

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	52	1	19–34	2004
--	----	---	-------	------

Regular research paper

Krystyna KALINOWSKA

Centre for Ecological Research, Polish Academy of Sciences
Hydrobiological Station
Leśna 13, 11-730 Mikołajki, Poland
e-mail: jolanta@onet.pl

BACTERIA, NANOFLAGELLATES AND CILIATES AS COMPONENTS OF THE MICROBIAL LOOP IN THREE LAKES OF DIFFERENT TROPHIC STATUS

ABSTRACT: The major components of the microbial loop (dissolved organic carbon, bacteria, nanoflagellates and ciliates) were examined in three Polish lakes (Masurian Lakeland, North-Eastern Poland): highly eutrophic (Lake Ryńskie), mesotrophic (Lake Kuc) and humic, acid (Lake Smolak Duży).

Microbial loop was distinctly differentiated among studied lakes. In the eutrophic lake, the microbial loop was characterized by a wide variety of biotic components, great taxonomic, trophic and size differentiation of ciliates (dominated by bacterivorous and predatory taxa). Probably, in this lake autochthonous dissolved organic carbon (DOC) prevailed. In the mesotrophic lake, the microbial loop comprised fewer components and the taxonomic and trophic variability of ciliates (dominated mainly by bacterivorous and algivorous taxa) was smaller. This lake contained almost the same amount of DOC, but part of it was probably less available and allochthonous origin. Much of the DOC in the humic lake being poorly available (humic substances prevailed) and hence there were lower densities of bacteria and still lower of nanoflagellates and ciliates (dominated by large-sized mixotrophic and small-sized bacterivorous species). The only significant correlation between bacteria and ciliates suggests that the food chain in this lake is short and that the high concentrations of DOC of allochthonous origin are not readily assimilated. Additionally, low pH values restricted growth of the studied groups of organisms and

decomposition of DOC by bacteria.

The number of significant correlations differed among lakes and in different temporal scales. In the eutrophic lake the relationships were stronger in both seasonal and diel cycle. Practically no relationships were found in the humic lakes in both scales. Generally, diel correlations were stronger than those in the seasonal scale.

KEY WORDS: DOC, bacteria, nanoflagellates, ciliates, microbial loop

1. INTRODUCTION

Bacteria, nanoflagellates and ciliates constitute the "microbial loop" which is a distinct and important element of the trophic food web in aquatic ecosystems affecting carbon and nutrient flows (Pomeroy 1974, Azam *et al.* 1983, Sherr and Sherr 1984). Heterotrophic flagellates are considered the main consumers of bacteria and picoplanktonic algae in both marine and freshwater habitats (Porter *et al.* 1985, Fenchel 1986, Sherr *et al.* 1987, Bloem *et al.* 1989, Sanders *et al.* 1989, Šimek *et al.* 1990, Weisse 1990, Berninger *et al.* 1991, Jürgens and Stolpe 1995, Kankaala *et al.* 1996).

Flagellates control bacterial populations and are themselves food for many ciliates. Ciliates play a significant role as consumers of small heterotrophic flagellates and pico- and nanophytoplankters, and are thus a link to higher trophic levels (Sanders *et al.* 1989, Šimek *et al.* 1990, Sherr *et al.* 1991, Szeląg-Wasielewska and Fyda 1999). Ciliates may be also active bacterivores particularly in eutrophic lakes, where bacterial densities are sufficient to maintain ciliate populations (Pace 1982, Fenchel 1984, Sanders *et al.* 1985, Sherr *et al.* 1987, Christoffersen *et al.* 1990). Epstein and Shiaris (1992) found in the inshore bay waters of the USA that ciliates consumed bacteria 17 times faster on average than did flagellates. Thus ciliates and nanoflagellates may play a similar role in controlling bacteria.

According to Porter *et al.* (1988), the importance of the microbial loop is greater in oligo- than in eutrophic lakes. However, Weisse *et al.* (1990) demonstrated, that almost 50% of carbon passed through the microbial loop in a meso-eutrophic lake. This suggests that the microbial loop may also be important in habitats of higher productivity. According to many authors (Tranvik 1988, Tranvik and Sieburth 1989, Amblard *et al.* 1995), the microbial loop in humic lakes has a different structure, because the large pool of allochthonous organic matter represents an additional and potentially important carbon source for bacteria (Jones 1992, Arvola *et al.* 1996). Functioning and the role of the microbial loop rely on many factors, for example on other zooplankton, like *Daphnia*, which can eat bacteria, algae, and especially nanoflagellates and might thus compete with ciliates for food and may display interference competition with smaller ciliates (Jürgens 1992, Jürgens and Stolpe 1995).

Less than 10% of available limnological information is focused on the organisms and metabolic processes in freshwater microbial loops (Wetzel 2000). Relations between bacteria and bacterivores are not fully understood particularly in respect to their changes with the eutrophication of waters, which might be decisive for the succession and functioning of temperate lowland lakes (e.g. Weisse 1990, Berninger *et al.* 1993, Amblard *et al.* 1995, Mayer *et al.* 1997). Therefore, the general aim of this work was to determine the tro-

phic structure of the microbial loop in lakes differently supplied with organic matter and nutrients and to analyse relationships between components of the microbial loop and selected indices of lake trophic status (TP, TN, DOC, chlorophyll) and between studied groups of organisms. The relationships within lakes were examined with correlation coefficients and must be treated with caution. However, the discussion on the relationships was based on a large number of previous laboratory experiments, field observations and manipulations, which indicate that organisms forming the microbial loop are tightly direct and/or indirect coupled, (e.g. Błöem *et al.* 1989, Sanders *et al.* 1989, Šimek *et al.* 1990, Šimek and Straškrabová 1992, Berninger *et al.* 1993, Amblard *et al.* 1995, Carrias *et al.* 1998, Simon *et al.* 1998, Hitchman and Jones 2000) and that the abundance of the main components of food chain are closely related to trophic state of lakes as measured by TP, TN, DOC, chlorophyll (Hillbricht-Ilkowska 1977, Hillbricht-Ilkowska *et al.* 1979, Beaver and Crisman 1982, 1990, Pace 1986, Laybourn-Parry 1994, Gajewski and Chróst 1995, James *et al.* 1995). In naturally acid, humic lakes the data indicate that low pH values reduced plankton abundances (Beaver and Crisman 1990). Thus, it was assumed that the abundance of the microbial loop components should be higher in both eutrophic and mesotrophic lakes than in humic one. Basing on the qualitative data, it was tested hypothesis that the humic lake differ from non-humic lakes in their trophic and taxonomic composition of ciliates. Based on the quantitative data, the question is addressed of whether ferti-lization of lakes and the input of humic substances inflowing to the lakes have impacted on the abundance of the microbial loop components and on the number and strength of the correlations (r) between particular links of the microbial loop. In addition, it was tested hypothesis that correlations type food-consumer should be more visible in the diel scale than in seasonal scale because small size of organisms and high rates of reproduction.

Summing up, the detail aims were: 1) analysis of general relations between the abundance (numbers and biomass) of the microbial loop components: DOC, bacteria, nanoflagellates and ciliates – with attention given to seasonal and diel varia-

tions, 2) identification of diversity and the trophic structure of the ciliate communities, 3) analysis of relationships between: components of the microbial loop (DOC, bacteria, nanoflagellates, ciliates) – type of food-consumer and between abundance of components of the microbial loop and trophic parameters of a lake, such as: TP (total phosphorus), TN (total nitrogen), DOC, chlorophyll *a*.

2. MATERIAL AND METHODS

The studies were conducted in three lakes of various trophic status situated in the Masurian Lakeland District (north-eastern Poland): highly eutrophic Lake Ryńskie, mesotrophic Lake Kuc and humic, acid Lake Smolak Duży. The morphometric and trophic characteristics of these lakes are summarized in Table 1.

Table 1. Morphometric and trophic characteristics of the study lakes (data for epilimnion in summer). D – dimictic, P – polymictic, SD – visibility of Secchi's disc, TP – total phosphorus, TN – total nitrogen, DOC – dissolved organic carbon, Chl *a* – chlorophyll *a*. * – The high concentration of chlorophyll was due to the large *Gonyostomum semen* (Raphidophyceae) and small chlorococcal algae, which were abundant at this time.

Characteristics	Lake		
	Ryńskie	Kuc Smolak	Duży
Mixis	D	D	P
Area (ha)	661.1	98.0	9.2
Maximum depth (m)	50.8	28.0	4.2
Mean depth (m)	10.5	8.0	1.8
SD (m)	1.1	5.8	0.7
pH	8.9	8.6	5.4
TP ($\mu\text{g l}^{-1}$)	42	33	52
TN (mg l^{-1})	1.42	0.49	0.58
DOC (mg l^{-1})	9.93	12.12	28.40
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	39.9	5.5	104.8*
Bacterial numbers ($\times 10^6 \text{ ml}^{-1}$)	12.56	11.86	5.45
Catchment	agricul- tural	agricul- tural	forest-peat bog
Trophy	eu- trophic	meso- trophic	humic

Monthly samples were collected out from May to November 1998. Diel studies were performed between 8 and 20 August 1999 by taking samples every four hours during a day in each lake. Samples for water analyses were taken from the deepest sites of each lake. In the shallow Lake Smolak Duży, water samples were taken

every metre from surface to the bottom. In deeper lakes, during thermal stratification, samples were pooled separately for each the three layers. Epi- and metalimnetic samples were taken every metre and hypolimnetic samples were collected every 3 m in Lake Kuc and every 5 m in Lake Ryńskie. When these lakes were mixed (October–November) samples were taken every metre from the surface to the bottom. One litre water samples from every sampled depth were combined for each thermal zone, mixed and preserved.

Temperature and oxygen concentration were measured with an oxymeter type OXI 197 (WTW, Germany) at depth intervals of 1 m. Total phosphorus (TP) was analysed from unfiltered water after mineralization with 60% perchloric acid (1 ml/50 ml of water sample) using the molybdenum blue method. Total nitrogen (TN) was analysed by the standard Kjeldahl procedure (Standard Methods 1960). Chlorophyll *a* concentration was determined by the spectrophotometric analysis of acetone extracts of algae retained on Whatman GF/C filters according to Golterman (1969). Dissolved organic carbon (DOC) in 0.45 μm filtered samples was analysed using a Shimadzu TOC-5050A analyser according to Górnica and Zieliński (1999).

Epifluorescence microscopy was used to determine bacterial and nanoflagellate cell numbers. Heterotrophic bacteria were DAPI stained according to Porter and Feig (1980) and filtered on 0.2 μm pore-size black filters. Nanoflagellates were primulin stained according to Caron (1983) and filtered on 1.0 μm pore-size black filters. For calculating biovolumes of bacteria and nanoflagellates, cell shapes were approximated by simple geometric forms. Ciliate samples were preserved with Lugol's solution and concentrated subsamples were counted with phase and light microscopy using the classic Utermöhl technique. Living observation was used for the taxonomic and trophic identification based mainly on Foissner and Berger (1996), Foissner *et al.* (1991-95), Foissner *et al.* (1999). Biovolumes of ciliates were calculated from measurements of dimensions of animals and approximations to geometric shapes.

Mean values and confidence intervals were used to compare results. Correlation coefficients were calculated between pairs of

variables in order to determine the relationships between particular components of the microbial loop. All statistical analyses were carried out using the STATISTICA software. Correlations were performed for the series of the whole study season for the three combined thermal layers (for stratified lakes $n = 17$ in the seasonal scale and $n = 18$ in the daily scale, for humic lake $n = 7$).

3. RESULTS

3.1. Abundance and general relations between microbial loop components in lakes

Biomasses of particular components of the microbial loop markedly differed between the lakes. The eutrophic lake was characterised by the highest biomass of all biotic components of the microbial loop (bacteria, nanoflagellates and ciliates) compared with the two other lakes. In the humic lake, concentration of DOC was significantly higher and the biomass of bacteria, nanoflagellates and ciliates was markedly lower than in the non-humic lakes (Fig. 1).

From all the studied lakes, the highest mean concentration of DOC was noted in the humic lake ($27.6 \pm 1.8 \text{ mg l}^{-1}$). In both

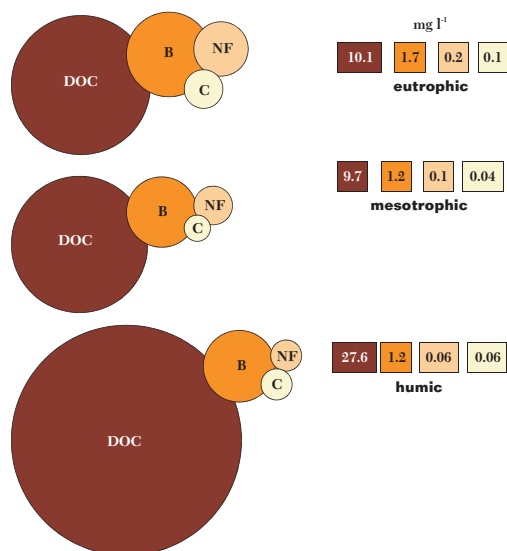


Fig. 1. Comparison of the major components of the microbial loop in Masurian lakes. The size of fields are proportional to the mean concentration of dissolved organic carbon (DOC) and mean biomasses of particular groups of organisms. B – bacteria, NF – nanoflagellates, C – ciliates.

stratified lakes the concentration of dissolved organic carbon was similar and about 3 times lower ($10.1 \pm 1.1 \text{ mg l}^{-1}$ and $9.7 \pm 0.7 \text{ mg l}^{-1}$ in the eutrophic and mesotrophic lakes, respectively) as compared to the humic lake, therefore the differences between stratified lakes were not statistically significant (t-test, $P > 0.05$). Maximum DOC concentration in the eutrophic and the humic lakes were noted during spring month, while in the mesotrophic – during summer.

The highest mean bacterial numbers and biomass were noted in the eutrophic lake ($13.3 \pm 0.7 \times 10^6 \text{ ml}^{-1}$ and $1.7 \pm 0.2 \text{ mg l}^{-1}$), the lower values were characteristic for the mesotrophic lake ($9.6 \pm 0.7 \times 10^6 \text{ ml}^{-1}$ and $1.2 \pm 0.1 \text{ mg l}^{-1}$). The humic lake was characterized by the lowest numbers ($8.5 \pm 1.5 \times 10^6 \text{ ml}^{-1}$), while the biomass ($1.2 \pm 0.2 \text{ mg l}^{-1}$) was higher than in the mesotrophic one. The statistical analysis did not show significant differences between the mesotrophic and the humic lakes (t-test, $P > 0.05$). All the studied lakes were characterized by the occurrence of the spring peak both in the numbers and biomass of bacteria. Additionally, two peaks: in summer and in autumn, were noted in stratified lakes, while in the humic lake – two observed peaks were separated by the low numbers in summer.

The highest mean numbers and biomass of nanoflagellates ($5.0 \pm 0.9 \times 10^3 \text{ ml}^{-1}$ and $172.4 \pm 30.7 \text{ ng ml}^{-1}$) were in the eutrophic lake, slightly less values were noted in the mesotrophic reservoir ($3.2 \pm 0.5 \times 10^3 \text{ ml}^{-1}$ and $87.3 \pm 8.6 \text{ ng ml}^{-1}$). The humic lake had especially low numbers and biomass of these organisms ($1.9 \pm 0.8 \times 10^3 \text{ ml}^{-1}$ and $56.8 \pm 16.12 \text{ ng ml}^{-1}$). The studied lakes were statistically different both in numbers and biomass of nanoflagellates (t-test, $P < 0.05$). In both non-harmonic lakes the peaks of the numbers were noted in the period of spring and/or summer, while in the humic one the peak appeared in autumn. The biomass of nanoflagellates submitted to greater changes and the peaks were usually observed in summer in the eutrophic and the humic lakes, while in the mesotrophic lake – in autumn.

The studied lakes differed in the annual mean numbers and biomass of ciliates. The highest mean ciliate numbers ($7.4 \pm 2.5 \text{ ind. ml}^{-1}$) and biomass ($87.8 \pm 23.5 \mu\text{g l}^{-1}$) were noted in the eutrophic Lake Ryńskie.

The mean numbers of ciliated protozoa in the mesotrophic Lake Kuc were about two times (3.6 ± 0.3 ind. ml⁻¹), and in the humic Lake Smolak Duży three times (2.2 ± 0.9 ind. ml⁻¹) lower as compared with the eutrophic lake. The higher individual weight of ciliates resulted the ciliate biomass in the humic lake higher than that in the mesotrophic lake. The differences between the studied lakes were statistically significant except the differences in ciliate biomass between the eutrophic and the humic lake (t-test, $P < 0.05$). The highest numbers of ciliate communities in the eutrophic and the humic lakes were noted in September, while in the mesotrophic lake – in the middle of summer. The biomass of ciliates had two-peak character in all lakes. The density and biomass of ciliated protozoans during the autumn circulation were low.

The data on vertical distribution and diel dynamics of the major components of the microbial loop will be presented elsewhere (Kalinowska, in prep.).

3.2. Diversity and trophic composition of ciliates

Forty two ciliate taxa were found from the studied lakes. The richest taxonomic composition (31 taxa) was found in the most eutrophic lake, slightly poorer (29 taxa) in the mesotrophic lake and the least diversified (18 taxa) in the humic lake. Eleven (i.e. 26%) taxa were common for all three lakes. These were mainly ciliates of the order Oligotrichida (*Strombidium* spp., *Strobilidium humile*, *Halteria* spp., *Codonella cratera*) feed on bacteria, autotrophic and heterotrophic flagellates and algae, and bacterivorous Peritrichida and Scuticociliatida. Other orders were represented by *Urotricha* spp., *Askenasia* spp., *Mesodinium* sp. Each of the studied lakes contained characteristic species, noted in only one lake. Most of these taxa, represented mainly by predacious Haptorida (*Monodinium* sp., *Didinium* sp., *Spathidium* spp.), large bacterivorous and algivorous Heterotrichida (*Spirosto-*

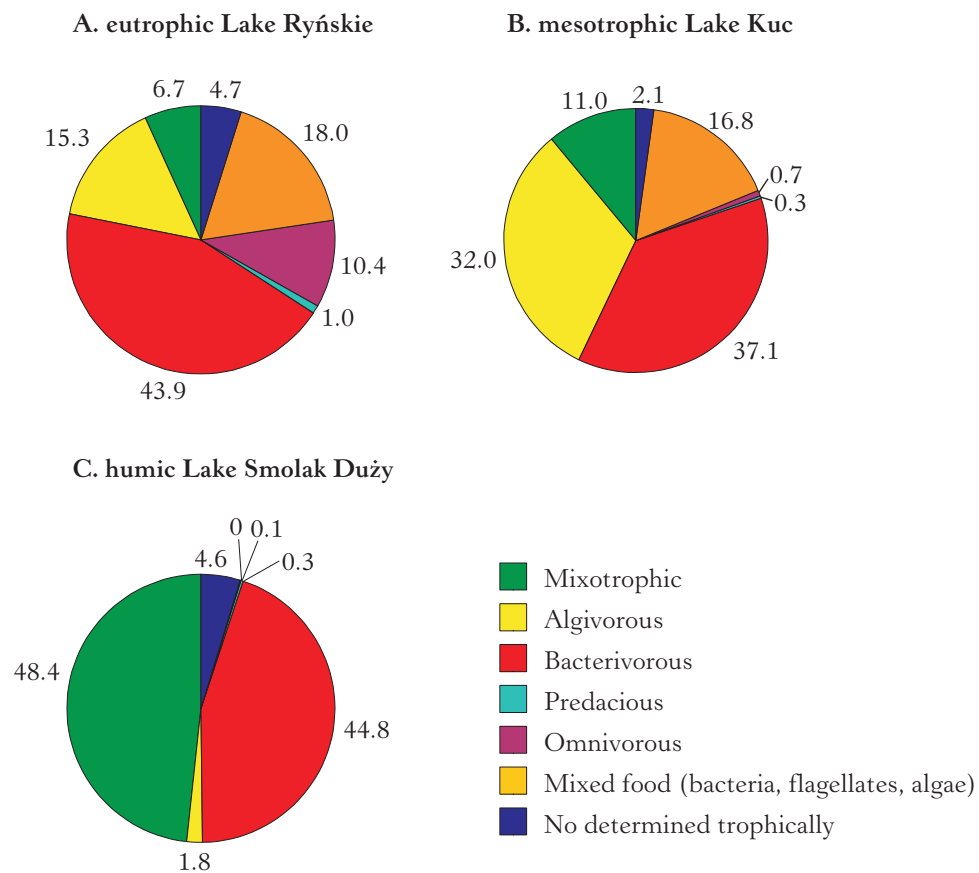


Fig. 2. Mean annual percentage share of main trophic groups of ciliates in total ciliate numbers in Masurian lakes.

mum, *Metopus*) and bacterivorous Hymenostomatida (*Frontonia* sp., *Marituja pelagica*, *Colpidium* sp.), were found in the eutrophic lake. Characteristic species in the mesotrophic lake were *Phialina*, *Lagynophrya acuminata* (Haptorida) and in the humic lake mixotrophic *Stokesia vernalis* (Hymenostomatida) – an important component of the ciliate fauna during the period spring-summer (7–19% of the total number and 83–92% of the total biomass).

Lakes differed in the annual mean percentage share of main trophic groups of ciliates in the total numbers. The eutrophic lake was mainly dominated by 15–90 μm -sized filter-feeding bacterivorous ciliates (43.9%) represented by small-sized Scuticociliatida and larger-sized Peritrichida. A high percentage of large predatory ciliates, as compared with other lakes, was also noted there (Fig. 2A). In the mesotrophic lake taxa feeding on bacteria (37.1%, mainly sessile Peritrichida living on the Cyanobacteria *Anabaena* sp.), and algae (32.0%) prevailed (Fig. 2B). Large-sized mixotrophic taxa (48.4%, represented by *Strombidium viride* and *Stokesia vernalis*), and small-sized bacterivores (44.8%, especially scuticociliate *Cyclidium*), were characteristic of the humic lake (Fig. 2C).

3.3. Relations between microbial loop components on seasonal and diel scale

The number of significant correlations between the components of the microbial loop and correlation coefficients differed among lakes and in different temporal scales. In the eutrophic lake the relationships were stronger in both seasonal and diel cycle. In this lake, most significant correlations between the components of the microbial loop on a seasonal basis were found (Table 2A). Bacterial biomass correlated most significantly and positively with bacterivorous Peritrichida ($r = 0.50$). The total biomass of nanoflagellates correlated positively with the density and biomass of Oligotrichida feed on bacteria, flagellates and algae ($r = 0.69$ and $r = 0.79$, respectively). The number and significance of correlations between the components of the microbial loop showed a different pattern in a diel cycle. All components were positively and strongly correlated with each other (Table 2A). The most signifi-

cant positive relationship was found between the density and biomass of ciliates and the density ($r = 0.81$ and $r = 0.74$, respectively) and biomass ($r = 0.81$ and $r = 0.76$) of nanoflagellates. Highly significant positive correlation was also found between the density and biomass of bacteria and the density and biomass of nanoflagellates and ciliates. Among ciliates, the highest correlations were found between the biomass of bacterivorous Peritrichida and bacterial density ($r = 0.71$) and between the biomass of Oligotrichida and bacterial biomass ($r = 0.72$). The numbers and biomass of bacteria were also positively correlated with DOC ($r = 0.56$ and $r = 0.70$, respectively).

In the seasonal scale the number of correlations in the mesotrophic lake was c. two times lower than in the eutrophic lake (Table 2B). Bacterial biomass correlated most significantly and negatively with bacterivorous Peritrichida ($r = -0.56$). The density of nanoflagellates correlated positively with the total density of ciliates ($r = 0.53$). The relationships between the elements of bacterial loop in the diel cycle were similar to those in the seasonal cycle (Table 2B). Highly significant negative correlations were noticed between bacteria and ciliates (small-sized bacterivorous Scuticociliatida, raptorial Haptorida, algivorous and bacterivorous Oligotrichida). A strong relationship was found in this lake between nanoflagellates and ciliates, of which most important seemed to be the genus *Histiobalantium* sp. feed on algae ($r = 0.72$ – 0.91).

In the humic lake, there was only one significant and positive correlation between bacterial biomass and small-sized bacterivorous Scuticociliatida represented by *Cyclidium* sp. ($r = 0.77$) in the seasonal cycle. No statistically significant relationships between the elements of microbial loop were found in the daily scale (Table 2C). None of the analysed parameters showed a significant correlation with nanoflagellates.

No significant correlation between bacteria and nanoflagellates was found in any of the studied lakes.

Generally, diel correlations (i.e. when changes were recorded every 4 hours) were stronger than those in the seasonal scale, which were correlated every month.

3.4. Relations between microbial loop components and lake trophic indices

Most statistically significant correlations between the components of the microbial loop and trophic state indices in the seasonal scale were found in the eutrophic lake (Table 3A). The numbers and biomass of nanoflagellates were negatively correlated with the total phosphorus concentration ($r = -0.78$ and $r = -0.54$, respectively) and positively with the concentration of chlorophyll *a* ($r = 0.69$). Total number of ciliates, the density of particular taxonomic groups (Oligotrichida, Haptorida) and of the genus *Histiobalantium* sp.

were correlated with the concentration of chlorophyll *a*. Correlation coefficient varied between 0.58 and 0.82 for particular groups. No expected correlation between DOC and the density or biomass of bacteria was found (Table 3A). In the eutrophic lake much more significant relationships between the components of the microbial loop and trophic factors were noted in the diel cycle than in the seasonal one (Table 3A). In this lake all studies groups of organisms were found to correlate with DOC. Negative correlations were found between TP concentration and: bacterial biomass ($r = -0.54$), density and biomass of nanoflagellates ($r = -0.82$ and $r = -0.83$, respectively),

Table 2. Correlation matrix for the major components of the microbial loop in the seasonal and diel cycles in Masurian lakes. Dissolved organic carbon (DOC), abundance (number and biomass) of bacteria (Bac), nanoflagellates (NF), total ciliates (Cil), Oligotrichida (Oli) feed on bacteria, flagellates and various algae, bacterivorous Peritrichida (Per), omnivorous Prostomatida (Pro), algivorous *Histiobalantium* (His), predacious Haptorida (Hap) mainly feed on heterotrophic protists, small-sized bacterivorous Scuticociliatida (Scu), ns – not significant, ■ – significant correlations at $P < 0.05$.

A eutrophic lake

	seasonal cycle				daily cycle			
	DOC	Bac	NF	Cil	DOC	Bac	NF	Cil
DOC	–	ns	ns	ns	–	■	■	■
Bac	ns	–	ns	ns	■	–	ns	ns
NF	ns	ns	–	■	■	■	–	■
Cil	ns	ns	■	–	■	■	■	–
Oli	ns	ns	■	–	ns	■	■	–
Per	ns	■	ns	–	ns	■	ns	–
Pro	–	–	–	–	ns	■	■	–
His	ns	ns	ns	–	–	–	–	–
Hap	ns	ns	■	–	ns	■	■	–
Scu	ns	ns	ns	–	ns	ns	ns	–

B mesotrophic lake

	seasonal cycle				daily cycle			
	DOC	Bac	NF	Cil	DOC	Bac	NF	Cil
DOC	–	ns	ns	ns	–	ns	ns	ns
Bac	ns	–	ns	ns	ns	–	ns	ns
NF	ns	ns	–	■	ns	ns	–	■
Cil	ns	ns	■	–	ns	ns	■	–
Oli	ns	■	ns	–	ns	■	■	–
Per	ns	■	ns	–	ns	ns	ns	–
Pro	–	–	–	–	ns	ns	ns	–
His	–	–	–	–	ns	ns	■	–
Hap	ns	ns	ns	–	ns	■	■	–
Scu	ns	ns	ns	–	ns	■	ns	–

C humic lake

	seasonal cycle				daily cycle			
	DOC	Bac	NF	Cil	DOC	Bac	NF	Cil
DOC	–	ns	ns	ns	–	ns	ns	ns
Bac	ns	–	ns	ns	ns	–	ns	ns
NF	ns	ns	–	ns	ns	ns	–	ns
Cil	ns	ns	ns	–	ns	ns	ns	–
Oli	ns	ns	ns	–	ns	ns	ns	–
Scu	ns	■	ns	–	ns	ns	ns	–

lake the components of the microbial loop correlated most significantly with DOC. In both seasonal and diel cycles the components showed a negative correlation with TP in the two non-humic lakes. In general, much more correlations were noted in the eutrophic lake than in two other. In the humic lake there were practically no such correlations.

4. DISCUSSION

4.1. Differences of microbial loop between lakes of various trophic status

Relations between the links of the microbial loop were different in the studied lakes and in different temporal scales thus one may assume variable functioning and the role of the microbial loop. Significant combinations between particular components of the microbial loop in the eutrophic lake were more numerous and stronger in the diel than in the seasonal cycle. In the mesotrophic lake no differences were found between the two time scales. Relation between bacteria and ciliates demonstrated in the seasonal cycle may point to an important process of carbon flow from bacteria to metazooplankton in the humic lake. This study suggest that in the seasonal cycle ciliates were the main consumer of bacteria in all lakes being an important and direct link between bacterioplankton/algal picoplankton and higher trophic levels. It was found, however, that various taxonomic and trophic groups of ciliates showed different correlations with bacterial abundance in particular lakes. In the diel cycle both ciliates and nanoflagellates probably played important role in reducing bacterioplankton in the eutrophic lake. Negative correlations between bacteria and ciliates in the mesotrophic lake indicate a possibility of other factors (e.g. organisms of higher trophic levels) responsible for controlling bacteria. No significant correlations between the components of microbial loop were found in the humic lake.

Since functioning and the role of the microbial loop rely on many factors, one should analyse not only the relationships within the microbial loop but also with other metazooplanktonic invertebrates or fishes, which might affect the microbial loop through the lower trophic levels.

Experiments carried out in meso- and eutrophic lakes on *Daphnia* feeding intensively on heterotrophic nanoflagellates and bacteria and thus controlling all components of microbial loop may serve as an example of such analyses. Studies in a eutrophic lake in Denmark demonstrated that 23–66% of bacterial production in fishless experiments were consumed by crustaceans $>200 \mu\text{m}$ while in the presence of planktivorous fishes small zooplankton gradually became the dominating bacterivore (Jürgens 1992).

Literature data show that in eutrophic lakes relatively high bacterial production and density are not the limiting factor for the growth of bacterivorous ciliates. Therefore, in productive lakes these small bacterivorous ciliates may, apart from heterotrophic nanoflagellates, play a key role in carbon transfer to higher trophic levels (Porter *et al.* 1979, Beaver and Crisman 1989). Many authors (e.g. Pace 1982, Christoffersen *et al.* 1990, James *et al.* 1995) showed positive correlations between the total biomass, density of larger groups or particular ciliate taxa and the abundance of bacterioplankton indicating thus an important role of ciliates as consumers of bacteria and nutrient recyclers. Consuming much of bacterial production ciliates become an important link between bacteria and higher trophic levels.

In oligo- and mesotrophic lakes rotifers may be the most significant link in bacterial and nanoplanktonic carbon flow to macrozooplankton (Stockner and Shortreed 1989). As shown by Laybourn-Parry (1992) lakes of low nutrient content are dominated in spring by diatoms and the density of picoplankton is low. Therefore, part of the "new primary production" goes to "classic" consumers of the food chain. Weisse (1990) demonstrated that the linear food chain (bacteria–heterotrophic nanoflagellates–ciliates) is the main way of transferring bacterial production to higher trophic levels. It seems, however, that trophic relations between bacteria and bacterivores in mesotrophic lakes reveal only in some periods. For example, Šimek *et al.* (1990) demonstrated that ciliates were important consumers of bacteria only in summer and that feeding by meso- and macrozooplankton was more important than that by protozoans in controlling bacterial densities. Carrias *et al.* (1998)

did not find correlations between ciliates and bacteria in an oligo-mesotrophic lake while Simon *et al.* (1998) demonstrated that protozoans and *Daphnia* were most important in controlling bacterioplankton dynamics. As given in Šimek *et al.* (1998) the role of heterotrophic nanoflagellates in grazing on bacteria decreases and that of ciliates increases with the increasing trophic status of lakes.

There are few data on mutual trophic relationships in humic lakes. Amblard *et al.* (1995) noted close correlations between the biomass of auto- and heterotrophic nanoflagellates and the biomass of ciliates. They did not find, however, the relations between bacterial biomass and the biomass of nanoflagellates or ciliates. Kankaala *et al.* (1996) reported, however, that heterotrophic nanoflagellates were the important consumer of bacteria in a humic lake. According to the data of Stockner and Porter (1988) and Amblard *et al.* (1995) a large load of allochthonous organic matter in humic lakes favours "new production" at the cost of production by recycling decreasing thus the importance of the microbial loop in the matter and energy flow as compared with the classical food chain.

Despite a common belief that the role of the microbial loop is greater in less productive habitats, this study (a number of mutual relationships between the components of the microbial loop) and literature data demonstrate that it may be of importance for carbon flow from bacteria to higher trophic levels even in such a productive habitat as the eutrophic Lake Ryńskie.

4.2. Ciliate communities of various lakes

Pelagic ciliates are the main component of microzooplankton and may constitute up to 34% of the total zooplankton biomass in eutrophic lakes and up to 62% in the hypertrophic ones (Pace and Orcutt 1981, Beaver and Crisman 1990). Undoubtedly, their role in the functioning of lakes of various trophic state is important.

Among the studied lakes the highest species diversity was noted in the eutrophic lake though the number of recorded ciliate taxa in the mesotrophic lake was only by 7% lower. In lakes of low concentrations of organic matter the total number of observed ciliate taxa varies between 20 and

30 while in eutrophic lakes species diversity is higher (Beaver and Crisman 1989, Laybourn-Parry 1992, 1994, Carrias *et al.* 1998). In all studied lakes numerous Oligotrichida, feed on bacteria, autotrophic and heterotrophic flagellates and various algae, thus being an important component of the microbial loop (Foissner *et al.* 1999), were the constant component of the fauna. They are widespread organisms found in all types of surface waters. The dominance of Oligotrichida (*Halteria*, *Strobilidium*, *Strombidium*) has been observed in both eutrophic (e.g. in Lake Oglethorpe in USA – Pace 1982, Ontario in Canada – Taylor and Heynen 1987, Esthwaite in England – Laybourn-Parry *et al.* 1990, Okaro in New Zealand – James *et al.* 1995, Alte Donau in Austria – Mayer *et al.* 1997), and oligo-mesotrophic lakes (Constance in Germany – Müller *et al.* 1991, Taupo in New Zealand – James *et al.* 1995, Pavin in France – Carrias *et al.* 1998, Houhu in China – Biyu 2000). Beaver and Crisman (1982, 1990) studying Florida lakes of various degree of eutrophication found decreasing importance of Oligotrichida (and also predacious Haptorida) and increasing importance of bacterivorous Scuticociliatida along with increasing trophic status. Similar dependence on the trophic status was found in the present study. There is an evidence (Šimek *et al.* 1995, Wiąckowski *et al.* 2001) that, at least in some mainly eutrophic lakes, small bacterivorous Scuticociliatida might be the dominating element of the ciliate fauna. Their dominance in lakes of differentiated trophic status, as found in this study, may differ in different periods and thermal layers. Cited studies by Beaver and Crisman (1982, 1990) did not involve the presence of Peritrichida. They are considered the organisms common in eutrophic temperate lakes (Müller 1989, Laybourn-Parry 1992). In the present study Peritrichida were found to dominate over the larger part of the year. High contribution of these bacterivores was also noted in the spring in the mesotrophic lake. Being present in such high numbers they may significantly affect the numbers of bacterioplankton. A detailed discussion of results based on ciliate composition in lakes and thermic layers will be given elsewhere (Kalinowska, in prep.).

The least taxonomically diversified

appeared to be the humic lake. The number of recorded taxa (18) was similar to that noted by Szelaż-Wasilewska and Fyda (1999) in Polish lobelian (soft water lakes with endemic atlantic species, *Lobelia dortmanna*) lakes of the Kaszub Lakeland (Pomerania, North Poland) (maximum number = 15). Much poorer species composition – up to 5 taxa – were noted in Polish humic lakes of a pH < 6.2 in Masurian Lakeland (Kalinowska 2000). The latter studies were based on samples collected once or twice a year in spring and summer. In Lake Smolak Duży, however, the greatest species diversity was observed in the autumn. The taxa recorded there represented two main groups of ciliates: Oligotrichida and Scuticociliatida. Beaver and Crisman (1989) found that small Scuticociliatida tended to dominate in lakes of pH > 5.0 while in more acidic lakes they were replaced by large Oligotrichida. Humic lakes, due to low pH, are often characterised by a lower number of taxa and lower densities (Beaver and Crisman 1990).

4.3. Seasonal and diel relations among the components of microbial loop

In the seasonal cycle total phosphorus was the trophic index which correlated negatively with the numbers and biomass of bacteria in the mesotrophic lake. The lake showed rather low TP concentrations (below 20 $\mu\text{g l}^{-1}$) in surface waters, particularly in spring and early autumn. This correlation may suggest that other factors such as predation or competition were important in determining the abundance of bacteria. In the stratified lakes densities and/or biomasses of bacteria were found to depend on the density of bacterivorous Peritrichida. These sessile ciliates typical for meso- and eutrophic lakes (Laybourn-Parry *et al.* 1990, Müller *et al.* 1991) even at low densities may strongly affect bacteria because of the high grazing rate (Šimek *et al.* 1995, Carrias *et al.* 1996). According to Šimek *et al.* (1995) the grazing rate on bacteria by a single individual of *Vorticella* (4200 bacteria per hour) is much higher than by *Cyclidium* (470 bacteria per hour) or by Oligotrichida (380–2130 bacteria per hour). Due to relatively high density of these ciliates in the both studied lakes one may infer their deci-

sively limiting effect on bacterioplankton. Bacterial biomass and the density of small-sized bacterivorous Scuticociliatida were also correlated in the humic lake, which might suggest that ciliates were one of the factors responsible for changes in bacterial biomass. The degree of correlation might also suggest that ciliates were more important in the mesotrophic and humic than in the eutrophic lake. Contrary to the expectations, no relationship was found between bacteria and DOC, the main energy source for bacteria (Chróst 1986, Münster and Chróst 1990), in any of studied lakes. A lack of such correlation could be the effect of other, not studied limiting factors. On the other hand, it is the chemical composition and availability of DOC rather than the amount, which are important for heterotrophic bacteria (Chróst 1986). The author found a close relationship between heterotrophic bacteria and the concentration of dissolved organic carbon excreted by algae but not with the total DOC pool. The majority of cellular photosynthetic matter has a polymeric structure and must be depolymerized outside the bacterial cell, ectoenzymatic hydrolysis is the limiting step of its availability for microheterotrophs. In addition, products of hydrolysis could be bound to the seston particles abundant in lakes and become unavailable for bacterial transport systems (Gajewski and Chróst 1995). So, in the studied lakes DOC could be possibly poorly available to bacteria. Another explanation for the lack of correlation could be the finding by Berninger *et al.* (1993) that not all bacteria actively participate in DOC uptake.

The significant correlations between bacteria and ciliates may indicate that the density of bacteria was in all studied lakes determined by ciliates. This finding negates the hypothesis given by Sanders *et al.* (1992) that in oligo-mesotrophic habitats the bottom-up effect is more important in bacterial control, while in eutrophic ones the top-down control is more significant. Similar relationship between the total number and particular ciliate species and the numbers of bacteria was noted in a eutrophic Lake Okaro in New Zealand by James *et al.* (1995), who underlined that ciliates were more significant consumer of particles < 2 μm than of nanoplankton (particles > 2 μm).

In the two stratified lakes the abun-

dance (numbers and biomass) of nanoflagellates might be controlled by both food availability and by grazing by ciliates. The number of factors determining their presence was, however, higher in the eutrophic (TP, Chlorophyll *a*, Oligotrichida, Haptorida) than in the mesotrophic lake (chlorophyll *a*, total numbers of ciliates). The strongest relationship in the eutrophic lake was that between nanoflagellates and Oligotrichida and in the mesotrophic lake – between nanoflagellates and chlorophyll *a*. None of the analysed factors was found to control nanoflagellates in the humic Lake Smolak Duży. In none of the lakes there was a correlation between bacteria and nanoflagellates, which might suggest that the latter were not important consumers of bacteria. Many studies pointed out a significant role of nanoflagellates as consumers of bacteria. There are, however, examples of a weak relationships between them, particularly in eutrophic lakes where top-down pressure exerted by predators is more important in controlling nanoflagellate dynamics than the availability of bacteria (Wright and Coffin 1984, Jürgens and Güde 1990, Weisse 1991, Wiąckowski *et al.* 2001). There is also some evidence (Caron *et al.* 1993) that only part of heterotrophic nanoflagellates are really bacterivorous. Mathes and Arndt (1995) demonstrated that c. one fourth of the biomass of heterotrophic nanoflagellates (*Kathablepharis*) in a meso-eutrophic lake in Germany were potential consumers of small algae. A lack of correlation between bacteria and nanoflagellates was also noted in humic lakes e.g. in Lake Vassievriere in France (Amblard *et al.* 1995). High bacterial biomasses, which were not the factor limiting nanoflagellates were the reason by which the authors explained missing correlation. It seems, however, that in the studied Masurian lakes nanoflagellates were determined not only by bacteria but also by autotrophic picoplankton, which might be a source of their food (Weisse 1990).

Positive correlations between the numbers and/or biomass of ciliates and chlorophyll found in all studied lakes seem to suggest the relationship between these components. One may expect that chlorophyll was a significant factor controlling ciliate density – the effect recorded also by Wiąckowski *et al.* (2001) in eutrophic

Lake Köyliönjärvi in Finland. Positive relationship between nanoflagellates and chlorophyll may indicate indirect relationship i.e. increased concentration of chlorophyll is followed by an increase in the abundance of substratum and detritus for bacteria, which in turn results in the increased number of nanoflagellates.

Studies carried out by Berninger *et al.* (1993) in a highly productive basin demonstrated that the flow of organic carbon was faster than sampling intervals (every 1–3 days) applied by the authors. Bacteria, nanoflagellates and ciliates are characterised by a high rate of reproduction. As given in Czapiak (1992) most protozoans divide on average once a day and in some ciliates the divisions take place every several hours. Since the life span of mentioned organisms is short – of the order of several hours – trophic relations can be traced in studies carried out at the same frequency. Therefore, more highly correlated relations were found in the diel cycles analysed in this paper than in the seasonal studies but they mostly pertained to the eutrophic lake.

In the eutrophic lake all studied groups of organisms were negatively correlated with TP and positively with DOC indicating that these were the factors controlling not only the bacterial abundance but also – indirectly – other groups of organisms (nanoflagellates and ciliates) feeding on bacteria. There was also a relationship between bacteria and total nitrogen concentration. Negative correlations between bacteria and TP and TN may indicate a high impact of bacterivores or an intensive N and P uptake by bacteria. Direct relationship between bacteria and nanoflagellates and ciliates confirms that bacteria were consumed by the two groups of organisms. Higher degree of correlation between bacteria and some ciliate taxa (Oligotrichida, Peritrichida and Haptorida) indicates that greater importance should be prescribed to ciliates than to nanoflagellates. Strong correlation between nanoflagellates and ciliates might suggest that ciliates were responsible for controlling nanoplanktonic flagellates.

In the mesotrophic lake the relations between the links of the microbial loop in the diel cycle were similar to those in the seasonal cycle. Chlorophyll was most correlated with the abundance of nanoflagel-

lates and ciliates. Highly significant correlation between bacteria and ciliates confirms their direct relationship. Noteworthy, bacteria in the diel cycle were correlated with Scuticociliatida and Haptorida but in the seasonal – with Peritrichida. It appears that the relationships are closely determined by taxonomic composition of ciliates. Correlation between ciliates (mostly *Histiobalantium* and Haptorida) and nanoflagellates suggests that the former were the direct consumer of nanoplankton.

In the humic lake I expected a highly significant correlation between the density of numerous *Cyclidium* and bacteria, their potential food. No such correlation was found, possibly due to the fact that these small ciliates (<30 μm) might utilise various food sources from picoplankton (Fenchel 1986, Šimek *et al.* 1990, Šimek and Straškrabova 1992, Weisse 1993) to nanoplankton (Sherr *et al.* 1991). Positive relationship between small-sized bacterivorous ciliates and large autotrophic flagellates composed of bacterivorous *Dinobryon cylindricum* was shown by Carrias *et al.* (1998) in an oligo-mesotrophic lake in France. The authors underlined that organisms of similar trophic requirements are more dependent on each other than on their food. Autotrophic picoplankton was not analysed within this study but from microscopic observations it appears that autotrophic picoplankton was present in large amounts and could constitute a source of food for both ciliates and nanoflagellates. Since picoplankton and bacteria fall in the same size class they may produce equally valuable food for protozoans.

ACKNOWLEDGEMENTS: I thank my colleagues for their technical assistance during chemical analysis of water samples. Special thanks go to Prof. A. Hillbricht-Ilkowska for her help during the work and many valuable suggestions. I am very grateful to Prof. L. Kufel for his comments and careful English correction and two anonymous reviewers for critical and valuable comments on the manuscript.

5. SUMMARY

The trophic structure of the microbial loop and relationships between the components of the microbial loop and selected indices of lake trophic status (TP, TN, DOC, chlorophyll) were examined in three Polish lakes of

different trophic status: highly eutrophic Lake Ryńskie, mesotrophic Lake Kuc and humic, acid Lake Smolak Duży (Table 1).

Biomasses of particular components of the microbial loop markedly differed between the lakes (Fig. 1). The studied lakes differed in percentage share of main trophic groups of ciliates in the total numbers. Bacterivorous taxa dominated in the eutrophic lake, bacterivorous and algivorous taxa were most abundant in the mesotrophic lake and large mixotrophic and small bacterivorous taxa dominated in the humic lake (Fig. 2). In the seasonal cycle the abundance of bacteria was correlated most significantly with bacterivorous Peritrichida in both stratified lakes, whereas with bacterivorous Scuticociliatida – in the humic lake. Nanoflagellate biomass was the strongly correlated with the abundance of Oligotrichida in the eutrophic lake and with ciliate numbers in the mesotrophic lake (Table 2). Diel correlations between the major components of the microbial loop were stronger than those in the seasonal scale, especially in the eutrophic lake (Table 2). In the seasonal cycle, chlorophyll was the major trophic indices positively correlated with both ciliate and nanoflagellate densities (Table 3). In diel cycle, all components of the microbial loop were the strongest correlated with DOC concentration in the eutrophic lake (Table 3). In the both cycles the components of the microbial loop were negatively correlated with TP in stratified lakes.

6. REFERENCES

- Amblard C., Carrias J.-F., Bourdier G., Maurin N. 1995 – The microbial loop in a humic lake: seasonal and vertical variations in the structure of different communities – *Hydrobiologia*, 300/301: 71–84.
- Arvola L., Kankaala P., TOLONEN T., Ojala A. 1996 – Effects of phosphorus and allochthonous humic matter enrichment on the metabolic processes and community structure of plankton in a boreal lake (Lake Pääjärvi) – *Can. J. Fish. Aquat. Sci.* 53: 1646–1662.
- Azam F., Fenchel T., Field J. G., Gray J. S., Meyer-Reil L. A., Thingstad F. 1983 – The ecological role of water column microbes in the sea – *Mar. Ecol. Prog. Ser.* 10: 257–263.
- Beaver J. R., Crisman T. L. 1982 – The trophic response of ciliated protozoans in freshwater lakes – *Limnol. Oceanogr.* 27: 246–253.
- Beaver J. R., Crisman T. L. 1989 – The role of ciliated protozoa in pelagic freshwater ecosystems – *Microb. Ecol.* 17: 111–136.
- Beaver J. R., Crisman T. L. 1990 – Seasonality of planktonic ciliated protozoa

- in 20 subtropical Florida lakes of varying trophic state – *Hydrobiologia*, 190: 127–135.
- Berninger U.-G., Finlay B. J., Kuuppo-Leinikki P. 1991 – Protozoan control of bacterial abundances in freshwater – *Limnol. Oceanogr.* 36: 139–147.
- Berninger U.-G., Wickham S. A., Finlay B. J. 1993 – Trophic coupling within the microbial food web: a study with fine temporal resolution in a eutrophic freshwater ecosystem – *Freshwat. Biol.* 30: 419–432.
- Biyu S. 2000 – Planktonic protozooplankton (ciliates, heliozoans and testaceans) in two shallow mesotrophic lakes in China – a comparative study between a macrophyte-dominated lake (Biandantang) and an algal lake (Houhu) – *Hydrobiologia*, 434: 151–163.
- Bloem J., Ellenbroek F. M., Bär-Gilissen M.-J. B., Cappenberg T. E. 1989 – Protozoan grazing and bacterial production in stratified lake Vechten estimated with fluorescently labeled bacteria and by thymidine incorporation – *Appl. Environ. Microbiol.* 55: 1787–1795.
- Caron D. A. 1983 – Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy and comparison with other procedures – *Appl. Environ. Microbiol.* 46: 491–498.
- Caron D. A., Sanders R. W., Lim E. L., Marrasé C., Amaral L. A., Whitney S., Aoki R. B., Porter K. G. 1993 – Light-dependent phagotrophy in the freshwater mixotrophic chrysophyte *Dinobryon cylindricum* – *Microb. Ecol.* 25: 93–111.
- Carrias J.-F., Amblard C., Bourdier G. 1996 – Protistan bacterivory in an oligomesotrophic lake: importance of attached ciliates and flagellates – *Microb. Ecol.* 31: 249–268.
- Carrias J.-F., Amblard C., Bourdier G. 1998 – Seasonal dynamics and vertical distribution of planktonic ciliates and their relationship to microbial food resources in the oligomesotrophic Lake Pavin – *Arch. Hydrobiol.* 143: 227–255.
- Christoffersen K., Riemann B., Hansen L. R., Klynsner A., Sørensen H. B. 1990 – Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria – *Microb. Ecol.* 20: 253–272.
- Chróst R. J. 1986 – Algal-bacterial metabolic coupling in the carbon and phosphorus cycle in lakes (In: *Perspectives in Microbial Ecology*, Eds. F. Megusar, M. Gantar) – *Proc. IV ISME*, pp. 360–366.
- Czapik A. 1992 – *Podstawy protozoologii [Fundamentals of Protozoology]* – PWN – Polish Scientific Publishers, Warszawa.
- Epstein S. S., Shiaris M. P. 1992 – Size-selective grazing of coastal bacterioplankton by natural assemblages of pigmented flagellates, colorless flagellates, and ciliates – *Microb. Ecol.* 23: 211–225.
- Fenchel T. 1984 – Suspended marine bacteria as a food source (In: *Flows of energy and materials in marine ecosystems*, Ed. M. R. Fasham) – Plenum Press, New York, pp. 301–315.
- Fenchel T. 1986 – The ecology of heterotrophic microflagellates – *Adv. Microb. Ecol.* 9: 57–97.
- Foissner W., Berger H. 1996 – A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology – *Freshwat. Biol.* 35: 375–482.
- Foissner W., Berger H., Blatterer H., Kohmann F. 1991–95 – *Taxonomische und ökologische Revision der Ciliaten des Saprobiensystems. Band I–IV* – Bayer. Landesamt für Wasserwirtschaft, München.
- Foissner W., Berger H., Schaumburg J. 1999 – *Identification and ecology of limnetic plankton ciliates* – Bayer. Landesamt für Wasserwirtschaft, München.
- Gajewski A. J., Chróst R. J. 1995 – Microbial enzyme activities and phytoplankton and bacterial production in the pelagial of the Great Mazurian Lakes (north-eastern Poland) during summer stratification – *Ekol. pol.* 43: 245–265.
- Golterman H. L. 1969 – *Methods for Chemical Analysis of Fresh Waters*. IBP Handbook No 8 – Blackwell Scientific Publications, Oxford, Edinburgh, 172 pp.
- Górniak A., Zieliński P. 1999 – *Rozpuszczone związki węgla organicznego w jeziorze Wigry [Soluble organic carbon compounds in Lake Wigry]* (In: *Funkcjonowanie i ochrona ekosystemów wodnych na obszarach chronionych [The functioning and protection of aquatic ecosystems on the protected areas]* Eds. B. Zdanowski, M. Kamiński, A. Martyniak – Institute of Inland Fisheries, Olsztyn, pp. 141–151.
- Hillbricht-Ilkowska A. 1977 – Trophic relations and energy flow in pelagic plankton – *Pol. Ecol. Stud.* 3: 3–98.
- Hillbricht-Ilkowska A., Spodniewska I., Węgleńska T. 1979 – Changes in the phytoplankton-zooplankton relationships connected with the eutrophication of lakes – *Symp. Biol. Hung.* 19: 59–75.
- Hitchman R. B., Jones H. L. J. 2000 – The role of mixotrophic protists in the population dynamics of the microbial food web in a small artificial pond – *Freshwat. Biol.* 43: 231–241.
- James M. R., Burns C. W., Forsyth D. J.

- 1995 – Pelagic ciliated protozoa in two monomictic, southern temperate lakes of contrasting trophic state: seasonal distribution and abundance – *J. Plankton Res.* 17: 1479–1500.
- Jones R. I. 1992 – The influence of humic substances on lacustrine planktonic food chains – *Hydrobiologia*, 229: 73–91.
- Jürgens K. 1992 – Is there plenty of food for bacterivorous flagellates in eutrophic waters? – *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 37: 195–205.
- Jürgens K., Güde H. 1990 – Incorporation and release of phosphorus by planktonic bacteria and phagotrophic flagellates – *Mar. Ecol. Prog. Ser.* 59: 271–284.
- Jürgens K., Stolpe G. 1995 – Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake – *Freshwat. Biol.* 33: 27–38.
- Kalinowska K. 2000 – Ciliates in small humic lakes (Masurian Lakeland, Poland): relationship to acidity and trophic parameters – *Pol. J. Ecol.* 48: 169–183.
- Kankaala P., Arvola L., Tulonen T., Ojala A. 1996 – Carbon budget for the pelagic food web of the euphotic zone in a boreal lake (Lake Pääjärvi) – *Can. J. Fish. Aquat. Sci.* 53: 1663–1674.
- Laybourn-Parry J. 1992 – Protozoan plankton ecology – Chapman and Hall, London, 231 pp.
- Laybourn-Parry J. 1994 – Seasonal successions of protozooplankton in freshwater ecosystems of different latitudes – *Mar. Microb. Food Webs* 8: 145–162.
- Laybourn-Parry J., Olver J., Rogerson A., Duvergé P. L. 1990 – The temporal and spatial patterns of protozooplankton abundance in a eutrophic temperate lake – *Hydrobiologia*, 203: 99–110.
- Mathes J., Arndt H. 1995 – Annual cycle of protozooplankton (ciliates, flagellates and sarcodines) in relation to phyto- and metazooplankton in Lake Neumühler See (Mecklenburg, Germany) – *Arch. Hydrobiol.* 134: 337–358.
- Mayer J., Dokulil M. T., Salbrechter M., Berger M., Posch T., Pfister G., Kirschner A. K. T., Velimirov B., Steitz A., Ulbricht T. 1997 – Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliate and bacteria in a hypertrophic shallow lake in Vienna, Austria – *Hydrobiologia*, 342/343: 165–174.
- Müller H. 1989 – The relative importance of different ciliate taxa in the pelagic food web of Lake Constance – *Microb. Ecol.* 18: 261–273.
- Müller H., Schöne A., Pinto-Coelho R. M., Schweizer A., Weisse T. 1991 – Seasonal succession of ciliates in Lake Constance – *Microb. Ecol.* 21: 119–138.
- Münster U., Chróst R. J. 1990 – Origin, composition and microbial utilization of dissolved organic matter (In: *Aquatic microbial ecology*, Eds. J. Overbeck, R. J. Chróst) – New York, pp. 8–46.
- Pace M. L. 1982 – Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake – *Can. J. Fish. Aquat. Sci.* 39: 1106–1116.
- Pace M. L. 1986 – An empirical analysis of zooplankton community size structure across lake trophic gradients – *Limnol. Oceanogr.* 31: 45–55.
- Pace M. L., Orcutt Jr. J. D. 1981 – The relative importance of protozoans, rotifers and crustaceans in a freshwater zooplankton community – *Limnol. Oceanogr.* 26: 822–830.
- Pomeroy L. R. 1974 – The oceans food web, a changing paradigm – *BioScience*, 24: 499–504.
- Porter K. G., Feig Y. S. 1980 – The use of DAPI for identifying and counting aquatic microflora – *Limnol. Oceanogr.* 25: 943–948.
- Porter K. G., Pace M. L., Battey J. F. 1979 – Ciliate protozoans as links in freshwater planktonic food chains – *Nature*, 277: 563–565.
- Porter K. G., Pearl H., Hodson R., Pace M. L., Prisco J., Riemann B., Scavia D., Stockner J. G. 1988 – Microbial interactions in lake food webs (In: *Complex Interactions in Lake Communities*, Ed. S. R. Carpenter) – Springer-Verlag, Berlin, pp. 209–227.
- Porter K. G., Sherr E. B., Sherr B. F., Pace M. L., Sanders R. W. 1985 – Protozoa in planktonic food webs – *J. Protozool.* 32: 409–415.
- Sanders R. W., Caron D. A., Berninger U.-G. 1992 – Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an interecosystem comparison – *Mar. Ecol. Prog. Ser.* 86: 1–14.
- Sanders R. W., Porter K. G., Bennett S. J., DeBiase A. E. 1989 – Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community – *Limnol. Oceanogr.* 34: 673–687.
- Sanders R. W., Porter K. G., McDonough R. 1985 – Bacterivory by ciliates, microflagellates and mixotrophic algae: factor influencing particle ingestion – *EOS* 66: 1314.
- Sherr B. F., Sherr E. B. 1984 – Role of heterotrophic protozoa in carbon and energy flow in aquatic environments (In: *Current Perspectives in Microbial Ecology*, Eds. M. J. Klug, C. A. Reddy) – American Society for Microbiology, Washington, D.C, pp. 412–423.
- Sherr B. F., Sherr E. B., Fallon R. D. 1987 –

- Use of monodispersed, fluorescently labeled bacteria to estimate in situ protozoan bacterivory – *Appl. Environ. Microbiol.* 53: 958–965.
- Sherr E. B., Sherr B. F., Berman T., Hadas O. 1991 – High abundance of picoplankton-ingesting ciliates during late fall in Lake Kinneret, Israel – *J. Plankton Res.* 13: 789–799.
- Simon M., Tilzer M. M., Müller H. 1998 – Bacterioplankton dynamics in a large mesotrophic lake: I. Abundance, production and growth control – *Arch. Hydrobiol.* 143: 385–407.
- Standard Methods for the Examination of Water and Wastewater 1960 – Am. Publ. Health Assoc. Inc., New York, 626 pp.
- Stockner J. G., Porter K. G. 1988 – Microbial food webs in freshwater planktonic ecosystems. (In: *Complex Interactions in Lake Communities*, Ed. S. R. Carpenter – Springer-Verlag, Berlin, pp. 69–83.
- Stockner J. G., Shortreed K. S. 1989 – Algal picoplankton production and contribution to food webs in oligotrophic British Columbia lakes – *Hydrobiologia*, 173: 151–166.
- Szelaż-Wasielewska E., Fyda J. 1999 – Phytoplankton and ciliate communities of ten lobelian Pomeranian lakes (NW Poland) – *Acta Hydrobiol.* 41: 153–164.
- Šimek K., Straškrabová V. 1992 – Bacterioplankton production and protozoan bacterivory in a mesotrophic reservoir – *J. Plankton Res.* 14: 773–787.
- Šimek K., Bobková J., Macek M., Nedoma J., Psenner R. 1995 – Ciliate grazing on picoplankton in a eutrophic reservoir during the summer phytoplankton maximum: A study at the species and community level – *Limnol. Oceanogr.* 40: 1077–1090.
- Šimek K., Macek M., Seda J., Vyhnálek V. 1990 – Possible food chain relationships between bacterioplankton, protozoans, and cladocerans in a reservoir – *Int. Rev. ges. Hydrobiol.* 75: 583–596.
- Šimek K., Armengol J., Comerma M., Garcia J. C., Chrzanowski T. H., Macek M., Nedoma J., Straškrabová V. 1998 – Characteristics of protistan control of bacterial production in three reservoirs of different trophic – *Int. Rev. ges. Hydrobiol.* 83: 485–494.
- Taylor W. D., Heynen M. L. 1987 – Seasonal and vertical distribution of ciliophora in Lake Ontario – *Can. J. Fish. Aquat. Sci.* 44: 2185–2191.
- Tranvik L. J. 1988 – Availability of dissolved organic carbon for planktonic bacteria in oligotrophic lakes of differing humic content – *Microb. Ecol.* 16: 311–322.
- Tranvik L. J., Sieburth J. McN. 1989 – Effects of flocculated humic matter on free and attached pelagic microorganisms – *Limnol. Oceanogr.* 34: 688–699.
- Weisse T. 1990 – Trophic interactions among heterotrophic microplankton, nanoplankton, and bacteria in Lake Constance – *Hydrobiologia*, 191: 111–122.
- Weisse T. 1991 – The annual cycle of heterotrophic freshwater nanoflagellates: role of bottom-up versus top-down control – *J. Plankton Res.* 13: 167–185.
- Weisse T. 1993 – Dynamics of autotrophic picoplankton in marine and freshwater ecosystems – *Adv. Microb. Ecol.* 13: 327–370.
- Weisse T., Müller H., Pinto-Coelho R. M., Schweizer A., Sprigmann D., Baldringer G. 1990 – Response of the microbial loop to the phytoplankton spring bloom in a large prealpine lake – *Limnol. Oceanogr.* 35: 781–794.
- Wetzel R. G. 2000 – Freshwater ecology: changes, requirements, and future demands – *Limnology*, 1: 3–9.
- Wiackowski K., Ventelä A.-M., Moilanen M., Saarikari V., Vuorio K., Sarvala J. 2001 – What factors control planktonic ciliates during summer in a highly eutrophic lake? – *Hydrobiologia*, 443: 43–57.
- Wright R. T., Coffin R. B. 1984 – Measuring microzooplankton grazing on planktonic marine bacteria by its impact on bacterial production – *Microb. Ecol.* 10: 137–149.

(Received after revising August 2003)