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Seasonal abundance and vertical distribution of Protozoa (flagellates, ciliates) and bacteria in Lake Kinneret, Israel

Ora Hadas*, Tom Berman

Israel Oceanographic & Limnological Research, The Yigal Allon Kinneret Limnological Laboratory, PO Box 345, Tiberias 14102, Israel

ABSTRACT: The seasonal and vertical abundances of ciliates and flagellates are described over a 2 yr period in Lake Kinneret, Israel, a warm meso-eutrophic monomictic lake. Ciliate numbers ranged from 3 to 47 cells ml^{-1}. At the thermocline and oxycline region, the highest ciliate numbers were observed in autumn, with *Coleps hirtus* as the dominant species. Maximum heterotrophic nanoflagellate abundance (1300 cells ml^{-1}) was found in the epilimnion in winter-spring, minimum numbers (66 cells ml^{-1}) occurred in autumn. Bacteria ranged from 10^5 to 3.10^7 cells ml^{-1} with highest numbers at the decline of the *Peridinium gatunense* bloom and the lowest during winter. Protozoa, especially ciliates, appeared to be important food sources for metazooplankton. Top-down control is an important factor determining the structure of the microbial loop in Lake Kinneret.

KEY WORDS: HNAN · Ciliates · Bacteria · Lake Kinneret

INTRODUCTION

The abundance and distribution of microorganisms in aquatic ecosystems result from a complex of environmental factors and trophic interactions among a multitude of biotic components. In lakes, as in the marine habitat, important fluxes of carbon nutrients and energy are mediated by the microbial food web (Pomeroy 1974, Azam et al. 1983), consisting of bacteria, picophytoplankton and protozoa (Nagata 1988, Bloem & Bar-Gilissen 1989, Sanders et al. 1989, 1992, Weisse & Muller 1990, Berninger et al. 1991). In some circumstances, the predation of metazoan zooplankton on components of the microbial food web may transfer carbon, other nutrients and energy into the classical food chain, i.e. to fish via metazoan zooplankton (Dolan & Gallegos 1991). Thus, several studies have suggested that ciliates can be an important food source for zooplankton in both marine and aquatic environments (Beaver & Crisman 1989, Pace et al. 1990, Stoecker & Capuzzo 1990).

The abundance of each component within the microbial loop, i.e. bacteria, picophytoplankton, flagellates and ciliates, is controlled by some combination of bottom-up (nutrient supply) and top-down (grazing) regulation. Heterotrophic nanoflagellates (HNAN) are frequently the dominant consumers of bacteria and picoplankton, determining the abundance of the latter in many aquatic ecosystems. Ciliates, mixotrophic flagellates, rotifers and cladocerans can also be significant grazers of bacteria and picophytoplankton (Bird & Kalff 1984, Sherr et al. 1986, Nagata 1988, Pace et al. 1990, Weisse & Muller 1990, Berninger et al. 1991, Sanders et al. 1992). In freshwaters, daphnid zooplankters with their broad feeding capabilities have also been reported to be important consumers of bacteria, protozoa and small algae (Porter et al. 1979, Pace et al. 1990, Sanders & Porter 1990).

*E-mail: orah@ocean.org.il

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Although many aspects of the ecosystem of Lake Kinneret, Israel, have been extensively studied and much information is available about the phytoplankton and zooplankton of this warm, mesotrophic-eutrophic lake, as yet relatively little has been published about the protozoan components of the plankton. An early paper of Pollingher & Kimor (1967) listed some of the tintinnids and Madoni (1990) reported on the major ciliate species in this lake. Sherr et al. (1982) and Hadas et al. (1990) described experimental studies with lake flagellates which clearly indicated the importance of these organisms as agents of nutrient recycling and breakdown of organic detritus. Other work (Sherr et al. 1991) showed the potential of ciliates as grazers of picophytoplankton in this lake. In this paper we give an overview of the seasonal abundance and vertical distribution of heterotrophic flagellates, ciliates and bacteria in Lake Kinneret from November 1988 to September 1992.

MATERIALS AND METHODS

Sampling was carried out twice a month in 1989 and monthly in 1990 and 1991 at Stn A, the deepest (42 m) location at the center of the lake, representative for the pelagic waters, at different depths (1, 5, 10, 20, 30 and 40 m). At each depth, water was taken with a Rodhe-Aberg sampler and transferred to the laboratory in dark glass bottles (1.5 l). Flagellate, ciliate and bacterial numbers in these samples were determined from November 1988 to July 1991. Subsamples (20 ml) for protozoan counts were preserved with 10 µl of alkaline-Lugol's, 0.5 ml of 40% formalin and 30 µl of thiosulfate (Sherr et al. 1991). For determination of bacterial abundance, 20 ml samples were fixed with 1.4 ml of 0.2 µm filtered 5% formaldehyde and stored at 4°C until counting. Aliquots (5 ml) of the preserved subsamples of protozoa and bacteria were filtered onto 0.8 and 0.2 µm Nuclepore membrane filters respectively and stained with DAPI (Porter & Feig 1980). Enumeration of heterotrophic nanoflagellates and bacteria was made at 1000× and ciliates at 400× using a Zeiss epifluorescence microscope (Axioscope) with a HBO 50 W bulb and with optical filter settings: excitation 365; beam splitter FT 395; barrier filter: P420. At least 60 fields per filter were counted for HNAN and ciliates. Biovolumes of these organisms were estimated based on their geometrical shapes: ciliates as oblate spheroids, and heterotrophic flagellates as spheres or oblate spheroids. Conversion to carbon biomass was made using a factor of 0.14 for ciliates (Putt & Stoecker 1989) and 0.22 pg C μm^{-3} for HNAN (Borsheim & Bratbak 1987). For bacteria a minimum of 400 to 500 cells was always counted. The bacterial dimensions were calibrated with an optical micrometer. Dissolved oxygen was determined by the Winkler method according to Standard Methods (APHA 1989).

RESULTS

Environmental conditions during the study period (1989 to 1991)

Seasonal stratification and oxic conditions

During January through April the lake was homothermic with temperatures of about 15°C within the whole water column. Strong thermal stratification which was established in the lake in May and June lasted until the middle or end of December. From the end of April until August, the temperature of the epilimnetic layer increased from 15 to 28°C and then decreased till the end of December. The depth of the thermocline varied from 14 to 22 m with most rapid deepening starting in October. Hypolimnetic water temperatures ranged from 14 to 16°C with little seasonal variation.

During the homothermic period, dissolved oxygen (DO) was distributed evenly in the water column at Stn A, reaching values of 11 to 14 mg O_2 l^{-1}. In April, a thermocline began to develop in the upper water layer at 3 to 5 m whereas an oxycline at 40 m formed as the result of H_2S release from the sediments, which lowered hypolimnetic oxygen concentrations to 1.5 mg l^{-1}. Thus, the thermocline and oxycline during April were located at distinctly different depths. By early summer, the hypolimnion became completely depleted of oxygen and remained anoxic until mid- to late December. In summer and autumn, DO in the epilimnion ranged from 8.2 to 8.8 mg O_2 l^{-1}. The oxycline coincided with the thermocline, with DO concentrations in the metalimnion varying from 0.2 to 5.9 mg O_2 l^{-1}.

Phytoplankton

The annual bloom of *Peridinium gatunense* from February-March through early June coincided with the greater part of the homothermic period in the lake. The dinoflagellates contributed more than 90% of the total phytoplankton biomass during winter and spring with maxima in April or May; 184, 243 and 251 g wet weight m^{-2}, in 1989, 1990 and 1991 respectively (data: U. Pollingher; Fig. 1). During summer and autumn when the phytoplankton community consisted mostly of chlorophyta, the total biomass ranged from 7.0 to 50 g wet weight m^{-2}. The decline of the dinoflagellate bloom in late May or early June supplied the water col-

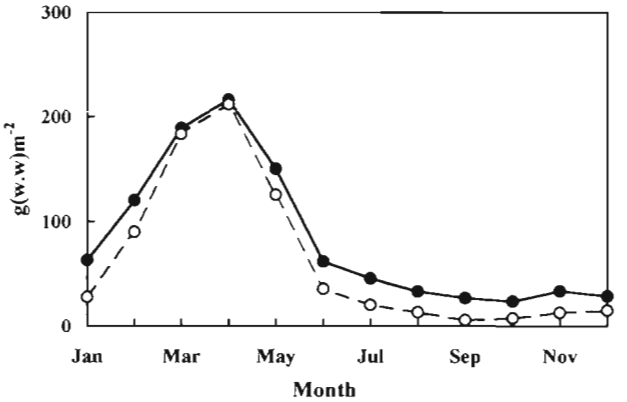


Fig. 1. Seasonal variations in phytoplankton biomass. (●) Total phytoplankton biomass; (○) *Peridinium* biomass. Average 1989 to 1991

umn and the sediment with organic matter, stimulating bacterial heterotrophic activity (Berman et al. 1979, Cavari & Hadas 1979).

Annual and seasonal abundance of ciliates

The abundance of ciliates expressed in terms of cell numbers and carbon biomass, averaged for the entire water column at Stn A from November 1988 to August 1991, is shown in Fig. 2. The greatest numbers of ciliates occurred in autumn (October 1989) and in spring. Carbon biomass and cell numbers were usually, but not always, well correlated (see Table 1). Ciliate numbers and carbon biomass ranged from 3 to 47 cells ml^{-1} and 1.4 to 17 mg C m^{-3}, respectively.

The vertical distribution of ciliate numbers and biomass during different seasons in 1989 is presented in Fig. 3. Relatively low numbers of ciliates were seen in February. In April, a peak of 64 ciliates ml^{-1} with a biovolume of 433 mm^3 m^{-3} (carbon biomass, 61 mg C m^{-3}) was recorded at 40 m which consisted mostly of anaerobic or facultative ciliates. After the onset of thermal stratification, and with the demise of the *Peridinium gatunense* bloom (May-June), high densities of ciliates were found in the thermocline or/and hypolimnion. With the deepening of the thermocline and oxycline below the photic zone after October there was an increase in ciliate numbers and biovolume (99 cells ml^{-1} and 275 mm^3 m^{-3} respectively).

Ciliate populations in Lake Kinneret

The major ciliate classes observed in Lake Kinneret were the Oligohymenophorea and Spirotrichea (Madoni 1990). In Fig. 4, we show the seasonal pattern of relative abundance of the major ciliate orders in the lake from November 1988 through November 1989.

Within the Oligohymenophorea, the order Scuticociliatida (*Cyclidium* sp., *Dexiotricha* sp., *Pleuronema* sp.) was abundant in autumn; 59 ind. ml^{-1} were counted in November 1988. *Cyclidium* was mainly found in the epilimnion, while *Dexiotricha* was domi-

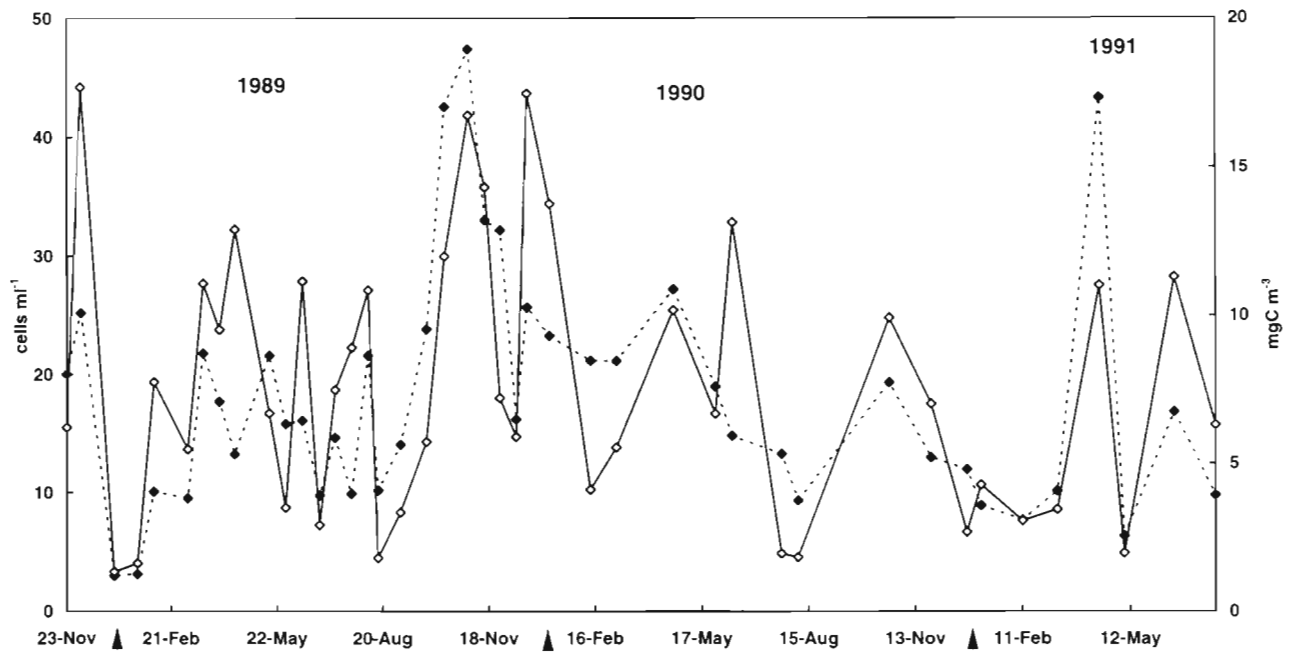
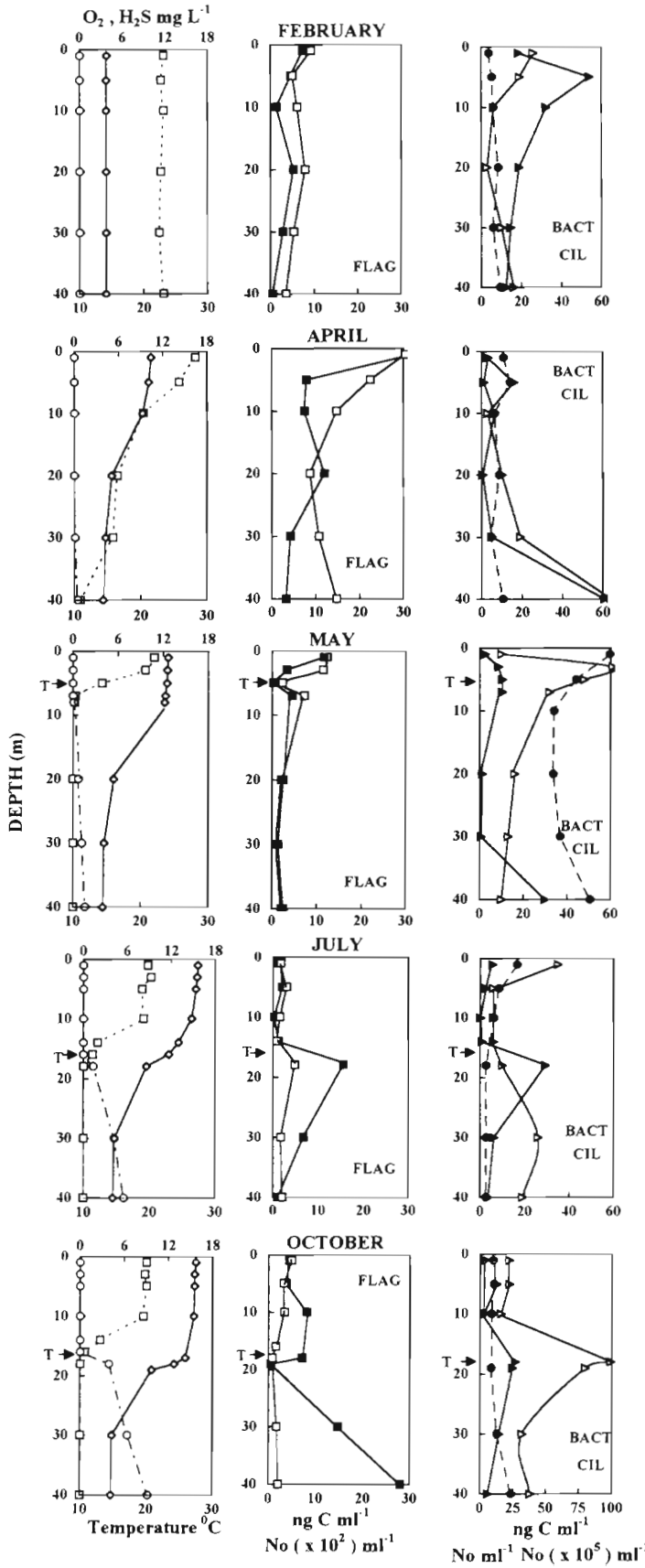


Fig. 2. Seasonal abundance of Lake Kinneret ciliates: (◆) average (0 to 10 m) cell numbers ml^{-1}, (◇) carbon biomass



nant in the anaerobic hypolimnion. With the decline of the dinoflagellate bloom in May 1989, an additional peak of Scuticociliatida was observed within the thermocline region in which there were high concentrations of organic matter and bacteria. *Colpoda steinii* (16 ind. ml^{-1} in June 1989), which has a high tolerance to NH_4 and to low concentrations of dissolved oxygen (Bick 1972), was particularly prominent in this water layer.

The order Sessilida (primarily represented by *Vorticella mayerii*) reached its highest densities (13 ind. ml^{-1}) in February, during the period of lake homothermy.

Within the class of Spirotrichea, the orders Choreotrichida and Oligotrichida were abundant throughout the year. However, the genera tintinnidium were observed only in February and early March, when the entire water column was strongly mixed and dissolved oxygen concentrations were high. Microscopic observation indicated that these organisms were mainly feeding on diatoms, flagellates and bacteria.

The order Haptorida (represented by *Didinium* sp., *Askensia* sp., *Mesodinium* sp.) was found during autumn, winter and spring but only occasionally during summer (May to August). These organisms are carnivorous, feeding on other ciliates (Bick 1972).

The most abundant ciliate species in Lake Kinneret during our study was *Coleps hirtus* (class Prostomatea, order Prorodontida) which was generally found dispersed throughout the water column. Maximum numbers of this organism were observed in October 1989 (59 ind. ml^{-1}) and high abundances were located within the thermocline and hypolimnion during the stratified period. Individuals of *C. hirtus* contained zoochlorellae and microscopic observation indicated that they were feeding on nano- and pico-sized algae, flagellates and small ciliates.

During the period of lake stratification (from May through December), we noted relatively large ciliate populations in the anaerobic hypolimnetic water which contained high con-

Fig. 3. Vertical distribution of: (left panels) temperature (◇), oxygen (□) and H_2S (○); (centre panels) flagellate numbers (□) and biomass (■); (right panels) ciliate numbers (▷), ciliate biomass (▶) and bacterial numbers × 10^5 ml^{-1} (●), in Lake Kinneret in 1989. T▶: depth of thermocline

centrations of H_2S (ranging from 1 to 12 mg S l^{-1}). The major ciliate genera observed in this region were *Metopus*, *Caenomorpha*, *Epalxella*, *Plagiopyla*, *Brachonella* and *Saprodinium*, all which are known to tolerate anaerobic conditions and the presence of H_2S (Fenchel et al. 1990). These ciliates were feeding on sulfur cycle bacteria (e.g. *Thiovulum* sp., *Beggiatoa* sp., and other bacteria as well as organic detritus (Hadas unpubl. data).

Heterotrophic nanoflagellates

The seasonal abundance of flagellates from November 1988 through August 1991 and their vertical distribution in 1989 are shown in Figs. 3 & 5. Small (2 to 5 µm) monads were the most abundant HNAN forms. The numbers of HNAN showed definite seasonal peaks during the late winter-spring months of 1989 and 1990, concomitantly with the bloom of *Peridinium gatunense*. Maximum flagellate numbers (averaged for the whole water column) were recorded in March and April 1989 (1350 cells ml^{-1}), while minimum numbers (66 cells ml^{-1}) were found in November 1989 (Fig. 3). Flagellates increased from January (900 cells ml^{-1} with a biovolume of 32 mm^3 m^{-3} at 5 m depth) to a maximum 3000 cells ml^{-1} and a biovolume of 146 mm^3 m^{-3} in April coincident with the peak of *P. gatunense* biomass (Fig. 3). Although HNAN were distributed throughout the water column including the anaerobic hypolimnion during the entire year, the maximum numbers of these organisms were found in the upper water layers in winter and spring.

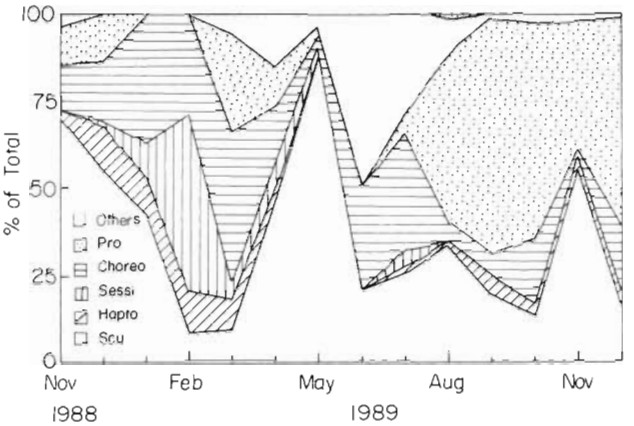


Fig. 4. Abundance of major ciliate orders in Lake Kinneret from November 1988 to November 1989. Scu: Scuticociliatida; Choreo: Choreotrichida; Hapto: Haptorida; Pro: Prorodontida; Sessi: Sessilida; Others: Saprodinium, Caenomorpha, Colpoda

The carbon biomass of HNAN did not show the same clear seasonal pattern as HNAN cell numbers although both parameters exhibited apparent 2 to 3 mo minimum-maximum cycles similar to those found for the ciliates (Figs. 3 & 5).

Sometimes small numbers of large flagellates were responsible for relatively high HNAN biomass carbon in the vertical profiles. For example, in October, most of the flagellate biomass in the hypolimnion was due to the presence of a few large organisms. In contrast, the

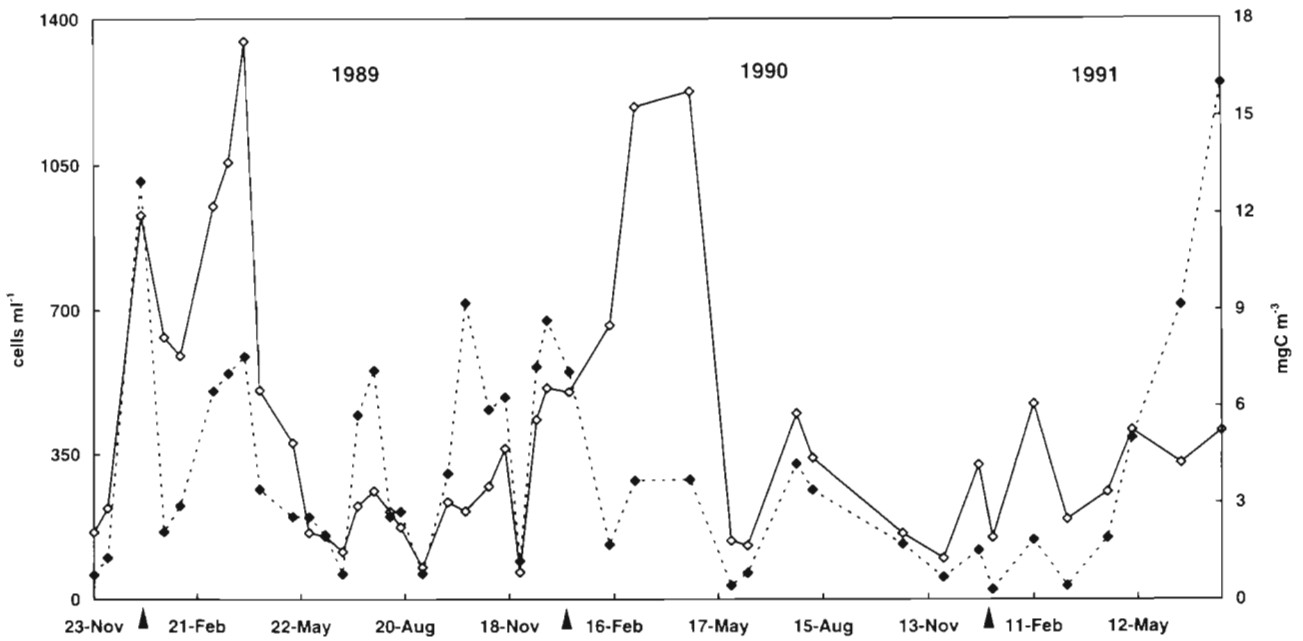


Fig. 5. Seasonal abundance of Lake Kinneret flagellates: (◆) average (0 to 10 m) cell numbers ml^{-1}, (◇) carbon biomass

high standing stock of HNAN biomass carbon in epilimnic waters during winter and spring was due to large numbers of small flagellates (Figs. 3 & 5). The profiles in July showed a maximum for HNAN biomass at the thermocline.

Bacterial abundance

Bacterial numbers ranged from 10^5 to 3×10^7 cells ml^{-1} over the period from January 1988 to July 1991. The average numbers and fluctuations of bacteria were surprisingly similar in both the upper and the lower water strata (Fig. 6). Generally the highest abundances of bacteria were found towards the end of the dinoflagellate bloom (late April and May) and minimum numbers were observed in June to August 1989 and during winter (January) of 1988 and 1989 (Fig. 6).

In epilimnetic waters, most bacteria were cocci, 0.5 to 1.0 µm in diameter (biovolume 0.07 to 0.5 $µm^3$) or small rods about 0.5 to 1.0 µm in width and 3 to 5 µm in length (biovolume 0.6 to 3.9 $µm^3$). A few larger cells were occasionally observed.

Bacterial populations from the anaerobic hypolimnion could be easily distinguished from those in the epilimnion. The former were generally larger cells typically filamentous or curved in shape and ranging in size from 1.0 to 2.0 µm in width and 2 to 7 µm in length (biovolume 5.5 to 6.28 $µm^3$). During stratification, a significant portion of the hypolimnetic bacterial population consisted of small vibrios or of sulphate reducers such as *Desulphovibrio* sp. mostly curved or sigmoid in form which are actively involved in sulphate reduction processes (Hadas & Pinkas 1995).

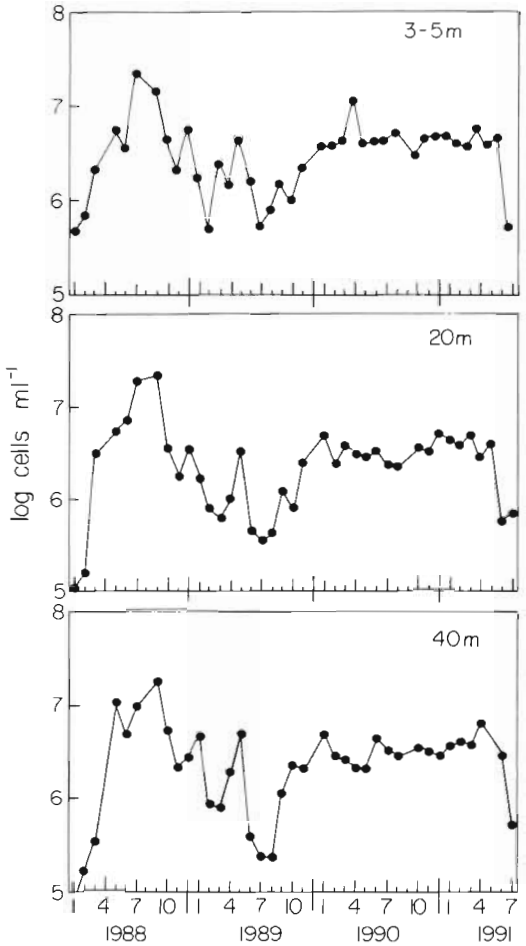


Fig. 6. Bacterial abundance in Lake Kinneret from November 1988 to July 1991 at depths of 3 to 5, 20 and 40 m

Interparameter correlations

We examined our data set for interrelationships between measured parameters (Table 1). Reasonably close correlations were found between the standing stocks of flagellate carbon and flagellate cell numbers and also between ciliate carbon and ciliate standing stock numbers. Flagellate numbers were correlated significantly with chlorophyll and with phytoplankton wet weight biomass standing stocks. An inverse relationship was found for the regression of flagellate numbers and picophytoplankton (mostly pico-

Table 1. Regressions between HNAN, ciliates, phytoplankton and picophytoplankton. Protozoan values (cells m^{-2} or mg C m^{-2}, integrated values from 0 to 10 m); picophytoplankton (cells m^{-2}); phytoplankton biomass (g wet weight m^{-2}); chlorophyll (µg l^{-1}, average of 15 m integrated values) and bacterial production (cells d^{-1}, average 0 to 10 m integrated values measured by ^{3}H-thymidine uptake; Berman et al. 1994)

Parameters		Equation	n	r^2	p
y	*x*	(*y* =)			
Flagellate carbon	Flagellate cell no.	$1.18\,x^{0.78}$	40	0.41	<0.0001
Ciliate carbon	Ciliate cell no.	$31.56\,x^{0.91}$	40	0.55	<0.0001
Flagellate cell no.	Phytoplankton biomass	$33.7\,x^{0.56}$	28	0.35	0.0007
Flagellate cell no.	Chlorophyll	$-178 + 232.8\,\ln(x)$	37	0.27	<0.0001
Flagellate cell no.	Picophytoplankton cell no.	$1142 - 161.7x$	27	0.23	0.009
Flagellate cell no.	Bacterial production	$23.3\,x^{0.19}$	34	0.16	0.016

cyanobacteria, see Malinsky-Rushansky et al. 1995). Flagellate or ciliate cell numbers were not significantly correlated to bacterial numbers but flagellate cell numbers were correlated to bacterial productivity albeit with a probability of only $p = 0.016$. No other correlates were found for parameters of flagellate or ciliate abundance or carbon biomass.

DISCUSSION

Seasonal patterns of Protozoa in Lake Kinneret

Our observations in Lake Kinneret indicate a definite seasonal pattern of protozoan distribution which resulted from physical conditions, biological factors and top-down predation pressures.

From February until the beginning of June, Lake Kinneret may be considered eutrophic. Maximum phytoplankton abundance reaches ~250 g m^{-2} (wet weight biomass) or ~300 mg m^{-2} (chlorophyll) and primary production ~2.5 g C m^{-2} d^{-1} (Berman et al. 1995). Most of the dominant *Peridinium* biomass is not grazed by metazoan zooplankton (Serruya et al. 1980). It has been shown that much of the *Peridinium* cell material is broken down in the water column (Hertzig et al. 1981), thus implying a 'detrital pathway' of degradation (Serruya et al. 1980) and the presence of a very active microbial loop.

Our observations substantiate this idea. Heterotrophic nanoflagellates dominated the water column from January to June, reaching maximum numbers of 3×10^3 cells ml^{-1}. In January 1988 and 1989, after lake overturn, we observed low bacterial numbers and high HNAN abundance (Figs. 5 & 6). The decreased bacterial numbers may have been partly due to relatively low (15 to 16°C) water temperatures (Cavari & Hadas 1979) but possibly a more important factor was the grazing pressure of HNAN on bacteria which led to an increase in the former at the expense of the latter.

The role of some ciliate species (including *Vorticella*, *Cyclidium*, *Coleps* sp.) as grazers of picoplankton in a freshwater lake has recently been reported in detail by Šimek et al. (1995). We suggest that picophytoplankton may also be a significant food source for ciliates in Lake Kinneret at this season.

In Lake Kinneret in February, peritrich ciliates, mostly *Vorticella mayerii*, were abundant. These organisms, which filter small particles, are mainly bacterivores (Munawar et al. 1994) and could have been partly responsible for the lowered bacterial and picocyanobacterial numbers in winter. With the onset of the *Peridinium* bloom in February there was a rise in ciliate abundance, concomitant with the increase of particulate organic detritus (e.g. dinoflagellate theca released with each cell division) and dissolved organic matter which stimulated bacterial (Berman et al. 1979, Cavari & Hadas 1979) and HNAN outgrowth. As in other freshwater ecosystems, the numbers of HNAN were highest in spring, coinciding with peaks of chl *a* and primary production (Nagata 1988, Sanders et al. 1989, Munawar et al. 1994).

Low bacterial numbers during winter may be attributed to both decreased water temperatures and the high abundance of flagellates. There were no seasonal fluctuations in bacterial numbers during 1990 perhaps due to the exceptionally mild winter and extremely low rainfall that winter. In winter-spring, the intake requirements (as carbon) of the herbivorous zooplankton have been estimated at ~1.5 g C m^{-2} d^{-1} (Serruya et al. 1980). At this time, herbivorous cladocera (*Ceriodaphnia reticulata*, *Diaphanosoma brachyurum*, *Bosmina longirostris*) dominated the zooplankton. Phytoplanktonic primary production during winter-spring in 1989 and 1990 averaged ~2.0 g C m^{-2} d^{-1} (Berman et al. 1995) and was due mainly to *Peridinium*. Since dinoflagellates are not directly grazed by cladocera there appeared to be a shortfall in algal sources to supply the carbon demand of the herbivorous zooplankton (Serruya et al. 1980). Stone et al. (1993) have suggested that some of this requirement may be supplied by protozoa, with ciliates providing almost half of the food needs of the copepods.

In laboratory experiments, cladocerans and young cyclopoid copepods isolated from Lake Kinneret were shown to feed upon the ciliates *Stylonichia*, *Cyclidium* and *Colpoda* (Berman & Gophen pers. comm.). These food sources enabled growth and reproduction of the metazoan zooplankton although at lower rates than when nanoplanktonic algae were grazed.

A short transition period from about mid-May through June prior to the onset of typical summer-autumn conditions is characterized by intense bacterial activity. Cavari & Hadas (1979) observed the highest bacterial numbers and a 78% increase in bacterial glucose assimilation rates at the beginning of summer after the decline of the *Peridinium* bloom. In addition, the increase of epilimnetic water temperatures from ~20 to 26°C and the onset of strong thermal and chemical stratification creates a layer rich in food sources for bacteria. At this time high numbers of ciliates and flagellates were found in the metalimnic layer (Fig. 3; May) as has been reported elsewhere (Berninger et al. 1991).

Similarly to observations in many other water bodies (Fenchel et al. 1990, Cole et al. 1993), bacterial cells in the anaerobic hypolimnion of Lake Kinneret were generally larger than those in the upper water layers (Schmaljohann et al. 1987). The smaller size of bacteria in epilimnetic waters might be due to the pressure of

protozoa and cladocerans, which appear to feed selectively on larger cells (Gonzalez et al. 1990), and/or to the different taxonomic composition, since anaerobic (hypolimnetic) taxa generally have much larger cell size.

During the summer and autumn (from July through December), Lake Kinneret is mesotrophic with chlorophyll concentrations of 5 to 8 µg l^{-1} and primary production of ~1.2 to 1.6 g C m^{-2} d^{-1}. Despite a switch in phytoplankton to a population dominated by small chlorophyta that maintain high levels of primary production, the herbivorous zooplankton may still require supplemental food sources, especially in view of their increased respiratory rates. On the basis of model simulations, Stone et al. (1993) suggested that, at this season too, ciliates are an important food source for the copepods while bacteria might provide about 10% of cladoceran requirements. Note that the protist carbon biomass (780 to 1160 mg C m^{-2}) in autumn was somewhat greater than that of the metazooplankton, 620 mg C m^{-2} (Sherr et al. 1991).

From August to December, copepods were usually the dominant metazooplankton. Although adult copepods are strict predators (Gophen 1978) and may have imposed strong pressure on ciliates, HNAN and cladocera at this season (Stone et al. 1993), nevertheless high numbers and biomass of ciliates were observed in autumn. *Cyclidium* sp. was abundant in the epilimnion while in the hypolimnion, *Coleps hirtus*, a macropredator able to feed on a large variety of food sources (Madoni et al. 1990), was dominant. In turn, predation by ciliates may have limited the HNAN population which dropped to 66 cells ml^{-1}.

Sediment-water interface

The ciliate community had the greatest numbers of individuals at the sediment-water interface. Here the ciliate species were characteristic of a sulfuretum. The large numbers of ciliates observed in the metalimnic layer may have been feeding on colorless sulfur bacteria which are numerous and show high chemosynthetic activity at the aerobic/anaerobic interface (Hadas unpubl. data). A similar phenomenon was found in the Black Sea (Zubkov et al. 1992) where the protist community was reported to be a major factor in the utilization of chemotrophic bacterial production.

Patterns of protozoan abundance

A priori we expected to find some relationship between the abundance of bacteria and that of the bacterivorous protozoa, especially HNAN. However, considering the lengthy intervals between sampling times (2 or 4 wk) and the rapid growth rates reported for HNAN in this lake (0.03 to 0.11 h^{-1}; Hadas et al. 1990), the absence of any evident relationship between HNAN standing stocks and bacteria is perhaps not surprising. Moreover, it seems reasonable that a direct relationship should exist between HNAN (cell numbers) and bacterial productivity (see Table 1), especially if the majority of bacteria cropped by the HNAN tend to be larger, actively dividing cells (Gonzalez et al. 1990). Clearly, in order to study the dynamics of HNAN and bacterial populations in the natural environment, more frequent (~12 hourly) sampling would be required.

In Lake Kinneret, cell numbers of both HNAN (Fig. 5) and ciliates (Fig. 2) showed regular oscillating patterns which were less evident in the biomass data. These oscillations had a periodicity of 2 to 3 mo, much longer than the cyclical patterns usually found for protozoan predator-prey relationships, which are generally in the order of 1 or 2 wk. This cyclical phenomenon was most pronounced throughout 1989 and less so in 1990. It would seem unlikely that the patterns observed in Figs. 2 & 5 were due to some sampling or counting artifact but at present we have no clear explanation for these observations. Elsewhere HNAN numbers have also shown considerable fluctuations (Nagata 1988, Bennett et al. 1990, Laybourn-Parry & Rogerson 1993). These fluctuations suggest that HNAN do not increase as much as they could because some other consumers (ciliates, zooplankton) can quickly respond to any increase in HNAN (Gasol & Vaqué 1993). Such long-term cyclical behaviour for natural protozoan populations may reflect shifts in the structure of the microbial loop which act to maintain an overall system stability in the face of environmental perturbations.

Our observations suggest that significant amounts of bacterial production may be transferred to higher levels of the plankton via HNAN and ciliates in Lake Kinneret. Protozoan grazing appears to be a major determinant of both bacteria and picocyanobacterial abundance in this lake as in other aquatic environments (Scavia & Laird 1987, Weisse 1990, Berninger et al. 1991, Sanders et al. 1992, Kuuppo-Leinikki et al. 1994). Predation by metazooplankton on components of the microbial food web, especially on ciliates, may be responsible for an important transfer of carbon to higher trophic levels in this lake.

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