Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake

K. David Hambright[1]
Israel Oceanographic and Limnological Research, Kinneret Limnological Laboratory, Migdal, 14950 Israel, University of Oklahoma Biological Station and Department of Zoology, Kingston, Oklahoma, 73439

Tamar Zohary
Israel Oceanographic and Limnological Research, Kinneret Limnological Laboratory, Migdal, 14950 Israel

Hans Güde
Landesanstalt für Umweltschutz, Institut für Seenforschung, D-88085 Langenargen, Germany

Abstract

In a series of grazer-gradient and dilution microcosm experiments, we compared grazing and nutrient mineralization by naturally co-existing crustacean and microzooplankton assemblages from mesoeutrophic Lake Kinneret. Across two distinct seasonal plankton assemblages, microzooplankton dominated both phytoplankton and bacteria grazing and nitrogen (N) and phosphorus (P) mineralization. Mass-specific ingestion rates by microzooplankton were ~20 times higher than ingestion rates of crustaceans. Although most carbon ingested by microzooplankton was in the form of bacteria, microzooplankton inflicted substantially higher mortalities (both in absolute terms and relative to maximum potential growth rates) on both phytoplankton and bacteria compared with crustaceans. Mass-specific P and N excretion rates were also higher (by 70 and 50 times, respectively) than crustacean excretion rates. These results suggest that microzooplankton grazing and nutrient mineralization are driving forces affecting bacteria and phytoplankton dynamics, playing important roles in carbon and nutrient transfer to upper trophic levels even in pelagic freshwater systems containing abundant crustaceans.

Traditionally, food web studies have considered the direct transfer of living primary production and detritus to higher trophic levels separately (reviewed by Moore et al. 1988; Hairston and Hairston 1993), but recent advances in food web ecology explicitly demonstrate that most food webs are based, and their top predators are supported, through both the "green" (live primary production-based) and "brown" (detrital-based) portions of the food web (Moore et al. 2004). In terrestrial systems, the live primary production–based and the detrital-based food webs are often separated in space: one primarily above ground, the traditional plant–herbivore–carnivore food web; the other primarily below ground, the soil and litter bacteria and

fungus–microbivore–carnivore food web. Although separated in space, these food webs are often strongly linked through common predators as well as through indirect effects such as increased nutrient mineralization in which nutrients supplied to the green portion of the food web can be augmented by nutrients mineralized by grazing bacterivores and fungivores (Wardle et al. 2004; Bezemer et al. 2005). In aquatic systems, particularly pelagic ones, the linkages can be even stronger because living primary production and nonliving detritus coexist spatially and both serve as food resources for grazing zooplankton. Also, bacteria, the predominant consumer of pelagic detritus (including dissolved organic carbon), and protists, the dominant bacterivores, both can be important food resources for crustacean zooplankton. Thus the distinction between the green and brown portions in pelagic food webs is often less apparent.

For nearly three decades, bacteria, protists, and their interactions (the microbial loop) have been considered essential components of open ocean pelagic food webs, dominating carbon (C) and nutrient fluxes (Kirchman 2000; Landry 2002). Yet despite numerous studies documenting the presence and activity of the microbial loop in freshwater systems (e.g., Sanders et al. 1992; Pace et al. 1998), limnologists continue to focus efforts to understand aquatic pelagic food webs on the classic phytoplankton–zooplankton–fish food chain (Drenner and Hambright 2002, but *see* Zollner et al. 2003). The role of detritus has been studied in a variety of pelagic systems, and although some studies have documented

substantial energy flow from bacteria to zooplankton and presumably to fish, most bacterial production is believed to be lost to respiration (Cole 1999). Thus, freshwater food web studies and modeling efforts have tended to focus primarily on the green portion of pelagic food webs (Moore et al. 2004).

In relatively productive freshwater pelagic systems, crustacean zooplankton are considered not only as dominant links between primary production and upper trophic levels, but also as crucial sources of mineralized nutrients for producers (Sterner and Elser 2002). Microbial grazers (also known as microzooplankton) are usually considered more important in these roles in oligotrophic systems in which bacterial production can be an important source for upper trophic level carbon (Capblancq 1990). Recent work in freshwater systems suggests that this dichotomy is more a function of the grazer assemblage than of the level of ecosystem trophy. Large crustacean grazers, especially *Daphnia*, may play a central role in determining the importance of microbial grazers because (1) large grazers are considered to be competitively superior to smaller crustaceans and microzooplankton because of relatively high consumption efficiency across a broad range of particle sizes (Tessier et al. 2001), thus they have a larger total resource base, and (2) many microzooplankton are vulnerable to predation or interference from large crustacean zooplankton (Gilbert 1989; Burns and Schallenberg 1996; Gaedke and Wickham 2004). Hence, the ecological function of microbial grazers may be restricted by the presence of large crustaceans (Jürgens 1994; Zollner et al. 2003) much in the same way that the ecological function of large crustaceans can be restricted by planktivorous fish (sensu Brooks and Dodson 1965). It is therefore logical to predict that in systems containing abundant planktivorous fish and thus few large crustacean zooplankton, microbial grazers could be important food web constituents, playing major roles in both carbon and nutrient transfer, particularly from detritus, to higher trophic levels.

To examine this possibility, we measured grazing and nutrient mineralization rates by naturally coexisting crustacean zooplankton and microzooplankton feeding on seasonal bacteria and phytoplankton assemblages in Lake Kinneret, Israel. Results show that microzooplankton dominate both grazing of phytoplankton and bacteria and mineralization of phosphorus (P) and nitrogen (N) in this highly productive system. These results strengthen the assertion that because of their ubiquitous occurrence in freshwaters and patterns of allometric scaling between body size and biological rates (Brown et al. 2004), microzooplankton can play key roles in freshwater carbon and nutrient fluxes (Pace et al. 1998), even in systems in which they are relatively scarce compared with crustacean zooplankton. Given that microzooplankton are also important components of omnivorous copepod diets in Lake Kinneret (Blumenshine and Hambright 2003), these results suggest that much of the production in the top predators in Lake Kinneret, planktivorous fishes, is based on detrital sources of carbon and nutrients.

Materials and methods

Study site—Lake Kinneret, situated between 32°42′ to 32°53′N, at −209 m altitude in the north of Israel in the Dead Sea Rift Valley (part of the Afro-Syrian Rift Series), is a warm monomictic lake, with average temperatures typically ranging from 14°C during the homeothermic winter period to 28°C in the epilimnion during the peak of thermal stratification (Hambright et al. 1994). The lake is approximately 168 km² in surface area and has mean and maximum depths of 26 m and 43 m, respectively. Generally, Lake Kinneret is classified as mesotrophic (Serruya 1978), although an annual phytoplankton production of 1.2–2.3 g m^{-2} d^{-1}, a seasonally anoxic hypolimnion with hydrogen sulfide (H$_2$S) concentrations >10 mg L^{-1}, and massive algal blooms (Zohary 2004) are more indicative of eutrophic conditions.

The zooplankton assemblage of Lake Kinneret is subject to intense fish planktivory and is therefore dominated by small crustaceans (mainly the Cladocera *Ceriodaphnia*, *Bosmina*, and *Chydorus* and Copepoda *Mesocyclops* and *Thermocyclops*) and a rich microzooplankton assemblage consisting of ~20 rotifer species, numerous ciliated and flagellated protists, and naupliar stages of copepods (Serruya 1978; Hadas and Berman 1998). The phytoplankton of Lake Kinneret has been described as consisting of two separate, seasonal assemblages (Zohary 2004). The winter and spring phytoplankton assemblages are dominated (up to 95% of the biomass and 50% of the production) by relatively large, bloom-forming species such as filamentous diatoms and thecate dinoflagellates that are not consumed by herbivorous zooplankton. Rather, upon senescence and death, these netphytoplanktonic species sink through the epilimnion and hypolimnion of the lake, as well as to the bottom sediments, fueling an array of bacterial processes collectively referred to as decomposition (Serruya 1978). By contrast, the summer and autumn phytoplankton are characterized by low-biomass, diverse assemblages of mostly nanoplanktonic species small enough to be readily grazeable by zooplankton. Thus the majority of primary production (as well as sequestered nutrients) in summer and fall is considered to be available for directly supporting higher trophic levels.

Experimental design—Using simultaneous application of separate methods for crustacean zooplankton (grazer-gradient assays) (Lehman and Sandgren 1985) and microzooplankton (dilution assays) (Landry and Hassett 1982) in paired mesocosm experiments with seasonal Lake Kinneret plankton assemblages (two each in winter–spring and two each in summer–autumn), we quantified grazing and nutrient mineralization (i.e., excretion) rates of coexisting crustacean and microzooplankton grazer assemblages. Because of the large overlap in size ranges between microzooplankton and phytoplankton, microzooplankton were always present in crustacean experiments and therefore always potentially important in phytoplankton and bacteria mortality and nutrient excretion measured in crustacean experiments. However, because microzooplankton experiments were run simultaneously with the same
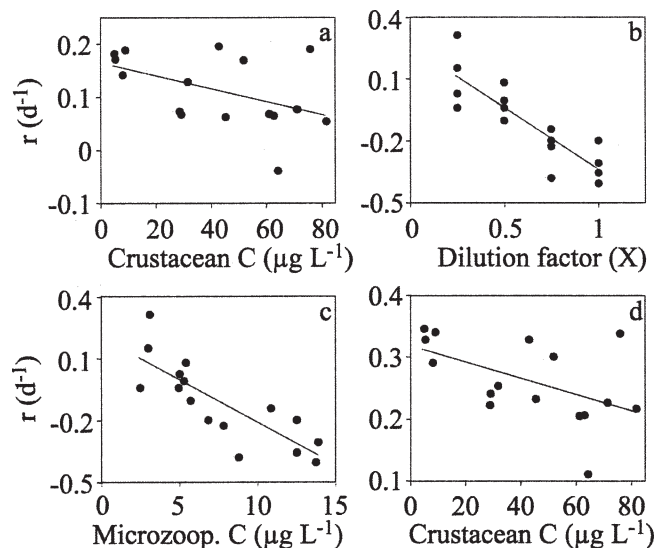
Fig. 1. Results from a paired grazer-gradient and dilution experiment showing estimation of phytoplankton grazing by crustaceans and microzooplankton. Direct results from a representative paired set of grazer-gradient and dilution experiments showing (a) an estimated clearance rate, CR, for total phytoplankton of 1.22 mL μgC$_Z^{-1}$ d^{-1} ($r^2 = 0.224$, $p = 0.032$) for crustaceans before correcting for microzooplankton grazing and (b) estimated grazing mortality, g, by microzooplankton of -0.60 d^{-1} ($r^2 = 0.740$, $p < 0.001$). After enumeration of microzooplankton, CR of microzooplankton (c), estimated as 41.6 mL μgC$_Z^{-1}$ d^{-1} ($r^2 = 0.662$, $p < 0.001$), enabled the correction of final total phytoplankton biomass due to losses by microzooplankton grazing, resulting in (d) a corrected clearance rate, CR_{CORR} of 1.32 mL μgC$_Z^{-1}$ d^{-1} ($r^2 = 0.277$, $p = 0.018$) (*see* text for details). In this example, the presence of microzooplankton affected the estimated total phytoplankton maximum potential growth rate, μ (0.163 d^{-1} before correction vs. 0.317 d^{-1} following correction; ANCOVA, $p < 0.001$), but did not affect estimated crustacean clearance rate ($CR = 1.22$ mL μgC$_Z^{-1}$ d^{-1} vs. $CR_{CORR} = 1.32$ mL μgC$_Z^{-1}$ d^{-1}; ANCOVA, $p = 0.906$).

plankton assemblages, excluding crustaceans, their impact on phytoplankton, bacteria, and nutrients could be mathematically subtracted from the effects of crustaceans (Nejstgaard et al. 2001) (Fig. 1).

Crustacean experiments were conducted in 10-liter, clear polystyrene bottles filled with lake water (collected from the central lake at 5 m) filtered through 150-μm mesh netting to remove crustaceans but retain the natural assemblage of phytoplankton, bacteria, and microzooplankton. Microscopic analyses revealed occasional juvenile cyclopoid copepodids up to 350 μm in length (stages I–III) present after filtration, but their biomass was only a small fraction of the microzooplankton biomass (mean $\pm$ SD; 12% $\pm$ 14%). Four replicate bottles each were then stocked with crustacean zooplankton (using the >150-μm fraction retained above) at either 0$\times$, 1$\times$, 2$\times$, and 4$\times$ naturally occurring densities. All 16 bottles were enriched with inorganic N (as NH$_4$Cl) and P (as Na$_2$HPO$_4$) at concentrations sufficient for saturating algal and bacterial uptake rates (as determined in preliminary experiments as $\sim$10% more than the amount producing maximum

phytoplankton growth rate and constrained to a molar N : P of 22 : 1, similar to the total nitrogen : total phosphorus of ambient lake water). Bottles were suspended for 24 h at 1.5–2-m depth in 5-m^3 outdoor tanks to provide natural light and thermal regimes. All bottles were sampled at 0 h and 24 h to determine initial and final concentrations of ammonia, total dissolved phosphorus, bacteria, chlorophyll *a*, phytoplankton, and zooplankton.

Microzooplankton experiments were conducted in 2-liter, clear polystyrene bottles suspended in outdoor tanks, as described above for crustacean experiments. Forty liters of lake water were collected from the central lake, filtered through 150-μm mesh to remove crustaceans and transferred to the laboratory. Half of this water, sequentially filtered through 63-μm mesh Nitex, 1.2-μm mesh glass-fiber, and 0.2-μm Nucleopore filters to remove all plankton (checked microscopically), was combined with the remaining nonfiltered lake water in ratios of unfiltered to filtered water of 1 : 0 (100% unfiltered, 1$\times$), 3 : 1 (0.75$\times$), 1 : 1 (0.50$\times$), and 1 : 3 (0.25$\times$) to create a series of dilutions. Four 2-liter bottles were filled with each dilution mixture, and excess N and P was added to each bottle as described above. All 16 bottles were sampled as in the crustacean experiments, except that only the 1 : 0 dilution bottles were sampled at 0 h. Concentrations of the various parameters in the remaining dilution treatments were calculated according to the dilution factor. All bottles were sampled at 24 h.

Laboratory analyses—Analyses of nutrient and plankton parameters were conducted according to standard methods. Ammonium and dissolved phosphorus concentrations were determined by flow-injection auto-analysis of 0.2-μm filtered water after, for phosphorus only, persulfate digestion at 100°C for 1 h (American Public Health Association 1998). Phytoplankton biomass$_{wet\ weight}$ was estimated by analyzing size-fractionated chlorophyll using fluorometry on whole and filtered (<2 μm, picophytoplankton; 2–25 μm, nanophytoplankton; >25 μm, netphytoplankton) water after 90% acetone extraction and by taxon-specific cell enumeration using an inverted microscopy on 3$\times$ concentrated (by sedimentation) samples after preservation in acidified Lugol's solution (Zohary 2004). Chlorophyll concentrations and cell densities were converted to equivalent phytoplankton biomass$_{wet\ weight}$ using conversion factors and geometric shape equivalents (Serruya 1978; Hart et al. 2000; Zohary 2004). Crustaceans and rotifers were enumerated and measured using microscopy and image analysis (Hambright and Fridman 1994) after preservation in 70% ethanol; densities were converted to biomass$_{wet\ weight}$ using Lake Kinneret–specific length-weight regressions. Flagellated protists and bacteria were enumerated and measured (bacteria only) using epifluorescent microscopy and image analysis after preservation in 1% glutaraldehyde (flagellates) or 0.5% filtered (0.45 μm) Formalin (bacteria) and staining using 4′,6-diamidino-2-phenylindole (Hadas and Berman 1998). Ciliated protists were enumerated using inverted microscopy on 10$\times$ concentrated (by sedimentation) samples after preservation in acidified Lugol's solution (Hadas and Berman 1998).

Protist and bacterial densities were converted to equivalent biomass$_{\text{wet weight}}$, and the biomass of all plankton components was converted to C (Simon and Azam 1989; Hart et al. 2000).

Grazing and nutrient mineralization calculations—For crustacean experiments, instantaneous rates of change, r, for each food resource, A (bacteria, picophytoplankton, nanophytoplankton, and netphytoplankton, as well as individual phytoplankton species) during the 24-h experiments were calculated as $\ln(A_f A_0^{-1})t^{-1}$, where A_0 and A_f are initial and final concentrations of the resource and t is experiment duration in days. Values of r_A were regressed (by least squares) against zooplankton biomass, Z, in the separate bottles to estimate the clearance rate, CR, as the $-$slope of the regression, $r = k - (CR)\,(Z)$, where k is the maximum potential growth rate of the resource (Lehman and Sandgren 1985). Ingestion rate, IR, was calculated as the product of CR and mean biomass of a resource, A', where $A' = (A_0 - A_f)[(r_A)\,(\Delta t)]^{-1}$ (i.e., $IR = CR \times A'$). Grazing mortality, g, was calculated as the product of CR and mean zooplankton biomass, Z', in each experiment.

For microzooplankton experiments, r for each food resource was regressed against the dilution factor, X, and g was estimated directly as the $-$slope of the linear equation, $r = k - gX$, where X is the dilution factor (i.e., $0.25\times$, $0.5\times$, $0.75\times$ and $1\times$ whole water) in the experimental bottles (Landry and Hassett 1982). After microzooplankton enumeration, mass-specific ingestion rates by microzooplankton for each resource were calculated as described above for crustaceans and used to correct the final (24 h) biomass of each resource in each 10-liter mesocosm in the paired crustacean experiments for losses caused by microzooplankton grazing (Nejstgaard et al. 2001), where, for example, $A_{t\text{-}CORR} = A_t + (IR_{microzoopl.} \times Z_{microzoopl.} \times r_A)$. Mean ($\pm$ SD) corrections as $\%A_t$ for bacteria, and picophytoplankton, nanophytoplankton, netphytoplankton, and total phytoplankton were $100.2\% \pm 81.7\%$, $62.5\% \pm 23.6\%$, $50.8\% \pm 46.7\%$, 0%, and $16.1 \pm 11.9\%$.

In both crustacean and microzooplankton experiments, absolute changes in nutrient concentrations during the 24-h period, standardized to the sum of algal and bacterial C, were regressed against zooplankton biomass (also standardized to algal and bacterial C) to estimate nutrient mineralization rates. Mass-specific nutrient mineralization rates for microzooplankton were used to correct final nutrient concentrations in each mesocosm of the paired crustacean experiment to account for changes in nutrient concentrations caused by microzooplankton mineralization. For all grazing and nutrient mineralization regressions, significance was set at $p \leq 0.05$ for the null hypothesis, H$_0$: $-$slope ≤ 0.

Results and discussion

In the winter–spring and summer–autumn plankton assemblages, crustaceans consumed bacteria and phytoplankton at daily rates equivalent to their own body mass as C (i.e., $\sim 1 \mu gC_{P+B} \mu gC_Z^{-1} d^{-1}$) (Fig. 2). These rates are similar to ingestion rates reported previously for other
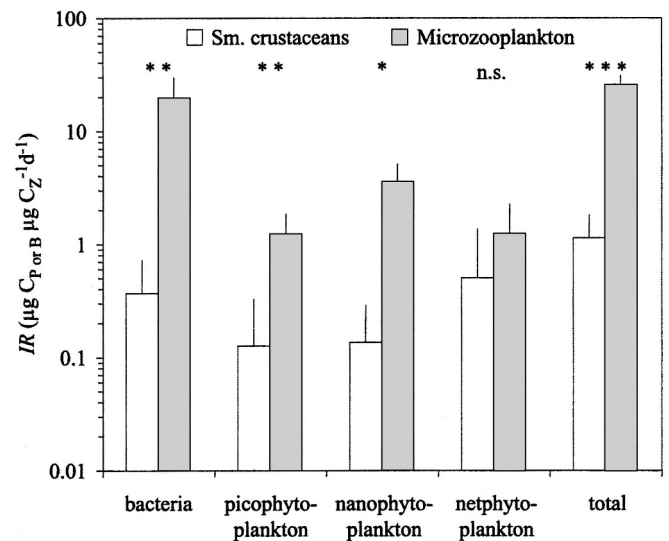

Fig. 2. Mean ($\pm$ SE, n = 4) mass-specific ingestion rates, IR ($\mu gC_{B \text{ or } P} \mu gC_Z^{-1} d^{-1}$), on bacteria (B) and phytoplankton (P) by small crustaceans and microzooplankton in Lake Kinneret. Phytoplankton was determined as size-fractionated chlorophyll for three sizes (picophytoplankton = <2.0 μm, nanophytoplankton = 2–25 μm, netphytoplankton = >25 μm); "total" refers to the sum of bacteria and phytoplankton C. Symbols above each pair of bars indicates results of paired t-tests; n.s. (not significant), $+(p \leq 0.1)$, $*(p \leq 0.05)$, $**(p \leq 0.01)$, $***(p \leq 0.001)$.

crustacean zooplankton (Cyr 1998), with $\sim 40\%$ of crustacean C derived from bacteria and $\sim 60\%$ from phytoplankton. In contrast, mass-specific ingestion rates of microzooplankton were ~ 20 times higher than ingestion rates of crustaceans, with most (>90%) C ingested by microzooplankton in the form of bacteria. These ingestion rates seem high, for example, compared to the findings of Hadas et al. (1998), in which the ciliate *Colpoda steinii* isolated from Lake Kinneret grazed fluorescently labeled bacteria at rates equivalent to $\sim 2 \mu gC \mu gC^{-1} d^{-1}$. Nevertheless, our measured ingestion rates are well within the range of rates reported for other systems. Assuming a carbon content of 10–14% wet weight for algae and ciliates (Putt and Stoecker 1989; Hart et al. 2000), Müller (1991) and Kenter et al. (1996) report ciliate ingestion rates equivalent to 1–24 $\mu gC \mu gC^{-1} d^{-1}$. Mass-specific ingestion rates by heterotrophic nanoflagellates can be 1–30 times higher than ciliate ingestion rates (Sanders et al. 1989). Moreover our results are in line with predictions derived from body size and metabolic rate relationships (Brown et al. 2004). For example, assuming metabolism varies as a negative quarter power of body mass (i.e., mass$^{-0.25}$), the metabolism (and presumably ingestion rates) of an individual *Ceriodaphnia* ($\sim 5 \mu g_{\text{dry weight}}$) would be expected to be approximately 20% of the metabolic rate of a 7 ng$_{\text{dry weight}}$ ciliate and only about 5% of the metabolic rate of a 30 pg$_{\text{dry weight}}$ flagellate. Jürgens et al. (1996) reported ciliate clearance rates $\sim 3–6$ times higher than those of *Ceriodaphnia* and *Bosmina*, and Tirok and Gaedke (2006) assumed similarly high values in their analysis of the relative importance of ciliates in Lake Constance.
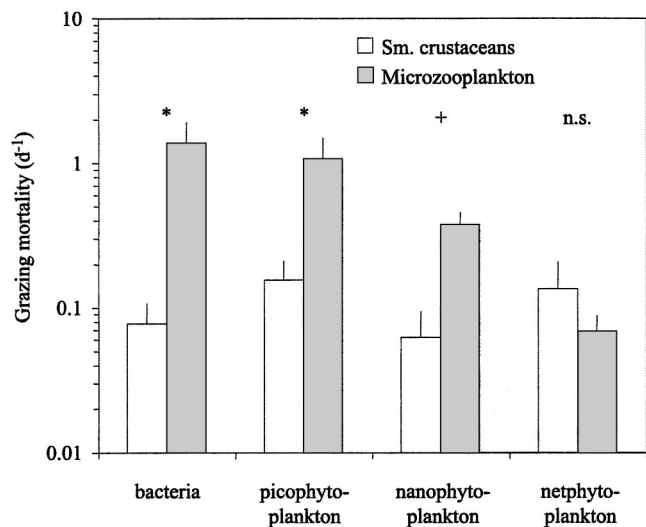
Fig. 3.   Mean ($\pm$ SE, n = 4) grazing mortalities, g (d^{-1}), for bacteria and phytoplankton inflicted by small crustaceans and microzooplankton in Lake Kinneret. Labels as in Fig 2.

From the viewpoint of population dynamics, microzooplankton grazing inflicted substantially higher mortalities (up to 10 times higher) on both phytoplankton and bacteria than did crustaceans (Fig. 3). Bacterial and phytoplankton mortalities caused by grazing by crustaceans amounted to a fraction of maximum potential growth rates for bacteria and picophytoplankton, nanophytoplankton, and netphytoplankton (mean $\pm$ SE; 12% $\pm$ 8%, 25% $\pm$ 12%, 42% $\pm$ 25%, and 0%), whereas mortalities due to microzooplankton grazing were similar in magnitude to measured maximum potential growth rates for these four food resources (103% $\pm$ 21%, 184% $\pm$ 65%, 96% $\pm$ 26%, 100% $\pm$ 0%). Moreover, crustaceans showed little size selectivity across food resources, whereas microzooplankton inflicted the highest mortalities on bacteria (mean $\pm$ SE; 1.37 $\pm$ 0.54 d^{-1}) and picophytoplankton (1.07 $\pm$ 0.41 d^{-1}) and progressively lower mortalities on nanophytoplankton (0.38 $\pm$ 0.08 d^{-1}) and netphytoplankton (0.07 $\pm$ 0.02 d^{-1}). These results suggest that microzooplankton grazing may be a strong, if not the major, driving force affecting bacteria and phytoplankton population and community dynamics in this system.

In addition to size-selective grazing, microscopic analyses of the phytoplankton revealed a strong taxonomic selection of phytoplankton resources by both grazer guilds and that taxon-specific grazing was seasonally dependent.

Table 1.   Number of phytoplankton taxa grazed in single winter–spring or summer–fall grazer-gradient or dilution experiments with Lake Kinneret grazers.

Grazer	Number of phytoplankton taxa	
	Winter–spring	Summer–fall
Small crustaceans*	16	5
Microzooplankton†	19	17
Both grazers	4	2
Neither grazer	15	28

* Small crustaceans are *Bosmina*, *Ceriodaphnia*, *Chydorus* and juvenile cyclopoid copepods.
† Microzooplankton are ciliated and flagellated protists and rotifers.

Of the nearly 50 phytoplankton taxa abundant enough for statistically valid counts in each season (Zohary 2004), 80% of the taxa in the winter–spring assemblage was grazed by one or the other grazer guild, whereas only 42% of the taxa in the summer–fall assemblage was grazed (Table 1). There was little overlap in resource use, however, as only four phytoplankton taxa were significantly grazed by both microzooplankton and crustacean grazers in the winter–spring and only two in the summer–fall assemblages. Analysis of taxonomic affiliation (e.g., division), size, motility, growth form (e.g., single cell, colony, or coenobium), and the presence or absence of gelatinous sheaths revealed no discernible patterns in selection (data not shown).

Nutrient mineralization rates of phosphorus and nitrogen by crustaceans were 0.04 μgP μgC$_Z$$^{-1}$ d^{-1} and 0.36 μgN μgC$_Z$$^{-1}$ d^{-1} (Table 2), notably higher than those typically measured for large crustaceans, such as *Daphnia* (Attayde and Hansson 1999), but expected, given the small body sizes of Lake Kinneret crustaceans (sensu Brown et al. 2004). Excretion rates by microzooplankton were substantially higher (2.8 μgP μgC$_Z$$^{-1}$ d^{-1} and 20 μgN μgC$_Z$$^{-1}$ d^{-1}) than crustacean excretion rates. It is important to note that these measurements of nutrient excretion were made under nutrient uptake rate–saturating conditions and should therefore be considered maximal estimates of nutrient mineralization by the grazers. Nevertheless, because resource conditions (i.e., algal and bacterial assemblages, nutrient concentrations) were similar across grazer-gradient and dilution experiments, a comparison of excretion rates between the two grazers is meaningful. Moreover, the 50- to 70-fold higher mass-specific nutrient mineralization rates by microzooplankton correspond well with expectations from general metabolic theory (Brown et

Table 2.   Crustacean and microzooplankton nutrient mineralization. Mean ($\pm$ 95% CI) mass-specific crustacean and microzooplankton nutrient mineralization rates (μgP or N μgC$_Z$$^{-1}$d^{-1}) for Lake Kinneret grazers, n = 3 for each grazer. Nutrient pool turnover rates were calculated from representative concentrations of total dissolved phosphorus (7.5 μg P L^{-1}) and ammonia (150 μg N L^{-1}) and biomass of crustaceans (53 μgC$_Z$ L^{-1}) and microzooplankton (7.5 μgC$_Z$ L^{-1}) (data from the Lake Kinneret Database of the Kinneret Limnological Laboratory, Migdal, Israel).

Grazer	Excretion rate (μgP μgC$_Z$$^{-1}$d^{-1})	P pool turnover (d)	Excretion rate (μgN μgC$_Z$$^{-1}$d^{-1})	N pool turnover (d)
Crustaceans	0.04 ($\pm$0.02)	3.6	0.36 ($\pm$0.24)	10.2
Microzooplankton	2.8 ($\pm$1.1)	0.36	20.0 ($\pm$0.9)	1.1

al. 2004). Although the molar N : P of k (maximum potential nutrient uptake rates by phytoplankton and bacteria from the regression of change in nutrients with grazer biomass [Lehman and Sandgren 1985]) indicated that the phytoplankton and bacterial assemblages were generally P-limited (mean $\pm$ 95% CI N : P$_k$ = 9.1 $\pm$ 1.9), little evidence suggests grazer P excretion rates were substantially enhanced by the higher uptake of P by phytoplankton and bacteria. Enhanced P uptake by phytoplankton and bacteria may have positively affected the rate of P excretion by the crustaceans. The mean ($\pm$ 95% CI) N : P of their excretion rates (14.4 $\pm$ 4.0) was slightly lower than the initial nutrient spike of 22 : 1. However, the mean ($\pm$ 95% CI) N : P of mineralization by microzooplankton (19.8 $\pm$ 3.9) was not different from the initial nutrient spike, nor from the crustacean excretion N : P. Alternatively, selective retention of N by crustaceans (which would also lower the N : P of excretion) is consistent with the relatively high abundances of cyclopoid copepodids in Lake Kinneret crustacean assemblage (sensu Sterner and Elser 2002).

Given the above considerations, some speculation regarding both the absolute and relative potential impacts of microzooplankton and crustaceans on nutrient cycling in the lake is valid. Based on representative concentrations of total dissolved phosphorus and ammonia and grazer biomass in the lake, microzooplankton excretion could account for more than 85% of the daily P and N mineralization, turning over the ambient dissolved pools of these nutrients in the lake in a tenth of the time of nutrient turnover by crustaceans (Table 2). Such high nutrient turnover by microzooplankton in this highly productive system is more typical of that found in substantially less productive lakes (Hudson and Taylor 1996). Thus, not only are microzooplankton potentially driving bacteria and phytoplankton population dynamics through high grazing mortalities in this mesoeutrophic lake, but our results also suggest that microzooplankton are primary sources of nutrients available (via mineralization) for primary production in Lake Kinneret, even during winter–spring when external nutrient loading is highest and internal recycling of nutrients is considered to be of secondary importance (Hart et al. 2000). Our comparisons also suggest that because the pool of dissolved P in Lake Kinneret may be recycled nearly three times faster than the ambient pool of ammonia, conclusions of general P limitation in Lake Kinneret based on nutrient bioassays and static measures of ambient nutrients in the lake (Hart et al. 2000) may actually underestimate the importance of recycling by the grazer assemblage. Higher rates of nutrient mineralization by smaller zooplankton, coupled with warmer temperatures, may provide a reasonable explanation for the general observation of higher primary production relative to nutrient loading in tropical and subtropical lakes (Mazumder and Havens 1998; Wetzel 2001).

There is growing recognition in terrestrial ecology that the decomposer (below ground) and primary producer (above ground) components of food webs are inextricably linked, influencing structure, composition, and functioning of community- and ecosystem-level processes (Wardle et al.

2004; Bezemer et al. 2005). Marine ecologists have long appreciated the importance of bacteria and microbial grazers in carbon and nutrient fluxes in the open ocean (Azam et al. 1983). Similarly, intensive study of allochthonous carbon inputs from riparian vegetation and the associated microbes and invertebrate grazers that process these materials have documented major roles of allochthonous carbon in energy and nutrient budgets of streams (Allan 1995). Limnologists have described similar important roles for bacteria and microzooplankton in predominantly oligo- and mesotrophic freshwater pelagic habitats (Porter 1996; Cole 1999), although detailed analyses of microzooplankton ecology across systems differing in trophic structure and dynamics (e.g., oligotrophic and eutrophic, with and without fish, with and without *Daphnia*) are lacking. The complex assemblage of coexisting small crustacean zooplankton and microzooplankton in Lake Kinneret offered a unique opportunity to examine both grazing and nutrient mineralization in these two important grazer guilds simultaneously and under the same environmental and food conditions. Even though microzooplankton standing stock biomass was low (only 14% of the standing biomass of crustaceans), our study demonstrates that in a mesoeutrophic freshwater pelagic system regulated by high fish zooplanktivory, in which the crustacean zooplankton assemblage is dominated by small species, coexisting microzooplankton can be major consumers of phytoplankton and bacteria and thus be key sources of mineralized nutrients supporting production. Similar experiments (i.e., gradient assays) (Blumenshine and Hambright 2003) have revealed that the diets of omnivorous and predatory crustaceans in Lake Kinneret (predominantly cyclopoid copepods) are composed of herbivorous crustaceans ($\sim$80%) and microzooplankton ($\sim$20%). Because cyclopoid copepods are key constituents in planktivorous fish diets in the lake (Blumenshine and Hambright 2003), we believe that our results challenge traditional views of aquatic food webs, suggesting that the current paradigm of pelagic trophic dynamics may need reformulation to address appropriately the general role of microbial grazers and the transfer of detrital-based carbon and nutrients to higher trophic levels in freshwater lakes.

In a review of potential roles of detritus in trophic dynamics and biodiversity, Moore et al. (2004) conclude that the infusion of detrital-based energy into a community and its passage to top predators can affect the diversity, structure, and dynamic properties of those communities and call for further study of the consumption and assimilation of detritus and microbes to better reconcile the brown and green pathways in food webs. Our study in the pelagic community of a subtropical mesoeutrophic lake corroborates their assertion that the distinction between living primary production-based and detrital-based portions of food webs is an artificial construct and may impede our understanding of food webs in nature.

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