

Carbon partitioning in the food web of a high mountain lake: from bacteria to zooplankton

Cristiana CALLIERI*, Alessandra PUGNETTI and Marina MANCA

C.N.R. Istituto Italiano di Idrobiologia, 28922 Verbania-Pallanza, Italy

*e-mail correspondig author: c.callieri@iii.to.cnr.it

ABSTRACT

The organisms of the microbial loop in Lake Paione Superiore (LPS), a high mountain lake in the Italian Alpine region, were studied together with phytoplankton and zooplankton for three successive years. The biomass of bacteria, HNF (heterotrophic nanoflagellates), ciliates and phytoplankton, as mean carbon concentration in the three years, was 30 and 37 $\mu\text{g C l}^{-1}$ near the surface (SUR) and the bottom (BOT) respectively. Under the ice-cover the mean biomass carbon decreased especially at the BOT, whereas at SUR the decrease was less evident due to the maintenance of higher phytoplankton biomass (mixotrophic flagellates). In LPS ~50% of the carbon was confined in bacteria, 20% in protozoa and 30% in phytoplankton. The ratio Autotrophs/Heterotrophs was lower than 1 (mean: 0,97 at SUR and 0,58 at BOT) thus indicating a system with a predominance of the heterotrophs. This might be the result of light inhibition of algal growth coupled to a production of dissolved carbon, utilized by bacteria. During late summer the peak of *Daphnia longispina*, the main component of the zooplankton of LPS, increased the carbon content in the lake to a total of 158 and 300 $\mu\text{g C l}^{-1}$ in 1997 and 1998 respectively. At the late summer peaks, zooplankton represented from 78 to 89% of the total carbon of the pelagic communities. Furthermore, the presence of *Daphnia* could be responsible for a decrease in the biomass carbon of a variety of organisms (algae, protozoa and bacteria). It may be possible that this is an instance of zooplankton grazing on algae, protozoa and also bacteria, as *Daphnia* has very broad niches and may eat pico-, nanoplankton and small ciliates. In the oligotrophic LPS, a diet which also includes protozoa could give *Daphnia* a further chance of survival, as ciliates are an important source of fatty acids and sterols.

Key words: microbial loop, high mountain lake, phytoplankton, zooplankton

1. INTRODUCTION

Since the importance of the microbial loop in ecosystem functioning was recognized (Pomeroy 1974; Williams 1981; Sieburth & Davis 1982; Azam *et al.* 1983), limnologists have devoted more and more effort to studying this part of the food web. Researches focussed on standing stock quantification (Amblard *et al.* 1995; Hadas & Berman 1998) and on carbon flux measurements in the loop (Weisse 1990; Nagata 1988, Nagata *et al.* 1996; Amblard *et al.* 1994; Šimek *et al.* 1995). Micro and mesocosm experiments were performed (Jürgens 1994; Jürgens *et al.* 1997) to investigate the food linkage among metazoans, protozoans and the bacterial population. Different studies emphasized the interactions among microorganisms and organisms in the microbial and classical food web in lakes (see review by Jürgens 1994; Pace *et al.* 1990; Carrick *et al.* 1991; Mathes & Arndt 1995; Šimek *et al.* 1997). Nevertheless, information is limited on carbon partitioning of natural assemblages of all the components of the microbial loop and zooplankton simultaneously (Porter 1996). Stockner & Porter (1988) outlined the different efficiency in carbon transfer in two food chains, one dominated by *Daphnia* and the others by picoplankton and microheterotrophs: the longer the chain the higher the losses. The microbial loop may be a sink for energy

flow, as much carbon is respired at different trophic levels so that the chain tends to support a lower standing stock of fish. But what happens if in the lake there are no fish at all, the water is acid, cold, ice-covered for five-six months and with a clear, light-unprotected water column?

This question prompted us to begin a study of the entire food web, from bacteria to zooplankton, of a simplified high mountain lake ecosystem which was slightly acid in 1991-1993 (Mosello *et al.* 1993), to quantify the carbon in the different compartments of the food web. The study constitutes the part of the EU MOLAR Project involved in Pelagic Food Web Research. Specifically, this was a three-year study on the pelagic community composition of the high mountain lake: Lake Paione Superiore (LPS) in the Italian Central Alps above 2000 m (Mosello *et al.* 1993, 1994). The absence of fish, the simplification of the other compartments with relatively few species and the almost exclusive presence of *Daphnia* in the summer zooplankton population (Cammarano & Manca 1997) made this small lake unique for studying the microbial loop and its relationship with *Daphnia* and phytoplankton.

In this paper we will mainly discuss the carbon partitioning in the food web during a three-year study, comparing the carbon content of the different autotrophic and heterotrophic compartments in the ice-free and ice-cover periods. In a more detailed paper published in

this issue (Callieri & Bertoni 1999) the study of the dynamics of the components of the microbial loop will be described also in relation to changes in pH and the light climate. Another paper will show the results of the activity measurements of autotrophic production, bacterial production and protozoan grazing (Callieri & Bertoni, in preparation).

2. MATERIALS AND METHODS

Field samplings were performed monthly from July 1996 to October 1998 at the point of maximum depth (11.7 m) of Lake Paione Superiore (LPS), a small glacial cirque lake at an altitude of 2269 m in the Bognanco Valley (Pennine Alps, Italy) (Bianchini 1952). Its geographic and morphometric features, together with the hydrochemical variables measured in 1991-1994, were reported in synthesis by Cammarano & Manca (1997). More recent data on water chemistry can be found in The MOLAR Water Chemistry Group (1999, this issue). A light extinction profile during summer and winter is presented by Callieri & Bertoni (in prep.). The water column is well irradiated, with 12% of surface irradiance present at the bottom. The measurements of underwater light, as PAR ($\mu\text{E m}^{-2} \text{s}^{-1}$), were performed with a LI-COR 250, and the extinction coefficient (k) was 0.22-0.32 m^{-1} in summer. The k values measured in 1991-93 were 0.1-0.2 m^{-1} (Bettinetti 1994; Pugnetti & Bettinetti 1995). The temperature in August is around 14 °C and a stratification appeared in August 1997 and July 1998.

During the ice-free period, we sampled picoplankton, protozoa, phytoplankton and zooplankton at two depths, namely, one meter under the surface in summer (SUR) and one meter above the bottom (BOT). Except for zooplankton, on which information was already available, we also collected samples under the ice-cover (one meter under the ice-water interface and one meter above the bottom). Zooplankton net integrated samples were also collected on each date in replicates, to obtain the carbon biomass directly from dry weight and carbon content (for details see Manca & Comoli 1999, this issue). To fix and count bacteria or HPP (heterotrophic picoplankton), APP (autotrophic picoplankton), HNF (heterotrophic nanoflagellate), phytoplankton and ciliates, the protocols described by Straškrabová *et al.* (1999, this issue) were followed, to obtain results comparable with the other lakes included in the MOLAR project. One exception was the dyeing of bacteria, which was done using Acridine Orange instead of DAPI, and the use of Anopore filters instead of Nucleopore membranes of the same porosity (0.2 μm pore size diameter) (Straškrabová *et al.* 1999, this issue). All the counting and biovolume measurement data were converted to carbon using the conversion factors and the equations reported in the protocols (Straškrabová *et al.* 1999, this issue). The statistical analyses performed were ANOVA tests.

3. RESULTS

In figure 1 the biomass temporal variations of HPP, APP, HNF, ciliates, phytoplankton and zooplankton are shown at SUR and BOT depths respectively. The depth of the BOT changed as the lake level fluctuated: in winter it was 7-8 m and in summer 9-10 m. These depths guaranteed sampling without contamination due to sediment resuspension.

APP, both eukaryots and cyanobacteria, were almost absent, reaching a maximum value of 0.1 $\mu\text{g C l}^{-1}$. On these rare occasions they were small eukaryotic algae, as picocyanobacteria were absent. Stockner & Shortreed (1991) have reported a situation of complete absence of pico-blues and dominance of eukaryotic picoplankton in low pH, humic Danish lakes. Both the acid conditions of LPS waters and the possibility of PAR and UV inhibition at 2200 m could be evoked as the possible causes of the absence of picocyanobacteria.

HPP (bacteria) constituted around 50% of the carbon of the microbial food web (microbial loop plus phytoplankton) and their seasonal dynamics were quite similar at the two depths, with the sole exception of early summer 1998, when an isolated peak of 56 $\mu\text{gC l}^{-1}$ was measured, due to the presence of large rods and long filaments at the BOT. Under the ice the bacterial carbon concentration was around 5 $\mu\text{g C l}^{-1}$, which nevertheless represents 40% of the organic carbon in the microbial food web. During early summer the bacterial carbon concentration, as a mean, was 36 $\mu\text{g C l}^{-1}$.

HNF showed a density range from 4 10^4 l^{-1} to 4 10^6 l^{-1} and were composed of a predominance of <3 μm cells and by 3 to 8 μm cells, which were relatively more important but in low numbers, under the ice. In Callieri & Bertoni (1999, this issue) the structure of the HNF population is described in more detail. Their carbon ranged from 0.4 to 42 $\mu\text{g C l}^{-1}$ and their mean concentration was 3 and 5 $\mu\text{g C l}^{-1}$ at the two depths respectively. Here it is important to note that these flagellates were less abundant under the ice (range: 60-750 10^3 l^{-1}) than in summer (range: 250-17,260 10^3 l^{-1}), when an increase in size diversity and numbers was also observed. They decreased in correspondence with the September increase in zooplankton at the BOT. They were also very low in May-June 1998 at the ice melt.

Ciliate biomass was lower than HPP and phytoplankton. The carbon concentrations ranged from 0.01 to 12 $\mu\text{g C l}^{-1}$ with a mean of 2 $\mu\text{g C l}^{-1}$. During the winter ice-cover the ciliate carbon was very low at both depths, but the abundance of prostomatids with *Urotricha* spp. and of the oligotrich *Halteria grandinella* reached values of 1500-2000 ind l^{-1} . Although the description of the ciliate species succession will be presented elsewhere (Callieri & Bertoni 1999, this issue), by simply looking at their total biomass it is clear that, especially at BOT, their importance in terms of carbon is restricted to the ice-free period, when the oligotrichs are represented by the large *Strombidium* sp. At SUR a

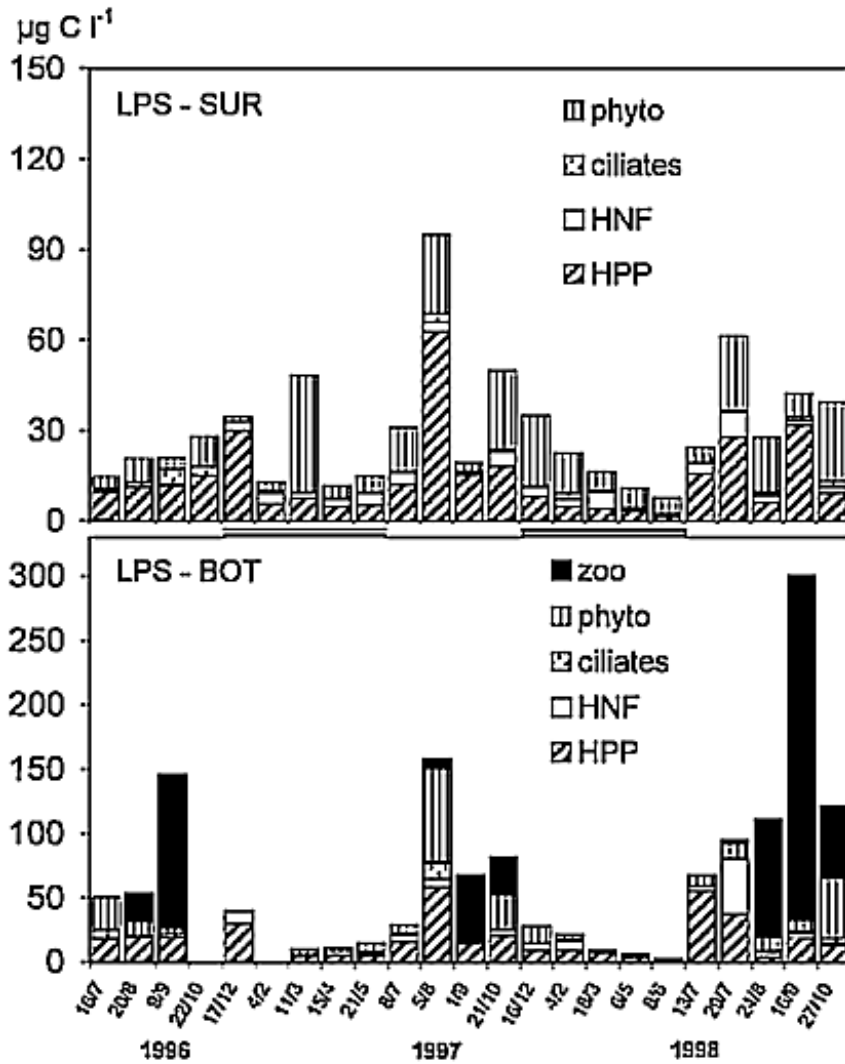


Fig. 1. Temporal variations of APP, HPP, HNF, ciliates and phytoplankton biomass, as carbon ($\mu\text{g C l}^{-1}$), at SUR (1 m under the surface) and BOT (1 m under the bottom) of Lake Paione Superiore (LPS) during 1996, 1997, 1998. Double line indicates the ice-cover.

peak of ciliate carbon due to *Halteria* was observed just once under the ice (February '97). The presence of the small prostomatid *Urotricha* throughout the year is not visible in the graphs shown in figure 1. The absence of large mixotrophic ciliates in LPS during winter constituted a significant difference from other MOLAR lakes. For example, comparing the carbon data of LPS with those from Lake Redó (Camarero & Felip, personal communication), in December 1996 it appears that while in the deeper part of the lakes similar concentrations were measured ($0.2\text{--}0.3 \mu\text{g C l}^{-1}$; 11 m LPS and 18 m Redó respectively), at 1 m in Lake Redó the carbon in the ciliate was more than one order of magnitude higher than in LPS.

Phytoplankton was mainly represented by: *Chromulina* sp., *Dinobryon sertularia*, *Mallomonas alveolata* and *Gymnodinium* sp., which were present throughout the year at both depths. Most of these species (*Dino-*

bryon sertularia and also some species of *Chromulina* and *Gymnodinium*) are known from the literature to be potentially mixotrophic, showing facultative bacterial feeding (Porter 1988; Jones & Rees 1994; Isaksson 1998). The phytoplankton carbon ranged from 1 to $38.9 \mu\text{g l}^{-1}$, with a mean value of $11.5 \mu\text{g l}^{-1}$. As a general pattern the total phytoplankton dynamics are characterized by a decline that begins after some months of ice-cover (even though quite high values at the end of the period could be observed) and lasts until the end of the ice melting, by an increase during early summer, when the yearly maxima are usually attained, and by a late summer decrease. The results of the spatial and temporal species dynamics can be found in Pugnetti & Bettinetti (1999, this issue). *Chromulina* sp., *Mallomonas alveolata* and *Gymnodinium* sp. were also the dominant species in the years 1991–1993 (Pugnetti & Bettinetti 1995), while *Dinobryon sertularia* has greatly increased

its importance in the present study. In comparison with the years 1991-1993 the total number of species has now increased (Pugnetti & Bettinetti 1999, this issue).

Zooplankton biomass is always negligible in the surface samples, because of the benthic habits of zooplankton during the day. Biomass peaks vary from year to year, both in their absolute values and in their timing, reflecting meteorological conditions and the time of ice melt, which are responsible for the initial increase in the carbon confined in the microbial food web. The development of zooplankton starts after this phase of phytoplankton, protozoa and bacteria increase (Fig. 1, BOT). In August 1997, when nauplii and rotifers contribute most to the total zooplanktonic carbon, it is likely that no effect on the phytoplankton, protozoa and bacteria is evident. In July and at the beginning of August, when *Daphnia* carbon was low, the compartments of the microbial loop represented 49, 77 and 85% of the total carbon in 1996, 1997 and 1998, at BOT. In the three consecutive years the importance of the microbial loop and in particular of bacteria increased, whereas the phytoplankton proportionally decreased. In late summer, both the autotrophic and the heterotrophic communities are preyed upon by *Daphnia longispina*, the main component of the zooplankton of LPS (Fig. 2) (Manca & Comoli 1999, this issue). This pattern is particularly evident in September 1997 and August 1998 when the massive presence of *Daphnia* increased the carbon content in the lake to a total of 158 and 300 $\mu\text{g C l}^{-1}$ respectively. At the late summer peaks zooplankton represent from 78 to 89% of the total carbon of the pelagic communities. In August 1998 the earlier development of *Daphnia* reflects a more effective control on phytoplankton growth by a most efficient community of grazers. To quantify the carbon transfers in the food web due to the activities of various organisms, the positive increments of carbon in the zooplankton compartment and the concomitant negative ones, confined in the microbial loop and phytoplankton, were calculated (Fig. 3).

The first observation is that the presence of *Daphnia* is responsible for a decrease in the carbon of a variety of organisms. It may be possible that this is an instance of zooplankton grazing on algae, protozoa and bacteria too.

In terms of carbon the heterotrophic organisms like HNF, bacteria and ciliates taken separately are not as important as the mixotrophic algae, particularly at SUR. Nevertheless, by summing up the carbon from all the microbial heterotrophic compartments (ciliates, HNF and bacteria) and making a ratio with the phytoplankton (A/H, ratio), in the ice-free period the mean value is 0.68 at SUR and 0.65 at BOT, which in any case demonstrates the tendency of the system to confine more carbon to the heterotrophs. If we include also the zooplankton among the heterotrophs the ratio decreases to 0.33, but only in September its contribution to the car-

bon of the heterotrophic communities is significant. The ratio increases to a maximum of 4 during the ice-cover at SUR and also the mean value of the two ice-cover period is low (1.28).

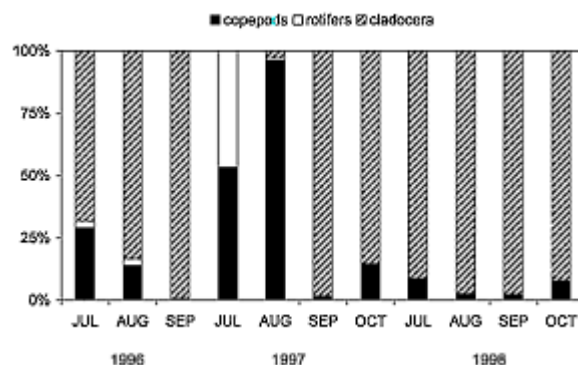


Fig. 2. Relative contribution of different groups to the total carbon biomass of zooplankton in the BOT samples (1 m above the bottom) of Lake Paione Superiore in the three years under study.

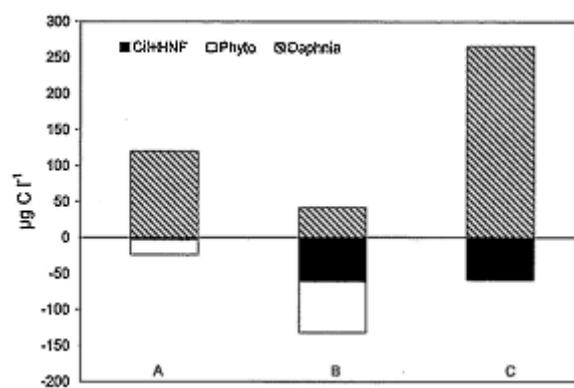


Fig. 3. Increments in the carbon ($\mu\text{g l}^{-1}$) of the ciliates, HNF, phytoplankton and zooplankton calculated by the difference between two measurements, in three ice-free periods, at BOT (1 m above the bottom). A: July - September 1996; B: August - September 1997; C: July - September 1998.

From the three-year data, statistically analyzed, no significant difference between the SUR and BOT total carbon (excluding zooplankton) exists. Nevertheless, if we split up the total carbon into its components, the resulting pie graph (Fig. 4) shows a slightly higher phytoplankton carbon content in SUR and conversely a higher heterotrophic component (HPP, HNF and ciliates) in BOT.

A comparison of the carbon concentrations of ice-cover and ice-free periods in 1997 and 1998 results in a significant difference (ANOVA, $P < 0.05$ in SUR and $P < 0.02$ in BOT) with higher concentrations in summer. During summer 1996 the concentrations were lower than in the subsequent years (Fig. 5), but as we lack the data from the ice-cover period we did not include them in the statistical elaborations. Mixotrophic algae survive

under the ice-cover in December, before the snow accumulation completely obscures the water column, also at the ice-water interface. It is from them that the carbon content found at the SUR under the ice derives (Pugnetti & Bettinetti 1999, this issue).

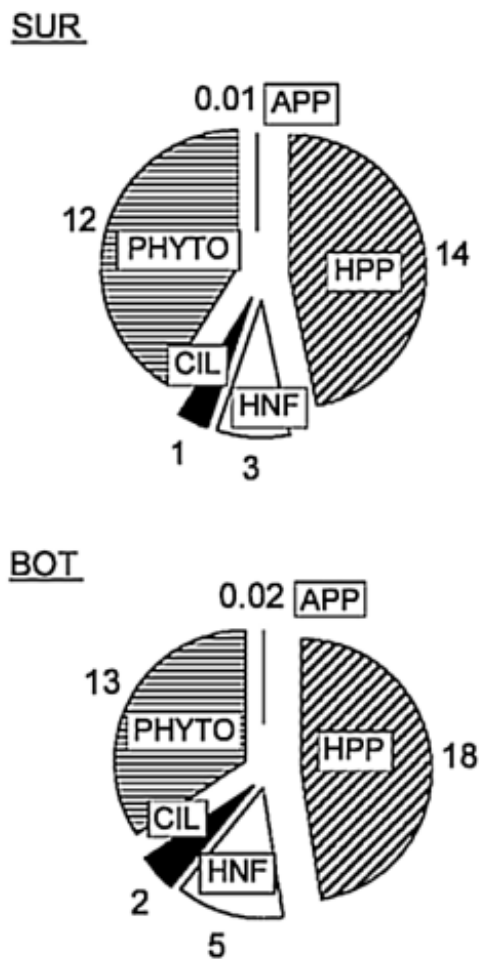


Fig. 4. Autotrophic and heterotrophic organisms of the microbial food web at the SUR (1 m under the surface) and BOT (1 m above the bottom) of Lake Paione Superiore expressed as a mean value of the three-year study. The values are in $\mu\text{g C l}^{-1}$.

4. DISCUSSION AND CONCLUSIONS

The seasonal pattern of the organisms of the pelagic food web of Lago Paione Superiore shows a cycle characterized by an increase in carbon from the beginning of the ice-free period to mid-September, followed by a consistent decrease during ice-cover. Apparently the ice does not have a strong negative effect on the presence at SUR of the phytoplankton; some of them, like *Dinobryon*, show a peak in winter 1997 which suggests that these peculiar organisms can grow in nature with low light. However, as light has a regulatory effect on phagotrophy, its considerable reduction due to the accumulation of snow on the ice explains the decline of mixotrophic organisms at certain dates during winter. Under

laboratory conditions (Jones & Rees 1994) *Dinobryon* appears to be an obligate phototroph in the sense that it ceases its activity if placed in the dark for a period longer than one day. Temperature too has an influence on the uptake rate of *Dinobryon*: at 5 °C the *Dinobryon sertularia* clearance rate was lower than at 20 °C in uptake experiments (Jones & Rees 1994). In LPS the low temperature does not have a negative influence on the abundance of *Dinobryon*, although we have no data on the uptake activity under the ice. We must remember that the advantage of phagotrophy is the exploitation of an unfavorable environment to obtain essential resources (Veen 1991) and this is the case of our oligotrophic high mountain lake, where inorganic carbon (0.7 mg l^{-1}), nitrogen and phosphorus are low (The MOLAR Water Chemistry Group 1999, this issue).

The A/H ratio low values demonstrate the prevalence of heterotrophic carbon in LPS. In the oligotrophic lake La Caldera this ratio fluctuated around 1 during the three years of study due to changes in the community structure, which was strongly influenced by different precipitation regimes (Medina-Sánchez *et al.* 1999, this issue). As a matter of fact the stability in the dominance of heterotrophic organisms (also not including zooplankton) is an exception, if compared with the other lakes included in the MOLAR project, where the autotrophic organisms generally prevail.

The low A/H ratios are due to low algal carbon and might be the result of light inhibition of algal growth. At 2200 m, in this clear water lake, the underwater PAR near the surface can exceed $1200 \mu\text{E m}^{-2} \text{ s}^{-1}$, which might likely cause an inhibition effect on growth of phytoplankton in most of the water column.

As appears from the activity measurements performed in 1997 and 1998 (Callieri & Bertoni, in prep.), the presence of *Daphnia* in the lake reduces drastically phytoplankton production, bacterial production and protozoa grazing on bacteria. The decrease in biomass and activity of organisms in the size range from less than $1 \mu\text{m}$ to more than $100 \mu\text{m}$ and the occurrence of a large spectrum filter feeder like *Daphnia* is more than a coincidence. Cladocerans have very broad niches and may eat pico-, nanoplankton and small ciliates (Gophen & Geller 1984; Lampert 1987; Jürgens 1994). Though we did not measure zooplankton grazing activity, from all the other data available and from observation of well-fed individuals with full guts we hypothesized a top-down control of *Daphnia* on phytoplankton and on the microbial loop. Furthermore, the different situations of August 1997 (when *Daphnia* biomass was still low) and August 1998 (when *Daphnia* dominated) seem well related to the different levels of food items (microorganism carbon) reached in the corresponding periods, being higher in 1997 than in 1998 (Fig. 1, BOT). The control on phytoplankton biomass by *Daphnia*, suggested in previous studies from observation of the mirror-shaped curves of phyto- and zooplankton (Pugnetti

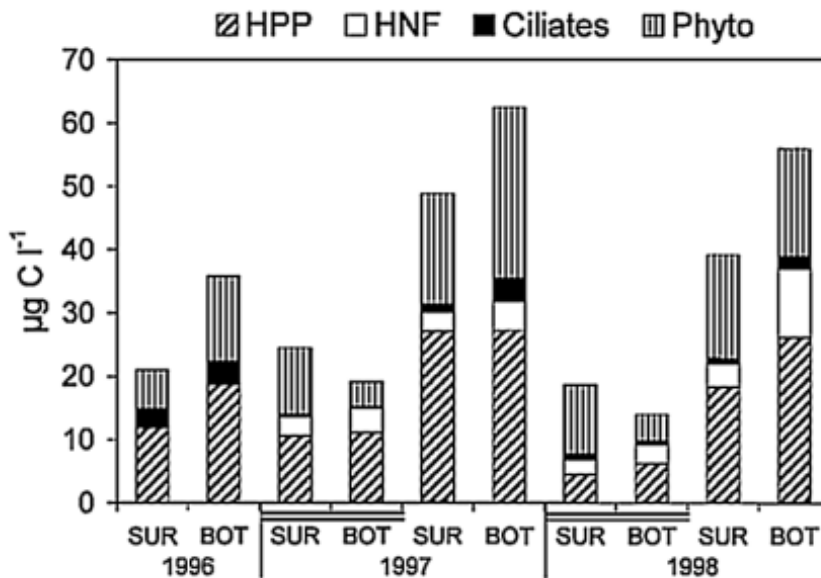


Fig. 5. Mean carbon values of the microorganisms of the microbial food web (APP, HPP, HNF, ciliates, phytoplankton) in the ice-free and ice-cover (double line) periods at the SUR (1m under the surface) and BOT (1 m above the bottom) of Lake Paione Superiore.

& Bettinetti 1995; Cammarano & Manca 1997), can be extended to the microorganisms of the microbial loop. It is likely that protozoa are an important source of fatty acids and sterols, thus representing a supplementary diet to enhance survival, growth and fecundity (Stoecker & McDowell Capuzzo 1990) especially during periods of nutrient limitation (Sanders *et al.* 1996). In the oligotrophic LPS a diet which also includes protozoa could give *Daphnia* a further chance of survival. In similar extreme environments, like Antarctica, with limited primary production, the microbial food webs are an important source of nutrition for metazoans (Bröckel 1981; Buck & Garrison 1988). A visual inspection of *Daphnia* indicates that they are well-fed, although there is a general depletion of eggs, probably related to the *Cyclops-Daphnia* feeding interactions (Manca & Comoli 1999, this issue). Food is probably not so scarce in Lago Paione Superiore. If we take microorganism carbon concentration as a measure of food availability (chlorophyll-*a* is not a good measure of food in this lake; Cammarano & Manca 1997; Pugnetti & Bettinetti 1999, this issue), we find that the *Daphnia* population starts to grow when levels are above the threshold limit reported in literature for large-bodied species (Gliwicz 1990).

The importance of *Daphnia* in LPS could also extend to bacteria because the protozoan control of the bacterial production occurs only in July - early August, as demonstrated by bacterial production measurements and protozoa grazing (Callieri & Bertoni, in prep.). The protozoa bacterivory in 1997 is responsible for 27 µg C l⁻¹ d⁻¹ in absence of *Daphnia* and for only 0.3 µg C l⁻¹ d⁻¹ when *Daphnia* increases. Other Authors (Šimek *et al.* 1990; Vaquè & Pace 1992; Jürgens 1994) have emphasized that Cladocerans become the main consumers of bacterial production during population peaks. Another

observation is that in 1997 and 1998 the decrease in carbon food items is not restricted near the bottom, where *Daphnia* was present in the morning, during samplings. This could indicate that the predators migrate, in the dark, along the water column (Ringelberg 1993).

In conclusion, the data of the seasonal changes in the organisms of the microbial loop, phyto- and zooplankton, and of their relative contribution to the organic carbon in the food web of Lake Paione Superiore, are evidence of the existence of a well-defined succession. The carbon partitioning shows the dominance of heterotrophic over autotrophic organisms, near the surface and the bottom. The key organisms are bacteria, flagellates and *Daphnia*; in the absence of fish this Cladoceran shows a peak in September during which it exerts a top-down control of the smaller organisms. Mixotrophic rather than heterotrophic flagellates occupy the near-surface layers during the ice-cover. Bacteria, thanks to the formation of long filaments, can contribute significantly (~50%) to the carbon in the microbial food web.

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