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Floral shift in the phytoplankton of Lake Baikal, Siberia: Recent dominance of *Nitzschia acicularis*

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Abstract: Earlier this century, the cosmopolitan diatom *Nitzschia acicularis* was reported to inhabit river deltas (especially the Selenga River delta), lake shallows, and to only occasionally be found in the pelagic plankton of Lake Baikal. This paper attempts to estimate the progress of *N. acicularis* beginning from the early 1960s: its increased abundance and subsequent expansion into the pelagic zone of the lake. Between 1963 and 1995, large annual fluctuations in the number of its cells were recorded in the euphotic zone (0–50 m) of southern Lake Baikal, with maximum values of 2.0×10^6 cells l^{-1}. The spatial distribution of *N. acicularis* was assessed in 1987, 1991 and 1995 in the 0–50 m layer over the entire lake; highest cell concentrations were found off the Selenga delta (1987, 1991), off the Upper Angara estuary (1991), and in the Kultuk Bay (1991, 1995). It is suggested that *N. acicularis* has become a major component of the Lake Baikal plankton, probably as a result of anthropogenic influence.

Key words: floral shift, phytoplankton, *Nitzschia acicularis*, Lake Baikal

Introduction

Over the last few decades there have been numerous reports of changes in the structure of the phytoplankton community of Lake Baikal (Fig. 1). One of these changes is a decreased abundance of the diatom *Aulacoseira baicalensis* (Meyer) Simonsen, a typical representative of pelagic phytoplankton, and a considerable increase of another diatom *Nitzschia acicularis* W. Smith (Popovskaya 1979; Zagorenko & Kaplina 1981). Previously, the latter species was not listed among taxa prevailing in the pelagic zone. This is what Meyer (1930) wrote in his summary concerning the distribution of this alga in Lake Baikal: "A large number of *N. acicularis* was often found in the silt of sors, bays and rivers. This alga was also found in the Selenga River, near Sakhalin (an island in the Selenga shallows), in Proval Bay, Istokskiy Sor (July 1925), near Kultuk (July 1915)".

In July–September 1952–1953, Kozhova (1959) found low concentrations of the alga (a few hundred cells l^{-1}) in the pelagic water of Lake Baikal. During this period she also observed an intense development of *N. acicularis* (3×10^5 cells l^{-1}) in the Mukhor Bay and the Strait of Olkhonskie Vorota in the Maloe More, in the Selenga River delta and the shallows nearby (2×10^5–4×10^5 cells l^{-1}). In the summer–autumn of 1957, Kozhova (1960) recorded concentrations of 5000 cells l^{-1} of *N. acicularis* (along with *Synedra acus*) in the Listvenichnoye Bay, close to the place where the Angara River flows out of the lake. She reported that at the same period *N. acicularis* was also abundant in the shallows off the Selenga River. Yasnitsky & Skabichevsky (1957) believed that *N. acicularis* was just an incidental member of the pelagic plankton and would not develop any noticeable numbers in the pelagic waters of Lake Baikal. They contended that those isolated specimens of *N. acicularis* cells that were found in the pelagic waters had most likely been brought there from the littoral zone by currents. According to Antipova (1974), since 1963 *N. acicularis* had become dominant in the Bolshie Koty region from May to August. Popovskaya (1971) studied the phytoplankton composition of the shallows near the Selenga River delta and recorded high abundances of the alga (reaching 9×10^5 cells l^{-1} in 1958) between 1958 and 1965. In 1969, *N. acicularis* was found for the first time in great numbers in the pelagic zone of southern Lake Baikal (Popovskaya 1987). From that time on *N. acicularis* has become one of the dominant and constant inhabitants of the pelagic water of Lake Baikal (Popovskaya 1987).

Earlier reports by Popovskaya (1971) and Antipova (1974) claimed that the maximum of this species occurred in summer. But in the 1970s and 1980s, a very intense de-

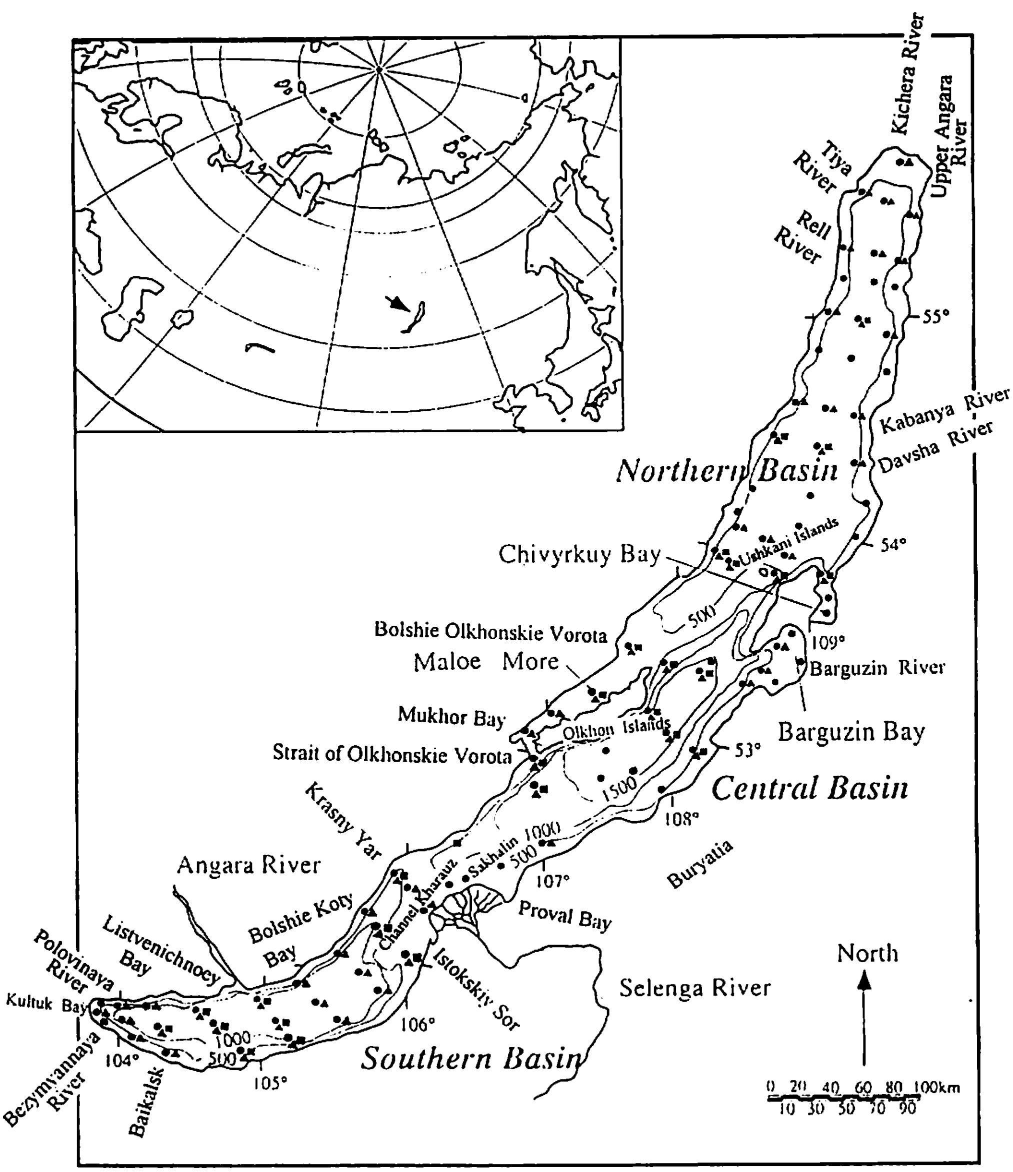

Fig. 1. Map of Lake Baikal showing station locations for 1987 (●), 1991 (▲) and 1995 (■).

velopment of *N. acicularis* was noticed under ice in spring and after ice break-up in early summer (June), when its concentrations reached 4.0×10^6 to 7.0×10^6 cells l^{-1} (Popovskaya 1991). The same author noticed another interesting feature of the *N. acicularis* population dynamics, i.e., a large interannual fluctuation in cell concentrations; *N. acicularis* was usually most abundant in the years when *Synedra* and *Aulacoseira* were at their lowest.

Popovskaya (1991) concluded that *N. acicularis* now constituted an inseparable part of the spring-summer phytocoenosis of Lake Baikal, with the highest abundance in spring. But analysing the state of phytoplankton off Baikalsk (a city with a large cellulose factory) in southern Lake Baikal, Kozhova & Pavlov (1995) found that in early 1990s the summer abundance of *N. acicularis* suffered a dramatic decline (from 7.0×10^6 to 500 cells l^{-1}), and this despite summer being a time of an annual peak of this alga. They could not find any considerable numbers of *N. acicularis* either in the pelagic or littoral zones in the subsequent years.

Mikhaylov & Popovskaya (1986) compared the fine structures of *N. acicularis* frustules between the Selenga River and Lake Baikal and found only small differences, linked to the ecological conditions of the regions in question. They concluded that a large increase of *N. acicularis* in the Selenga River over the previous ten years had been one of the main causes of the increased abundance of the alga in the Lake Baikal pelagic zone and it could signal a start of ecological changes in the lake. This stipulated culture studies of *N. acicularis* to be made (Bondarenko & Guselnikova 1988, 1994). Cultivated *N. acicularis* was found to have a higher growth rate than the diatoms en-

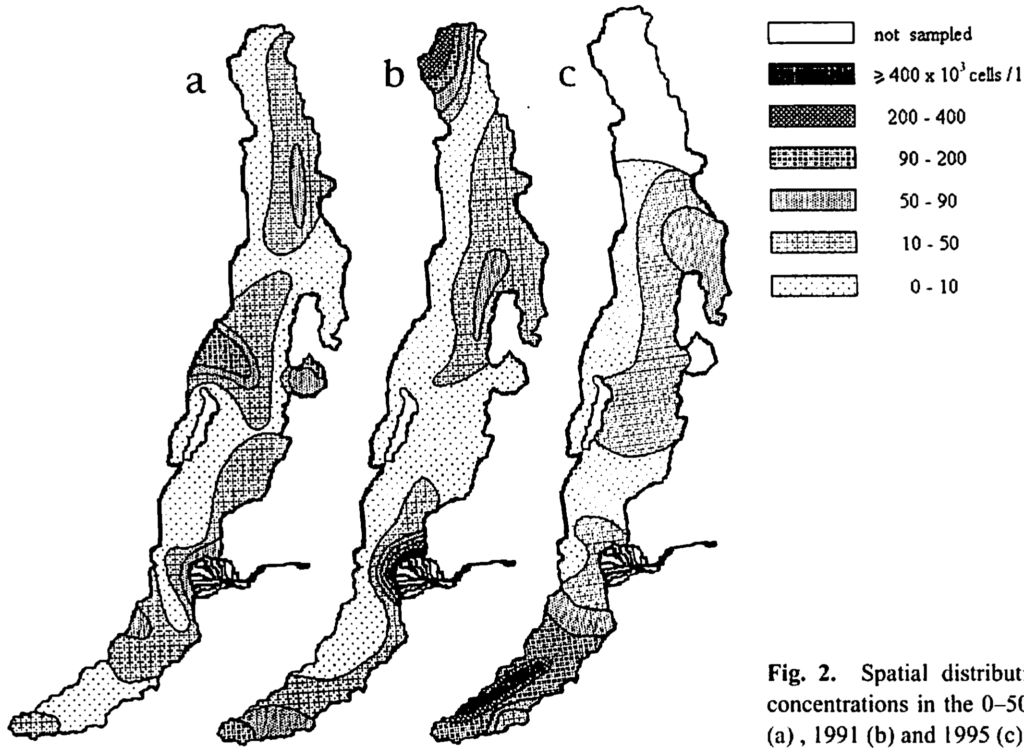

Fig. 2. Spatial distribution of *Nitzschia acicularis* cell concentrations in the 0–50 m layer of Lake Baikal in 1987 (a), 1991 (b) and 1995 (c).

demic to Lake Baikal, such as *A. baicalensis* and *Cyclotella baicalensis* Skvortzow et Meyer. The maximum division rate was 2.1 d^{-1} under optimal conditions (temperature, 12–14°C; light, 59 mmol $m^{-2} s^{-1}$). Studies of the mineral nourishment of *N. acicularis* have revealed that this alga responded most strongly to phosphorus (P): a concentration of 0.05 mg l^{-1} in the medium led to a 40% increase in the photosynthetic rate. This shows that the Lake Baikal population of this species is highly limited by P.

The purpose of this study is to assess the role of *N. acicularis* in the phytoplankton community of Lake Baikal by comparing the original results of recent investigations of annual and spatial variations in this diatom with the results of the previous studies.

Materials and Methods

The spatial distribution of *Nitzschia acicularis* was investigated in 1987, 1991, and 1995 at 90, 63 and 27 stations (Fig. 1), respectively; the years were chosen so as to represent different levels of development of *N. acicularis* in Lake Baikal. The abundances of *N. acicularis* were estimated from samples of phytoplankton collected with a Nansen bottle-type water sampler. One-liter samples were taken from 0, 5, 10, 25 and 50 m depths. Samples were fixed with acidified Lugol's iodine solution (1-ml solution per 1-liter sample) and 4% formalin. The routine procedures for concentrating and treating samples were outlined by Kiselev (1956). The weighted mean values of algal cell number were calculated for the upper 0–50 m layer (Kozhova & Melnik 1978).

Data for the interannual population densities in Southern Lake Baikal in May–July (peak for *N. acicularis* development) were compiled from Antipova (1974) for Bolshie Koty Bay, Popovskaya (1971, 1987, 1991) for the regions close to Bolshie Koty Bay, and from my own results for Bolshie Koty and Listvenichnoye Bay since 1975 (Bondarenko 1997).

Results

Figure 2 shows that the spatial distribution of *Nitzschia acicularis* in Lake Baikal differs over the three years concerned, but some similarities can still be found.

In the summer of 1987 (21 July–8 August) high algal concentrations were found in some regions of the central basin such as the Barguzin Bay (1.62×10^5 cells l^{-1}), and the Bolshie Olkhonskie Vorota area (1.2×10^5 cells l^{-1}). In the northern basin, they ranged from 4.3×10^4 to 5.0×10^4 cells l^{-1} in the areas affected by affluent river waters (Upper Angara) (Fig. 2a). *N. acicularis* was also abundant in the southern basin but did not exceed 9.0×10^4 cells l^{-1}.

High concentrations were locally observed on 1–4 June 1991 in the shallows off the Selenga River delta (4.54×10^5 cells l^{-1}) and in the northern part of the lake (regions near the larger rivers: Rell, Tiya, Upper Angara and Kichera) (0.85×10^5 to 2.09×10^5 cells l^{-1}). Other notable areas were in the Davsha River delta (1.9×10^4 cells l^{-1} and the Ushkani Islands region (4.7×10^4 to 8.0×10^4 cells l^{-1}).

In the southern basin, 5.4×10^4 to 5.8×10^4 cells l^{-1} were registered near the Polovinaya River mouth, and 1.66×10^5 cells l^{-1} in Kultuk Bay, off the Bezymyannaya River

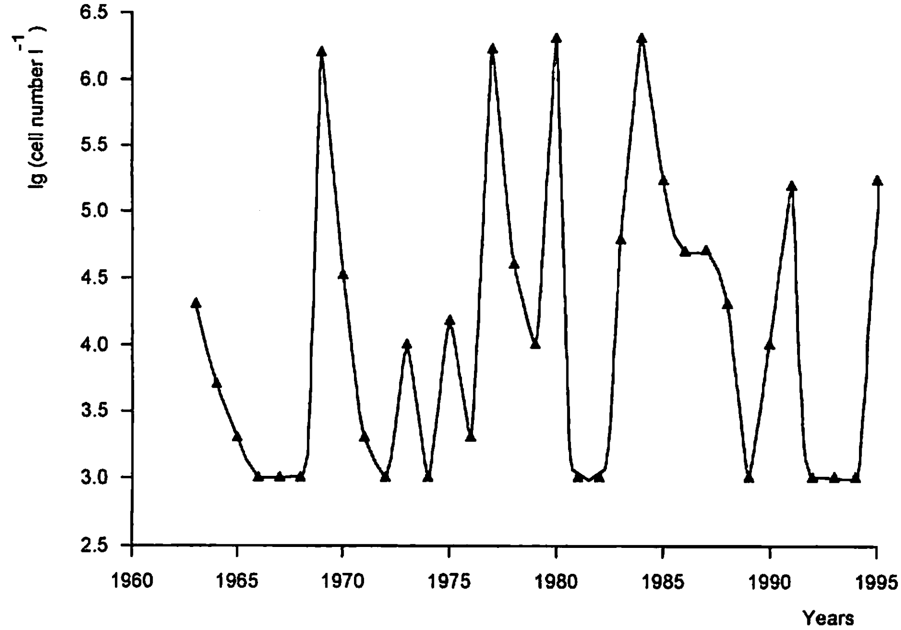

Fig. 3. Interannual fluctuations in the maximum cell concentrations of *Nitzschia acicularis* in the 0–50 m layer of Southern Lake Baikal between 1963 and 1995.

(9.0×10^4 to 1.44×10^5 cells l^{-1} near the west bank of this river) (Fig. 2 b).

Highest abundance of *N. acicularis* within the period of investigations (1987, 1991, 1995) has been registered in 1995. The alga numbered over 1.0×10^6 cells l^{-1} at the mouth of the Polovinaya River, and 1.0×10^5 to 2.0×10^5 cells l^{-1} in the Kultuk Bay area on 24–31 May 1995 in the southern basin of the lake (Fig. 2 c).

These results show that the most intensive development of *N. acicularis* has been detected primarily in the river delta areas. In some years (e.g. 1995) local *N. acicularis* blooms were so intense that they spread out to significant areas of the pelagic zone of the lake.

Maximum cell concentrations of *N. acicularis* in May–July of each year between 1963 and 1995 exhibited large interannual fluctuations (Fig. 3), similar to other major species of phytoplankton in Lake Baikal (Popovskaya 1987; Bondarenko 1997). Highest concentrations of *N. acicularis* in the lake were observed in 1969, 1977, 1980, 1984 and cell concentrations reached the high level of 1.6×10^6–2.0×10^6 cells l^{-1}.

Discussion

Nitzschia acicularis is a widely distributed species and is found simultaneously in its planktonic and attached forms. *N. acicularis* is a typical inhabitant of rivers, ponds, and sometimes found in streams and bogs, but is only very rarely found in lakes (Skabichevsky 1960; Talling 1987). Hustedt (1930) considered this species to be planktonic but Skabichevsky (1960) regarded its role in the plankton biocoenosis as important only for rivers. Algae of the genus *Nitzschia* in African freshwater lakes grow well even at low phosphate supply and had moderate requirements for silicate (Kilham et al. 1986). In some lakes they even dominated over other diatoms, e.g. *Synedra*, because of a relatively low Si level in the water and their lower Si requirement for growth. In an isolated bay of Lake Kivu, Africa, the growth rate of *Synedra* species was limited by Si, while that of *Nitzschia* was limited by P. Apparently, in such circumstances these species may even coexist. Experiments of Sommer (1983, 1985) showed that *Nitzschia* multiplied very rapidly under conditions of pulsed nutrient additions at moderate to high Si : P ratios.

In Lake Baikal, an interesting phenomenon exists concerning high interannual fluctuations of phytoplankton cell concentrations under ice in March–May: periodically occurring highly-productive, so-called "*Melosira* years", named so after the genus that formerly included the dominant *Aulacoseira* species (Antipova 1963, 1974). This intensive bloom usually continues after ice break in June. Besides the dominating *A. baicalensis* (formerly *Melosira baicalensis*), several other large diatom species, like *A. skvortzowii* Edlund, Stoermer et Taylor; *Stephanodiscus binderanus* var. *baicalensis* Popovskaya et Genkal and *Synedra acus* var. *radians* Kützing prosper in the spring of typical *Melosira* years. For Southern Lake Baikal, a typical interval between *Melosira* years is 2 to 4 years but sometimes they succeed each other immediately (Antipova 1974). In 1970s the regularity of the dominance of *A. baicalensis* was disturbed and intense vegetation of this species occurred only every 6 to 8 years. The highly productive years of this period were: 1968 (dominant species: *A. skvortzowii*, *A. baicalensis*) (Antipova 1974), 1974 (*A. baicalensis*) (Popovskaya 1987), 1976 (*A. skvortzowii*), 1979 (*A. skvortzowii*), 1982 (*A. baicalensis*), 1983 (*S. acus*), 1990 (*A. baicalensis*), 1994 (*A. baicalensis*) (Bondarenko 1997). Comparing the years of high *Nitzschia* abundance to years favourable for other diatoms (Table 1), it is clear that, except 1975, the "*Nitzschia* year" immedi-

Table 1. Years of high cell concentrations of *Nitzschia acicularis* and other diatoms (*Melosira* years) in the Southern basin of Lake Baikal.

Dominant diatoms	Years													
N. acicularis		1969			1977		1980			1984		1991		1995
Other diatoms	1968		1974	1976		1979		1982	1983		1990		1994	

ately followed the productive year. In the years when *N. acicularis* was abundant it acted as the main producer of organic matter in the under-ice and late-spring periods. Earlier, Antipova (1974) reported that in the period from the 1950s to the 1970s it was *S. acus* that grew abundantly in the under-ice and spring periods of the year immediately after the *Melosira* year. But in 1969, 1977, 1980, 1991, and 1995 its place was taken by *N. acicularis.*

The causes of the increased abundance of the *Nitzschia* population in the pelagic zone of Lake Baikal during the 1960s and 1970s are not yet completely understood, but they are most likely to be linked to the economical developments that took place in the areas around the lake over the past few decades. In the late 1950s the Irkutsk hydroelectric power station on the Angara River was built causing a 1.2-m rise in the lake water level. Agricultural land usage almost doubled during the 1950s and 1960s on the territory of Buryatia, in the basins of the Selenga River and the Barguzin River, entailing an increased use of organic and mineral fertilisers containing such elements as P, K and N (Anonymous 1973). Increased industrial activities also led to an increased supply of nutrients into the river waters. In 1971, a big flood took place due to heavy rains and consequent snow-melting in the Khamar-Daban Ridge, where the sources of many of the Lake Baikal affluents are located, and the run-off of all the rivers rose many times. Popovskaya (1991) reported that the number of algal cells entering the lake from the Selenga River (which carries 60% of the water entering the lake) in the 1970s was 3–3.5 times greater than in late 1950s.

The above-mentioned activities in the Lake Baikal area may be one of the possible causes for the observed increase in the abundance of *N. acicularis* in the pelagic zone of Lake Baikal, acting as the pulsed nutrient additions like those in the experiments of Sommer (1983, 1985). The spacial distribution of *N. acicularis* in Lake Baikal, observed in 1987, 1991 and 1995, is consistent with this hypothesis. In general, the shallow waters near the Selenga River and rivers of the north and south basins of Baikal were the richest in algal concentrations, especially at the stations located close to the deltas, i.e., the maximum concentrations of *N. acicularis* in Baikal have always been found in the places with the permanent additions of nutrients of allochtonic origin.

But despite its progress, the dominance of *N. acicularis* in the pelagic plankton has not yet been stabilised. This has been confirmed by the shift of its maximum abundance from summer to under-ice period (Popovskaya 1991): although *N. acicularis* is a very competitive species, it is probably less successful in competing for nutrients than native species of the lake prevailing in summer, such as blue-green and green picoplankton algae (Popovskaya 1987; Bondarenko 1997), hence it had to try to occupy a free niche of the under-ice plankton when the regularity of *Melosira* years was disturbed. The restored regularity of *Melosira* years in the 1990s, as well as decrease of the maximum concentrations of *N. acicularis* in the 1990s as compared to the 1970–1980s (Fig. 3), suggests that it will probably be difficult for *N. acicularis* to retain its dominant position in the pelagic zone of Lake Baikal.

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