

Standing crops of planktonic ciliates and nanoplankton in oceanic waters of the western Pacific

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ABSTRACT: The vertical distribution of planktonic ciliates and nanoplankton was investigated in 3 types of oceanic waters in the western Pacific. Ranges of their standing crops, in abundance and biomass, were 50 to 2540 cells l⁻¹ and 4.89 × 10⁴ to 6.32 × 10⁶ pg C l⁻¹ for ciliates and 7.2 × 10⁴ to 1.97 × 10⁶ cells l⁻¹ and 2.45 × 10⁵ to 4.92 × 10⁷ pg C l⁻¹ for nanoplankton in the spring subarctic water, <1080 cells l⁻¹ and <1.27 × 10⁶ pg C l⁻¹ for ciliates and 7.5 × 10⁴ to 2.76 × 10⁶ cells l⁻¹ and 1.01 × 10⁵ to 1.03 × 10⁷ pg C l⁻¹ for nanoplankton in the fall subarctic water, and <570 cells l⁻¹ and <1.59 × 10⁶ pg C l⁻¹ for ciliates and 1.45 × 10⁵ to 3.18 × 10⁶ cells l⁻¹ and 3.05 × 10⁵ to 2.62 × 10⁷ pg C l⁻¹ for nanoplankton in the subtropical water. The standing crop of ciliates, as a whole, was positively correlated to that of nanoplankton especially in biomass: $B_c = 0.211 \times B_n^{0.994}$, $r = 0.81$, $p < 0.001$, where B_c and B_n are biomass of ciliates and nanoplankton, respectively. This suggests that nanoplankton and ciliate stocks are tightly linked in oceanic waters.

KEY WORDS: Planktonic ciliates · Nanoplankton · Quantitative relationship · Oceanic waters

INTRODUCTION

Planktonic ciliates are abundant and ubiquitous in every ocean (Pierce & Turner 1992). They are known to ingest picoplankton or bacterioplankton (Sherr & Sherr 1987, Bernard & Rassoulzadegan 1990) and nanoplankton (Gifford 1985, Verity 1985). Some microplankton, in a size range similar to or larger than the planktonic ciliates, can also serve as ciliate prey (Wessenberg & Antipa 1970, Ishiyama et al. 1993). Previous studies on the standing crops and feeding activities of planktonic ciliates have demonstrated that they can be the dominant heterotrophs in the microbial loops (Sorokin 1981, Porter et al. 1985). Lynn & Montagnes (1991) compared bacterioplankton biomass with ciliate biomass reported from a variety of marine environments and found a poor correlation between the two on a logarithmic scale. On the other hand, an

analysis of biomasses of ciliates and nanoplankton in the North Atlantic Ocean revealed a significant negative correlation between autotrophic nanoplankton and ciliates but a non-significant correlation between heterotrophic nanoplankton and ciliates (Stoecker et al. 1994b). However, there are few data on nanoplankton and ciliates for the oligotrophic open ocean, where the role of microbial components may be more important. This study analyzes the relationship between both components based on the data sets obtained by consistent investigations in the western Pacific Ocean.

Planktonic ciliates, except for the autotrophic *Mesodinium rubrum*, are classified as heterotrophs or mixotrophs (Stoecker et al. 1989, Suzuki & Taniguchi 1993). Although both may feed on heterotrophic nanoplankton, the latter require autotrophic nanoplankton to continuously sequester functional chloroplasts (Stoecker et al. 1988, Stoecker 1991). Therefore, we considered quantitative relationships for the following 4 pairs: between total ciliates and total nanoplankton, between heterotrophic ciliates and total nanoplankton, between mixotrophic ciliates and total nanoplankton, and between mixotrophic ciliates and autotrophic nanoplankton.

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METHODS

Water samples were collected with a CTD-Rosette Multi Sampler from 6 to 12 layers in the top 100 or 200 m of the water column in 3 types of oceanic waters of the western Pacific, i.e. spring subarctic (6 stations), fall subarctic (3 stations) and subtropical (6 stations) waters on 3 cruises of RV 'Hakuho Maru' (Fig. 1, Table 1). Vertical profiles of water temperature were recorded with the CTD. A total of 131 water samples were analyzed to determine chlorophyll *a* (chl *a*) concentration by a fluorometric method (Strickland & Parsons 1972) and abundances and size composition of nanoplankton and ciliate communities. Plankters of 2 to 20 μm in equivalent spherical diameter (ESD) were categorized as nanoplankton except ciliates less than 20 μm in ESD which were counted as ciliates.

For the nanoplankton cell enumeration, 25 to 50 ml aliquots were fixed with glutaraldehyde (0.5% final concentration) and stained with proflavine (0.00066% final concentration) and then filtered onto a black prestained Nuclepore polycarbonate filter (0.6 μm pore size, 25 mm diam.) (Haas 1982). The filter was mounted on a slide and kept frozen at -80°C until examination. Slides were examined with an epifluorescence microscope (Nikon Optiphot) at 1000 \times with B-excitation light (line spectra of 405 and 435 nm and continuous spectrum around 490 nm). More than 50 cells in the dozens of randomly selected microscopic fields were counted for the spring subarctic samples, and over 100 fields for fall subarctic and subtropical samples, which were equivalent in sample size to 0.03–1.6 ml for the spring subarctic water (detection limit: 600 cells l^{-1}) and to 0.12–0.48 ml for the fall subarctic and subtropical waters (detection limit: 2000 cells l^{-1}). Cell size was measured simultaneously for individual cells. Nanoplankton cell carbon was calculated based on Strathmann's (1967) equation.

Water samples for ciliate cell counts were fixed with neutralized formaldehyde (2% final concentration). Counts and size measurement were done by Utermöhl method using an inverted epifluorescence microscope (Olympus IMT-2) at 200 \times on 100 ml (detection limit: 10 cells l^{-1}) and cell volume was calculated individually. The cell volume was converted to carbon biomass by using the factor of 0.14 $\text{pg C } \mu\text{m}^{-3}$ (Putt & Stoecker 1989). Mixotrophic ciliates were identified by possession of chlorophyll pigments with bright red fluorescence under a B-excitation, which is different from the spotted and faded red emission of the autotrophic plankton in food vacuoles of ciliates. *Mesodinium rubrum*, if any, were omitted because of their autotrophic mode and absence of feeding relationship with nanoplankton (Lindholm 1985).

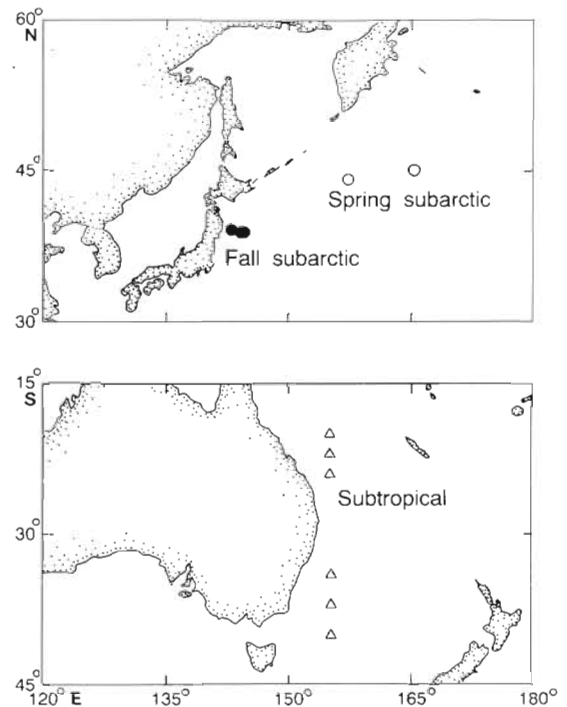


Fig. 1. Location of sampling stations. (○) Spring subarctic water (5 points are almost overlapping around 45°N , 165°E); (●) fall subarctic water; (Δ) subtropical water

RESULTS

Autotrophic nanoplanktonic populations consisted of pigmented flagellates and diatoms. The flagellates always predominated over the diatoms in abundance and biomass. All heterotrophic nanoplankters were heterotrophic flagellates. Both auto- and heterotrophic nanoplankton were dominated by small cells, less than 4 μm in ESD. The mixotrophic ciliates observed were dominated by cells of around 30 μm ESD. Heterotrophic ciliates consisted of both aloricate forms and tintinnids, the aloricate forms predominated in abundance and biomass over tintinnids in most samples. The dominant size of the heterotrophic ciliates was around 20 μm in ESD.

Standing crops in abundance (A_c) and biomass (B_c) of total ciliates in spring subarctic water (50 to 2540 cells l^{-1} , 4.89×10^4 to 6.32×10^6 $\text{pg C } \text{l}^{-1}$) were larger than those in fall subarctic (<1080 cells l^{-1} , $<1.27 \times 10^6$ $\text{pg C } \text{l}^{-1}$) and subtropical waters (<570 cells l^{-1} , $<1.59 \times 10^6$ $\text{pg C } \text{l}^{-1}$). Abundance of total nanoplankton (A_n) showed a different trend, being higher in subtropical (1.45×10^5 to 3.18×10^6 cells l^{-1}) than in fall subarctic (7.5×10^4 to 2.76×10^6 cells l^{-1}) and spring subarctic waters (7.2×10^4 to 1.97×10^6 cells l^{-1}) (Table 1). However, in terms of biomass, nanoplankton (B_n) in spring subarctic (2.45×10^5 to 4.92×10^7 $\text{pg C } \text{l}^{-1}$) was higher

Table 1. Data on samplings at 6, 3 and 6 stations respectively in the spring subarctic, fall subarctic and subtropical Pacific waters and data on abundance and biomass of nanoplankton and planktonic ciliates. ANP: autotrophic nanoplankton; HNP: heterotrophic nanoplankton; TNP: total nanoplankton (ANP + HNP); HC: heterotrophic ciliates; MC: mixotrophic ciliates; TC: total ciliates (HC + MC). nd: not detected; —: no data

| Date | Position | Depth (m) | Temp. (°C) | Chl <i>a</i> (µg l ⁻¹) | Abundance (10 ³ cells l ⁻¹) | | | | | Biomass (pg C l ⁻¹) | | | | | | |
|------------|-----------------------|-----------|------------|------------------------------------|--|-----|------|------|------------------------|---------------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | | | | ANP | HNP | TNP | HC | MC | TC | ANP | HNP | TNP | HC | MC | TC |
| 1 Jun 1991 | 44° 13' N, 157° 14' E | 0 | 5.20 | 0.79 | 589 | 134 | 723 | 1440 | 480 | 1920 | 7.29 × 10 ⁶ | 2.67 × 10 ⁶ | 9.96 × 10 ⁶ | 3.46 × 10 ⁶ | 1.51 × 10 ⁶ | 4.97 × 10 ⁶ |
| | | 10 | 4.95 | 0.79 | 1133 | 272 | 1405 | 820 | 480 | 1300 | 1.86 × 10 ⁷ | 2.48 × 10 ⁶ | 2.11 × 10 ⁷ | 4.16 × 10 ⁶ | 5.61 × 10 ⁶ | 4.72 × 10 ⁶ |
| | | 20 | 4.91 | 0.65 | 1400 | 334 | 1734 | 1090 | 510 | 1600 | 2.64 × 10 ⁷ | 3.20 × 10 ⁶ | 2.96 × 10 ⁷ | 3.82 × 10 ⁶ | 2.49 × 10 ⁶ | 6.32 × 10 ⁶ |
| | | 30 | 4.52 | 0.64 | 426 | 125 | 551 | 1390 | 200 | 1590 | 5.05 × 10 ⁶ | 8.69 × 10 ⁵ | 5.92 × 10 ⁶ | 5.22 × 10 ⁶ | 8.19 × 10 ⁵ | 6.04 × 10 ⁶ |
| | | 40 | 2.74 | 0.69 | 932 | 276 | 1208 | 1350 | 1190 | 2540 | 4.21 × 10 ⁶ | 2.11 × 10 ⁶ | 6.32 × 10 ⁶ | 3.57 × 10 ⁶ | 6.31 × 10 ⁵ | 4.20 × 10 ⁶ |
| | | 50 | 2.58 | 0.48 | 529 | 140 | 669 | 1070 | 150 | 1220 | 7.61 × 10 ⁶ | 3.53 × 10 ⁶ | 1.11 × 10 ⁷ | 2.47 × 10 ⁶ | 2.13 × 10 ⁵ | 2.68 × 10 ⁶ |
| | | 75 | 2.37 | 0.20 | 307 | 159 | 466 | 400 | 10 | 410 | 5.21 × 10 ⁶ | 2.28 × 10 ⁶ | 7.49 × 10 ⁶ | 1.04 × 10 ⁶ | 2.48 × 10 ³ | 1.04 × 10 ⁶ |
| | | 100 | 1.75 | 0.12 | 207 | 152 | 359 | 190 | 10 | 200 | 2.00 × 10 ⁶ | 1.69 × 10 ⁶ | 3.69 × 10 ⁶ | 3.79 × 10 ⁵ | 2.48 × 10 ³ | 3.81 × 10 ⁵ |
| | | 125 | 2.00 | 0.07 | 92 | 97 | 189 | 160 | nd | 160 | 5.48 × 10 ⁵ | 9.48 × 10 ⁵ | 1.50 × 10 ⁶ | 2.50 × 10 ⁵ | nd | 2.50 × 10 ⁵ |
| | | 150 | 2.23 | 0.04 | 65 | 140 | 205 | 200 | 40 | 240 | 3.64 × 10 ⁵ | 1.15 × 10 ⁶ | 1.51 × 10 ⁶ | 1.71 × 10 ⁵ | 9.90 × 10 ³ | 1.81 × 10 ⁵ |
| 175 | 2.43 | 0.02 | 73 | 117 | 190 | 240 | 10 | 250 | 1.33 × 10 ⁶ | 1.02 × 10 ⁶ | 2.35 × 10 ⁶ | 1.59 × 10 ⁵ | 2.48 × 10 ³ | 1.61 × 10 ⁵ | | |
| 200 | 2.57 | 0.02 | 56 | 88 | 144 | 180 | nd | 180 | 8.66 × 10 ⁵ | 3.75 × 10 ⁵ | 1.24 × 10 ⁶ | 3.87 × 10 ⁵ | nd | 3.87 × 10 ⁵ | | |
| 2 Jun 1991 | 45° 09' N, 165° 14' E | 0 | 5.01 | 0.71 | 1413 | 326 | 1739 | 720 | 620 | 1340 | 3.54 × 10 ⁷ | 9.22 × 10 ⁶ | 4.46 × 10 ⁷ | 2.04 × 10 ⁶ | 3.51 × 10 ⁶ | 5.55 × 10 ⁶ |
| | | 10 | 5.01 | 0.64 | 1275 | 351 | 1626 | 500 | 270 | 770 | 2.33 × 10 ⁷ | 5.66 × 10 ⁶ | 2.90 × 10 ⁷ | 7.17 × 10 ⁵ | 7.72 × 10 ⁵ | 1.49 × 10 ⁶ |
| | | 20 | 5.02 | 0.64 | 602 | 443 | 1045 | 560 | 100 | 660 | 1.06 × 10 ⁷ | 5.65 × 10 ⁶ | 1.62 × 10 ⁷ | 7.49 × 10 ⁵ | 1.17 × 10 ⁵ | 8.66 × 10 ⁵ |
| | | 30 | 5.04 | 0.70 | 1463 | 510 | 1973 | 410 | 50 | 460 | 2.83 × 10 ⁷ | 2.08 × 10 ⁷ | 4.92 × 10 ⁷ | 9.34 × 10 ⁵ | 2.60 × 10 ⁴ | 9.60 × 10 ⁵ |
| | | 40 | 5.04 | 0.67 | 950 | 315 | 1265 | 740 | 110 | 850 | 1.66 × 10 ⁷ | 5.27 × 10 ⁶ | 2.19 × 10 ⁷ | 1.78 × 10 ⁶ | 6.68 × 10 ⁴ | 1.85 × 10 ⁶ |
| | | 60 | 5.05 | 0.58 | 1101 | 376 | 1477 | 970 | 140 | 1110 | 2.21 × 10 ⁷ | 5.00 × 10 ⁶ | 2.71 × 10 ⁷ | 3.11 × 10 ⁶ | 2.97 × 10 ⁵ | 3.41 × 10 ⁶ |
| | | 80 | 4.98 | 0.44 | 1048 | 353 | 1401 | 420 | 40 | 460 | 2.07 × 10 ⁷ | 6.11 × 10 ⁶ | 2.68 × 10 ⁷ | 4.27 × 10 ⁵ | 1.88 × 10 ⁵ | 6.15 × 10 ⁵ |
| | | 100 | 4.54 | 0.12 | 247 | 224 | 471 | 250 | 20 | 270 | 4.10 × 10 ⁶ | 1.52 × 10 ⁶ | 5.62 × 10 ⁶ | 3.74 × 10 ⁵ | 9.39 × 10 ⁴ | 4.68 × 10 ⁵ |
| | | 120 | 4.27 | 0.07 | 69 | 123 | 192 | 100 | nd | 100 | 7.12 × 10 ⁵ | 7.80 × 10 ⁵ | 1.49 × 10 ⁶ | 1.25 × 10 ⁵ | nd | 1.25 × 10 ⁵ |
| | | 150 | 4.23 | 0.02 | 109 | 142 | 251 | 60 | nd | 60 | 1.30 × 10 ⁶ | 8.97 × 10 ⁵ | 2.20 × 10 ⁶ | 6.08 × 10 ⁴ | nd | 6.08 × 10 ⁴ |
| 200 | 3.66 | 0.01 | 127 | 142 | 269 | 50 | nd | 50 | 1.11 × 10 ⁶ | 6.93 × 10 ⁵ | 1.81 × 10 ⁶ | 4.89 × 10 ⁴ | nd | 4.89 × 10 ⁴ | | |
| 2 Jun 1991 | 45° 07' N, 165° 17' E | 0 | 5.21 | 0.76 | 1363 | 456 | 1819 | 1160 | 520 | 1680 | 3.06 × 10 ⁷ | 5.42 × 10 ⁶ | 3.61 × 10 ⁷ | 1.71 × 10 ⁶ | 2.12 × 10 ⁶ | 3.83 × 10 ⁶ |
| | | 10 | 5.17 | 0.63 | 137 | 152 | 289 | 1110 | 100 | 1210 | 2.31 × 10 ⁶ | 9.29 × 10 ⁵ | 3.24 × 10 ⁶ | 1.12 × 10 ⁶ | 2.34 × 10 ⁵ | 1.36 × 10 ⁶ |
| | | 20 | 5.16 | 0.65 | 1342 | 569 | 1911 | 1730 | 80 | 1810 | 3.20 × 10 ⁷ | 1.66 × 10 ⁷ | 4.86 × 10 ⁷ | 2.62 × 10 ⁶ | 2.00 × 10 ⁵ | 2.82 × 10 ⁶ |
| | | 30 | 5.13 | 0.73 | 1133 | 468 | 1601 | 900 | 160 | 1060 | 2.48 × 10 ⁷ | 7.22 × 10 ⁶ | 3.20 × 10 ⁷ | 1.67 × 10 ⁶ | 2.47 × 10 ⁵ | 1.92 × 10 ⁶ |
| | | 40 | 5.13 | 0.70 | 1099 | 343 | 1442 | 560 | 80 | 640 | 2.07 × 10 ⁷ | 1.16 × 10 ⁷ | 3.23 × 10 ⁷ | 8.07 × 10 ⁵ | 6.80 × 10 ⁵ | 1.49 × 10 ⁶ |
| | | 60 | 5.08 | 0.51 | 772 | 410 | 1182 | 750 | 70 | 820 | 1.22 × 10 ⁷ | 8.64 × 10 ⁶ | 2.09 × 10 ⁷ | 1.36 × 10 ⁶ | 2.26 × 10 ⁵ | 1.58 × 10 ⁶ |
| | | 80 | 4.38 | 0.15 | 281 | 326 | 607 | 180 | 10 | 190 | 5.00 × 10 ⁶ | 5.73 × 10 ⁶ | 1.07 × 10 ⁷ | 1.19 × 10 ⁶ | 4.70 × 10 ⁴ | 1.24 × 10 ⁶ |
| | | 100 | 4.57 | 0.08 | 184 | 186 | 370 | 100 | nd | 100 | 2.13 × 10 ⁶ | 1.13 × 10 ⁶ | 3.26 × 10 ⁶ | 1.52 × 10 ⁵ | nd | 1.52 × 10 ⁵ |
| | | 120 | 4.69 | 0.03 | 166 | 246 | 412 | 100 | nd | 100 | 1.41 × 10 ⁶ | 8.57 × 10 ⁵ | 2.98 × 10 ⁶ | 5.97 × 10 ⁴ | nd | 5.97 × 10 ⁴ |
| | | 150 | 4.43 | 0.01 | 159 | 171 | 330 | 70 | nd | 70 | 1.41 × 10 ⁶ | 8.57 × 10 ⁵ | 2.27 × 10 ⁶ | 1.96 × 10 ⁵ | nd | 1.96 × 10 ⁵ |
| 200 | 3.75 | nd | 32 | 40 | 72 | 70 | nd | 70 | 1.09 × 10 ⁵ | 1.36 × 10 ⁵ | 2.45 × 10 ⁵ | 5.60 × 10 ⁴ | nd | 5.60 × 10 ⁴ | | |
| 2 Jun 1991 | 45° 10' N, 165° 17' E | 0 | 5.15 | 0.68 | 1241 | 451 | 1692 | 1750 | 600 | 2350 | 3.54 × 10 ⁷ | 7.96 × 10 ⁶ | 4.34 × 10 ⁷ | 2.23 × 10 ⁶ | 2.90 × 10 ⁶ | 5.13 × 10 ⁶ |
| | | 10 | 5.15 | 0.61 | 82 | 104 | 186 | 1790 | 420 | 2210 | 9.90 × 10 ⁵ | 7.92 × 10 ⁵ | 1.78 × 10 ⁶ | 2.77 × 10 ⁶ | 1.99 × 10 ⁶ | 4.75 × 10 ⁶ |
| | | 30 | 5.07 | 0.75 | 1003 | 307 | 1310 | 960 | 110 | 1070 | 2.05 × 10 ⁷ | 9.87 × 10 ⁶ | 3.04 × 10 ⁷ | 2.00 × 10 ⁶ | 1.94 × 10 ⁶ | 3.94 × 10 ⁶ |
| | | 40 | 5.06 | 0.71 | 1124 | 238 | 1362 | 800 | 100 | 900 | 1.90 × 10 ⁷ | 4.03 × 10 ⁶ | 2.31 × 10 ⁷ | 1.31 × 10 ⁶ | 2.36 × 10 ⁵ | 1.55 × 10 ⁶ |
| | | 60 | 5.06 | 0.56 | 1062 | 415 | 1477 | 560 | 310 | 870 | 1.86 × 10 ⁷ | 1.32 × 10 ⁷ | 3.18 × 10 ⁷ | 1.18 × 10 ⁶ | 3.84 × 10 ⁵ | 1.56 × 10 ⁶ |
| | | 80 | 4.98 | 0.26 | 817 | 464 | 1281 | 630 | 10 | 640 | 1.24 × 10 ⁷ | 1.24 × 10 ⁷ | 2.48 × 10 ⁷ | 6.67 × 10 ⁵ | 5.87 × 10 ³ | 6.73 × 10 ⁵ |
| 100 | 4.34 | 0.07 | 127 | 254 | 381 | 110 | nd | 110 | 2.18 × 10 ⁶ | 3.76 × 10 ⁶ | 5.94 × 10 ⁶ | 1.86 × 10 ⁵ | nd | 1.86 × 10 ⁵ | | |

(Table continued on next page)

Table 1 (continued)

| Date | Position | Depth Temp. (m) (°C) | Chl <i>a</i> (µg l ⁻¹) | Abundance (10 ³ cells l ⁻¹) | | | | | | Biomass (pg C l ⁻¹) | | | | | |
|----------------|--------------------------|-------------------------|---------------------------------------|---|------|------|------|-----|------------------------|---------------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | | | ANP | HNP | TNP | HC | MC | TC | ANP | HNP | TNP | HC | MC | TC |
| 3 Jun 1991 | 45° 09' N, 165° 19' E | 0 | 0.67 | 457 | 184 | 641 | 1890 | 200 | 2090 | 1.16 × 10 ⁷ | 2.82 × 10 ⁶ | 1.44 × 10 ⁷ | 2.51 × 10 ⁶ | 8.90 × 10 ⁵ | 3.40 × 10 ⁵ |
| | | 10 | 0.70 | 1116 | 343 | 1459 | 1900 | 290 | 2190 | 2.00 × 10 ⁷ | 9.25 × 10 ⁶ | 2.93 × 10 ⁷ | 2.42 × 10 ⁶ | 1.09 × 10 ⁶ | 3.51 × 10 ⁵ |
| | | 20 | 0.69 | 1041 | 380 | 1421 | 1730 | 460 | 2190 | 2.14 × 10 ⁷ | 7.67 × 10 ⁶ | 2.91 × 10 ⁷ | 3.03 × 10 ⁶ | 1.54 × 10 ⁶ | 4.56 × 10 ⁵ |
| | | 30 | 0.68 | 895 | 330 | 1225 | 1170 | 260 | 1430 | 1.83 × 10 ⁷ | 7.83 × 10 ⁶ | 2.61 × 10 ⁷ | 1.75 × 10 ⁶ | 1.94 × 10 ⁶ | 3.69 × 10 ⁵ |
| | | 40 | 0.71 | 1183 | 314 | 1497 | 1360 | 180 | 1540 | 2.69 × 10 ⁷ | 1.07 × 10 ⁷ | 3.76 × 10 ⁷ | 3.21 × 10 ⁶ | 3.44 × 10 ⁵ | 3.56 × 10 ⁵ |
| | | 60 | 0.52 | 1250 | 334 | 1584 | 1450 | 430 | 1880 | 2.74 × 10 ⁷ | 1.05 × 10 ⁷ | 3.79 × 10 ⁷ | 3.03 × 10 ⁶ | 2.26 × 10 ⁶ | 5.29 × 10 ⁵ |
| 3 Jun 1991 | 45° 08' N, 165° 17' E | 80 | 0.24 | 230 | 201 | 431 | 420 | 40 | 460 | 3.36 × 10 ⁶ | 3.48 × 10 ⁶ | 6.83 × 10 ⁶ | 4.18 × 10 ⁵ | 7.71 × 10 ⁵ | 1.19 × 10 ⁵ |
| | | 100 | 0.10 | 184 | 256 | 440 | 110 | 20 | 130 | 2.40 × 10 ⁶ | 1.91 × 10 ⁶ | 4.32 × 10 ⁶ | 2.12 × 10 ⁵ | 9.39 × 10 ⁴ | 3.06 × 10 ⁵ |
| | | 0 | 0.61 | 915 | 293 | 1208 | 970 | 350 | 1320 | 1.70 × 10 ⁷ | 1.65 × 10 ⁶ | 1.86 × 10 ⁷ | 1.23 × 10 ⁶ | 1.58 × 10 ⁶ | 2.80 × 10 ⁵ |
| | | 10 | 0.59 | 1137 | 443 | 1580 | 960 | 380 | 1340 | 1.93 × 10 ⁷ | 8.89 × 10 ⁶ | 2.82 × 10 ⁷ | 1.34 × 10 ⁶ | 1.73 × 10 ⁶ | 3.07 × 10 ⁵ |
| | | 20 | 0.58 | 786 | 360 | 1146 | 1080 | 110 | 1190 | 1.79 × 10 ⁷ | 7.07 × 10 ⁶ | 2.50 × 10 ⁷ | 2.28 × 10 ⁶ | 3.27 × 10 ⁵ | 2.61 × 10 ⁵ |
| | | 30 | 0.56 | 920 | 456 | 1376 | 1140 | 270 | 1410 | 1.86 × 10 ⁷ | 1.27 × 10 ⁷ | 3.14 × 10 ⁷ | 2.46 × 10 ⁶ | 1.81 × 10 ⁶ | 4.27 × 10 ⁵ |
| 16 Nov 1991 | 39° 11' N, 142° 57' E | 40 | 0.56 | 999 | 406 | 1405 | 1010 | 210 | 1220 | 1.70 × 10 ⁷ | 8.39 × 10 ⁶ | 2.54 × 10 ⁷ | 1.50 × 10 ⁶ | 6.46 × 10 ⁵ | 2.14 × 10 ⁵ |
| | | 60 | 0.53 | 995 | 385 | 1380 | 1070 | 210 | 1280 | 1.77 × 10 ⁷ | 7.11 × 10 ⁶ | 2.48 × 10 ⁷ | 2.17 × 10 ⁶ | 5.32 × 10 ⁵ | 2.71 × 10 ⁵ |
| | | 80 | 0.16 | 100 | 54 | 154 | 170 | 30 | 200 | 1.34 × 10 ⁶ | 4.10 × 10 ⁵ | 1.75 × 10 ⁶ | 3.70 × 10 ⁵ | 4.34 × 10 ⁵ | 8.04 × 10 ⁵ |
| | | 100 | 0.08 | 177 | 226 | 403 | 100 | nd | 100 | 3.46 × 10 ⁶ | 2.66 × 10 ⁶ | 6.13 × 10 ⁶ | 1.75 × 10 ⁵ | nd | 1.75 × 10 ⁵ |
| | | 0 | 0.98 | 855 | 275 | 1130 | 380 | 100 | 480 | 2.48 × 10 ⁶ | 1.11 × 10 ⁶ | 3.59 × 10 ⁶ | 7.36 × 10 ⁵ | 1.67 × 10 ⁵ | 9.03 × 10 ⁵ |
| | | 10 | 1.30 | 1969 | 436 | 2405 | 370 | 90 | 460 | 3.97 × 10 ⁶ | 1.26 × 10 ⁶ | 5.22 × 10 ⁶ | 4.90 × 10 ⁵ | 4.67 × 10 ⁵ | 9.58 × 10 ⁵ |
| 19 Nov 1991 | 38° 58' N, 144° 30' E | 20 | 1.17 | 1903 | 331 | 2234 | 450 | 30 | 480 | 5.40 × 10 ⁶ | 2.57 × 10 ⁶ | 7.98 × 10 ⁶ | 7.86 × 10 ⁵ | 2.54 × 10 ⁵ | 8.12 × 10 ⁵ |
| | | 30 | 1.24 | 1264 | 406 | 1670 | 340 | 50 | 390 | 3.52 × 10 ⁶ | 9.99 × 10 ⁵ | 4.52 × 10 ⁶ | 4.97 × 10 ⁵ | 1.02 × 10 ⁵ | 6.00 × 10 ⁵ |
| | | 50 | 1.07 | 2195 | 430 | 2625 | 230 | 60 | 290 | 8.76 × 10 ⁶ | 1.52 × 10 ⁶ | 1.03 × 10 ⁷ | 3.08 × 10 ⁵ | 5.91 × 10 ⁴ | 3.67 × 10 ⁵ |
| | | 75 | 0.10 | 533 | 243 | 776 | 30 | 10 | 40 | 7.66 × 10 ⁵ | 5.15 × 10 ⁵ | 1.28 × 10 ⁶ | 4.48 × 10 ⁵ | 2.52 × 10 ⁵ | 7.00 × 10 ⁵ |
| | | 100 | 0.09 | 357 | 352 | 709 | 70 | nd | 70 | 4.33 × 10 ⁵ | 8.52 × 10 ⁵ | 1.29 × 10 ⁶ | 1.54 × 10 ⁵ | nd | 1.54 × 10 ⁵ |
| | | 150 | 0.01 | 55 | 115 | 170 | nd | nd | nd | 2.72 × 10 ⁵ | 1.32 × 10 ⁵ | 4.04 × 10 ⁵ | nd | nd | nd |
| 20 Nov 1991 | 38° 56' N, 144° 05' E | 200 | 0.01 | 40 | 79 | 119 | nd | nd | nd | 3.79 × 10 ⁴ | 3.21 × 10 ⁵ | 3.59 × 10 ⁵ | nd | nd | nd |
| | | 0 | 1.02 | 1534 | 619 | 2153 | 960 | 120 | 1080 | 5.22 × 10 ⁶ | 1.68 × 10 ⁶ | 6.90 × 10 ⁶ | 1.01 × 10 ⁶ | 2.66 × 10 ⁵ | 1.27 × 10 ⁶ |
| | | 10 | 1.13 | 1752 | 399 | 2151 | 640 | 90 | 730 | 6.40 × 10 ⁶ | 1.14 × 10 ⁶ | 7.54 × 10 ⁶ | 6.20 × 10 ⁵ | 2.74 × 10 ⁵ | 8.94 × 10 ⁵ |
| | | 30 | 0.54 | 800 | 351 | 1151 | 240 | 60 | 300 | 3.37 × 10 ⁶ | 9.00 × 10 ⁵ | 4.27 × 10 ⁶ | 3.47 × 10 ⁵ | 1.49 × 10 ⁴ | 3.62 × 10 ⁵ |
| | | 50 | 0.21 | 456 | 190 | 646 | 80 | nd | 80 | 9.86 × 10 ⁵ | 2.94 × 10 ⁵ | 1.28 × 10 ⁶ | 1.12 × 10 ⁵ | nd | 1.12 × 10 ⁵ |
| | | 75 | 0.03 | 48 | 58 | 106 | 20 | nd | 20 | 6.61 × 10 ⁴ | 8.35 × 10 ⁴ | 1.50 × 10 ⁵ | 8.35 × 10 ³ | nd | 8.35 × 10 ³ |
| 20 Nov 1991 | 40° 01' S, 155° 10' E | 100 | 0.02 | 59 | 67 | 126 | 20 | nd | 20 | 1.73 × 10 ⁵ | 2.39 × 10 ⁵ | 4.12 × 10 ⁵ | 3.13 × 10 ⁴ | nd | 3.13 × 10 ⁴ |
| | | 150 | 0.01 | 21 | 103 | 124 | 30 | nd | 30 | 3.41 × 10 ⁴ | 1.71 × 10 ⁵ | 2.05 × 10 ⁵ | 1.42 × 10 ⁴ | nd | 1.42 × 10 ⁴ |
| | | 200 | 0.01 | 2 | 73 | 75 | 30 | nd | 30 | 3.96 × 10 ² | 1.01 × 10 ⁵ | 1.01 × 10 ⁵ | 3.98 × 10 ⁴ | nd | 3.98 × 10 ⁴ |
| | | 0 | 0.69 | 1101 | 347 | 1448 | 670 | 50 | 720 | 2.69 × 10 ⁶ | 8.64 × 10 ⁵ | 3.55 × 10 ⁶ | 1.16 × 10 ⁶ | 9.56 × 10 ⁴ | 1.25 × 10 ⁶ |
| | | 30 | 0.65 | 2488 | 268 | 2756 | 390 | 20 | 410 | 2.75 × 10 ⁶ | 2.14 × 10 ⁶ | 4.89 × 10 ⁶ | 6.21 × 10 ⁵ | 1.39 × 10 ⁴ | 6.35 × 10 ⁵ |
| | | 200 | 0.39 | 1491 | 218 | 1709 | 210 | 30 | 240 | 2.13 × 10 ⁶ | 2.74 × 10 ⁵ | 2.41 × 10 ⁶ | 1.47 × 10 ⁵ | 4.21 × 10 ⁴ | 1.89 × 10 ⁵ |
| 17 Oct 1992 | 40° 01' S, 155° 10' E | 50 | 0.33 | 867 | 102 | 969 | 130 | nd | 130 | 1.30 × 10 ⁶ | 1.14 × 10 ⁶ | 1.41 × 10 ⁶ | 1.13 × 10 ⁵ | nd | 1.13 × 10 ⁵ |
| | | 75 | 11.84 | 535 | 48 | 583 | 90 | nd | 90 | 6.42 × 10 ⁵ | 7.17 × 10 ⁴ | 7.14 × 10 ⁵ | 1.65 × 10 ⁵ | nd | 1.65 × 10 ⁵ |
| | | 100 | 0.21 | 168 | 118 | 286 | 70 | nd | 70 | 1.73 × 10 ⁵ | 1.55 × 10 ⁵ | 3.28 × 10 ⁵ | 3.31 × 10 ⁴ | nd | 3.31 × 10 ⁴ |
| | | 150 | 0.03 | 138 | 144 | 282 | 100 | 10 | 110 | 1.52 × 10 ⁵ | 3.64 × 10 ⁵ | 5.16 × 10 ⁵ | 9.21 × 10 ⁴ | 1.98 × 10 ⁴ | 1.12 × 10 ⁵ |
| | | 200 | 2.92 | 26 | 77 | 103 | 20 | nd | 20 | 6.13 × 10 ⁴ | 2.19 × 10 ⁵ | 2.80 × 10 ⁵ | 2.23 × 10 ⁴ | nd | 2.23 × 10 ⁴ |
| | | 0 | 0.36 | 2849 | 327 | 3176 | 180 | 60 | 240 | 2.37 × 10 ⁷ | 2.52 × 10 ⁶ | 2.62 × 10 ⁷ | 1.95 × 10 ⁵ | 8.59 × 10 ⁴ | 2.81 × 10 ⁵ |
| | 10 | 0.44 | 1769 | 246 | 2015 | 350 | 140 | 490 | 1.10 × 10 ⁷ | 1.46 × 10 ⁶ | 1.25 × 10 ⁷ | 4.25 × 10 ⁵ | 1.20 × 10 ⁵ | 5.45 × 10 ⁵ | |
| | 30 | 0.40 | 2175 | 231 | 2406 | 310 | 130 | 440 | 1.34 × 10 ⁷ | 1.02 × 10 ⁶ | 1.44 × 10 ⁷ | 3.01 × 10 ⁵ | 1.29 × 10 ⁵ | 4.29 × 10 ⁵ | |
| | 50 | 0.20 | 829 | 95 | 924 | 230 | 40 | 270 | 4.68 × 10 ⁶ | 4.78 × 10 ⁵ | 5.16 × 10 ⁶ | 3.73 × 10 ⁵ | 2.23 × 10 ⁵ | 3.96 × 10 ⁵ | |

Table 1 (continued)

| Date | Position | Depth (m) | Temp. (°C) | Chl <i>a</i> ($\mu\text{g l}^{-1}$) | Abundance | | | | Biomass (pg C l ⁻¹) | | | | TC | | | |
|----------------|--------------------------|--------------|---------------|--|--|------------------------------|------------------------------|-----------------------------|---------------------------------|-----|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | | | | ANP $\times 10^3$ cells l ⁻¹ | HNP cells l ⁻¹ | TNP cells l ⁻¹ | HC cells l ⁻¹ | MC cells l ⁻¹ | TC | ANP | HNP | | TNP | HC | MC |
| 19 Oct 1992 | 37° 00' S, 155° 10' E | 75 | 13.33 | 0.23 | 729 | 231 | 960 | 240 | 50 | 290 | 4.92 × 10 ⁶ | 7.61 × 10 ⁵ | 5.68 × 10 ⁶ | 4.41 × 10 ⁵ | 6.27 × 10 ⁴ | 5.03 × 10 ⁵ |
| | | 100 | 13.27 | 0.18 | 553 | 272 | 825 | 250 | 10 | 260 | 2.07 × 10 ⁶ | 1.36 × 10 ⁶ | 3.43 × 10 ⁶ | 3.99 × 10 ⁵ | 3.15 × 10 ⁴ | 4.30 × 10 ⁵ |
| | | 150 | 12.92 | 0.04 | 257 | 156 | 413 | 110 | 10 | 120 | 6.97 × 10 ⁵ | 4.01 × 10 ⁵ | 1.10 × 10 ⁶ | 2.53 × 10 ⁵ | 2.52 × 10 ⁵ | 5.05 × 10 ⁵ |
| | | 200 | 12.68 | 0.03 | 387 | 246 | 633 | 40 | nd | 40 | 1.39 × 10 ⁶ | 6.90 × 10 ⁵ | 2.08 × 10 ⁶ | 5.69 × 10 ⁴ | nd | 5.69 × 10 ⁴ |
| | | 0 | 17.40 | 0.23 | 552 | 206 | 758 | 40 | 150 | 190 | 2.44 × 10 ⁶ | 1.64 × 10 ⁶ | 4.08 × 10 ⁶ | 8.25 × 10 ⁴ | 1.75 × 10 ⁵ | 2.58 × 10 ⁵ |
| 20 Oct 1992 | 34° 00' S, 155° 10' E | 10 | 16.15 | 0.25 | 901 | 170 | 1071 | 80 | 70 | 150 | 3.68 × 10 ⁶ | 5.79 × 10 ⁵ | 4.26 × 10 ⁶ | 1.20 × 10 ⁵ | 3.70 × 10 ⁵ | 4.90 × 10 ⁵ |
| | | 30 | 16.00 | 0.34 | 764 | 175 | 939 | 50 | 90 | 140 | 6.11 × 10 ⁶ | 5.56 × 10 ⁵ | 6.66 × 10 ⁶ | 1.14 × 10 ⁵ | 4.25 × 10 ⁵ | 5.39 × 10 ⁵ |
| | | 50 | 15.53 | 0.33 | 849 | 201 | 1050 | 110 | 40 | 150 | 4.93 × 10 ⁶ | 5.23 × 10 ⁵ | 5.45 × 10 ⁶ | 1.65 × 10 ⁵ | 1.03 × 10 ⁵ | 2.68 × 10 ⁵ |
| | | 75 | 14.52 | 0.11 | 205 | 151 | 356 | 40 | nd | 40 | 1.44 × 10 ⁶ | 4.89 × 10 ⁵ | 1.93 × 10 ⁶ | 6.02 × 10 ⁴ | nd | 6.02 × 10 ⁴ |
| | | 100 | 14.34 | 0.11 | 190 | 256 | 446 | 30 | nd | 30 | 1.49 × 10 ⁶ | 1.06 × 10 ⁶ | 2.55 × 10 ⁶ | 2.88 × 10 ⁴ | nd | 2.88 × 10 ⁴ |
| 20 Oct 1992 | 34° 00' S, 155° 10' E | 150 | 13.74 | 0.05 | 55 | 90 | 145 | 10 | nd | 10 | 1.30 × 10 ⁵ | 1.75 × 10 ⁵ | 3.05 × 10 ⁵ | 9.17 × 10 ⁴ | nd | 9.17 × 10 ⁴ |
| | | 200 | 13.31 | 0.01 | 60 | 121 | 181 | 20 | nd | 20 | 2.11 × 10 ⁵ | 1.79 × 10 ⁵ | 3.90 × 10 ⁵ | 4.29 × 10 ⁴ | nd | 4.29 × 10 ⁴ |
| | | 0 | 17.40 | 0.27 | 1755 | 447 | 2202 | 200 | 290 | 490 | 8.30 × 10 ⁶ | 1.68 × 10 ⁶ | 9.98 × 10 ⁶ | 3.94 × 10 ⁵ | 1.01 × 10 ⁶ | 1.40 × 10 ⁶ |
| | | 10 | 17.24 | 0.26 | 1584 | 332 | 1916 | 150 | 418 | 568 | 6.42 × 10 ⁶ | 1.32 × 10 ⁶ | 7.74 × 10 ⁶ | 3.17 × 10 ⁵ | 1.28 × 10 ⁶ | 1.59 × 10 ⁶ |
| | | 30 | 17.12 | 0.27 | 1398 | 332 | 1730 | 140 | 260 | 400 | 5.89 × 10 ⁶ | 1.34 × 10 ⁶ | 7.23 × 10 ⁶ | 2.33 × 10 ⁵ | 5.75 × 10 ⁵ | 8.08 × 10 ⁵ |
| 23 Oct 1992 | 24° 00' S, 155° 00' E | 50 | 16.15 | 0.18 | 613 | 171 | 784 | 350 | 20 | 370 | 2.19 × 10 ⁶ | 1.18 × 10 ⁶ | 3.37 × 10 ⁶ | 1.12 × 10 ⁶ | 3.13 × 10 ⁴ | 1.16 × 10 ⁶ |
| | | 75 | 15.87 | 0.15 | 478 | 282 | 760 | 130 | 10 | 140 | 1.25 × 10 ⁶ | 1.07 × 10 ⁶ | 2.32 × 10 ⁶ | 1.06 × 10 ⁶ | 2.48 × 10 ³ | 1.09 × 10 ⁵ |
| | | 100 | 15.23 | 0.05 | 266 | 216 | 482 | 100 | nd | 100 | 1.70 × 10 ⁶ | 1.22 × 10 ⁶ | 2.93 × 10 ⁶ | 9.52 × 10 ⁴ | nd | 9.52 × 10 ⁴ |
| | | 150 | 14.39 | 0.02 | 120 | 145 | 265 | 60 | nd | 60 | 3.39 × 10 ⁵ | 7.93 × 10 ⁵ | 1.13 × 10 ⁶ | 9.24 × 10 ⁴ | nd | 9.24 × 10 ⁴ |
| | | 200 | 13.68 | 0.01 | 90 | 140 | 230 | nd | nd | nd | 3.00 × 10 ⁵ | 1.34 × 10 ⁶ | 1.64 × 10 ⁶ | nd | nd | nd |
| 23 Oct 1992 | 22° 00' S, 155° 00' E | 0 | 24.30 | 0.05 | 588 | 168 | 756 | 50 | 30 | 80 | 2.11 × 10 ⁶ | 5.19 × 10 ⁵ | 2.62 × 10 ⁶ | 1.27 × 10 ⁵ | 4.21 × 10 ⁴ | 1.69 × 10 ⁵ |
| | | 10 | 23.11 | 0.05 | 974 | 175 | 1149 | nd | 60 | 60 | 3.05 × 10 ⁶ | 1.43 × 10 ⁶ | 4.48 × 10 ⁶ | nd | 8.03 × 10 ⁴ | 8.03 × 10 ⁴ |
| | | 30 | 23.10 | 0.06 | 571 | 362 | 933 | 30 | 60 | 90 | 2.60 × 10 ⁶ | 4.05 × 10 ⁶ | 4.05 × 10 ⁶ | 7.11 × 10 ⁴ | 9.09 × 10 ⁴ | 1.62 × 10 ⁵ |
| | | 50 | 22.65 | 0.07 | 1193 | 479 | 1672 | 30 | 50 | 80 | 3.98 × 10 ⁶ | 2.57 × 10 ⁶ | 6.55 × 10 ⁶ | 3.71 × 10 ⁴ | 7.60 × 10 ⁴ | 1.13 × 10 ⁵ |
| | | 75 | 22.41 | 0.15 | 604 | 293 | 897 | 60 | 10 | 70 | 1.51 × 10 ⁶ | 1.31 × 10 ⁶ | 2.82 × 10 ⁶ | 7.70 × 10 ⁴ | 3.15 × 10 ⁴ | 1.08 × 10 ⁵ |
| 23 Oct 1992 | 22° 00' S, 155° 00' E | 100 | 22.07 | 0.11 | 328 | 126 | 454 | 20 | nd | 20 | 1.15 × 10 ⁶ | 4.13 × 10 ⁵ | 1.56 × 10 ⁶ | 1.12 × 10 ⁵ | nd | 1.12 × 10 ⁵ |
| | | 150 | 21.18 | 0.02 | 75 | 142 | 217 | 20 | nd | 20 | 1.76 × 10 ⁵ | 1.53 × 10 ⁶ | 1.71 × 10 ⁶ | 8.67 × 10 ⁴ | nd | 8.67 × 10 ⁴ |
| | | 200 | 20.59 | nd | 59 | 218 | 277 | 10 | nd | 10 | 1.09 × 10 ⁵ | 4.98 × 10 ⁵ | 6.07 × 10 ⁵ | 1.15 × 10 ⁴ | nd | 1.15 × 10 ⁴ |
| | | 0 | 24.10 | 0.06 | 865 | 478 | 1343 | 50 | 50 | 100 | 2.00 × 10 ⁶ | 1.47 × 10 ⁶ | 3.47 × 10 ⁶ | 4.53 × 10 ⁵ | 1.51 × 10 ⁵ | 6.04 × 10 ⁵ |
| | | 10 | 23.96 | 0.06 | 1007 | 319 | 1326 | 50 | 130 | 180 | 2.19 × 10 ⁶ | 8.43 × 10 ⁵ | 3.03 × 10 ⁶ | 5.37 × 10 ⁴ | 3.84 × 10 ⁵ | 4.38 × 10 ⁵ |
| 24 Oct 1992 | 20° 00' S, 155° 00' E | 30 | 23.97 | 0.07 | 730 | 327 | 1057 | 60 | 160 | 220 | 2.50 × 10 ⁶ | 1.29 × 10 ⁶ | 3.78 × 10 ⁶ | 1.99 × 10 ⁵ | 5.08 × 10 ⁵ | 7.07 × 10 ⁵ |
| | | 50 | 23.93 | 0.06 | 504 | 402 | 906 | 10 | 50 | 60 | 1.24 × 10 ⁶ | 1.24 × 10 ⁶ | 2.48 × 10 ⁶ | 1.15 × 10 ⁴ | 1.91 × 10 ⁵ | 2.02 × 10 ⁵ |
| | | 75 | 23.66 | 0.11 | 689 | 193 | 882 | 10 | 100 | 110 | 1.76 × 10 ⁶ | 5.79 × 10 ⁵ | 2.34 × 10 ⁶ | 1.98 × 10 ⁴ | 2.12 × 10 ⁵ | 2.31 × 10 ⁵ |
| | | 100 | 23.02 | 0.15 | 847 | 243 | 1090 | 10 | 30 | 40 | 1.78 × 10 ⁶ | 7.67 × 10 ⁵ | 2.54 × 10 ⁶ | 1.15 × 10 ⁴ | 3.15 × 10 ⁴ | 4.30 × 10 ⁴ |
| | | 150 | 21.63 | 0.12 | 377 | 126 | 503 | 40 | 10 | 50 | 1.40 × 10 ⁶ | 2.76 × 10 ⁵ | 1.68 × 10 ⁶ | 9.24 × 10 ⁴ | 5.87 × 10 ³ | 9.83 × 10 ⁴ |
| 24 Oct 1992 | 20° 00' S, 155° 00' E | 200 | 20.70 | 0.03 | 143 | 126 | 269 | 10 | nd | 10 | 2.48 × 10 ⁵ | 4.04 × 10 ⁵ | 6.52 × 10 ⁵ | 3.15 × 10 ⁴ | nd | 3.15 × 10 ⁴ |
| | | 0 | 24.30 | 0.05 | 1032 | 310 | 1342 | 30 | 10 | 40 | 3.11 × 10 ⁶ | 1.33 × 10 ⁶ | 4.44 × 10 ⁶ | 5.11 × 10 ⁴ | 2.48 × 10 ³ | 5.36 × 10 ⁴ |
| | | 10 | 23.59 | 0.06 | 983 | 419 | 1402 | 50 | 100 | 150 | 2.61 × 10 ⁶ | 1.69 × 10 ⁶ | 4.30 × 10 ⁶ | 1.09 × 10 ⁵ | 1.63 × 10 ⁵ | 2.73 × 10 ⁵ |
| | | 30 | 23.58 | 0.07 | 915 | 455 | 1370 | 120 | 50 | 170 | 2.81 × 10 ⁶ | 2.59 × 10 ⁶ | 5.39 × 10 ⁶ | 4.68 × 10 ⁵ | 5.38 × 10 ⁴ | 5.22 × 10 ⁵ |
| | | 50 | 23.56 | 0.11 | 999 | 402 | 1401 | 50 | 20 | 70 | 3.41 × 10 ⁶ | 2.19 × 10 ⁶ | 5.60 × 10 ⁶ | 5.38 × 10 ⁴ | 3.96 × 10 ⁴ | 9.34 × 10 ⁴ |
| 24 Oct 1992 | 20° 00' S, 155° 00' E | 75 | 23.39 | 0.13 | 755 | 369 | 1124 | 150 | 90 | 240 | 2.17 × 10 ⁶ | 1.21 × 10 ⁶ | 3.38 × 10 ⁶ | 2.04 × 10 ⁵ | 1.57 × 10 ⁵ | 3.61 × 10 ⁵ |
| | | 100 | 22.73 | 0.04 | 235 | 134 | 369 | 50 | nd | 50 | 4.70 × 10 ⁵ | 2.27 × 10 ⁵ | 6.97 × 10 ⁵ | 1.09 × 10 ⁵ | nd | 1.09 × 10 ⁵ |
| | | 150 | 21.53 | nd | 76 | 168 | 244 | 10 | nd | 10 | 1.85 × 10 ⁵ | 5.19 × 10 ⁵ | 7.04 × 10 ⁵ | 5.87 × 10 ³ | nd | 5.87 × 10 ³ |
| | | 200 | 20.08 | nd | 101 | 168 | 269 | nd | nd | nd | 1.97 × 10 ⁵ | 4.93 × 10 ⁵ | 6.90 × 10 ⁵ | nd | nd | nd |
| | | 0 | 24.30 | 0.05 | 1032 | 310 | 1342 | 30 | 10 | 40 | 3.11 × 10 ⁶ | 1.33 × 10 ⁶ | 4.44 × 10 ⁶ | 5.11 × 10 ⁴ | 2.48 × 10 ³ | 5.36 × 10 ⁴ |

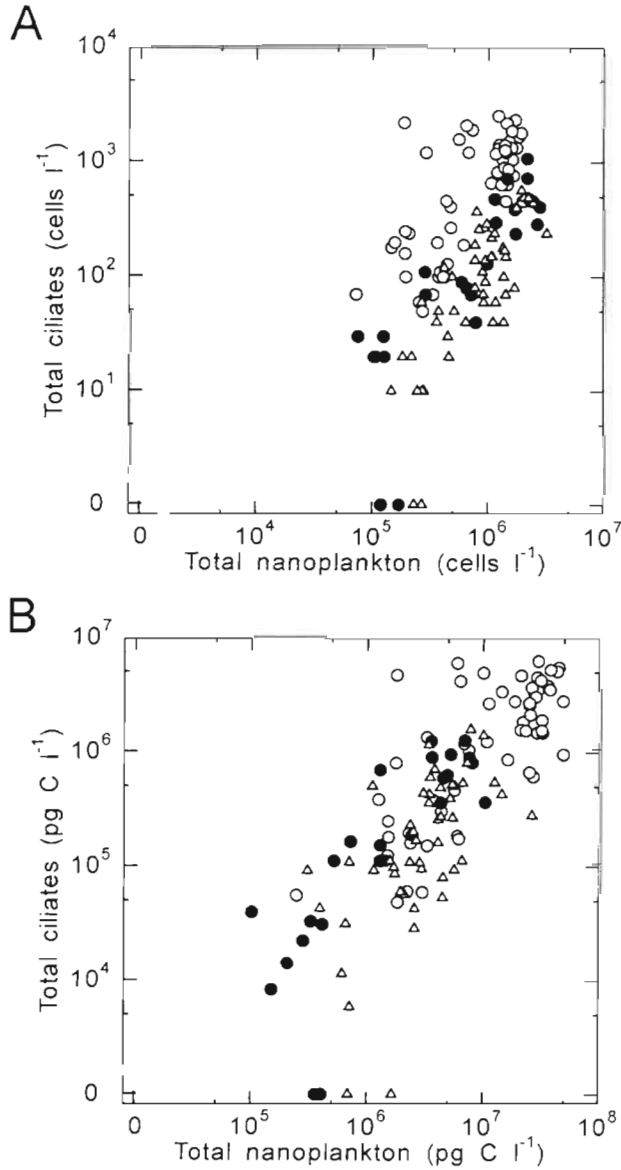


Fig. 2. Relationship in (A) abundance and (B) biomass between total nanoplankton and total planktonic ciliates. (O) Spring subarctic water; (●) fall subarctic water; (▲) subtropical water

than in fall subarctic (1.01×10^5 to 1.03×10^7 pg C l^{-1}) and subtropical waters (3.05×10^5 to 2.62×10^7 pg C l^{-1}) (Table 1). Positive correlations were observed both between A_c and A_n and between B_c and B_n (Fig. 2) on logarithmic scales. When 4 samples with zero A_c were excluded, the regression equation in abundance over 3 oceanographic regimes was: $A_c = 3.24 \times 10^{-4} \times A_n^{0.996}$ ($r = 0.61$, $p < 0.001$, $n = 126$). On the other hand, the regression equation in biomass was: $B_c = 0.211 \times B_n^{0.944}$ ($r = 0.81$, $p < 0.001$, $n = 126$). The correlation coefficient observed in biomass ($r = 0.81$) was significantly larger ($p < 0.01$) than that in abundance ($r = 0.61$).

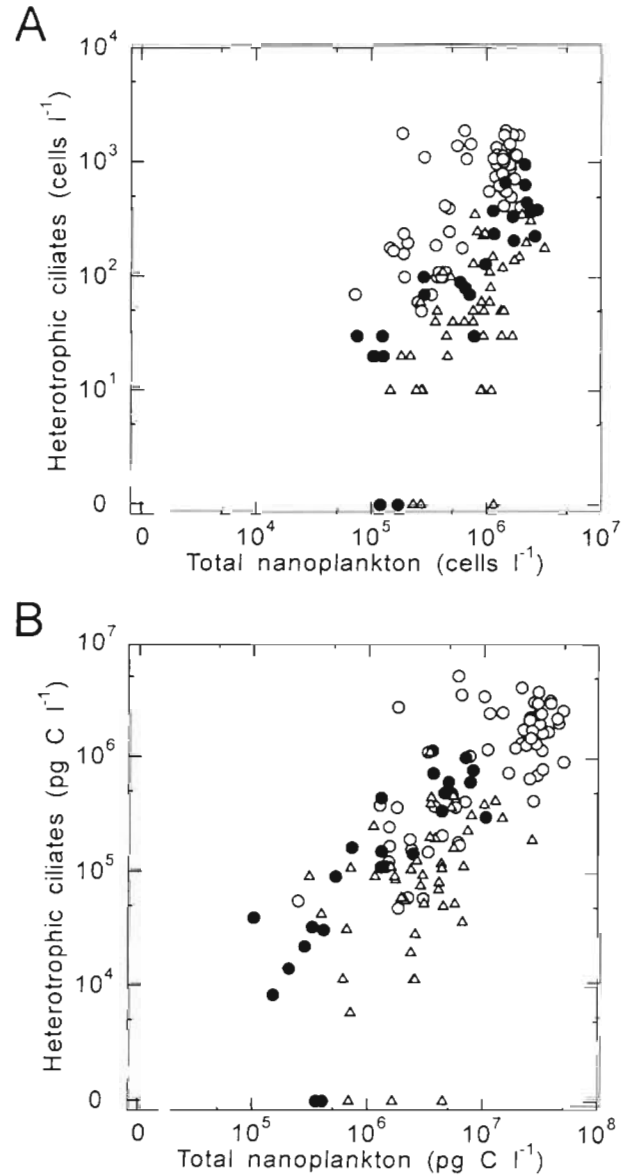


Fig. 3. Relationship in (A) abundance and (B) biomass between total nanoplankton and heterotrophic planktonic ciliates. (O) Spring subarctic water; (●) fall subarctic water; (▲) subtropical water

The relationship between heterotrophic ciliates and total nanoplankton (Fig. 3) was almost the same as that between total ciliates and total nanoplankton, since abundance (A_{hc}) and biomass (B_{hc}) of heterotrophic ciliates were generally higher in spring subarctic (50 to 1900 cells l^{-1} , 4.89×10^4 to 5.22×10^6 pg C l^{-1}) than in fall subarctic (< 960 cells l^{-1} , $< 1.16 \times 10^6$ pg C l^{-1}) and subtropical waters (< 350 cells l^{-1} , $< 1.12 \times 10^6$ pg C l^{-1}) (Table 1). The overall regression equation in abundance excluding 5 exceptional samples with zero A_{hc} was: $A_{hc} = 2.00 \times 10^{-3} \times A_n^{0.842}$ ($r = 0.50$, $p < 0.001$, $n = 125$). The regression equation in biomass was: $B_{hc} =$

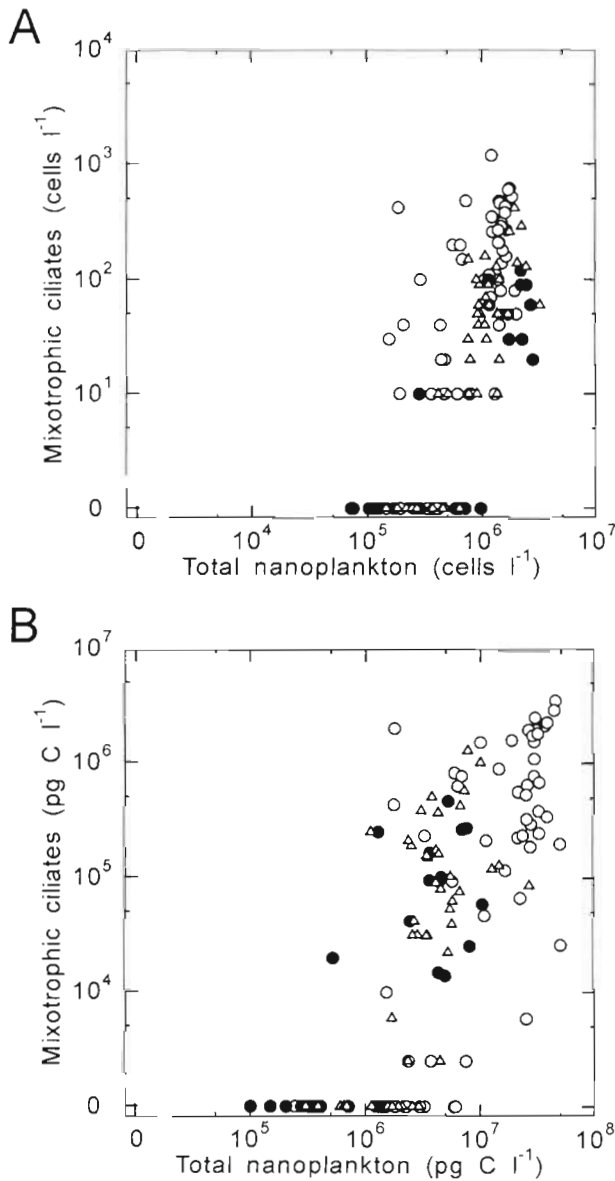


Fig. 4. Relationship in (A) abundance and (B) biomass between total nanoplankton and mixotrophic planktonic ciliates. (O) Spring subarctic water; (●) fall subarctic water; (Δ) subtropical water

$0.478 \times B_n^{0.868}$ ($r = 0.77$, $p < 0.001$, $n = 125$). The correlation coefficient in biomass ($r = 0.77$) was significantly higher ($p < 0.001$) than in abundance ($r = 0.50$).

Slight differences were observed in standing crop of mixotrophic ciliates over 3 oceanographic regimes, i.e. the highest values of mixotrophic ciliate abundance (A_{mc}) were 1190, 120 and 420 cells l^{-1} and those of biomass (B_{mc}) were 3.51×10^6 , 4.67×10^5 and 1.28×10^6 pg C l^{-1} in spring subarctic, fall subarctic and subtropical waters, respectively (Table 1). Mixotrophic ciliates did not correlate well with total nanoplankton in both abundance and biomass (Fig. 4). Overall regression of A_{mc} on A_n ex-

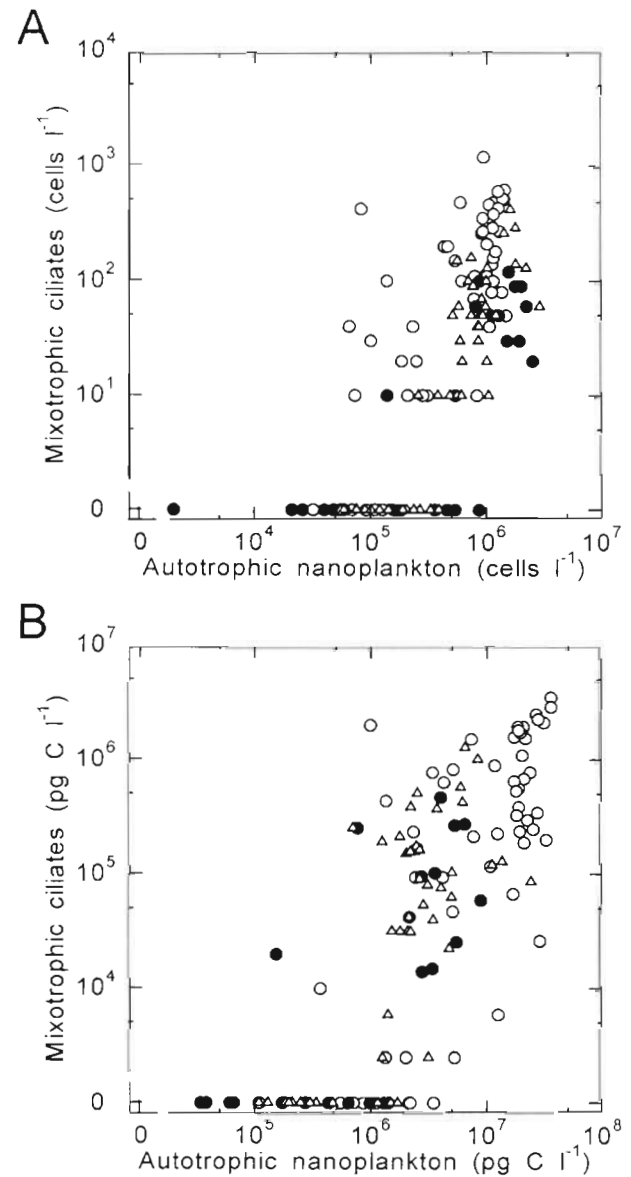


Fig. 5. Relationship in (A) abundance and (B) biomass between autotrophic nanoplankton and mixotrophic planktonic ciliates. (O) Spring subarctic water; (●) fall subarctic water; (Δ) subtropical water. One biomass datum (3.96×10^2 , 0) at 200 m in fall subarctic water of 19 November 1991 ($38^\circ 58' N$, $144^\circ 30' E$) is excluded from (B)

cluding 38 samples with zero A_{mc} was: $A_{mc} = 2.09 \times 10^{-3} \times A_n^{0.757}$ ($r = 0.38$, $p < 0.001$, $n = 92$). The regression equation in biomass was: $B_{mc} = 0.339 \times B_n^{0.823}$ ($r = 0.48$, $p < 0.001$, $n = 92$). Correlation of mixotrophic ciliates to autotrophic nanoplankton was not close either (Fig. 5), being $A_{mc} = 1.74 \times 10^{-2} \times A_{an}^{0.621}$ ($r = 0.39$, $p < 0.001$, $n = 92$) in abundance, and $B_{mc} = 0.682 \times B_{an}^{0.797}$ ($r = 0.51$, $p < 0.001$, $n = 92$) in biomass. Abundance (A_{an}) and biomass (B_{an}) of autotrophic nanoplankton were 3.2×10^4 to 1.46×10^6 cells l^{-1} and 1.09×10^5 to 3.54×10^7 pg C l^{-1} in spring

subarctic, 2×10^3 to 2.49×10^6 cells l^{-1} and 3.96×10^2 to 8.71×10^6 pg C l^{-1} in fall subarctic and 5.5×10^4 to 2.85×10^6 cells l^{-1} and 1.09×10^5 to 2.37×10^7 pg C l^{-1} in subtropical waters (Table 1).

Correlations of total ciliates and heterotrophic ciliates to chl *a* concentration were high. These coefficients (*r*) on logarithmic scales were 0.83 ($p < 0.001$, $n = 124$) in abundance and 0.81 ($p < 0.001$, $n = 124$) in biomass of total ciliates and 0.79 ($p < 0.001$, $n = 123$) in abundance and 0.77 ($p < 0.001$, $n = 123$) in biomass of heterotrophic ciliates, when the samples with zero chl *a* concentration and zero ciliate abundance or biomass were excluded. On the other hand, that between mixotrophic ciliates and chl *a* concentration was not high: 0.57 ($p < 0.01$, $n = 92$) in abundance and 0.49 ($p < 0.05$, $n = 92$) in biomass.

DISCUSSION

Standing crops of ciliates observed in this study were < 2540 cells l^{-1} in abundance, or $< 6.32 \times 10^6$ pg C l^{-1} in biomass. These values are comparable to those reported from other oceanic waters. In Georges Bank in July, mean ciliate abundance in the water column above the depth of 1% light level was 580 to 13 153 cells l^{-1} (Stoecker et al. 1989). In the East China Sea in August, ciliate abundance and biomass in the top 200 m were 30 to 3040 cells l^{-1} and 2.02×10^4 to 1.07×10^7 pg C l^{-1} , respectively (Ota 1995). In the northwestern Indian Ocean during September and October, mean values of ciliate abundance and biomass in the euphotic zone were respectively 31 to 823 cells l^{-1} and 1×10^5 to 1.2×10^6 pg C l^{-1} (Leakey et al. 1996).

Abundance and biomass of nanoplankton observed in this study were 7.2×10^4 to 3.18×10^6 cells l^{-1} and 1.01×10^5 to 4.92×10^7 pg C l^{-1} , respectively. These values are also comparable to previously reported values from oceanic waters. In the Sargasso Sea during October and November, nanoplankton abundance in the top 20 m was 6.9×10^5 to 1.38×10^6 cells l^{-1} (Caron 1983). In the Antarctic Ocean in March, average standing crop of nanoplankton in the surface water was 6.02×10^5 cells l^{-1} , or 2.97×10^6 pg C l^{-1} (Ishiyama et al. 1993).

Shrinkage and loss of cells due to fixation and preservation are serious problems in measurements of volume and abundance of ciliate cells. Fixation with 1% buffered formaldehyde causes significant shrinkage of the cells to 80–86% of live volume (Choi & Stoecker 1989). Loss of cells by addition of formaldehyde is up to 20% of live counts (Dale & Burkill 1982). Even so, formaldehyde is reported to cause less shrinkage than other fixatives such as glutaraldehyde and acid Lugol's (Choi & Stoecker 1989) and is considered to be the most appropriate fixative for examination of

chlorophyll pigments contained in mixotrophic ciliates (Stoecker et al. 1994a). The ciliate cells examined in this study were subjected to such artifacts. However, correlations between ciliates and nanoplankton are likely valid, because the same fixation procedure was consistently employed throughout this study.

The correlation between ciliates and nanoplankton in biomass was strong ($r = 0.81$, $p < 0.001$, $n = 126$) when all the data from the top 100 or 200 m of the water column are pooled (Fig. 2B). Correlation coefficients between them were also significantly high when the water column was divided into the surface layer shallower than 50 m ($r = 0.64$, $p < 0.002$, $n = 67$) and the underlying layer ($r = 0.80$, $p < 0.001$, $n = 59$) (Fig. 6). This indicates that standing crops of ciliates and nanoplankton co-vary geographically in a similar manner in both the layers, according to water types.

Planktonic ciliates are known to consume primarily both nanoplankton (Gifford 1985, Verity 1985) and picoplankton (Sherr & Sherr 1987, Bernard & Rasoulzadegan 1990). Standing crops of total ciliates and heterotrophic ciliates are correlated with nanoplankton at the community level (Figs. 2 & 3). Since the correlation coefficients were larger when the standing crops were expressed in biomass, their predator-prey linkage might be very tight in the oceanic waters. Correlations between ciliates and picoplankton (bacterioplankton) were unknown in this study, because the latter was not measured. It is reported that the standing crop of bacterioplankton is stable over seasonal scales in various aquatic environments (e.g. Wright & Coffin 1984, Tanaka et al. 1997) and this may explain the fact

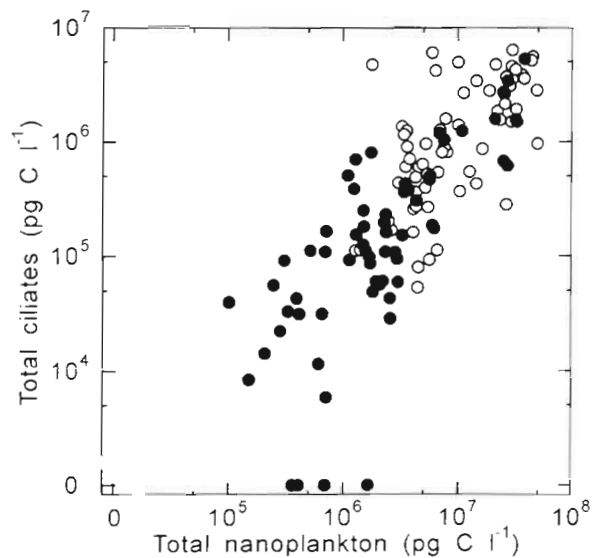


Fig. 6. Relationship in biomass between total nanoplankton and total planktonic ciliates. (○) Samples from the surface layer shallower than 50 m; (●) those from the underlying layer deeper than 51 m

that the correlation between ciliates and picoplankton in biomass over various sea areas is poor ($r = 0.14$, $n = 87$) (Lynn & Montagnes 1991).

Mixotrophic ciliates did not show significant correlations with either total nanoplankton or autotrophic nanoplankton (Figs. 4 & 5). Very few mixotrophic ciliates below the detection limit were frequently counted in deeper layers. Mixotrophic ciliates might be more or less selective feeders as they sequester the chloroplasts of particular types of algae (Jonsson 1987, Stoecker & Silver 1987, Stoecker 1991), which remain functional (Jonsson 1987). If such a stenophagous character of mixotrophic ciliates is the case, differential vertical distributions of different nanoplankters (Furuya & Marumo 1983, Olson et al. 1991) are likely the main reason for the lack of a significantly positive relationship between mixotrophic ciliates and total nanoplankton as well as autotrophic nanoplankton at the community level.

Whether prey organisms control size of predator populations or predator organisms control size of prey populations is an interesting question. If nanoplankton control ciliates, positive relationships are observed between the two (Gasol 1994). Although this study does not cover many components such as picoplankton, nanoplankton feeders other than ciliates and predators on ciliates, the strong positive correlations of the total ciliates and the heterotrophic ciliates on the nanoplankton are evident (Figs. 2 & 3). Size of the ciliate populations at community level is, as a whole, likely to be controlled in bottom-up manner by nanoplankton in open ocean. This trend indicates that the situation in the open ocean is possibly different from those in some coastal waters where top-down control on ciliate populations by metazoan predators prevails (e.g. Smetacek 1981, Dolan 1991, Nielsen & Kiørboe 1991, 1994, Kivi et al. 1993).

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LITERATURE CITED

- Bernard C, Rassoulzadegan F (1990) Bacteria on microflagellates as a major food source for marine ciliates: possible implications for the microzooplankton. *Mar Ecol Prog Ser* 64:147–155
- Caron DA (1983) Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. *Appl Environ Microbiol* 46:491–498
- Choi JW, Stoecker DK (1989) Effects of fixation on cell volume of marine planktonic Protozoa. *Appl Environ Microbiol* 55:1761–1765
- Dale T, Burkill PH (1982) 'Live counting' — a quick and simple technique for enumerating pelagic ciliates. *Ann Inst Oceanogr* 58:267–276
- Dolan JR (1991) Guilds of ciliate microzooplankton in the Chesapeake Bay. *Estuar Coast Shelf Sci* 33:137–152
- Furuya K, Marumo R (1983) The structure of the phytoplankton community in the subsurface chlorophyll maxima in the western North Pacific Ocean. *J Plankton Res* 5:393–406
- Gasol JM (1994) A framework for the assessment of top-down vs bottom-up control of heterotrophic nanoflagellate abundance. *Mar Ecol Prog Ser* 113:291–300
- Gifford D (1985) Laboratory culture of marine planktonic oligotrichs (Ciliophora, Oligotrichida). *Mar Ecol Prog Ser* 23:257–267
- Haas LW (1982) Improved epifluorescence microscopy for observing planktonic micro-organisms. *Ann Inst Oceanogr* 58:261–266
- Ishiyama M, Hiromi J, Tanimura A, Kadota S (1993) Abundance and biomass distribution of microbial assemblages at the surface in the oceanic province of Antarctic Ocean. *Proc NIPR Symp Polar Biol* 6:6–20
- Jonsson PR (1987) Photosynthetic assimilation of inorganic carbon in marine oligotrich ciliates (Ciliophora, Oligotrichina). *Mar Microb Food Webs* 2:55–68
- Kivi K, Kaitala S, Kuosa H, Kuparinen J, Leskinen E, Lignell R, Marcussen B, Tamminen T (1993) Nutrient limitation and grazing control of the Baltic plankton community during annual succession. *Limnol Oceanogr* 38:893–905
- Leakey RJG, Burkill PH, Sleigh MA (1996) Planktonic ciliates in the northwestern Indian Ocean: their abundance and biomass in waters of contrasting productivity. *J Plankton Res* 18:1063–1071
- Lindholm T (1985) *Mesodinium rubrum* — unique photosynthetic ciliate. *Adv Aquat Microbiol* 3:1–48
- Lynn DH, Montagnes DJS (1991) Global production of heterotrophic marine planktonic ciliates. In: Reid PC, Turley CM, Burkill PH (eds) *Protozoa and their role in marine processes*. Springer, London, p 281–307
- Nielsen TG, Kiørboe T (1991) Effects of a storm event on the structure of the pelagic food web with special emphasis on planktonic ciliates. *J Plankton Res* 13:35–51
- Nielsen TG, Kiørboe T (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol Oceanogr* 39:508–519
- Olson RJ, Zettler ER, Chisholm SW, Dusenberry JA (1991) Advances in oceanography through flow cytometry. In: Demers S (ed) *Particle analysis in oceanography*. Springer-Verlag, Berlin, p 351–399
- Ota T (1995) Biomass and production of microzooplankton in the East China Sea with special reference to planktonic ciliates. Master's thesis, Tohoku Univ, Sendai (in Japanese with English abstract)
- Pierce RW, Turner JT (1992) Ecology of planktonic ciliates in marine food webs. *Rev Aquat Sci* 6:139–181
- Porter KG, Sherr EB, Sherr BF, Pace M, Sanders RW (1985) Protozoa in planktonic food webs. *J Protozool* 32:409–415
- Putt M, Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. *Limnol Oceanogr* 34:1097–1103
- Sherr EB, Sherr BF (1987) High rates of consumption of bacteria by pelagic ciliates. *Nature* 325:710–711
- Smetacek V (1981) The annual cycle of protozooplankton in the Kiel Bight. *Mar Biol* 63:1–11
- Sorokin YI (1981) Microheterotrophic organisms in marine ecosystems. In: Longhurst AT (ed) *Analysis of marine ecosystems*. Academic Press, New York, p 293–342
- Stoecker DK (1991) Mixotrophy in marine planktonic ciliates:

- physiological and ecological aspects of plastid-retention by oligotrichs. In: Reid PC, Turley CM, Burkill PH (eds) Protozoa and their role in marine processes. Springer, London, p 161–179
- Stoecker DK, Gifford DJ, Putt M (1994a) Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. *Mar Ecol Prog Ser* 110:293–299
- Stoecker DK, Sieracki ME, Verity PG, Michaels AE, Haugen E, Burkill PH, Edwards ES (1994b) Nanoplankton and protozoan microzooplankton during the JGOFS North Atlantic bloom experiment: 1989 and 1990. *J Mar Biol Assoc UK* 74:427–443
- Stoecker DK, Silver MW (1987) Chloroplast retention by marine planktonic ciliates. *Endocytobiology III. Ann NY Acad Sci* 503:562–565
- Stoecker DK, Silver MW, Michaels AE, Davis LH (1988) Obligate mixotrophy in *Laboea strobila*, a ciliate which retains chloroplasts. *Mar Biol* 99:415–423
- Stoecker DK, Taniguchi A, Michaels AE (1989) Abundance of autotrophic, mixotrophic and heterotrophic planktonic ciliates in shelf and slope water. *Mar Ecol Prog Ser* 50:241–254
- Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell or plasma volume. *Limnol Oceanogr* 12:411–418
- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis. *Bull Fish Res Bd Can* 167
- Tanaka T, Fujita N, Taniguchi A (1997) Predator-prey eddy in heterotrophic nanoflagellate-bacteria relationships in a coastal marine environment: a new scheme for predator-prey associations. *Aquat Microb Ecol* 13:249–256
- Verity PG (1985) Grazing, respiration, excretion, and growth rates of tintinnids. *Limnol Oceanogr* 30:1268–1282
- Wessenberg H, Antipa GA (1970) Capture and ingestion of *Paramecium* by *Didinium nasutum*. *J Protozool* 17:250–270
- Wright RT, Coffin RB (1984) Factors affecting bacterioplankton density and productivity in salt marsh estuaries. In: Klug MJ, Reddy CA (eds) *Current perspectives in microbial ecology*. American Society for Microbiology, Washington, DC, p 485–494

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