Components, structure and fluxes of the microbial food web in a small, stratified lake

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ABSTRACT: We studied the planktonic community established in Lake Cisó (Girona, Spain) during summer stratification, with the aim of describing the food web of a system as completely as possible. The lake was sampled 19 times during 1990 and 1991 We first determined which populations contributed significantly to total summer biomass. Then, we determined the trophic role of these populations by several independent approaches, and aggregated the community into functional groups. The binary food web obtained indicated that the structure of the food web in Lake Cisó was similar to that found in other systems. Finally, we quantified the trophic fluxes among populations using a simple algorithm which considers the vertical distribution of organisms and the functional responses of the different predators. The trophic food web obtained revealed 2 interesting properties. First, the compartments with larger biomass were relatively stable during stratification and presented slow growth and low predatory losses. Second, there was a very inefficient transfer of organic matter from the lower levels (bacteria, algae and protozoans) to the higher levels (rotifers and zooplankton) of the food web. Both properties could be explained by the fact that most biomass of the system accumulated in the metalimnion, along opposite gradients of oxygen and sulfide, which determined an environment with reduced competition and predation. We postulate that metalimnetic communities above anaerobic hypolimnia can be regarded as sinks of organic matter off the epilimnion.

KEY WORDS: Lake Cisó · Binary food web · Trophic food web · Prey refuge

INTRODUCTION

The description of the food web of an ecosystem is fundamental to understanding how it functions (Cohen 1989, Pimm et al. 1991). The food web structure determines how the energy and organic matter are channeled and dissipated through the different trophic levels, affecting their biomass and activity. There are several approaches to studying the food web of a particular system, each one requiring more data (Gaedke 1995). In the first approach, the abundance and size of all organisms are determined and the size distribution of the community is obtained. We used this approach with the Lake Cisó (Girona, Spain) community in a previous paper (Gasol et al. 1991b). Addition of the trophic role of each population results in the binary

food web, which qualitatively shows trophic links among living compartments. Next, fluxes among compartments can be quantified in order to obtain the trophic food web, which describes the flow of matter through the community. Finally, dynamic simulation models can be applied to understand and predict the temporal changes of the ecosystem. Each of these 4 approaches by itself gives interesting information about the structure, function and regulation of the food web.

The aim of the present work was to attempt as complete a description of the trophic food web of a pelagic system as possible. For this purpose, we chose Lake Cisó. Lakes are supposed to have a simpler food web than marine systems, since they are closed habitats with clear boundaries (Pomeroy 1991). In addition, Lake Cisó has some interesting advantages that made its study easier than the study of other lakes. It is a well known system (Pedrós-Alió & Guerrero 1993). In recent years, detailed data on the community composi-

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tion and biomass size distribution (Gasol et al. 1991b, 1992), primary production (García-Cantizano 1992) and bacterial production (Calderón-Paz et al. 1993, García-Cantizano et al. 1994) have been obtained. The community is rather simple, with an absence of fishes and just a few microbial populations composing most of the biomass. Moreover, the community established during spring remains in the metalimnion with minor changes throughout the summer until the fall mixing (Gasol et al. 1992, Massana et al. 1994b), and thus a single food web structure seems to hold throughout stratification. These special characteristics of Lake Cisó have allowed us to study its food web in great detail.

The community found in Lake Cisó is an example of a widespread type of community, found in many other thermally stratified or meromictic lakes in places as distant and with as diverse climates as Japan (Matsuyama & Shirouzu 1978), Tasmania (Baker et al. 1985), Spain (Finlay et al. 1991) and Finland (Arvola et al. 1992). These systems are characterized by an extraordinary accumulation of biomass in the metalimnion, at the boundary between oxic and sulfide containing waters. The trophic fate of such biomass is not clear, and whereas some authors have postulated that metalimnetic organisms can represent a significant fraction of the food of some epilimnetic zooplankters (Sorokin 1970, Mazumder & Dickman 1989), other authors have proposed the contrary, suggesting the metalimnetic biomass to be a sink of carbon from the epilimnion (Fry 1986, Mas et al. 1990). The study of the food web of Lake Cisó can provide the appropriate data set to assess the fate of the metalimnetic biomass in such an ecosystem.

MATERIALS AND METHODS

Lake Cisó. Lake Cisó is a small holomictic lake located in the karstic region of Banyoles (Girona, Spain). The physico-chemical properties of the water column and vertical distributions of organisms have been previously characterized (Gasol et al. 1992, Pedrós-Alió & Guerrero 1993, Massana & Pedrós-Alió 1994a, b, Massana et al. 1994a, b). During the mixing period (from October to March) the entire water column is anoxic with sulfide, and only bacteria (heterotrophic and phototrophic) and anaerobic ciliates are found. During summer stratification (from April to September), a strong thermal gradient appears in the water column that isolates the hypolimnion (which remains rich in sulfide) from the epilimnion (which oxygenates completely). A dense community of organisms develops in the metalimnion along opposite gradients of oxygen and sulfide. This study is based on the

information obtained on 19 sampling dates (3 to 12 depths sampled each date) during 1990 and 1991, with a total of 141 samples analyzed.

Determination of integrated biomass of the populations. Linear dimensions (length and width) of several individuals of each population were measured under the microscope with a graduated eyepiece (zooplankton, protozoans and algae) or by a digital image analysis system (bacteria). Individual volumes (μm^3 ind.$^{-1}$) were calculated assuming simple geometrical shapes and converted to carbon content (pg C ind.$^{-1}$) using conversion factors taken from the literature: 0.20 pg C μm^{-3} for bacteria (Bratbak 1993), 0.14 pg C μm^{-3} for ciliates (Putt & Stoecker 1989), and 0.15 pg C μm^{-3} for algae (Strathmann 1967). For *Thermocyclops dybowskii* (adults, copepodites and nauplii) we used an empirical regression between length (L, μm) and dry weight (DW, pg): DW = $11 \times L^{1.89}$ (Dumont et al. 1975). For the rotifers *Polyarthra* sp. and *Keratella* sp., dry weights given in Stemberger & Gilbert (1985) for rotifers of the same genera and size were assumed. Carbon content was considered to be 45% of dry weight. Dry weight was converted to volume considering that it is 19% of the wet weight (Båmstedt 1986) and has a density of 1 pg μm^{-3}.

For each sampling date, several samples were taken at different depths, and the abundance (ind. ml^{-1}) of the most important populations was determined. Integrated abundance (ind. cm^{-2}) was calculated in a water column from 0 to 500 cm depth (see Eq. 1 in Massana & Pedrós-Alió 1994a). Integrated biomass (μg C cm^{-2}) was obtained by multiplying integrated abundance times the carbon content.

Determination of trophic roles. Photosynthetic organisms were identified by the presence of pigments through phase contrast and epifluorescence microscopy. In addition, in order to identify the autotrophic populations in a broader sense, also including chemolithoautotrophic bacteria, natural samples were incubated for 4 h with radioactive bicarbonate ($NaH^{14}CO_3$) and organisms were then examined directly by micro-autoradiography (details of the methods in García-Cantizano 1992).

The food spectrum of each phagotrophic organism was determined using 3 sources of information. First, a literature search was done looking for the grazing habits of these or similar organisms. Second, the morphology and autofluorescence of the material ingested by the phagotrophs was examined under the microscope. Chlorophyll *a* gives red autofluorescence when irradiated with blue light, and phycobilins, present in cryptomonads and cyanobacteria, give a strong red autofluorescence when irradiated with green light (Craig 1987). Third, *in situ* experiments of incorporation of fluorescent particles were performed on

selected dates. Two bacterial suspensions, stained with FITC according to Sherr et al. (1987), were used: FLB (fluorescently labeled bacteria; dimensions of 1.1 × 0.8 µm; volume 0.42 µm^3) and FLC (fluorescently labeled *Chromatium*; dimensions of 3.2 × 1.4 µm; volume 4.2 µm^3). We also used 2 suspensions of fluorescent latex beads: SL (small latex; 0.49 µm diameter; volume 0.06 µm^3) and LL (large latex; 2.44 µm diameter; volume 7.6 µm^3). These particles were added to natural samples as tracers of colorless bacteria (FLB and SL) or phototrophic bacteria (FLC and LL). After a short incubation time, samples were fixed with formaldehyde and ingested particles inside predators were observed by epifluorescence microscopy. Uptake rates were measured counting the ingested particles at different times, and clearance rates (µl ind.$^{-1}$ h^{-1}) were calculated from uptake rates and particle concentrations.

Quantification of trophic fluxes. The integrated predation (prey eaten cm^{-2} h^{-1}) of each single prey-predator relationship was computed from vertical profiles of abundance of prey and predator populations and the functional response of the predator, using an algorithm described in Massana & Pedrós-Alió (1994a). Two parameters defined the functional response: the maximal uptake rate (U_m, µm^3 ind.$^{-1}$ h^{-1}) and the half-saturation constant for ingestion (k, µm^3 ml^{-1}). These parameters have been extracted from the literature for each predator (Table 1). The functional response of *Thermocyclops dybowskii* was assumed to be the same as that of *Tropocyclops prasinus mexicanus* (Adrian & Frost 1992). For *Polyarthra* sp. and *Keratella* sp. we used the functional response described for *Brachionus rubens*

(Rothhaupt 1990), modifying U_m to represent in both cases around 18% of the individual volume ingested per hour, as it is in *B. rubens*. The functional responses of *Anuraeopsis fissa* and *Coleps* sp. have been described previously (Massana & Pedrós-Alió 1994a, Pedrós-Alió et al. 1995). The functional response of *Prorodon* sp. was considered to be similar to that of *Coleps* sp., but modifying U_m to obtain the same U_m/V ratio. For bacterivorous ciliates (and nauplii), we used the data presented in Fenchel (1980), relating maximal uptake rates with the size of ciliates and half-saturation constants with the size of ingested particles. To obtain the values of U_m and k corresponding to each prey organism (U_m, prey eaten ind.$^{-1}$ h^{-1}; k, prey ml^{-1}), the values of these 2 parameters expressed in biovolume (as they are shown in Table 1) are divided by the individual volume of the prey. Therefore, we assumed the functional response to be identical (in terms of total biovolume ingested) for each prey considered. We will discuss the significance and reliability of all these assumptions.

RESULTS

Components of the food web: biomass and seasonal changes

Dimensions, individual volume and carbon content of the most important organisms found in Lake Cisó during the years 1990 and 1991 are shown in Table 2. We considered all populations which composed at least 0.5% of the total biomass at some time. Crus-

Table 1 Parameters of the functional response of each predator used in this study. U_m: maximal uptake rate; k: half-saturation constant; V: individual volume (µm^3 ind.$^{-1}$); F_m: maximal clearance rate (U_m/k)

Organism	U_m (µm^3 ind.$^{-1}$ h^{-1})	k (10^6 µm^3 ml^{-1})	U_m/V (% h^{-1})	F_m (µl ind.$^{-1}$ h^{-1})	Source
Crustaceans					
Thermocyclops dybowskii	333000	16.5	9.4	20	Adrian & Frost (1992)
Nauplii	40000	50	11.5	0.80	Fenchel (1980)
Rotifers					
Polyarthra sp.	37000	6.7	17.6	5.5	Rothhaupt (1990)
Keratella sp.	19000	6.7	18.1	2.8	Rothhaupt (1990)
Anuraeopsis fissa	15400	20	24.3	0.77	Massana & Pedrós-Alió (1994a)
Ciliates					
Coleps sp.	495	0.73	3.4	0.68	Massana & Pedrós-Alió (1994a)
Prorodon sp.	1600	0.73	3.4	2.2	Massana & Pedrós-Alió (1994a)
Cyclidium sp.	3200	50	40.1	0.064	Fenchel (1980)
Paramecium sp.	14590	50	22.5	0.29	Fenchel (1980)
Vorticella sp.	10690	50	25.0	0.21	Fenchel (1980)
Strombidium sp.	2060	50	45.0	0.041	Fenchel (1980)

Table 2. Dimensions (length and width), individual volume and carbon content of the main organisms in Lake Cisó. Contribution of each population to total biomass during summer stratification (12 sampling dates during 1990 and 1991) is also shown. HNF: heterotrophic nanoflagellates

Organism	Dimensions (µm)	Volume (µm^3 ind.$^{-1}$)	Carbon content (pg C ind.$^{-1}$)	% summer biomass Average	Range
Crustaceans					
T. dybowskii	340 × 70	3 520 000	301 000	0.24	0.00–1.30
Nauplii	100 × 75	349 000	30 000	0.15	0.00–0.63
Rotifers					
Polyarthra sp.	95 × 65	211 000	18 000	0.63	0.00–2.42
Keratella sp.	100 × 50	105 000	9 000	0.16	0.00–1.80
Anuraeopsis fissa	77 × 40	63 250	5 410	1.88	0.00–6.77
Ciliates					
Coleps sp.	42 × 23	14 700	2 060	5.48	0.00–19.05
Prorodon sp.	53 × 39	47 600	6 660	10.78	0.00–26.45
Cyclidium sp.	31 × 21	8 000	1 120	0.95	0.05–6.25
Paramecium sp.	108 × 48	64 800	9 080	0.68	0.00–5.28
Vorticella sp.	44 × 43	42 750	5 990	0.79	0.00–4.42
Strombidium sp.	21 × 21	4 580	640	0.17	0.00–0.74
HNF	4 × 4	34	4.7	0.19	0.04–0.59
Phytoplankton					
C. phaseolus	16 × 10	570	84	31.88	14.00–56.54
Other algae	6 × 6	115	21	5.24	0.00–15.77
Bacterioplankton					
Colorless bacteria	0.95 × 0.45	0.13	0.026	26.51	10.41–48.20
Chromatium sp.	5.0 × 2.7	23.5	4.7	5.64	0.00–25.61
Amoebobacter sp.	2.0 × 1.8	3.6	0.71	8.49	2.68–19.36

taceans, rotifers and ciliates were identified to genus or species level, whereas heterotrophic nanoflagellates (HNF) and algae other than Cryptomonas (other algae, with different species each sampling date) were pooled together. Two bacterial species, the phototrophic purple bacteria Chromatium (probably C. minus) and Amoebobacter (probably A. purpureus),

were morphologically recognized and counted separately. The remaining bacteria, mostly typical-looking cocci and rods, were called 'colorless bacteria' The only significant planktonic organisms present in Lake Cisó and not included in Table 2 were anaerobic ciliates. These were the object of a separate study (Massana & Pedrós-Alió 1994b).

Populations stratified at different depths of the water column. In a typical summer date (Fig. 1), there was a strong thermocline and most organisms accumulated at the metalimnion, in a narrow region where sulfide coexists with low concentrations of oxygen (Gasol et al. 1991a). There was a slight vertical segregation: in general the peak of phototrophic bacteria was placed below the peak of Cryptomonas, and the latter was found below the peak of algivorous ciliates and Anuraeopsis fissa. As we will see, such vertical distribution of populations and the presence of sulfide have strong implications for the flow of organic carbon through the food web.

We studied the changes in the integrated biomass of these populations for 2 yr (Fig. 2). Crustaceans (Fig. 2A), rotifers (Fig. 2B), algivorous protozoans (Fig. 2C) and bacterivorous protozoans (Fig. 2D) were found only during summer stratification (shaded region
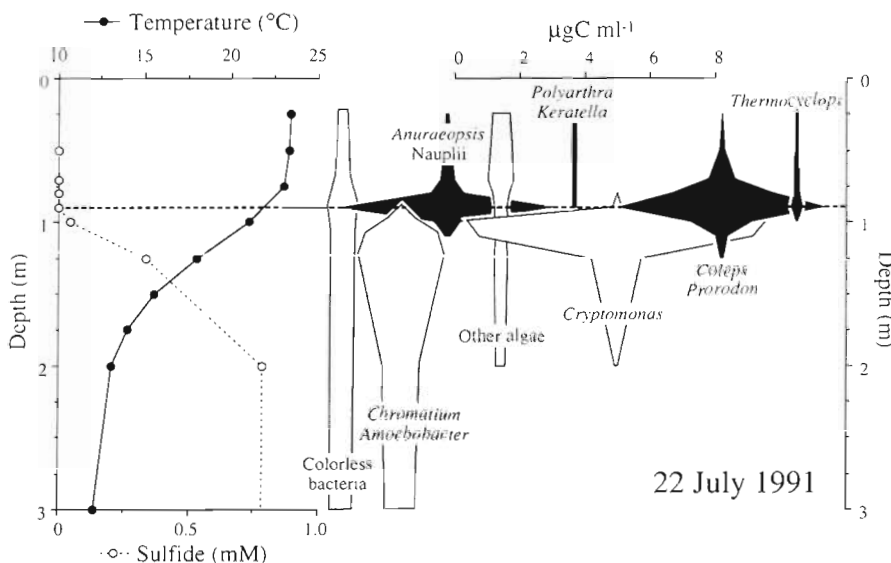

Fig. 1 Vertical profile of temperature and sulfide, and vertical distribution of the most significant populations in Lake Cisó on 22 July 1991. Black and gray kites indicate phagotrophic and osmotrophic groups, respectively. Horizontal dashed line: depth at which sulfide first appears
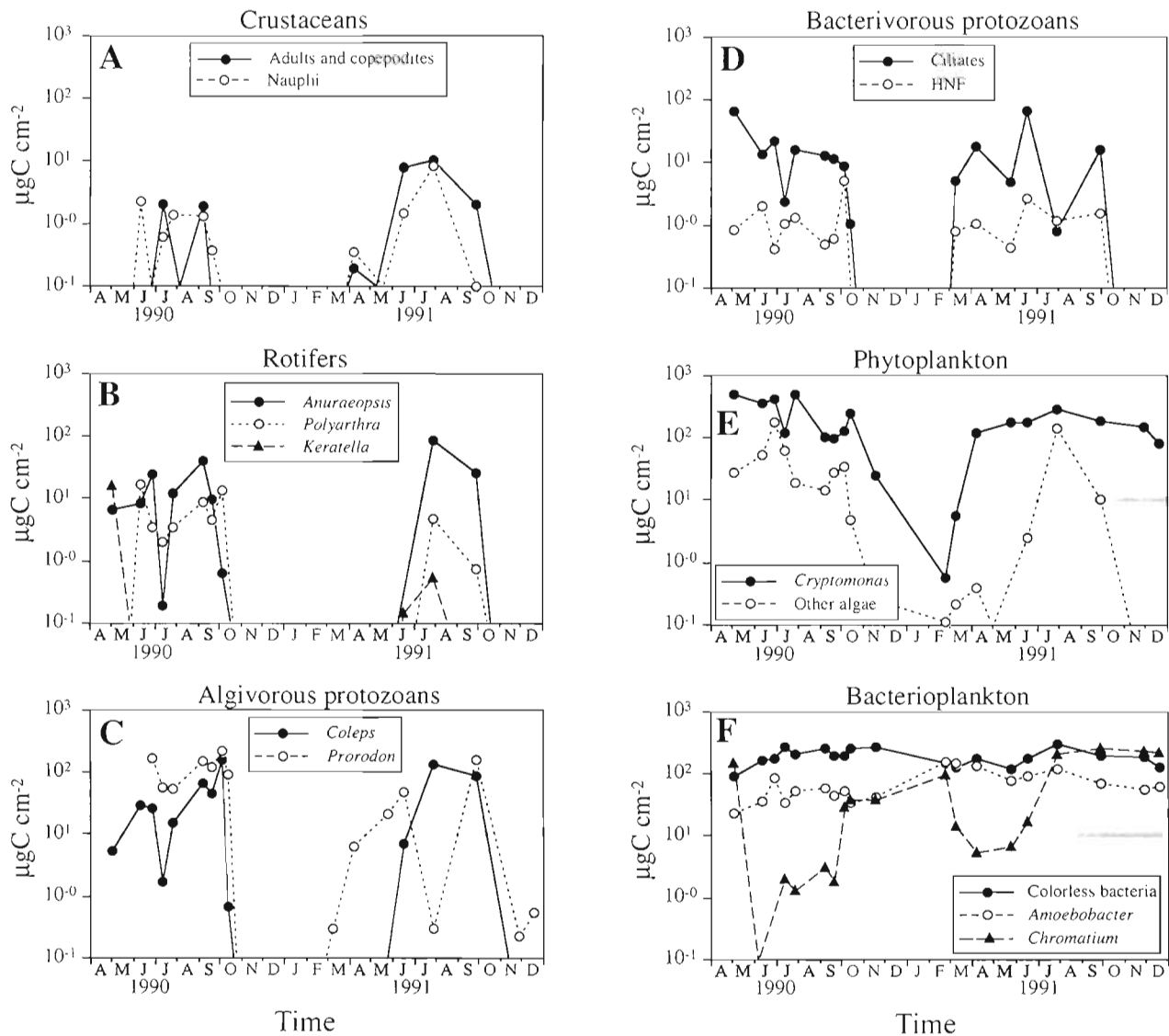
Fig. 2. Seasonal changes in integrated biomass of (A) crustaceans, (B) rotifers, (C) algivorous protozoans, (D) bacterivorous protozoans, (E) phytoplankton and (F) bacterioplankton in Lake Cisó from April 1990 to December 1991. Shaded region on the x-axis: stratification period (April to September). Horizontal line at 10 μg C cm^{-2} included to facilitate comparisons

in the horizontal axis) and disappeared during winter mixing Phytoplankton organisms (Fig. 2E) decreased during the mixing period to very low numbers, and all bacterial groups (Fig. 2F) were always present at a relatively constant biomass. The same populations that had disappeared during the mixing period developed during the summer of the second year, reaching similar biomass. This suggests the existence of a characteristic community that develops regularly every spring, changes very slightly during summer, and disappears with the fall mixing, when sulfide appears throughout the water column. A few populations dominated this summer community (Table 2): *Cryptomonas*, *Prorodon*, *Coleps*, *Amoebobacter*, *Chromatium* and colorless bacteria accounted for 90% of the total biomass.

Trophic roles and functional groups: binary food web

The trophic role of each significant population in the lake was determined by different approaches. Phototrophic bacteria, phytoplankton and some colorless bacteria incorporated inorganic carbon, as visualized by microautoradiography (data not shown, García-Cantizano 1992). The *Chlorella* cells endosymbiont in the ciliates *Coleps* and *Prorodon* also incorporated inorganic carbon, although their contribution to the growth of the ciliates (Massana unpubl. results) and to total primary production (García-Cantizano 1992) appeared to be insignificant. The food spectrum of phagotrophic organisms was determined by observa-

tion of ingested material in natural or experimental samples (Table 3).

Populations with similar trophic habits were aggregated into functional groups, guilds or 'trophic species', an assemblage of organisms that eat the same food items and are eaten by the same predators (Cohen 1989, Pimm et al. 1991, Gaedke 1995). The community of Lake Cisó was aggregated into 8 functional groups. *Thermocyclops dybowskii* constituted the first functional group. This is a small cyclopoid copepod, a typical inhabitant of small bodies of water (Maier 1990), a raptorial feeder specialized in particles of the size of rotifers, ciliates and algae (Nilssen 1978). The second functional group included the algivorous rotifers *Polyarthra* and *Keratella*, which feed preferentially on *Cryptomonas*, although they can also ingest other algae (Bogdan & Gilbert 1982). The third functional group was formed by the algivorous ciliates *Coleps* and *Prorodon*, that feed on *Cryptomonas* but never on bacteria or other algae. Such a selective predation behavior has also been observed by other investigators (Klaveness 1984, Finlay et al. 1991). The fourth group included the organisms feeding on the microbial component of the community, bacteria and other algae, and were named microphagous. The rotifer *Anuraeopsis fissa* dominated this assemblage, composed also of nauplii and the ciliates *Vorticella*, *Paramecium*, *Cyclidium* and *Strombidium*. Clearance rates of these organisms

have been determined *in situ* (Table 3). The 4 remaining functional groups were not phagotrophic but osmotrophic. Three of them were phototrophic: *Cryptomonas*, other algae and phototrophic bacteria (*Chromatium* and *Amoebobacter*). The last group comprised the colorless bacteria, with a regular morphology but heterogeneous metabolism: heterotrophy, anoxygenic photosynthesis and chemolithoautotrophy.

Determination of the trophic role of the significant populations resulted in the binary food web, a qualitative diagram that shows the trophic links connecting the different compartments and gives information about the structure of the food web. Several standard parameters have been described to compare binary food webs. These parameters were calculated in Lake Cisó (Table 4), both considering the unaggregated community formed by the 16 populations or assemblages presented in Table 2 (excluding HNF), or the community aggregated into the 8 previously described functional groups. The values obtained are in good concordance with those found in other systems (Table 4). The increase of the fraction of top-basal links and the lack of the intermediate-intermediate links is a typical trait of the smallest webs (Havens 1992). The very short maximal length is also expected in such a system with a reduced spatial dimensionality (Briand & Cohen 1987), where most populations grow at the same depth of the lake.

Table 3. Observation of the ingestion of different prey by phagotrophic organisms in Lake Cisó. Numbers correspond to clearance rates determined *in situ* (μl ind.$^{-1}$ h^{-1}). +: microscopic evidence of ingestion; –: microscopic evidence of non-ingestion. [+], [–]: information taken from the literature. All other numbers and signs are from our observations. FLB: fluorescently labeled bacteria; SL: small latex; FLC: fluorescently labeled *Chromatium*; LL: large latex; HNF: heterotrophic nanoflagellates

Phagotrophic organism	Particles ingested						Source
	FLB	SL	FLC	LL	Algae	*Cryptomonas*	
Crustaceans							
T. dybowskii	–	–	–	–	[+]	[+]	Adrian & Frost (1992), Nilssen (1978)
Nauplii	[+]	[+]	+	5.4	+	[–]	Nilssen (1978)
Rotifers							
Polyarthra sp.	–	–	–	–	+	+	Bogdan & Gilbert (1982)
Keratella sp.	[+]	[+]	[+]	[+]	[+]	[+]	Bogdan & Gilbert (1982), Ooms-Wilms (1991)
Anuraeopsis fissa	0.02	0.05	0.52	0.06	+	–	Ooms-Wilms (1991), Wilms et al. (1991)
Ciliates							
Coleps sp.	–	–	–	–	–	+	Klaveness (1984), Finlay et al. (1988, 1991), Madoni et al. (1990)
Prorodon sp.	–	–	–	–	–	+	Finlay et al. (1988)
Cyclidium sp.	0.02	+	0.02	+	–	–	Fenchel (1980), Finlay et al. (1988)
Paramecium sp.	+	0.02	0.35	0.24	+	–	Fenchel (1980)
Vorticella sp.	0.11	0.06	0.94	1.47	+	–	Finlay et al. (1988)
Strombidium sp.	0.04	+	0.42	+	+	–	Finlay et al. (1988)
HNF	0.0003	+	–	–	–	–	Fenchel (1986)

Table 4. Standard parameters of the binary food web of Lake Cisó. S: number of species (or functional groups); L: number of links; d: linkage density (L/S); TF, IF and BF: fractions of top, intermediate and basal species, respectively; Lti/L, Ltb/L, Lii/L and Lib/L: fractions of top-intermediate, top-basal, intermediate-intermediate and intermediate-basal links, respectively. Mean values reported in 2 comparative studies with unaggregated (Havens 1992) and aggregated (Cohen & Briand 1984) binary food webs are also shown for comparison

System	S	L	d	TF	IF	BF	Lti/L	Ltb/L	Lii/L	Lib/L
Lake Cisó										
Unaggregated	16	41	2.56	0.06	0.62	0.32	0.24	0.05	0	0.71
Aggregated	8	11	1.37	0.13	0.37	0.50	0.27	0.18	0	0.55
Literature mean values										
Unaggregated	–	–	–	0.06	0.44	0.50	0.10	0.05	0.32	0.53
Aggregated	–	–	–	0.19	0.53	0.29	0.35	0.08	0.30	0.27

Carbon fluxes among functional groups: trophic food web

For each sampling date, we calculated the integrated biomass of each functional group and the carbon fluxes among them, considering only the links presented in Table 3. Since the community was similar during the entire summer, we averaged the values of biomass and fluxes calculated in 9 sampling days
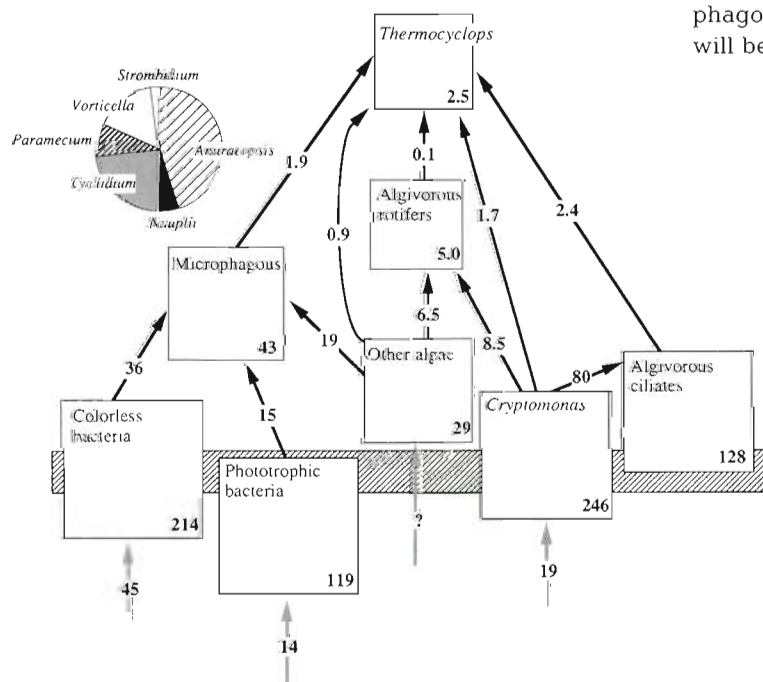

Fig. 3. Trophic food web in Lake Cisó obtained averaging the values of biomass and fluxes on 9 dates from summers 1990 and 1991. Biomass of compartments are shown inside boxes (in µg C cm^{-2}) and fluxes are shown above arrows (in µg C cm^{-2} d^{-1}). Compartments are drawn in a position relative to oxygen-sulfide interface (striped horizontal bar). Pie chart (left) shows the contribution of the different populations to total microphagous biomass. Average values during the stratification period of algal and bacterial production are also shown

(Fig. 3). As reference, the figure also shows the averaged value, during summer stratification, for primary production (García-Cantizano 1992) and for heterotrophic bacterial production (Calderón-Paz et al. 1993, García-Cantizano et al. 1994). The groups directly related with the sulfide interface (both bacterial groups, *Cryptomonas* and algivorous ciliates) show a large biomass and an apparent slow growth. In comparison, the biomass of *Thermocyclops* and algivorous rotifers is 1 or 2 orders of magnitude lower. Some compartments, especially algivorous ciliates and microphagous organisms, are severely unbalanced. This will be discussed later.

DISCUSSION

Limitations of the study

We repeatedly sampled Lake Cisó for 2 yr, accounting for both the vertical and seasonal distribution of populations. We determined which populations contributed significantly to the biomass of the summer community and what was their trophic role. Then, we quantified the carbon fluxes among populations. Whereas biomass and trophic roles are likely well determined, the quantification of carbon fluxes has a degree of uncertainty, especially due to the use of the functional response of predators. The parameters defining this response, U_m and k, were found independently and might not represent *in situ* conditions in Lake Cisó. In general, however, maximal clearance rates (F_m; Table 1) were in the same range than *in situ* clearance rates (Table 3). The same values of U_m and k (in µm^3) were applied to each prey, assuming that predators were feeding on all prey

with the same efficiency. In fact, predators normally have an optimal prey, depending on its size, shape, texture or behavior. Moreover, most organisms developed in depths with strong vertical gradients of temperature, oxygen and sulfide, which could cause changes of U_m and k with depth. For these reasons, the values of carbon fluxes obtained (Fig. 3) must be viewed as approximate estimates (likely overestimates), with a certain degree of variability associated. This exercise, however, remains valuable since it reveals some major trends in the flow of organic carbon through the community.

Analysis of the trophic food web of Lake Cisó

With the information on biomass, trophic roles and carbon fluxes presented in Fig. 3, we built a simplified diagram of the food web showing its main properties (Fig. 4). The first property was the presence of some functional groups (dark circles in Fig. 4) with high biomass, which was relatively stable all summer (Fig. 2) and had low predation losses. The growth of both bacterial groups was balanced by predation losses, with doubling times of 4 and 6 d for colorless and phototrophic bacteria, respectively. Losses by bacterivorous anaerobes were insignificant (Massana & Pedrós-Alió 1994b). The other 2 slow-growing compartments, *Cryptomonas* and algivorous ciliates, appeared unbalanced. We think this is due to the predation by the ciliates on *Cryptomonas* being overestimated. Most of the coexistence between both groups occurred in sulfide containing waters (Fig. 1), where the ciliates are
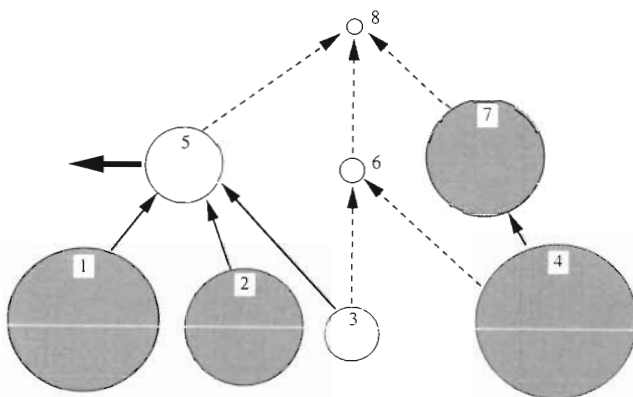

Fig. 4. Simplified diagram of the food web of Lake Cisó. Area of each compartment is proportional to its biomass. Dark compartments indicate slow growth and low predation losses. Dashed arrows: inefficient transfer of organic matter. Thick horizontal arrow: unknown mortality. 1. Colorless bacteria; 2: phototrophic bacteria; 3: other algae; 4: *Cryptomonas*; 5: microphagous organisms; 6: algivorous rotifers; 7: algivorous ciliates; 8: *Thermocyclops*

suboptimally adapted (Pedrós-Alió et al. 1995). Moreover, *Cryptomonas* migrated daily to spend the night in sulfide containing waters (Gasol et al. 1991a), thus reducing its predatory losses (Pedrós-Alió et al. 1995). To obtain balanced conditions that agree with observations of stable biomass, the predation by algivorous ciliates should be roughly equivalent to the growth of *Cryptomonas*, and this would result in doubling times of 9 d for *Cryptomonas* and 12 d for algivorous ciliates (40% gross growth efficiency; Jonsson 1986).

The remaining groups (light circles in Fig. 4) presented different dynamics. A doubling time of 1 d was calculated for other algae assuming a growth to compensate predation losses. This assemblage seemed to have a fast growth, high predation losses and the typical succession of species throughout the summer (Sommer et al. 1986, Gasol & Pedrós-Alió 1991). Microphagous organisms appeared unbalanced, with a potential fast growth (doubling time of 2 d; 40% gross growth efficiency; Jonsson 1986), minor predation losses and stable biomass (Fig. 2). The predation calculated could be overestimated (due to a similar mechanism of prey refuge), and the replacement of populations, especially of ciliates, suggests unknown mortality factors. The 2 zooplankton compartments always show low biomass (see below).

The second property of the food web of Lake Cisó was the inefficient transfer of organic matter from lower trophic levels to zooplankton (dashed lines in Fig. 4). This can be deduced by analyzing the values of both biomass and carbon flux. Theoretical models of steady-state food chains suggest a rather similar biomass in consecutive trophic levels (Fenchel & Finlay 1990). This seemed true for the pairs bacteria-microphagous organisms and *Cryptomonas*-algivorous ciliates, whereas the biomass of *Thermocyclops* was much lower. This indicated an efficient transfer of energy (although slow) between the first and the second trophic levels and an uncoupling between the second and the third. Data on carbon fluxes showed that *Thermocyclops* could ingest enough food to develop optimally in the lake. Despite the absence of predatory losses, its biomass always remained low, and its small size (Table 2) indicated that it was able to develop only to copepodite stages. Again, this suggests an inefficient transfer of organic matter to the highest level of the system.

Both properties of the food web can be explained by the same reason: the presence of opposite gradients of oxygen and sulfide at the metalimnion and the differential adaptation of certain populations to thrive in such an environment, a compromise between suboptimal growth and a spatial refuge from predators. This was well exemplified by *Cryptomonas*, the aerobic organism better adapted to survive in sulfide waters: its large biomass grew slowly, with only a minor fraction

being consumed by the ciliates *Coleps* and *Prorodon*. These ciliates presented a similar trend: in the metalimnion they could escape from their predators, build a large biomass, and grow slowly by feeding on *Cryptomonas*. Phototrophic bacteria were truly anaerobes, and their large biomass was due to the same mechanism, predation refuge. The zooplankton of Lake Cisó was not able to consume efficiently the metalimnetic biomass, likely because they do not tolerate sulfide at all. Moreover, we had the chance to follow the invasion of a new predator in Lake Cisó during summer 1992, *Daphnia pulex*, which was better adapted than *Thermocyclops* to microoxic waters (Massana et al. 1994a). *D. pulex* consumed most aerobic organisms (*Cryptomonas*, algivorous ciliates, microphagous organisms) and reached a huge biomass, indicating an efficient transfer of organic matter from the metalimnetic community to the epilimnetic zooplankton. Again, the populations better adapted to sulfide waters, such as phototrophic bacteria, escaped predation.

General implications of our study

Many properties of the food web of Lake Cisó differ from what is known from other freshwater or marine systems. First, most of the biomass is formed by a few populations, resulting in a very low diversity. Second, there is a dramatic vertical heterogeneity, with most of the biomass accumulated at the metalimnion and existence of spatial refuges for prey. Third, the turnover time of most of the metalimnetic biomass is long, with slow growth and low predation losses. Fourth, there is a lack of seasonal succession, unlike in many lakes of the temperate region (Sommer et al. 1986). This has been interpreted as a result of the absence of the forces driving succession, i.e. competition and predation (Gasol & Pedrós-Alió 1991, Massana et al. 1994b). Fifth, the bacterial component is very important: it represents 40% of the biomass of the system (Table 2), and total bacterial production is always higher than algal production (Fig. 3). The microbial loop, regarded as the routing of organic carbon from algae to protozoans through heterotrophic bacteria, is only a part of this bacteria-based food web, since the heterotrophic bacterial production also depends on imported organic matter (likely from leaves of the surrounding trees) and there is an important contribution of autotrophic bacterial production. Contrary to what has been described in most aquatic systems (Fenchel 1986), bacterivory is performed by ciliates and rotifers, and heterotrophic nanoflagellates are never significant in terms of biomass (Table 2, Fig. 2D).

The characteristics of the community of Lake Cisó allow a description of its food web with a detail that is normally impossible in other systems (Pomeroy 1991). Since the data derive from several samplings during the summer period it is more than an instantaneous description of the food web (Pimm et al. 1991). The binary food web is similar to that found in other communities (Table 4), suggesting that general ecological theory also applies in systems dominated by microorganisms and with a strong spatial heterogeneity. The finding of an inefficient transfer of organic matter from the metalimnetic biomass to the epilimnetic zooplankton can be applied to other systems with similar properties, such as thermally stratified or meromictic lakes with anoxic deep water and biomass accumulation in the oxic-anoxic interface. Metalimnetic communities can be regarded as systems with large and slow-growing biomass, with a minor fraction of the biomass channeled to epilimnetic zooplankton. The presence of sulfide seems to be the key factor, providing a refuge from predation.

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