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Calanoid copepods versus cladocerans: Consumer effects on protozoa in lakes of different trophic status

Abstract—Through their consumption of protozoa, cladocerans and copepods link classical food chains and microbial food webs in aquatic ecosystems. Published results of studies of the effects of these metazooplankton on protozoa in lakes allow few generalizations to be made. To determine if general patterns exist along a trophic gradient, we measured the effects of cladocerans and calanoid copepods on heterotrophic nanoflagellates (HNF) and ciliates in four lakes that ranged from ultraoligotrophic to eutrophic using the same methodology. Copepods (*Boeckella* spp.), and to a lesser extent cladocerans (*Daphnia*, *Ceriodaphnia*), had significant negative effects on the growth of protozoa, and the rates at which both groups cleared protozoa from the water were higher in nutrient-poor conditions than in nutrient-rich conditions. In two oligotrophic lakes, calanoid copepods ingested HNF at biomass-specific rates that were 2.2 times higher than those of cladocerans. Rates of ciliate ingestion by copepods, relative to cladocerans (top-down effects on the ciliate community), increased with lake productivity from 2.5 times higher in an ultraoligotrophic lake to 9.5 times higher in a mesotrophic lake. Our study shows that copepods are more effective consumers of protozoa than cladocerans, particularly in eutrophic conditions.

Protozoa are integral components of the microbial food webs in lakes and the sea where they provide trophic links between primary producers, bacteria, and the metazoan zooplankton. The major protozoa in these aquatic systems are generally ciliates and heterotrophic flagellates (HNF). It is now well established that cladocerans and calanoid copepods will consume HNF and ciliates (e.g., Stoecker and Capuzzo 1990; Burns and Gilbert 1993; Pace and Vaqué 1994), but most studies of the top-down effects of metazooplankton on microbial food webs have focused only on one lake (e.g., Carrick et al. 1991; Wiackowski et al. 1994; Havens and Beaver 1997; Wickham 1998; Adrian and Schneider-Olt 1999; Jürgens et al. 1999), only on one group of protozoa (e.g., Wiackowski et al. 1994; Gasol et al. 1995; Havens and Beaver 1997; Herbst 1998), or only on *Daphnia* as consumers (e.g., Pace and Funke 1991; Jürgens et al. 1994; Pace et al. 1998).

The effect of cladocerans and copepods on populations of protozoa in lakes in these studies is inconsistent. For example, cladocerans appeared to control HNF in some eutro-

phic and mesotrophic lakes (Jürgens et al. 1994; Pace and Vaqué 1994; Herbst 1998) but had no detectable effect on the growth of HNF in other lakes (Pace and Vaqué 1994; Burns and Schallenberg 1998). In mesotrophic Schöhsee, North Germany, *Daphnia* reduced the ciliate community significantly in early summer, but had no effect on ciliates 1 month earlier (Wickham 1998). Calanoid copepods reduced the growth of HNF in eutrophic Lake Biwa, Japan (Nagata et al. 1996), and in some oligotrophic lakes (Carrick et al. 1991; Burns and Schallenberg 1998), but not in other oligotrophic and mesotrophic lakes (Jürgens et al. 1994; Burns and Schallenberg 1996; Carrias et al. 1998). Cyclopoid copepods had little or no effect on ciliates in eutrophic Lake Okeechobee (Havens and Beaver 1997) but had strong effects in mesotrophic Schöhsee (Wickham 1998) and a hypertrophic lake in Denmark (Jürgens et al. 1999). Differences in methods, experimental design, and data analysis reduce the extent to which the results of these studies can be compared and the conclusions generalized.

Although calanoid copepods and cladocerans occur in most lakes, there have been only a few comparisons of their consumer effects on microbial food webs. In studies of the short-term effects of *Daphnia* and calanoid copepods on protozoa in mesotrophic lakes in New Zealand and Germany, the negative effect of copepods on ciliates was much stronger than that of *Daphnia* (Burns and Schallenberg 1996; Adrian and Schneider-Olt 1999). In contrast, *Daphnia rosea* was as effective as the copepod, *Diaptomus novamexicanus* in depressing ciliate growth in a short-term study in Castle Lake, California (Brett et al. 1994; Wiackowski et al. 1994).

Numerous factors have the potential to influence the effect of cladocerans and copepods on planktonic microbial food webs. Among them are the diversity, the biomasses and production of microorganisms, and the feeding behaviors and biomasses of the crustacean zooplankton. Our aim was to compare the consumer effects of cladocerans and calanoid copepods on protozoa in lakes of different trophic state to determine if general patterns exist that might be related to microbial or phytoplankton biomass. Our study developed from a more intensive investigation of the effects of nutrients and crustacean zooplankton on microbial food webs of lakes

Table 1. Description of Lakes Wakatipu, Manapouri, Mahinerangi, and Hayes (data from Livingston et al. 1986) and characteristics at the time of experiments. Dc, *Daphnia carinata*; Cd, *Ceriodaphnia dubia*; Bh, *Boeckella hamata*; Bd, *Boeckella dilatata*. Mean biomass ($\mu\text{g dw}$) per adult in parentheses. DIN is dissolved inorganic nitrogen; SRP is soluble reactive phosphorus.

	Wakatipu	Manapouri	Mahinerangi	Hayes
Latitude, longitude	45°02'S, 168°42'E	45°34'S, 167°34'E	45°52'S, 169°58'E	44°59'S, 168°48'E
Surface area (km ²)	289	143	18.6	2.03
Maximum depth (m)	380	444	31.2	35
Epilimnetic temperature (°C)	14	16	13.1	18.3
Secchi depth (m)	8.5	10.3	1.05	2.48
Chl <i>a</i> ($\mu\text{g L}^{-1}$)	0.31	0.85	3.10	5.78
Total nitrogen (μM)	4.9	4.0	8.1	18.6
Total phosphorus (μM)	0.14	—	0.32	0.36
Nutrients added to enclosures				
DIN as NH_4Cl (μM)	7.1	18.6	17.1	22.9
SRP as KH_2PO_4 (μM)	0.16	0.9	0.65	1.48
Zooplankton added to enclosures				
Cladocera (number L^{-1})	Cd 2,8(7)	Dc 1,4(38)*	Dc 2,8(36)	Dc 2,8(36)
Copepoda (number L^{-1})	Bd 1,4(11)	Bh 1,4(10.9)*	Bh 2,8(11)	Bd 2,8(10.7)

* Collected in another lake. —, no data.

of different trophic state in New Zealand, some results of which have been published (Burns and Schallenberg 1996, 1998). We determined the composition and biomass of the major components of the microbial food webs of four lakes in South Island, New Zealand, that range from ultraoligotrophic to eutrophic (Table 1). By manipulating nutrients and zooplankton in enclosures in the lakes, we show that calanoid copepods are more effective than cladocerans at removing protozoa, particularly ciliates. As phytoplankton and microbial biomasses increase (lakes becomes more eutrophic), copepods become increasingly more effective than cladocerans as potential consumers of ciliates. A strength of our study is that the same experimental design and procedures were used in each lake.

Materials and methods—Epilimnetic water collected in each lake in summer was screened through 150- μm mesh to remove most of the metazooplankton and mixed in large, covered, plastic barrels. Thirty, 4.25-liter clear, polyethylene enclosures were filled with the well-mixed water, after which nutrients and zooplankton at two densities were added in a combined factorial and gradient design. To stimulate production, inorganic nutrients (NH_4Cl and KH_2PO_4) were added to half of the enclosures to approximate the highest concentrations of these nutrients that have been recorded in the lakes (Table 1). Because variation in zooplankton-imposed mortality of protozoa is strongly related to body size of *Daphnia* (Pace and Vaqué 1994) and calanoid copepods (Burns and Gilbert 1993), we used similar-sized adult zooplankton where possible. Adult cladocerans (*Daphnia carinata* King, length 1.9–2.2 mm; *Ceriodaphnia dubia* Richard, length \sim 0.9 mm) and calanoid copepods (*Boeckella hamata* Brehm, prosome length 0.91–1.06 mm; *Boeckella dilatata* Sars, prosome length \sim 0.97 mm) were added to the enclosures at densities of 0, 1, 2, 4, or 8 individuals L^{-1} (Table 1). These densities were within the recorded ranges for the lakes. Each treatment with added nutrients and cladoceran or copepod grazers was replicated three times, as were con-

trol enclosures without nutrients and/or grazers, to make a total of 30 enclosures per lake.

The enclosures were suspended below the surface in the epilimnion of each lake for 4 d. Samples of the water used to fill the enclosures were taken at time 0 for analysis of chlorophyll *a* (Chl *a*) and microorganisms (see below). The enclosures were sampled after 1 d, when top-down (consumer) effects of the crustaceans were expected to be strongest because 24 h is too short for most microorganisms to multiply significantly in response to nutrients (e.g., Carrick et al. 1991), and again after 4 d to allow the microbial community to respond to the combined effects of consumption and nutrient recycling. Water that was removed during sampling after 1 d was replaced with freshly collected 150- μm -filtered water from the lake, and the fertilized enclosures received a second dose of nutrients at the same level as the initial dose before they were resuspended at the incubation depth for a further 3 d. When the enclosures were removed on day 4, they were subsampled again for microorganisms, after which the entire content of each enclosure was filtered through 150- μm netting to retrieve the crustacean zooplankton, which was sorted, rinsed, dried, and weighed on a microbalance (Sartorius; \pm 0.5 μg) to obtain the biomass of cladocerans or copepods in each enclosure.

The methods of analysis of nutrients, microorganisms, and zooplankton have been described by Burns and Schallenberg (1996, 1998). Concentrations of Chl *a* were measured fluorometrically; samples for ciliates and small algae were preserved with Lugol's iodine solution and counted under an inverted microscope; samples for autotrophic picoplankton (APP) and flagellates were fixed with glutaraldehyde, stained with primulin (Bloem et al. 1986), and collected on 0.2- and 0.8- μm black polycarbonate filters, respectively, for counting by epifluorescence microscopy; bacteria were fixed with formalin, stained with 4',6-diamidino-2-phenylindole (DAPI), and concentrated on black 0.2- μm filters for counting under an epifluorescence microscope.

Net daily growth rates of microorganisms in each enclosure were calculated as:

$$\ln[(N_t/N_0)]/t, \quad (1)$$

where N_0 is the initial concentration of microorganisms and N_t is the concentration after 1 or 4 d. The net effects of zooplankton biomass on the growth rates of protozoa in the fertilized and unfertilized enclosures were analyzed by regression with biomass as the independent variable. Clearance rates, or the rates at which cladocerans and copepods removed protozoa from the water ($\text{ml } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) were derived from the slopes of simple linear regressions that related protozoan growth rate to zooplankton biomass ($\mu\text{g dwt L}^{-1}$) (Lehman 1980) when $P < 0.15$. Ingestion rates ($\text{ng C } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) were calculated as the product of clearance rates and the average biomass of protozoa in enclosures without added zooplankton at the start and end of the incubation period.

Biomasses of the major components of the microbial food webs in each lake were expressed in units of carbon (C, in $\mu\text{g C L}^{-1}$) derived from Chl *a* concentrations, cell densities, and cell volumes of protozoa (based on measurements of ~ 40 cells of each major taxon) and published conversion factors. These factors were: phytoplankton = Chl *a* ($\mu\text{g L}^{-1}$) $\times 50$ (Strickland and Parsons 1972); heterotrophic bacteria = $20 \text{ fg C cell}^{-1}$ (Li et al. 1992); APP = $250 \text{ fg C cell}^{-1}$ (Li et al. 1992); protozoa = $0.4 \text{ pg dwt } \mu\text{m}^{-3}$ and $0.5 \mu\text{g C } (\mu\text{g dwt})^{-1}$ (Borsheim and Bratbak 1987).

Results—Microbial food web composition: The total carbon biomass of microplankton ($<150 \mu\text{m}$) in the epilimnion of the four lakes and the relative contributions of autotrophs and heterotrophs are shown in Fig. 1. There was a clear gradient of increasing microplankton biomass in the epilimnion of the four lakes with biomasses in Lakes Manapouri, Mahinerangi, and Hayes that were 1.9 times, 5.6 times, and 13 times larger, respectively, than the $40 \mu\text{g C L}^{-1}$ in Lake Wakatipu (Fig. 1, upper panel). Autotroph biomass was 18 times higher in Lake Hayes than in Lake Wakatipu and contributed $>50\%$ of the total microplankton biomass in all of the lakes except Lake Wakatipu, where it contributed 41% (Fig. 1, lower panel). In Lakes Wakatipu and Manapouri, picocyanobacteria were the dominant autotrophs, whereas eukaryotic phytoplankton dominated the autotrophic biomass in the other two lakes. Ranked in order of increasing trophic state based on autotrophic biomass, the lakes were: Lake Wakatipu $<$ Lake Manapouri $<$ Lake Mahinerangi $<$ Lake Hayes.

The biomasses of heterotrophs increased also with lake trophic state. The biomass of heterotrophic bacteria ranged from $5.4 \mu\text{g C L}^{-1}$ in Lake Wakatipu to $175 \mu\text{g C L}^{-1}$ in Lake Hayes and accounted for 13.6 and 33.7%, respectively, of total microplanktonic carbon in these lakes. HNF biomass was lowest in Lake Manapouri ($12.6 \mu\text{g C L}^{-1}$) and highest in Lake Hayes ($44 \mu\text{g C L}^{-1}$); HNF decreased as a percentage of total microplanktonic carbon with increasing lake trophic state (Fig. 1, lower panel). Ciliate biomass and contributions to total microplanktonic carbon increased 77-fold across the lake trophic gradient from $0.15 \mu\text{g C L}^{-1}$ in Lake Wakatipu (0.4% of biomass) to $11.5 \mu\text{g C L}^{-1}$ in Lake Hayes (2.3% of biomass). The relative contribution of protozoa (HNF, ciliates) to total microplanktonic carbon in the lakes decreased

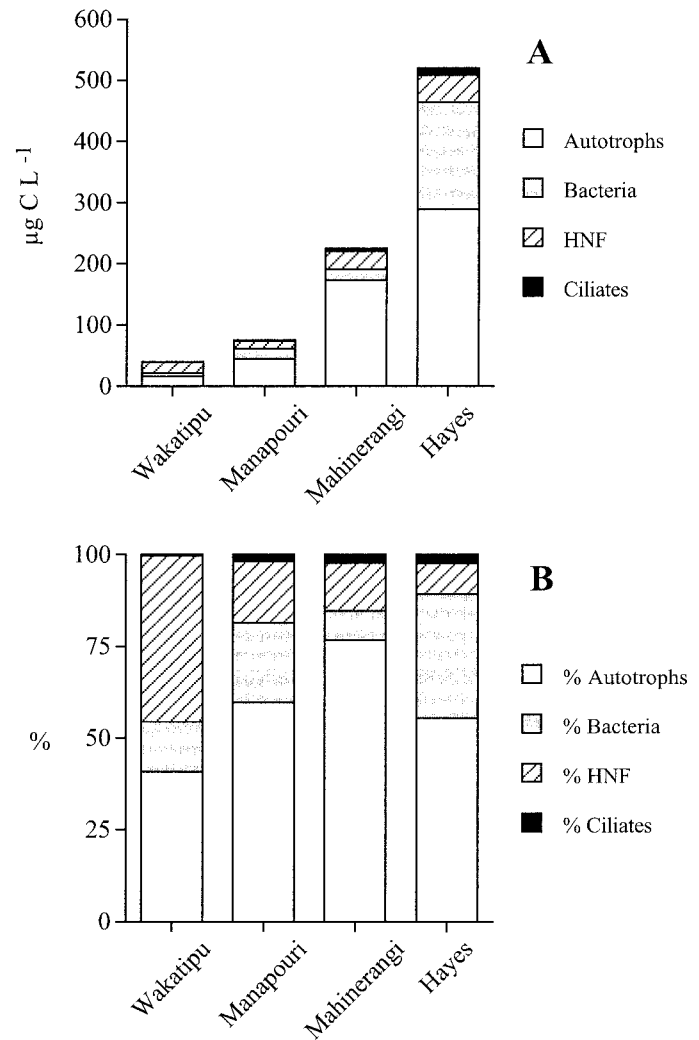


Fig. 1. Biomass of microplankton $<150 \mu\text{m}$ in the epilimnion of Lakes Wakatipu, Manapouri, Mahinerangi, and Hayes in summer. (A) Biomass, expressed as $\mu\text{g C L}^{-1}$, of autotrophs (derived from Chl *a*) and the major heterotrophs (bacteria, HNF, ciliates). (B) Percentage of contributions of autotrophs and the major heterotrophs to total carbon biomass $<150 \mu\text{m}$.

with increasing trophic state owing to the dominant contribution of HNFs to total protozoan biomass in the lakes.

Clearance and ingestion rates: The rates at which the added zooplankton removed and ingested protozoa after 1 and 4 d are shown in Figs. 2, 3 and Tables 2, 3. The individual mean dry biomasses ($\mu\text{g dwt}$) of the copepods and cladocerans added to the enclosures are shown in Table 1. After 1 d, *Boeckella* cleared HNF from Lake Wakatipu at rates of $9.6\text{--}10 \text{ ml } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$ (ingestion rates, $169\text{--}178 \text{ ng C } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$), and *Ceriodaphnia* removed them from Lake Wakatipu at a rate of $4.8 \text{ ml } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$ (ingestion rate, $85 \text{ ng C } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) (Fig. 2, Table 2). The rates of removal of HNF by copepods and cladocerans after 4 d ranged from $0.7 \text{ ml } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$ to $6.2 \text{ ml } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$ and tended to decrease with lake trophic state (Fig. 2). Ingestion rates by *Daphnia* ranged from $46 \text{ ng C } (\mu\text{g dwt})^{-1}$

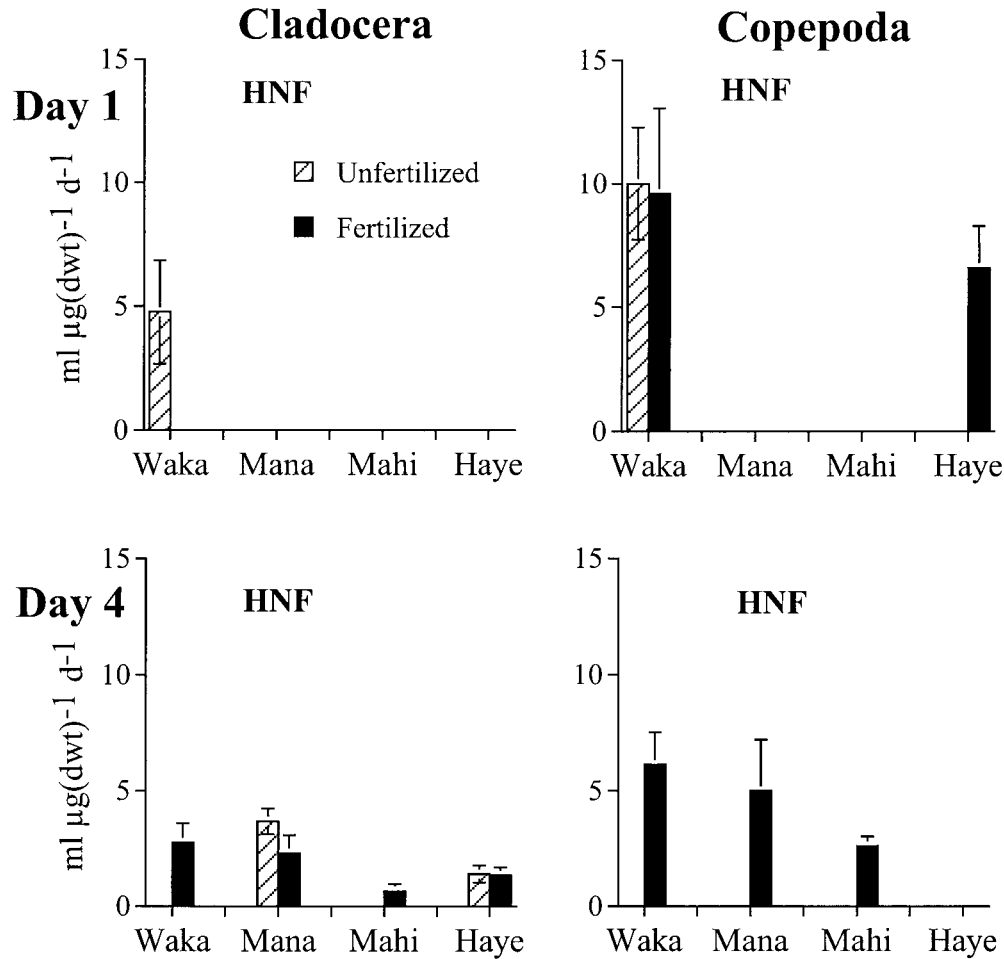


Fig. 2. Rates of clearance (± 1 SE) of HNF by cladocerans and copepods ($\text{ml } [\mu\text{g dwt}]^{-1} \text{d}^{-1}$) from unfertilized and fertilized enclosures in Lakes Wakatipu (WAKA), Manapouri (MANA), Mahinerangi (MAHI), and Hayes (HAYE) after 1 (upper panels) and 4 d (lower panels). Clearance rates were not calculated when linear regressions relating HNF growth rate to crustacean biomass were $P > 0.15$.

Table 2. Ingestion rates ($\text{ng C } [\mu\text{g dwt}]^{-1} \text{d}^{-1}$) of cladocerans and copepods, derived from their rates of clearance of HNFs and ciliates, and the mean biomasses of protozoa in enclosures without added zooplankton after 1 d. Inorganic nutrients (N, P) were added to some enclosures (Nutrients). —, Clearance rates not calculated.

	Cladocerans		Copepods	
	No nutrients	Nutrients	No nutrients	Nutrients
HNFs				
Wakatipu	84.7	—	178.0	169.3
Manapouri	—	—	—	—
Mahinerangi	—	—	—	—
Hayes	—	—	—	457.3
Ciliates				
Wakatipu	—	—	7.9	8.4
Manapouri	10.4	5.9	26.3	26.3
Mahinerangi	—	—	25.8	23.5
Hayes	—	—	77.8	—

d^{-1} in oligotrophic Lake Manapouri to $264 \text{ ng C } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in eutrophic Lake Hayes (Table 3).

The rates of removal of ciliates after 1 d ranged from $4 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ for *Daphnia* in Lake Manapouri to $37.6 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ for *Boeckella* in Lake Wakatipu (Fig. 3). These rates of ciliate removal by copepods declined with increasing lake trophic state and were lower in enriched enclosures than in enclosures without added nutrients. This pattern, after 1 d, of decreasing clearance rates with increasing lake productivity also was evident after 4 d, when rates of ciliate clearance by copepods decreased from $23 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in Lake Wakatipu to $2.5 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in Lake Hayes, and the clearance rates of cladocerans decreased from $9 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in Lake Wakatipu to $0.4 \text{ ml } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in Lake Mahinerangi; clearance rates were also lower in nutrient-enriched than in unfertilized enclosures (Fig. 3, day 4; paired *t*-test on mean clearance rates; $n = 7$, $t = 2.084$, $P = 0.041$).

The rates at which copepods ingested ciliates increased with lake trophic state from $8 \text{ ng C } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in fertilized enclosures in Lake Wakatipu to $65 \text{ ng C } (\mu\text{g dwt})^{-1} \text{d}^{-1}$ in

Table 3. Ingestion rates ($\text{ng C } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) of cladocerans and copepods, derived from their rates of clearance of HNFs and ciliates, and the mean biomasses of protozoa in enclosures without added zooplankton after 4 d. Inorganic nutrients (N, P) were added to some enclosures (Nutrients). —, Clearance rates not calculated.

	Cladocerans		Copepods	
	No nutrients	Nutrients	No nutrients	Nutrients
HNFs				
Wakatipu	—	52.5	—	116.4
Manapouri	55.1	45.6	—	99.3
Mahinerangi	—	—	—	—
Hayes	131.5	264.1	—	—
Ciliates				
Wakatipu	5.6	3.6	14.3	8.4
Manapouri	4.7	2.7	19.4	17.3
Mahinerangi	2.8	3.0	24.4	28.6
Hayes	—	—	51.1	64.9

the fertilized enclosures in Lake Hayes (Table 3). In contrast, cladocerans ingested ciliates at $<6 \text{ ng C } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$.

Protozoan contributions to crustacean carbon: We estimated the potential contributions of protozoa to the carbon requirements of cladocerans and copepods in our study from their rates of ingestion of HNF and ciliates and from ratios of carbon to dry weights of similar-sized adult *Daphnia* and a calanoid copepod, *Eudiaptomus gracilis* (Muck and Lampert 1984). Based on these ratios, the carbon contents of adult *D. carinata* (mean = $37 \mu\text{g dwt}$) and *Boeckella* ($11 \mu\text{g dwt}$) in our study were assumed to be $13.4 \mu\text{g C}$ and $4.8 \mu\text{g C}$, respectively. *Daphnia* replaces approximately 3.5%, and *Eudiaptomus* 1%, of body carbon per hour (Muck and Lampert 1984), which amounts to $11.26 \mu\text{g C d}^{-1}$ for *D. carinata* and $1.15 \mu\text{g C d}^{-1}$ for *Boeckella* at the same rates of carbon replacement. Based on these rates of carbon replacement, the ingestion of ciliates provided less than 3.4% of the daily carbon needs of *Daphnia* in our study, but 7.5–74.3% of the daily carbon requirements of *Boeckella*, thereby confirming the importance of ciliates in the diet of cal-

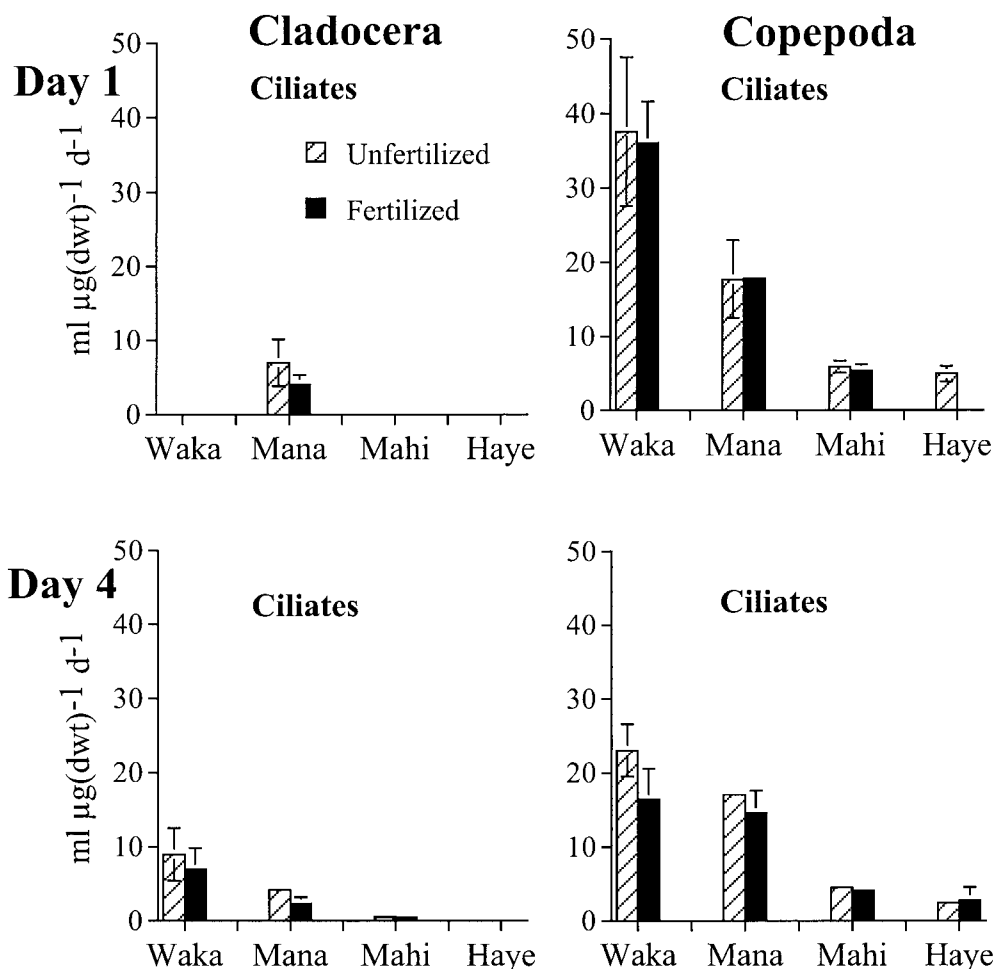


Fig. 3. Rates of clearance ($\pm 1 \text{ SE}$) of ciliates by cladocerans and copepods ($\text{ml } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) from unfertilized and fertilized enclosures in Lakes Wakatipu (WAKA), Manapouri (MANA), Mahinerangi (MAHI), and Hayes (HAYE) after 1 (upper panels) and 4 d (lower panels). Clearance rates were not calculated when linear regressions relating ciliate growth rate to crustacean biomass were $P > 0.15$.

anoid copepods (Sanders et al. 1996). The potential contribution of HNF exceeded that of ciliates, however. The consumption of HNF by *Daphnia* met 15–86.6% of their daily carbon requirements, and HNF provided 94.8% to more than four times the daily carbon needs of *Boeckella*. HNF may have been utilized poorly by copepods, however. In experiments to determine the reproductive success of cladocerans and calanoid copepods fed diets of algae and protozoa, a HNF (*Paraphysomonas*) was a high-quality food for *Daphnia pulicaria* but was of little utility to *Diaptomus oregonensis*, despite being ingested by the copepod at a rate of $\sim 1,400 \text{ ng C } (\mu\text{g dwt})^{-1} \text{ d}^{-1}$ (Sanders et al. 1996). Calanoid copepods also have nutritional requirements beyond carbon content, and nutrient ratios that are poorly understood (Von Elert and Stampfl 2000). We might also have overestimated ingestion rates if predation on HNF by other protozoa in the enclosures contributed to lowering the abundance of HNF in the presence of copepods and cladocerans, although this is unlikely. In experiments in two eutrophic lakes using similar methods to ours, Pace and Vaqué (1994) found that predation on protozoa by larger protozoa and microzooplankton was insignificant.

Lake productivity and crustacean control of protozoa: Calanoid copepods were clearly more effective per unit biomass than cladocerans at removing protozoa from lakes of different productivity. In the four lakes that we studied, the biomasses of HNF and ciliates increased with increasing autotrophic biomass (Fig. 1), so that protozoan biomass was also an index of lake productivity. When biomass-specific ingestion rates of HNF by copepods and cladocerans are plotted against HNF biomass on the same days in the absence of metazooplankton, they increased with increasing HNF biomass (Fig. 4) and with Chl *a* (copepods, $n = 5$, $r = 0.91$, $P = 0.035$; cladocerans, $n = 6$, $r = 0.94$, $P = 0.006$). The rate at which copepods consumed ciliates also increased with ciliate biomass (Fig. 4) and Chl *a* ($n = 15$, $r = 0.45$, $P = 0.093$) and supports an earlier prediction from a study of *Epischura* and two species of *Diaptomus* that large changes in algal biomass associated with eutrophication or season will not reduce the vulnerability of ciliates to predation by calanoid copepods (Burns and Gilbert 1993). In contrast, rates of ciliate consumption by cladocerans decreased with increasing ciliate biomass (Fig. 4) and were unrelated to Chl *a* ($n = 8$, $r = 0.45$, $P = 0.26$). As the biomass of Chl *a* (not shown), HNF, and ciliates increased (Fig. 4), the differential in the rates of consumption of protozoa by copepods and cladocerans increased, which implies that copepods become even more effective than cladocerans in exploiting protozoa as a food resource as lakes become more productive.

Further insight into the relative effectiveness of copepods and cladocerans in controlling ciliates is gained by plotting copepod ingestion rates of ciliates (IR_{cope}) as a ratio of cladoceran ingestion rates of ciliates (IR_{clad}) under the same conditions (same lake and same treatment) against phytoplankton biomass (Chl *a*) in enclosures without added zooplankton (Fig. 5). An $\text{IR}_{\text{cope}} : \text{IR}_{\text{clad}}$ of 1.0 would indicate that there was no difference between the two groups of zooplankton in their biomass-specific rates of consumption of ciliates. As phytoplankton increased across the gradient from ultra-

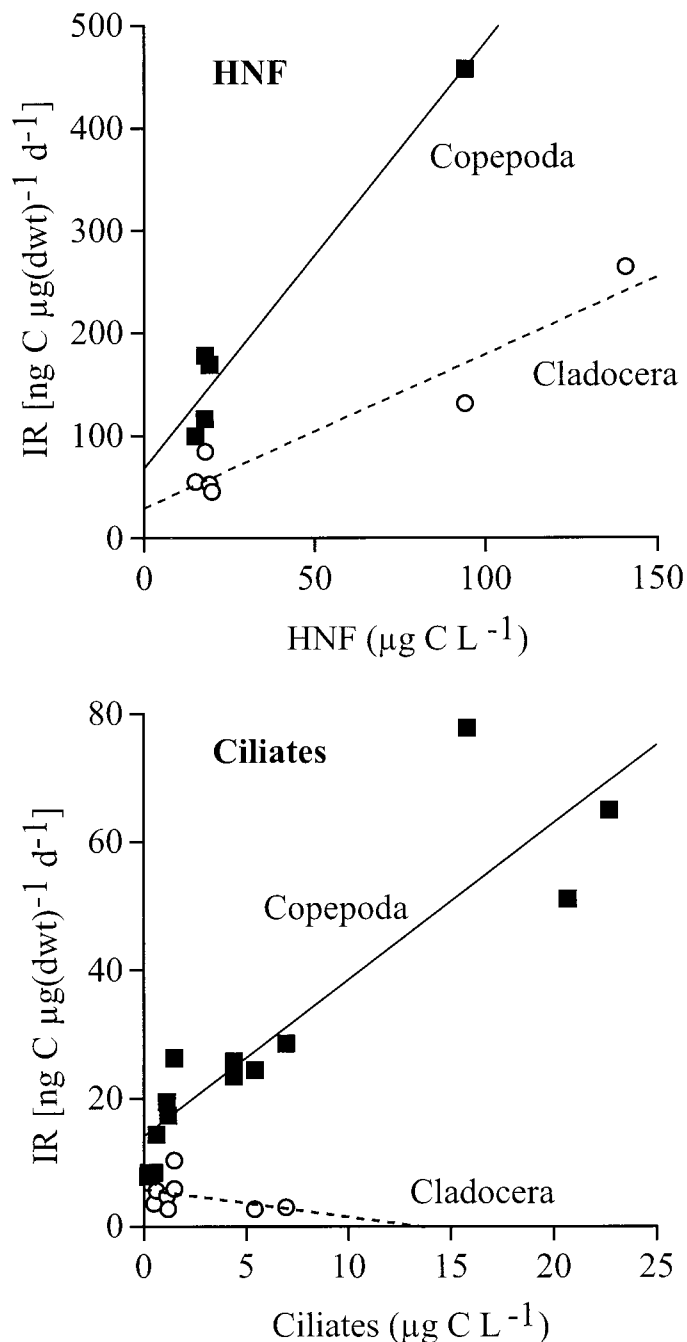


Fig. 4. Rates of ingestion ($\text{ng C } [\mu\text{g dwt}]^{-1} \text{ d}^{-1}$) of HNF and ciliates by copepods and cladocerans after 1 or 4 d plotted against the mean biomasses ($\mu\text{g C L}^{-1}$) of HNF and ciliates in enclosures in the same lake and treatment without added zooplankton. Regression lines relate protozoan biomass to ingestion rate of copepods (solid line) and cladocerans (broken line).

oligotrophic Lake Wakatipu to mesoeutrophic Lake Mahinerangi, the effectiveness of calanoid copepods at removing ciliates increased from 2.5 times as effective to 9.5 times as effective as cladocerans.

The increasing effectiveness of copepods, compared to cladocerans, at removing protozoa from the microbial food webs of lakes as they become more eutrophic is consistent

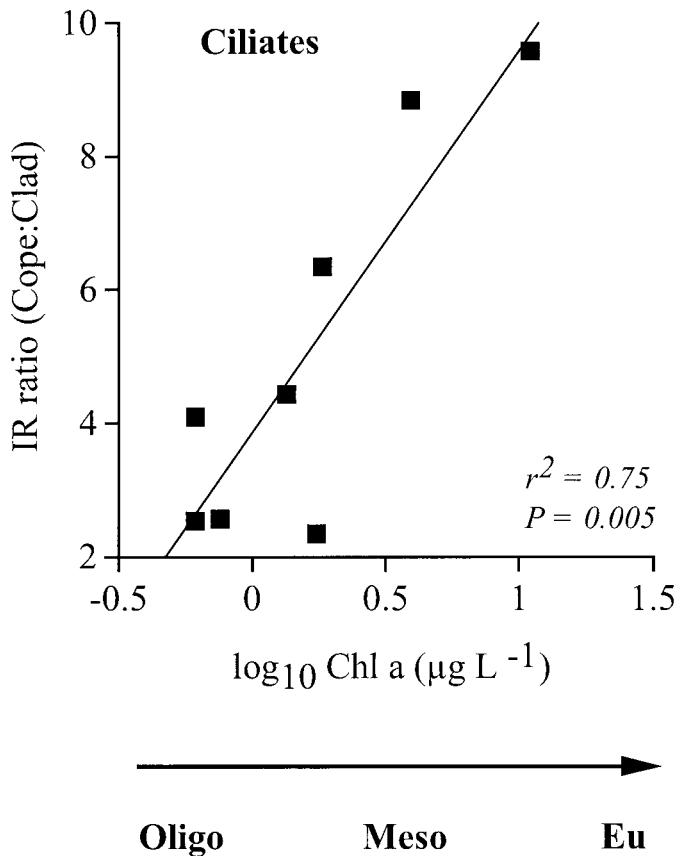


Fig. 5. Ratios of the rates at which copepods and cladocerans ingested ciliates in enclosures in the same lake with the same nutrient treatment (fertilized, unfertilized) after 4 d, plotted against phytoplankton biomass (Chl *a*, $\mu\text{g L}^{-1}$) in enclosures in the same lake and treatment without added zooplankton. There is no ingestion ratio for zooplankton in Lake Hayes because ingestion of ciliates by cladocerans was not detected in this lake. The regression line relates ingestion ratio to increasing trophic state of the water.

with the different feeding behaviors of *Daphnia* and calanoid copepods. Suspension-feeding cladocerans, such as daphnids, feed largely automatically. As particle concentrations in the water increase (for example, when phytoplankton biomass increases), their food collection system clogs with excess particles, which they clear away unselectively so that some ciliates will be rejected. In contrast, copepods are able to select and ingest ciliates from mixtures of other particles (e.g., Stoecker and Capuzzo 1990; Burns and Gilbert 1993), and the rates at which they do so are relatively unaffected by the presence of algae (Burns and Gilbert 1993).

The effects of calanoid copepods and *Daphnia* on ciliates are known to be influenced by the species and size of ciliate (Burns and Gilbert 1993; Jack and Gilbert 1993). Some species (e.g., *Halteria*) have jumping behaviors that reduce their vulnerability to predation by metazooplankton. It is likely that taxonomic differences in the ciliate communities in our four study lakes contributed to variance in the regressions that relate zooplankton ingestion rates to ciliate biomass (Figs. 4, 5) and that predictions based on these regressions may not hold in lakes dominated by ciliates that are particularly large or small or have evasive behaviors.

Summary—Our aim was to assess the relative effectiveness of cladocerans and copepods as consumers of protozoa in lakes of different trophic state. We show that protozoa are potentially important components of the diets of copepods and cladocerans in lakes of different productivity. These trophic interactions link the microbial food web and classical food chain in lakes. The link between ciliates and calanoid copepods is consistently stronger than that between ciliates and cladocerans. Furthermore, the consumer link between calanoid copepods and ciliates strengthens relative to that between cladocerans and ciliates in lakes of increasing trophic state.

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Upwelling and the condition and diet of juvenile rockfish: A study using ^{14}C , ^{13}C , and ^{15}N natural abundances

Abstract—Juvenile *Sebastes jordani* individuals sampled in late spring 1995, 1996, and 1997 near Monterey Bay, California, were analyzed for $\Delta^{14}\text{C}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. As anticipated, a strong negative correlation was found between mean annual juvenile rockfish $\Delta^{14}\text{C}$ and the preceding 3-month average Bakun upwelling index for this region. The sensitivity of this isotopic response by juvenile rockfish to upwelling variations was similar to that previously observed in surface-water inorganic carbon in nearby Half Moon Bay (Robinson 1981). This indicates that the $\Delta^{14}\text{C}$ of surface-dwelling marine fish can be used as a measure of fish feeding in freshly upwelled ^{14}C -depleted water. However, we found no correlation between this parameter and fish somatic condition as measured by deviations in the regressions of individual fish (1) weight on length, (2) otolith size on fish length, or (3) total lipid content on dry weight. This questions the role upwelling plays in affecting juvenile rockfish condition. Also unrelated to fish condition were fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, implying that the condition of juvenile *S. jordani* is unaffected by variation in the consumption of specific, isotopically discernible food resources.

The advection of nutrients critical to plant life is facilitated by the upwelling of subsurface water and has long been recognized as an important process for both neritic and open ocean ecosystems (Smith 1968; Cushing 1975; Hermann et al. 1989). The transport of micro- and macronutrient-rich deep water to the photic zone via winds, internal waves, and ocean currents can significantly stimulate primary, and subsequently secondary, production when those nutrients are otherwise limiting to plant and microbial growth. These processes are thought to play a pivotal role in determining the spatial, temporal, and taxonomic patterns of life in the ocean. Although nutrient supply and overall ecosystem productivity are necessarily intimately linked, it has proven more difficult to directly demonstrate by field measurement that a relationship exists between upwelling (nutrient supply) and the health and abundance of the more diffuse and mobile higher consumers.

The rockfishes (*Sebastes*) are one such example. This genus forms one of the most important segments of the U.S.