Vol. 10: 273–282, 1996 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published June 27

Micro- and mesoprotozooplankton at 140° W in the equatorial Pacific: heterotrophs and mixotrophs

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ABSTRACT: Abundance, biomass and presence or absence of plastids in micro- (>20 to 200 µm) and meso- (>200 µm to 2 mm size range) protozooplankton were determined during March-April and October 1992 at 140° W on the equator as part of the United States' participation in the Joint Global Ocean Flux Study (JGOFS). The March-April cruise took place during strong El Niño conditions but the October 1992 cruise was during a relaxation in El Niño. Protistan zooplankton biomass in the 20 to 64 µm size range was dominated by planktonic ciliates, in the >64 to 200 µm size range by ciliates, heterotrophic dinoflagellates, foraminifera and acantharia, and in the >200 µm size range by acantharia, foraminifera and polycystine radiolaria. Presence of algal plastids, indicating mixotrophic nutrition, was common. In October, plastidic cells contributed ~27, 47 and 56% of the protozooplankton biomass in the 20–64, >64–200 and >200 µm size classes, respectively. During October, the protistan micro- and mesozooplankton biomass was generally higher than in March-April 1992. Most of the increase in biomass was due to ciliates and foraminifera. These data suggest that the numerical responses of ciliates may be important in coupling changes in primary productivity of nanoplankton to their removal by grazing in the equatorial Pacific. The increased biomass of foraminifera in October may be linked to the relaxation in El Niño. Foraminifera may be particularly important in the coupling between primary production and biogenic flux of organic carbon and carbonate in the equatorial Pacific.

KEY WORDS: El Niño · Ciliates · Heterotrophic dinoflagellates · Sarcodines · Foraminifera · Radiolaria · Acantharia · Mixotrophy · JGOFS · Microzooplankton · EqPac · Equatorial Pacific

INTRODUCTION

The structure of planktonic food webs is hypothesized to have an important influence on the export of organic carbon and carbonate from surface waters (reviewed in Michaels & Silver 1988, Peinert et al. 1989, Legendre & Le Fèvre 1995). Microphytoplankton cells, such as large diatoms, can be directly involved in the flux of particulate carbon from the mixed layer (Lampitt 1985, Goldman 1993), but most oceanic phytoplankters only contribute to flux after they have been grazed. Consumption of primary production by bacteria and small protists results in the respiration of a large proportion of the fixed carbon in surface waters. Consumption of primary production by larger protists, such as some thecate dinoflagellates and sarcodines, or by metazoan grazers, has the potential to result in the export of particulate carbon, as cells, bodies or fecal pellets. Sedimentation of plankton with carbonate sketetal structures, such as planktonic foraminifera, also contributes to the export of inorganic carbon as calcium carbonate (reviewed in Bé 1977, Caron & Swanberg 1990, Legendre & Le Fèvre 1995, Michaels et al. 1995).

In tropical, oceanic waters, such as the equatorial Pacific, the role of the microbial food web in controlling the export of biogenic carbon (organic and inorganic) from surface waters may be particularly important. In these waters, most of the chlorophyll is accounted for by <5 µm cells (Murray et al. 1994) which are too small to have appreciable sinking velocities. These cells are also too small to be efficiently utilized by most, but not all, metazoan grazers (reviewed in Sherr et al. 1986).

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In tropical and subtropical oceans, planktonic sarcodines are important generalists, preying on bacteria, other protists and metazoa as well as often being sites of enhanced primary production due to algal endosymbionts (reviewed in Caron & Swanberg 1990, Anderson 1993). Surface dwelling sarcodines are often particularly important in biogenic flux because when they lose buoyancy, due to death or as part of their life cycle, they can sink rapidly (Takahashi & Bé 1984). Many surface water dwelling planktonic sarcodines drop their spines and become more mineralized at the onset of gametogenesis or cyst formation, which causes them to sink (reviewed in Caron & Swanberg 1990, Antia et al. 1993). In oceanic waters, the planktonic sarcodines with mineralized skeletal structures are thought to play particularly important roles in the export of organic and inorganic carbon to the deep ocean and in strontium and silicate cycling (Michaels 1991, Boltovskoy et al. 1993, Michaels et al. 1995). Biogenic oozes, containing foraminiferal and radiolarian remains, dominate the equatorial Pacific deep sea sediments (reviewed in Steineck & Casey 1990, Zeitzschel 1990).

The >20 µm protozooplankton are an important part of the plankton in tropical oceans and often account for a significant proportion of the photosynthesis in the >20 and >200 µm size classes, as well as being important grazers on phytoplankton and predators on other protozooplankton and copepods (reviewed in Michaels & Silver 1988, Caron & Swanberg 1990, Swanberg & Caron 1991). In oceanic environments, they can be an important component of organic carbon and biogenic carbonate flux (Michaels 1991, Legendre & Le Fèvre 1995, Michaels et al. 1995). Most investigations of the larger protozooplankton in tropical waters have been largely taxonomic and have been limited to a particular taxon or have not distinguished between strict heterotrophs and mixotrophs (Bé 1977, Sorokin 1981, Boltovskoy & Jankilevich 1985).

Herein we report the abundance, biomass and trophic status of the major categories of micro- and mesoprotozooplankton in surface waters (0 to 120 m) during the March-April (23 March to 10 April 1992) and October (1 to 10 October 1992) United States Joint Global Ocean Flux Study (USJGOFS) time series cruises at 140° W on the equator (for an overview of the USJGOFS equatorial Pacific study, refer to Murray et al. 1992, 1994).

METHODS

The >20 µm protozooplankton includes over an order of magnitude range in size and average numerical abundance, and thus several methods were used for sampling. Greater than 20 µm ciliates and heterotrophic dinoflagellates and solitary skeleton bearing sarcodines in the classes Granuloreticulosea (foraminifera), Polycystinea (polycystine radiolaria) and Acantharea (acantharia) were included. Some of the photosynthetic dinoflagellates can consume other cells (Bockstahler & Coats 1993), but we could not distinguish the phagocytic plastidic dinoflagellates (mixotrophs) from strictly autotrophic dinoflagellates, and thus did not include them. Colonial radiolaria, although protozooplankton, are part of the macroplankton and were not included.

In the equatorial Pacific, a diverse upper ocean microbial community is found down to about 120 m. During the time series cruises, most microphytoplankton and protozooplankton biomass occurred above 90 m, with dramatic decreases in abundance between 90 and 120 m (Iriate & Fryxell 1995, Verity et al. in press). For these reasons, we sampled to 90 or 120 m.

The first method we used was typical 'bottle' sampling for microplankton. For each profile, 30 l Niskin bottles on a CTD rosette were used to collect samples at 15, 30, 45, 60, 75, 90, 100 and 120 m depths. During the March-April cruise, 5 profiles (March 23, 28, 31, April 4, 9) were collected and during the October cruise, 4 profiles (October 2, 8, 14, 20) were collected. One liter samples were preserved with 2% (final concentration) formaldehyde buffered with hexamethylamine for examination with transmitted light and epifluorescence microscopy (Stoecker et al. 1994b). A second set of 1 l samples was preserved with 10% (final concentration) acid Lugol's solution (Stoecker et al. 1994a, b). The formaldehyde fixed samples were stored at 4°C in the dark and returned to the laboratory for processing. The acid Lugol's solution fixed samples were stored in a box on deck or in the hold of the ship and then, after several months, shipped to our home institution.

In the laboratory, the fixed samples were concentrated by sedimentation to approximately 300 ml and then 100 ml subsamples were settled in Utermöhl chambers and examined with an inverted microscope (sedimentation or SED samples). Dense, flocculent material had formed in the acid Lugol's fixed samples, possibly due to high storage temperatures, and thus these samples were discarded.

The formaldehyde fixed samples were used to enumerate the ≥20 µm aplastidic, thecate and non-thecate dinoflagellates, plastidic and non-plastidic ciliates (oligotrichs, tintinnids and other taxa), and plastidic and non-plastidic foraminifera and radiolaria (Lessard & Swift 1986, Laval-Peuto & Rassoulzadegan 1988). Protozooplankton cells with plastids were classified as mixotrophic.

Within each broad category, cells were enumerated by species or morphotype and, whenever possible, 20 or more cells of each type were sized using a calibrated ocular micrometer. Appropriate geometric approximations were used to calculate average cell volume or lorica volume for each morphotype of ciliate or dinoflagellate (Edler 1979). The dimensions of sarcodine spicules and capsules were measured for calculation of biomass using the formulae of Michaels et al. (1995). Appropriate volume:carbon factors for nonloricate ciliates (Putt & Stoecker 1989), tintinnids (Verity & Langdon 1984), and heterotrophic dinoflagellates (Lessard 1991) were used. Placement of cells in size classes (20–64, >64–200 and >200 µm) were based on equivalent spherical diameter, rather than on length.

The other methods we used to sample were designed to capture the larger, rarer sarcodines. The first of these was use of a 1 m opening and closing net system (MOCNESS) fitted with 26 µm mesh nets (NET samples). In March-April, we collected 4 profiles (March 25, 29, April 4, 6) with tows at 0–20, 20–40, 40–60, 60–90, and 90–120 m depth intervals. Volume filtered per net ranged from 13 to 102 m^3. A 5% split of each net sample was preserved in 2% buffered formaldehyde with added $SrCl_2$ (final concentration, 0.16 mg ml^{-1}) to prevent dissolution of acantharian spicules (Beers & Stewart 1970). In October, 3 profiles (October 9, 15, 21) were collected with the MOCNESS system. Sampling parameters were similar to the first cruise, except that the depth intervals were 0–20, 20–40, 40–60, 60–80, 80–100, and 100–120 m and the volume filtered per net ranged from 21 to 126 m^3.

On the October cruise, sarcodine samples were also collected using a third method. A 30 l Niskin bottle (measured volume obtained, ~26 l) was used to collect 5 profiles (October 2, 8, 9, 14, 21) with samples from 0, 30, 60 and 90 m. The bottom (not the spigot) of the bottle was opened and the contents concentrated on a 30 µm Nitex mesh. The collected material was washed with filtered seawater into a glass jar and preserved with 2% buffered formaldehyde (30 l samples). $SrCl_2$ was added to prevent the dissolution of acantharian spicules. Both the MOCNESS and 30 l concentrated samples were stored at 4°C in the dark. In the laboratory, subsamples were examined in Utermöhl chambers with a combination of transmitted light and epifluorescence microscopy.

RESULTS

Comparison of methods for sarcodines

For both cruises, the average abundance of radiolaria estimated from whole water samples concentrated by sedimentation (SED) was higher than that estimated from samples collected with the MOCNESS system (NET) (Figs. 1 & 2). On the second cruise, when samples were collected with bottles and concentrated on a Nitex mesh (30 l), the estimate of average radiolarian abundance based on the SED samples was higher than that based on the 30 l samples (Fig. 2). Estimates of radiolarian average biomass were also higher based on the settled samples (SED) than on the MOCNESS (NET) or Nitex mesh concentrated samples (30 l), but these differences were not statistically significant (Figs. 1 & 2). For the foraminifera, there were no statistically significant differences among the abundance or biomass estimates based on the different techniques (Figs. 1 & 2), although biomass estimates based on the 30 l concentrate appeared to be lower than estimates of biomass based on the SED or NET samples (Fig. 2). Estimates of acantharian abundance and biomass appeared to be much higher based on the 30 l concentrated samples than on the NET samples, but these differences were not quite statistically significant due to the variability among profiles (Fig. 2).

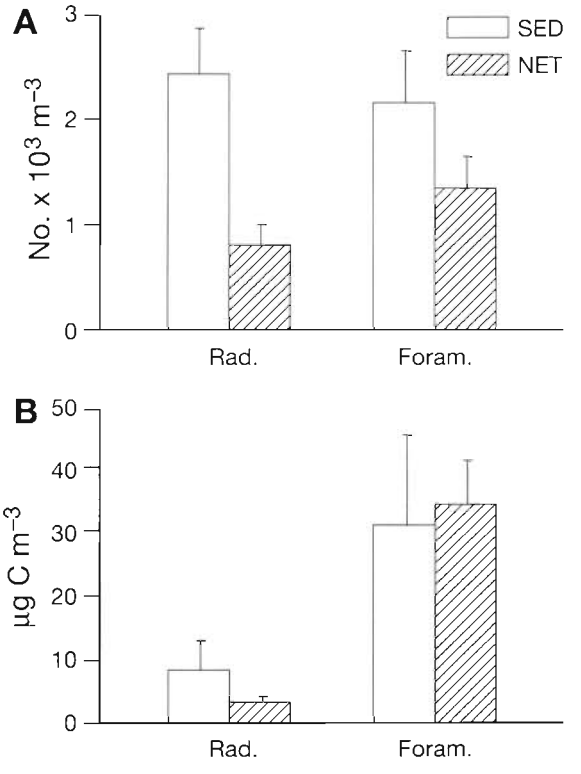

Fig. 1. Comparison of (A) abundance and (B) biomass of radiolaria (Rad.) and foraminifera (Foram.) determined from water samples concentrated by sedimentation (SED) and from MOCNESS collection (NET) on the March-April 1992 cruise. Means for upper 120 m, +SE. Significance of differences between methods tested by 1-way ANOVA for abundance and biomass of each taxon: Rad.: abundance, $p = 0.0086$; biomass, $p = 0.2492$; Foram.: abundance, $p = 0.1623$; biomass, $p = 0.8373$

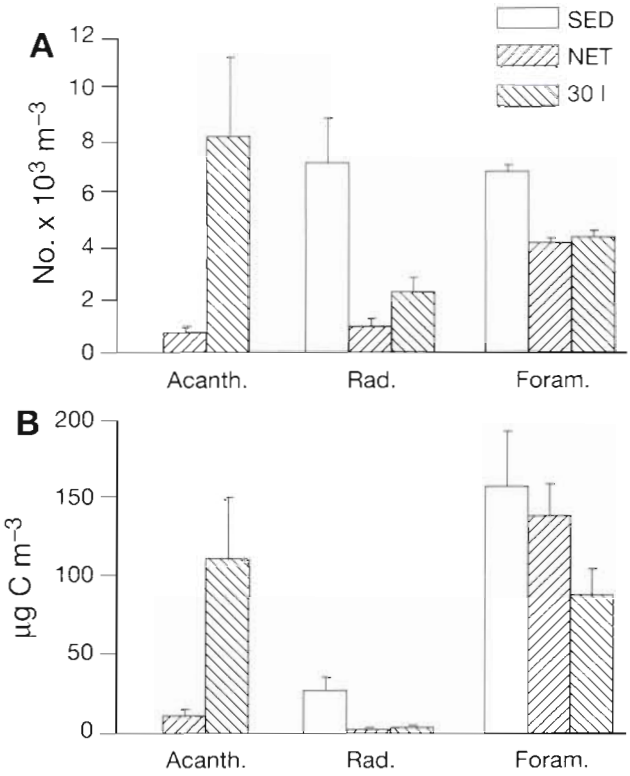

Fig. 2. Comparison of (A) average abundance and (B) biomass of acantharia (Acanth.), radiolaria (Rad.) and foraminifera (Foram.) determined from water samples concentrated by sedimentation (SED), by concentration above a mesh (30 l) and from MOCNESS collection (NET) on the October 1992 cruise. No data on acantharia for SED. Means for upper 90 m, +SE. Significance of differences between methods tested by 1-way ANOVA for abundance and biomass of each taxon: Acanth.: abundance, $p = 0.0504$; biomass, $p = 0.0514$; Rad.: abundance, $p = 0.0315$; biomass, $p = 0.0523$; Foram.: abundance, $p = 0.2294$; biomass, $p = 0.6680$

Contribution by size class

Data from the SED samples were used to estimate the average biomass contribution of various taxa of microzooplankton to the 20–64, >64–200 and >200 µm size classes (Figs. 3 & 4). For the October cruise, data on acantharia from the 30 l samples are included as well (30 l bottle samples are not available for the March-April cruise). On both cruises, ciliates clearly dominated the protistan microzooplankton biomass in the 20 to 64 µm size range. Ciliates, heterotrophic dinoflagellates and sarcodines all contributed to the microzooplankton biomass in the >64 to 200 µm size range, with cells in this size range being more abundant during October than during March-April. During the March-April time series, there was very little protistan microzooplankton biomass in the >200 µm range, but during October, foraminifera and acantharia each contributed about 25 µg C m^{-3} in the >200 µm size range (Figs. 3 & 4).

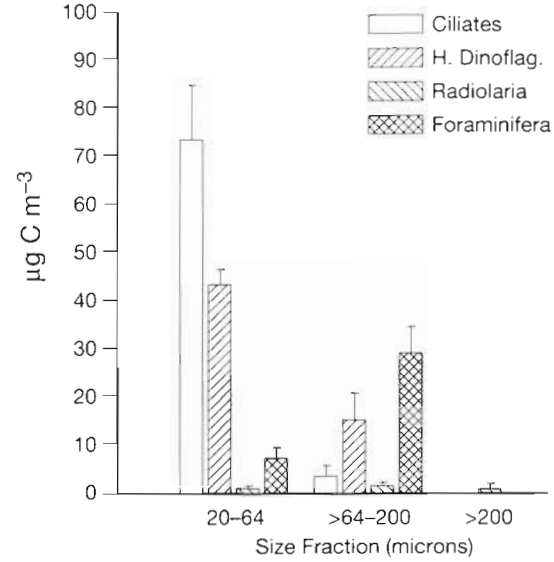

Fig. 3. Distribution of biomass of protistan microzooplankton among taxa and size classes, March-April time series, 0 to 120 m, based on SED samples. Means +SE

Incidence of mixotrophy

During the March-April time series, about 10% of the ciliates contained plastids (Fig. 5). In contrast, during October, mixotrophic ciliates contributed <10% to ciliate abundance (Fig. 5). On both cruises, all of the mixotrophic, plastidic ciliates were oligotrichs. Mixotrophic ciliates were only contributors to biomass in the 20 to 64 µm size class (Table 1).

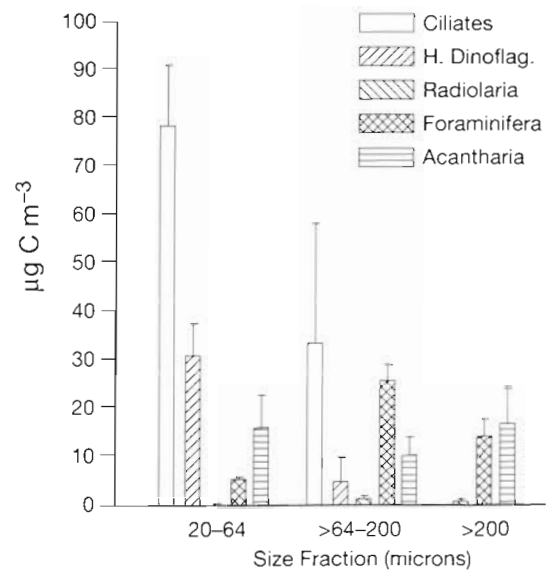

Fig. 4. Distribution of biomass of protistan microzooplankton among taxa and size classes, October time series, 0 to 90 m. SED samples except for data on acantharia which are from 30 l samples. Means +SE

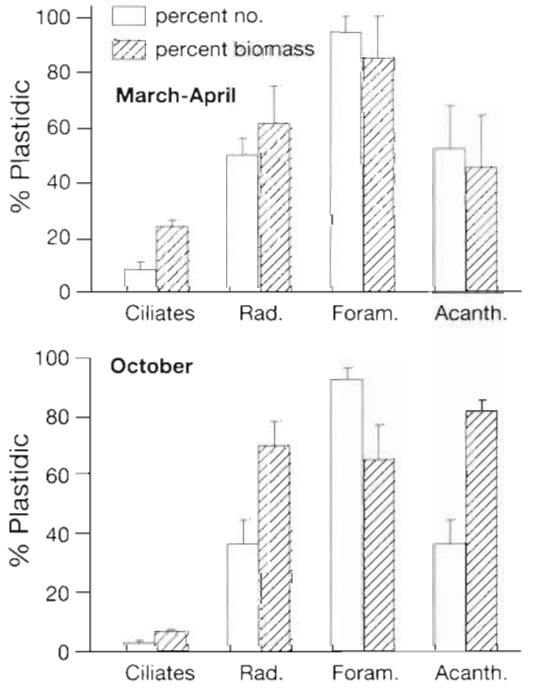

Fig. 5. Percent abundance and biomass of microprotozooplankton with plastids. Integrated data, 0 to 120 m. Means + SE

Among the solitary skeleton bearing radiolaria, 30 to 50% had algal endosymbionts. Plastidic specimens contributed over 50% of the average radiolarian biomass during both cruises (Fig. 5). Mixotrophic radiolaria contributed primarily to the >64 to 200 and >200 µm size ranges (Table 1).

During both cruises, over 80% of the foraminifera were plastidic (Fig. 5). The contribution of plastidic specimens to biomass was lower than their contribution to abundance (Fig. 5). The biomass contribution of plastidic foraminifera was primarily to the >64 to 200 µm size range (Table 1).

About 40% of the acantharia had plastids (Fig. 5). During the March-April time series, about 40% of the acantharian biomass was accounted for by plastidic specimens, but during October about 80% of the acantharian biomass was plastidic (Fig. 5). Plastidic acantharia made an important contribution to biomass in all size classes, but they were most important in the >200 µm size class (Table 1).

Table 1. Calculated contribution of mixotrophs to protistan biomass by size class during the October 1992 time series

Taxon	µg C m^{-3}, average 0 to 90 m		
	20–64 µm	>64–200 µm	>200 µm
Plastidic oligotrichs	14.9	0.0	0.0
Plastidic radiolaria	0.3	1.6	0.9
Plastidic foraminifera	15.1	35.0	0.0
Plastidic acantharia	31.4	20.0	45.8
Sum plastidic protozoa	61.7	56.6	46.7
Sum non-plastidic protozoa	232.8	121.26	36.8
Mixotrophic[a]	27%	47%	56%

[a]Does not include the plastidic dinoflagellates that are potentially mixotrophic

In Table 1, the total contribution of mixotrophs to the >20 µm protozoan biomass is underestimated because mixotrophic, plastidic dinoflagellates are not included. Nevertheless, mixotrophs contributed an estimated 27, 47 and 56%, respectively, of the biomass in the 20–64, >64–200, and >200 µm size range of protozooplankton. Plastidic sarcodines contributed the most to the mixotrophic biomass in all 3 size fractions.

Comparison of March-April and October 1992 time series

The abundance and biomass of protozooplankton taxa and trophic types during the 2 time series are compared based on water samples concentrated by sedimentation (SED) in Table 2 and on MOCNESS samples (NET) in Table 3. Abundance and biomass of >20 µm thecate heterotrophic dinoflagellates were generally higher during October than during March-April, but the differences between cruises were not statistically significant (Tables 2 & 3). Non-thecate dinoflagellates >20 µm in size were only enumerated in the SED samples, and there appeared to be no difference between cruises (Table 2).

Ciliates were only enumerated in the SED samples. Non-plastidic oligotrichs dominated both ciliate numbers and biomass during both cruises (Table 2). Both abundance and biomass of non-plastidic oligotrichs were generally higher in October than during March-April, but the differences were not statistically significant (Table 2). In contrast, the numbers and biomass of plastidic ciliates appeared to be higher in March-April than in October (Table 2). The contribution of plastidic ciliates was variable, but during March-April they contributed about 30% of oligotrich biomass. In contrast, during October, plastidic ciliates only contributed about 7% of oligotrich biomass. Tintinnids were a minor component of the ciliate assemblage during both cruises, but during October average tintinnid size was greater than during the earlier time series and tintinnid biomass was significantly higher than in March-April (Table 2). Other ciliate taxa (i.e. not members of subclass Choreotrichia) appeared to be about twice as abundant during October than during March-April, but the difference between cruises was not statistically significant (Table 2).

No significant differences between cruises in radiolarian abundance and biomass were detected based on the SED or NET samples (Tables 2 & 3). Based on SED

Table 2. Comparison of average micro- and mesoprotozooplanktonic abundance and biomass (0 to 120 m) during March-April and October 1992 time series cruises based on water samples concentrated by sedimentation. Mean ± SE. P-values are for differences between cruises tested by 1-way ANOVA. n = 5 for March-April and n = 4 for October

Taxon	No. × 10^3 m^{-3}		p-value	µg C m^{-3}		p-value
	Mar–Apr	Oct		Mar–Apr	Oct	
Heterotrophic dinoflagellates						
Thecate	6.72 ± 1.06	10.51 ± 1.04	0.53	30.32 ± 6.43	49.90 ± 9.53	0.54
Non-thecate	9.89 ± 2.02	8.73 ± 1.19	0.37	28.88 ± 2.52	35.30 ± 6.30	0.95
Ciliates						
Plastidic oligotrichs	4.53 ± 1.65	1.77 ± 0.72	0.15	22.05 ± 9.74	11.19 ± 5.04	0.31
Non-plastidic oligotrichs	39.48 ± 4.21	67.67 ± 8.99	0.40	51.47 ± 4.89	146.23 ± 26.76	0.12
Tintinnids	4.02 ± 1.26	3.22 ± 0.75	0.42	1.91 ± 0.62	12.80 ± 2.36	0.04
Other ciliates	1.26 ± 0.99	0.68 ± 0.36	0.56	9.90 ± 8.05	22.33 ± 15.85	0.69
Radiolaria						
Plastidic	1.20 ± 0.20	3.03 ± 0.85	0.26	6.58 ± 4.54	13.54 ± 5.81	0.60
Non-plastidic	1.23 ± 0.25	2.64 ± 0.90	0.40	1.66 ± 0.62	8.23 ± 6.05	0.41
Foraminifera						
Plastidic	2.07 ± 0.54	5.00 ± 0.20	0.14	28.35 ± 15.01	93.51 ± 36.59	0.29
Non-plastidic	0.07 ± 0.06	0.35 ± 0.11	0.16	2.78 ± 2.49	30.06 ± 16.83	0.23

and NET samples, the average abundance and biomass of foraminifera apppeared to be 2- to 3-fold higher during the October than during the March-April time series, but the differences between cruises were not statistically significant (Tables 2 & 3). Based on the NET samples, the abundance and biomass of acantharia on the 2 cruises were about the same (Table 3).

DISCUSSION

Sampling problems

For radiolaria and foraminifera, standard microplankton sampling methods, involving fixation of whole water samples and concentration of fixed water samples by sedimentation, resulted in the highest estimates of numerical abundance and biomass. Some sarcodines, especially the radiolaria, are sticky and may adhere to sampling devices and meshes when samples are manipulated or concentrated. Losses of radiolaria with nets were more severe than of foraminifera. Precise estimates of sarcodines are difficult to obtain using the sedimentation technique because relatively small (generally <1 l) samples are enumerated and sarcodines usually occur at low densities per liter. Calculation of averages based on several individual samples (our integrated averages were based on data from 8 samples in each profile) or fixation and sedimentation of larger volume samples should improve precision.

Our estimates of acantharia were based on concentrated (either in a net or on a mesh after collection with bottles) and then fixed samples. As discussed in Michaels (1988), net tows severely underestimate acantharian abundance compared to bottle samples that are concentrated on a mesh. In general, fixation

Table 3. Comparison of average micro- and mesoprotozooplankton abundance and biomass (0 to 120 m) during March-April and October 1992 time series cruises based on net samples. Mean ± SE. P-values are for differences between cruises tested by 1-way ANOVA. n = 4 for March-April and n = 3 for October

Taxon	No. × 10^3 m^{-3}		p-value	µg C m^{-3}		p-value
	Mar–Apr	Oct		Mar–Apr	Oct	
Thecate heterotrophic dinoflagellates	1.16 ± 0.22	2.05 ± 0.43	0.60	9.52 ± 1.15	37.20 ± 7.18	0.15
Radiolaria						
Plastidic	0.44 ± 0.17	0.29 ± 0.07	0.35	2.32 ± 0.49	2.08 ± 0.68	0.47
Non-plastidic	0.31 ± 0.08	0.55 ± 0.14	0.65	0.96 ± 0.54	0.17 ± 0.03	0.23
Foraminifera						
Plastidic	1.23 ± 0.35	3.61 ± 0.33	0.20	26.75 ± 7.79	50.15 ± 8.82	0.55
Non-plastidic	0.10 ± 0.03	0.24 ± 0.03	0.30	7.88 ± 2.00	69.18 ± 15.55	0.09
Acantharia						
Plastidic	0.19 ± 0.04	0.27 ± 0.01	0.91	3.25 ± 0.51	5.22 ± 1.70	0.76
Non-plastidic	0.48 ± 0.20	0.36 ± 0.08	0.92	5.52 ± 2.28	4.22 ± 2.26	0.71

and then concentration of whole water samples by sedimentation resulted in higher counts of most microplankters than concentration with nets or meshes prior to fixation (Figs. 1 & 2). We would probably have obtained higher abundance estimates for acantharia if we had added $SrCl_2$ to our microplankton samples and thus had been able to enumerate this taxon in the samples that had been fixed and then concentrated by sedimentation.

None of the sampling methods we employed can give accurate measurements of the colonial radiolaria or other >2 mm sarcodines that can make an important contribution to plankton biomass (Caron & Swanberg 1990). In order to obtain accurate estimates of abundance for the full size spectrum of sarcodines in oceanic waters it might be necessary to complement water sampling and microscopy for the smaller, more abundant types with video observation and enumeration of the larger, rarer forms (Michaels et al. 1995).

Unfortunately, we were not able to enumerate ciliates in the microplankton samples fixed with 10% acid Lugol's solution because of sample preservation problems. The estimates of ciliate abundance were based on enumeration of samples preserved in 2% buffered formaldehyde. Laboratory and field experiments have demonstrated that fixation with 2% formaldehyde results in underestimation of oligotrich abundance by 50 to 65% (Stoecker et al. 1994a). Thus, oligotrich abundance and biomass is probably underestimated by this amount in the data presented herein.

Mixotrophy

Mixotrophy was common in all the major taxa of micro- and mesoprotozooplankton. Among the oligotrichous ciliates, on average ≤10% of the cells were plastidic. This frequency is low compared to neritic and shelf/slope waters and oligotrophic subtropical gyres (reviewed in Stoecker 1991). We did not enumerate the plastidic dinoflagellates, but Iriate & Fryxell (1995) reported that *Ceratium*, *Dinophysis*, and *Gymnodinium* spp. were common at times, and at least some members of these genera are mixotrophic (Bockstahler & Coats 1993, Li et al. 1996). Among the sarcodines, which dominated the larger size range of protistan zooplankton, the presence of algal endosymbionts was very common. Plastidic sarcodines are mixotrophic, deriving energy both from ingestion of prey and from photosynthesis by their endosymbionts (reviewed in Caron et al. 1995). Chlorophyll contents and rates of photosynthesis in sarcodine symbioses are usually as high or higher than in free living algae, probably because the endosymbionts are not nutrient limited (reviewed in Caron & Swanberg 1990, Caron et al. 1995).

For radiolaria and acantharia during the October time series, the proportion of abundance contributed by plastidic specimens was lower than the proportion of biomass (Fig. 5). Larger specimens were more likely to be plastidic than smaller specimens. In contrast, among the foraminifera, plastidic specimens contributed more to numbers than to biomass. The largest foraminifera usually lacked endosymbionts. Foraminifera with algal endosymbionts often digest their symbionts at the onset of gametogenesis (reviewed in Caron & Swanberg 1990) and thus the larger specimens would tend to be aplastidic. Relatively large, spineless, aplastidic foraminifera were more common during October than during the March-April cruise. Lunar periodicities occur in the maturation of some foraminifera (Caron & Swanberg 1990), and a full moon occurred during the middle of the October time series but not during the earlier time series. It is possible that lunar periodicity affected the degree of mixotrophy observed among the foraminifera.

Based on the data presented in Tables 2 & 3, the estimated contribution of mixotrophic sarcodines to the photosynthetic biomass was approximately 5×10^3 µg C m^{-2} during March-April and 13×10^3 µg C m^{-2} during October; this is considerably lower than the range reported for the microplanktonic diatoms, $12–114 \times 10^3$ and $90–298 \times 10^3$ µg C m^{-2}, respectively (Iriate & Fryxell 1995). Although the standing stock of sarcodines is usually lower than that of microdiatoms, primary production within sarcodines probably makes a disproportionately higher contribution to photosynthesis in the largest size classes.

Comparison of El Niño and non-El Niño conditions

Although seasonal variability is very low or nonexistent in the equatorial Pacific, interannual variability is high due to El Niño Southern Oscillation (ENSO) events (Murray et al. 1992, 1994, McPhaden 1993). Both time series cruises were during the 1991–1993 ENSO event, but the March-April 1992 cruise was during intense El Niño conditions whereas the October 1992 cruise was during a pronounced relaxation of El Niño conditions (McPhaden 1993). During October, surface water temperatures were lower (average 25.1 vs 28.6°C) and integrated primary production was about 40% higher than during the March-April cruise (Murray et al. 1994). A greater proportion of the chlorophyll *a* (11.5 vs 2.6%) was in the >14 µm size fraction and microplanktonic diatoms were generally more abundant during October than during the first time series (Murray et al. 1994, Iriate & Fryxell 1995). However, differences between the 2 time series in integrated chlorophyll values, hetero-

trophic nanoplankton abundance and integrated mesozooplankton biomass were slight (Murray et al. 1994, Roman et al. 1995).

Likewise, we found slight differences in microzooplankton abundance and biomass between the March-April (El Niño) and October (non-El Niño conditions) cruises. There appeared to be considerable variability among microzooplankton taxa in their response to the relaxation in El Niño conditions that began in August.

Abundance and biomass of the non-thecate heterotrophic dinoflagellates, radiolaria and acantharia showed little or no difference between cruises (Tables 2 & 3). The only taxa that were consistently more abundant or higher in biomass during the relaxation in El Niño than in March-April were the planktonic ciliates and the foraminifera. Among the planktonic ciliates, the increase was almost entirely due to non-plastidic oligotrichs (mostly *Strombidium* spp.) and tintinnids. Oligotrichs prey on nanoplankton (Rassoulzadegan et al. 1988) which, judging from chlorophyll size fractions and biomass of heterotrophic nanoplankton (Murray et al. 1994, Verity et al. in press) were more abundant during October than during March-April. Heterotrophic nanoflagellate populations were about 10% greater during the October than during the March-April time series (Verity et al. in press) compared to the approximately 2-fold increase in ciliate biomass (Table 2). Thus, it seems likely that oligotrichous ciliates and tintinnids were important in the tight coupling between growth and grazing of nanophytoplankton that was observed in dilution experiments done during both time series (Verity et al. in press).

The only other major taxon that showed a consistent difference between cruises was the foraminifera, largely due to increased biomass of large, rare, non-plastidic specimens during the October time series. This is most evident from the NET data. The differences between time series could represent a response to increased surface primary production (Boltovskoy et al. 1993) but could also be due to lunar periodicities in reproduction (Michaels et al. 1995).

Contribution of protozooplankton to vertical flux

Particulate organic carbon (POC) flux from the mixed layer in the equatorial Pacific appears to be surprisingly low (Murray et al. 1994). Bacon et al. (in press) estimated POC flux at 120 m to have averaged only about 2% of the primary production during both the March-April and the October time series. Although primary production in October was about double that in March-April (Barber et al. in press), there was only a slight increase in export flux of carbon as measured by ^{234}Th measurements (Bacon et al. in press). However, sediment trap data from survey cruises indicate that particulate carbon flux was 3- to 4-fold higher during February than during August 1992 in the vicinity of the equator at 140° W (Murray et al. 1994). The results of the JGOFS in the equatorial Pacific indicate that the major proportion of the new production must be removed in the form of dissolved organic matter by advection from surface waters of the region (Bacon et al. in press).

During both cruises, grazing by the <200 µm fraction consumed most of the daily primary production (Landry et al. 1995, Verity et al. in press). The tight coupling between primary production and consumption by microzooplankton may largely account for the low rates of POC vertical flux from surface waters. The increases in oligotrichous ciliate populations with increases in primary productivity should dampen changes in vertical flux of POC associated with new production.

Among the planktonic protozoa that were abundant in the equatorial Pacific during our study, the sarcodines are probably the most important in terms of vertical flux. The reasons include the following: (1) the average sarcodine is usually larger (64 to 200 µm equivalent spherical diameter, ESD) than the average heterotrophic flagellate or ciliate and thus can sink faster (Takahashi & Bé 1984) and carries relatively more carbon; (2) the life cycle of planktonic sarcodines often involves sinking of mature specimens or cysts due to increases in specific gravity (due to increased mineralization) and decreased drag (loss of spines), thus undegraded (live) carbon can be lost from the mixed layer (Antia et al. 1993, Michaels et al. 1995); (3) foraminifera transport both organic carbon and biogenic carbonate; and (4) a large proportion of the planktonic sarcodines in surface waters are mixotrophic during most of the vegetative part of their life cycle (Caron et al. 1995), and photosynthate derived from endosymbionts is more likely to contribute to vertical flux than that of the average <5 µm phytoplankter (Chavez et al. 1990).

Sarcodines are usually a conspicuous component of sediment trap material from the open ocean (Honjo et al. 1982, Pisias et al. 1986, Deuser & Ross 1989, Silver & Gowing 1991, Boltovskoy et al. 1993). At the JGOFS site near Bermuda, Michaels et al. (1995) reported that on average, 15.5% of the total carbon flux at 150 to 160 m is due to sarcodines, and that when large foraminifera and radiolaria are abundant, episodes occur in which sarcodines account for up to 43% of the total carbon flux. At the VERTEX seasonal station in the North Pacific Central Gyre, Michaels (1991) found that acantharia alone could represent up to 9% of the total sinking organic carbon flux at 150 m. The deep sea

sediments in the equatorial Pacific are largely foraminiferal and radiolarian oozes, indicating the flux of these organisms to the deep sea over geologic time (reviewed in Steineck & Casey 1990, Zeitzschel 1990). However, sarcodine flux is often not immediately linked to surface primary productivity, probably because the skeleton bearing sarcodines have relatively long life spans (ca 1 mo) (Boltovskoy et al. 1993).

Acknowledgements. We thank our EqPac colleagues for help at sea and for sharing their data, in particular Drs M. Roman and G. Fryxell and Ms A. Gauzens for splits of the MOCNESS samples, Ms H. Quinby for her technical suggestions, and Ms S. Kadar for logistics. We thank the captain and crew of the RV 'Thomas G. Thompson' We thank Dr M. E. Sieracki for coordination of our project and for his comments on the manuscript. Drs D. A. Caron and N. R. Swanberg were very generous in giving us needed advice on sarcodines, providing preprints of their manuscripts and lending us difficult-to-find references. This research was supported by NSF grant OCE-90-22318. This is UMES CEES contribution number 2739 and USGOFS contribution number 226.

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Responsible Subject Editor: R. W. Sanders, Philadelphia, Pennsylvania, USA

Manuscript first received: September 26, 1995
Revised version accepted: April 16, 1996