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Recent dynamics of bacterioplankton in Lake Ladoga

Larisa Kapustina

Institute of Limnology, Russian Academy of Sciences, Sevastyanov Str. 9, RUS-196199, St. Petersburg, Russia

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New data are presented on the dynamics of total bacterioplankton numbers (BN) and dark CO_2-fixation (DCF) in 1989–1993. During this period, both BN and DCF have been much higher than in the preceding years. Summer averages of DCF and BN for the period 1985–1988 were 0.49 µg C l^{-1} d^{-1} and 0.54×10^6 cells ml^{-1}, and for 1989–1993 they were 2.4 µg C l^{-1} d^{-1} and 1.02×10^6 cells ml^{-1}, respectively. The summer 1992 averages of BN, 2.26×10^6 cells ml^{-1} in epilimnion and 1.16×10^6 cells ml^{-1} in hypolimnion are the highest values recorded since the beginning of bacterioplankton investigations in Lake Ladoga in 1977. The increase of DCF and BN has been accompanied with a considerable decrease (from 9 down to 6.3–8.3 mg l^{-1}) of total organic carbon levels in Lake Ladoga.

Introduction

Our previous studies demonstrated marked changes in the bacterial community of Lake Ladoga since the year 1977, along with the eutrophication of the lake (Kapustina 1992, 1996). As a result of anthropogenic influence, the typical oligotrophic state of the lake was changed to a mesotrophic level with significant spatial gradients of bacterial densities and activities (1977–1978). Further eutrophication resulted in a recurrent homogenization of numbers of bacteria and activity on a new trophic level (1978–1987). The present work concentrates on the further evolution of bacterioplankton community in the period 1989–1993. Main tasks of the present work are:

— to analyse numbers of bacteria (BN) and dark CO_2-fixation (DCF) obtained during 1989–1993;
— to investigate temporal (seasonal and annual) and spatial (between different limnetic zones) distribution of bacterial densities and DCF-values and their relationships with some other parameters;
— to compare the data with those of preceding years in order to assess the long-term trends and potential future development of the bacterial communities of the lake.

Material and methods

Bacterial samples were taken from altogether 20 sites, representing different limnetic regions of the lake during the years 1989–1993. The sampling was mainly repeated during tree seasons (spring, summer and autumn), and at each site, between 2 and 6 water layers were sampled, depending on the depth of the site.

The total numbers of bacteria (BN) were estimated with the carbolic erythrosine direct count method of Romanenko and Kuznetsov (1974). The 100-ml bacterial count samples were fixed with formaldehyde (2% final concentration). Two 5–10 ml subsamples of each of these were filtered through 0.23-µm Synpore filters (diam. 35 mm), stained with carbolic erythrosine for 24 h, rinsed, dried and counted with microscope. About 500 bacteria were counted on each slide under a Reichert Zetopan light microscope (magnification 1500×); typically 20 to 30 microscope fields were counted.

The dark CO_2-fixation (DCF) or heterotrophic bacterial activity was measured followng the method of Romanenko and Kuznetsov (1974) in 100-ml samples (two replicates for each site). Samples of the euphotic zone were prefiltered through 0.8–1.0-m Synpore filters to avoid measuring the dark CO_2-fixation by algal cells. $NaH^{14}CO_3$ solution (0.5–1.0 ml; specific activity 5–10 µCi ml^{-1}) was added to each sample, and they were incubated for 16–24 h in the dark in a reservoir containing lake water close to the *in situ* temperature. After incubation, 50–100 ml of the samples were filtered through 0.23-µm Synpore cellulose filters, which were treated with 1% HCL for 5 min to remove carbonate precipitates, and then radioactivity of the filters was determined with a β-2 liquid scintillation counter. The above treatment and measurements were applied also to two blank samples prepared by adding formaldehyde (2% final concentration) to a standard sample.

4. Results

Weighted averages of numbers of bacteria and dark carbon fixation were calculated, where appropriate, for the water column and for epi- and hypolimnion at each sampling site. Table 1 summarizes the seasonal BN and DCF values calculated for the nearshore and offshore zones for each year.

There are prominent seasonal patterns in the values of microbiological parameters; the highest values of BN and DCF were usually encountered in the summer. In spring, the highest values of both BN- and DCF-were always obtained in the nearshore zone. This is mainly due to the spring thermal front, which separates the stratified (warmer) near-shore water mass from the isothermally mixing cold pelagial waters and is accompanied with significant temperature gradients in the euphotic zone (Terzhevik and Kryuchkov 1982, Naumenko *et al*. 1996). The difference of BN and DCF between the near-shore and off-shore zones was most pronounced during high-discharge years (e.g. 1989, 1990 and 1993) from late May to early June, when the flood-waters of tributaries have accumulated inshore the thermal front border. These gradients usually dissipate by the end of June, when the thermal front has traversed

Table 1. Weighted averages of total numbers of bacteria (BN × 10^6 cells ml^{-1}) and dark CO_2-fixation (DCF, µg C l^{-1} d^{-1}) in the nearshore (NS) and offshore (OS) zones of Lake Ladoga during the spring, summer and autumn seasons in the years 1989–1993. – = no data.

Year	Spring				Summer				Autumn			
	NS		OS		NS		OS		NS		OS	
	BN	DCF	BN	DCF	BN	DCF	BN	DCF	BN	DCF	BN	DCF
1989	1.83	0.15	0.45	0.13	1.4	1.2	1.07	4.9	0.88	0.88	0.46	2.07
1990	1.60	0.17	0.57	0.02	1.3	–	0.96	–	–	–	–	–
1991	1.22	0.30	0.75	0.14	2.08	5.17	1.4	1.77	1.28	2.63	0.75	1.2
1992	–	–	–	–	3.4	1.82	1.7	0.61	–	–	–	–
1993	1.20	–	0.41	–	2.0	0.36	0.9	0.27	0.87	0.21	0.56	0.15

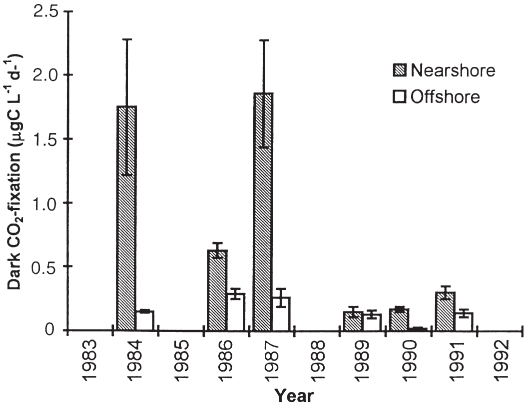

Fig. 1. Spring weighted averages of dark CO_2-fixation (DCF) in the nearshore and offshore regions of Lake Ladoga in 1984–1991.

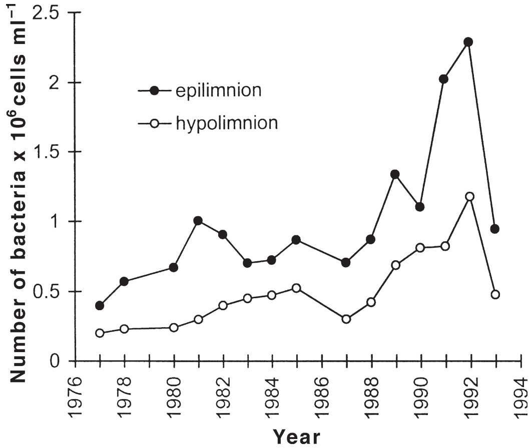

Fig. 2. Annual average summer values of numbers of bacteria (BN) in epilimnion and hypolimnion of Lake Ladoga in the period of 1977–1993.

towards the open lake. In spring 1989, the DCF was clearly lower than in the preceding years, especially in the near-shore zone (Fig. 1).

The summers 1989–1992 were characterized by a marked increase in numbers of bacteria as compared with all the previous years of observations (Fig. 2). The highest values of BN encountered so far (4.9–5.3 × 10^6 cells ml^{-1}) were measured in July 1992 in the Petrokrepost Bay; this maximum was followed by a relatively pronounced decrease in 1993. The same temporal variation: a sharp increase in 1989–1992 with subsequent decline in 1993 was evident also in the summer DCF-values (Fig. 3). It is worth noticing that the hypolimnetic offshore zone (depths of 60–70 m) values of BN were only slightly reduced, reflecting relatively high temperature of the water during 1989–1992.

In autumn (end of September–October), the distribution patterns of bacteria were more homogeneous than during the summer season, which is a reflection of the hydrological mixing processes. It is to be noted that the spatial patterns of BN observed in 1989, 1991 and 1993 represent the isothermal mixing period; the late autumn is usually characterized by the development of a thermal front with inverse stratification in the nearshore. At the time of sampling in these years, no region in the lake had cooled down to +4 °C, which is a prerequisite for the autumn thermal front initiation. Features of the summer distribution were thus preserved and the values of bacterial densities in the nearshore zone still exceeded those in the offshore zone by up to 2 times. In both nearshore and offshore zones the autumn BN and DCF-values were reduced to roughly half of those observed in the summer (Table 1). In the epilimnion the difference between summer and autumn values of the parameters is typically more pronounced than in the hypolimnion.

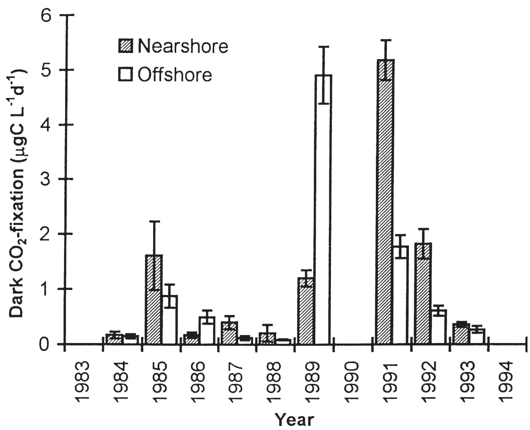

Fig. 3. Summer weighted averages of dark CO_2-fixation (DCF) in the nearshore and offshore regions of Lake Ladoga in 1984–1993.

Discussion and conclusions

All three seasons are characterized by greater values of the observed parameters in the nearshore zone. In spring, however, relatively high values of BN were caused mainly by allochtonous microorganisms with low DCF activity, discharged by flood waters to the littoral region. Microbiological processes are thus strongly dependent on the temporal hydrological situation during sampling.

Most representative data on the trends of bacterioplankton development were obtained for the summer seasons, when water temperatures are at their maximum, a steady vertical stratification prevails, and the bacterial densities reach their annual peaks. During our previous investigations in the period 1980–1985 a rather uniform distribution of BN and DCF values over the whole lake were detected, often with the highest values in the deep-water regions (Kapustina 1996). In contrast to the preceding years, in the most recent period of observations higher values of BN and DCF were observed in the littoral and the profundal slope regions; similar spatial patterns were also detected during the period of 1977–1978 (the beginning of microbiological monitoring). In 1989–1992 the values of BN and DCF increased and then again declined in 1993 (Fig. 2, Table 2), the latter reduction can be explained by a relatively cold summer. Nevertheless, the summer BN and DCF averages for the whole period of 1989–1993 were clearly higher than in 1985–1988. The weather conditions of 1993 also caused changes in primary production (Letanskaya 1997) and biomass of phyto- and zooplankton (Andronikova and Avinski 1994, Letanskaya and Protopopova 1994). The variations of BN and DCF were accompanied by a notable decrease of total organic carbon (TOC) in 1989–1992 (from 9 down to 6.3–7.7 mg l^{-1}) followed by an increase up to the former level (8.8 mg l^{-1}) in 1993 (Table 2, Kortichko *et al.* 1995). At the same time, the bulk input and output of TOC into and from the lake were nearly constant. A strong negative correlation is obtained between BN and TOC ($r = -0.81$, $n = 7$) over the years of the investigation. The same tendencies were already observed in 1981–1983. The TOC concentration in Lake Ladoga was rather constant before 1981. Seasonal (open water period) TOC averages in the 1976–1979 varied from 8.2 to 8.5 mg l^{-1}. In 1981 an essential decrease of the spring and summer TOC averages (down to 5.8 mg l^{-1} in spring) was observed. In 1983, the TOC concentrations raised sharply up to 9.3 mg l^{-1} and showed small variations (9.0–9.57 mg l^{-1}) in the period 1984–1987. Rather high DCF values were obtained for 1981–1982, but in 1983 they decreased strongly (Tregubova *et al.* 1987) (Table 2). BN averages for the whole water column showed no pronounced changes in the 1981–1983, even though a small raise in 1981 and decrease in 1983 of BN were observed in the epilimnion (Fig. 2).

Table 2. Summer averages of bacterial densities (BN $\times 10^6$ cells ml^{-1}), dark CO_2-fixation (DCF, µg C l^{-1} d^{-1}), primary production (PP, mg C m^{-2} d^{-1}), and total organic carbon (TOC, mg l^{-1}) in Lake Ladoga in the years 1981–1993. – = no data.

Year	BN	DCF	PP	TOC
1981	0.45	3.4	–	6.7
1982	0.40	1.5	–	7.3
1983	0.44	0.06	–	9.3
1989	0.81	4.18	1 031	7.7
1990	0.85	–	–	7.8
1991	1.10	2.4	–	6.3
1992	1.40	0.85	433	7.6
1993	0.56	0.29	356	8.8

Microbiological and chemical data, taken together, suggest that bacterioplankton consumes not only the organic carbon produced by phytoplankton but also high-molecular matter (humic matter), which constitutes more than 80 % of total dissolved organic C in Lake Ladoga (Kortichko *et al.* 1995). The utilization by bacterioplankton of organic carbon of nonphytoplanktonic origin is increasingly recognized as essential for the observed trophic flux rates in fresh-water ecosystems (Tranvik 1992; Coveney and Wetzel 1995). In Lake Ladoga in contrast to most other large lakes, the organic carbon input with tributaries (about 1.04×10^{12} g C yr^{-1}) is of the same order of magnitude as primary production (about 0.80×10^{12} g C yr^{-1}) (Tregubova *et al.* 1987). Thus, the allochthonous organic C appears to be an important source of carbon for bacterioplankton of Lake Ladoga.

Results of the present work, combined with earlier observations and other limnological data on ake Ladoga, can be summarized as follows:

1. In general, the period 1989–1993, with the exception of spring observations, was characterized by rather high total numbers of bacteria and values of dark CO_2 fixation all over

the lake. Generally, the values in the nearshore zone exceed those in the deep-water region. Eutrophication of Lake Ladoga has led to continuous increase in bacterial density and activity, even though other factors (e.g. climatic) cause short-termed fluctuations.

2. A sharp increase of the microbiological parameters from the 1985–1988 values to those in 1989, together with the simultaneous reduction of total organic carbon imply instability of the lake. A similar change was observed was in 1981–1983, even though the measured respective values of BN and DCF were lower.
3. Evolution of the trophic state of Lake Ladoga, as evidenced by the microbiological parameters appears as a sequence of more or less stable periods alternating by transitional conditions, leading stepwise to a new (higher) level of eutrophication. However, scarcity of data prevents from definite conclusions on the duration or regularity of these cycles.

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