Characteristics of the distribution of bacteria, heterotrophic nanoflagellates and ciliates in Hiroshima Bay in summer

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ABSTRACT: The distribution of the main microbial loop components (bacteria, heterotrophic nanoflagellates (HNF), ciliates) was investigated at three sites: the inner, central and outer regions of Hiroshima Bay, Seto Inland Sea, Japan, in summer (June and August 1996 and July 1997). At the inner region site, lower salinity and higher concentrations of nutrients and chlorophyll a were observed than in the other regions. Bacterial, HNF and ciliate biomasses ranging from 32.6 to 170.1 μg C/L, from 1.5 to 84.8 μg C/L and from 0.1 to 91.7 μg C/L, respectively, were generally highest at the inner region site. The ciliate assemblages were mostly dominated by mixotrophic aloricate ciliates in the surface and near-surface layers. The relationship between the biomass of aloricate ciliates and their prey organisms showed significant linear correlations at the three sites. The slope of the regression line was lowest and the X-axis intercept of the line was highest at the inner region site, possibly suggesting relatively low energy transfer efficiency between them in this site. Hence, high biomass of less than 20 μm phytoplankton, bacteria and HNF may not be efficiently utilized by ciliates in the inner region of Hiroshima Bay, compared with the situation in other regions of the bay.

KEY WORDS: bacteria, biomass, ciliate, distribution, heterotrophic nanoflagellate, Hiroshima Bay.

INTRODUCTION

Recent studies on the roles of microbial loop components, such as bacteria, heterotrophic nanoflagellates (HNF), heterotrophic dinoflagellates and ciliates, have demonstrated that significant energy flows from bacteria to higher trophic levels occur in various oceanic regions.1-4 This also implies that some parts within the microbial loop effectively link with the grazing food chain and may enhance fisheries.5-7 Especially, in eutrophic bays where the bacterial biomass and production are very high, it is likely that the bacterial production strongly influences planktonic food webs, which enhance the productivity of higher trophic levels, even if there is significant loss due to the numerous trophic levels.8

Hiroshima Bay is a semi-enclosed bay and is one of the eutrophic areas in the Seto Inland Sea of Japan. The northern, inner region of the bay is strongly influenced by riverine inputs and has a very low seawater exchange rate with the outer region, with a freshwater residence time of 20.6 days.9 Also, like chlorophyll a concentrations, the biomass and production of bacteria are high in the Seto Inland Sea,10-12 implying that microbial food webs play important roles in the ecosystem of the bay. Abundances and/or biomasses of bacteria, HNF and ciliate assemblages have been reported for Hiroshima Bay.11-20 However, information on simultaneous investigation of bacteria, HNF and ciliates is limited to the findings of Kamiyama et al.20 but even this information is limited to the case of a bloom period at one site.

Hiroshima Bay is an important area for the production of planktivorous shellfish and fish. There are many rafts for aquaculture of oysters throughout the whole bay and adjacent areas, and oyster production in these areas constitutes 50–60% of the total Japanese production. Furthermore, the productivity of planktivorous fish such as anchovies and sardines in Hiroshima Bay is very high.21 To utilize the fisheries resources in the bay effec-
tively and sustainably, it is necessary to clarify the food web components and the energy flow between them, including the microbial loop system, together with the environmental characteristics of the bay.

In the present study, the distributions of the main microbial loop components (bacteria, HNF and ciliates) and the environmental conditions in Hiroshima Bay in summer were examined and compared with different regions of the bay.

MATERIALS AND METHODS

Study sites and sampling programs

Environmental factors were investigated at six sites in Hiroshima Bay (Fig. 1). Sampling was performed from the research vessel R/V Shirafuji-Maru, belonging to the National Research Institute of Fisheries and Environment of Inland Sea in summer (13–15 June and 20–22 August 1996, and 1–3 July 1997). Vertical profiles of temperature, salinity and dissolved oxygen concentration (DO) were measured at all sites with a portable temperature-salinity bridge (Model 602; YEO-KAL Electronics, Brookvale, NSW, Australia) and a portable DO meter (Model 8500; Nester Instruments, PA, USA). Seawater was collected from the surface with a plastic bucket and from 2-m and 5-m depth layers and then every 10-m depth layer to 1 m above the bottom (B-1 m) with a Van Dorn (Rigo, Tokyo, Japan) water sampler. The main microbial loop components (bacteria, HNF and ciliates) were also investigated at three of the six sites: the inner (Stn. 1), central (Stn. 3) and outer (Stn. 5) regions of the bay.

Sample treatment for measuring environmental parameters

Two subsamples (50–100 mL), one of the unfractionated seawater sample (total fraction) and the other one filtered through a 20-µm mesh screen (<20 µm fraction), from each depth layer were filtered onto glass-fiber filters (GF/F; Whatman, Kent, UK) using gentle vacuum pressure (<150 mmHg). The <20 µm fraction of phytoplankton is considered to equate with the amount of pico- and nano-phytoplankton, which are main prey organisms for ciliates. The chlorophyll a on the filters was extracted with N,N-dimethylformamide at −20°C under dark conditions, and then measured with a Turner Designs fluorometer (Turner Designs, Sunnyvale, Canada).

Another seawater subsample from each depth was filtered through a Millipore Milex HV-filter (pore size: 0.45 µm; Millipore, Billerica, MA, USA), and the concentrations of nutrients (NO₂-N, NO₃-N, NH₄-N, PO₄-P and SiO₂-Si) in each filtrate were measured using a TrAAcs 800 autoanalyzer (Bran+Luebbe, Roselle, IL, USA), based on the method of Strickland and Parsons.

Treatment and observation of the main microbial loop components

To investigate both abundance and biomass of the ciliate assemblages, two seawater subsamples (500 mL and 100 mL) from each depth were fixed with Lugol's iodine and buffered formaldehyde, respectively (final concentrations: both 2%), and stored at approximately 2°C in the dark. The seawater subsample fixed with Lugol's iodine was con-
centrated by settling to a volume of 1–3 mL. Ciliates were counted in 1 mL of the concentrated sample with a phase contrast microscope at magnifications of ×100 or ×200, using a Sedgewick-Rafter chamber (Toshinriko, Tokyo, Japan). The dimensions of the lorica or cell body were measured as described below. The seawater subsample fixed with buffered formaldehyde was allowed to settle in an Utermöhl (Phycotech, St Joseph, MI, USA) chamber and the aloricate ciliates were counted with an inverted epifluorescence microscope (IX-70; Olympus, Tokyo, Japan) at a magnification of ×150 to discriminate the mixotrophic ciliates from the heterotrophic ones; the cell dimensions of each ciliate were measured as described below. Finally, the ratio of the mixotrophic ciliates and the heterotrophic ciliates to the total aloricate ciliate abundance (RMA and RHA, respectively) and the ratio to the total aloricate ciliate cell volume (RMV and RHV, respectively) were calculated for each sample.

In the ciliate assemblages, most of the tintinnids were identified to species from the lorica morphology based on the same references used in Kamiyama and Tsujino. However, heterotrophic and mixotrophic aloricate ciliates could not be readily identified into genus or species. Hence, they were grouped into separate morphotypes that were based on size and shape. In the present study, the autotrophic ciliate Mesodinium rubrum (= Myrionecta rubra) was not included in the aloricate ciliates. The dimensions of the lorica of tintinnids or the cell body of aloricate ciliates were measured using a calibrated ocular micrometer or Scion Image (Scion, Frederick, MD, USA) for up to a maximum of 10 individuals for each taxon. The mean lorica volume for tintinnids and the mean cell volume for aloricate ciliates were calculated by approximating the shape of each ciliate taxon to a standard geometric configuration.

There is a possibility that fixation with formaldehyde causes an underestimation of aloricate ciliate abundance. Hence, the abundance and cell volume of aloricate ciliates fixed with Lugol’s iodine were adopted (AC and VC, respectively), and abundances and cell volumes of mixotrophic ciliates (AMC and VMC, respectively) and heterotrophic ciliates (AHC and VHC, respectively) were calculated with the following equations:

\[ \text{AMC} = RMA \times AC, \quad \text{VMC} = RMV \times VC \]

for mixotrophic ciliates

\[ \text{AHC} = RHA \times AC, \quad \text{VHC} = RHV \times VC \]

for heterotrophic ciliates

Seawater from each depth layer was fixed with glutaraldehyde (final concentration 1%) and the abundances of bacteria and HNF were quantified with an epifluorescence microscope according to the method of Iwamoto et al. based on the procedures of Porter and Feig and Sherr and Sherr. Bacteria in 0.3 mL of the fixed subsamples were stained with 4′,6-diamidino-2-phenylindole (DAPI; final concentration: 0.5 μg/mL), and then filtered onto Sudan black B-stained Nucleopore (Nomura Micro Science, Atsugi, Kanagawa, Japan) polycarbonate filters (pore size: 0.2 μm) with <300 mmHg vacuum pressure. The HNF in 5–20 mL of the fixed subsamples were stained with DAPI (final concentration 0.1 μg/mL) and fluorescein isothiocyanate (FITC; final concentration 1 μg/mL) solutions and then filtered onto a Sudan black B-stained Nucleopore filter (pore size 1.0 μm) with <100 mmHg vacuum pressure. At least 200 bacterial cells in more than 10 fields and at least 50 HNF cells in more than 25 fields were counted with an epifluorescence microscope at ×1250 magnification. The length and width of each HNF cell were measured using a calibrated ocular micrometer, and then the cell volume was calculated as an elliptical sphere.

**Estimation of the biomass of the microbial loop components**

The carbon content of tintinnid ciliates (Ct, pg) was estimated by fitting the lorica volume (LV, μm³) of each species into the equation:

\[ Ct = 444.5 + 0.053 \times LV \]

and the carbon content of aloricate ciliate cells preserved in 2% Lugol’s iodine solution was calculated from the cell volume data using a carbon conversion factor of 0.19 pg C/μm³. The carbon content of bacteria was converted from the mean cell volume (0.098 μm³/cell) from annual Hiroshima Bay data and an allometric conversion equation (29.6 fgC/cell). The carbon values of HNF were estimated from measured cell volumes, using a carbon conversion factor of 0.22 pg C/μm³.

**RESULTS**

**Patterns of distribution of temperature, salinity and nutrients**

Temperature and salinity ranged from 15.6°C to 26.8°C and from 14.2 to 34.1 p.s.u. over the study period, and were vertically stratified at all the sites (Fig. 2). Dissolved oxygen concentration (DO) exceeded 4 mg/L except in the B-1 m layer at Stn. 1 in August, indicating that DO did not strongly regulate the distribution of plankton assemblages.
in almost all the sites of Hiroshima Bay (data not shown). In July 1997, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP) and SiO$_2$-Si concentrations were comparatively high in the surface layer at the innermost site (Stn. 1; Fig. 2), indicating that riverine inputs strongly influenced the seawater environment at Stn. 1. However, the riverine influence on nutrient con-
centrations probably did not reach Stn. 3. In August, high concentrations of DIN and DIP occurred in the 10-m and B-1 m layers at Stn. 2, while these nutrients were generally low in the surface layer at this site (Fig. 2). These high nutrient concentrations in the middle and near-bottom layers are probably due to release from the bottom sediments.

**Patterns of distribution of chlorophyll a concentration**

Chlorophyll a concentrations ranged from 0.45 µg/L to 40.2 µg/L over the study period. Generally, higher concentrations were recorded in the surface and near-surface layers in the inner regions of the bay (Stns. 1 and 2; Fig. 3). The maximum at Stn. 1 in July was lower than the maxima in other months, possibly indicating that the temporary decline of salinity in the surface layer (Fig. 2) due to riverine input led to a decrease of phytoplankton abundance at Stn. 1. The contribution of the <20 µm fraction to total chlorophyll a concentration mostly exceeded 60% in June 1996 and in July 1997. In August 1996, more than 60% of the contribution of the <20 µm fraction was also recorded in almost all the layers at Stns. 1 and 2 although less than 40% of the contribution was partly observed in the central and outer regions of the bay. This result indicates that the phytoplankton assemblage is generally dominated by nano- and picoplankton in the inner region of the bay in summer.

**Abundance and biomass of main microbial loop components at the three sites in Hiroshima Bay**

Abundance of bacteria ranged from $1.10 \times 10^6$ cells/mL to $5.75 \times 10^6$ cells/mL, and biomass of bacteria ranged from 32.6 µg C/L to 170.1 µg C/L (Fig. 4). The biomass of bacteria in each of the surface, 2-m and 5-m layers at Stn. 1 were 1.1–4.1-fold higher than at the other two sites in each month. Abundance and biomass of HNF ranged from $0.52 \times 10^3$ cells/L to $11.06 \times 10^3$ cells/L and from 1.5 µg C/L to 84.8 µg C/L, respectively (Fig. 5). The highest abundance and biomass of HNF on each occasion were recorded in either of the surface, 2-m or 5-m layers at Stn. 1 (Fig. 5), which is similar to the distribution of bacterial abundance and biomass.

The abundance of total ciliates ranged from $0.6 \times 10^2$ ind./L to $20.5 \times 10^3$ ind./L during the study. Ciliate assemblages were generally dominated by aloricate forms except for samples col-

![Fig. 3 Horizontal and vertical distributions of the chlorophyll a concentration and the percentage of the chlorophyll a concentration accounted for by the <20 µm fraction.](image-url)
lected in August 1996 at Stns. 1 and 5 (Fig. 6). In the August 1996 samples, tintinnids accounted for 11–91% of total ciliate abundance. The maximum abundance of total ciliates was observed in the surface or 2-m layers at Stn. 1 in all months (Fig. 6). In July, the maximum abundance of ciliates, especially the tintinnid forms at Stn. 1, was considerably lower than in June and August (Fig. 6). The biomass of total ciliates ranged from 0.1 μg C/L to 91.7 μg C/L over the study period (Fig. 7). In general, the patterns of the vertical distribution of ciliate biomass were similar to those of the abundance. How-
ever, ciliate biomass was remarkably low at Stn. 1 in July and the biomass of tintinnid ciliates was particularly high at Stn. 5 in August (Fig. 7). This high biomass of tintinnid ciliates in the surface and near-surface layers at Stn. 5 in August was largely due to the mass occurrence of *Metacylis gorbula*, but in most other cases mixotrophic ciliates dominated the ciliate biomass in the surface and near-surface layers (Fig. 7). The biomass of mixotrophs reached 93% of the total ciliate value and the average values in the water column accounted for 9–79% of total ciliate biomass.

**Comparisons of abundance and biomass of the main microbial loop components and environmental conditions among the three sites**

Data at each depth for all parameters were integrated over depth and, thus, mean water column data were obtained. The average temperature and

DO of the mean water-column data were similar among sites, but the average salinity was significantly lower at Stn. 1 than at the other sites (Table 1). Average nutrient concentrations, chlorophyll *a* concentrations and abundances and biomasses of bacteria, HNF and ciliates were generally higher at Stn. 1 than at the other sites. However, the differences among sites in DIN, DIP and ciliates were not significant (*P* > 0.05; Table 1).

**DISCUSSION**

**Distribution of environmental factors and main microbial loop components**

The vertical distribution of temperature and salinity showed that the water column in Hiroshima Bay in summer was stratified. Low salinity was observed in the surface waters from Stn. 1 to Stns. 3 or 4, suggesting that riverine inputs can influence
the surface environment from the inner to the middle regions of the bay. However, high concentrations of DIN and DIP in the surface layer were limited to the innermost site where chlorophyll a concentrations were high (Stns. 1, 2). Similar phenomena were observed in a previous study in Hiroshima Bay. Riverine nutrient inputs may rapidly be taken up by phytoplankton in the vicinity of the river mouth areas in Hiroshima Bay.5

In the inner region of the bay, abundance and biomass of the main microbial loop components are higher than in the other regions. The maximum abundance of bacteria and HNF reached $5.75 \times 10^6$ and $11.1 \times 10^3$ cells/mL, respectively. These values are equal to or higher than those reported in previous studies ($4.3-4.9 \times 10^6$ cells/mL for bacteria and $9.1-10.0 \times 10^3$ cells/mL for HNF), conducted in the coastal area of north-western Hiroshima Bay in summer.11,13,14 The maximum chlorophyll a concentration observed in the present study (mean water column data: $31.5 \mu g/L$) at Stn. 1 is higher than the concentrations ($14.5-14.7 \mu g/L$) reported by previous studies.13,14 Hence, the higher abundance of bacteria in the inner region may be associated with organic matter produced by phytoplankton and/or direct riverine input,2 although HNF abundance differed little among locations.

In the present study, the maximum abundance and biomass of total ciliates reached $20.5 \times 10^3$ ind./L and $91.7 \mu g C/L$, respectively. The maximum abundance is similar to the data previously reported for Hiroshima Bay ($25 \times 10^3$ ind./L).15 However, the maximum biomass is considerably higher than data previously reported in this bay in summer ($1 \text{ to } 3 \mu g C/L$).17,19 Even higher biomass values have been recorded in coastal waters of the UK ($219 \mu g C/L$)33 and in Hiroshima Bay during the decay of a red tide ($134 \mu g C/L$).20

The ciliate assemblages were frequently dominated by mixotrophs. This was particularly apparent in the surface and near-surface layers at all

![Fig. 7 Vertical distributions of the carbon biomass of ciliates at Stns. 1, 3 and 5 in Hiroshima Bay.](image)
Table 1  Average data on environmental conditions and the microbial loop components for the 3 months combined

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Station (mean ± SD)</th>
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<tr>
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<td>1</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>20.43 ± 3.73</td>
</tr>
<tr>
<td>Salinity (p.s.u.)</td>
<td>30.58 ± 0.55*</td>
</tr>
<tr>
<td>DO (mg/L)</td>
<td>8.07 ± 2.66</td>
</tr>
<tr>
<td>DIN (µM)</td>
<td>6.5 ± 6.6</td>
</tr>
<tr>
<td>DIP (µM)</td>
<td>0.22 ± 0.11</td>
</tr>
<tr>
<td>SiO₂-Si (µM)</td>
<td>34.6 ± 8.3*</td>
</tr>
<tr>
<td>Chlorophyll a (µg/L)</td>
<td>19.0 ± 10.8*</td>
</tr>
<tr>
<td>Bacteria (× 10⁶ cells/mL)</td>
<td>3.90 ± 0.85*</td>
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<tr>
<td></td>
<td>115.0 ± 25.0*</td>
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<tr>
<td>HNF (µg C/L)</td>
<td>4.10 ± 0.92</td>
</tr>
<tr>
<td>Aloricate ciliates (× 10⁶ cells/L)</td>
<td>34.8 ± 10.9*</td>
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<tr>
<td></td>
<td>4.82 ± 3.74</td>
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<tr>
<td></td>
<td>9.2 ± 7.6</td>
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<tr>
<td>Tintinnid ciliates (× 10⁶ cells/mL)</td>
<td>2.31 ± 3.66</td>
</tr>
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<td>10.7 ± 17.5</td>
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Each datum indicates the mean water-column value ± standard deviations. * indicates a significant difference from both values at the other stations (P < 0.05).

DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; DO, dissolved oxygen concentration.

sites, consistent with observations from Georges Bank in the North-west Atlantic, the Nordic Sea and the Aegean Sea in the eastern Mediterranean. Stoecker et al. found that mixotrophic ciliates commonly occurred in seawater, and reported that mixotrophy in some samples constituted over 90% of the total ciliate assemblage in the harbor of Woods Hole, MA, USA. The contribution of mixotrophic ciliate abundance (mean water-column data) to the total ciliate assemblage in our study (7–79%) approximated the previous general records (40–50%). There have been very few reports of information on the mixotrophic ciliates in Japanese coastal waters. Results from the present study indicate that mixotrophic ciliates are an important component of the ciliate assemblage in this region.

Ciliate community dynamics related to environmental conditions in the inner region of the bay

One of our aims in the present investigation was to clarify the abundance and biomass of the microbial loop components in summer in Hiroshima Bay; however, the abundance and biomass of tintinnid and aloricate ciliates markedly varied among the sampling periods. Large fluctuations in ciliate abundance and biomass have also been reported in other seasonal investigations. Biomass of the microbial loop components has been shown to dramatically change over short intervals (a few days) in the course of bloom formation and collapse. In particular, at Stn. 1 in the present study, changes in the ciliate biomass were probably greatly influenced by changes in environmental factors associated with riverine inputs. Hence, at this site it is necessary to carefully consider the environmental conditions (salinity, nutrients and chlorophyll a) together with the dynamics of the ciliate community in each month.

At Stn. 1 in July 1997, low salinity in the surface layer occurred with a lower chlorophyll a concentration and ciliate abundance than in the other months, and the high concentrations of nutrients (e.g. DIN) presumably indicate that phytoplankton and the ciliate assemblages, which had declined due to intensive riverine input, were recovering. In June 1996, high concentrations of chlorophyll a and nutrients, and high densities of ciliates were observed, suggesting that phytoplankton increased under high nutrient conditions, and the increasing phytoplankton might have led to the increase in ciliate abundance. In August, high abundances of phytoplankton and ciliates, but low nutrient concentrations, may indicate that the phytoplankton assemblages temporarily reached a growth peak and the population of ciliates was still developing. These interpretations suggest that the biomass of the ciliate assemblages was influenced
by prey conditions in June and August 1996 while the assemblages in July 1997 were directly affected by riverine inputs rather than prey availability.

Transfer efficiency from primary producers to their grazers

Among Stns. 1, 3 and 5 in the present study, Stn. 1 was characterized by high nutrient concentrations, high chlorophyll a concentrations and high abundance of the microbial loop components. High biomass of primary producers probably sustains the high production of the grazing plankton that feeds on them. Further, it is interesting to evaluate the transfer efficiency of energy from the primary producers to their grazers. Assuming that the carbon conversion factor of the < 20 \mu m fraction of chlorophyll a was 30,38,39 we analyzed the relationships of the carbon biomass between each ciliate assemblage (tintinnid or aloricate ciliate) and the prey organisms (bacteria, HNF and < 20 \mu m chlorophyll a). For this analysis, stable prey–predator conditions are necessary; biomass of ciliate is directly influenced by the prey biomass and the quality of prey does not influence the prey–predator relationships. Considering these preconditions, data from Stn. 1 in July were not used for the analysis because of extremely low salinity from riverine inputs, resulting in unstable conditions for the ciliate assemblage at this site, as discussed above.

The positive linear correlations between aloricate ciliates and the < 20 \mu m fraction of chlorophyll a \((r^2 = 0.47–0.78, P < 0.05)\), and between aloricate ciliates and total prey organisms \((r^2 = 0.45–0.73, P < 0.05)\) were significant at all sites (Fig. 8a). Also, significant correlations of several parameters with the biomass of tintinnids were observed. However, the parameters linearly correlating with the biomass of tintinnids were not uniform among the three sites, probably because the biomass levels of tintinnids were considerably low in June and July, irrespective of the variation of their prey biomass. Regarding the relationships between aloricates and the total prey organisms, the slope of the linear regression at Stn. 3 was significantly higher than those at Stns. 1 and 5 \((P < 0.01)\). Furthermore, the mean carbon–biomass ratio of aloricate ciliates to their prey organisms on all occasions was significantly lower at Stn. 1 than at Stns. 3 and 5 \((P < 0.01)\) (Fig. 8b). Additionally, the X-axis intercept in Fig. 8a at Stn. 1 was significantly higher than those at Stns. 3 and 5 \((P < 0.01)\) (Fig. 8b). These interpretations demonstrate that the energy transfer efficiency from primary production and microbes to aloricate ciliates may be
low in the inner region of the bay (Stn. 1) compared to the central region of the bay (Stn. 3).

We cannot exactly explain the reason why the energy transfer efficiency in the inner region of the bay was low, but can speculate as follows. Small cyclopoid copepods *Oithona* spp., which feeds on ciliates, abundantly occur in this area in summer, possibly indicating that top down control by these copepods is one of the causes. Growth rates and abundance of ciliates usually saturate under high prey concentrations. This can also explain the relatively lower biomass ratio of aloricate ciliates to their prey in the inner region where their prey biomass is high.

To consider the energy transfer efficiency, it is necessary to practically measure the primary production and subsequent grazing impact, because biomass relationships are caused by the production of the predator and prey species and the interactions between them. In spite of such limitations, biomass relationships between prey and predators in the present study were clear and characteristics differed among areas in the bay, suggesting that the biomass relationship may be one of the factors to evaluate the efficiency of energy flow in planktonic food webs.

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