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Influence of water motion on the spatial distribution of *Spirogyra* in Lake Baikal

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ABSTRACT

We investigated the diversity of benthic algal communities as well as phytoplankton in Lake Baikal. The structure of benthic algal communities changed in comparison to the period before 2000 due to intense development of filamentous algae, particularly *Spirogyra*. Percent cover of filamentous algae in different areas of the coastal zone varied from 0 to 100%. The lowest *Spirogyra* biomass was recorded in the surf and wave-breaking zones, whereas the highest biomass was observed in the area of the bottom less affected by waves. Fragments of *Spirogyra* thallomes were also recorded in the phytoplankton community of Lake Baikal's southern basin which is a new phenomena not previously recorded in the lake. Hydraulic characteristics of *Spirogyra* were similar to those of planktonic diatoms. Currents and wave effects on the bottom favored transfer and distribution of *Spirogyra* from locations with intense development to the coastal area of Lake Baikal. *Spirogyra* is now found throughout Lake Baikal.
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Introduction

Along with the effects of global warming and direct anthropogenic impact, algal blooms have been recorded in the coastal areas of seas and lakes (Nozaki et al., 2003; Hiraoka et al., 2011; Smith et al., 2006), which causes deterioration of both water quality and the environment in recreational areas. A similar phenomenon has been shown to exist in the ecosystem of Lake Baikal, a UNESCO World Heritage site. In the coastal zone close to settlements, we have observed overgrowth of the bottom with filamentous algae for the past decade, among which there are members of the genus *Spirogyra* atypical of algal communities in Lake Baikal (Kravtsova et al., 2014; Timoshkin et al., 2016, 2018). *Spirogyra* was found in the composition of the benthic phytocenoses of not only Listvennichny Bay (an area of the open Baikal coast located in a human activity zone with >2000 permanent residents and 300,000 tourists per year), but also on Olkhon Island (1350 permanent residents and >500,000 tourists in summer). Moreover, the biomass of *Spirogyra* in benthic phytocenoses reached 100–135 g m^{-2} opposite the densely populated villages of the island (Khuzhir and Kharin-Irgi), whereas, on the other side of the island with no permanent residents and tourists, *Spirogyra* was not observed or was insignificant (a few separate filaments) (Timoshkin et al., 2018). Large clumps of filamentous algae were found on the Baikal beaches in Senogda Bay, but in other areas, e.g. Amnundakan Cape and Davsha Valley, *Spirogyra* was only observed sporadically (Timoshkin et al., 2016). Previously, single *Spirogyra* filaments were recorded only in warmer bays and shallow shoals of Lake Baikal and its tributaries (Izhboldina, 2007; Kozhova and Izhboldina, 1994). In addition to the increase in the benthic phytocenoses, *Spirogyra* has become reported in phytoplankton communities; which was not been found in earlier investigations (Kozhov, 1972; Popovskaya, 1977). For example, in June 2012, there were from 17.5 to 25.5 thousand cells L^{-1} of *Spirogyra* in the phytoplankton of Barguzin Bay near Maksimikha Village (Kobanova et al., 2016). In the southern basin of Lake Baikal, opposite Kultuk Settlement and the towns of Baikalsk and Slyudyanka, *Spirogyra* was found in the spring phytoplankton (Bondarenko and Logacheva, 2016). At present, it is unclear whether the appearance of *Spirogyra* in the phytoplankton of open Baikal waters is accidental or permanent. We hypothesize that the presence of *Spirogyra* filaments in the coastal zone of the lake is due to the circulation currents of Lake Baikal, which transport these algae from locations of mass development to all areas of the lake.

The hydrodynamic regime, together with other environmental factors, affect the biota of sea and freshwater lakes (Liu et al., 2015; Peters et al., 2006; Wang et al., 2012; Wolcott, 2007).

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Specifically, characteristics of water motion, including the velocity of currents, wave action, dynamic pressure, and turbulence, directly affect mobility and transfer of aquatic organisms (Cross et al., 2014; Durham et al., 2013; Luhar et al., 2010). Wind-induced waves and ripples affecting higher aquatic plants and benthic communities may also limit their growth (Raspopov et al., 1990). For example, the diversity and spatial distribution of hydrobionts are indirectly affected by water motion through changes in sedimentation dynamics, transport of particulates and detritus in the coastal area of waterbodies (Airoldi, 1998; Snelgrove et al., 1998). The characteristics of water movement in Lake Baikal have been studied using long-term in-situ measurements, instrumental investigation, and mathematical models. General patterns of formation of currents, wave activity, surging, turbulence and upwelling are known (Afanasyev and Verbolov, 1977; Aibund, 1973; Fialkov, 1983; Pomytkin, 1960; Shimaraev et al., 2012; Zhdanov et al., 2009). But there is less information on the direct effect of hydrodynamics on the biota of Lake Baikal, including the effect of wave activity on distribution of benthic organisms in the coastal area of the lake (Karabanov and Kulishenko, 1990) and the effect of water movement on plankton (Jewson et al., 2010; Likhoshway et al., 1996). Here, we investigate the spatial distribution of filamentous algae and its biomass to better understand the effect of water motion on the transfer of *Spirogyra* in the coastal zone of Lake Baikal.

Material and methods

Environmental setting

Lake Baikal (N 53°14′ E 108°05′) is a unique lake with three basins (southern, central and northern) and as well as differences in the composition of debris in the bottom sediments in the coastal zone. In the western coastal zone, coarse deposits (boulders, pebble, gravel, outcrops of bedrocks, sand), unrounded rock fragments and outcrops of bedrock prevail. Along the eastern coastal zone, bottom sediments are fine (sand, silt), and coarse material (boulders, pebble) is well-rounded. Benthic algae (137 species and variations of lower plants — meiophytes are 0.5–2 mm and macrophytes over 2 mm) inhabit bottom sediments of the coastal zone of Lake Baikal. Vertical zonation is observed in the spatial distribution of benthic algae. They form vegetation belts around Lake Baikal, with species replacements as depth increases (Meier, 1930; Izhboldina, 2007). *Ulothrix zonata* Kütz. forms the first vegetation belt at a depth of 0–1.5 m. The second belt is formed by dominant species of *Tetraspora cylindrica* (Wahl.) Ag. var. *bullosa* C. Meyer and *Didymosphenia geminata* (Lingb.) M. Schmidt at a depth of 1.5–2.5 m along the entire shore. The third vegetation belt occupies depths from 2.5–3.5 m to 10–12 m with dominant endemic species of the genus *Draparnaldioides*. Benthic algae can detach from the substrate under the influence of orbital and reciprocating water motions caused by wave activity (Karabanov and Kulishenko, 1990). A large number of floating fragments of algae and higher plants, as well as their mass clumps on the shore of Lake Baikal after storms, have been recorded since the previous century (Kozhov, 1972; Timoshkin et al., 2016; Votintsev, 1961).

Wave processes in the open areas of the coastal zone

In Lake Baikal, wind and wind-induced wave activity play a significant role in water motion. The navigation period in summer is characterized by low wind speeds and little wave activity (waves height up to 0.5 m). Occasional higher wind speeds can give wave heights of 1–1.1 m (Galazy, 1993). According to the wind regime and wave activity, as well as specific characteristics of the bottom, Fialkov (1983) distinguishes 35 regions based on geomorphology (Fig. 1A) in Lake Baikal. During wave activity, the water moves around circular orbits. The sizes of these circulations decrease towards the shore (with a decrease in depth), and their orbits acquire the shape of flat ellipses. Moreover, near-bottom velocities of water flow increase. The interaction between the water motion and the bottom distinguishes three zones: I – offshore zone of undeformed waves; II – transformation of waves (deformation zone and breaker zone); and III – surf zone (Fig. 2A). Sediment movement takes place in the wave-breaking and the surf zones.

Currents

In Lake Baikal currents are primarily influenced by the dynamic atmosphere — wind regime and pressure gradient — above the lake surface (Afanasyev and Verbolov, 1977; Aibund, 1973). The system of currents at Lake Baikal comprises cyclonic alongshore circulation covering the entire lake, and secondary circulations in the southern, central and northern basins of Lake Baikal (Fig. 1B).

Nutrients of Baikal water

Since the previous century, a low content of nutrients has characterized the open waters of Lake Baikal in summer due to the growth of benthic algae, higher aquatic plants and, most importantly, the sinking of the spring diatom bloom out of the photic zone (0–50 m). Moreover, low concentrations of nutrients are due to the huge volume of water (23,000 km^3), intense water exchange, wave mixing, currents, etc. The reference values for N and P in open parts of the lake are 80 $\mu g\ L^{-1}$ and 7 $\mu g\ L^{-1}$, respectively. However, the nutrient content is substantially higher along the lakeshore where human activity is greatest (Khodzher et al., 2017; Timoshkin et al., 2018). Particularly, in July–August 2011, high concentrations of nutrients NO_3^--N up to 200 $\mu g\ L^{-1}$ and PO_4^{3-}-P up to 420 $\mu g\ L^{-1}$ were recorded in the near-shore waters of Listvennichny Bay, in the area opposite the settlement of Listvyanka (Kravtsova et al., 2014). This area is affected by the growing tourist industry and poorly treated wastewaters. Mass development of filamentous algae in Listvennichny Bay opposite the settlement creates secondary pollution of the coastal zone. Destruction of algal mats causes higher concentrations of nutrients in depressions along the coast. In 2015, the content of nutrients in the near-bottom water was high (in $\mu g\ L^{-1}$): $NH_4^+ = 560$; $NO_2^- = 55$; $NO_3^- = 690$; $P_{mineral} = 25$; $P_{organic} = 24$; $P_{total} = 49$ (Kulakova et al., 2017).

Field studies

We studied the algal flora in the coastal zone of Lake Baikal in August 2016, on board the research vessel *Titov*. Temperature and transparency of water were measured. In addition, water samples were collected for hydrochemical analyses from the near-bottom water layer up to 10-m isobath, and from the surface of lake. Water was sampled with 50-mL and 500-mL syringes.

Sampling to determine the spatial distribution of filamentous algae alongshore of Lake Baikal

Scuba divers collected 117 qualitative samples of benthic algae from depths of 0–12 m in southern, central and northern basins of Lake Baikal at 29 stations located at sites which differed in wind-wave characteristics and bottom geomorphology (Fig. 1A, Table 1). Qualitative samples were collected in each vegetation belt at the corresponding depths. Additionally, at 11 sites (Table 1), scuba divers mapped benthic algae at 15 transects (T) using frames (area of 1 m^2) divided into 100 equal quadrats to assess percent cover of the bottom with filamentous algae (Fig. 1A, B). There were five transects at site 3, two transects both at sites 1 and 30 and one transect at other sites. At the transects, a percent cover were

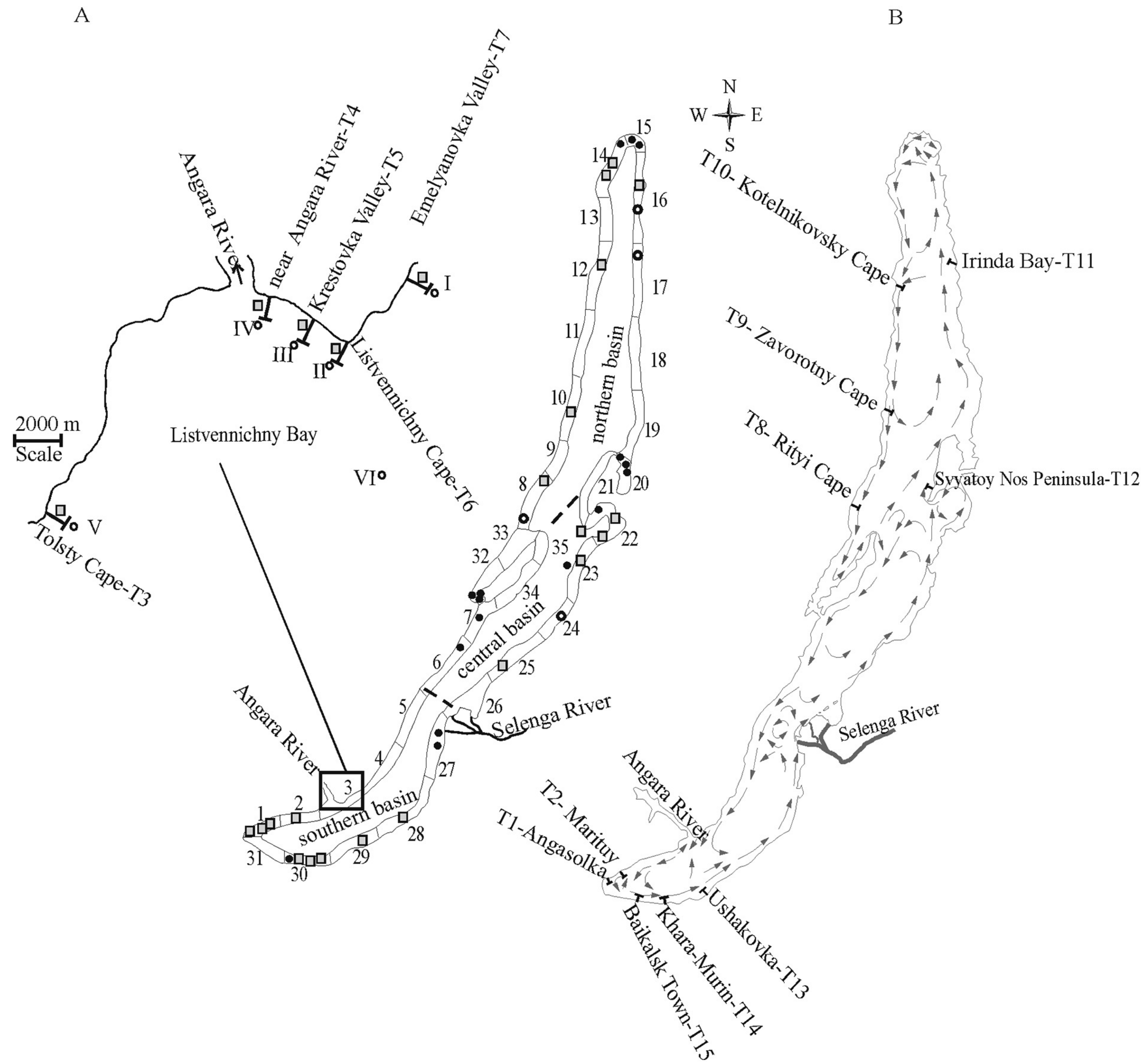

Fig. 1. Schematic map of algae sampling in different areas of Lake Baikal (A, B). A: Numbers 1–35 are shoreline reaches of different wind-wave characteristics and bottom geomorphology (according to Fialkov, 1983). Grey squares indicate stations studied in 2016, where *Spirogyra* was found in qualitative samples: 1 – Kultuk, Angasolka, Marituy, 2 – Polovinny Cape, 3 – Tolsty Cape, near the Angara River, Krestovka Valley, Listvennichny Cape, Emelyanovka Valley, 8 – Rytyi Cape, 10 – Zavorotny Cape, 12 – Kotelnikovsky Cape, 14 – Tiya River, Senogda Bay, 16 – Frolikha Bay, 21 – Peninsula Svyatoy Nos, 22 – Ust-Barguzin, Maksimikha Settlement, 23 – Tonky Cape, 25 – Sukhinsky Cape, 28 – Boyarsky Cape, 29 – Ushakovka River, 30 – Murinskaya Banka, Khara-Murin, Baikalsk Town; white circles indicate stations, where *Spirogyra* was not found: 8 – Arul Cape, 16 – Khakusy, 17 – Irinda Bay, 24 – Talanka Bay; black circles indicate stations studied before 2000, where singular *Spirogyra* filaments were found (archive data of L. Izhboldina): 6 – Anga Bay, 7 – Ulan-Nur Cape, 32 – Zagli, Kharin-Irgi, Khuzhir-Nugo, 14 – Toshka Brook, 15 – opposite the Angara-Kichera Shoal, Dagarskaya Bay, 20 – Sorozhya, Big Kaltygey Island, Chivyrkuy River, 22 – Makarovo Village, 23 – Listvennichny Island, 27 – Istokskiy Sor, Posolsky Sor, 30 – Baikalsk Town. Inset to A: I-VI – stations of phytoplankton sampling in Listvennichny Bay; the alongshore solid line indicates the conventional boundary of the coastal zone divided into sites 1–35, and the dashed line indicates the boundaries between the Baikal basins. B – percent cover of filamentous algae at transects (T): 1 – Angasolka (1%), 2 – Marituy (0–6%), 3 –Tolsty Cape (0–60%), 4 – near the Angara River (0–90%), 5 – Krestovka Valley (1–90%), 6 – Listvennichny Cape (1–70%), 7 – Emelyanovka Valley (0%), 8 – Rytyi Cape (0%), 9 – Zavorotny Cape (0–1%), 10 – Kotelnikovsky Cape (0–3%), 11 – Irinda Bay (0%), 12 – Peninsula Svyatoy Nos (1–3%), 13 – Ushakovka River (1–90%), 14 – Khara-Murin (1–15%), 15 – Baikalsk Town (1–100%); C-arrows show cyclonic, alongshore currents covering the entire lake and secondary circulations of water masses in the southern, central and northern basins of Lake Baikal (according to Afanasyev and Verbolov, 1977).

measured at intervals of 0.5–1 m. Three or four qualitative samples of benthic algae were collected from each transect.

Sampling to determine the structure of algal communities at the site with the uniform hydrodynamic environment and different recreational activity within its boundaries

To assess the proportion of *Spirogyra* biomass in the current algal communities, the scuba divers collected 18 quantitative samples of benthic algae from two transects perpendicular to the shoreline. One transect was located in the impact zone, in Listvennichny Bay opposite Krestovka Valley, an area of recreational activity (Fig. 1A). A second transect was located 5 km to the north of Listvennichny Cape in the reference area opposite Emelyanovka Valley (outside the impact zone of human activity). The scuba divers collected three samples in each vegetation belt at transects using a frame with an area of 0.16 m^2. They put stones covered with algae into sacks of strong fabric and lifted them on board the vessel. The stones were then put into a large cuvette with water. The algae were cut with a scalpel from the surface or brushed off. The water was poured into the sieve of a mill-gauze No. 23. The algae were put into flasks and fixed in 4% formalin.

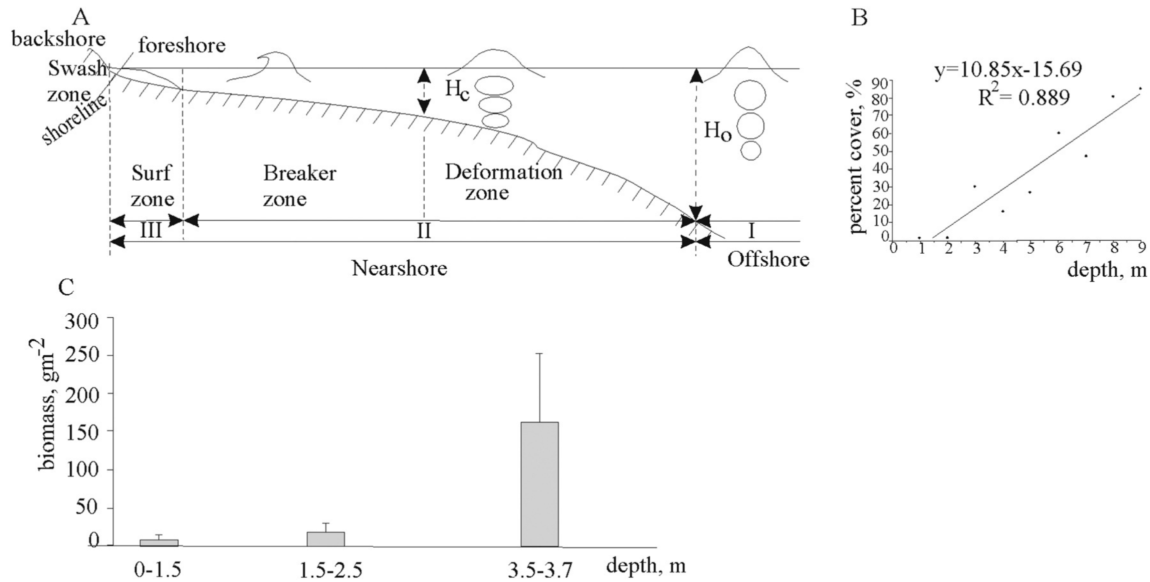

Fig. 2. Zones of wave effect on the bottom (A), the correlation between percent cover of filamentous algae and depth (B), and the biomass of *Spirogyra* in the coastal zone of Listvennichny Bay (August 2016) (C). H_c - a depth with a wave effect on the bottom, and H_0 – a depth without wave effect on the bottom.

We collected samples of phytoplankton to study the distribution of *Spirogyra* in the water of the southern basin of Lake Baikal (Fig. 1A). Phytoplankton samples (1.5 L of water) were collected by bathometer at six stations (I–VI), with a water sampler at depths of 0, 5 and 15 m. Stations I–V were located at a distance of approximately 50–100 m off the shore in the southern basin of Lake Baikal. Station VI was 7 km away from the shore (open water of Lake Baikal) in the direction from Listvennichny Cape to Tankhoy Settlement. At this station, samples were taken at 5 m intervals from the surface to 50 m. All quantitative phytoplankton samples (22) were fixed in Utermohl's solution.

Laboratory analyses

Nutrients (NH_4^+-N, NO_2^--N, NO_3^--N, PO_4^{3-}-P) as indicators of the state of the water environment and dissolved oxygen concentrations, were measured using spectrophotometry and the Winkler test respectively (Boeva, 2009; Wetzel, 1991). The pH values were measured on a pH-meter "Expert PH" (Econix-Expert, Russia).

Benthic algae were sorted according to taxon level under an MBC-10 microscope at 2 × 8 magnification. Species were identified from the temporary algal preparations under an Amplival microscope at 12 × 10 and 12 × 40 magnifications. Cell sizes (width and length in μm) were measured with an ocular micrometer. To determine biomass (wet weight) of each species from quantitative samples, benthic algae were dried on the filter paper and weighed on a torsion balance (WT, Poland) (precision ±1 mg). The data obtained were converted to 1 m^2 of the bottom (g m^{-2}).

Phytoplankton samples were settled in a 15–20 mL volume for about 14 days. Algae were counted in 0.1 mL. Individual volumes of cells were taken into account to determine algal biomass (mg m^{-3}) (Makarova and Pichkily, 1970).

Analytical design

The dependence of filamentous algae growth on the hydrodynamic environment was estimated by principal component analysis (PCA) using the following parameters as variables: x_1 – percent cover of the bottom with filamentous algae, %; x_2 – the prevalent type of bottom sediments at studied sites was classified visually from one to seven based on coarseness of material (Table 1 for composition); x_3 – depth (H, m); x_4 – width of the coastal zone, m; x_5 – wave height (h, m); x_6 – wave length (λ, m); x_7 – frequency of wave activity (τ, s); x_8 – slope ratio (angle) of the coastal zone; x_9 – orbital velocity of the water motion (V_{orb}, m·s^{-1}); x_{10} – shear velocity (V_{sh}, m·s^{-1}) of sediment movement; x_{11} – coefficient of sediment mobility (K_m); x_{12}–x_{18} – hydrodynamic pressure (P, g m^{-2}) on vertical surface at certain depths (0.5 m, 1.5 m, 2 m, 3 m, 4 m, 5 m). The orbital velocity of the water motion in zones of undeformed waves (I) or transformation (II) of waves and in the surf zone (III) was calculated by Petrov (1985). The shear velocity (the initial velocity of sediment movement) was estimated by Longinov (1963). The mobility coefficient of bottom sediments and hydrodynamic pressure on vertical surface were calculated by Karabanov and Kulishenko (1990). In our calculations, we used the highest values of wave activity (λ, τ) at the prevailing wind velocity (5–10 m·s^{-1}) during the August navigation (Galazy, 1993). All values of the database were transformed by $\log_{10}$ (x + 1) and presented means ± SE and 95% confidence interval.

Structure of algal communities

The structure of both phytobenthos and phytoplankton was identified by species ranking from maximal percent (dominance) to minimal percent (sub-dominance) of total biomass. We did not consider minor species with biomass <1%. The algal communities were characterized using Shannon's species diversity index (H), dominance index (D) and equitability (e) (Odum, 1971). To clarify whether *Spirogyra* is a permanent component of algal communities in Lake Baikal, we compared the composition of algal communities with previous years, referring to the data by L. Izhboldina on phytobenthos for August in 1966–1988 (southern, central and northern basins of Lake Baikal –298 qualitative samples as well as the Krestovka Valley and Emelyanovka Valley – 37 quantitative samples) and S. Vorobyova on phytoplankton in August 1992 (southern basin of Lake Baikal – 35 quantitative samples). All samples were collected using the same methods as in 2016.

Calculating hydraulic characteristics non-spherical algal cells

We calculated the sinking velocity of *Spirogyra* during the settling in a laminar flow from the Stokes formula:

Table 1
Physical characteristics of coastal locations sampled in different years. Composition of benthic algae in the coastal zone of Lake Baikal. Taxa atypical of the coastal zone are in bold; total taxon number are given in parentheses.

No. of sites (Fialkov, 1983)	Length of coastal zone, km	Width of coastal zone, m and bottom sediment composition	Slope of the coastal zone (angle), °	Depth (boundary) is where the shallow-water terrace merges into the slope, m	Composition of benthic algae	
					Before 2000	In 2016
1	40	75 boulders, pebble	3.8	5	*Chaetocladiella pumila*, *Cladophora compacta*, *C. kursanovii*, *Didymosphenia geminata*, *Draparnaldioides baicalensis*, *D. pilosa*, *Nostoc verrucosum*, *Tetraspora cylindrica* var. *bullosa*, *Ulothrix zonata* (9)	*Calothrix* sp., *Chaetocladiella pumila*, *Chaetomorpha curta*, *Cladophora floccosa*, *C. glomerata*, *C. kursanovii*, *Dermatochrysis reticulata*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Draparnaldioides baicalensis*, ***Oedogonium* sp.**, *Oscillatoria amoena*, *Rivularia borealis*, ***Spirogyra* conf. *calospora***, ***Spirogyra* sp.**, *Tolypothrix distorta*, *Ulothrix zonata* (17)
3	45	111 boulders, pebble, gravel, outcrops of bedrocks, sand, unrounded rock fragments	5.1	10	*Calothrix* sp., *Chaetocladiella pumila*, *Cladophora compacta*, *C. floccosa*, *C. kursanovii*, *Didymosphenia geminata*, *Draparnaldioides baicalensis*, *Nostoc verrucosum*, *Oscillatoria amoena*, *Schizothrix* sp., *Tetraspora cylindrica* var. *bullosa*, *Tetrasporopsis reticulata*, *Tolypothrix distorta*, *Ulothrix tenerrima*, *Ulothrix zonata*, *Ulothrix zonata* (16)	*Calothrix parietina*,*Calothrix* sp., *Chaetocladiella pumila*, *Chaetophora elegans*, *Cladophora compacta*, *C. floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. glomerata*, *C. kursanovii*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Draparnaldioides arnoldii*, *D. baicalensis*, *D. pilosa*, *Nitella* sp., *Nostoc verrucosum*, ***Oedogonium* conf. *flavescens***, ***Oedogonium* sp.**, *Oscillatoria amoena*, *Phaeoplaca baicalensis*, *Schizothrix* sp., ***Spirogyra* sp.**, *Tetraspora cylindrica* var. *bullosa*, *Tolypothrix distorta*, *T. distorta* f. *penicillata*, *T. distorta* f. *distorta*, *Ulothrix zonata* (28)
8	55	200 boulders, pebble	3.4	12	*Chaetocladiella pumila*, *Cladophora compacta*, *C. floccosa* f. *floccosa*, *Didymosphenia geminata*, *Draparnaldioides arenaria*, *D. arnoldii*, *D. baicalensis*, *D. pumila*, *Nostoc verrucosum*, *Tetraspora cylindrica* var. *bullosa*, *Tolypothrix distorta* f. *penicillata*, *Ulothrix zonata* (12)	*Chaetocladiella microscopica*, *Chaetomorpha baicalensis*, *C. moniliformis*, *C. solitaria*, *Cladophora compacta*, *C. floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. glomerata*, *C. meyeri*, *C. pulvinata*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Draparnaldioides arnoldii*, *D. baicalensis*, ***Mougeotia* sp.**, *Nostoc verrucosum*, ***Oedogonium* sp.**, *Oscillatoria amoena*, *O. tenuis*, *Schizothrix* sp., ***Spirogyra* sp.**, *Tolypothrix distorta*, *Tolypothrix distorta* f. *penicillata*, *T. distorta* f.*distorta*, *Ulothrix zonata* (26)
10	54	241 boulders, pebble	3.3	14	*Didymosphenia geminata*, *Draparnaldioides arenaria*, *D. arnoldii*, *D. baicalensis*, *D. pumila*, *D. vilosa*, *Tetraspora cylindrica* var. *bullosa*, *Ulothrix zonata* (8)	*Calothrix* sp., *Chaetocladiella pumila*, *Chaetomorpha moniliformis*, *Cladophora compacta*, *C. floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. glomerata*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Draparnaldioides arenaria*, *D. arnoldii*, *D. baicalensis*, *D. pilosa*, *Gemmiphora compacta*, *Microcoleus subtorulosus*, *Microcystis muscicola*, *Nostoc verrucosum*, ***Oedogonium* sp.**, *Oscillatoria amoena*, *O. tenuis*, *Schizothrix* sp., ***Spirogyra* conf. *weberi***, ***Spirogyra* sp.**, *Tolypothrix distorta*, *T. distorta* f. *penicillata*, *T. distorta* f.*distorta*, *Ulothrix zonata* (28)
12	52	154 boulders, pebble, sand	4.1	11	*Cladophora floccosa* f. *floccosa*, *Draparnaldioides baicalensis*, *Tetraspora cylindrica* var. *bullosa*, *Tolypothrix distorta* f. *penicillata*, *Ulothrix zonata* (5)	*Chaetomorpha moniliformis*, *Cladophora floccosa*, *C. kursanovii*, *Didymosphenia geminata*, ***Oedogonium* sp.**, ***Spirogyra* sp.**, *Tolypothrix distorta* (7)
14	64	828 sand, boulders	1.0	14	*Cladophora floccosa* f. *floccosa*, *Cladophora kursanovii*, *Didymosphenia geminata*, *Draparnaldioides pumila*, *Microcystis muscicola*, *Nostoc verrucosum*, *Tetraspora cylindrica* var. *bullosa* (7)	*Cladophora floccosa* var. *irregularis*, *C. glomerata*, *Draparnaldioides pumila*, *Microcoleus subtorulosus*, *Nitella* sp., ***Oedogonium* sp.1**, *Oscillatoria amoena*, *O. tenuis*, ***Spirogyra* sp.**, *Ulothrix zonata* (10)
17	69	580 boulders, sand	1.4	14	*Cladophora floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *Didymosphenia geminata*, *Draparnaldioides pumila*, *Nostoc verrucosum*, *Tetraspora cylindrica* var. *bullosa* (6)	*Calothrix* sp., *Chaetomorpha moniliformis*, *Cladophora floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. glomerata*, *C. kursanovii*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Draparnaldioides arnoldii*, *D. arnoldii f. compacta*, *D. baicalensis*, *D. pilosa*, *Nostoc verrucosum*, *Rivularia borealis*, *Schizothrix* sp., *Tolypothrix distorta* f. *penicillata*, *T. distorta F. distorta*, *Ulothrix zonata* (19)

(*continued on next page*)

Table 1 (*continued*)

No. of sites (Fialkov, 1983)	Length of coastal zone, km	Width of coastal zone, m and bottom sediment composition	Slope of the coastal zone (angle), °	Depth (boundary) is where the shallow-water terrace merges into the slope, m	Composition of benthic algae	
					Before 2000	In 2016
21	56	375 boulders, pebble, sand	2.7	18	*Cladophora floccosa* f. *floccosa*, *C. glomerata*, *Draparnaldioides arenaria*, *D. arnoldii*, *D. baicalensis* (5)	*Calothrix* sp., *Chaetomorpha moniliformis*, *Cladophora compacta*, *C. floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. fracta*, *C. glomerata*, *C. kursanovii*, *Dermatochrysis* sp., *Didymosphenia geminata*, *Nostoc verrucosum*, *Oscillatoria amoena*, *Schizothrix* sp., ***Spirogyra* sp.**, *Tolypothrix distorta* f. *distorta*, *Ulothrix zonata* (17)
22	83	2450 sand, gravel, boulders	0.5	22	*Chara* sp., *Cladophora floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. fracta*, *Nitella* sp., *Nostoc pruniforme*, *N. verrucosum* (7)	*Chaetomorpha moniliformis*, *Cladophora floccosa* f. *floccosa*, *C. fracta*, *C. glomerata*, *Nostoc verrucosum*, *Oedogonium* sp., ***Oedogonium* sp.1**, ***Spirogyra* sp.**, *Tolypothrix distorta* (9)
25	56	1400 boulders, sand	0.5	12	*Cladophora fracta*, *C. glomerata*, *Dermatochrysis reticulata*, *Gloeothrichia pisum*, *Nostoc verrucosum* (5)	*Cladophora kursanovii*, *Didymosphenia geminata*, ***Spirogyra* sp.**, *Tolypothrix distorta* f. *penicillata*, *Ulothrix zonata* (5)
30	47	574 sand, silt sand, boulders	1.1	11	*Didymosphenia geminata*, *D. arenaria*, *D. pilosa*, *Tetraspora cylindrica* var. *bullosa*, *Ulothrix zonata* (5)	*Cladophora floccosa*, *C. floccosa* f. *floccosa*, *C. floccosa* var. *irregularis*, *C. glomerata*, *C. kursanovii*, *Didymosphenia geminata*, *Draparnaldioides pilosa*, *D. pumila*, *Microcystis muscicola*, *Mougeotia* sp., *Nitella* sp., *Nostoc verrucosum*, ***Oedogonium* sp.**, *Schizothrix* sp., ***Spirogyra* sp.**, *Tolypothrix distorta*, *T. distorta* f. *penicillata*, *T. distorta* f. *distorta*, *Ulothrix zonata* (19)

Taxa untypical of the coastal zone are in bold.

$$W = 2r^2g(\rho - \rho_0)/(9\,\mu),$$

where W is the sinking velocity of a spherical particle in the water, cm s^{-1}; r is its radius, cm; g is the gravity acceleration (normal, 980.655 cm s^{-2}); ρ is the particle density, g cm^{-3}; ρ_0 is the water density (1 g cm^{-3}); μ is the water dynamic viscosity, g cm^{-1} s^{-1}.

To reduce non-spherical algal cells to a conditionally spherical shape, we calculated the equivalent radius according to cell volume:

$$r_e = \left(\frac{3V}{4\pi}\right)^{1/3}$$

The geometric form coefficient ζ was used to estimate non-spherical particles:

$$\zeta = S/S_0,$$

where S is the particle surface area; S_0 is the sphere area of the same effective radius.

Dynamic coefficient of the particle shape $\Gamma(\zeta)$ in the linear area of environmental resistance was calculated from Velikanov et al. (2013):

$$\Gamma(\zeta) = 1 + 0.348(\zeta - 1),$$

where ζ is the geometric form coefficient.

The density of living *Spirogyra* (ρ_s) was calculated from the following formula:

$$\rho_s = v\rho_{dry} + v_w\rho_w,$$

where v and v_w are the volumes of the dry substance and water, respectively; ρ_{dry} is the density of the dry substance; ρ_w is the water density at the given temperature.

The density of the dry substance (ρ_{dry}) was calculated from the volume of a solid tablet of *Spirogyra* filaments and its weight. First, *Spirogyra* filaments were dried on filter paper and then subjected to pressing in a compression mould to a solid tablet to determine the true weight of the dry mass. The water content was estimated from the difference between the wet weight of *Spirogyra* filaments dried on filter paper (until a wet spot disappeared) and the dry weight of these filaments (quantity weighed 20 g dried at 103 °C). The temperature of the cell content was set as equal to the water temperature for estimating the density of living *Spirogyra*. The water density (ρ_w) at this temperature was determined from standard tables.

Additionally, hydraulic characteristics were calculated for comparison of diatoms: namely, *Asterionella formosa* Hass., as a dominant of the phytoplankton community and *Aulacoseira baicalensis* (Meyer) Simonsen as a typical member of the algal community in the open water of Lake Baikal.

Results

Water environment

During this study in 2016, the water temperature was 15–17 °C at a depth of up to 15 m in the coastal zone and in the adjacent areas of the open pelagic zone. Secchi depth was 9 m. Dissolved oxygen concentrations in water at different stations varied from 10.5 mg L^{-1} to 13.1 mg L^{-1}. Content of nutrients was low except for some areas (Table 2). In the areas of human activity (Angasolka, Marituy, Krestovka Valley, Ushakovka River, Khara-Murin, Baikalsk Town) the content of nutrients in the surface water was slightly increased on average NO_3^--N (109 ± 38 µg L^{-1}) and PO_4^{3-}-P (26 ± 4 µg L^{-1}) for these stations. In the areas without anthropogenic impact (Rytyi Cape, Zavorotny Cape, Kotelnikovsky Cape, Irinda Bay of the northern basin, Peninsula Svyatoy Nos of the central basin, and Emelyanovka Valley of the southern basin), the

Table 2
Nutrient concentrations (µg L^{-1}) in surface (0) and near-bottom (1) water samples collected from different areas of Lake Baikal.

Transect	Station	Water layer	pH	NO_2^--N	NH_4^+-N	NO_3^--N	PO_4^{3-}-P
1	Angasolka	0	7.8	2	18	306	38
		1	7.8	2	0	338	33
2	Marituy	0	7.9	3	4	149	3
		1	8.0	3	0	232	23
3	Tolsty Cape	0	7.9	4	10	90	2
		1	7.9	3	12	150	3
4	Near the source of the Angara River	0	8.2	0	5	110	2
		1	8.4	0	4	110	3
5	Krestovka Valley	0	7.4	16	6	110	31
		1	8.2	2	6	110	2
6	Listvennichny Cape	0	8.1	1	7	110	3
		1	8.2	1	6	150	2
7	Emelyanovka Valley	0	7.9	1	8	100	3
		1	8.0	1	6	120	3
8	Rytyi Cape	0	8.5	3	7	4	1
		1	8.2	4	0	2	33
9	Zavorotny Cape	0	8.4	3	0	1	1
		1	8.5	4	14	1	1
10	Kotelnikovsky Cape	0	8.3	3	3	16	5
		1	7.9	11	3	235	36
11	Irinda Bay	0	8.4	0	7	8	9
		1	8.4	0	19	12	7
12	Peninsula Svyatoy Nos	0	8.2	12	0	37	0
		1	8.2	18	6	118	0
13	Ushakovka River	0	8.5	0	12	26	22
		1	8.5	0	8	0	13
14	Khara-Murin	0	8.2	0	14	66	34
		1	8.2	0	12	1	14
15	Baikalsk Town	0	8.5	0	44	0	23
		1	8.1	0	12	66	23

values of mineral forms of nitrogen and phosphorus are within the reference characteristics in the surface water and reached on average 28 ± 15 µg L^{-1} (NO_3^--N) and 3 ± 1 µg L^{-1} (PO_4^{3-}-P).

Spatial distribution of Spirogyra alongshore of Lake Baikal

In 2016, the benthic flora in the studied sites (Table 1) alongshore of Lake Baikal consisted of 56 taxa of benthic algae, which was more diverse than in the past century. There are filamentous algae *Mougeotia* sp., *Oedogonium* conf. *flavescens*, *Oedogonium* sp., *Spirogyra* conf. *calospora*, *Spirogyra* conf. *weberi*, *Spirogyra* sp., and *U. zonata*. The occurrence of *Spirogyra* at the study sites of the open coastal zone of Lake Baikal was 75%; other filamentous algae were rare (except for *Oedogonium*; its occurrence was 40%). In the previous century, algae of the genus *Spirogyra* occurred only in certain areas (shoal zone) of the lake as singular filaments, and sometimes was recorded in the grab samples collected at a depth of 40–80 m (Dagarskaya Bay, opposite Angara-Kichera Shoal and Ulan-Nur Cape) (Fig. 1A).

PCA analysis showed that the main percentage of variability (80%) of the whole database was provided by the first two principal components. In the space of the first two principal components the point set is divided into two non-overlapping subsets, *I* and *II* (Fig. 3). Subset *I* includes stations located in the zone of waves transformation. At stations Listvennichny Cape, Krestovka Valley, near the source of the Angara River, and Baikalsk Town, the vertical zoning of the spatial distribution of benthic algae was disturbed due to mass development of filamentous algae (percent cover at a depth of over 2 m reached 40–100%). The same subset includes the stations (Kultuk Settlement, Maximikha Settlement and the area opposite the Ushakovka River) where we found free-lying clumps formed by filamentous algae on the sandy bottom (Fig. 4). In addition, subset *I* includes the stations where the percent cover of the bottom with filamentous algae was up to 15%; however, the vertical zoning of algal distribution was not disturbed. The percent cover of filamentous algae at the stations forming a subset *I* is closely associated with such factors as shear velocity, the composition of bottom sediment, slope ratio, and

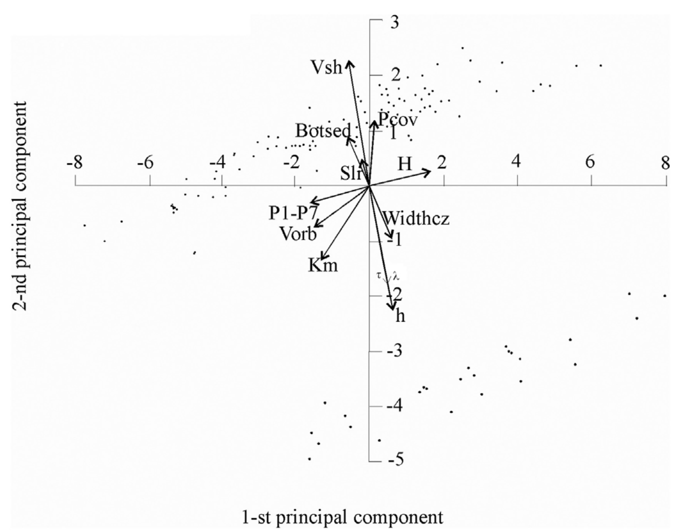

Fig. 3. Location of sampling points in the space of two principal components. The subset *I* includes stations in the zone of waves transformation: Angasolka, Marituy, Tolsty Cape, near the Angara River, Krestovka Valley, Listvennichny Cape, Emelyanovka Valley, the area opposite the Ushakovka River, Khara-Murin and Baikalsk Town, where shear velocity (V_{sh}), composition of bottom sediment (*Botsed*), slope ratio (*Slr*) and a depth (*H*) are the most significant factors, and where filamentous algae are often recorded. The subset *II* includes points Rytyi Cape, Zavorotny Cape, Kotelnikovsky Cape, Irinda Bay and Peninsula Svyatoy Nos in the zone of wave deformation, where width of the coastal zone (*Widthcz*), wave height (*h*), length (λ) and frequency of waves (τ) are the most significant factors, and filamentous algae are rare or not recorded. Orbital velocity (H_{orb}) of the water motion, coefficient of sediment mobility (*Km*) and hydrodynamic pressure (P_1-P_7) on the vertical surface are significant factors for some stations from subsets *I* and *II* located in the surf zone at depths of 0.6–1.5 m, where filamentous algae either are missing or their percent cover is 1%.

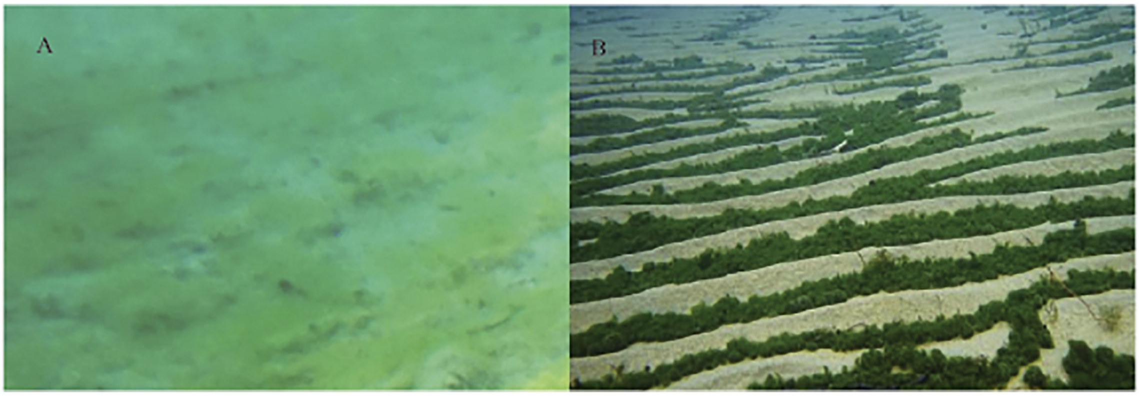

Fig. 4. The photograph of bottom covered with filamentous algae at a depth of 3 m in Lake Baikal: A (left image)– before the storm, B (right Image – after the storm with a wave height of approximately 2 m (Photo by I.V. Khanaev).

depth (Fig. 3). Subset *II* comprises stations located in the zone of wave transformation in which the vertical zonality in the spatial distribution of benthic algae persists and where filamentous algae were not present or present in low numbers (percent cover 1–3%): Rytyi Cape, Zavorotny Cape, Kotelnikovsky Cape, Irinda Bay, Peninsula Svyatoy Nos. Such factors as wave height, length and frequency of waves as well as width of the coastal zone are the most significant for these stations (Fig. 3).

Orbital velocity of the water motion, coefficient of sediment mobility and hydrodynamic pressure on the vertical surface are the most significant for some stations from subsets *I* and *II* located at depths of 0.6–1.5 m (surf zone), where the percent cover of the bottom with filamentous algae was 0–1%.

The percent cover of the bottom with filamentous algae increased at depths of over 1.5–2.5 m; depths with lower wave effects on the bottom (Fig. 2B). At depths corresponding to three vegetation belts, the orbital velocity in the zone of wave deformation (at a depth of 2.5–3.5 m) was on average 0.40 ± 0.03 m s^{-1}, in the zone of wave breaking (depths of 1.5–2.5 m) – 1.37 ± 0.22 m s^{-1}, and in the surf zone at the beginning of surge (depth of up to 1.5 m) – 3.34 ± 0.31 m s^{-1}. Shear velocity varied from 0.07 to 0.15 m s^{-1}. Such velocities were observed at wave lengths of 14 m and 21 m, periodicity of 3 s and 5.1 s, respectively, and at wave heights of 1–1.2 m. K_m in these zones was >1, indicating the mobility of bottom sediments.

Comparisons structure of benthic algal communities at the site with the uniform hydrodynamic environment and different recreational activity within its boundaries

The structure of benthic algal communities was changed in the zone of anthropogenic impact opposite the settlement of Listvyanka (Krestovka Valley) (Table 3). Here, in 2016, we recorded a change of dominants in all three vegetation belts. The communities with the dominance of *Spirogyra* untypical of the open coastal zone of Lake Baikal formed there for the first time (for the period of observations since the beginning of the previous century). A share of *Spirogyra* in the communities of benthic algae ranged between 56% and 76% of the total biomass, whereas the share of other filamentous algae, in particular, the formerly dominant *U. zonata*, was <0.1%. Previously (1987), filamentous algae *U. zonata* was 95% of the total biomass of the community in the first vegetation belt, but *Spirogyra* was not recorded (Table 3). At the transect opposite the anthropogenically impacted Krestovka Valley, the distribution of *Spirogyra* biomass depends on the hydrodynamic environment. Its lowest content was recorded in the surf and wave-breaking zones, whereas the highest values were registered in the zone of weak effect of wave activity on the bottom (Fig. 2C).

In 2016, in the reference area at transect opposite Emelyanovka Valley, the structure of benthic algae communities did not change significantly compared to that in 1987 (Table 3). In different vegetation belts, the communities had from 12 to 16 taxa dominated by the common Baikal species *Calothrix* sp., *Chaetocladiella pumila* (C. Meyer) C. Meyer et Skabitsch. and *Draparnaldioides baicalensis* Meyer et Skabitsch. Filamentous algae *U. zonata* and a few separate filaments of *Spirogyra* were observed in the communities only among minor species, and their percentage was lower than 0.1% of the total biomass. In 1987, *U. zonata* dominated in the first vegetation belt, and among subdominant or minor species of all algal communities; there were no specimens of the genus *Spirogyra* (Table 3).

Geometric and hydraulic characteristics of Spirogyra cells and possibilities of their transfer to phytoplankton communities

During our investigation, the length of filament strands of *Spirogyra* reached 50–70 cm in some areas of the lake, but according to the visual observations of I. Khanaev, in June–August in Listvennichny Bay filament strands could reach >150 cm. The longest filament strands usually form at depths below 8 m (up to 12 m), i.e. beyond the zone of wave effect on the bottom during summer storms (*h* = 1–1.2 m). Cells forming the *Spirogyra* thallomes were represented by two size groups. Some cells (n = 38 measurements) were on average 30 ± 1 μm wide (range 14–40 μm) and 152 ± 14 μm long (29–345 μm). Others (n = 23) were on average of 45 ± 1 μm wide (41–68 μm) and 208 ± 20 μm long (81–378 μm). The cell walls of *Spirogyra* consist of the outer pectin layer (mucus) and two or more inner cellulose layers. The dimensions of thallomes in a single alga range between several millimetres to 8–15 cm. Intertwined with each other, they form long filament strands at the bottom of Baikal. During summer storms, in zones where waves affect the bottom, filament strands are destroyed, and thallome fragments of *Spirogyra* enter the water column. Thallome fragments of *Spirogyra* consisting mainly of one to three cells were found in phytoplankton samples at all depths sampled in the southern basin of Lake Baikal (the abundance was 650 to 5440 cells L^{-1}).

Geometric and hydraulic characteristics of both *Spirogyra* and diatoms are consistent with their possible transfer with coastal currents. The density of dry *Spirogyra* was 1.36 g cm^{-3}, and the water content of the living alga was 90%. The density ρ_s of the living *Spirogyra* was 1.036 g cm^{-3}. The sinking velocity at 10 °C of one *Spirogyra* cell with the volume of 28,600 μm^3 and equivalent radius of 19 μm was 22×10^{-3} mm s^{-1} (actual surface area

Table 3
Structure of benthic algal communities in different years at the site 3 with the uniform hydrodynamic environment and different human activity within its boundaries. Indicators of benthic algal communities in 2016 are (underlined) and in 1987 just below; the contribution of the species (in %) to the total biomass of benthic algae is given in parentheses.

Site 3	Vegetation zone	Zone of depth, m	Total taxa in community	Means biomass (±SE) of community, gm^{-2}	Shannon index, H	Dominance index, D	Equitability, e	Dominant and sub-dominant species of community in 2016, (%)	Dominant and sub-dominant species of community in 1987, (%)
Krestovka Valley - Impacted	1	0–1.5	16 7	11 ± 4.9 45.7 ± 26.0	0.8 0.2	0.61 0.92	0.29 0.11	*Spirogyra* sp.1 (76), *Cladophora glomerata* (14), *Dermatochrysis* sp. (6), *Cladophora floccosa* f. *floccosa* (2)	*Ulothrix zonata* (95), *Didymosphenia geminata* (3), *Cladophora glomerata* (1)
	2	1.5–2.5	13 13	26.3 ± 13.5 76.0 ± 42.0	0.8 1.1	0.56 0.44	0.31 0.42	*Spirogyra* sp.1 (72), *Nitella* sp. (14), *Draparnaldioides pilosa* (13)	*Nitella flexilis* (60), *Cladophora floccosa* (29), *Tetrasporopsis reticulata* (6), *Didymosphenia geminata* (2), *Ulothrix zonata* (2)
	3	2.5–3.5 up to 12	15 16	289.4 ± 167.6 225.4 ± 105.9	0.9 2.4	0.47 0.11	0.33 0.85	*Spirogyra* sp.1 (56), *Draparnaldioides pilosa* (39), *Nitella* sp.(2), *Didymosphenia geminata* (2)	*Dermatochrysis reticulata* (21), *Tetraspora cylindrica* var. *bullosa* (15), *Stratonostoc verrucosum* (12), *Cladophora compacta* (9), *Draparnaldioides simplex* (9), *Myxonemopsis crassimembranaceae* (7), *Tetraspora lubrica* (6), *Nitella* sp. (6), *Cladophora floccosa* (4), *Schizothrix* sp. (4) *Didymosphenia geminata* (3), *Chaetocladiella pumila* (2)
Emelyanovka Valley - Reference	1	0–1.5	16 3	5.6 ± 2.0 7.8 ± 5.4	1.6 0.4	0.28 0.78	0.56 0.35	*Calothrix* sp. (46), *Schizothrix* sp. (15), *Chaetocladiella pumila* (12), *Cladophora glomerata* (12), *Tolypothrix distorta* f. *distorta* (7), *Nostoc verrucosum* (6), *Cladophora floccosa* (1)	*Ulothrix zonata* (87), *Draparnaldioides baicalensis* (12)
	2	1.5–2.5	12 13	59.9 ± 14.6 117.0 ± 78.6	0.9 1.6	0.62 0.31	0.36 0.61	*Chaetocladiella pumila* (78), *Nostoc verrucosum* (6), *Tolypothrix distorta f. distorta* (6), *Schizothrix sp.* (5), *Calothrix parietina* (2), *Draparnaldioides baicalensis* (1)	*Draparnaldioides baicalensis* (50), *Cladophora floccosa* (10), *Tetraspora* f. sp. (9), *Chaetocladiella pumila* (9), *Cladophora compacta* (8), *Cladophora kursanovii* (6), *Tetraspora cylindrica* var. *bullosa* (2), *Stratonostoc verrucosum* (1)
	3	2.5–3.5 up to 12	13 13	427.7 ± 95.3 171.5 ± 55.8	0.3 1.4	0.87 0.34	0.13 0.54	*Draparnaldioides baicalensis* (93), *Schizothrix* sp. (4), *Tolypothrix distorta* f. *distorta* (2)	*Draparnaldioides baicalensis* (52), *Chaetocladiella pumila* (19), *Schizothrix* sp. (16), *Tetraspora* f. sp. (5), *Tolypothrix distorta* (4), *Gemmiphora compacta* (3)

(S) = 6729 μm^2, sphere area (S_0) = 4523 μm^2, geometric coefficient (ζ) = 1.49, dynamic coefficient (Γ) = 1.17). A fragment of *Spirogyra* thallome from three cells with a volume of 85,800 μm^3 and equivalent radius of 27.4 μm (S = 20,188 μm^2, S_0 = 9407 μm^2, ζ = 2.15, Γ = 1.40) sinks at a velocity of 45×10^{-3} mm s^{-1}. The density of a thin-walled diatom *A. baicalensis* calculated from the data shown in Jewson et al. (2010) was 1.27 g cm^{-3}. Therefore, its cell, with a volume of 14,300 μm^3 and equivalent radius of 15 μm sinks at a velocity of 90×10^{-3} mm s^{-1} (S = 3908 μm^2, S_0 = 2827 μm^2, ζ = 1.38, Γ = 1.13). Another diatom, *A. formosa*, sinks at 15×10^{-3} mm s^{-1}, with a cell volume of 800 μm^3 and equivalent radius of 5.76 μm (S = 907 μm^2, S_0 = 423 μm^2, ζ = 2.14, Γ = 1.40). This diatom is likely to be of the same density as *A. baicalensis*. Because *A. formosa* is able to form star colonies consisting of several cells, e.g. five, its sinking velocity, in this case, is 44×10^{-3} mm·s^{-1}(volume 4000 μm^3, equivalent radius 9.8 μm, S = 4535 μm^2, S_0 = 1207 μm^2, ζ = 3.76, Γ = 1.96). Thus, the dynamic coefficient in the linear area of resistance for a *Spirogyra* cell and for thallome fragments of several cells are comparable to that of diatoms. The density of living algal cells (excluding diatoms) at this temperature is close to water density. Even in these large cells like *Spirogyra*, the sinking velocity is lower than in diatoms *A. baicalensis* and *A. formosa* with a silicon frustule. The sinking velocity of one *Spirogyra* cell indicates that it can remain in the photic layer (0–50 m) of the Baikal water column in calm weather for a long time (26 days). Low sinking velocities contribute to the transfer of *Spirogyra* cells by circulation currents (Fig. 1B) over long distances along the Baikal shores.

In the water column, *Spirogyra* cells stay alive and continue to function. In 2016, the phytoplankton of the open Baikal pelagic zone contained 4 mg m^{-3} of the *Spirogyra* biomass in the surface layer (0 m), and 16 mg m^{-3} at a depth of 50 m (Fig. 5A). The largest *Spirogyra* biomass (28 mg m^{-3}) was in coastal phytoplankton at a depth of 5 m. In general, current algal communities of phytoplankton were characterized by a more diverse composition than in 1992. They contained 40–44 taxa dominated by *A. formosa* (16–20% of the total biomass of communities, 194–238 mg m^{-3}). At the same time, the share of *Spirogyra* in the total biomass of different communities ranged between 4 and 12% (Fig. 5B). In all studies of deep horizons, planktonic communities had high Shannon diversity indices (2.6–2.7), low dominance values (0.08–0.10) and high evenness (0.69–0.72) in comparison with those of 1992: H = 1.2–1.5, D = 0.39–0.41, e = 0.39–0.46. In 1992, fewer species were recorded in communities (23–29). Picoplankton (60–69%), as well as species *Rhodomonas pusilla* (Bachm.) Javorn. (10–22%) and *Gymnodinium coeruleum* Ant. (5–7%), dominated the biomass, but specimens of the genus *Spirogyra* were not recorded (Fig. 5C).

Discussion

In the past decade, the diversity of benthic algal flora in different areas of Lake Baikal has increased not only due to the common inhabitants of the coastal zone but also to species not typical of the open coasts (Table 1). One of them is *Spirogyra*, whose spatial distribution along the coastal zone of open Baikal is very uneven (Fig. 1A). Normally, in the areas subject to local anthropogenic impact, *Spirogyra* occurs as separate patches or forms dense or freely lying clumps on the bottom (Fig. 4). In particular, in the coastal zone of Listvennichny Bay, percent cover varies from 0–1% (in the first vegetation belt) to 80–90% (in the third vegetation belt). The same picture was observed in the areas opposite Baikalsk Town and the Ushakovka River. In other Baikal areas (Rytyi Cape, Zavorotny Cape, Kotelnikovsky Cape of the northern basin, Peninsula Svyatoy Nos of the central basin and Emelyanovka Valley of the southern basin), there are only a few *Spirogyra* filaments attached to larger algae or other substrates, and this can only be found under a microscope. On the one hand, the uneven distribution of *Spirogyra* is due to anthropogenic impact, which was previously shown in (Kravtsova et al., 2014; Timoshkin et al., 2016, 2018). On the other hand, it can be due to such abiotic factors as hydrodynamics. The growth and development of benthic algae in aquatic ecosystems are known to be closely related to hydrodynamics, in particular wave activity (Engelen et al., 2005; Nozaki et al., 2003; Raspopov et al., 1990; Reiter, 1986). In Lake Baikal, the intensive development of dominant algae in the vegetation zones, e.g. *U. zonata*, *T. cylindrica* var. *bullosa* and *D. geminata*, and species of the genus *Draparnaldioides* occurs in summer when wind speeds and wave activity (h = 0.5 m) are low. Later, when the waves reach their maximum height (late autumn and early winter), the above listed algae stop growing (Izhboldina, 2007). Now, algal mats of filamentous algae can be found in the coastal zone at a depth of 3 m and below in the area of anthropogenic impact in Listvennichny Bay (Kravtsova et al., 2014).

According to in situ data, *Spirogyra* forms the longest filament strands at depths of over 8–10 m. In this habitat, rare storms with a wave height of >1 m, and current velocities near bottom (V_{orb} = 0.03–0.10 m s^{-1}) are unable to detach filaments from the substrate. At depths of 3.5–4.6 m in the third vegetation belt, orbital velocities from 0.22 m s^{-1} to 0.36 m s^{-1} are also unlikely to affect the development of *Spirogyra*, and so its percent cover and biomass are high there (Fig. 2B,C). These velocities are comparable to those from the experimental research by Peterson and Stevenson (1992), which showed that *Spirogyra* develops at current velocities of 0.12 m s^{-1} and 0.29 m s^{-1} forming the greater biomass in the first case and slightly lower biomass in the second case.

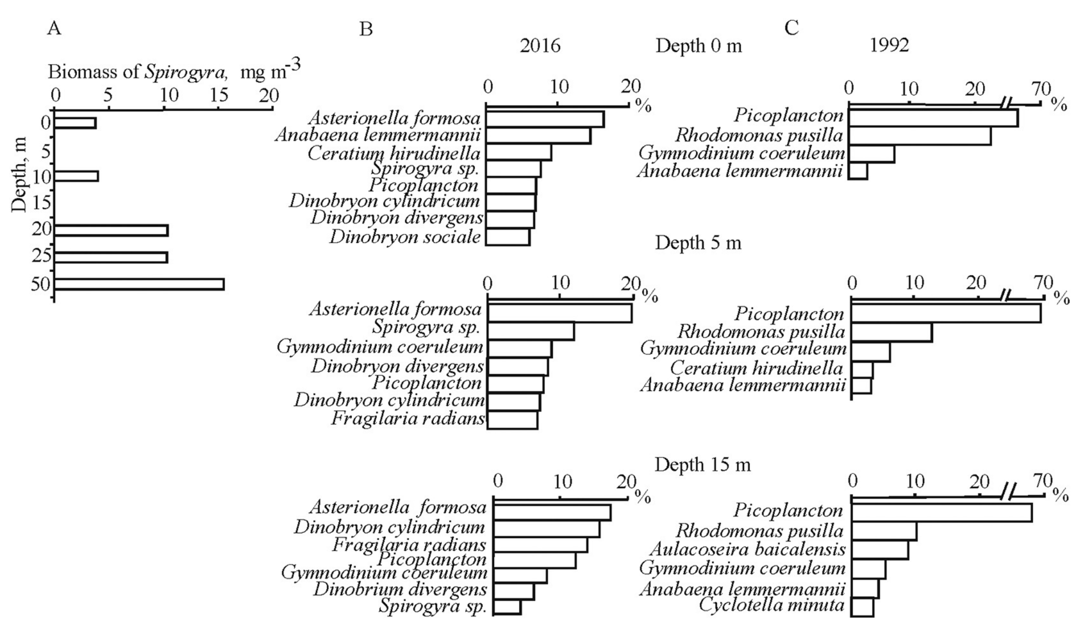

Fig. 5. Composition of phytoplankton communities in the southern basin of Lake Baikal during different years: A – depth distribution of biomass of planktonic *Spirogyra* in 2016 at VI station Listvennichny Bay in; B – depth distribution of relative abundance of phytoplankton in 2016; and C - in 1992 in the southern basin of Lake Baikal showing change in contribution of *Spirogyra* to phytoplankton community. Along X-axis – a percentage of species biomass from the total biomass of community, along Y-axis – species ranking in the order of decrease of percentage.

In Baikal, the first and second vegetation belts show significantly higher current velocities than the third; orbital velocities (at $h = 1.0$ m) can be 3.8–6.2 m s^{-1} and 0.58–1.6 m s^{-1}, respectively, and *Spirogyra* biomass is several times lower than in the third vegetation belt (Fig. 2C). Such velocities are likely to create unfavorable conditions for the growth of *Spirogyra*, because not only fine-grained material but also coarser material are set in motion at the bottom. In the coastal zone of seas and large lakes, orbital velocities (0.5 m s^{-1}) are able to re-suspend fine sand particles (Rasmussen and Rowan, 1997). According to Volkov and Ionin (1962), the movement of debris (1–20 cm in diameter) in water bodies emerges when near bottom current velocity exceeds critical values (0.5–1.7 m·s^{-1}) and depends on its size and bottom slope. A probable abundance of *Spirogyra* at lesser depths in Lake Baikal is not higher due to the abrasive effect of moving sandy particles and gravel-pebble material. Additionally, the length of other algal filaments of *U. zonata* was small, from 10–15 cm to 0.5–0.6 cm, at higher velocities in the surf zone when coarse pebbles and boulders (30 cm in diameter) were in movement (Karabanov and Kulishenko, 1990). In the surf zone, bottom sediments can be free from algae due to the transfer, mobility, friction and turbidity of debris of different sizes. Filaments detached from the substrate entered the water column.

Shear and orbital velocities in vegetation belts of the coastal zone of Lake Baikal contribute to the horizontal transfer of fine sand particles and fragments of *Spirogyra* by cyclonic currents. In storm periods, orbital velocities with a regime probability of 0.1% near the bottom can stir up the sand around the entire area of the coastal zone (Fialkov, 1983). The system of currents (Afanasyev and Verbolov, 1977) and turbulent diffusion distribute terrigenous suspended sediments brought with river waters around the water area of Lake Baikal. According to a mathematical model (Mizandrontsev and Sudakov, 1981), suspended sediments (diameter of 0.005 mm, density of 2.65 g cm^{-3} and sinking velocity of 17×10^{-3} mm·s^{-1}) are transported along the western coast of the northern basin of Lake Baikal at current velocities of some centimetres per second for a distance of hundreds of kilometers from the mouths of large tributaries located in the northern part of the lake. Offshore secondary circulations (Fig. 1B) and horizontal turbulent diffusion promote the removal of suspended particles in the open areas of the lake (Mizandrontsev and Sudakov, 1981). The diatoms *A. formosa* and *A. baicalensis*, as well as fine mineral sediments, can be transferred by coastal currents significant distances. This relates to planktonic algae, without denser mineral cell walls, with densities close to the density of the lake water and fragments of *Spirogyra* thallomes. Moreover, the density of living planktonic algae without silicon cell walls is close to 1 g cm^{-3} and can be lower than the water density (at this temperature) due to the presence of gas vacuoles and fat inclusions (Henderson-Sellers, 1987; Smith, 1982). The transfer mechanism of filaments and their fragments within the water column, considering the geometric and hydraulic characteristics, is similar to that of planktonic diatoms. The sinking velocity of *A. baicalensis* (10,000 μm^3) in the laminar water flow is 39×10^{-3} mm s^{-1} (Votintsev, 1961) and that of marine phytoplankton, particularly, dinoflagellates (taking into account the equivalent radius of cells and their non-spherical shape), is from 3×10^{-3} mm s^{-1} to 45×10^{-3} mm s^{-1} (Kamykowski et al., 1992). The sinking velocity of *Spirogyra* (22×10^{-3} mm s^{-1}) is lower than that of Baikal diatoms. Because sedimentation rates are very low, it allows filament fragments and diatoms to remain within the water column for a long time. Findings of *Spirogyra* in the planktonic samples at studied depths in the southern basin of Lake Baikal support this fact (Fig. 5A, B). The *Spirogyra* cells are found not only in the phytoplankton of the southern basin but also the central (Goryachinsk Settlement, Boldakovo Valley) and northern basin of Lake Baikal (near the Tiya River and Senogda Bay) (personal communications by Bondarenko and Vorobyova). Thallome fragments of filamentous algae *Spirogyra* removed by currents (Fig. 1B) from the coastal area can move along the perimeter in each basin of the lake and around the entire lake. For example, algal fragments will be transferred from Listvennichny Cape to Tolsty Cape (Fig. 1A) in 11 days at the wind with regime probability of 50% and at the velocity of current of 9 cm s^{-1} in the middle water layer. Moreover, of interest are earlier findings of singular *Spirogyra* filaments outside the coastal zone at depths of 40–80 m. Their occurrence in the deep zone, as well as the thermophilic diatom *A. formosa*, at depths of 300–600 m, may be attributed to the run-off of warm waters along the slope at the boundary of the thermal bar (Likhoshway et al., 1996).

Conclusions

Hydrodynamics plays an important role in the formation of the current structure of algal communities in Lake Baikal. Under conditions of global warming and flux of nutrients into the coastal zone, we observe the bottom overgrowing with filamentous algae. The blooms of filamentous algae change the historical benthic communities. At the initial stage of anthropogenic succession of the benthic algae communities, there is a change in vertical zonation, and *Spirogyra* replaces the formerly dominant species. During storms, filaments detach from the substrate and are either washed ashore, forming aggregates on the beaches or enter the water column. Because the hydraulic characteristics of filamentous algae, particularly *Spirogyra*, are comparable with those of planktonic diatoms, the existing system of currents in Lake Baikal causes their transfer from regions of mass development to areas outside the zones of local anthropogenic impact. In the open parts of the coastal zone of Lake Baikal remote from settlements, we observed singular filaments or thallome fragments of *Spirogyra*. Bays and coastal shoals, i.e. traditional habitats of this alga, also serve as a source of replenishment of algal fragments by currents into the open water zone. Only in recent years has *Spirogyra* been detected in the plankton of the open parts of Lake Baikal, even though benthic diatoms were constantly recorded in the open-water plankton. If the nutrient loading into the coastal zone increases, the role of filamentous algae in the Baikal ecosystem will also increase, and hydrodynamics will promote the spreading of these algae throughout the lake. Understanding how hydrodynamic processes affect the biotic component of aquatic ecosystems is important for understanding mechanisms associated with ecosystem function. Coastal blooms of filamentous algae in inland waters have become a critically important issue for both the natural and the social environment. Long-term monitoring must, therefore, consider the human factor controlling these blooms and their impact on the water supply in Lake Baikal as well as on other large lakes threatened by accelerating eutrophication.

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