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Seasonal variations in the dynamics of microbial plankton communities: first estimates from experiments in the Gulf of Trieste, Northern Adriatic Sea

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ABSTRACT: Heterotrophic plankton grazing was studied in the Gulf of Trieste (Northern Adriatic Sea) from November 1998 to August 1999 using the dilution method. Four sets of experiments were carried out quarterly in order to assess the impact on communities of both phototrophic and heterotrophic prey. Four different trophic models were observed: during the autumn microzooplankton fed on small dinoflagellates, and phototrophic (PNAN) and heterotrophic nanoflagellates (HNAN), but not on the abundant bulk of diatoms. The entire initial HNAN standing stock was removed; we therefore did not observe any mortality of bacteria, whose biomass was the highest in the whole period. In late winter, the intense diatom bloom of *Lauderia annulata* remained almost untouched as the microzooplankton fed only on a less abundant small sized diatom (*Chaetoceros*). Microzooplankton also fed on HNAN, halving the mortality of bacteria induced by HNAN grazing only. In late spring, microzooplankton grazed effectively on a large array of prey (small diatoms, PNAN and HNAN). Reduction of bacterial mortality, exerted by microzooplankton through grazing on HNAN, was less evident, possibly due to direct microzooplankton grazing on bacteria. During the summer, we observed an intense grazing on bacteria by microzooplankton, which shifted from the usual nano-sized prey organisms, due to their extreme paucity, to bacteria. In conclusion, microzooplankton grazing was highly selective and variable due to the prey composition and to the predator community structure, which were investigated at the species to genus level. Microzooplankton was unable to control a bloom of large-sized diatoms, but showed a high level of control on most of the PNAN fractions. The result of this selection contributed significantly to the shaping of the phytoplankton community structure. Microzooplankton controlled HNAN biomass even more efficiently with relevant indirect effects on bacterial mortality.

KEY WORDS: Microzooplankton herbivory · Microzooplankton bacterivory · HNAN bacterivory · Microbial food web · Seasonal trophic models

INTRODUCTION

The Northern Adriatic and the Gulf of Trieste have been intensely investigated since the 19th century (e.g. Fonda Umani 1996). However, before this project, there were no studies on the grazing impact of either microzooplankton (20 to 200 µm protozoa of various taxa, and small metazoa larvae and nauplii) or heterotrophic nanoplankton (HNAN; 2 to 20 µm nanoflagellates and ciliates). The occurrence and distribution of microzooplankton and HNAN has been studied in the Gulf of Trieste (e.g. Fonda Umani et al. 1995); however, the mortality induced by grazing on phototrophic and heterotrophic plankton components has only been inferred by distribution analyses (e.g. Del Negro et al. 2001). Direct determination of the relative grazing rates of microzooplankton and HNAN, and quantification of specific prey mortality rates is critical for understanding the patterns of energy and material flows through the pelagic food web. Microzooplankton and

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HNAN are able to select food and display rapid responses to changes in food availability. Therefore, they play significant roles in structuring plankton communities (e.g. Paranjape 1990, Fahnenstiel et al. 1995, Froneman & Perissinotto 1996, Verity et al. 1996, James & Hall 1998, Lessard & Murrell 1998). Studies in other marine environments have shown that through their grazing impact, microzooplankton and HNAN can control phytoplankton production (e.g. Gifford 1988, Verity et al. 1993, Burkill et al. 1995, Cotano et al. 1998) and dynamics (e.g. Landry et al. 1993, Strom & Strom 1996, Latasa et al. 1997, Ruiz et al. 1998, Stelfox-Widdicombe et al. 2000) as well as play a significant role in nutrient regeneration (Goldman et al. 1987).

Our knowledge of protozoan grazing in controlling energy fluxes from producers to higher trophic levels has steadily increased over the last 2 decades, leading to a new perception of the marine food webs that has dramatically changed from the classic grazing food chain to a more complex multivorous food web (Pomeroy 1974, Azam et al. 1983, Rassoulzadegan 1993, Legendre & Rassoulzadegan 1995), where the microbial loop plays a pivotal role. In most of the oceanic environments, major fluxes of organic matter move via dissolved organic matter to bacteria and the microbial loop. A significant part of this energy can be channelled to higher trophic levels via protozoan grazing on bacteria.

Many studies have considered the sum of the grazing impact of microzooplankton and HNAN (e.g. Caron et al. 1991, Murrell & Hollibaugh 1998), but only few measured the relative effects of HNAN and microzooplankton in combined experiments (Kuuppo-Leinikki 1990, Reckermann & Veldhuis 1997) or the predator communities composition (e.g. Gifford 1988, Paranjape 1990, Verity et al. 1993, Froneman & Perissinotto 1996, Froneman et al. 1996, Strom & Strom 1996, James & Hall 1998, Dolan et al. 2000).

The main goals of our study were: (1) to quantify the carbon fluxes through the microbial community; (2) to identify any prey selectivity exerted by heterotrophic communities; and (3) to analyse the relationships between the microzooplankton and HNAN grazing impact on picoplankton prey. Therefore, we attempted to analyse both predator and prey communities at genus to species level, and determined both specific growth and grazing rates of the predators represented by microzooplankton and HNAN, as well as specific growth and mortality rates of the prey represented by bacteria, nanoplankton and microphytoplankton.

A number of approaches have been used to measure the grazing impact of both micro- and nano-predators on a wide range of prey, but most used the dilution method (Landry & Hasset 1982, reviewed by Dolan et al. 2000). In addition to the classical approach of monitoring chl *a* concentration following dilution, several researchers estimated taxon- or pigment-specific mortality rates using pigment analysis by HPLC (e.g. Strom & Welschmeyer 1991, McManus & Ederington-Cantrell 1992, Verity et al. 1993, Waterhouse & Welschmeyer 1995, Latasa et al. 1997, Schlüter 1998) and flow cytometry (e.g. Landry et al. 1995, Reckermann & Veldhuis 1997, Kuipers & Witte 1999, Stelfox-Widdicombe et al. 2000). We conducted microscopical counts of microzooplankton and phytoplankton (e.g. McManus 1995, Verity et al. 1996, Nejstgaard et al. 1997, Fonda Umani & Zanon 2000), and enumeration of phototrophic and heterotrophic nano- and picoplankton by epifluorescence microscopy (e.g. Campbell & Carpenter 1986, Verity et al. 1993, Ayukai 1996, James & Hall 1998).

The study was carried out under a 3 yr monitoring project (INTERREG 2, Italy and Slovenia) from July 1998 to June 2001 in the Gulf of Trieste (Northern Adriatic Sea), conducted on a biweekly to monthly basis. The sampling grid comprised 30 stations; in 3 of these, we analysed most of the biotic components in the water column (e.g. pico-, nano-, microphyto- and microzooplankton compositions). The dilution experiments were performed in the most coastal 'biological' station. Based on the monitoring results and the historical data set, we selected 4 distinct periods which correspond to 4 different environmental conditions: the moment of the first annual diatom bloom which appeared in February (e.g. Fonda Umani 1992), the shift from diatoms to nanoflagellates in the phytoplankton composition in May (e.g. Malej et al. 1995), the lowest yearly phytoplankton biomass in August (e.g. Mozetic et al. 1998) and the autumn diatom bloom (e.g. Malej et al. 1995).

In the 4 periods, we performed separate parallel dilution experiments with natural assemblages to assess the grazing impact of both microzooplankton and HNAN. Therefore, we were able to consider microzooplankton and HNAN separately as potential grazers, as well as microphytoplankton, and phototrophic (PNAN) and heterotrophic (HNAN) nanoplankton as potential prey. This also enabled us to distinguish between microzooplankton and HNAN grazing induced mortality of bacteria.

MATERIALS AND METHODS

Study area. The Gulf of Trieste is a semi-enclosed shallow system (maximum depth 25 m), in the northernmost eastern part of the Northern Adriatic Sea (Fig. 1). It stretches from the Isonzo (Soca) River, the most important source of fresh waters to Punta Salvore (Istrian peninsula). It is mostly controlled by pulsing

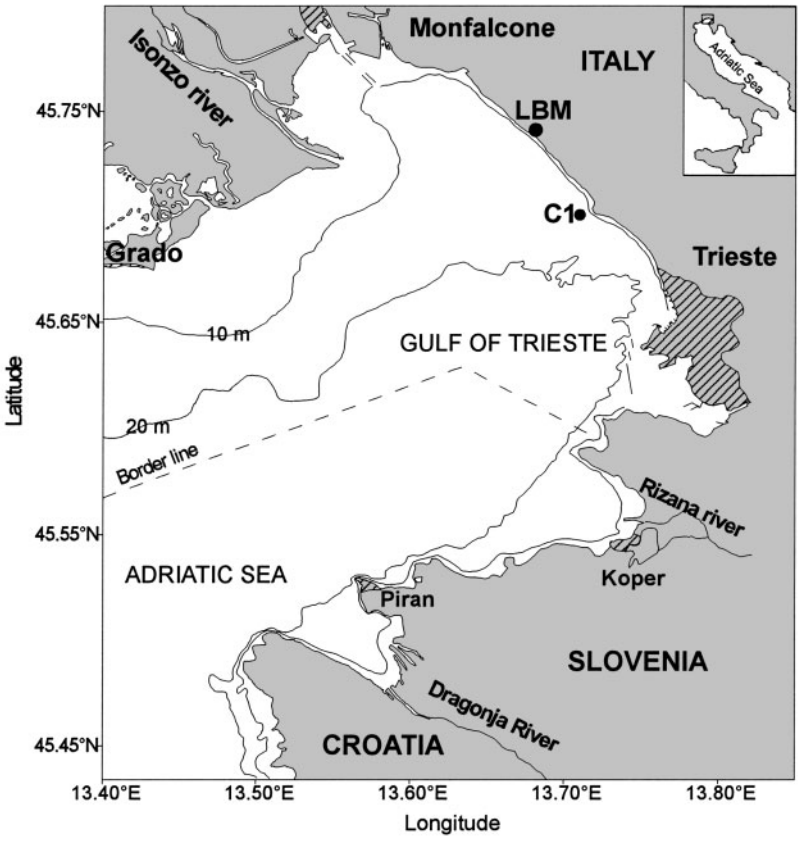

Fig. 1. The Gulf of Trieste (Northern Adriatic Sea). C1 = sampling site, LBM = land laboratory

external inputs (e.g. terrigenous supply, freshwater run-off, injections from the Mid-Adriatic Sea, etc.). The river inputs show a high temporal variability that affects salinity (ranging from 32.7 ± 0.48 to 37.6 ± 0.34, as average surface values; Fonda Umani 1991). The highest river discharges are generally observed in late spring and autumn; whereas the lowest discharge occurs during winter and summer. However, during these seasons a high inter-annual variability has been observed (Malej et al. 1995). The concentration of inorganic nutrients, mainly due to the river inputs, can be highly variable (e.g. at the surface between 2–3 and 84.2 µM for total disolved nitrogen; Burba et al. 1994). Allochthonous inputs of phosphates, which range between 0.05 and >3 µM at the surface, are mainly due to the sewage supply, since the discharge from the karstic system is very low. The temperature shows a regular annual pattern from winter minima as low as 6°C in February to higher than 25°C summer maxima (Cardin & Celio 1997). A 3-layer model can be used to represent the water mass circulation in the Gulf of Trieste. The bottom (below 10 m depth) and intermediate layers (from 5 to 10 m) flow almost permanently counterclockwise in the NE part of the Gulf. The surface layer (from 0 to 5 m), usually flows clockwise towards Trieste (Stravisi 1983). The primary production, which is around 50 g C m^{-2} yr^{-1} (Faganeli & Malej 1981, Fonda Umani 1991), is supported by >10 µm producers in late winter and by the <10 µm size class in the rest of the year (Malej et al. 1995).

The composition and annual dynamics of pico-, nano-, microphyto-, microzoo- and netzooplankton have already been described over the last 15 yr, as well as their carbon content (Cabrini et al. 1989, Turk et al. 1990, Fonda Umani 1991, 1992, Lipej & Malej 1992, Cataletto et al. 1993, 1995, Fonda Umani et al. 1995, Malej et al. 1995, Del Negro et al. 1996, Lipej 1996, Malej & Fonda Umani 1998, Mozetic et al. 1998, Salvi et al. 1998). Besides the year-to-year variations, the system is characterised by a typical cold temperate annual cycle with an intense late winter diatom bloom, a nutrient-depleted summer and a second short-lasting autumn bloom (Mozetic et al. 1998, Harding et al. 1999).

Sampling. Surface water (ca. 0.5 m depth) for the experiments was collected quarterly (November 1998, February, May and August 1999) using Niskin bottles in the Gulf of Trieste at a site (C1) 200 m offshore (13° 42.60′ E, 45° 42.06′ N) where the average depth was 17 m (Fig. 1). Pressure, temperature, conductivity and oxygen data were collected by means of an Idronaut Ocean Seven (Model 401) multiparametric probe, calibrated at 6 mo time intervals. Analyses of the dissolved nutrients were performed on seawater samples pre-filtered on glass fibre filters (Whatman GF/F) using an Alliance auto analyzer, according to Koroleff (1983). For chl *a*, triplicate water samples of 150 ml were filtered on board through Whatman GF/F filters, frozen in the dark and returned to the land laboratory. Filters were extracted at –20°C overnight in 90% acetone, centrifuged and the extract was measured on a Perkin Elmer Model LS50B fluorometer, according to Lorenzen & Jeffrey (1980).

To eliminate any possible mesozooplanktonic grazers, immediately after collection the samples were poured gently through a nylon sieve with a 200 µm mesh into 25 l polypropylene carboys. The screening effectiveness was checked microscopically after sampling. All the samples were kept in the dark, at sampling temperature, and transferred to the Laboratorio di Biologia Marina (LBM, Fig. 1) in less than 1 h.

Dilution protocols. To estimate the grazing activity, incubations were prepared according to the dilution method by Landry & Hasset (1982), e.g. Landry (1993).

Equipment used for the experiments was washed in diluted HCl and rinsed with deionised water. Only precleaned and rinsed silicone tubing was used. Incubation vessels, filter holders, etc., for the experiments on HNAN and picoplankton were sterilised by autoclaving. The predator- and prey-free water for the dilutions was prepared directly from the water samples within 1 h at the land laboratory.

Dilution experiments regarding microzooplankton grazing were carried out using water pre-filtered on hydrophilic fluorocopolymere 0.22 µm pore size Durapore filters. All parts of the filtration apparatus in contact with the water were made of Teflon. This filtration step eliminated all but some very small bacteria, mostly vibrios. To verify the possible presence and growth of bacteria in the filtered water, samples were analysed microscopically on 3 replicates at the beginning and at the end of the experiment. Counts remained below 10^{-5}% of the total bacterial titre.

Five serial dilutions (20, 40, 60, 80 and 100% whole water) were prepared in 20 l polypropylene carboys and incubated in triplicate 1.3 l polycarbonate bottles. To check for growth of microzooplankton, 3 additional bottles of whole water were added. While pouring, water was gently mixed to prevent clustering of planktonic organisms. In 2 bottles of each dilution, we added nitrate and phosphate supplements (5 µM $NaNO_3$ and 1 µM KH_2PO_4, respectively). The third replicates were incubated without any nutrient addition. All the bottles were incubated under simulated *in situ* conditions (free floating in a container flushed with running seawater) for 24 h.

Special care was taken to control the effect of the manipulations: for all parameters and all dilutions, 2 initial blanks were taken. The success of the initial dilutions was verified by regression analysis. Only parameters whose results were significant were considered for the final elaboration.

Triplicate microzoo-, microphyto-, nano- and picoplankton samples were taken after 24 h. In parallel treatments for the determination of HNAN grazing pressure on picoplankton, the standard serial dilution was modified to removing grazers >10 µm. This was accomplished by pre-screening through a 10 µm mesh nylon sieve. The removal of larger organisms was checked microscopically in the nanoplankton samples (see below). The bacteria-free water for these dilutions was obtained after a second filtration step using sterile in-line filters with 0.1 µm Durapore membranes (Millipore). This step eliminated even vibrios, as confirmed by the controls. The incubations were carried out in 175 ml polycarbonate bottles.

Sample analysis. Picoplankton samples were preserved in formaldehyde (2% final concentration) and filtered onto black 0.2 µm polycarbonate membrane filters (Nuclepore) laid over pre-wetted 0.45 µm nitrocellulose backing filters (Millipore). Cells were stained in the dark with DAPI (5 µg ml^{-1} final concentration) following a modification of the Porter & Feig (1980) method. Filters were stored at –20°C until processed. Sample volumes were adjusted per dilution: 6 ml for 20 and 40% dilutions, and 3 ml for 60, 80 and 100% whole water. Picoplankton enumeration was conducted with a 100× oil immersion objective using an Olympus BX60 epifluorescence microscope equipped with a 100 W high-pressure mercury burner (HPO 100W/2). The abundance of coccoid cyanobacteria was determined on the same filter used for bacteria enumeration using blue excitation (450 to 490 nm) and counting at least 200 cells. Cell numbers of hetero- and autotrophic picoplankton were converted to carbon biomass using a factor of 20 fg C $cell^{-1}$ (Ducklow & Carlson 1992) and 200 fg C $cell^{-1}$ (Caron et al. 1991), respectively.

Nanoplankton was preserved in 1% glutaraldehyde and processed as described by Verity et al. (1993). Sample volume was 80 ml for 20 and 40% dilutions, and 40 ml for 60, 80 and 100% whole water. Samples were filtered onto black 0.8 µm polycarbonate filters (Nuclepore) positioned on 1.2 µm nitrocellulose backing filters (Millipore). Cells were stained with DAPI (5 µg ml^{-1} final concentration) and stored at –20°C before being processed. Nanoplanktonic cells were counted by a 100× oil immersion objective using a Leitz Dialux epifluorescence microscope equipped with a 50 W high-pressure mercury burner (HBO 50W/2). Carbon content was calculated using a conversion factor of 14 pg C $µm^{-3}$ $cell^{-1}$ (Lessard 1991).

Phytoplankton samples (500 ml) were preserved in 1% hexamethylenetetramine buffered formaldehyde. Volumes of sedimentation chambers used for this purpose, according to Utermöhl (1958), ranged from 50 to 100 ml depending on the cell concentration. When needed, several chambers were screened. The method of enumeration was adapted to fit the abundance of the various groups: cells of abundant groups were counted in defined fields, whereas rare species were counted on the whole chamber. For counts to be considered significant, at least 100 cells per sample of each observed group had to be counted. Species with negligible abundance were not included in the elaborations. At least 100 cells of each species were measured and linear dimensions were converted to cell volumes using standard geometric formulae (Edler 1979). Cell volumes were converted to carbon content using standard conversion formulae (Strathmann 1967).

Microzooplankton was analysed following 2 methods. To distinguish between heterotrophic and autotrophic dinoflagellates, 100 ml samples were fixed and processed as described for nanoplankton. As this sam-

ple size is too small for significant counts, 1 l samples were fixed with 1% hexamethylenetetramine-buffered formaldehyde to determine microzooplankton abundance (Verity et al. 1996). Formaldehyde was chosen instead of acid Lugol because it does not stain mucus aggregates and detritus that can be abundant in the Northern Adriatic. To compensate for any loss of choreotrichs due to fixation in formaldehyde, cell numbers were corrected by multiplying them by a factor of 1.56 (Stoecker et al. 1994a,b). Samples were pre-concentrated to 100 ml by sedimentation (Dolan et al. 2000). At least 50 ml of these pre-concentrated samples were settled in sedimentation chambers and examined using a Leitz inverted microscope (20× objective). Only chambers with at least 100 cells from each observed group or species were considered for their significance. Acantharia, Heliozoa, Radiolaria and Foraminifera were always found at low concentrations (always $<10\ l^{-1}$) and were therefore not included. Sample enumeration and determination were performed within 2 mo. At least 100 cells were looked at for each species or genera were measured and grouped according to size and standardised geometrical forms. Cell volume was transformed into carbon content using the conversion factor for formaldehyde fixed samples of 14 pg C μm^{-3} (Putt & Stoecker 1989) and the formula of 444.5 pg C + (lorica volume in $\mu m^{-3} \times 0.053$ pg C) per cell for tintinnids (Verity & Langdon 1984).

Data analysis. Growth rates of pico-, nano- and microphytoplankton, and nano- and microzooplankton grazing rates were calculated from Model I regressions of apparent growth against dilution factor, based on Landry & Hasset (1982) (e.g. Landry 1993). The apparent prey growth is described by:

$$C_t = C_0 e^{(k-g)t}$$

where C_0 is the carbon concentration of the prey at the beginning, C_t the carbon concentration at the end of the experiment (time t), k the apparent growth coefficient and g the grazing coefficient. Production (P) and ingestion (I) were calculated as $P = k \times C_m$ and $I = g \times C_m$, where C_m is the average carbon concentration during the incubation:

$$C_m = \frac{P_0 e^{(k-g)} - P_0}{k - g}$$

as according to Frost (1972) (e.g. Strom & Strom 1996).

Microzooplankton growth was calculated based on carbon concentrations found in whole water samples at the beginning and at the end of the incubations. HNAN growth, besides the growth rate obtained as described above, was also calculated in the pre-screened (>10 µm) initial and final water samples. Instantaneous phytoplankton growth rates were recalculated according to Caron (2000). As suggested by Strom (2000), we measured the bacterial carbon production (BCP) by a modification of the Smith & Azam (1992) method, in which tritiated thymidine (20 nM) rather than leucine was used as the radiolabelled substrate. BCP was transformed into the respective net growth rates (k_n) dividing BCP by the estimated bacteria biomass (Ducklow & Carlson 1992).

RESULTS

Environmental variables and microbial standing stocks

Water quality variables for all dates are summarised in Table 1. Vertical profiles of salinity and temperature changed from the well-mixed autumn to winter structure, to the spring to summer stratification, which was almost undetectable in August because of the intense warming which reached the bottom layer. Inorganic nutrient concentrations (such as N_{total}, PO_4 and SiO_2) were always very low and homogeneous, except for in August. This was particularly the case below the surface layer due to the remineralisation processes. The low nutrient concentration in February 1999 indicated that the phytoplankton bloom had started some days before. Chl *a* ranged between 0.4 µg l^{-1} in August and 5.9 µg l^{-1} at the surface in February.

Micro- and phytoplankton constituted the most important fraction of the total living carbon in 3 out of 4 experiments; only in August did picoplankton significantly contribute to the total biomass (Table 2). Diatoms were the major contributors in February when 1 species alone (*Lauderia annulata*) made up to 92% of the living carbon bulk. In November dinoflagellates, and in May PNAN, provided the largest portions of the biomass.

In November, the microzooplankton community (Table 3) was largely dominated by tintinnids (e.g. *Stenosemella ventricosa*) and heterotrophic dinoflagellates, which were still dominant in February. In May, the microzooplankton community reached the highest diversity with the appearance of large choreotrich ciliates (e.g. *Strombidium cornucopiae*, the mixotroph *Laboea strobila*), numerous tintinnids (e.g. *Stenosemella nivalis*, *Tintinnopsis levigata*, *T. compressa*) and nauplii of copepods. Large-sized ciliates (>50 µm) also dominated the community in August.

Microzooplankton grazing on phototrophic fractions

Phytoplankton net growth rates (k_n), recalculated as suggested by Caron (2000), were always very close to k values obtained in the replicates with added nutri-

Table 1. Ambient environmental conditions at the beginning of the experiments at Site C1. nd = not determined

Depth (m)	Temperature (°C)	Salinity (psu)	O_2 (% saturation)	N_{total} (µM l^{-1})	PO_4 (µM l^{-1})	SiO_2 (µM l^{-1})	Total chl *a* (µg l^{-1})
Nov 98							
0	14.5	36.2	88	1.41	0.06	0.98	1.6
5	14.5	36.2	89	1.23	0.03	0.72	nd
10	14.7	36.2	87	1.26	0.03	0.69	1.6
15	14.6	36.2	87	1.65	0.02	0.82	1.3
Feb 99							
0	8.0	37.8	102	0.49	0.07	0.89	5.9
5	8.0	37.8	103	1.75	0.11	0.74	3.3
10	8.2	37.8	101	1.59	0.11	1.88	3.7
15	8.3	37.9	99	0.76	0.09	1.73	2.7
May 99							
0	17.5	36.2	104	1.51	0.11	1.88	1.2
5	16.3	36.7	106	1.18	0.12	1.15	0.8
10	14.8	37.1	103	0.44	0.12	1.40	1.1
15	13.9	37.3	101	0.46	0.11	1.41	1.0
Aug 99							
0	24.2	37.6	98	0.92	0.07	2.16	0.4
5	23.9	37.5	99	10.9	0.91	5.02	0.4
10	23.8	37.5	99	11.1	1.02	4.96	nd
15	23.7	37.5	97	3.96	0.53	1.90	nd

ents (Table 2). The growth rate in nutrient-enriched bottles (k) was either the same or only slightly higher than k_n, the growth rate in unenriched bottles. Nutrient enrichment did not enhance the phytoplankton growth rates in our experiments. In November, microzooplankton grazed efficiently on PNAN and small-sized dinoflagellates (20 × 25 µm), but not diatoms (Table 2). Small dinoflagellates were grazed at rates (g = 1.35 d^{-1}) higher than their net growth rate (k_n = 0.79 d^{-1}). This indicates a top-down control exerted by microzooplankton. The corresponding ingestion rate was 64.9 µg C l^{-1} d^{-1}. Grazing rates on PNAN were in the same range (g = 0.73 and 0.81 d^{-1} for <10 µm and 10 to 20 µm size classes, respectively), and were higher than the corresponding net growth rate (k_n = 0.07 d^{-1}) for the <10 µm size class and lower (k_n = 0.97 d^{-1}) for the larger one. The ingestion rates were 0.37 and 7.91 µg C l^{-1} d^{-1}, respectively.

In February, the impact of microzooplankton grazing was evident only on the smallest (≤20 µm) autotrophic fraction consisting of *Chaetoceros* spp. and on HNAN, but not at all on the blooming large-sized diatom *Lauderia annulata*. There was a weak sign of some possible grazing activity on autotrophic picoplankton by microzooplankton, but its abundance was too low to calculate any significant ingestion.

In May (Fig. 2, Table 2), phytoplankton was dominated by PNAN which consisted mainly of euglenophytes, prasinophytes and cryptophytes. Microzooplankton exerted significant grazing on diatoms (g = 0.45 d^{-1}). Mortality was more than counterbalanced by their net growth rate (k_n = 0.84 d^{-1}); therefore, grazing reduced their daily potential production by only 49%. On the other hand, PNAN (10 to 20 µm) was greatly affected by microzooplankton grazing which eliminated more than 100% of the daily potential production. Grazing on the various groups of flagellates was differentiated. Grazing eliminated 163% of the daily potential production of the cryptophytes. This resulted in a remarkable reduction of their standing stock. For the other flagellates, grazing was more than counterbalanced by growth with a mortality of 80% of the daily potential production for euglenophytes and of 85% for prasinophytes.

In August, phytoplankton was scarce and grazing additionally reduced the standing stock. Microzooplankton grazed on diatoms, with a pressure higher (g = 1.03 d^{-1}) than their net growth rate (k_n = 0.62 d^{-1}), which led to a loss of 169% of their daily potential production (Table 2). The grazing impact was also high on part of the PNAN (Chlorophyceae) <10 µm, whose production was significantly reduced by 145%.

The growth of microzooplankton was analysed over the 24 h period of incubation. Significant microzooplankton growth (Table 3) was only detectable in August, when it showed a significant production of 3.02 µg C l^{-1} d^{-1}. We calculated the ingestion and clearance rates as well as the weight-specific ingestion rates (Table 4) on the whole data set. On the base of our results, in August we also included bacteria (see 'Discussion'). The weight-specific ingestion rates ranged from 2.50 to 11.4 d^{-1} with an average of 7.31 d^{-1}. Clearance rates ranged from 0.11 to 1.29 ml $cell^{-1}$ d^{-1} with an average of 0.53 ml $cell^{-1}$ d^{-1}.

Grazing on heterotrophic fractions

Microzooplankton grazed significantly on HNAN (<10 µm) in 3 out of 4 experiments: only in August did we not detect any grazing impact on this fraction (Table 2). In the other cases, grazing rates were higher than HNAN apparent growth rates that led to a removal of more than 100% of the daily potential HNAN production and of 50 to 100% of the initial standing stock.

Table 2. Microzooplankton grazing on microphytoplankton, phototrophic nanoflagellates (PNAN), heterotrophic nanoflagellates (HNAN) and picoplankton. k_n = net growth rate (d^{-1}), k = growth coefficient (d^{-1}), g = grazing coefficient (d^{-1}), $^{\star}p < 0.05$, $^{\star\star}p < 0.01$, $^{\star\star\star}p < 0.001$, C_0 = initial concentration (µg C l^{-1}). P = production (µg C l^{-1} d^{-1}), I = ingestion (µg C l^{-1} d^{-1}), P_g = production grazed (% d^{-1}), $^{\star}p < 0.05$, $^{\star\star}p < 0.01$, $^{\star\star\star}p < 0.001$, nd = not determined, ns = not significant, unid = unidentified. Prevalent microphytoplankton species: November, *Chaetoceros* spp. and dinoflagellates (20 × 25 µm); February, *Lauderia annulata* and *Chaetoceros* spp.; May, >10 and <20 µm PNAN (Cryptophyceae, Euglenophyceae, Prasinophyceae), *Chaetoceros* cfr. *affinis* and *Chaetoceros* spp.; August, Dinophyceae (*Ceratium furca*) and *Pseudo-nitzschia seriata*. *Heterotrophic nanoflagellates (HNAN) grazing on picoplankton in the experiments without microzooplankton

	k_n	SD	k	±SE	g	±SE	C_0	P	I	P_g
Nov 98										
Total phytoplankton	0.37	0.02	0.40	0.11	0.41	0.17*	126**	50.0	51.2	103
Bacillariophyceae	nd	nd	ns	ns	ns	ns	51.7*	nd	nd	nd
Dinophyceae	0.79	0.04	0.74	0.12	1.35	0.19***	64.2*	35.6	64.9	182
Unid. PNAN >10 <20 µm	0.97	0.00	0.97	0.17	0.81	0.26**	9.01**	9.48	7.91	84
Unid. PNAN <10 µm	0.07	0.14	0.27	0.14	0.73	0.22**	0.63**	0.14	0.37	270
Unid. HNAN	nd	nd	0.78	0.27	1.03	0.41*	0.23*	0.16	0.21	132
Heterotrophic picoplankton	0.45	nd	ns	ns	ns	ns	44.4***	nd	nd	nd
Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	5.87***	nd	nd	nd
*Unid. Heterotrophic picoplankton	0.45	nd	0.32	0.08	0.45	0.13**	46.2***	13.9	19.5	141
*Unid. Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	5.70***	nd	nd	nd
Feb 99										
Total phytoplankton	nd	nd	ns	ns	ns	ns	1105***	nd	nd	nd
Bacillariophyceae	nd	nd	ns	ns	ns	ns	1088***	nd	nd	nd
Lauderia annulata	nd	nd	ns	ns	ns	ns	1029***	nd	nd	nd
Chaetoceros spp.	−0.12	0.08	−0.01	0.16	0.52	0.23*	59.6*	nd	24.0	nd
Unid. PNAN >10 and <20 µm	nd	nd	ns	ns	ns	ns	15.8***	nd	nd	nd
Unid. PNAN <10 µm	nd	nd	ns	ns	ns	ns	0.59**	nd	nd	nd
Unid. HNAN	nd	nd	−0.01	0.13	0.61	0.19*	2.16**	nd	0.98	nd
Heterotrophic picoplankton	2.54	nd	1.29	0.10	0.68	0.16**	5.51***	9.79	5.16	53
Autotrophic picoplankton	nd	nd	0.67	0.26	1.22	0.38*	0.08	nd	nd	nd
*Unid. Heterotrophic picoplankton	2.54	nd	1.43	0.10	1.21	0.15***	8.47***	13.5	11.5	85
*Unid. Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	0.21**	ns	ns	ns
May 99										
Total phytoplankton	0.58	0.03	0.62	0.06	0.44	0.09***	147***	99.8	70.8	71
Bacillariophyceae	0.84	0.06	0.92	0.08	0.45	0.13**	54.0***	63.4	31.0	49
Dinophyceae	nd	nd	ns	ns	ns	ns	10.2***	nd	nd	nd
Cryptophyceae	0.19	0.06	0.27	0.07	0.44	0.10***	7.16**	1.78	2.90	163
Euglenophyceae	0.60	0.01	0.59	0.13	0.47	0.19*	23.0***	14.4	11.5	80
Prasinophyceae	0.63	0.06	0.55	0.11	0.47	0.16**	7.30***	4.18	3.57	85
Unid. PNAN >10 < 20 µm	0.40	0.02	0.37	0.11	0.54	0.16**	43.6***	14.8	21.6	146
Unid. PNAN <10 µm	nd	nd	ns	ns	ns	ns	1.65**	nd	nd	nd
Unid. HNAN	nd	nd	0.24	0.08	0.63	0.12***	1.68***	0.33	0.88	263
Heterotrophic picoplankton	2.74	nd	1.54	0.12	0.67	0.19**	9.80***	24.1	10.5	44
Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	2.95***	nd	nd	nd
*Unid. Heterotrophic picoplankton	2.74	nd	1.42	0.10	0.72	0.15***	10.6***	21.7	11.0	51
*Unid. Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	2.62***	nd	nd	nd
Aug 99										
Total phytoplankton	nd	nd	ns	ns	ns	ns	25.2**	nd	nd	nd
Bacillariophyceae	0.62	0.01	0.61	0.29	1.03	0.39*	0.67**	0.33	0.56	169
Dinophyceae	nd	nd	ns	ns	ns	ns	22.1**	nd	nd	nd
Chlorophyceae < 10 µm	1.02	0.03	0.97	0.12	1.41	0.18***	0.46***	0.36	0.52	145
Unid. PNAN < 10 µm	nd	nd	ns	ns	ns	ns	1.92*	nd	nd	nd
Unid. HNAN	nd	nd	ns	ns	ns	ns	0.87*	nd	nd	nd
Heterotrophic picoplankton	0.35	nd	1.72	0.27	1.47	0.40**	23.6***	46.1	39.4	85
Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	23.0***	nd	nd	nd
*Unid. Heterotrophic picoplankton	0.35	nd	0.95	0.08	0.67	0.12***	24.1***	26.4	18.6	71
*Unid. Autotrophic picoplankton	nd	nd	ns	ns	ns	ns	23.7***	nd	nd	nd

Table 3. Growth and abundance of potential grazers, microzooplankton and heterotrophic nanoflagellates (HNAN). k = growth coefficient (d^{-1}), C_0 = initial concentration (µg C l^{-1}), P = production (µg C l^{-1} d^{-1}), nd = not determined, ns = not significant. Predominating Ciliophora non-Tintinnida: November, *Strombidium* spp.; February, small choreotrichs; May, small *Strombidium* spp., *S. cornucopiae*; August, strombidiid ciliates >100 µm and small *Strombidium* spp. Predominating Protozoa non-Ciliophora (heterotrophic dinoflagellates): November to May, small *Gyrodinium* spp.; August, *Gyrodinium* spp. and *Protoperidinium* spp. Predominating Tintinnida: November, *Stenosemella ventricosa*; February and May, *S. nivalis*; August, hyaline loricate unidentified Tintinnida (50 µm). Predominating Metazoa: in all experiments copepod nauplii, in February many larvae of Bivalvia. *HNAN growth in the experiments without microzooplankton

	k	SD	C_0	SD	P
Nov 98					
Total microzooplankton	ns	ns	6.43	1.01	nd
Total Protozoa	ns	ns	5.35	0.49	nd
Ciliophora non Tintinnida	ns	ns	0.13	0.02	nd
Tintinnida	ns	ns	5.01	0.46	nd
Protozoa non Ciliophora	ns	ns	0.21	0.05	nd
Metazoa	ns	ns	1.08	0.51	nd
*HNAN	0.51	0.18	0.20	0.06	0.13
Feb 99					
Total microzooplankton	ns	ns	9.63	0.86	nd
Total Protozoa	ns	ns	8.43	0.24	nd
Ciliophora non Tintinnida	ns	ns	1.14	0.07	nd
Tintinnida	ns	ns	0.01	0.02	nd
Protozoa non Ciliophora	ns	ns	7.29	0.17	nd
Metazoa	ns	ns	1.19	0.60	nd
*HNAN	0.21	0.01	0.91	0.09	0.21
May 99					
Total microzooplankton	ns	ns	8.46	1.66	nd
Total Protozoa	ns	ns	6.89	1.00	nd
Ciliophora non Tintinnida	ns	ns	6.40	0.89	nd
Tintinnida	ns	ns	0.49	0.17	nd
Protozoa non Ciliophora	ns	ns	0.13	0.10	nd
Metazoa	ns	ns	1.44	0.60	nd
*HNAN	1.02	0.24	0.85	0.08	1.52
Aug 99					
Total microzooplankton	0.41	0.15	5.90	0.41	3.02
Total Protozoa	0.44	0.16	5.62	0.46	3.10
Ciliophora non Tintinnida	0.32	0.21	4.84	0.53	1.85
Tintinnida	1.16	0.07	0.59	0.07	1.29
Protozoa non Ciliophora	ns	ns	0.19	0.03	nd
Metazoa	ns	ns	0.28	0.07	nd
*HNAN	0.25	0.08	0.92	0.26	0.27

During the experiment performed without microzooplankton, in November 1998, HNAN grazed only on heterotrophic picoplankton (bacteria) with a grazing rate (g = 0.45 d^{-1}) equal to the picoplankton net growth rate (k_n = 0.45 d^{-1}) measured as ^{3}H-thymidine incorporation. The result from the grazing experiment with an apparent growth rate of k = 0.32 d^{-1} would suggest a slightly stronger potential consumer control on the prey.

In the experiment performed in the presence of microzooplankton, we did not detect any significant grazing on bacteria. In this case, the grazing impact of microzooplankton on HNAN was strong enough to remove more than 100% of the potential production, eliminating most of the HNAN. On the other hand, the microzooplankton itself did not show any direct grazing impact on picoplankton.

In the February and May experiments (Table 2), the grazing impact of HNAN alone on bacteria was significant, leading to slightly lower ingestions than in November.

When the effect of microzooplankton was investigated in both experiments, similar results were obtained: a lower grazing impact of microzooplankton and HNAN together on bacteria than in the experiments with HNAN alone. In February, the decrease was more evident, when ingestion of bacteria by microzooplankton and HNAN was halved (from 11.5 to 5.16 µg C l^{-1} d^{-1}); whereas, in May, it showed a 5% reduction (from 11.0 to 10.5 µg C l^{-1} d^{-1}). In all cases (with or without microzooplankton consumers), the grazing rates were lower than the apparent growth rates of bacteria, which was also true for the net (^{3}H-thymidine determined) growth rates.

In the summer experiment (Table 2), the HNAN grazing rate on bacteria was slightly higher than in November, and led to an ingestion close to that in November, when the bacterial biomass had been almost double.

The cumulated effect of the grazing impact of microzooplankton and HNAN was to enhance bacterial mortality in summer. In this case, we did not observe any direct microzooplankton grazing impact on HNAN, while the direct impact of microzooplankton grazers on bacteria was evident and very strong. It is also necessary to highlight the increase of the apparent growth rate of bacteria (k = 0.95 d^{-1} without and k = 1.72 d^{-1} with microzooplankton), while the net (^{3}H-thymidine determined) growth rate was much lower (k_n = 0.35 d^{-1}). Only in this set of experiments were grazing rates higher than the net bacteria growth, suggesting a control exerted by grazers on bacterial biomass development.

Growth of HNAN turned out to be significant in all experiments except in November (Table 3). The growth coefficient was particularly high in May (1.02 d^{-1}), while in the other months, it was quite homogeneous and lower (from 0.21 to 0.51 d^{-1}). In all

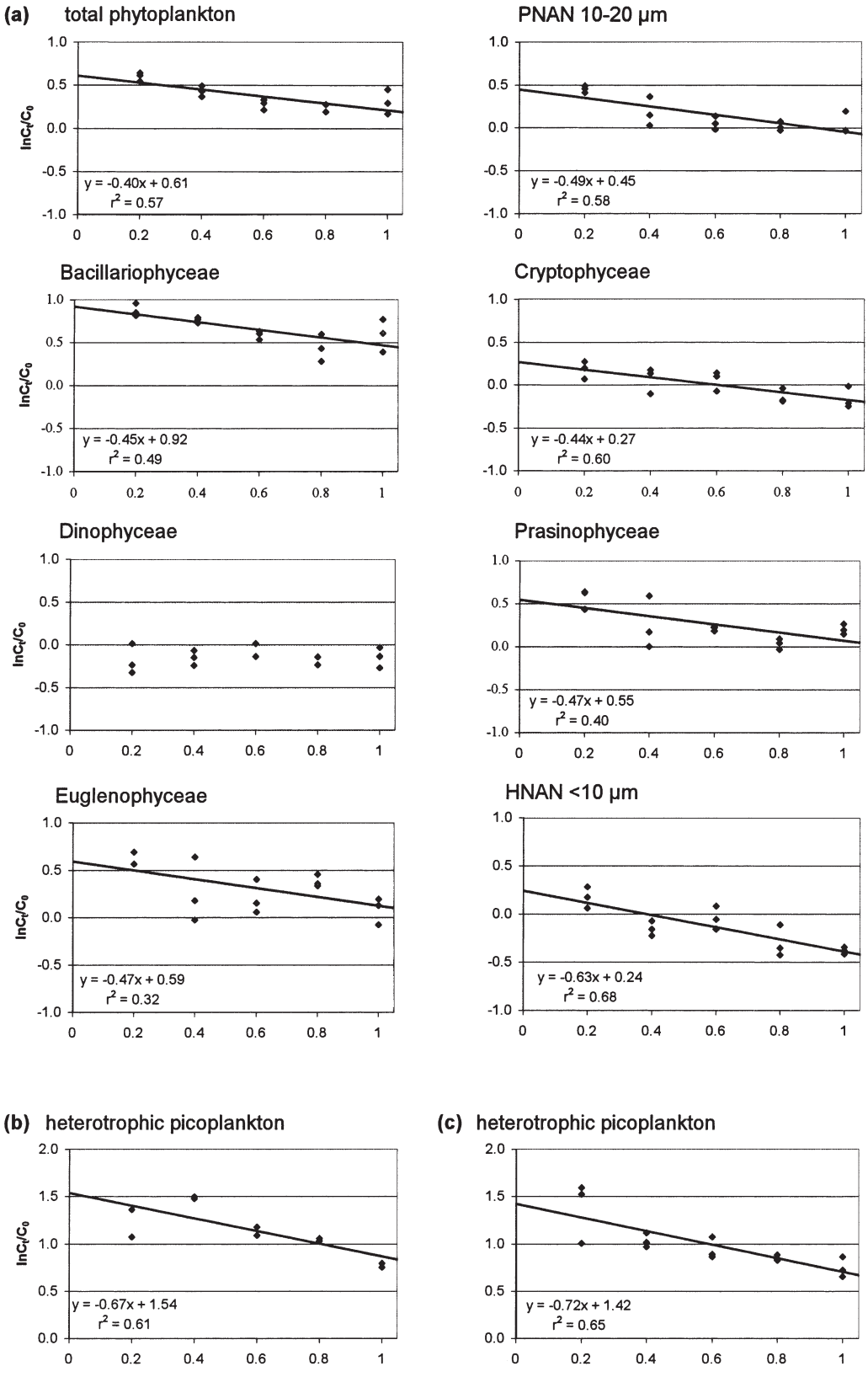

Fig. 2. Dilution plots from the experiment at Site C1 in May 1999. (a) Grazing of microzooplankton on total phytoplankton, subgroups of phytoplankton and heterotrophic nanoflagellates (HNAN); (b) microzooplankton and nanoplankton grazing on heterotrophic picoplankton; (c) grazing of HNAN alone on heterotrophic picoplankton. PNAN: phototrophic nanoflagellates

Table 4. (a) Microzooplankton grazing on corresponding prey. (b) Heterotrophic nanoflagellates (HNAN) grazing on picoplankton. *C* = carbon content of grazers (µg C l^{-1}), *I* = ingestion (µg C l^{-1} d^{-1}), I_{sp} = weight-specific ingestion rate represented by ingestion in carbon (µg C l^{-1} d^{-1}):carbon content grazers (µg C l^{-1}), Cl_{sp} = specific clearance rate (ml cells of grazers^{-1} d^{-1})

	C	*I*	I_{sp}	Cl_{sp}
(a) Microzooplankton				
Nov 98	6.43	73.4	11.4	1.29
Feb 99	9.63	24.1	2.50	0.11
May 99	8.46	71.5	8.45	0.20
Aug 99	5.90	1.08	0.18	0.68
Aug 99 + bacteria	5.90	40.5	6.86	0.51
Average (including August with bacteria)			7.31	0.53
	C	*I*	I_{sp}	Cl_{sp} ($\times 10^{-3}$)
(b) HNAN				
Nov 98	0.20	19.5	97.5	4.16
Feb 99	0.91	11.5	12.6	1.19
May 99	0.85	11.0	13.0	0.91
Aug 99	0.92	18.6	20.3	1.64
Average (excluding November)			15.3	1.25

cases, ingestion was calculated based on the average concentrations found (Frost 1972). HNAN ingestion and clearance rates and the weight-specific ingestion rates were high (Table 4). The weight-specific ingestion rates ranged from 12.6 to 20.3 d^{-1} with an average of 15.3 d^{-1}. The extremely high data of November were not included in the average (see 'Discussion'). Clearance rates for HNAN (Table 4) had an average value of 1.25×10^{-3} ml $cell^{-1}$ d^{-1} with a minimum of 9.1×10^{-4} ml d^{-1} and a maximum of 4.16×10^{-3} ml $cell^{-1}$ d^{-1}.

DISCUSSION

One of the aims of the experiments was to assess the grazing impact of microzooplankton on the phototrophic fraction; this was fully achieved in all the experimental settings. In our study, phytoplankton proved not to be nutrient-limited although nutrients, especially phosphorus, were always scarce. It was always possible to show the influence of microzooplankton on phytoplankton, but only by distinguishing the different groups of prey and the selective grazing impact on each of them. In 2 out of 4 experiments, grazing on total phytoplankton (including micro- and nano-sized organisms) was not significant. However, we detected mortality induced by grazing on some of the phototrophic components: in February on small *Chaetoceros*, and in August on diatoms and <10 µm Chlorophyceae. In November and May, when microzooplankton grazed on the most important constituents of the phytoplankton assemblage (e.g. dinoflagellates, PNAN, diatoms), grazing on total phytoplankton was also significant. This result indicates strong selection by micro-grazers on food items. In all cases, nano-sized prey were preferred. This confirms similar results found by other authors (e.g. Kamiyama 1994, Fahnenstiel et al. 1995, Gifford et al. 1995, Froneman et al. 1996). This selectivity is not only limited to different size classes, but may concern different groups inside a single size class as can be seen in May (Fig. 2, Table 2).

Microzooplankton grazing on the natural phototrophic assemblage determined only a partial consumption of the available photosynthesised carbon, which varied from less than 5% of the total carbon in August up to almost 100% in May. During this month, the high grazing impact was counterbalanced by the high growth rates, particularly of diatoms: their potential daily production decreased by only 49%. In November, when the grazing-induced mortality was higher than 100% of the total phytoplankton daily potential production, diatoms were not consumed at all. Overall, the selective grazing pressure contributed to shaping the phytoplankton community structure. Mortality induced by microzooplankton grazing did not affect large diatoms, which remained available for other predators or were shifted to the sea floor.

However, the question remains: did microzooplankton live on phytoplankton alone? In August, microzooplankton had very scanty resources in the nano-sized class. Therefore, it would be reasonable to predict that it preyed on other items as well. When comparing the results of the experiments with and without micrograzers (Table 2), it is obvious that they must have used bacteria as a food source to a large extent. If we suppose that the difference in ingestion is a result of microzooplankton grazing, it must have grazed nearly exclusively on bacteria.

James & Hall (1998) found a 27 to 67% depletion of the standing stock in bacterial biomass by microzooplankton. In this case, there are no indications of the sizes of the grazers, and it is likely that they estimated the combined effect of HNAN and microzooplankton on bacteria. Several authors used fluorescent-labelled bacteria (e.g. Sherr et al. 1989, Caron et al. 1999) to show how the smaller fraction of the ciliate population can feed on bacteria (see the recent review by Strom 2000). Bernard & Rassoulzadegan (1990) showed that small ciliates (e.g. *Strombidium sulcatum*) feed on bacteria-sized particles, even if they prefer slightly larger prey (*Nannochloris* sp. >2.5 µm). Kivi & Setälä (1995) demonstrated the ability of some large aloricate ciliates and tintinnids to feed on 1.4 µm sized particles, even if they generally preferred larger-sized prey (e.g. from 2.8 up to 15.4 µm).

Microzooplankton used HNAN as a food source in almost all experiments. When HNAN were grazed (November, February, May), the grazing rates always exceeded the apparent growth rates. This indicates a strong and often preferential control on the heterotrophic nano-fraction.

In general, microzooplankton used the most abundant resource in the most suitable dimension. As an example, in February, it grazed on *Chaetoceros* (20 µm), but not on 10 to 20 µm PNAN, which was far less abundant. In May, among the smallest fraction, only HNAN was grazed, while there was no significant grazing on <10 µm PNAN. Still more generally, the microzooplankton grazing impact exceeded the apparent and net growth rates in most of the cases, showing good overall control on the small phototrophic and heterotrophic fractions. Only in the case of scarcity of nanoplankton did we find a high direct influence on picoplankton. On the other hand, mortality induced by microzooplankton grazing did not affect large diatoms (e.g. *Lauderia annulata*). This confirms data obtained by Gallegos et al. (1996) during the February bloom of the large diatom *Odontella sinensis* in Manukau Harbour, New Zealand.

Our results confirmed the strong grazing impact of HNAN on heterotrophic bacteria (e.g. Rassoulzadegan & Sheldon 1986, Kuuppo-Leinikki et al. 1994 and references therein; Calbet & Landry 1999, Becquevort et al. 2000, Calbet et al. 2001), but not on cyanobacteria. This may be due to the extreme scarcity of cyanobacteria in our samples, whose number, after dilution, decreased to values which were not significant (Campbell & Carpenter 1986), as well as to clear selection by HNAN on heterotrophic bacteria, as observed by Caron et al. (1991) both in laboratory studies with cultured species and in field experiments.

In our study, HNAN biomass (from 0.20 to 0.92 µg C l^{-1}) as well as its grazing rate on bacteria (from 0.45 to 0.72 d^{-1}) remained quite stable, except for in February, when the bacterial biomass was very low. The combination of these 2 factors (grazing rate and initial biomass of bacteria) led to quite a stable ingestion, from 11.0 to 19.5 µg C l^{-1} d^{-1}, which is lower than figures reported by Reckermann & Veldhuis (1997) for a coastal site in the Somali basin. Despite the potential grazing impact exerted, HNAN seemed unable to control the biomass development of bacteria, whose growing rates exceeded the grazing rates in 3 out of 4 experiments. Only in August was the net growth rate lower than the grazing rates. In this set of experiments, the potential effect of the grazing of microzooplankton in enhancing the growth of bacteria, as suggested by Reckermann & Veldhuis (1997), was particularly evident (k_n = 0.35 d^{-1}, k = 0.95 d^{-1} with HNAN, k = 1.72 d^{-1} with HNAN and microzooplankton). These results confirmed the fast response of the bacteria population to the increasing grazing impact as suggested by Ferrier-Pages & Rassoulzadegan (1994). This may be due to the increase of DOM release by protist grazers that have been found to release 25% or more of the ingested prey carbon; some of this material appears to be quite labile and can be readily taken up by bacteria; thus, enhancing their growth rates (Strom 2000).

In November, the HNAN-specific ingestion rate was incredibly high, given the relatively small HNAN biomass; while in the other 3 experiments, it ranged from 12.6 to 20.3 µg C l^{-1} d^{-1} (Table 4). At the same time, small-unidentified PNAN were abundant. Our experimental techniques did not enable us to distinguish between mixotrophic and autotrophic nanoplankton. However, it is well known that mixotrophic flagellates can have a significant influence on picoplankton (e.g. Safi & Hall 1999). Only mixotrophy of part of the unidentified flagellates can explain the high bacterial mortality encountered. Another possible explanation, such as virus infections, which are able to reduce the bacterial biomass by 7 to 20% h^{-1} (Fuhrman & Noble 1995, Steward et al. 1996, Fuhrman 2000), seems unlikely as they should not be detected by the dilution method. When we tested the effect of microzooplankton grazing on bacteria in this month, it turned out that the impressive potential impact of HNAN on bacteria was completely inhibited by the control exerted by microzooplankton on HNAN (Fig. 3a) and the possibly mixotrophic flagellates. The final result was the absence of any bacterial mortality.

In February (Fig. 3b) and May (Fig. 3c), microzooplankton controlled the grazing pressure of HNAN on bacteria less efficiently, even if in February, it reduced bacterial mortality by suppressing some 50% of HNAN. In May, there was a considerable amount of mixotrophic cryptophytes, which were able to graze on bacteria as well. This fraction was less reduced than HNAN by microzooplankton grazing; however, the difference was insufficient to explain the observed lower interference of the microzooplankton on picoplankton mortality. A direct grazing impact of small microzooplankton on bacteria, such as small choreotrichs, which were abundant, seems more likely.

In August (Fig. 3c), the direct grazing impact of microzooplankton added to that of HNAN causing bacterial mortality to double. As discussed above, in this month, the available resources in the nano-sized class were very scarce, thus forcing at least part of the microzooplankton to feed on bacteria.

Our results confirmed the hypothesis by Thingstad & Rassoulzadegan (1995) (but see also Reckermann & Veldhuis 1997, Thingstad 2000) about the indirect control exerted by microzooplankton on bacteria biomass through HNAN removal in 3 out of 4 of the experi-

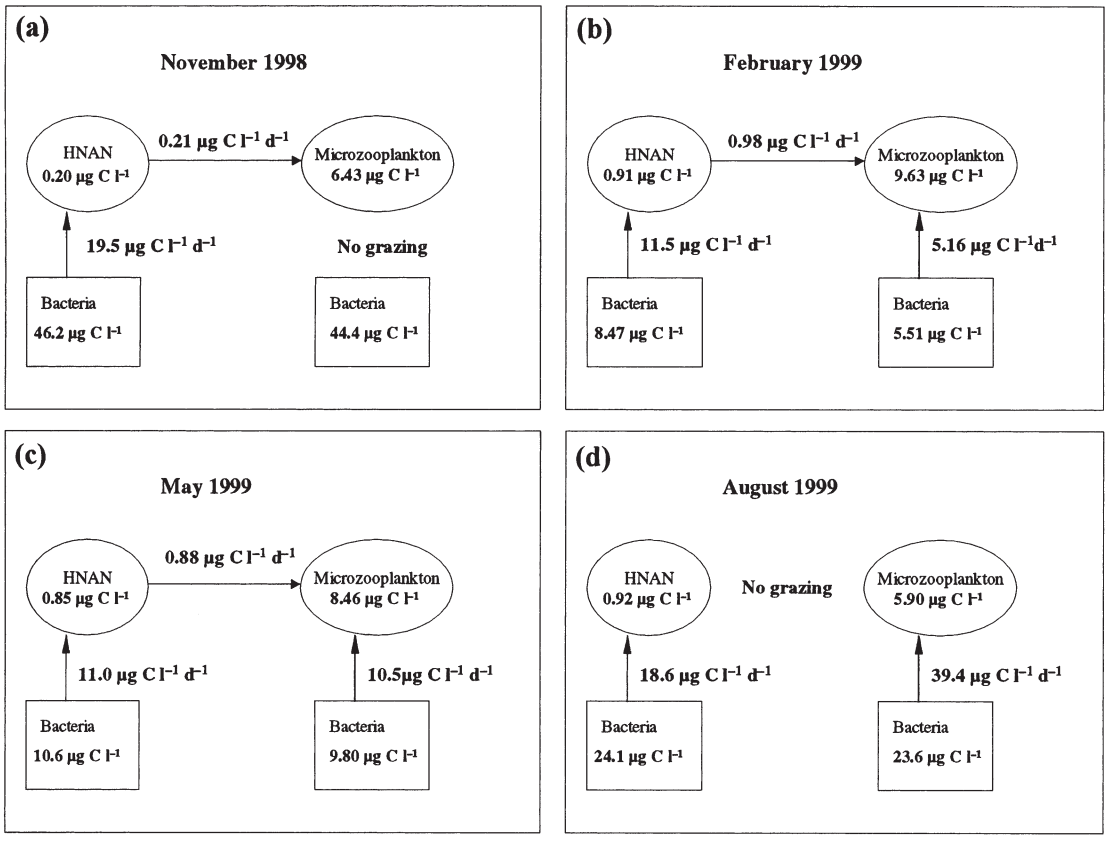

Fig. 3. Grazing impact of heterotrophic nanoflagellates (HNAN) alone on bacteria, and microzooplankton and HNAN on bacteria in November 1998 (a), February 1999 (b), May 1999 (c) and August 1999 (d). In November, no microzooplankton grazing impact on bacteria was detectable. In August, no microzooplankton grazing impact on HNAN was observed

ments. Only when the other more suitable resources were almost completely depleted did the microzooplankton shift its diet from nano-sized prey to bacteria.

Total ingestion of prey by microzooplankton (on both microphytoplankton, PNAN, HNAN and bacteria) ranged from 24.1 to 73.4 µg C l^{-1} d^{-1}; values that are comparable with data reported by Verity et al. (1993) and Reckermann & Veldhuis (1997). Verity and colleagues attempted to estimate the specific ingestion rates for some groups of predators using data derived from the literature and by comparing these estimated data with those obtained from chl *a* (after conversion into carbon content using a factor of 40). Using this data set, Paffenhofer (1998) later calculated that the weight-specific ingestion rates ranged from 0.36 d^{-1} (nauplii) to 3.12 d^{-1} (heterotrophic microflagellates). Our direct estimates (Table 4) gave us weight-specific ingestion rates for total microzooplankton ranging from 2.50 to 11.4 d^{-1} with a mean value of 7.31 d^{-1}, which is about twice the amount reported by Paffenhofer (1998). The differences between the 2 data sets might be explained by considering the 2 different methods used: our carbon estimates derive from cell counts of a field population including heterotrophic organisms and not from chl *a* transformation, which additionally seems to underestimate real grazing rates in dilution experiments by some 60% (Waterhouse & Welschmeyer 1995).

So, was there any grazing by mixotrophic microplankton? The high clearance rate encountered in November with 1.29 ml $cell^{-1}$ d^{-1} indicates possible grazing by the abundant dinoflagellates found in this experiment, but it is still well within the range of clearance rates found by Kivi & Setälä (1995) and the literature cited there.

Values for weight-specific ingestion rates (Table 4) for HNAN recalculated on the data set of Reckermann & Veldhuis (1997) ranged from 3.0 to 13.7 d^{-1}. Our results were slightly higher with a minimum of 12.6 d^{-1}, a maximum of 20.3 d^{-1} and a mean value of 15.3 d^{-1}. Clearance rates for nanoflagellates found by Sherr et al. (1991) using fluorescent-labelled prey on natural assemblages (9.6×10^{-5} to 2.0×10^{-2} ml $cell^{-1}$ d^{-1}), and the data of Landry et al. (1991) in culture on living bacteria (8.4×10^{-4} ml $cell^{-1}$ d^{-1}), correspond to the results of our study.

CONCLUSIONS

The results of this study demonstrate that most of the carbon flux in the Gulf of Trieste passed through microzooplankton, which was able to control the smaller-sized producers and consumers. Only larger diatoms were left for the higher consumers.

The microzooplankton community changed over the period of study both in terms of dimension and taxonomic composition. This was reflected in the diverse food selection observed in all 4 experiments, with the common feature of an evident preference for nano-sized organisms and particularly for HNAN. There was a high selectivity even within this size class. This proved to be particularly evident in spring. As a result of this selection, microzooplankton, when grazing significantly, contributed to the shaping of the phytoplankton community structure.

This study identified 4 different situations, which can be seen as responses by heterotrophic grazers to the different seasonal trophic states: (1) In the autumn, there was a modest diatom bloom, which was not grazed at all because microzooplankton preferred dinoflagellates and PNAN, as well as HNAN whose initial standing stock was completely removed. This eventually led to the absence of any evident mortality of bacteria whose biomass was the highest in the 4 experiments (Fig. 3a). (2) In late winter, an intense diatom bloom occurred which again remained almost untouched. Microzooplankton fed only on the smallest secondary blooming diatom (*Chaetoceros*) as well as on HNAN. In this case, the bacterial mortality induced by HNAN alone was halved (Fig. 3b). (3) In the spring, the microzooplankton grazed on a large array of prey, which included small diatoms, PNAN and HNAN. In this case, the reduction of the HNAN grazing impact was less evident. Given the fact that the reduction of the initial standing stock was very similar in the 2 last situations, we can infer that microzooplankton itself could have fed directly on bacteria (Fig. 3c). (4) During the summer, we clearly detected a direct impact of microzooplankton on bacteria probably due to the paucity of prey in the nano-sized class, which usually appeared to be the most suitable prey (Fig. 3d). At the same time, there was a distinct enhancement of bacterial growth in the presence of microplankton.

As shown above, 3 different models for the grazing on bacteria can be envisaged: the total depletion of the smallest predators by the larger ones (November), the reduction of the grazing pressure by partial elimination of the smallest predators (February and May), and the increase of the grazing impact by the direct uptake of bacteria by larger consumers (August). During August, phytoplankton production and biomass were extremely scarce. On the other hand, the microbial loop was particularly efficient in the presence of microplankton. The available dissolved organic matter fuelled the microbial food web, thereby enhancing bacterial production and biomass. This constituted the main carbon resource for microzooplankton. The microbial food web, therefore, was, in this case, the trophic basis for the whole community.

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