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Dedicated to the late Professor Jadwiga Siemińska

Green and charophytic algae of the high-mountain Nesamovyte and Brebeneskul lakes (Eastern Carpathians, Ukraine)

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Abstract. A study of green and charophytic algae diversity in two high-mountain lakes in the Eastern Carpathians (Ukraine) identified 99 species (109 taxa at species and intraspecific rank) in 35 genera from different ecotopes of the studied lakes. Algal species composition was characterized, and the ecological parameters of the lakes were determined from monitoring data recorded over the last century. Environmental analyses using bioindication methods based only on data on the composition of green and charophytic algae confirmed that the environmental inferences were accurate. Degradation of the Nesamovyte and Brebeneskul lake ecosystems, as compared with their earlier states, was noted.

Key words: algae, diversity, Eastern Carpathians, mountains lakes, bioindication, ecosystems

Introduction

Algae are an important component of mountain ecosystems, where they form a particular spectrum of taxonomic groups, with montane forms as well as rare and distinctive species. Algae exhibit geographical, zonal and stratigraphic specificity in their species composition and in their association with types of waterbodies and biotopes, and are considered to be indicators of climatic changes (Nauwerk 1966; Ettl 1968; Wasser 1989; Lampert & Sommer 1997; Kamenik et al. 2000; Nedbalova et al. 2006; Barinova et al. 2006, 2019; Cantonati & Spitale 2009; Bąk et al. 2012). Of particular indicator value are diatoms and green and charophyte algae, which often are subdominants or dominants in the waterbodies of these ecosystems (Kawecka 1970; Kopaček et al. 2004; Buczko & Wojtal 2007; Kawecka & Galas 2003; Kawecka & Robinson 2008; Robinson et al. 2010; Burchardt 2014; Wojtan et al. 2014; Khuram et al. 2019). In terms of composition, taxonomic structure and distribution, algal diversity is high in the mountain waterbodies of the Carpathian region (Szklarczyk-Gazdowa 1960; Sieminska 1967; Hindák & Kováčik 1993; Lukavsky 1994; Wojtal & Galas 1994; Fott 1999; Juriš & Kováčik 1987; Buczkó et al. 2009; Kot 2009; Cărăus 2012; Lenarczyk 2012; Lenarczyk & Tsarenko 2013).

Data on algal diversity in the Eastern (Ukrainian) Carpathians, and especially on their individual taxonomic groups and on the mountain ranges, are scarce and incomplete (Vodopian 1981; Palamar-Mordvintseva et al. 1992; Tsarenko et al. 1997, 1998, 2009, 2014, 2017; Tsarenko & Parchuk 1998; Tsarenko 2000; Tsarenko & Wasser 2000; Tsarenko & Palamar-Mordvintseva 2014, 2016; Mykitchak 2014; Tsarenko & Lilitska 2016; Bilous & Tsarenko 2018). This applies primarily to the waterbodies of the high-mountain ecosystems of this region and specifically to the largest subalpine lakes of the Chornohora Mts of the Eastern Carpathians in Ukraine (Tsarenko et al. 2014). Published algofloristic information for this area comes from the 20th century (Wołoszynska 1920; Asaul 1969; Palamar-Mordvintseva 1978a, b, 1982) and needs updating; the current state of algal diversity and species composition needs to be documented. Recently we obtained a general idea of the diversity and indicator value of algae in the lentic system of Chornohora (Tsarenko et al. 2014, 2015, 2017, 2018). The diatom species composition of Nesamovyte and Brebeneskul lakes, and also Maricheyka Lake from the forest zone of the Carpathians, was studied in detail (Kryvosheya & Tsarenko 2018; Tsarenko et al. 2016). In the present study we addressed the present-day species composition of "green" algal phyla (*Chlorophyta*, *Charophyta*) in the highest lakes of Chornohora (Nesamovyte, Brebeneskul), analysed monitoring data for the last century, and determined the ecological state of these

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lakes on the basis of algal indicator species occurring under recent environmental conditions[1].

Materials and methods

The investigated lakes are located in the highest part of the Ukrainian Carpathians (Fig. 1), the Polonyno-Chornohora geomorphological area (Tsys 1968), which is part of the Carpathian-Danube algofloristic sub-provinces according to the algofloristic zonation of Ukraine (Palamar-Mordvintseva & Tsarenko 2015).

The material for the study (16 samples of net plankton, the periphyton communities of algae on higher aquatic plants, and squeezes from moss from marshland) was collected along the perimeter of the lakes (more along the southern parts) in the summers of 2013–2017 (July–August 2013–15, August 2016–2017). Nesamovyte Lake is in a glacial cirque on the eastern slope of Mount Turkul (Chornohora Ridge, Eastern Carpathians) at 1750 m a.s.l. The lake covers ~0.3 hectares (88 × 45 m) and is ~2 m deep. It is characterized by atmospheric supply of water and food, with a sandy/muddy bottom and a long freezing period. The water in the lake is now β-mesosaprobic (Mikitschak & Kokish 2014).

Brebeneskul Lake is one of Ukraine's highest mountain lakes. It is in a glacial cirque on the southwestern slope of Chornohora Ridge at 1793 m a.s.l. in a depression between Mt. Brebeneskul (2035 m a.s.l.) and Mt. Gutin-Tomnatek (2016 m a.s.l.) in the Chornohora area of the Carpathian Biosphere Reserve (Mykitchak & Kokish 2014). The lake covers ~0.6 ha (146 × 67 m) and is up to 2.4 m deep. The lake is not drained but undergoes weak filtration through the ridge from the eastern side, and is supplemented by atmospheric precipitation and groundwater. The bottom is stony silt, and the weakly mineralized water is oligosaprobic (Mykitchak 2014). During the study period the water parameters were as follows: 18.4–12.6°C (upper to lower layer), pH 7.1, specific conductivity 26.74 μS/cm, turbidity 3.91 NTU (nephelometric turbidity units) and oxygen saturation 6.32 mg/L.

This study is based on living algal material from the plankton (accumulation cultures, with addition of liquid and agar Bold Basal Medium; Andersen 2005) and on samples fixed with 4% formaldehyde solution. In addition to the algological samples we collected in 2013–2017, we studied material from the Algoteca of the M.G. Kholodny Institute of Botany, National Academy of Science of Ukraine (AKW, accessions NN 16855–16898, samples from 1967 collected by Z.I. Asaul). The algae were observed and identified by light microscopy (Ergaval Carl Zeiss, Olympus BX-53).

Our ecological analyses of the two lakes is based on historical data for 1920 (only Nesamovyte Lake) and 1967 (both lakes), and recent data from 2013–2016. The following ecological characteristics were used: habitat preference (B – benthic; P-B – plankto-benthic; S – soil; Ep – epiphyte; P – planktonic), current and oxygenation (aer – aerophyles; St-str – inhabitants of low-flow, moderately oxygenated water; ae – aerophytes; st – inhabitants of standing water with low oxygenation), pH (Hustedt 1957) (ind – indifferent; acf – acidophile), salinity (Hustedt 1957) (i – indifferent; hb – halophobe; oh – oligohalobe), trophic state (Van Dam et al. 1994) (m – mesotraphentic; me – meso-eutraphentic; o-m – oligo- to mesotraphentic; e – eutraphentic; ot – oligotraphentic), and organic pollution (Sladecek 1973; Barinova et al. 2006, 2019) (x – xenosaprobe; x-o – xeno-oligosaprobe; o-x –oligo-xenosaprobe; x-b – xeno-betamesosaprobe; o – oligosaprobe; o-b – oligo-betamesosaprobe; b-o – beta-oligosaprobe; o-a – oligo-alphamesosaprobe; b – betamesosaprobe; b-a – beta-alphamesosaprobe; a – alpha-mesosaprobe). Organic pollution was calculated based on the values of the saprobity indices and indicator groups, and, accordingly, water quality classes. The above indicators were used to assign the water to the following quality classes: I – 0–0.5 (x, x-o); II – 0.6–1.5 (o-x, x-b, o, o-b); III – (b-o, o-a, b, b-a); and IV – (a) (Belous et al. 2013; Bilous et al. 2014, 2016; Barinova et al. 2019).

Valid names are given according to AlgaeBase (Guiry and Guiry 2019). The taxonomic list was compiled in accordance with the system used in Tsarenko et al. (2011, 2014).

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Table 1. Morphometry and basic parameters of the studied lakes (original measurements)

Location	Nesamovyte Lake	Brebeneskul Lake
Coordinates	48°07′36.6″N 24°32′26.4″E	48°06′′06.0″N 24°33′44.2″E
Elevation, m a.s.l.	1748	1793
Area, ha	0.3	0.6
Max. depth, m	~2.0	2.4
Water temp., °C	18.3 (16.2)	18.4 (–12.6)
pH	6.2–6.4	7.1
Conductivity, μS/cm	8.2–9.8	26.74
O_2, mg/l	10.7	6.32

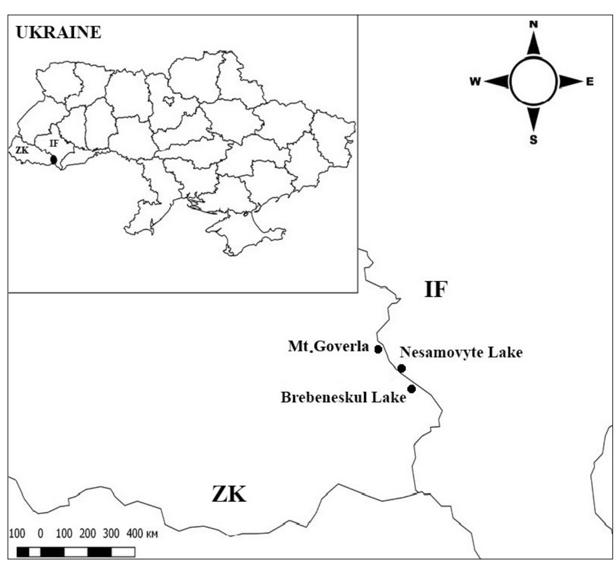

Figure 1. Location of Nesamovyte and Brebeneskul lakes (IF – Ivano-Frankivsk Region; ZK – Zakarpatia Region).

To compare the species composition of the lakes, we used Venny 2.1.0 software to construct Euler circles. Species occurrence in the samples was estimated on the Starmach scale (Wasser 1989). Ecological features of the species are presented according to Barinova et al. (2006, 2015, 2019) and Bilous et al. (2016).

Results and discussion

The material from 100 years of investigation of the two lakes contained 99 species of green and charophytic algae (109 taxa at species and intraspecific rank) belonging to four classes (*Trebouxiophyceae*, *Chlorophyceae* and *Oedogoniophyceae* from *Chlorophyta*; *Zygnematophyceae* from *Charophyta*), eight orders, 16 families and 35 genera (Table 2). Charophytic algae account for most of the algal diversity (84.4%). The families *Desmidiaceae* (75.2%) of the charophytic algae and *Scenedesmaceae* (6.5%) of the green algae together formed ~82% of the species composition of the algae. The richest genera were *Staurastrum* (22 species, 25 intraspecific; 22.9%), *Cosmarium* (17 species, 15.6%), *Euastrum* (13 species, 17 intraspecific; 15.6%), *Closterium* (6 species, 5.5%), *Tetmemorus* (2 species, 4 intraspecific; 3.7%), *Actinotaenium* and *Staurodesmus* (3 species, 2.8% each), *Pseudopediastrum* (2 species, 3 intraspecific; 2.8%), and *Gonatozygon* and *Penium* (2 species, 1.8% each). Twenty-one genera were represented by only one species each.

About 85% of the species composition were charophytic algae (*Zygnematophyceae*), which develop primarily in higher aquatic plant associations (58%). The share of this group in other biotopes is much lower: ~20% in the benthos and ~22% in the plankton. We found similar shares of ~85% for *Chlorophyta* in the water column of the two lakes, and small shares (7.5% each) in the benthos and in aquatic plant associations. Such an uneven biotopic distribution of algae is due to the ecological requirements and habit of the species and taxonomic groups. Most of the species diversity was contributed by the algae of Nesamovyte Lake (83 species, 92 intraspecific; 84.4%).

The first information about the diversity of algae in the Chornohora lakes, including this lake, was presented by Woloszynska (1920), based on material from the early 20th century (collected by R. Raciborski in 1910 and T. Wilezyński in 1914). Wołoszynska studied and analyzed the algal diversity of Nesamovyte Lake in detail by comparing it with that of other mountainous regions of Europe – the Alps, Tatras and Sudetes. She noted 80 taxa at species and intraspecific rank from six groups: *Cyanoprokaryota* (3), *Chrysophyta* (1), *Dinophyta* (2), *Bacillariophyta* (17), *Chlorophyta* (4) and *Charophyta* (43, according to the modern understanding of the rank and structure of the species as well as the identity of some of them). This information remained unchanged for almost half a century. Later, collections from 1967 (collected by Z.I. Asaul) enabled regular study of the *Desmidiales* algae of the lakes of the Chornohora region, including Nesamovyte and Brebeneskul lakes (Palamar-Mordvintseva 1978a, b, 1982). However, these publications only noted the presence of more than 100 *Desmidiales* taxa in 14 lakes of the region, without specifying the lakes, and mentioning several species of that group as well as coccoid green algae in the two lakes we studied (Palamar-Mordvintseva 1978a, b). That author noted the distinctiveness of the algal species composition of the Chornohora region and characterized the lakes as a different type of waterbody, and also determined the main factors contributing to the diversity and distribution of *Desmidiales* in the studied water bodies.

The algological samples housed in AKW, taken from these lakes in the 1960s, archival materials from Prof. G.M. Palamar-Morvintseva's studies, and the results of our research in 2013–2017 allowed us to track the species diversity of the green and charophytic algae of Nesamovyte and Brebeneskul lakes over time. Our research confirmed the diversity of *Desmidiales* in Nesamovyte Lake and its marsh (Table 2). A comparison of the algal species composition of this lake at 50-year intervals (1910–1967–2017) indicates a decrease in the species diversity of this group. There were 41 species (43 intraspecific) in the early 20th century (Wołoszynska 1920), 29 (31 intraspecific) in the 1960s (Palamar-Mordvintseva 1978a, b), and only 20 species recently. In the latter period, rare species of the genera *Hyalotheca*, *Euastrum* and *Tetmemorus* were observed; they are peculiar to waterbodies of mountain regions. However, taxa of the genera *Actinotaenium*, *Cylindrocystis*, *Micrasterias*, *Netrium*, *Teilingia* and *Coelastrum*, noted in material from 1910, were not confirmed, representatives of genera *Penium*, *Sphaerozosma*, *Spirotaenia* and *Tortitaenia*, found in material from 1967, were not noted in 2017. Along with this, species of the genera *Mougeotia*, *Spirogyra*, *Zygnema*, *Oedogonium*, *Botryococcus*, *Chlamydomonas*, *Mucidosphaerium*, *Dictyosphaerium*, *Mychonastes* and *Westella* appeared in 2017 for the first time. The presence of representatives of the latter genera apparently indicates degradation of the oligotrophic waterbody, its transformation to a mesotrophic state, and its colonization by common species having a wide ecological amplitude.

There was also a change in the quantitatively dominant species: at the beginning of the 20th century (Wołoszynska 1920) the dominants were *Cylindrocystis brebissonii*, *Actinotaenium cucurbita*, *Cosmarium staurastriforme*, *C. venustum* var. *excavatum*, *Euastrum insigne*, *E. humerosum* var. *humerosum* and var. *subintermedium*, *E. didelta* and *Staurastrum muricatiforme*. In the middle of the 20th century (Palamar-Mordvintseva 1978) the dominants were *Staurastrum senarium* f. *senarium* and f. *tatrica*, *Euastrum pinnatum*, *E. humerosum* var. *humerosum* and var. *affine*, *E. didelta*, *E. denticulatum* and *Closterium directum*. In the early 21st century the dominants were *Hyalotheca dissiliens*, *Netrium digitus*, *Euastrum humerosum* var. *affine*, *E. ansatum* and *Staurastrum polytrichum*. The recently noted algal blooms in Nesamovyte Lake, resulting from massive growth of the green colonial coccoid alga *Botryococcus terribilis*, confirm the instability of the lake's ecosystem and its increase in trophy (Tsarenko et al. 2015, 2016, 2018; Mykitchak 2017).

Table 2. The algal indicators of the Nesamovyte and Brebenskul Lakes with species ecology (Barinova et al., 2006, 2019). Habitat preferences: B – benthic; P-B – planktic-benthic; S – soil; Ep – epiphytes; P – planktonic. aer – aerophyles. Streaming and oxygenation: St-str, low-flow moderately oxygenated water inhabitants; ae – aerophytes; st – standing water with low oxygenation inhabitants. pH (Hustedt 1957): ind – indifferents; acf – acidophils. Salinity: i – indifferents; hb – halophobes; oh – olihohalobes. Trophic state (Tro) (Van Dam et al. 1994): m – mesotraphentic; me – meso-eutraphentic; o-m – oligo- to mesotraphentic; e – eutraphentic; ot – oligotraphentic. Organic pollution (SI, Sap): x – xenosaprobes, x-o – xeno-oligosaprobes, o-x –oligo-xenosaprobes, x-b – xeno-betamesosaprobes. o – oligosaprobes, o-b – oligo-betamesosaprobes, b-o – beta-oligosaprobes, o-a – oligo-alphamesosaprobes, b – betamesosaprobes, b-a – beta-alphamesosaprobes, a – alpha-mesosaprobes.

Taxa	Nesamovyte Lake			Brebenskul Lake		Hab	Oxy	pH	Hal	Sap	SI	Tro
	1920	1967	2013-2016	1967	2013–2016							
Actinotaenium clevei (Lund.) Teil.	+	–	+	–	–	B	.	acf	.	.	.	o-m
A. cucurbita (Bréb. ex Ralfs) Teiling ex Růžička	+	–	–	–	–	P-B	.	acf	.	.	.	o-m
A. silvae-nigrae var. *parallelum* (Willi Krieger) Kouwest & Coesel	+	–	–	–	–	B	ae	acf	.	o-x	0.7	m
Closterium archerianum Cleve ex P. Lundell	–	–	–	+	–	B	.	acf	.	.	.	m
C. intermedium Ralfs	–	+	–	–	–	P, B	st	acf	.	x-b	0.8	o-m
C. jenneri Ralfs	–	–	–	+	–	P-B	.	acf	.	o	1.0	m
C. rostratum Ehrenb. ex Ralfs	–	+	+	–	–	B	ae	ind	.	o-x	0.7	m
C. navicula var. *crassum* (West & G.S. West) Grönblad	–	+	–	–	–	.	.	.	.	.	.	o-m
C. striolatum Ehrenb.	+	–	–	–	–	P-B	.	acf	.	o	1.2	o-m
Cosmarium amoenum var. *annulatum* Eichl. & Gutw.	+	–	–	–	–	.	.	.	.	.	.	.
C. angulosum Bréb.	–	–	+	–	–	B	.	ind	.	.	.	m
C. bipunctatum Børgesen	–	–	–	+	–	.	.	.	.	.	.	.
C. brebissonii Menegh. ex Ralfs	–	–	+	–	–	.	.	.	.	.	.	.
C. costatum var. *tatrense* Gutw.	+	–	–	–	–	.	.	.	.	.	.	.
C. difficile Lütkem.	–	–	–	+	–	B	.	acf	hb	.	.	m
C. margaritiferum Menegh. ex Ralfs	–	–	–	+	–	B	.	acf	i	.	.	m
C. minutum Delponte forma	+	–	–	–	–	B	.	acf	.	.	.	m
C. nasutum f. *tatrica* Gutw.	+	–	–	–	–	.	.	.	.	.	.	.
C. obtusatum (Schmidle) Schmidle	–	–	–	–	+	B	.	ind	i	o	1.3	me
C. polonicum Racib.	+	–	–	–	–	.	.	.	.	.	.	.
C. pygmaeum W. Archer	–	+	–	–	–	.	.	.	.	.	.	.
C. staurastriforme Gutw.	+	–	–	–	.	.	.	.	.	.	.	.
C. staurastroides Eichl. & Gutw. forma	+	–	–	–	–	.	.	acf	.	.	.	ot
C. subcostatum var. *minus* (West & G.S. West) Kurt Forster	–	+	–	–	–	B	.	ind	.	.	.	m
C. umbilicatum Lütkem.	–	–	–	+	–	B	.	ind	hb	.	.	e
C. venustum (Bréb.) W. Archer var. *excavatum* (Eichl. & Gutw.) West & G.S. West	+	–	–	–	–	P-B	.	acf	.	.	.	o-m
Cylindrocystis brebissonii (Ralfs) de Bary	+	–	–	+	–	B, S	st,ae	acf	.	x-b	0.8	o-m
Euastrum aboense Elfv.	+	–	–	–	–	.	.	acf	.	x-o	0.5	m
E. ansatum (Ehenb Ralfs.)	–	–	1	–	–	P-B	.	acf	.	x-o	0.5	o-m
E. binale (Turp.) Ralfs var. *papilliferum* Gutw.	+	–	–	–	–	B	.	acf	.	o-x	0.6	ot
E. denticulatum (Kirchn.) Gay var. *denticulatum*	+	+	+	+	+	P-B	.	acf	.	x-o	0.4	o-m
E. denticulatum var. *angusticeps* Groenbl.	.	+	–	+	–	.	.	.	.	.	.	.
E. didelta Ralfs ex Ralfs	+	+	+	–	–	.	.	acf	.	x-o	0.4	m
E. elegans (Bréb.) Kütz.	+	–	–	–	–	P-B	.	acf	hb	x-o	0.5	m
E. humerosum Ralfs var. *humerosum*	+	+	+	–	–	B	.	acf	.	x-o	0.5	o-m

Table 2. Continued.

Taxa	Nesamovyte Lake			Brebenskul Lake		Hab	Oxy	pH	Hal	Sap	SI	Tro
	1920	1967	2013-2016	1967	2013–2016							
E. humerosum var. *affine* (Ralfs) Racib.	–	+	2	–	–	B	.	acf	.	x-o	0.5	o-m
E. humerosum var. *subintermedium* Schröd.	+	–	–	–	–	.	.	.	.	.	.	.
E. insigne Hassall ex Ralfs	+	–	–	–	–	B	.	acf	.	x-o	0.5	ot
E. montanum West & G.S. West	–	+	–	–	–	B	.	acf	.	x-o	0.5	o-m
E. obesum Josh. var. *obesum*	–	+	–	–	–	.	.	acf	.	x-o	0.5	ot
E. obesum var. *subangulare* West & G.S. West	–	–	–	+	–	.	.	.	.	.	.	.
E. pinnatum Ralfs	+	+	–	–	–	B	.	acf	.	x-o	0.5	o-m
E. tuddalense Ström	–	+	–	–	–	.	.	.	.	x-o	0.5	.
E. verrucosum Ehrenb. ex Ralfs	–	–	–	+	–	P-B	.	acf	hb	o-x	0.6	m
Gonatozygon monotaenium var. *pilosellum* Nordst.	–	–	–	+	–	B	.	acf	.	x-b	0.8	m
Hyalotheca dissiliens Bréb. ex Ralfs	–	+	2	–	–	P-B	.	ind	hb	x-b	0.9	m
H. mucosa (Mertens) Ehrenb.	+	.	+	–	–	P-B	.	acf	hb	.	.	o-m
Micrasterias fimbriata Ralfs	+	–	–	–	–	B	.	acf	.	x	0.3	m
Mougeotia sp.st	–	–	+	–	–	.	.	.	.	.	.	.
Netrium digitus (Ehrenb. ex Ralfs) Itzigs. & Rothe emend. Ohtani	+	–	2	+	+	P-B	.	acf	i	x-o	0.5	o-m
N. oblongum (De Bary) Lütkm.	+	–	–	–	–	B, aer	ae	acf	.	x-o	0.5	ot
N. oblongum var. *cylindricum* West & G.S. West	+	–	–	.	–	.	.	.	.	.	.	.
Penium cylindrus Bréb. ex Ralfs	+	+	–	+	–	B	.	acf	.	x-o	0.4	o-m
P. spirostriolatum J. Barker	.	+	–	–	–	B	.	acf	.	x-o	0.5	o-m
Pleurotaenium ehrenbergii (Ralfs) De Bary	+	–	–	–	–	B	.	ind	i	x-o	0.4	m
Sphaerozosma aubertianum West	–	+	–	–	–	B	.	acf	.	x-o	0.5	m
S. pulchellum var. *austriacum* Lütkem.	+	–	–	–	–	.	.	.	.	.	.	.
Spirogyra sp.	–	–	+	–	–	.	.	.	.	.	.	.
Spirotaenia condensata Bréb. ex Ralfs	+	–	+	–	–	B, aer	ae	acf	.	x-b	0.9	o-m
Staurastrum arcuatum var. *subavicula* (West) Coesel & Meesters	–	+	–	–	–	P-B	.	ind	.	.	.	m
S. avicula Bréb.	–	+	+	–	–	P-B	.	ind	.	.	.	m
S. coarctatus Breb.	–	–	+	–	–	.	.	.	.	.	.	.
S. conspicuum West & G.S.West	–	+	–	–	–	.	.	.	.	.	.	.
S. diacanthum Lemaire	–	+	–	–	+	.	.	acf	.	.	.	ot
S. dilatatum Ehrenb. ex Ralfs	–	–	–	+	+	P	.	.	.	.	.	.
S. hexacerum Wittrock	–	–	–	+	+	P	.	acf	.	o-b	1.5	m
S. hirsutum var. *muricatum* (Bréb. ex Ralfs) Kurt Förster	–	–	+	+	–	B	st-str	acf	.	.	.	ot
S. muricatiforme Schmidle	+	–	–	–	–	B, aer	ae	acf	.	.	.	o-m
S. muticum Bréb. ex Ralfs var. *muticum*	–	–	+	–	–	B	st	acf	i	.	.	m
S. muricatum f. *tatrica* Gutw.	+	–	–	–	–	.	.	.	.	.	.	.
S. pilosum Bréb.	–	–	–	+	+	P-B	st-str	acf	.	.	.	m
S. polytrichum (Perty) Rabenh.	.	+	1	–	–	B	.	acf	.	b-o	1.6	m
S. punctulatum Bréb.	–	–	–	+	+	P-B	st-str	ind	i	o	1.2	o-m

Table 2. Continued.

Taxa	Nesamovyte Lake			Brebenskul Lake		Hab	Oxy	pH	Hal	Sap	SI	Tro
	1920	1967	2013-2016	1967	2013–2016							
S. sebaldii Reinsch	+	–	–	–	–	B	.	ind	.	.	.	m
S. senarium (Ehrenb.) Ralfs f. *senarium*	.	+	–	–	–	B	.	acf	.	.	.	m
Staurastrum senarium f. *tatrica* Racib.	+	+	–	–	–	.	.	.	.	.	.	.
S. sexcostatum Bréb. ex Ralfs	.	+	–	–	–	B, aer	ae	acf	.	.	.	m
S. sexcostatum var. *productum* (West) West & G.S. West	–	+	–	–	–	B	.	acf	.	.	.	m
S. scabrum Bréb.	+	–	–	–	–	B	.	acf	.	.	.	o-m
S. subavicula var. *tyrolense* (Schmidle) Irenne-Maria	+	–	–	–	–	.	.	.	.	.	.	.
S. teliferum Ralfs var. *teliferum*	+	–	–	–	–	.	.	.	.	.	.	.
S. teliferum var. *gladiosum* (W.B. Turner) Coesel & Meesters	–	–	+	–	–	.	.	acf	.	.	.	m
S. turgescens De Not.	+	+	–		–	.	.	acf	.	.	.	m
S. vastum Schmidle	+	–	–	–	–	.	.	.	.	.	.	.
Staurodesmus dejectus (Bréb. ex Ralfs) Teiling	+	–	–	–	–	P-B	.	ind	hb	o-b	1.5	o-m
S. extensus var. *isthmosus* (Heimerl) Coesel	–	+	–	–	–	B	.	acf	.	.	.	o-m
S. glaber (Ehrenb. ex Ralfs) Teiling	–	+	+	–	–	B	.	acf	.	.	.	o-m
S. quadratus (Schmidle) Teiling	–	–	+	–	–	.	.	acf	.	.	.	m
Teilingia granulata (Roy & Bisset) Bourrelly	+	–	–	–	–	.	.	.	.	.	.	.
Tetmemorus brebissonii Ralfs var. *brebissonii*	–	–	+	–	–	B	.	acf	.	x-b	0.8	ot
T. brebissonii var. *minor* De Bary	+	–	–	–	–	B	.	acf	.	x-b	0.8	o-m
T. laevis Ralfs ex Ralfs var. levis	+	–	–	–	–	B, aer	ae	ind	.	x-o	0.5	o-m
T. laevis var. *intermedius* (Woronich.) Růžička	–	+	–	–	–	.	.	.	.	.	.	.
Tortitaenia alpina (Schmidle) Brook	+	–	+	–	–	.	.	.	.	.	.	.
Zygnema sp. st.	–	–	+	–	–	.	.	.	.	.	.	.
Botryococcus braunii Kütz	–	–	+	–	–	P-B	st	ind	i	o-b	1.5	.
B. terribilis Komarek & Marvan	–	–	5	–	–	.	.	.	.	.	.	.
Chlamydomonas reinhardtii P.A. Dangeard	–	–	+	–	–	P-B	st-str	.	oh	a	3.1	.
Coelastrum sp.	+	–	.	.	.	.	.	.	.	.	.	.
Crucigeniella irregularis (Wille) P.Tsarenko & D.M. John	–	–	–	+	–	P-B	st-str	ind	i	.	.	.
Dictyosphaerium chlorelloides (Nauman) Komárek & Perman	–	–	+	–	–	.	.	.	.	.	.	.
Desmodesmus communis (E. Hegew.) E. Hegew.	+	–	+	+	+	P-B, Ep	st-str	ind	i	b	2.15	.
Lemmermannia triangularis (Chodat) C. Bock & Krienitz	–	–	+	–	–	.	.	.	.	.	.	.
Mucidosphaerium pulchellum (H.C. Wood) C. Bock, Pröschold & Krienitz	–	–	+	+	–	P-B	st-str	ind	i	b	2.3	.
Mychonastes anomalus (Korschikov) Krienitz, C.Bock, Dadheech & Pröschold	–	–	+	–	–	.	.	.	.	.	.	.
Oedogonium sp. st.	–	–	+	.	.	.	.	.	.	.	.	.
Pediastrum braunii Wartmann	+	–	–	–	–	P	.	.	.	o	1.3	.
P. duplex Meyen	–	–	–	+	+	P	st-str	ind	i	b	2.1	.
Pseudopediastrum boryanum (Turpin) E. Hegew. var. boryanum	–	–	–	+	+	.	.	.	.	.	.	.
P. boryanum var. *longicorne* (Reinsch) P. Tsarenko	–	–	+	–	+	P-B	st-str	.	.	b	2.1	.
Tetradesmus dimorphus (Turpin) M.J. Wynne	+	–	+	–	–	.	.	.	.	.	.	.
Westella botryoides (West) De Wildeman	–	–	+	–	–	P	st-str	.	.	o-a	1.8	.

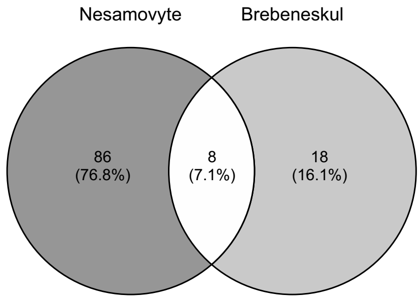

Figure 2. Degree of similarity of species composition of green and charophytic algae between Nesamovyte and Brebeneskul lakes.

The algae of Brebeneskul Lake show low floristic and taxonomic diversity, with only 23 species (26 intraspecific), which is ~24% of the total algal species of the investigated lakes. *Charophytes* account for ~77% of the identified algae; green algae are less diverse (23%) and are found occasionally, mostly in the marshy part of the lake environment among higher aquatic plant associations. The species composition of the plankton and benthos (the rocky bottom of the lake, slightly silted near shore) was depauperate. The most diverse genera are *Staurastrum*, *Cosmarium*, *Euastrum*, *Closterium* and *Pseudopediastrum*, and the remaining eight genera of both groups are represented by one species each. Such low species diversity in Brebeneskul Lake was noted earlier for euglenophytes and desmids (Asaul 1969; Palamar-Mordvintseva 1978a); this was apparently due to its oligotrophy, degree of mineralization, sharp temperature gradient from the upper to bottom layers of the water, and the lake's origin and location (at the bottom of a glacial cirque). The presence of rare or typical species (*Gonatozygon monotaenium* var. *pilosellum*, *Netrium digitus*, *Staurastrum diacanthum*, *Staurastrum punctulatum*) testifies to the algosozological value of this lake, the appropriateness of its being included in the Carpathian Biosphere Reserve, and the need for environmental protection measures to maintain this ecosystem.

The two lakes differed in algal species composition. Most of the taxa (83 species, 92 intraspecific; ~84%) were recorded in Nesamovyte Lake. The degree of similarity between the green and charophytic algae of this lake and those of Brebeneskul Lake was very low, only 7.1% (Fig. 2).

Only seven taxa were found in the material from both lakes. (*Cylindrocystis brebissonii*, *Euastrum denticulatum*, *Euastrum denticulatum* var. *angusticeps*, *Netrium digitus*, *Penium cylindrus*, *Desmodesmus communis*, *Pseudopediastrum boryanum* var. *longicorne*). The differences in the algal species composition of the two lakes can be explained by environmental factors and by features specific to these waterbodies – differences in their morphometric indicators, and the degree of modern transformation of their ecosystems. In particular, the species diversity of Nesamovyte Lake apparently has decreased as a result of anthropopression, changes in trophy, temperature increases and long dry periods in recent years,

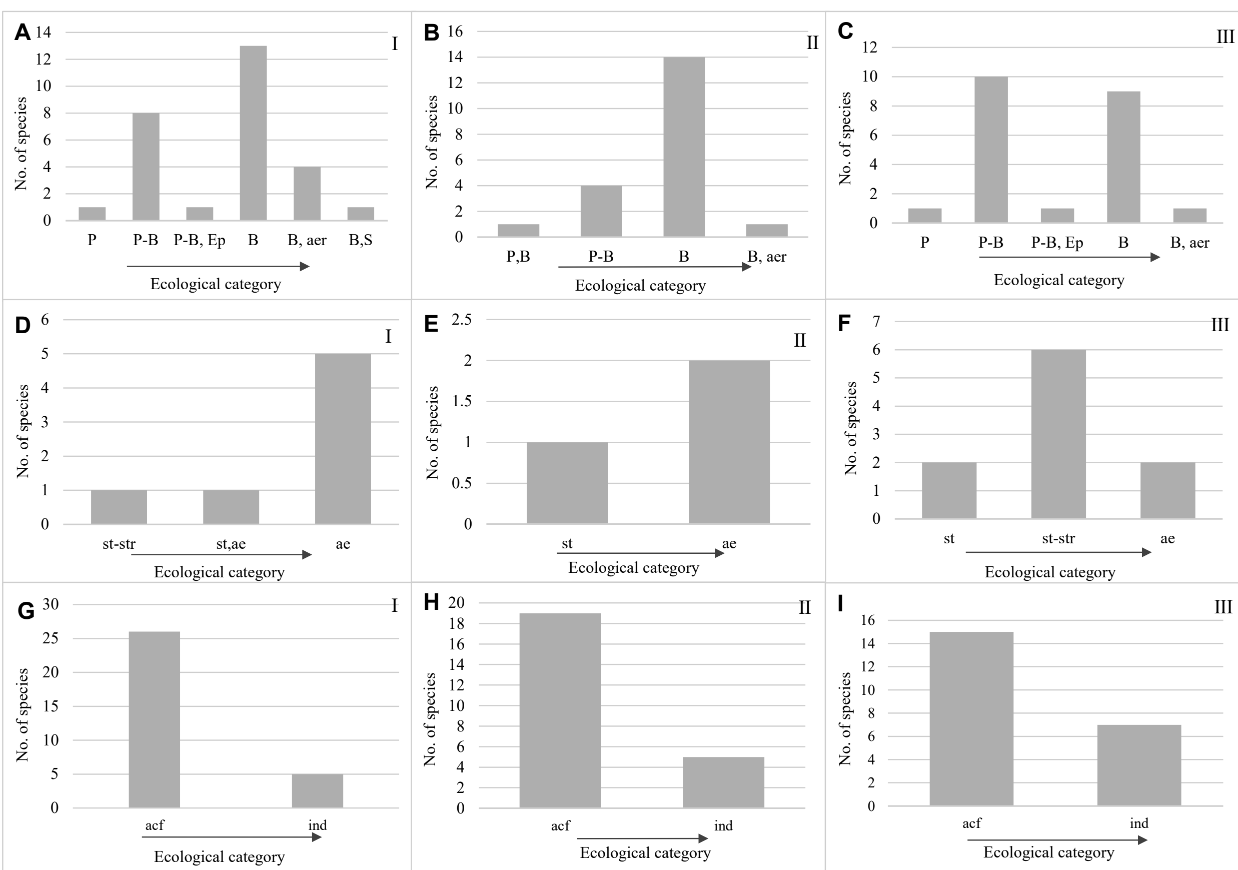

Figure 3. Bioindication plots for ecological analysis of habitat preference (A–C), current and oxygenation (D–F) and pH (G–I) in Nesamovyte Lake (for the periods: I – 1920, II – 1967, III – 2013–2016).

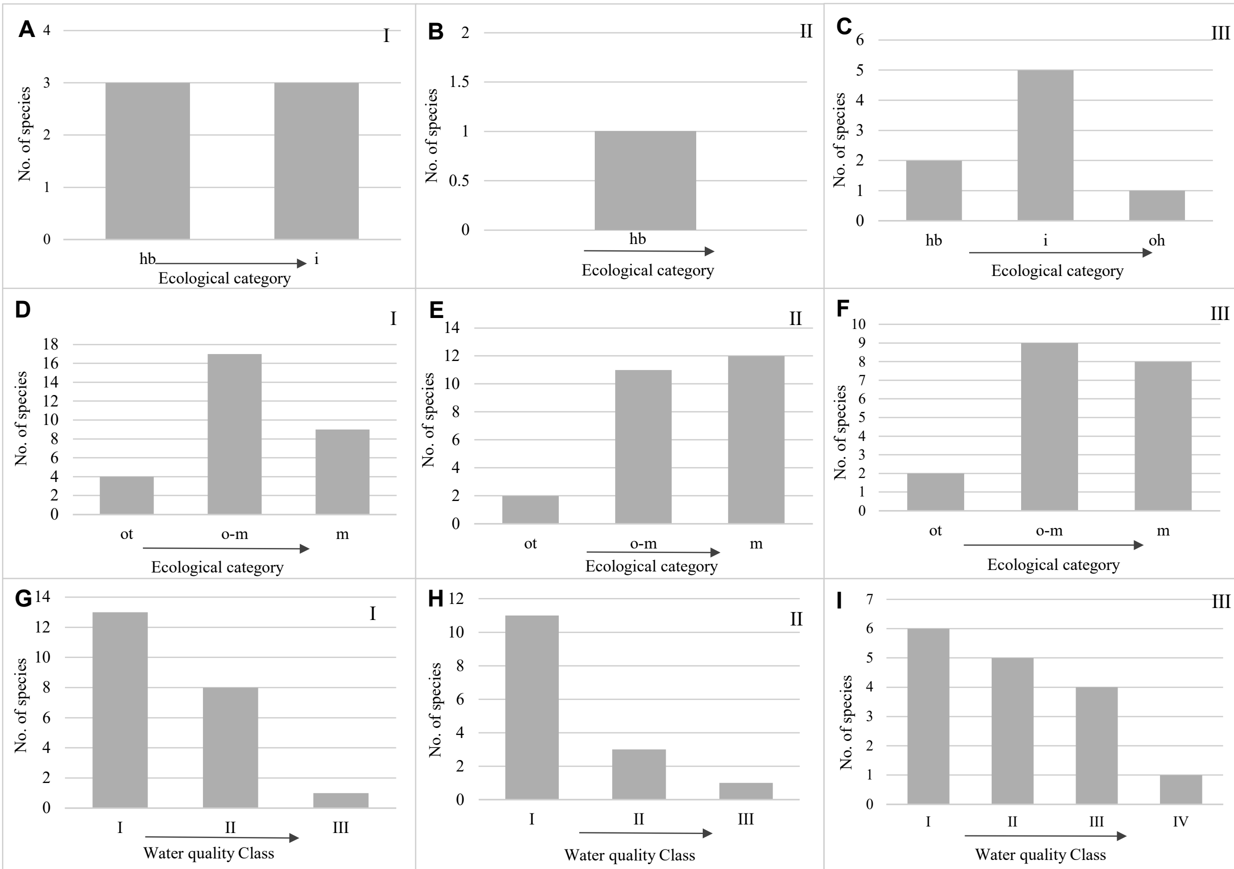

Figure 4. Bioindication plots for ecological analysis of salinity (A–C), Trophic state (D–F), water quality class (according to organic pollution) (G–I) in Nesamovyte Lake (for the periods: I – 1920, II – 1967, III – 2013–2016).

resulting in a decrease of the lake surface area and lower water content of the near-shore wetland, and the lack of characteristic types of oligotrophic waterbodies in the subalpine zone (Wołoszynska 1920; Palamar-Mordvintseva 1978a, 1982; Lukavsky 1994; Lenarczyk & Tsarenko 2013). Similar changes in the ecosystem and in its species composition of algae have also occurred in Brebeneskul Lake.

The changes in algal indicator taxa algae in Nesamovyte Lake in 1920, 1967 and 2013–2016 reflect changes in lake conditions. Taxa that inhabit different biotopes declined. In 1920 the dominant indicators were benthic (B) along with plankto-benthic (P-B), followed by benthic and aerophyles (B-aer), planktonic (P), benthic and soil (B, S), and plankto-benthic and epiphytes (P-B, Ep); in 2014–2016 we noted decreases of P-B, B, B-aer, P and P-B, and Ep, along with a decrease in the number of benthic forms, the predominance of plankto-benthic and disappearance of a group of algae that can occur in both benthos and soil (Fig. 3A, B, C). Perhaps this can be explained by the changes in the hydrological regime or by differences in the way algological material was sampled in the 1920s, as well as by the current state of the waterbody and its near-shore wetland.

Data on the algal indicators of oxygen regime and water movement confirm changes in the hydrological regime of the lake. Early data indicate the predominance of aerophytes (ae), indicating that the water was oxygen-enriched in 1920; along with the aerophytes there was a more or less uniform distribution of taxa indicating low-flow, moderately oxygenated water (st-str) and standing water with low oxygenation (st) (Fig. 3D). Data from 1967 show a gradual increase in the role of standing-water algae, with taxa indicating low oxygenation. By 2013–2016, the dominant taxa had shifted from aerophytes to taxa characteristic of low-flow, moderately oxygenated water (st-str) (Fig. 3E, F). This indication of lower oxygen may reflect environmental degradation.

The pH-indicating taxonomic groups remained stable over the studied years: only indifferents (ind) and acidophiles (acf) were found. Acidophiles prevailed in all the studied years, indicating neutral to slightly acid water (Fig. 3G, H, I), but the increasing share of indifferents suggests an upward trend of pH from neutral to 7, which is seen in Nesamovyte Lake (2013–2016) (Fig. 3I). In terms of salinity, indicators of typically fresh waterbodies were identified, characterizing the lakes as freshwater both earlier and recently, though we observed a tendency to increased mineralization, the appearance of low numbers of oligohalobes (Fig. 4A, B, C). The trophic state of the lake is determined by a multitude of interrelated physicochemical and biological processes; in these lakes those processes were reflected in the presence of mesotraphentic (m), oligo- to mesotraphentic (o-m) and oligotraphentic (ot) (Fig. 4D, E, F) indicator groups. In the recent period, as before, oligo- to mesotraphentic indicators prevailed, reflecting relatively clean water. However, as seen from Figure 6, a decrease of oligotraphentic

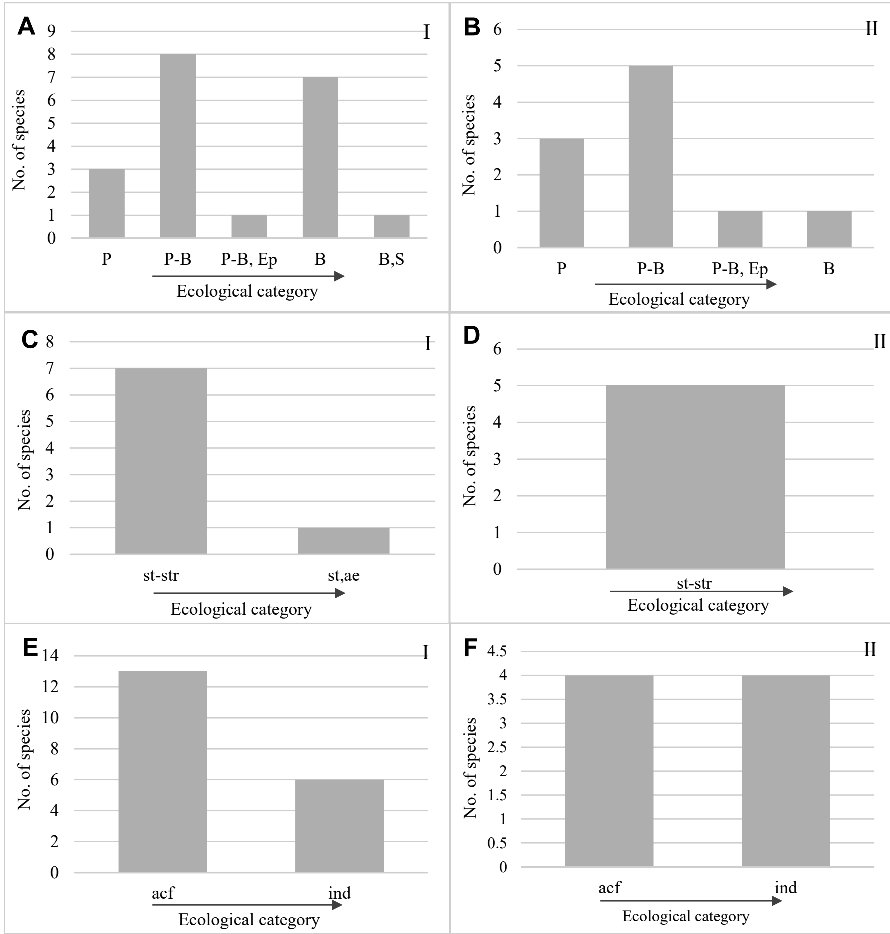

Figure 5. Bioindication plots for ecological analysis of habitat preference (A, B), current and oxygenation (C, D) and pH (E, F) in Brebeneskul Lake (for the periods: I – 1967, II – 2013–2016).

indicators and the growing share of mesotraphentic species testify to deterioration of lake trophy. In regard to organic pollution, taxa indicating the first (cleanest) class of water quality prevail (Fig. 4G, H, I). In Nesamovyte Lake the indicator taxa were distributed among the three water quality classes (I, II, III) at the beginning of the 20th century (1920) and also in subsequent periods (1967, 2013–2016). Recently, however, taxa indicating quality class V class were found; no taxa of that group were present in 1920 and 1967. Thus we see some deterioration of the state of the lake, despite the continued dominance of taxa indicating water quality class I.

In the ecosystem of Brebeneskul Lake, plankto-benthic species dominated the algal assemblage in both 1967 and 2013–2016. The shares of other habitat-limited organisms changed over time. In 1967 the number of benthic forms was higher; it decreased in 2013–2016, replaced by a larger number of planktonic forms (Fig. 5A, B); differences in sampling methods may be partly responsible for this. The 1967 samples contained benthic, plankto-benthic, planktonic, benthic, soil, plankto-benthic and epiphytic taxa; by 2013–2016 the benthic and soil species had vanished. This suggests a change in the lake's hydrological regime. Here we note that taxa of low-flow, moderately oxygenated water were observed in the recent period as well as earlier (Fig. 5C, D). Taxa indicating standing water (st) with low oxygenation, along with aerophytes (ae), were in the 1967 samples but not in the material from 2013–2016. This supports the suggestion of altered hydrology, but in view of the low number of indicators it is difficult to assert that with certainty. In Brebeneskul Lake, in both 1967 and 2013–2016 the same groups of water pH indicators were found, but in 1967 acidophiles dominated and there were few indifferents; the share of indifferents has increased since then, pointing to an increase in pH, closer to pH 7 (Fig. 5E, F). For salinity, indiferrents predominated both recently and earlier, but halophobes (hb), present in 1967, no longer occur in the lake (Fig. 6A, B). Halophobes are strictly freshwater species, disappearing with a slight increase in salinity. Thus, it can be assumed that small changes in the mineral regime have occurred, though the water remains fresh. Figure 6C, d shows the decline in the trophic state of the lake through time. In the earlier period, mesotraphentic indicators prevailed, followed by oligo- to mesotraphentic (o-m); eutraphentic (e) and oligotraphentic (ot) indicators were marginally represented. The picture has changed somewhat since then: oligo- to mesotraphentic species (o-m) are followed by mesotraphentic and a small number of meso-eutraphentic (me).

Organic pollution gives the final evidence about changes in the state of Brebeneskul Lake (Fig. 6E, F). In 1967, indicators of water quality class II prevailed, with few indicators of classes I and III; the material from

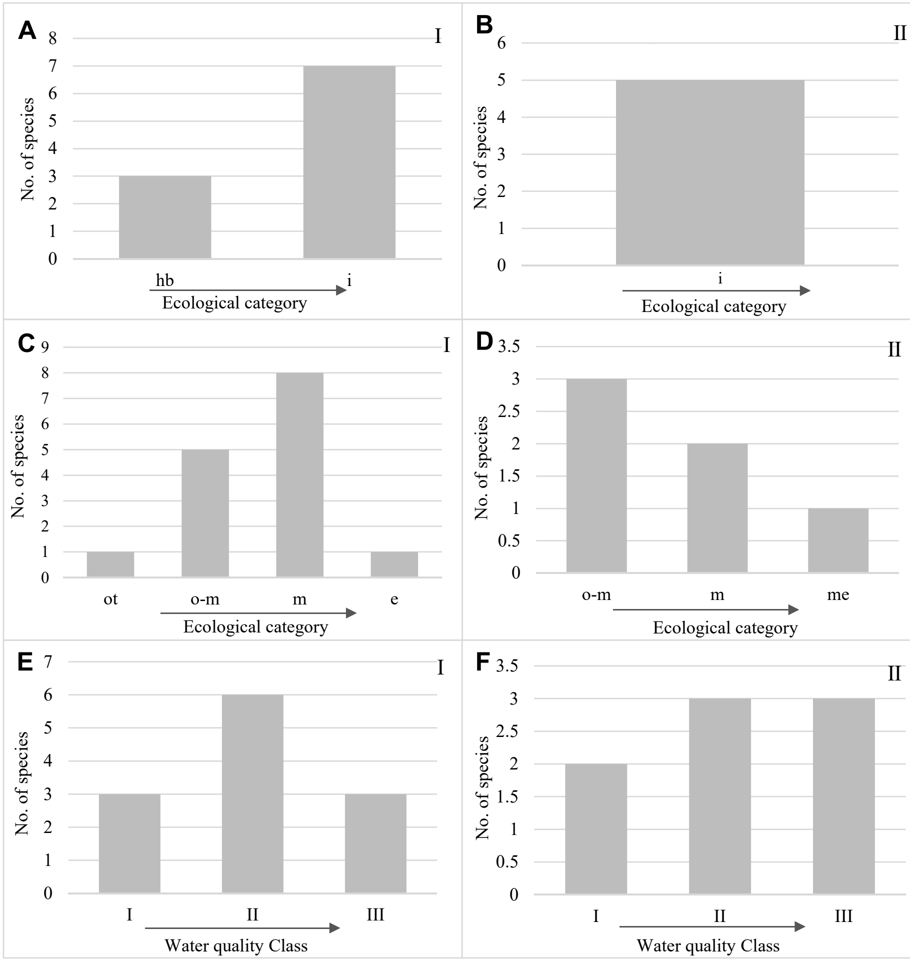

Figure 6. Bioindication plots for salinity (A, B), trophic state (C, D) and water quality class (according to organic pollution) (E, F) in Brebeneskul Lake (I: 1967, II: 2013–2016).

2013–2016 contains the same shares of class III and class II indicator taxa as noted in 1967, and fewer class I indicators. From this we infer that the water has changed from clean to moderately polluted.

Conclusions

Our bioindication-based environmental analysis focusing on the composition of green and charophyte algae produced conclusions restricted to several systematic groups. In terms of typology and biology, the two studied high-mountain lakes of Chornohora are oligo-mesotrophic and contain the corresponding range of aquatic organisms and algae. However, increased anthropopression, impacts of recreational use, and the accompanying changes in the ecosystem are transforming their biota. Such changes characterize the Nesamovyte Lake ecosystem over the more than century-long observation period: in particular, the transition from oligotrophic to beta-mesosaprobic (Wołoszynska 1920; Asaul 1969, Palamar-Mordvintseva 1978a, b, 1982; Mykitchak 2014). Confirmation is found in the results of studies of lake hydrobionts from 2012–2013 (Mykitchak et al. 2014; Tsarenko et al. 2014, Mykitchak 2017). Our study of the green and charophyte indicator species of the two lakes suggests that the ecosystems of Nesamovyte Lake and Brebeneskul Lake have deteriorated recently, and that the negative changes are worse in Brebeneskul Lake.

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