

Seasonal dynamics of the Lake Kinneret food web: The importance of the microbial loop

Deborah R. Hart¹ and Lewi Stone

Department of Zoology, Tel Aviv University, Israel

Tom Berman

Kinneret Limnological Laboratory, Tiberias, Israel

Abstract

The role of bacteria and protozoa in the food web of Lake Kinneret was examined for 14 seasons over a 4-yr period (1989–1992) using a mass-balanced carbon flux model and network analysis. These microorganisms supplied nearly half of the carbon requirements of metazoan zooplankton grazers during the late winter–spring *Peridinium* bloom, when the lake was in its most eutrophic phase. The level of primary productivity was not seen to have a significant effect on the relative amounts of carbon passing from bacteria and protozoa to higher trophic levels. Rather, this depended on the proportion of photosynthetically fixed carbon that originated from “inedible” net-phytoplankton and the efficiency with which bacterial carbon was transferred to metazoans. The importance of the microbial loop as a carbon source to higher trophic levels in Lake Kinneret was a result of the often high levels of inedible net-phytoplankton (mostly *Peridinium gatunense*). The higher levels also occurred because bacterial production was transferred to metazoans in a relatively efficient one- or two-step process. These results indicate that even in eutrophic environments, bacteria and protozoa can supply significant amounts of carbon to metazoans.

The so-called “microbial loop” is now a well-accepted component of aquatic ecosystems (Pomeroy 1974; Azam et al. 1983). It is often recognized that a significant, albeit variable, proportion of organic carbon fixed by primary producers is eventually released as dissolved organic carbon (DOC) and taken up by bacteria. Bacteria utilize the DOC as a food source and form the base of a microbial food web involving a host of microorganisms.

The extent to which the primary produced carbon is passed through heterotrophic microorganisms and actually becomes available to higher trophic levels such as metazoan zooplankters has been the subject of some debate (Ducklow et al. 1986; Sherr et al. 1987). Current evidence indicates that the quantity and importance of bacterial carbon production that is eventually transferred to metazoans varies widely. In general, it has been suggested that the proportion of primary production that flows through the microbial loop, as opposed to direct utilization by metazoan grazers, is highest in oligotrophic and least in eutrophic environments (Bird and Kalff 1984; Porter et al. 1988; Weisse 1991; Azam and Smith 1991).

Lake Kinneret, Israel, has been identified as a lake where heterotrophic microorganisms may play an important role

(Hadas et al. 1990; Sherr et al. 1991; Stone et al. 1993; Hadas and Berman 1998; Hadas et al. 1998). Both ciliates and flagellates, as well as bacteria, are significant components of this ecosystem, though their importance may vary seasonally. We studied the seasonal dynamics of the microbial loop in Lake Kinneret and examined its importance in the food web of the euphotic zone of this lake.

This food web was modeled in terms of 10 compartments that describe the main biotic components of the Kinneret pelagic ecosystem. The model computed and analyzed the expected fluxes or flows of carbon between all compartments in the Kinneret food web. Linear programming was used to calculate the pattern of fluxes through the food web that conformed as closely as possible with observed data, while still maintaining internal consistency constraints such as mass balance (Stone et al. 1993; Hart et al. 1997). We quantified the role of the microbial loop in the Kinneret system by applying network analysis (Ulanowicz 1986; Kay et al. 1989) to these flux charts. We used these techniques to measure the extent of microbially mediated carbon cycling and other important quantities such as the proportion of the metazoans’ diets originating from the microbial loop. We specifically examined the conditions associated with those periods in which microorganisms are important food sources for higher trophic levels.

Although there have been previous attempts to model the carbon flow through the Lake Kinneret food web, the approach presented here overcomes many of their shortcomings and provides considerably more detail. The studies of Serruya et al. (1980) and Walline et al. (1993) gave only superficial analyses of the microbial loop and considered annual averages only. Stone et al. (1993) provided more detailed pictures of flows through the microbial loop via mass-balanced carbon flow charts for two different seasons in 1989.

¹To whom correspondence should be addressed. Present address: Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543.

Acknowledgments

We would like to thank U. Gaedke, D. Straile, S. Hochstädter, O. Hadas, B. Azoulay, A. Nishri, S. Gafny, and the anonymous reviewers for useful discussions and comments. This work was supported by a grant from the Bundesministerium für Forschung und Technologie, joint German–Israeli research project number 4340981, and from the United States–Israel Binational Science Foundation, Jerusalem, Israel (Grant 95-2).

The present article represents a major extension and re-thinking of Stone et al. (1993) in several ways. First, we applied more refined estimation techniques (Hart et al. 1997) than were used previously; these yielded more reliable flux estimates. Second, after an extensive review of the data and the literature, several assumptions were altered. Most important here is the addition of a flux from nanophytoplankton to ciliates (Madoni et al. 1990; Sherr et al. 1991) and alteration of the assumptions on bacterial production and respiration. Third, by examining 14 seasonal periods over 4 yr, the present work allowed for more confidence that the observed seasonal patterns are not just artifacts of a particular year. Finally, the present work more accurately quantified the role of the microbial loop by giving an in-depth network analysis, including new techniques for measuring the importance of heterotrophic microorganisms to the system.

Study site—Lake Kinneret (the Sea of Galilee) is a warm monomictic lake covering an area of about 170 km² with an average depth of approximately 24 m. The lake is considered mesoeutrophic, though the algal biomass and productivity during the late winter–early spring bloom are well into the eutrophic range (Berman et al. 1995). There is a brief mixing period from late December to February, and the lake is strongly stratified from about April to November with an anoxic hypolimnion. There was a drought during the first 3 yr of our study (1989–1991), and in the summer of the latter two of these years, the lake level dropped to a record low level (about 212.9 m below mean sea level). The winter of 1991–1992 was one of the coldest and wettest on record and saw a rapid 4-m rise in the lake level and a delayed appearance of the spring algal bloom.

We divided each of the four study years (1989–1992) into four seasons. The timing of the seasons varied with events in the lake rather than strictly with the calendar. The spring season coincided with the major annual bloom of the dinoflagellate *Peridinium gatunense*. Because of its large size and hard polyglucan theca, this organism provides almost no direct food supply to zooplankton and is only grazed and digested by some fish (especially *Sarotherodon galilaeus*), and the rotifer *Asplanchna* spp. (Spartaru and Zorn 1976; Serruya 1978). During the spring, there was relatively little biomass of smaller, edible algae but high bacterial production. At the end of the *Peridinium* bloom, bacterial production was high because of the considerable accumulation of organic matter derived from the dinoflagellates (Cavari et al. 1978; Berman et al. 1979; Zohary et al. 1998). During summer, nanophytoplankton primary production was relatively high but decreased in late summer–autumn with increasing nutrient limitation. Bacterial production also diminished in the fall. For two of the study years (1991–1992), there was insufficient data in the autumn to construct complete flux charts; these periods were therefore omitted from the analysis. The winter season was taken as the period from just before complete lake mixing until the beginning of the *Peridinium* bloom. More information on the annual and seasonal patterns of phytoplankton standing stock and primary production can be found in Berman et al. (1995).

Methods

The Kinneret food web—The food web was divided into 10 compartments as in Stone et al. (1993; see Fig. 1). These included two phytoplankton compartments: net-phytoplankton (>20 μm) and nanophytoplankton (<20 μm). The latter included picophytoplankton, though nanophytoplankton comprised nearly all the biomass of this compartment during the 4-yr study period. The net-phytoplankton was dominated by *Peridinium* and was assumed to be mostly invulnerable to grazing by metazoans. However, a small amount of this compartment was taken to be grazed. This is to account both for the fact that some net-algae other than *P. gatunense* may have been edible and because zooplankton consumed some of the detrital remains of dead *Peridinium* cells. There were three compartments for the microbial loop (bacteria, heterotrophic flagellates, and ciliates), three metazoan zooplankton compartments (rotifers, cladocerans, and copepods), one fish compartment, and a single detrital organic carbon pool. Note that the latter included both dissolved and particulate organic carbon (DOC and POC).

Each living compartment was characterized by its biomass B , respiration R , excretion E to the POC/DOC pool, and by flows from and to other living compartments. The intake I of a compartment is the sum of its inflows or inputs, while its production is given by

$$P = I - E - R. \quad (1)$$

The gross and net growth efficiencies k_1 and k_2 of a compartment are defined by the equations

$$k_1 = \frac{P}{I} \quad \text{and} \quad k_2 = \frac{P}{P + R}. \quad (2)$$

Note that all data were based on integrated values for a water column from 0–15 m depth during stratification, corresponding approximately to the euphotic depth and that of the epilimnion. The integration was taken over the entire water column during lake turnover.

Compartmental parameters

Biomasses—The biomasses of the compartments were estimated from data obtained by routine regular sampling at the Kinneret Limnological Laboratory. Bacterial biomass was calculated from cell counts using an average cell biomass of 0.066 pgC cell⁻¹ (volume = 0.3 μm³ × 0.22 pgC μm⁻³; Bratbak 1985; Sherr et al. 1991). Carbon content of the other compartments, as a percentage of wet weight, was taken to be 20% for net-phytoplankton (Pollinger and Berman 1975), 6% for copepods (Gophen 1977), 8% for other metazoan zooplankton (Gophen 1992), and 10% for nanophytoplankton, protozoa, and fish. Fish biomass was based on acoustic surveys (Walline et al. 1992; Kalikhman and Walline 1994).

Primary producers—Primary production was measured using the ¹⁴C method. Based on the data from Pollinger and Berman (1982), the mass-specific production of net-phyto-

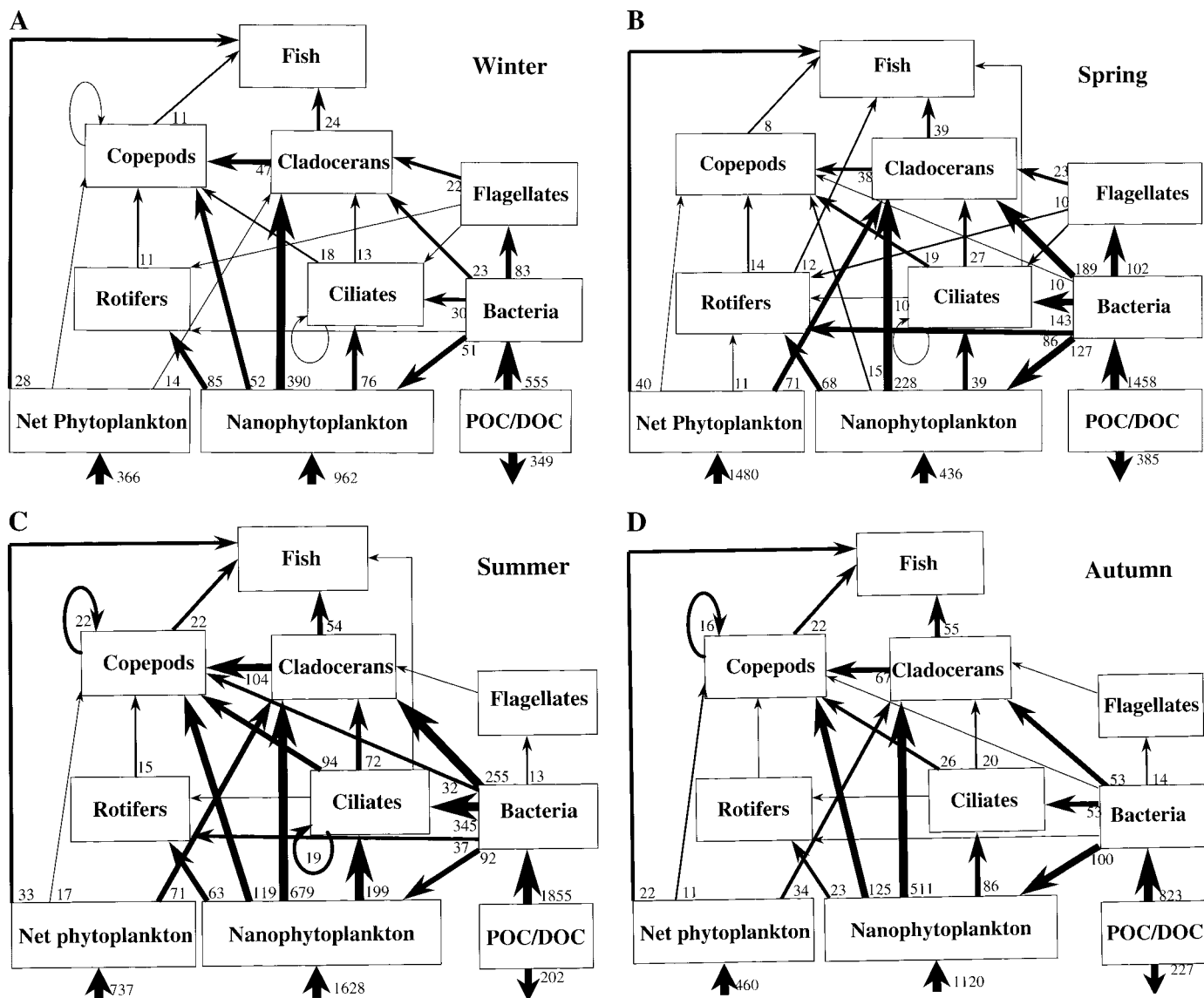


Fig. 1. Seasonally averaged compartmental carbon flux charts for the Kinneret food web during (A) winter (B) spring (C) summer (D) autumn. The arrows show fluxes (predation or uptake) between compartments that exceeded $3.5 \text{ mgC m}^{-2} \text{ d}^{-1}$; their thickness indicate the level of the flux. For fluxes of at least $10 \text{ mgC m}^{-2} \text{ d}^{-1}$, the numerical value of the flux is also given to the right or below the arrow. Respiration and fluxes to the POC/DOC compartment are not shown (see Figs. 2, 3).

plankton tended to decline relative to that of nanophytoplankton, as net-phytoplankton biomass increased. Using this data, we found a highly significant ($P < 0.001$, $r^2 = 0.96$) nonlinear relationship between the ratio of nano- to net-phytoplankton mass specific primary production and net-phytoplankton biomass. This relationship was used to apportion primary production between the two phytoplankton compartments.

Phytoplankton were assumed to respire 25% of gross primary production in winter and spring and 30% in summer and autumn. Direct losses of nanophytoplankton production to the POC/DOC pool, due to exudation or lysis by viruses (Fuhrman 1999), were generally taken as 10% of nanophytoplankton net primary production. However, in winter 1989, there was a large bloom of the diatom *Aulacoseira* (formerly

Melosira) spp. This alga, because of its large volume of intracellular vacuoles and prominent silica cell walls, is a poor-quality food (U. Pollinger pers. comm.), and it also has a high sinking rate. Therefore, we assumed that when *Aulacoseira* was dominant, 25% of net nanophytoplankton production went directly into the POC/DOC pool, after which much sedimented out of the system.

Microbial loop—Bacterial production was measured using the thymidine uptake method (Fuhrman and Azam 1982) with a conversion factor of $2 \times 10^{18} \text{ cell mol}^{-1}$. This factor was chosen as the one most consistent with the information obtained from the rest of the food web as well as being the most common literature estimate. Bacterial growth efficiency can vary depending on temperature and the availability of

easily assimilated material. Using short-term glucose uptake experiments in Lake Kinneret, Cavari et al. (1978) found that bacterial respiration was generally between 40% and 60% of carbon uptake. Because glucose is more easily assimilated than many other substrates, these experiments probably underestimated the level of respiration. For this reason, we estimated bacterial respiration to be between 50% and 70% of uptake, with the respiration percentage calculated according to the availability of substrate. This estimate for respiration losses is considerably higher, but probably more realistic, than the values (30% to 40% of carbon uptake) used by Stone et al. (1993). Lysis by phages (Fuhrman 1999) was assumed to deplete 10% of bacterial production.

Flagellates were assumed to consume only bacteria and picophytoplankton, with growth rates depending on food source availability and (negatively) on temperature (Hadas et al. 1990). The gross growth efficiency k_1 of this compartment was taken as 0.4 (Fenchel 1982). In addition to heterotrophic flagellates, mixotrophic flagellates (e.g., *Ochromonas* spp.) also can be significant consumers of bacteria in Lake Kinneret. We quantified the level of grazing on bacteria by mixotrophs using data from Paran (1994); these organisms were included as part of the nanophytoplankton compartment. Thus, the model contained a flux from bacteria to nanophytoplankton (see Fig. 1).

The ciliate community was dominated by the omnivore (primarily algivorous) *Coleps hirtus* and bacterivores such as *Vorticella mayeri*, *Colpoda* spp., and small scuticociliates (Madoni 1990; Sherr et al. 1991). The bacterivores occurred mostly during the times of high bacterial production (spring and early summer). In contrast, *Coleps* was more common during the later part of year when there was relatively little bacterial production (Hadas and Berman 1998). *Coleps* has a considerably slower growth rate than the bacterivorous ciliates (Madoni et al. 1990; Sherr et al. 1991; Hadas et al. 1998). Therefore, the growth rate of ciliates and the preference of these organisms to consume bacteria was increased during times of high bacterial production. Gross growth efficiency of the ciliates was taken to be 0.35 (Simek et al. 1996).

Metazoans—The rotifer community included species ranging from fine filter feeders such as *Keratella cochlearis* to the predatory *Asplanchna* spp. (Gophen 1978b). We assumed that rotifers have the same gross growth efficiency as cladocerans but somewhat higher mass-specific growth and grazing rates (Allan 1976; Bosselmann and Riemann 1986).

Cladocerans consisted primarily of the small to midsize species *Ceriodaphnia* spp., *Diaphanosoma brachyurum*, and *Bosmina longirostris* (Gophen 1978b). As these species are in general better at filtering nanoplankton than picoplankton (Bogdan and Gilbert 1984, 1987), we assumed that they have twice the preference to consume nanophytoplankton and flagellates than bacteria.

The copepods were dominated by the cyclopoid *Mesocyclops oregonus* (formerly *M. leucarti*; Gophen 1978b). Omnivorous calanoids and the cyclopoid *Thermocyclops dybowskii* also occurred in small numbers during this study period. We split this compartment into two subcompartments: one for the primarily herbivorous nauplius and early

copepodite stages and the other for the mostly carnivorous late copepodite and adult stages (Gophen 1977). Predation rates of the carnivorous stages were based on Gophen (1977) and were varied somewhat depending on food availability.

The fish compartment was divided into three subcompartments: zooplanktivores, consisting primarily of *Acanthobrama terraesanctae* (= *Mirogrex terraesanctae*, commonly known as lavnun or “Kinneret sardine”), filter feeders such as the St. Peter’s fish *Sarotherodon galilaeus*, and young of the year of all species. The predation rates (in units of gC per gC of predator per day) of zooplanktivores were varied between 0.015 in the winter to 0.03 in the summer (Gophen and Threlkeld 1989), whereas the ingestion of filter feeders was taken as ranging from 0.035 in autumn to 0.06 during the spring *Peridinium* bloom (Spartaru and Zorn 1976). Growth rates of young of the year fish were taken as 0.04 d⁻¹ in winter–spring, declining to 0.015 d⁻¹ in autumn (Azoulay and Gophen 1992; Gophen 1980). The gross growth efficiencies k_1 of the three subcompartments were estimated as 0.1 for zooplanktivores, 0.05 for filter feeders, and 0.25 for young of the year. *Acanthobrama* spawn in winter, whereas *Sarotherodon* reproduce in late spring and summer (Ben Tuvia et al. 1992).

Flux chart construction—For each season, we constructed food web flux charts that estimate the flows of carbon between the compartments of the food web. These charts needed to be consistent with known information about the biomass, production, and intake of each compartment as well as with mass-balance, i.e., the sum of the intake of a compartment must equal the sum of its outflow less any change in biomass over the period.

The construction of seasonal flux charts presents special challenges since gross growth efficiencies as well as mass-specific grazing and production rates can vary with food concentration and temperature (Peters and Downing 1984; Jumars et al. 1989; Gaedke and Straile 1994a). Thus, it may not be appropriate to apply the same literature values to periods where the prey densities are different. To account for the fact that herbivores increase their grazing rates with increasing food concentration, we assumed that all nanophytoplankton production was grazed, except for losses for respiration and a fixed small percentage (10% of net production, except in winter 1989) for exudation and viral lysis (cf. Gaedke and Straile 1994a,b). Note that “sloppy feeding” is accounted for by decreasing the assimilation efficiency of the consumer, so that it appears as a flux from prey to predator to POC/DOC, rather than a direct flux from prey to POC/DOC. Also, we assumed that the production of herbivores correspond to the calculated carbon demands of carnivores (based on the considerations discussed in the previous section). From this, we were able to estimate grazing and production rates as well as gross growth efficiencies k_1 of the herbivores. Net growth efficiencies k_2 were fixed at 0.5 for all protozoan and metazoan zooplankton compartments (Gaedke and Straile 1994a,b) except copepods. As the adult males do not contribute to production, the net growth efficiency of the copepod compartment was taken to be somewhat lower (about 0.42, depending slightly on the estimated age structure during the season). A summary of the

Table 1. Estimates of the ranges of production to biomass ratio, and gross and net growth efficiencies, for each living compartment.

Compartment	p/b (d^{-1})	k_1	k_2
Nanophytoplankton	0.11–0.67	0.57–0.67	0.65–0.72
Net-phytoplankton	0.015–0.11	0.55–0.60	0.65–0.71
Bacteria	0.01–0.59	0.27–0.45	0.28–0.48
Flagellates	0.20–1.30	0.4	0.5
Ciliates	0.10–0.90	0.35	0.5
Rotifers	0.08–0.31	0.11–0.22	0.5
Cladocerans	0.05–0.25	0.11–0.22	0.5
Copepods	0.02–0.13	0.08–0.16	0.40–0.44
Fish	0.003–0.005	0.09–0.13	0.24–0.31

p/b , k_1 and k_2 values used for all compartments during each season is given in Table 1.

The estimates of production P , gross and net growth efficiencies obtained as above gave us estimates of intake I , respiration R , and detrital flux E (from, e.g., excretion and sloppy feeding) for each compartment of the biota. These were obtained by the following transformations of Eq. 1 and Eq. 2:

$$I = \frac{P}{k_1}; \quad R = P \left(\frac{1}{k_2} - 1 \right); \quad E = P \left(\frac{1}{k_1} - \frac{1}{k_2} \right). \quad (3)$$

The fluxes t_{ij} from prey compartment j to consumer compartment i were then estimated using the formula

$$T_{ij} = \frac{d_i a_j r_{ij}}{\sum_k a_k r_{ik}}, \quad (4)$$

where d_i is the intake of compartment i and r_{ij} the relative preference of the j th compartment for the i th compartment as a food source (Hart et al. 1997). Here the parameter a_j is the available production of the j th compartment, which is defined as the production P less the rate of change in biomass B of the compartment from one season to the next (Gaedke and Straile 1994b). The relative preferences r_{ij} were based on literature reports on the feeding habits of the component species of each compartment, as noted above. A linear programming procedure as described in Stone et al. (1993) was then used to find the mass-balanced flux chart closest to the original estimates.

Network and sensitivity analysis—We used network analysis (Ulanowicz 1986; Kay et al. 1989) to analyze the role of recycling and the microbial loop in the food web. The importance of the microbial food chain to the dominant herbivores was evaluated by calculating the total dependency of cladocerans on the POC/DOC compartment. The total dependency of a consumer compartment on another compartment is defined as the fraction of the consumer's diet that passed through the other compartment at some time in the past. Thus, the total dependency of cladocerans on the detrital compartment measures the fraction of the cladoceran carbon intake (from bacteria, flagellates, and ciliates) that had passed through the POC/DOC pool.

We used Finn's cycling index (Finn 1976) as a statistic to quantify the level of carbon cycling in the system. Finn's index for a compartment measures the fraction of the flow into that compartment that has been in the compartment some time in the past. It represents the ratio of "recycled" flow to total throughput (total flow) of that compartment. The Finn's index of the system is the weighted (by the quantity of flow through each compartment) mean of the separate compartmental Finn's indices of that system. To calculate network statistics, we used the NETWK program of Ulanowicz and Kay (1991), as modified by C. Pahl-Wostl and D. Straile (pers. comm.) to account for the changes in biomass during different time intervals. Note, however, that we used the matrix based definition of Finn's cycling index given above (see Kay et al. 1989), which gives higher values than that of the NETWK program.

We defined the bacterial transfer efficiency (BTE) to be the percentage of bacterial production eventually consumed by metazoans. This is computed as

$$\text{BTE} = \frac{bc + fc \cdot dep_f + cc \cdot dep_c}{bp} \quad (5)$$

where bc , fc and cc are the amounts of bacteria, flagellates (including mixotrophs), and ciliates consumed by metazoans, respectively, dep_f and dep_c are the total dependency on POC/DOC of flagellates and ciliates, respectively, and bp is bacterial production.

In order to assess the robustness of our results, a sensitivity analysis was performed by constructing three alternate sets of flux charts in addition to the "standard" charts. In each case, one or two of the more important but uncertain inputs to our model were changed. For each alternative scenario, new sets of flux charts and network analysis statistics were found.

Results

Seasonal flux charts were constructed and mass-balanced for each of the 14 time periods from January 1989 to August 1992. Seasonal averages of these charts are shown in Fig. 1.

Production—Due to their higher mass-specific growth rate, nanophytoplankton were responsible for the majority of primary production except during the spring *Peridinium* bloom (Fig. 1), even though they usually comprised less than half of the phytoplankton biomass. In spring, the largely inedible *Peridinium* was responsible for most of the primary production. Because of this, almost 60% of net primary production (i.e., gross primary production less algal respiration) in the spring period was not grazed but moved directly to the POC/DOC compartment. In contrast, about 77% of net primary production was grazed during summer and autumn and 73% in the winter.

Bacterial production ranged from 2% to 48% of gross primary production (mean 23%) and was higher in spring and summer than in autumn and winter. It was higher during the low lake level years (1990 and 1991) than in 1989 and the 1992 flood year.

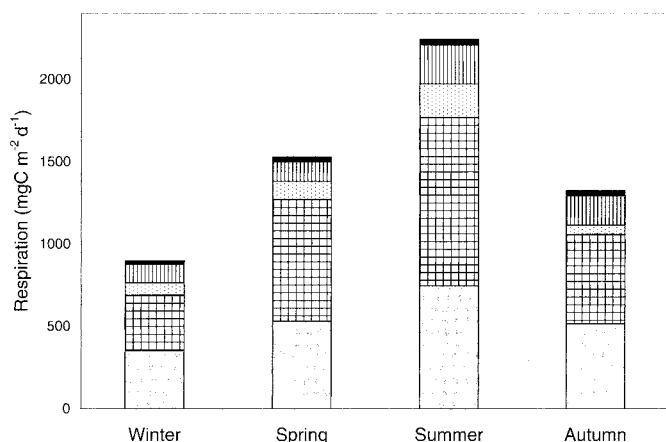


Fig. 2. Seasonally averaged contribution of phytoplankton (gray), bacteria (hatches), protozoa (dots), metazoan zooplankton (vertical lines), and fish (black) to community respiration.

Ciliates and cladocerans dominated zooplankton production. Ciliate production was especially high during the summers. Copepods and, during winter and spring, flagellates and rotifers, were also significant contributors to secondary production. Fish production averaged about $11 \text{ mgC m}^{-2} \text{ d}^{-1}$ or about 0.6% of gross primary production.

Grazing and predation—Average predation and grazing fluxes for each season are shown in Fig. 1. Cladocerans were the dominant grazers of phytoplankton, accounting on average for about 63% of all herbivory. Rotifers during spring, juvenile copepods during other seasons, and ciliates during most periods (especially during the summer) were also important grazers of phytoplankton.

Flagellates (both heterotrophic and mixotrophic), ciliates and cladocerans were all important consumers of bacteria. Flagellates were especially important in the winter when they accounted for about 60% of all grazing on bacteria. Ciliates were the major summer bacterial grazers, whereas cladocerans consumed about one-third of bacteria production in both spring and summer.

Copepods were the dominant predators on microzooplankton (i.e., ciliates, rotifers, and nauplii). Cladocera (preying on ciliates) and fish were less important predators on these organisms, consuming about one-quarter and one-eighth of microzooplankton production, respectively. Copepods also consumed a majority of cladocerans except in spring, when fish and copepods took roughly equal amounts.

Respiration and production of organic detritus—The main contributors to community respiration (Fig. 2) were bacteria (40% annual average) and phytoplankton (37%). The percentage contribution of phytoplankton and bacteria to community respiration ranged between 28–46% and 25–54%, respectively (excluding the unusual spring 1992 period, when bacterial production and respiration appeared to be abnormally low; however, these results may have been due to experimental error). The contribution by bacteria to community respiration was highest in spring and summer. Meta-

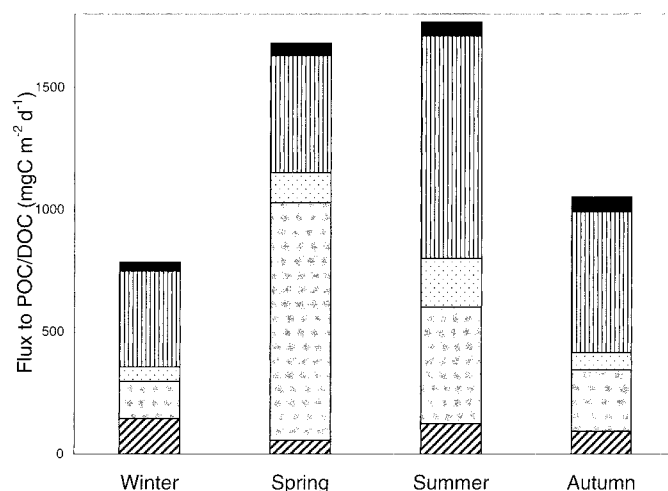


Fig. 3. Seasonally averaged fluxes to the POC/DOC pool from nanophytoplankton (diagonal lines), net-phytoplankton (gray), microorganisms (dots), metazoan zooplankton (vertical lines), and fish (black).

zoan zooplankton (14%), protozoa (7%), and fish (2%) were less important contributors to community respiration.

The main inputs to the POC/DOC detrital pool were from net-phytoplankton and zooplankton (Fig. 3). Net-phytoplankton was the dominant source of POC/DOC during spring, while zooplankton was the most important source in other seasons. Fish, protozoa, bacteria, and nanophytoplankton were less significant sources of detrital material.

Network analysis: The significance of the microbial loop—In order to assess the importance of carbon cycled through the microbial loop for the dominant herbivorous zooplankton (i.e., the cladocerans), we calculated the total dependency of cladocerans on the POC/DOC compartment. This parameter gave a measure of the fraction of the cladoceran diet deriving from recycled carbon (see Methods). The total dependency of cladocerans on POC/DOC for each season was the highest in the spring, with the exception of the unusual year 1992 and reached a maximum of 0.64 during the spring of 1991 (Fig. 4). If the spring 1992 season is excluded, the average total dependency in spring exceeded 0.5. Also, by calculating the total dependency of POC/DOC on each of the two phytoplankton compartments, we could find the ultimate source of the detrital carbon. The bulk of detrital carbon during spring was derived from net-phytoplankton (consisting almost completely of *Peridinium*), while at other times, most of this carbon originated from nanophytoplankton. The latter mostly reached the POC/DOC pool as a result of sloppy feeding and excretion by herbivores and their predators rather than through direct exudation from phytoplankton.

Finn's cycling index measures the fraction of the total carbon flow that has passed through a compartment more than one time (see Methods). This index, together with the ratio of bacterial production to primary production plus bacterial production and the bacterial transfer efficiency, is shown for each period in Fig. 5A. The seasonal averages of Finn's in-

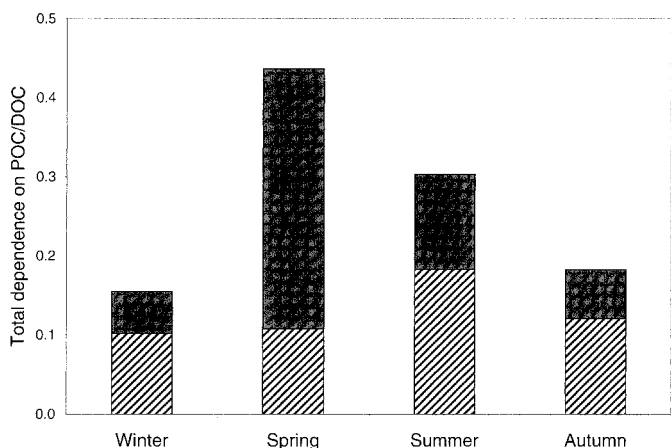


Fig. 4. Seasonal averages of the total dependency of cladocerans on detrital matter. The ultimate source of this detrital matter, either nano- (diagonal lines) or net- (gray) phytoplankton, is also shown.

dex, together with the bacterial transfer efficiency and the percentage of primary production stemming from net-phytoplankton, are shown in Fig. 5B.

The microbial food web efficiency was defined by Ducklow (1991) as the ratio of metazoan consumption of protozoa to total consumption by protozoa. This parameter measures the efficiency by which protozoa transfer energy to higher trophic levels. It did not vary much in different periods, ranging from a low of 0.29 in spring 1989 to a high of 0.35 in winter 1992 (average 0.32). Since metazoans can ingest bacteria directly as well as receive bacterial carbon indirectly via protozoa, it is of interest to compute the total fraction of bacterial production that reached metazoans. Thus, we defined the BTE as the fraction of bacterial production that is eventually consumed by metazoans. This quantity can be calculated using the total dependency coefficients obtained from network analysis (*see* Eq. 5). Seasonal averages of this quantity ranged from a low of 0.32 (in winter 1991) to a high of 0.68 (in spring 1990 and 1991), with an annual average of 0.53 (Fig. 5).

Sensitivity analysis—In order to assess the robustness of our results, we varied several of the more important but more uncertain assumptions and inputs to the model. We considered three alternative scenarios as outlined below.

First, the conversion factor used to estimate bacterial production from thymidine uptake measurements can vary considerably (Coveney and Wetzel 1988; Berman et al. 1994) and hence carries with it substantial uncertainty. Furthermore, reported values of bacterial respiration and growth efficiency have varied over a wide range (e.g., Coveney and Wetzel 1992). To consider the impact of variability in bacterial production and respiration on the carbon fluxes inferred by the model, we constructed alternative charts in which bacterial production was reduced by 45%, corresponding to a conversion factor of 1.1×10^{18} cell mol⁻¹, as used in some other food web studies (Gaedke and Straile 1994a,b). Concomitantly, bacterial respiration was increased

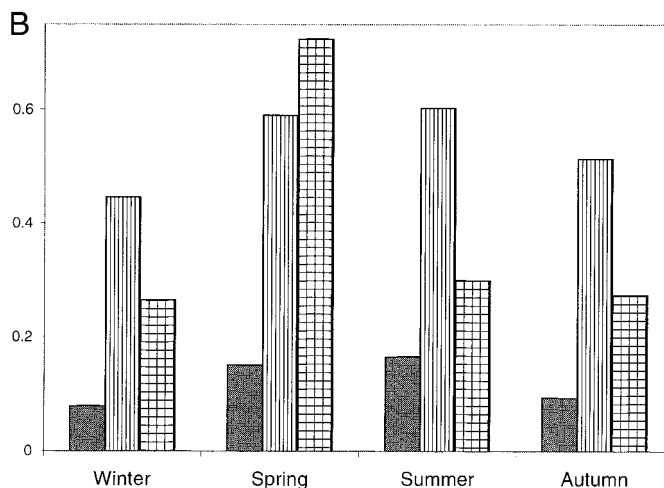
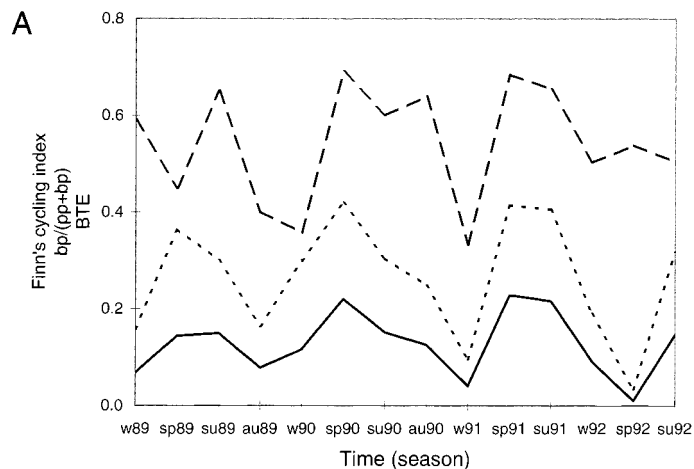


Fig. 5. (A) Finn's cycling index (solid line), the ratio of bacterial production to that of primary plus bacterial production (dotted line), and the bacterial transfer efficiency (dashed line) during each period studied. (B) Finn's index (gray bars), bacterial transfer efficiency (vertical lined bars), and the percent of primary production due to net-algae (checked bars), seasonally averaged.

by about 25% in order to retain rates of carbon sedimentation consistent with experimentally determined data.

Second, bacterial production cannot alone be increased much without assuming unrealistically high figures for bacterial efficiency. However, recent studies (Berman et al. 1994; B. Luz and J. Erez pers. comm.) have suggested that both primary production and bacterial production may have been underestimated in Lake Kinneret. To test how changes in these parameters might affect overall carbon fluxes in the model, we increased primary production by 50% and bacterial production by 75%; these numbers were chosen to remain consistent with experimentally obtained sedimentation data.

Third, the rates that we used for carbon flux into fish are taken from literature values based on laboratory measurements and may overestimate the true fish intake in the lake. Fish biomass estimates are also subject to considerable error (Walline et al. 1992). Since, unlike herbivorous zooplankton grazing, fish consumption was a direct model input, it is

Table 2. Sensitivity analysis. Values of key output parameters (cladoceran p/b , gross growth efficiency, total dependence on detrital matter, and system Finn's cycling index) under the standard and each of the alternative sets of assumptions.

Assumptions	Cladoc- eran p/b	Cladoc- eran k_1	Cladoc- eran de- pendence	Finn's cycling index
Standard	0.13	0.17	0.27	0.12
Low bacterial production	0.13	0.20	0.17	0.07
High primary and bacterial production	0.14	0.10	0.32	0.21
Low fish ingestion	0.12	0.15	0.28	0.13

worthwhile to explore what impact a change in the level of fish consumption would have on the other parts of the system. To evaluate the effect that overestimating fish consumption could have on other carbon fluxes, we created alternative charts in which the carbon intake of fish was reduced by 25%.

Some key output parameters from the model using the original flux charts and the three alternative assumptions are listed in Table 2. Under the low bacterial production assumption, there would be fewer microorganisms and total food available for consumption by metazoans. Because the cladocerans' food supply was diminished, but their production (as calculated by the estimated predation on cladocerans) was only slightly changed under this scenario, a higher cladoceran gross growth efficiency k_1 is required to obtain mass balance. A lower total dependency on POC/DOC and Finn's cycling index is also seen, due to the lower percentage of microbial food in the cladocerans' diet. Conversely, the high primary and bacterial production assumption implies a low k_1 value because food is so abundant. Also, since bacterial production is increased more than primary production, the indicators of the importance the microbial loop, the dependency on POC/DOC and Finn's index, were higher under this assumption. The lower fish predation assumption mainly resulted in slightly lower cladoceran production and gross growth efficiency but had little effect on the total dependency figure and Finn's index.

Discussion

It has been proposed that in aquatic systems, the microbial loop has a less important role under eutrophic conditions than in oligotrophic systems (Bird and Kalff 1984; Porter et al. 1989; Weisse 1991; Azam and Smith 1991; but see Riemann et al. 1986 for a contrary view). However, our results indicate that in mesoeutrophic Lake Kinneret, bacteria and protozoa were a significant portion of the diet of metazoan grazers. This has also been suggested on the basis of field observations (Hadas and Berman 1998). Heterotrophic microorganisms were an especially important component of the metazoans' diet during the spring bloom, when the lake is in its most eutrophic phase. However, the relationship between primary production and the total dependence of cladocerans on the microbial food web was not significant ($P = 0.2$, or excluding the spring 1992 season, $P = 0.15$),

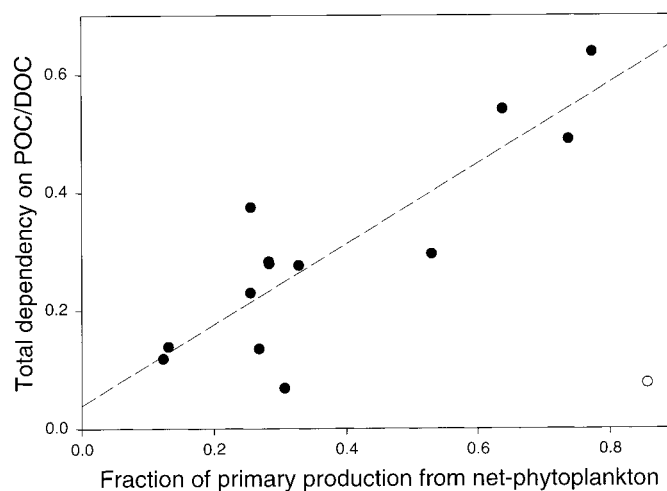


Fig. 6. Plot of the total dependency of cladocerans on POC/DOC as a function of the percentage of primary production stemming from net-phytoplankton. The regression line excluding the outlier spring 1992 point (open circle) is also shown.

though weakly positive. This suggests that there is no simple relationship between lake trophy per se and the relative importance of the microbial loop as a source of carbon to higher trophic levels.

We propose that two other factors can influence the relative importance of the microbial loop as a food source to metazoans in aquatic ecosystems. We found a relationship between total cladoceran dependence on carbon derived from the POC/DOC pool (i.e., via the microbial loop) and the fraction of phytoplankton productivity stemming from net-phytoplankton (see Fig. 6). The three highest levels of dependency on POC/DOC were all during the spring *Peridinium* bloom, when most of the primary production was due to net-phytoplankton. In this lake, the microbial loop organisms can be considered as providing a safety net for metazoan grazers in spring, serving as an alternative food source when edible nanophytoplankton were in short supply. (As previously noted, the spring of 1992 did not follow this pattern, but we are uncertain about the reliability of the recorded data for this period.)

The importance of microbes as sources for metazoan carbon requirements may also depend on the efficiency at which bacterial carbon is transferred to higher trophic levels; this is quantified by the BTE. To test this, we performed a multiple regression of the total cladoceran dependence on POC/DOC against net-phytoplankton production (logarithmically transformed) and BTE. The partial regression with the net-phytoplankton fraction was significant ($P = 0.04$), though the partial regression with BTE had only borderline significance ($P = 0.06$). However, when the aberrant spring 1992 data was removed, both predictors were strongly significant ($P < 0.001$ and $P = 0.002$, respectively), with a total r^2 of 0.9.

Bacterial growth is carbon limited in most, but not all, lakes (Coveney and Wetzel 1992). To check if this is the case in Lake Kinneret, we regressed log bacterial production against the log of the flux of detrital carbon flowing into the POC/DOC compartment, as given by the model. When the

outlier spring 1992 point was excluded, the regression was highly significant ($r^2 = 0.73$, $P < 0.001$) with a slope of 1.0. This indicates that bacterial production proportionally followed the supply of detrital carbon. Experiments (T. Berman unpubl. data) similarly demonstrated that bacteria was primarily carbon limited in Lake Kinneret, with occasional colimitation by phosphorus or nitrogen.

In Lake Kinneret and most other lakes, the response of bacterial production and the microbial loop to changes in primary production will thus be determined by the changes induced in the supply of POC/DOC. Because algal extracellular release of DOC relative to primary production tends to be greater in nutrient poor waters (Berman and Holm-Hansen 1974), the relative proportion of bacterial to primary production in these conditions may be higher in oligotrophic than in eutrophic systems. Additionally, allochthonous carbon inputs may be more important when autotrophic production is low (del Giorgio et al. 1999). Hence, the detrital chain may in some cases become less important as a food source with increasing levels of primary production.

However, under a range of mesotrophic to eutrophic conditions, increases in nutrients can induce the outgrowth of large or colonial forms of algae or cyanobacteria which are not readily grazed by metazoans (Watson and McCauley 1988). The ungrazed remains of these phytoplankton can be important carbon sources for bacteria. Additionally, the rate of viral infection of bacteria and phytoplankton may be greater in eutrophic environments because of higher concentrations of phages and viruses (Fuhrman 1999). This would increase the percentage of primary and bacterial production lost to viral lysis. Thus, when inedible phytoplankton or viral lysis are significant sources of POC/DOC, the microbial loop can become more important as a carbon source to metazoans with increasing lake trophy. In the case of Lake Kinneret, the remains of largely inedible net-phytoplankton were a much more important source of detrital carbon than phytoplankton exudates or allochthonous inputs. This explains partially why bacteria and protozoa are especially important carbon sources for metazoans during times of higher productivity in this lake.

In many lakes, where flagellates are the dominant grazers on bacteria, the transfer of bacterial carbon to macrozooplankton is an inefficient two- or three-step process. In Lake Kinneret, flagellates consumed a majority of bacterial production only during winter, and heterotrophic flagellates almost disappeared during summer and autumn. In place of the flagellates, ciliates, and metazoans were significant direct consumers of bacteria during these seasons. For this reason, the transfer of bacterial carbon to metazoans was mostly a one- or two-step process, which was reflected in the high BTE coefficients recorded in this lake. By partially short-circuiting the protozoan portion of the microbial loop, metazoans can utilize a larger proportion of bacterial production than otherwise would be possible. The importance and seasonal variation in the direct utilization of bacteria has been noted in other systems as well (Pace et al. 1990).

Another source for the idea that microorganisms play more important roles in oligotrophic waters is the work of Bird and Kalff (1984), who showed that the ratio of bacterial counts to chlorophyll *a* tends to decline with increasing eu-

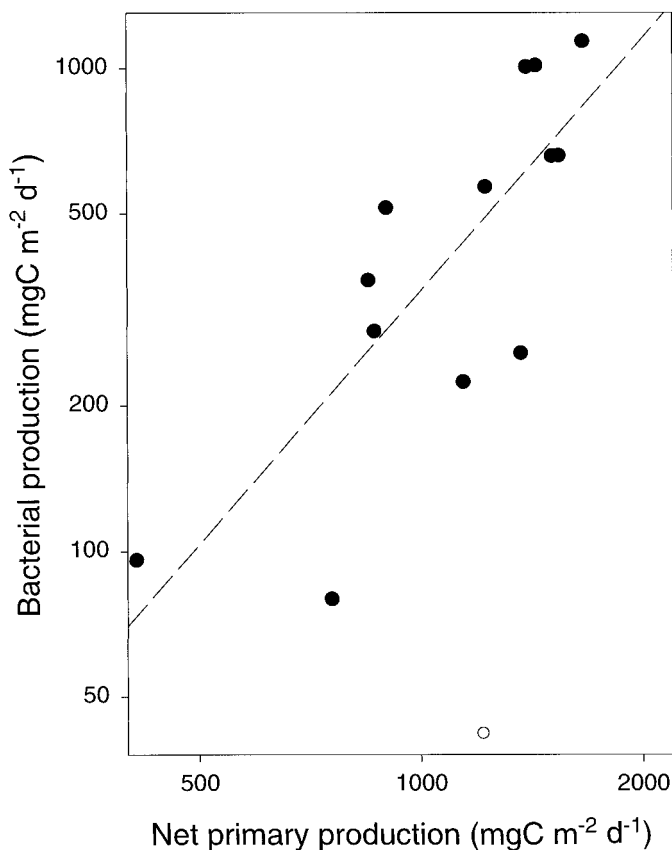


Fig. 7. Log-log plot of bacterial production versus primary production for each period studied. The regression line excluding the outlier spring 1992 point (open circle) is also shown.

trophication. Such a decline was also seen in Lake Kinneret. However, the ratio of bacterial productivity to chlorophyll *a* (data not shown) tended to rise with increasing primary productivity. A plot of bacterial productivity versus primary productivity, log transformed, for the 14 seasons studied here (Fig. 7) showed a similar trend. The slope of the regression line was considerably greater than 1 ($m = 1.7$; $r^2 = 0.62$, omitting the spring 1992 season), again indicating that bacterial production tended to be relatively more important in the more eutrophic periods. Although increasing primary productivity strongly stimulated bacterial production, grazing on bacteria also increased accordingly, thus maintaining more or less the same bacterial biomass. In this scenario, bacteria biomass was top-down controlled, and much of the increased bacterial production was transferred to higher trophic levels. As Bird and Kalff (1984) cautioned, bacterial numbers alone may not accurately reflect microbial loop activity.

The relatively high Finn's cycling index in spring and summer was another expression of the elevated bacterial activity during these seasons. Since recycled carbon must pass through the bacterial compartment, bacterial production is closely related to the level of recycling. The total throughput (i.e., the sum of all carbon fluxes through the system) should be closely related to the sum of primary and bacterial production. Therefore, as Fig. 5A demonstrates, the ratio z of

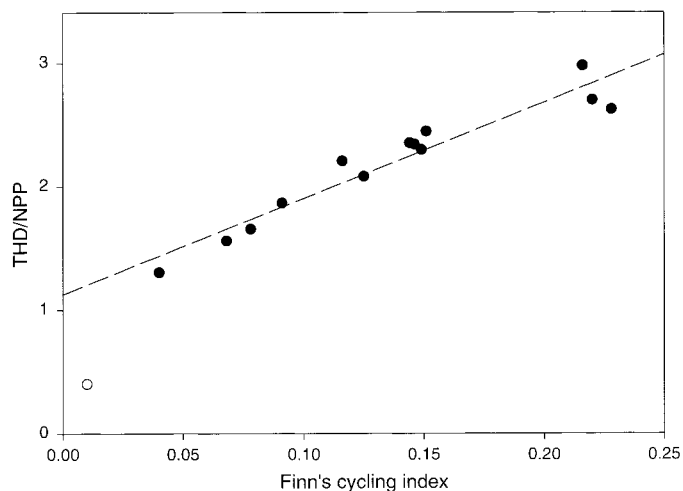


Fig. 8. Plot of the ratio of total heterotrophic demand (THD) to net primary production (NPP) versus Finn's cycling index. The regression line excluding the outlier spring 1992 point (open circle) is also shown.

bacterial production to the sum of primary and bacterial production had a close relationship to Finn's index Fi (a similar relationship was also found in Lake Constance [Straile 1994]). Linear regression of Fi versus z gave a highly significant fit ($Fi = 0.6z$; $r^2 = 0.97$; $P < 0.001$). This relationship permits the estimation of the importance of carbon cycling to the system, as measured by Finn's index, from primary and bacterial production data alone, without having to construct detailed carbon flux charts.

Strayer (1988) noted that the total heterotrophic demand (THD) in aquatic ecosystems can considerably exceed primary production because of the effects of recycling. Thus, the ratio of THD to net primary productivity should be connected with measures of recycling. To check this, we plotted this ratio against Finn's index for each of the 14 seasons studied (Fig. 8) and found a significant correlation ($r^2 = 0.87$; $P < 0.001$). Note that the heterotrophic demand often exceeded primary productivity by a factor of two or more, indicating that the Kinneret epilimnion is a very retentive system as defined by Strayer (1988).

Sediment trap measurements (A. Nishri unpubl. data) showed that the actual sedimentation is about 10–12% of primary production, only slightly lower than the estimates we obtained. Assuming that our estimates of primary production and bacterial respiration (60% of intake on average) are correct, this implies that our estimate of the thymidine conversion coefficient (2×10^{18} cell mol⁻¹) is also near to the mark. If the confidence interval for the average bacterial respiration is taken to be 40–80% of intake, this gives a thymidine conversion factor of between $1\text{--}3 \times 10^{18}$ cell mol⁻¹. Thus, ecosystem models such as ours can help give independent estimates of difficult-to-measure parameters such as the thymidine conversion factor and bacterial respiration (Cole et al. 1989).

Berman et al. (1994) reported an experimentally determined thymidine conversion factor (1×10^{19} cell mol⁻¹) much higher than the one used here. The sensitivity analysis indicates that the amount of bacterial production that such a

high conversion factor would imply could only be sustained if primary production has been drastically underestimated. Although it is possible that primary productivity has been underestimated to some extent (see Sensitivity analysis), here we chose to use the measured value of primary productivity and to reduce the thymidine conversion factor to a more commonly used value consistent with the reported values of primary productivity. Resolution of this discrepancy must await more definitive measurements of primary and bacterial productivity.

Our compartmental model is not a predictive model but rather a descriptive one that gives detailed seasonal pictures of the Kinneret food web. There have been only a few other food webs whose seasonal dynamics have been characterized in such a detailed way (e.g., Baird and Ulanowicz 1989; Gaedke and Straile 1994a,b). These pictures can aid considerably in the difficult task in building and parameterizing predictive dynamical food web models. The estimated fluxes found in this study, for example, have been used to parameterize a differential equation model of the Lake Kinneret food web, which shows that invertebrate predators can dampen the classical trophic cascade from fish to phytoplankton (Hart pers. comm.).

Because of the many estimates and assumptions required to build a whole ecosystem model such as the one presented here, our results carry a certain amount of uncertainty. However, the sensitivity analysis indicates that our results are relatively robust to changes in model assumptions. Large changes in one or more assumptions induced somewhat smaller changes in each of the key statistics listed in Table 2. Though there is some uncertainty in the exact values of the fluxes and network analysis parameters, the qualitative conclusions of this study were not substantially affected by changes in the tested assumptions. By combining information about all aspects of the food web, our results give a holistic picture of the Kinneret ecosystem and the interconnections between its components that could not be obtained by only studying these parts separately.

We have demonstrated here how such models can be used to quantify the role of heterotrophic microorganisms in the carbon budget of a pelagic system. In particular, we have measured the importance of heterotrophic microorganisms to the diet of metazoan grazers, and in addition, we have quantified the extent of recycling of organic material.

References

- ALLAN, J. D. 1976. Life history patterns in zooplankton. *Am. Nat.* **110**: 165–181.
- AZAM, F., T. FENCHEL, J. FIELD, J. GRAY, L. MEYER-REID, AND F. THINGSTAD. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* **10**: 257–263.
- , AND D. C. SMITH. 1991. Bacterial influence on the variability in the oceans' biogeochemical state: A mechanistic view, p. 213–236. *In* S. Demers [ed.], Particle analysis in oceanography. NATO-ISI Series G **27**.
- AZOULAY, B., AND M. GOPHEN. 1992. Feeding habits of larval *Mirrogrex terraesanctae* (Steinitz, 1952) in Lake Kinneret (Israel) II. Experimental study. *Hydrobiologia* **246**: 251–258.
- BAIRD, D., AND R. E. ULANOWICZ. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* **59**: 329–364.

- BEN-TUVIA, A., E. B. DAVIDOFF, J. SHAPIRO, AND D. SHEFLER. 1992. Biology and management of Lake Kinneret fisheries. *Isr. J. Aquacult. Bamidgah* **44**: 48–65.
- BERMAN, T., O. HADAS, AND U. MARCHIAM. 1979. Heterotrophic glucose uptake and respiration in Lake Kinneret. *Hydrobiologia* **62**: 275–282.
- , AND O. HOLM-HANSEN. 1974. Release of photoassimilated carbon as dissolved organic matter by marine phytoplankton. *Mar. Biol.* **28**: 305–310.
- , H. HOPPE, AND K. GOCKE. 1994. Response of aquatic bacterial populations to substrate enrichment. *Mar. Ecol. Prog. Ser.* **104**: 173–184.
- , L. STONE, Y. YACOBI, B. KAPLAN, M. SCHLICHTER, A. NISHRI, AND U. POLLINGHER. 1995. Primary production and phytoplankton in Lake Kinneret: A long-term record (1972–1993). *Limnol. Oceanogr.* **40**: 1064–1076.
- BIRD, D. F., AND KALFF, J. 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. *Can. J. Fish. Aquat. Sci.* **41**: 1015–1023.
- BOGDAN, K. G., AND J. J. GILBERT. 1984. Body size and food size in freshwater zooplankton. *Proc. Natl. Acad. Sci. USA* **81**: 6427–6431.
- , AND ———. 1987. Quantitative comparison of food niches in some freshwater zooplankton. A multi-cell-tracer approach. *Oecologia* **72**: 331–340.
- BOSELNAN, S., AND B. RIEMANN. 1986. Zooplankton, p. 199–236. *In* B. Riemann and M. Sondergaard [eds.], *Carbon dynamics in eutrophic, temperate lakes*. Elsevier.
- BRATBAK, G. 1985. Bacterial biovolume and biomass estimations. *Appl. Environ. Microbiol.* **49**: 1488–1493.
- CAVARI, B. Z., G. PHELPS, AND O. HADAS. 1978. Glucose concentrations and heterotrophic activity in Lake Kinneret. *Verh. Int. Ver. Limnol.* **20**: 2249–2254.
- COLE, J., N. CARARO, D. STRAYER, C. OCHS, AND S. NOLAN. 1989. A detailed organic carbon budget as an ecosystems level calibration of bacterial respiration in an oligotrophic lake during midsummer. *Limnol. Oceanogr.* **34**: 286–296.
- COVENEY, M. F., AND R. G. WETZEL. 1988. Experimental evaluation of conversion factors for the ³H thymidine incorporation assay of bacterial secondary productivity. *Appl. Environ. Microbiol.* **54**: 2018–2026.
- , AND ———. 1992. Effects of nutrients on specific growth rates of bacterioplankton in oligotrophic lake water cultures. *Appl. Environ. Microbiol.* **58**: 150–156.
- DEL GIORGIO, P. A., J. J. COLE, N. F. CARACO, AND R. H. PETERS. 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology* **80**: 1422–1431.
- DUCKLOW, H. W. 1991. The passage of carbon through microbial food webs: Results from flow network models. *Mar. Microb. Food Webs* **5**: 129–144.
- , D. A. PURDIE, P. WILLIAMS, AND J. M. DAVIES. 1986. Bacterioplankton: A sink for carbon in a coastal marine plankton community. *Science* **232**: 865–867.
- FENCHEL, T. 1982. Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. *Mar. Ecol. Prog. Ser.* **8**: 225–231.
- FINN, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol.* **56**: 363–380.
- FUHRMAN, J. 1999. Marine viruses and their biogeochemical and ecological effects. *Nature* **399**: 541–548.
- , AND F. AZAM. 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in a marine surface waters: Evaluation and field results. *Mar. Biol.* **66**: 109–120.
- GAEDKE, U., AND D. STRAILE. 1994a. Seasonal changes of trophic transfer efficiency in a plankton food web derived from biomass size distributions and network analysis. *Ecol. Model.* **75**: 435–445.
- , AND ———. 1994b. Seasonal changes of the quantitative importance of protozoans in a large lake. An ecosystem approach using mass-balanced carbon flow diagrams. *Mar. Microb. Food Webs* **8**: 163–188.
- GOPHEN, M. 1977. Food and feeding habits of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). *Freshw. Biol.* **7**: 513–518.
- . 1978a. The productivity of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). *Hydrobiologia* **60**: 17–22.
- . 1978b. Zooplankton, p. 297–311. *In* C. Serruya [ed.], *Lake Kinneret. Monographiae Biologicae* **32**. Junk.
- . 1980. Food sources, feeding behaviour and growth rates of *Sarotherodon galilaeum* (Linnaeus) fingerlings. *Aquaculture* **20**: 101–115.
- . 1992. Zooplankton developments in the Kinneret during the period 1969–1991. Kinneret Limnological Laboratory Report T7/92 (in Hebrew).
- , AND S. THRELKELD. 1989. An experimental study of zooplankton consumption by the Lake Kinneret sardine. *Arch. Hydrobiol.* **115**: 91–95.
- HADAS, O., AND T. BERMAN. 1998. Seasonal abundance and vertical distribution of protozoa (flagellates, ciliates) in L. Kinneret, Israel. *Aquat. Microb. Ecol.* **14**: 161–170.
- , N. MALINSKY-RUSHANSKY, R. PINKAS, AND T. E. CAPPENBERG. 1998. Grazing on autotrophic and heterotrophic picoplankton by ciliates isolated from Lake Kinneret, Israel. *J. Plankton Res.* **20**: 1435–1448.
- , R. PINKAS, C. ALBERT-DIEZ, J. BLOEM, T. CAPPENBERG, AND T. BERMAN. 1990. The effect of detrital addition on the development of nanoflagellates and bacteria in Lake Kinneret. *J. Plankton Res.* **12**: 185–199.
- HART, D. R., L. STONE, A. STERN, D. STRAILE, AND U. GAEDKE. 1997. Methods for constructing and balancing ecosystem flux charts: New techniques and software. *Environ. Model. Assess.* **2**: 23–28.
- JUMARS, P. A., D. L. PENRY, J. A. BAROSS, M. J. PERRY, AND B. W. FROST. 1989. Closing the microbial loop: Dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res.* **36**: 483–495.
- KALIKHMAN, Y., AND F. WALLINE. 1994. Population size and distribution of pelagic fish in Lake Kinneret determined using acoustic method. Kinneret Limnological Laboratory Report T11/94.
- KAY, J. J., L. E. GRAHAM, AND R. E. ULANOWICZ. 1989. A detailed guide to network analysis, p. 15–61. *In* F. Wulff, J. G. Field, and K. H. Mann, [eds.], *Network analysis in marine ecology, methods and applications, coastal and estuarine studies* **32**. Springer-Verlag.
- MADONI, P. 1990. The ciliated protozoa of the monomictic Lake Kinneret (Israel): Species composition and distribution during stratification. *Hydrobiologia* **190**: 111–120.
- , T. BERMAN, O. HADAS, AND R. PINKAS. 1990. Food selection and growth of the planktonic ciliate *Coleps hirtus* isolated from a monomictic subtropical lake. *J. Plankton Res.* **12**: 735–741.
- PACE, M. L., G. B. MCMANUS, AND S. E. G. FINDLAY. 1990. Planktonic community structure determines the fate of bacterial production in a temperate lake. *Limnol. Oceanogr.* **35**: 795–808.
- PARAN, N. 1994. Mixotrophic flagellates in the Kinneret. Ph.D. thesis, Bar Ilan University (in Hebrew).
- PETERS, R., AND J. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* **29**: 763–784.
- POLLINGHER, U., AND T. BERMAN. 1975. Temporal and spatial pat-

- terns of dinoflagellate blooms in Lake Kinneret, Israel (1969–1974). *Verh. Int. Ver. Limnol.* **19**: 1370–1380.
- , AND T. BERMAN. 1982. Relative contributions of net- and nano-phytoplankton to primary production in Lake Kinneret (Israel). *Arch. Hydrobiol.* **96**: 33–46.
- POMEROY, L. R. 1974. The ocean's food web, a changing paradigm. *Bioscience* **24**: 499–504.
- PORTER, K. G., AND OTHERS. 1988. Microbial interactions in lake food webs, p. 209–227. *In* S. Carpenter [ed.], *Complex interactions in lake communities*. Springer-Verlag.
- RIEMANN, B., M. SONDERGAARD, L. PERSSON, AND L. JOHANSSON. 1986. Carbon metabolism and community regulation in eutrophic, temperate lakes, p. 267–280. *In* B. Riemann and M. Sondergaard [eds.], *Carbon dynamics in eutrophic, temperate lakes*. Elsevier.
- SERRUYA, C. 1978. The origin of the Kinneret fauna, p. 465–473. *In* C. Serruya [ed.], *Lake Kinneret. Monographiae Biologicae* **32**. Junk.
- , M. GOPHEN, AND U. POLLINGHER. 1980. Lake Kinneret: Carbon flow patterns and ecosystem management. *Arch. Hydrobiol.* **88**: 265–302.
- SHERR, E. B., B. F. SHERR, AND L. J. ALBRIGHT. 1987. Bacteria: Link or sink? *Science* **235**: 88.
- , B. F. SHERR, T. BERMAN, AND O. HADAS. 1991. High abundance of picoplankton-ingesting ciliates during late fall in Lake Kinneret, Israel. *J. Plankton Res.* **13**: 789–799.
- SIMEK, K., M. MACEK, J. PERNTHALER, V. STRASKRABOVA, AND R. PSENNER. 1996. Can freshwater planktonic ciliates survive on a diet of picoplankton? *J. Plankton Res.* **18**: 597–613.
- SPARTARU, P., AND M. ZORN. 1976. Some aspects of natural feed and feeding habits of *Tilapia Galilaea* (Artemis) and *Tilapia Aurea* (Steindachner) in Lake Kinneret. *Isr. J. Aquacult. Bamidgah* **28**: 12–17.
- STONE, L., T. BERMAN, R. BONNER, S. BARRY, AND S. WEEKS. 1993. Lake Kinneret: A seasonal model for carbon flux through the planktonic biota. *Limnol. Oceanogr.* **38**: 1680–1695.
- STRAILE, D. 1994. Die saisonale Entwicklung des Kohlenstoffkreislaufes im pelagischen Nahrungsnetz des Bodensees—Eine Analyse von massenbilanzierten Flussdiagrammen mit Hilfe der Netzwerktheorie. Ph.D. Dissertation, Universität Konstanz.
- STRAYER, D. 1988. On the limits of secondary production. *Limnol. Oceanogr.* **33**: 1217–1220.
- ULANOWICZ, R. E. 1986. *Growth and development: Ecosystems phenomenology*. Springer-Verlag.
- , AND J. J. KAY. 1991. A package for the analysis of ecosystem flow networks. *Environ. Software* **6**: 131–142.
- WALLINE, P., S. PISANTY, AND T. LINDEM. 1992. Acoustic assessment of the number of pelagic fish in Lake Kinneret, Israel. *Hydrobiologia* **231**: 153–163.
- , M. GOPHEN, AND T. BERMAN. 1993. The ecosystem of Lake Kinneret, Israel, p. 103–109. *In* V. Christensen and D. Pauly [eds.], *Trophic models of aquatic ecosystems*. ICLARM.
- WATSON, S., AND E. MCCAULEY. 1988. Contrasting patterns of net- and nano-plankton production and biomass among lakes. *Can. J. Fish. Aquat. Sci.* **45**: 915–920.
- WEISSE, T. 1991. The microbial food web and its sensitivity to eutrophication and contaminant enrichment: A cross-system overview. *Int. Rev. Gesamten Hydrobiol.* **76**: 327–337.
- ZOHARY, T., U. POLLINGHER, O. HADAS, AND K. D. HAMBRIGHT. 1998. Bloom dynamics and sedimentation of *P. gatunense* in Lake Kinneret. *Limnol. Oceanogr.* **43**: 175–186.

Received: 31 March 1999

Accepted: 23 September 1999

Amended: 23 October 1999