J. Protozool.* **38**: 81–86.

Hashimoto, T., T. Yamamoto., K. Tada., O. Matsuda., T. Nagasue., T. Tada., A. Go & K. Nakaguchi 1996. Seasonal investigation of water quality characteristics of the Seto Inland Sea. *J. Fac. Appl. Biol. Sci., Hiroshima Univ.* **35**: 243–273.

Heinbokel, J. F. 1978. Studies on the functional role of tintinnids in the Southern California Bight. 1. Grazing and growth rates in laboratory cultures. *Mar. Biol.* **47**: 177–189.

Ikeda, T. & S. Motoda 1978. Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. *Fish. Bull.* **76**: 357–366.

Kamiyama, T. 1994. The impact of grazing by microzooplankton in northern Hiroshima Bay, the Seto Inland Sea, Japan. *Mar. Biol.* **119**: 77–88.

Kamiyama, T. & M. Tsujino 1996. Seasonal variation in the species composition of tintinnid ciliates in Hiroshima Bay, the Seto Inland Sea of Japan. *J. Plankton Res.* **18**: 2313–2327.

Kofoid, C. A. & A. S. Campbell 1929. A conspectus of the marine and freshwater ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the eastern tropical Pacific 1904–1905. *Univ. Calif. Publ. Zool.* **34**: 1–403.

Landry, M. R. & R. P. Hassett 1982. Estimating the grazing impact of marine microzooplankton. *Mar. Biol.* **67**: 283–288.

Leakey, R. J. G., P. H. Burkill & M. A. Sleigh 1992. Planktonic ciliates in Southampton water: abundance, biomass, production, and role in pelagic carbon flow. *Mar. Biol.* **114**: 67–83.

Leakey, R. J. G., P. H. Burkill & M. A. Sleigh 1994. A comparison of fixatives for the estimation of abundance and biovolume of marine planktonic ciliate populations. *J. Plankton Res.* **16**: 375–389.

Lessard, E. J. 1991. The trophic role of heterotrophic dinoflagellates in diverse marine environments. *Mar. Microb. Food Webs* **5**: 49–58.

Maeda, M. 1997. Suborder Oligotrichina, p. 397–420. In *An Illustrated Guide to Marine Plankton in Japan* (eds. Chihara, M. & M. Murano). Tokai Univ. Press, Tokyo.

Marshall, S. M. 1969. Protozoa Order Tintinnida, p. 117–127. In *Fishes d' Identification du Zooplankton Cons. Per. Int. Explor. Mer Zooplankton Sheet* (eds. Fraser, J. H. & V. Kr. Hansen). Charlottenlund, Denmark.

Müller, H. & W. Geller 1993. Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. *Arch. Hydrobiol.* **126**: 315–327.

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

Parsons, T. R., M. Takahashi & B. Hargrave 1984. *Biological Oceanographic Processes*, 3rd ed. Pergamon Press, Oxford, 330 pp.

Putt, M. & D. K. Stoecker 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. *Limnol. Oceanogr.* **34**: 1097–1103.

Revelante, N. & M. Gilmartin 1983. Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. *Oceanol. Acta.* **6**: 407–415.

Revelante, N., M. Gilmartin & N. Smodlaka 1985. The effects of Po River induced eutrophication on the distribution and community structure of ciliated protozoan and micrometazoan populations in the Northern Adriatic Sea. *J. Plankton Res.* **7**: 461–471.

Robertson, J. R. 1983. Predation by estuarine zooplankton on tintinnid ciliates. *Estuar. Coast. Shelf Sci.* **16**: 27–36.

Sanders, R. W. 1987. Tintinnids and other microzooplankton–seasonal distributions and relationship to resources and hydrography in a Maine estuary. *J. Plankton Res.* **9**: 65–77.

Stoecker, D. K. & D. A. Egloff 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *J. Exp. Mar. Biol. Ecol.* **110**: 53–68.

Stoecker, D. K. & J. D. Capuzzo 1990. Predation on protozoa: its implications to zooplankton. *J. Plankton Res.* **12**: 891–908.

Taniguchi, A. 1997. Suborder Tintinnina, p. 421–483. In *An Illustrated Guide to Marine Plankton in Japan* (eds. Chihara, M. & M. Murano). Tokai Univ. Press, Tokyo.

Taniguchi, A & R. Kawakami 1983. Growth rates of ciliate *Eutintinnus lusus undae* and *Favella taraikaensis* observed in the laboratory culture experiments. *Bull. Plankton Soc. Jpn* **30**: 33–40.

Utermöhl, H. 1958. Zur Vervolkommung der quantitativen phytoplankton. *Methodik. Mitt. Int. Verein. Theor. Angew. Limnol.* **9**: 1–38.

Uye, S., N. Nagano & H. Tamaki 1996. Geographical and seasonal variations in abundance, biomass and estimated production rates of microzooplanton in the Inland Sea of Japan. *J. Oceanogr. Soc. Jpn* **52**: 689–703.

Uye, S., N. Nagano & T. Shimazu 1998. Biomass, production and trophic roles of micro- and macrozooplankton in Dokai Inlet, a heavily eutrophic inlet, in summer. *Plankton Biol. Ecol.* **45**: 171–182.

Verity, P. G. 1985. Grazing, respiration, excretion and growth rates of tintinnids. *Limnol. Oceanogr.* **30**: 1268–1282.

Verity, P. G. 1986. Growth rates of natural tintinnid populations in Narragansett Bay. *Mar. Ecol. Prog. Ser.* **29**: 117–126.

Verity, P. G. 1987. Abundance, community composition, size distribution, and production rates of tintinnids in Narragansett Bay, Rhode Island. *Estuar. Coast. Shelf Sci.* **24**: 671–690.

Verity, P. G. & C. Langdon 1984. Relationship between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.* **66**: 859–868.

Verity, P. G. & T. A. Villareal 1986. The relative food value of diatoms, dinoflagellates, flagellates, and cyanobacterica for tintinnid ciliates. *Arch. Protistenkd.* **131**: 71–84.

Yamamoto, T., T. Kitamura & O. Matsuda 1996. Riverine inputs of fresh water, total nitrogen and total phosphorous in the Seto Inland Sea. *J. Fac. Appl. Biol. Sci., Hiroshima Univ.* **35**: 81–104.