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Environmental Factors Structuring Diatom Diversity of the Protected High Mountain Lakes in the Kaçkar Mountains National Park (Rize, Turkey)

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Abstract: The altitude of the habitat is one of the important regulators of species survival. Kaçkar Mountains National Park is located in the Eastern Black Sea region of Turkey. This is the first study on the benthic diatom flora of the high mountain lakes in Kaçkar Mountains National Park, which is situated between 2782 and 3075 m a.s.l. A total of 84 diatom species were identified from benthic communities of 15 habitats in summer (19 July, 28 August) and autumn (10 September) months of 2020. The genus *Pinnularia* (thirteen species) formed the basis of the taxonomic list, followed by *Eunotia* (five species), *Navicula* (five species), and *Frustulia* (four species) genera, respectively. The waters in all the studied lakes were fresh, low-saline, with low-alkaline or circumneutral pH and organically uncontaminated, as evidenced by prevailed bioindicator groups. Statistical methods and comparative floristic results confirm the role of the lake altitude for the diatom species distribution. The species richness of the studied lakes was higher in lakes with lower altitudes. The statistical approach also revealed the potential for an increase in the number of species in high mountain lakes if the study of the diatom flora of the Kachkar Mountains National Park is continued and the species composition of the lakes is replenished. Further studies will be needed to continue exploring this pattern. To protect studied high mountain lakes, their ecological conditions must be constantly monitored in the Kaçkar Mountains National Park.

Keywords: high mountain lakes; diatoms; benthic habitats; environmental factors; bioindicator; threatened and rare species; Kaçkar Mountains National Park; Turkey

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1. Introduction

Siliceous crystal mountain ranges are among the highest-altitude regions in the world. This feature allows them to harbor pristine biodiversity, provide recreation areas, and maintain healthy water resources. Therefore, they hold a prominent position among natural areas that need protection [1].

High mountain lakes are habitats where a limited number of species live, as they generally have low nutrient and ion concentrations [2]. They are also sensitive to climate change, dissolved organic carbon, and nitrogen inputs [3,4]. Increases in air temperature and changes in snow and ice cover on mountains in some regions have changed the functioning, diversity, and productivity of these lakes [5–7]. Despite these effects, high mountain lakes are still considered as undisturbed ecosystems [8].

Biodiversity, which bears the evidence of evolutionary processes, plays an important role in the maintenance of ecological functions and the stability of the ecosystem [9]. At the same time, biodiversity is also used to evaluate the environmental status of aquatic ecosystems [10]. Diatoms, which have very important ecological functions, contribute 20–25% to the world's global primary production, carbon fixation, and oxygen release to the atmosphere, thanks to their photosynthetic activities [11,12]. In addition, the annual amount of carbon fixation by diatoms represents 40% of total primary production in seawater, an amount equivalent to the total amount fixed by all terrestrial tropical forests [13]. Therefore, examining the diatom communities in the sediments of high mountain lakes and using the obtained information in the creation of diatom-based biomonitoring programs will be one of the most effective ways to understand the response of these lakes to climatic change [14].

The need to study the species richness and ecology of benthic diatoms becomes more obvious as data accumulate in the biomonitoring system of high mountain lake ecosystems of the Eastern Black Sea region. Studies have been carried out on the benthic diatom flora of high mountain lakes and the physico-chemical properties of their waters in the region since 1990 [15]. However, until now, no information has been obtained about the diatom flora of the high mountain lakes in the Kaçkar Mountains National Park.

The aim of this work was to describe the diversity of benthic diatoms collected from 14 lakes and a pond in the Kaçkar Mountains National Park, located in the Eastern Black Sea region of Turkey, and their relationship with environmental factors. Additionally, it determines the rarity and frequencies of diatom species based on the number of studied lakes where species were found.

2. Materials and Methods

2.1. Description of Study Site

The Kaçkar Mountains National Park was designated as a national park in 1994. It covers a total area of 51,550 hectares and is located administratively between Rize, Artvin, and Erzurum Provinces (40°57′49″–40°42′10″ N–41°14′45″–40°51′27″ E) (Figure 1) [16]. The Park is located in the northeastern part of the Eastern Black Sea Mountain Belt, which runs parallel to the southeastern Black Sea coast. It is approximately 600 km long and 200 km wide. The park mainly consists of granitic and volcanic rocks that range in age from the Late Cretaceous to the Eocene [17]. The area is primarily composed of Granodiorite and Cretaceous flysch, with occasional patches of Neogene deposits. These structures were brought to the surface during the mountain formation process that occurred during the Paleozoic (I Period) and Cretaceous periods (III Period) [16]. The Kaçkar Mountains are one of the few places where current glaciation is observed alongside traces of Pleistocene glaciers. This region boasts numerous glaciers, glacial lakes, glacial valleys, cirques, and moraines [18]. With an altitude of 3932 m, the Kaçkar Mountains are the fourth highest mountain in Turkey and are home to nearly 100 glacial lakes [16].

The area is classified under Turkey's climate classification system [19] as being under the influence of the Eastern Black Sea climate. This climate is characterized by cool summers, temperate winters, and rainfall throughout the year. In the lower, northern part of the Kaçkar Mountains National Park, such as around the Ayder Plateau, temperatures range from 0 °C to 4 °C during the winter months and rise above 18 °C in the summer. At an altitude of over 3000 m a.s.l. in the southern mountains of the park, temperatures drop to −6 °C in winter and range from 6 to 9 °C in summer. High alpine areas are typically covered in snow from late September to mid-May. The park receives an annual average precipitation of over 2000 mm. The park is composed of four major soil groups: high mountain meadow soils, limeless brown forest soil, red yellow soils, and gray brown soils [16]. The park area has significant biodiversity in terms of flora and fauna. Davis [20] identifies the research area as part of the Colchis (Colchis) region of the Euro-Siberian floristic region. The forest belt contains broad-leaved conifers, *Fagus orientalis*, *Castanea sativa*, and *Carpinus* sp. The alpine zone has a rich vegetation with many endemic and relict species. This location in Turkey is unique, as it is the only place where Rhododendrons grow at an altitude of 3000 m above sea level. The study area is one of three significant routes for bird migration, with the northeast–south migration route being the most important for daytime raptors in the Western Palearctic [21].

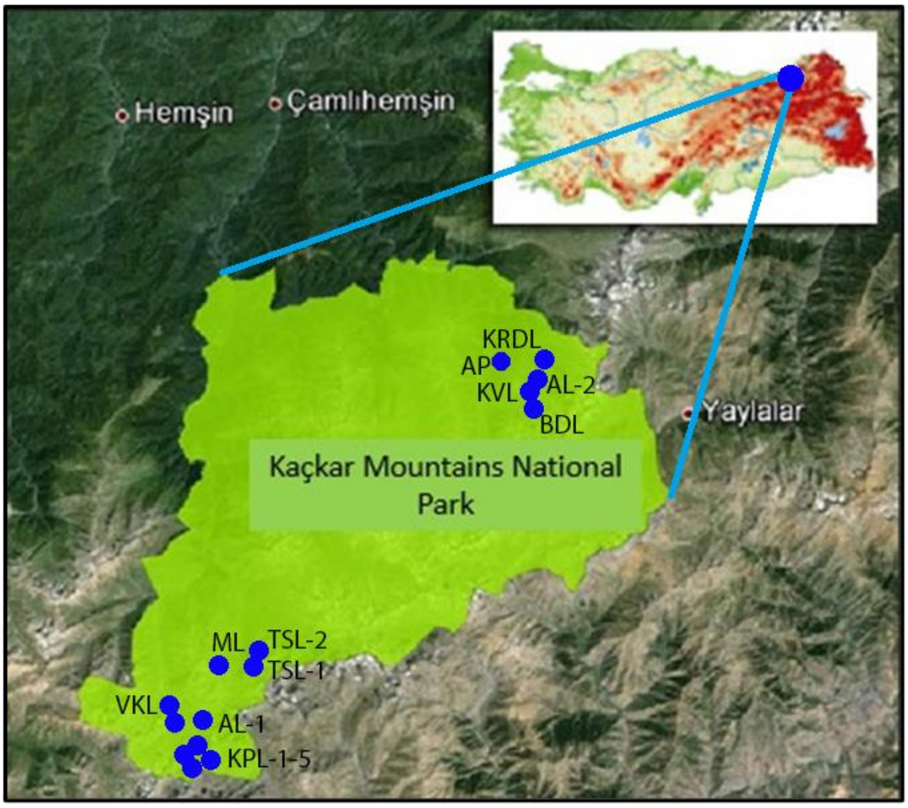


Figure 1. Geographical location of Kaçkar Mountains National Park, green colored (https://en.wikipedia.org/wiki/List_of_national_parks_of_Turkey (accessed on 10 January 2024)) and the studied lakes as blue dots.

2.2. Methods of Sampling and Laboratory Studies

A total of 39 samples of epipelic, epilithic, and epiphytic algae were collected from 14 lakes and a pond on 19 July, 28 August, and 10 September 2020 (Figure 2, Table 1). Due to the inaccessibility of the lakes, 2 or 3 fouling samples were taken from each. Epipelic algae were collected from the sediment surface of all studied waters using a glass pipe 1 m long and 0.8 cm in diameter. Epilithic samples from 2 or 3 stones were collected only from TSL-1, TSL-2, BDL, and KVL lakes. Randomly selected stones were scraped off with a toothbrush and the suspension was placed in plastic bottles.

Epiphytic species were collected by squeezing out from the macrophytes (*Potamogeton* sp. and *Juncus* sp.), where several parts of submerged plants were manually squeezed out, and the suspension was placed in a test tube found in KVL and AP [22,23]. All samples were preserved in 100 mL plastic bottles with 4% (v/v) formaldehyde. In the field, we measured in three repetitions the water temperature, dissolved oxygen, conductivity, and pH using Thermo Orion-4-Star pH and YSI-55 portable meters for all sampling points, excluding AP pond, where variables were not tested because the water sample was lost. The DSI General Directorate Laboratories DSI 22nd Regional Directorate Quality Control and Laboratory Branch Office conducted analyses of variables other than temperature, dissolved oxygen, conductivity, and pH: potassium, total hardness, calcium, magnesium, ammonium, chlorine, nitrate, nitrite, and phosphate hydrochemical parameters. Diatom samples were acid-purified using H_2SO_4 and HNO_3 in the lab, followed by washing with distilled water [22]. The cleaned diatom shells were then placed in Naphrax®. The diatoms were examined (up to 400 shells per slide) and photographed using a Leica DM 2500 light microscope and a Leica DFC 290 camera (Leica, Wetzlar, Germany).

To identify the diatom species, we consulted relevant literature, including [24–35]. We verified the nomenclature of all identified taxa on the Algaebase website [36].

Frequencies of algal taxa were determined based on the number of lakes in the Kaçkar Mountains Natural Park where species were found, according to the following scale: very rare (VR)—taxa recorded in 1–20% of investigated lakes; rare (R)—in 21–40%; common (C)—in 41–60%; frequent (F)—in 61–80%; very frequent (VF)—in 81–100% [37].

Bioindication methods were used to assess the ecological state of lake ecosystems [38]. For this purpose, the distribution of species with certain ecological preferences was identified across intervals of environmental factors [39]. Then, data on the abundance of species in a particular lake were summarized for each indicator group. The distribution of the number of species with the same indicator properties was plotted by ecological groups for each environmental variable. The class of water quality indicators of organic pollution was grouped by the range of the species-specific index of saprobity S: class 1, S = 0.0–0.5; class 2, S = 0.5–1.5; class 3, S = 1.5–2.5; class 4, S = 2.5–3.5 [39]. In total, groups of indicators for nine environmental and ecosystem variables (substrate preferences, temperature, oxygen, salinity, pH, organic pollution by Watanabe system [40], organic pollution by Sládeček system [41], autotrophy–heterotrophy nutrition type, trophic state) were used for analysis in this study. The arrangement of groups of indicators for each environmental variable on the histogram was in increasing order of the indicated variable.

Figure 2. View of the studied lakes in the Kaçkar Mountains National Park in 2020. North group: (**a**) Karadeniz Lake, (**b**) Büyük Deniz Lake; central group: (**c**) Moçar Lake, (**d**) Tatos Sulak Lakes 1–2; south group: (**e**) Kapılı Lakes 1–4, (**f**) Vercenik Kumlu Lake. Photo by Bülent Şahin.

Table 1. Geographic coordinates, altitude, and surface area information of the studied lakes in Kaçkar Mountains National Park, 2020.

Lake with Abbreviation	Geographic Coordinates	Altitude (m)	Area, km^2
Kapılı Lake-1 (KPL-1)	40°42′56″.59 N; 40°54′51″.71 E	2980	0.71
Kapılı Lake-2 (KPL-2)	40°43′08″.70 N; 40°54′55″.30 E	2973	0.15
Kapılı Lake-3 (KPL-3)	40°42′34″.73 N; 40°54′49″.02 E	3074	0.36
Kapılı Lake-4 (KPL-4)	40°42′43″.97 N; 40°54′47″.24 E	3028	0.05
Kapılı Lake-5 (KPL-5)	40°42′59″.03 N; 40°54′20″.06 E	2926	0.07
Vercenik Kumlu Lake (VKL)	40°43′17″.91 N; 40°54′16″.58 E	2864	0.03
Karadeniz Lake (KRDL)	40°52′39″.19 N; 41°10′ 02″.06 E	2782	0.24
Kavron Lake (KVL)	40°52′24″.39 N; 41°09′45″.73 E	2911	0.09
Büyük Deniz Lake (BDL)	40°52′04″.60 N; 41°09′38″.54 E	2922	0.68
Adsız Lake-1 (AL-1)	40°42′39″.75 N; 40°54′57″.65 E	3075	1.62
Adsız Lake-2 (AL-2)	40°52′21″.18 N; 41°10′06″.94 E	2868	0.04
Moçar Lake (ML)	40°44′11″.63 N; 40°56′05″.36 E	2958	0.22
Tatos Sulak Lake-1 (TSL-1)	40°44′16″.11 N; 40°56′42″.25 E	2976	0.46
Tatos Sulak Lake-2 (TSL-2)	40°44′25″.50 N; 40°56′51″.18 E	2940	0.17
AP pond (AP)	40°42′48″.06 N; 40°54′48″.01 E	3008	0.01

Bray–Curtis analysis was performed using BioDiversity Pro 9.0 and a similarity tree was constructed [42]. Pearson correlation coefficients were calculated using [43]. Correlation analysis of species data in each lake was performed as a network graph in JASP (Jeffrey's Amazing Statistics Program 0.16.4) statistics botnet package with R [44]. Three-dimensional (3D) surface plots of the number of species versus individual parameters were constructed in Statistica 12.0 using the distance-weighted least squares method. For comparison, for each 3D graph, one main parameter (species number) and two others are selected, within which the program calculates probable changes in the main parameter. Thus, the resulting graph shows the trends in each of the related parameters. From here, extreme values may appear that are not real, but only reflect trends for a given distribution. The graph can be interpreted as a trend of changes (increases or decreases) in the values of the main parameter (z-axis) when the other two parameters (x- and y-axis) change. Redundancy discriminant analysis (RDA) to calculate the relationship between biological dominant variables and environmental variables was performed using the CANOCO program [45].

3. Results

3.1. Physical and Chemical Properties of Waters

The water temperatures of the studied lakes fluctuated between 7.1 and 22.5 °C. While the pH values of the waters were determined to be between 6.10 and 8.21, the dissolved oxygen values were measured to be between 8.02 and 9.17 mg L^{-1}. Total dissolved solids were 9.92–44.27 mg L^{-1} and electrical conductivity values were found as 14.1–71.4 µSm cm^{-1}. Total hardness was measured in the range of 17.59–38.84 mg L^{-1} in the KPL-1,2,3,4,5, BDL, and ML. The amount of nitrate detected in the studied lakes was in the range of 0.207–0.575 mg L^{-1}, excluding lakes KPL-1, VKL, and KVL, where the nitrates were very low. Nitrite was detected as 0.020 mg L^{-1} in ML and TSL-1, while phosphate was detected as 0.113 mg L^{-1} only in KPL-5. Potassium, calcium, magnesium, ammonium, and chlorine values of the waters were also determined and are represented in Table 2, with some indeterminate values as a result of fresh soft water.

Table 2. Averaged physical and chemical data of the 14 high mountain lakes in the Kaçkar Mountains National Park, 2020.

Parameters	KPL-1	KPL-2	KPL-3	KPL-4	KPL-5	VKL	KRDL	KVL	BDL	AL-1	AL-2	ML	TSL-1	TSL-2
Temperature (°C)	14.2	14.0	14.5	14.0	14.8	22.5	12.5	14.7	11.2	17.6	7.1	12.2	13	13
DO (mg L^{-1})	8.03	8.33	8.14	8.02	8.20	8.18	8.89	8.55	8.69	7.98	8.97	9.03	9.17	8.90
pH	6.30	6.30	6.55	6.32	8.21	7.88	6.33	7.18	6.10	7.30	6.54	7.13	6.9	6.9
Conductivity (µSm cm^{-1})	23.4	23.2	27.1	26.0	29.30	22.9	36.8	19.9	71.4	14.1	38.9	46	40	40
TDS (mg L^{-1})	17.73	15.93	18.72	18.23	20.46	17.86	22.82	12.34	44.27	9.92	27.34	21.89	20.34	19.84
Potassium (mg L^{-1})	0.37	0.37	0.50	0.40	0.47	-	-	0.38	0.44	0.35	-	-	-	-
Total hardness $CaCO_3$ (mg L^{-1})	17.96	17.64	19.94	19.70	23.60	-	-	-	38.84	-	-	17.59	-	-
Calcium (mg L^{-1})	5.13	5.00	5.92	5.82	7.17	-	-	4.02	12.69	-	7.25	4.52	5.30	5.33
Magnesium (mg L^{-1})	-	-	-	-	1.38	-	-	-	1.73	-	-	1.53	-	-
Ammonium (mg L^{-1})	0.31	0.28	0.34	0.23	0.40	0.35	0.17	0.76	0.82	0.31	0.13	0.11	0.08	0.12
Chlorine (mg L^{-1})	2.11	1.77	2.20	2.70	1.98	1.51	7.51	2.44	1.70	2.02	7.48	7.26	7.03	7.74
Nitrate (mg L^{-1})	-	0.214	0.207	0.232	0.330	-	0.575	-	0.233	0.225	0.515	0.361	0.279	0.218
Nitrite (mg L^{-1})	-	-	-	-	-	-	-	-	-	-	-	0.020	0.020	-
Phosphate (P_2O_5) (mg L^{-1})	-	-	-	-	0.113	-	-	-	-	-	-	-	-	-

Note: (-): Could not be detected as below the determination level. Variables in AP pond were not tested because water sample was lost.

3.2. Floristic Composition and Diversity of Diatoms

A total of 84 species and intraspecific taxa of Bacillariophyta, belonging to three classes, 15 orders, 25 families, and 42 genera were identified in 14 lakes and the pond (Appendix A Figures A1–A4). While the two classes (Mediophyceae, Coscinodiscophyceae, four species in each class) represent a very small part of the benthic diatom flora (9.52%), class Bacillarophyceae formed the basis of the species richness of the flora (76 species, 90.47%). The top two orders of the flora composition of benthic diatoms included Naviculales (35 species) and Cymbellales (10 species). Among the dominant families were Pinnulariaceae (thirteen species), Naviculaceae (eight species), Surirellaceae (seven species), Cymbellaceae (five species), and Eunotiaceae (five species). The main part of the benthic diatom flora was formed by genera *Pinnularia* (thirteen species), *Eunotia* (five species), *Navicula* (five species), and *Frustulia* (four species) (Appendix A Table A1). One diatom species (*Eunotia cristagalli*) was identified for the first time in the freshwater diatom flora of Turkey. It is marked with an asterisk (*) in Appendix A Tables A1 and A2.

About 8.33% of the diatom species were found in more than 80% of investigated lakes (VF), whereas 72.61% were found in less than 40% of the investigated lakes (VR, R). The representation ratios of the species in the frequent (F) and common (C) groups are the same (eight species in each group, 9.52%). Thirty diatom species (35.71% of the flora) were identified in only one lake each.

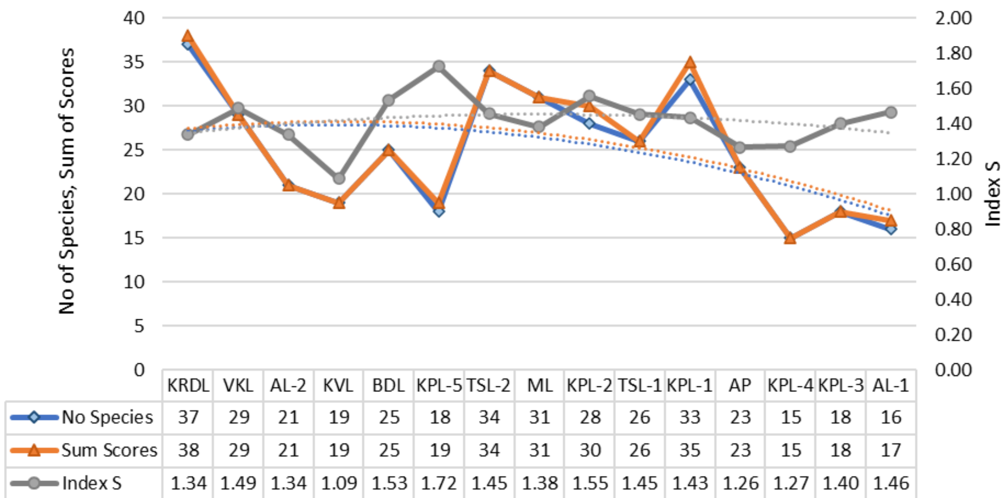
On the other hand, *Iconella capronii* is the only species identified in all studied lakes and the pond. Likewise, *Didymosphenia geminata* and *Encyonema minutum* were observed in 15 habitats. The *Caloneis silicula*, *Navicula cryptocephala*, *Pinnularia interrupta*, and *P. major* were found in 13 lakes (Appendix A Table A1; Appendix A Figures A1–A4).

When the benthic diatom flora of the studied lakes were compared, it was observed that the species diversity and relative abundances were different. In particular, the epilithic diatom species richness (81 species) was higher than that of epipelic and epiphytic diatoms. With regard to the geographical distribution of species, a significant part of the flora consisting of cosmopolitan species is of alpine and subalpine origin. The flora also includes northern alpine and alpine diatom species [24–35].

3.3. Bioindicators

The distribution of indicator properties of diatom species in studied lakes is represented in Appendix A Table A2 and summarized in Appendix A Table A3. It can be seen that the total number of diatom species in each lake strongly correlated with the abundance scores, R = 0.995, $p < 0.0001$ (Figure 3). The dashed trend lines show a decrease in both variables with increasing altitude of the lake. The organic pollution evidence is crucial for the protected lakes, and in the Kaçkar Mountains National Park, we can observe that the calculated Index of Saprobity (S) reflects clear waters in the studied lakes, falling within Class 2 or 3 of water quality (Figure 3), with a tendency for a slight decrease with increasing altitude.

The distribution of each group of indicators is represented in Figures 4 and 5. Benthic species dominated the examined samples. The plankto-benthic species were also observed (Figure 4a). It can be seen that the percentage of benthic inhabitants slightly increased with altitude from 60% in KRDL to 70% in AL1, but it appears to be rather stable in the lake community (Figure 4a). Among the indicators of water temperature belonging to four groups, species characteristic of temperate conditions strongly predominate in the surveyed lakes (Figure 4b). Three ecological groups of diatom species were found in relation to oxygenation, water velocity, and oxygen saturation. In the studied lakes, the species characteristics for standing water prevail (Figure 4c). The results of the pH bioindication show that indifferent species (45.45%) are common in the Kaçkar Mountains Natural Park. It was followed by alkaliphile (35.06%) and acidophile species (15.58%), respectively (Figure 4d). Additionally, alkalibionte species were also seen in VKL and KPL-3 lakes (Appendix A Table A3). As a whole, indicator groups consisting of indifferent alkaliphiles and acidophiles comprised 96.09% of the indicator species in each lake community (Figure 4d).



	KRDL	VKL	AL-2	KVL	BDL	KPL-5	TSL-2	ML	KPL-2	TSL-1	KPL-1	AP	KPL-4	KPL-3	AL-1
No Species	37	29	21	19	25	18	34	31	28	26	33	23	15	18	16
Sum Scores	38	29	21	19	25	19	34	31	30	26	35	23	15	18	17
Index S	1.34	1.49	1.34	1.09	1.53	1.72	1.45	1.38	1.55	1.45	1.43	1.26	1.27	1.40	1.46

Figure 3. Distribution of diatom species richness, abundance sum of scores, and Index of Saprobity S value over studied lakes in the Kaçkar Mountains National Park, 2022. The order of studied lakes is according to increasing lake altitude. Trend lines are dashed lines.

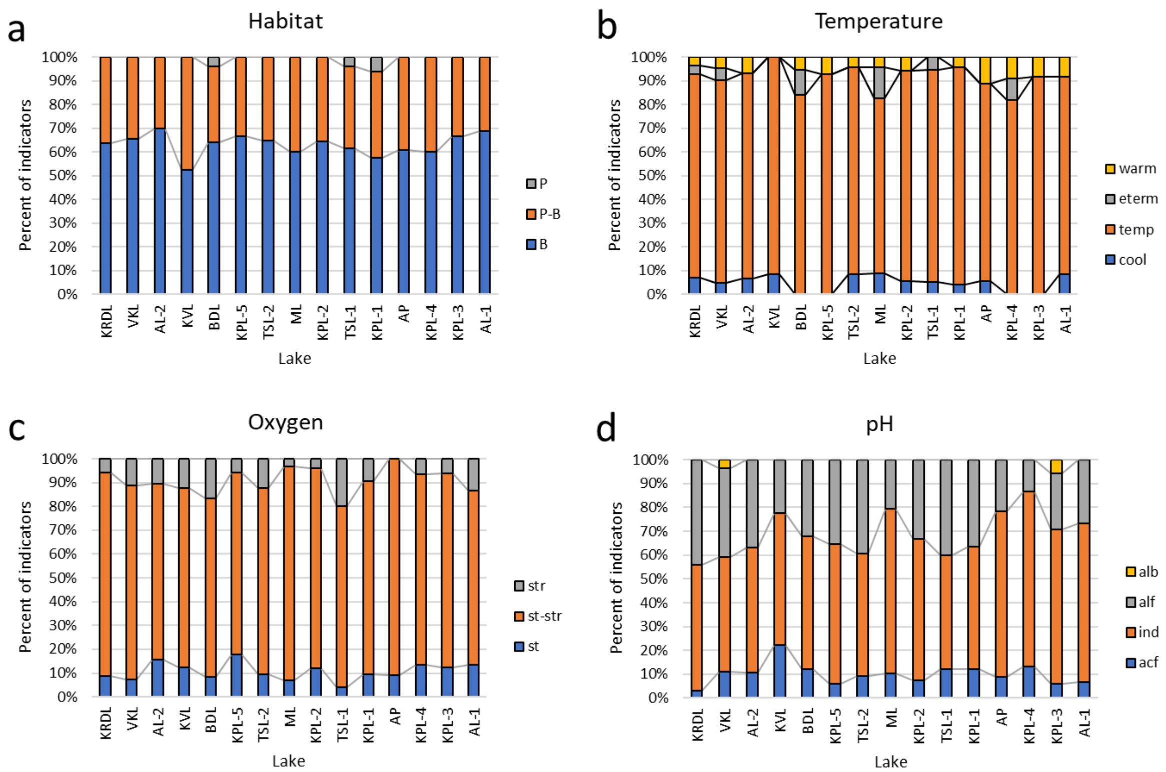


Figure 4. Distribution of indicator species by water temperature, oxygen, pH, and habitat preferences for benthic communities in the Kaçkar Mountains National Park. Habitat (**a**): P-B—plankto-benthic, B—benthic; temperature preferences (**b**): cool—cool water, temp—temperate, eterm—eurythermic, warm—warm water; oxygenation and water moving (**c**): str—streaming water, st-str—low streaming water; pH preference groups (**d**): alb—alkalibiontes; alf—alkaliphiles, ind—indifferent; acf—acidophiles. The lakes order is by increasing altitude. The indicator group order is according to increase in the indicated variable value.

Salinity is a crucial component of the total ion content in water, influencing the algal community. Bioindication based on water salinity reveals that the "indifferent" group of species dominates in all studied lakes. The other groups were oligohalobes/halophobes, halophiles, and mesohalobes (Figure 5a). Light and temperature are the basic climatic variables affecting photosynthesis, so these global climatic factors also define life and evolution [4]. Photosynthetic diatoms prevail in communities of all studied lakes (Figure 5b) and strongly prevail with increasing altitude.

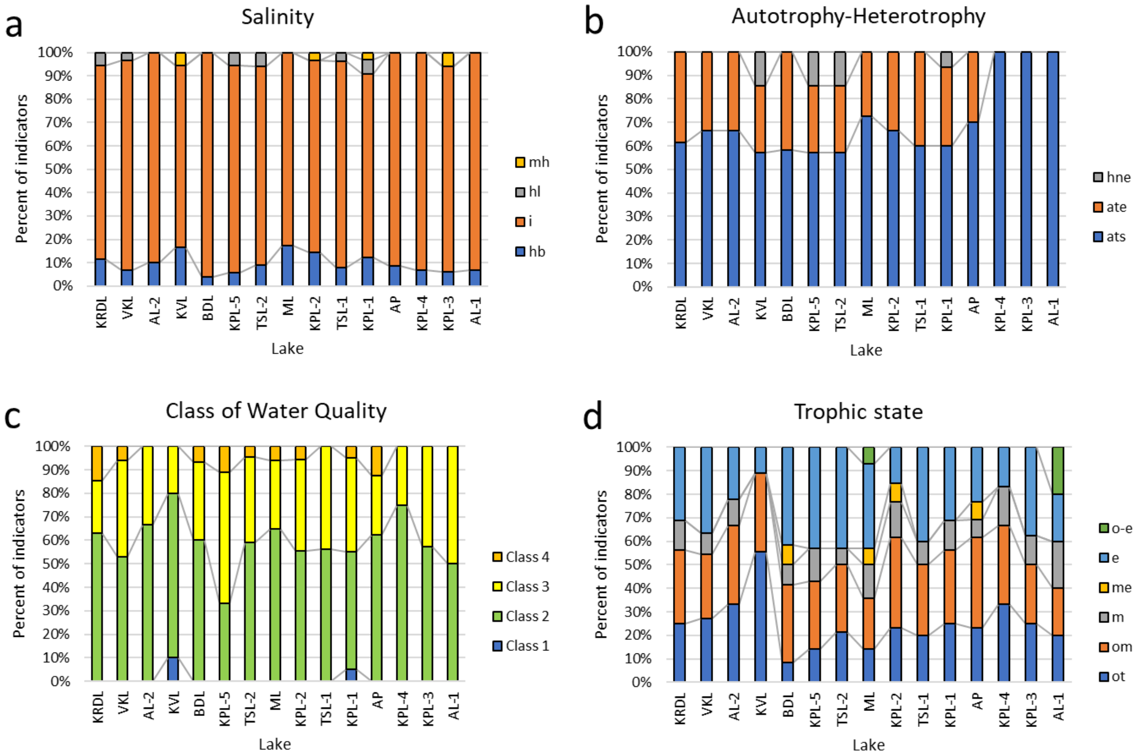


Figure 5. Distribution of indicators of salinity, nutrition type, class of water quality, and trophic state for benthic communities in the Kaçkar Mountains National Park. Abbreviations of ecological groups are given in Appendix A Table A2. Salinity ecological groups (**a**): hb—oligohalobes/halophobes, i—oligohalobes/indifferent, hl—halophiles; mh—mesohalobes, oh—oligohalobes of wide spectrum with optimum as indifferent. Nitrogen uptake metabolism (autotrophy–heterotrophy) (**b**): ats—nitrogen -autotrophic taxa, tolerating very small concentrations of organically bound nitrogen; ate—nitrogen-autotrophic taxa, tolerating elevated concentrations of organically bound nitrogen. The water quality class is determined as the sum of indicators whose species-specific index saprobity S from Appendix A Table A2 is within the range of each class. Classes of water quality colored in EU color code (**c**). Trophic state indicators (**d**): ot—oligotraphentic; om—oligomesotraphentic; m—mesotraphentic; me—mesoeutraphentic; e—eutraphentic; o-e—hypereutraphentic. The lakes are ordered by increasing altitude, and the indicator groups are arranged in increasing order of the indicated variable value.

The bioindication results of organic pollution obtained from the Sladecek's [41] systems are shown in Figure 5c. Organic pollution indicator groups of Watanabe's [40] method are not presented on the histogram but can be seen in Appendix A Table A3 and demonstrated the same results as Sládeček's method. While the indicators of Class 2 in Sládeček's [41] system contained a significant portion of the diatom community in all the studied waters, Class 3 was second. While Class 1 was represented in the KVL and KPL-1 lakes, Class 4 was also represented in the AP, KRDL, VKL, BDL, KPL-5, TSL-2, ML, KPL-2, and KPL-1. KPL-1 was the only lake where all class indicators were found. The indicators for water pollution in Class 5 were not identified. Figure 5c illustrates a decrease in Class 4 indicators with an increase in altitude, accompanied by a rising percentage of indicators corresponding to Class 3 water quality.

The trophic state of the lake usually correlates to organic matter content [46]. Oligotrophic diatom species constitute 15.47% of all diatom species and dominate the diatom communities of the studied lakes. They are followed by oligo-mesotrophic (13.09%) and eutrophic (11.90%) diatom species, respectively. In total, they comprise 40.46% of all diatom species. Additionally, mesotrophic, meso-eutrophic, and oligo-eutrophic diatoms were recorded, representing a smaller share in the diatom community (5.95%) (Figure 5d).

3.4. Comparative Analysis

A JASP Network plot of bioindicator correlation of the studied lakes in the Kaçkar Mountains National Park was constructed based on Appendix A Table A3. Four clusters can be seen in Figure 6a. Cluster 1, marked with a black dotted line, unites lakes AL-1 and KPL-3,4, the structure of diversity of which is similar, and the species composition is not high, as seen in Appendix A Table A3. These three lakes are located above all the others and are part of the southern group of lakes, and their floras are dominated by indicators of class 2 clean waters. Cluster 2, outlined by a red dotted line, consists of the floras of four lakes, the indicators of which occupy an intermediate position between the high mountain lakes of cluster 1 and the rest. Cluster 3 includes five lakes, among which are low-lying lakes with higher temperature and conductivity. The three lakes of cluster 4 have high species richness and are located in the group of southern and middle lakes. In general, the analysis did not reveal a strict relationship to groups of lakes and to altitude, but revealed a noticeable role of species richness as a grouping factor. We supplemented the current analysis with a comparison with the floras of the lakes of the Artabel Park [47] located in the mountainous region of Turkey, but somewhat to the west, and also included in the analysis two previously studied lakes of the Kaçkar part [15]. Figure 6b shows that the lake communities are grouped according to territorial characteristics, corresponding to two groups of protected areas, while the floras of two previously studied lakes located on the low spurs of the mountains in the Kaçkar Park are included in the western group of lakes of the Artabel Park, emphasizing the high individuality of those studied in this study of 14 lakes and ponds.

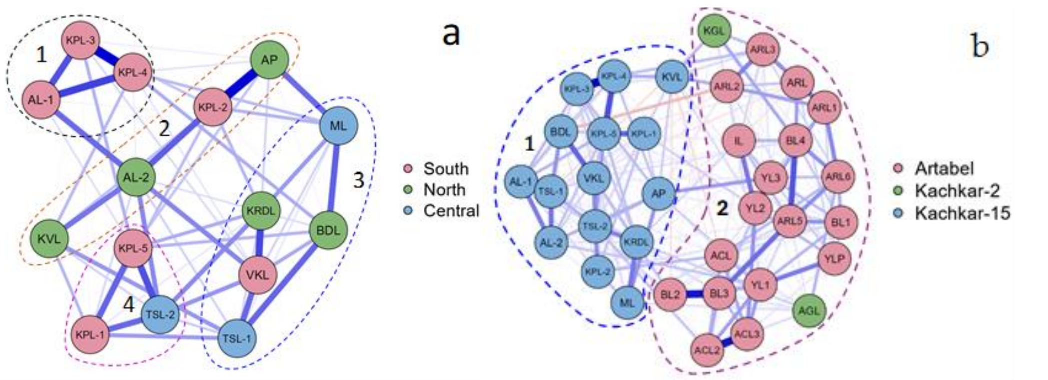


Figure 6. JASP Network plot of diatom bioindicator correlation (**a**) in the communities of the lakes of the Kaçkar Mountains National Park, $p < 0.5$, calculated based on Appendix A Table A3, and plot of comparison of the studied lake communities (Kachkar-15), previous studied diatom communities in Kaçkar Mountains National Park (Kachkar-2) [15] and in Artabel [47] (**b**). Major groups of the lakes abbreviated and colored in the legend. Blue lines are positive correlations, while red lines are negative correlations. The line thickness reflects the value of correlation. Dashed line outlined different clusters with numbers of 1-4 on Figure (**a**) and 1-2 on Figure (**b**).

The comparison of the species richness from Appendix A Table A1 by the Bray–Curtis calculation of similarity for diatom species composition shows two groups of lakes (Figure 7), outlined by a dashed line and represented by different colors. It can be observed that the smaller group of lakes includes only KPL lakes 3, 4, 5, and AL 1 and 2. All other diatom communities are outlined by the largest cluster. Both type analyses (JASP and Bray–Curtis) show similar results, because the smallest group also included the lakes with low species richness of diatoms placed at high altitude.

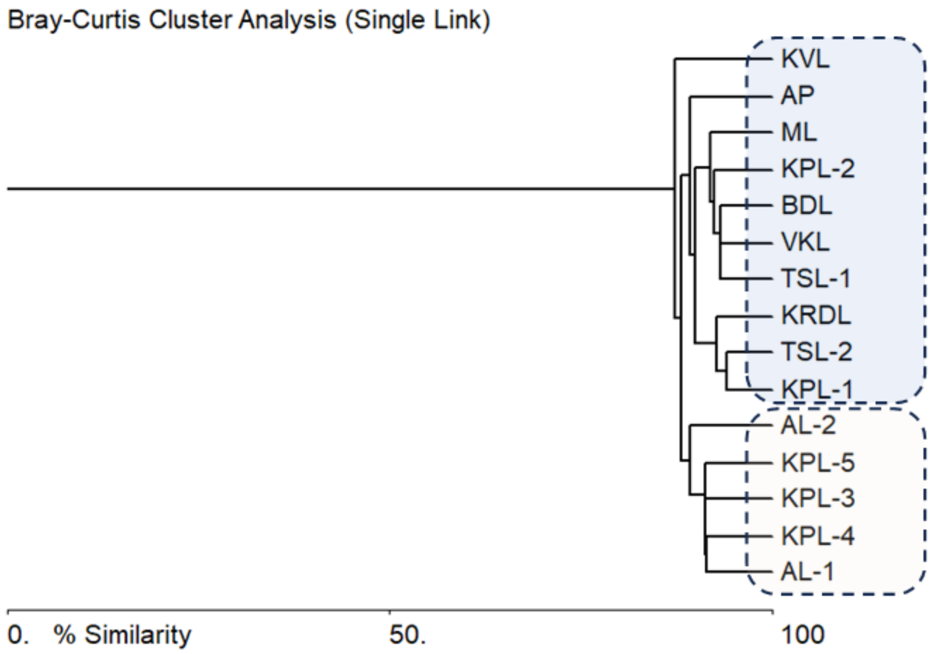


Figure 7. Tree of Bray–Curtis similarity analysis of diatom species composition in communities of the Kaçkar Mountains National Park, 2020. Clusters are outlined by dashed lines and represented by different colors.

3.5. Species–Environment Relationships

RDA plots of the relationship analysis of dominated ecological groups and environmental variables are represented in Figure 8a,b and in the correlation matrix in Appendix A Table A4. Data from fourteen lakes were used for this analysis, with seven environmental data points as independent variables and nine biological data points as dependent variables. Despite the fact that the test indicators are far from ideal (945 permutation; Eigenvalue = 0.488; p-value = 0.5), since this is a complex natural system of lakes, one can focus on the general trends in the dependence of the activity of indicator groups in the available environmental indicators. Figure 8a shows that the majority of indicators are combined into one set related to the increase in dissolved ions and oxygen concentration. The other set of environmental variables represents a negative influence on most indicator groups and includes ammonia, pH, and temperature variables. It is remarkable that one of the most species-rich indicator groups of oligotrophic waters stays in opposition to the Index Saprobity S value. An increase in the Index Saprobity S value is typically associated with eutrophication. Figure 8b reflects the lakes related to the groups of variables described above. So, ammonia is an important factor for KVL lakes, favoring oligotrophic species domination. The increasing water pH influenced diversity mostly in AL-1, while a decrease in pH is important for diatom species abundance in TSL-2 lake when total salt concentration was increased.

The relationships between species richness in the diatom community of the protected lakes in the Kaçkar Mountains National Park and the major climatic and water property variables were studied with the 3D plots in the Statistica program. Figures 9–12 show the surface plots in which the dependent variable was the number of diatom species in the community of 14 lakes and the independent variable for each plot was the lake altitude, but the third variable for each plot was different. Figure 9a shows an increase in the number of diatom species in the community when water conductivity and the lake altitude were low. The different tendency can be seen in relation to dissolved oxygen (Figure 9b) when species richness decreased in high-altitude lakes where DO increased.

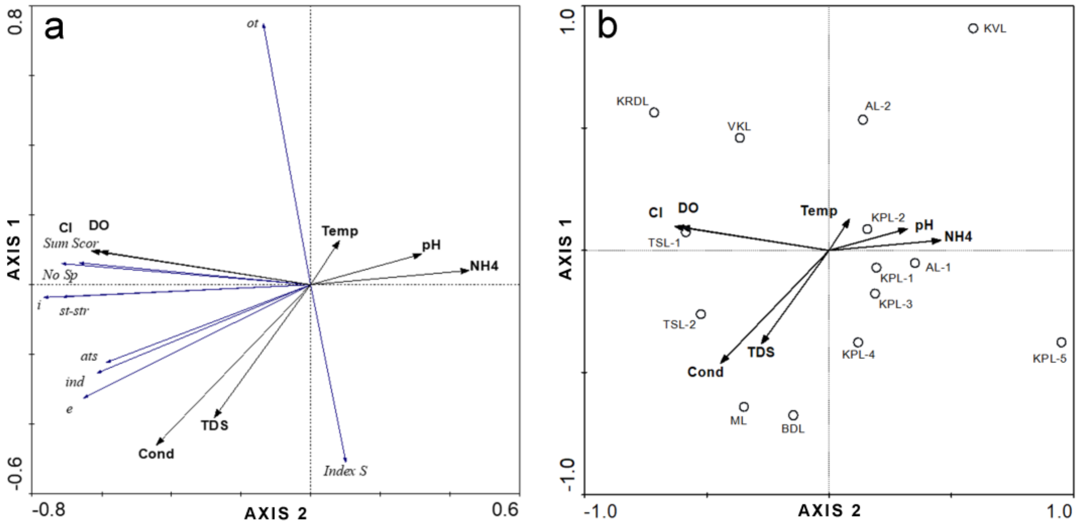


Figure 8. RDA plots for dominated groups of species indicators and environmental variables in 11 studied lakes based on data from Tables 1 and 2, and Appendix A Tables A1 and A4 in the Kaçkar Mountains National Park. RDA plot for species richness, sum of scores and environmental variables (**a**). RDA plot for environmental variables in the studied lakes (**b**).

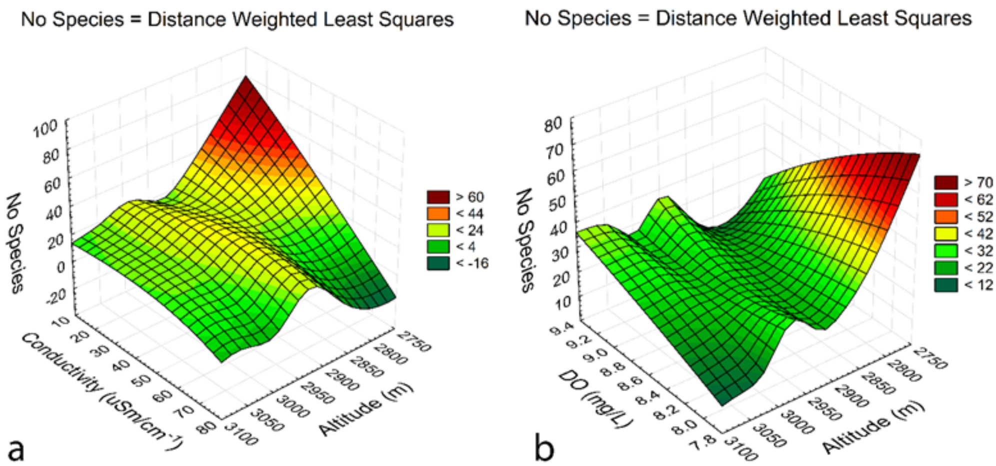


Figure 9. Three-dimensional surface plots of species richness in diatom community in relation to lake altitude and water conductivity (**a**), and lake altitude and dissolved oxygen (DO) (**b**) in the protected lakes in the Kaçkar Mountains National Park, 2020.

Figure 10a demonstrates the relationships of water pH that fluctuated between 6.0 and 8.4, in which, at the low-altitude lakes, the species number increased. In contrast, the temperature surface has a two-wave shape that reflects the complex relation of species richness with this environmental factor. In any case, species richness increased with the highest temperature in the low-altitude lakes (Figure 10b).

Index saprobity S is evidence of organic pollution, which is an important factor for the protected lakes' diversity. Figure 11a demonstrates that the relationships between species richness in the diatom community and organic pollution are complex, showing a two-wave pattern. But in general, there is an increase in species richness in the group of "low"-altitude lakes with an increase in organic pollution. The ammonium impact is reflected in the surface of Figure 11b when increasing, which stimulates the species richness in both high-altitude and low-altitude lakes.

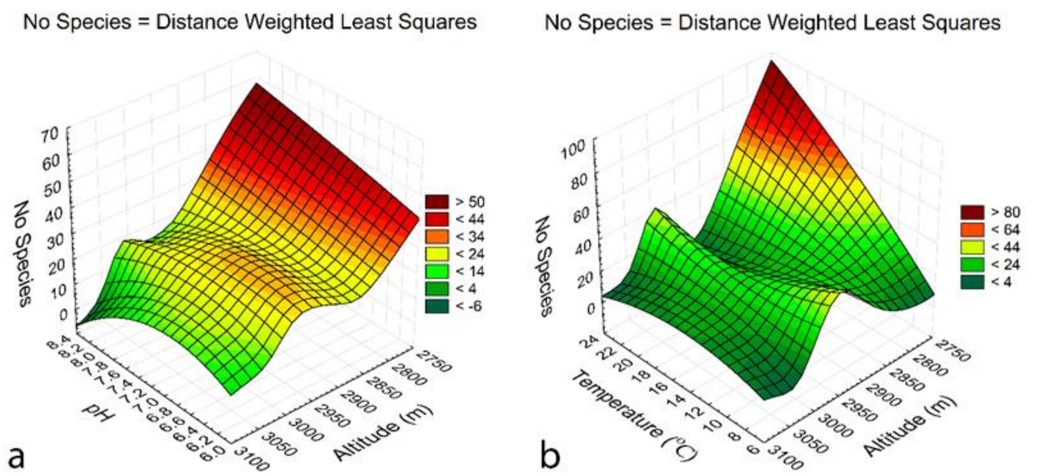


Figure 10. Three-dimensional surface plots of species richness in diatom community in relation to lake altitude and water pH (**a**), species richness in diatom community in relation to lake altitude and temperature (**b**) in the protected lakes in the Kaçkar Mountains National Park, 2020.

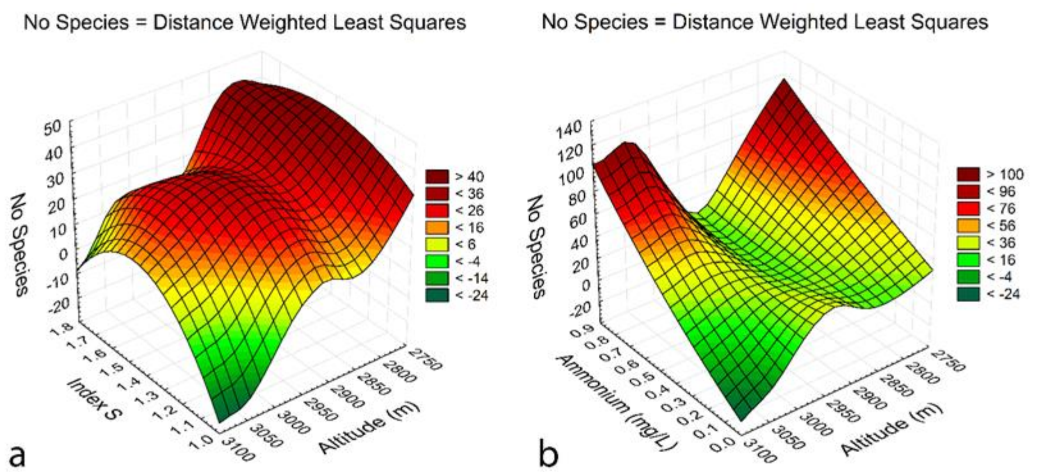


Figure 11. Three-dimesional surface plots of species richness in diatom community in relation to lake altitude and Index Saprobity S (**a**), and lake altitude and ammonium (**b**) in the protected lakes in the Kaçkar Mountains National Park, 2020.

There was a special part of the 3D analysis in which we tried to reveal the relationships of species richness with the calculated index of species number per lake area, and the lake area as an environmental factor for the Kaçkar Mountains National Park lakes. So, Figure 12a shows that the number of diatom species is decreasing in the lakes at low altitude and that have a large surface area. This may be the result of insufficient research, but in any case, it pointed to potential future research in the diatom studies in the protected areas. At the same time, Figure 12b shows an increase in the number of species per lake surface area in 'lowland' lakes if the Sp/Area index has low values. However, the left side of Figure 12b shows an increasing trend for both the number of species per lake area and species richness in high-altitude lakes if efforts are made to deplete diatom diversity in the Kaçkar Mountains National Park in future studies.

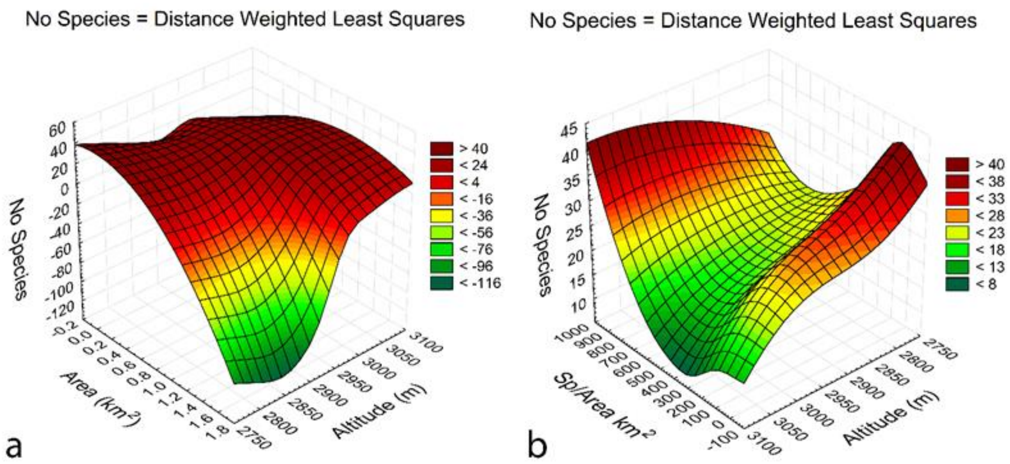


Figure 12. Three-dimensional surface plots of species richness in diatom community in relation to lake altitude and water area (**a**), and lake altitude and Index of Species per Area (**b**) in the protected lakes in the Kaçkar Mountains National Park, 2020.

4. Discussion

We investigated the diatom communities of 14 high mountain lakes and a pond in Kaçkar Mountains National Park and their relationship with environmental factors. The chemistry of the studied lakes characterizes their waters as fresh and soft, slightly saturated with salts, which unites them with the group of high mountain lake Artabel [47], but significantly distinguishes them from the sulfate alkaline lake Great Lota [48].

We identified 84 taxa of epipelic, epilithic, and epiphytic diatoms. The families (Pinnulariaceae, Naviculaceae, Surirellaceae, Cymbellaceae and Eunotiaceae) and genera (*Pinnularia*, *Eunotia*, *Navicula*, and *Frustulia*) that stand out in the flora are also characteristic members of other high mountain lakes that have been identified in the region. The flora, which generally consists of common species, is also similar to the diatom communities of the alpine and subalpine lakes in the region [15]. We suppose that the macro-climatic conditions, the similarity of the land structure, and the lake characteristics are the factors in the formation of this situation.

The common species were *Caloneis silicula*, *Encyonema minutum*, *Iconella capronii*, *Navicula cryptocephala*, and *Pinnularia interrupta* (Appendix A Table A1). These species occur in most of the lakes studied and thus may be indicators of the ecological health of the park as a whole (Appendix A Table A2). The most abundant and common species were benthic autotrophes, indicative for temperate well-oxygenated waters with circumneutral and low-alkaline pH and with low organic content of Class 2 of water quality.

The noticeable presence of species of the genus *Pinnularia* in the studied flora of the lakes of the park attracted attention, since these species are inherent in the floras of high-mountain and high-latitude reservoirs with fresh, slightly acidic waters and low electrical conductivity [46,49,50], which is confirmed by our chemical analyses (Table 2), that is, they allow us to classify the studied lakes as high mountain habitats not subject to anthropogenic influence. Thus, the ecological conditions of the waters form a suitable environment for the development of representatives of *Pinnularia* species. In addition, species of the genus *Pinnularia* are also known to inhabit extreme habitats, including highlands and arctic [49], indicators of diversity hotspots in the Ecotones, which are a border area of different landscapes [51]. *Pinnularia interrupta* and *P. maior*, which were found in 14 of the investigated lakes and pond, were recorded very frequently (VF) (86.66%) and were among the important species in the diatom flora of the park (Appendix A Table A1). *Pinnularia interrupta* occurs in low-mineral-content, circumneutral, oligosaprobic, and oligo-mesotrophic waters, while *P. maior* prefers low-mineral-content, circumneutral, β-mesosaprobic, and meso-eutrophic waters [34,38,46]. In addition, *Pinnularia borealis* and *P. viridis* species were also recorded as common (C).

Caloneis silicula is usually found in alkaliphilic, oligosaprobic, and meso-eutrophic waters, and in littoral areas of freshwater habitats with moderate electrolyte content [31,38,46], whereas Patrick and Reimer [34] state that the species has a wide ecological tolerance. *Didymosphenia geminata* prefers cool, low-conductivity, and circumneutral-pH waters [35,38,46]. *Encyonema minutum*, which has a wide geographical distribution, prefers oligo-mesotrophic freshwater habitats with medium electrolyte content, and circumneutral-pH waters [31,34,46]. According to Krammer and Lange-Bertalot [28], *Iconella capronii* is a cosmopolitan benthic form common throughout Europe and generally prefers meso-eutrophic waters with moderate to high electrolyte levels. In addition, Van Dam et al. [46] states that the species has alkaliphilic and oligosaprobic ecological properties. *Navicula cryptocephala*, which has a wide ecological tolerance, is found in oligo-eutrophic and eutrophic–polytrophic freshwater habitats with poor electrolyte content, and circumneutral-pH and alkaline waters. At the same time, this species also tolerates saprobic levels exceeding beta-alpha-mesosaprobic [31,34,38,46]. The detected physico-chemical properties in the studied lakes support the above-mentioned references.

A comparison of the influence of individual environmental parameters on the diatom communities of 14 lakes showed that the flora consists of diatom taxa that are influenced by the ionic composition of water and habitat altitude, which was demonstrated by RDA and 3D plot anslysis. Both statistical methods (JASP and Bray–Curtis) helped to reveal the high role of the lake altitude in the formation of diatom communities. At the same time, comparison with the other lake systems in the protected areas in the north of Turkey show high individuality of diatom community content of each natural reserve.

Eutrophication and acidification are among the important problems of high mountain lakes [52,53]. The bioindication and chemical data obtained from the research showed us that these problems do not exist in the lakes studied. In addition, the low species richness of the identified diatoms and the absence of a pronounced domination in the communities are among the notable features of the detected flora, and these features are inherent for the intact ecosystems of high mountain lakes [54–56].

In Appendix A Table A4, a strong correlation was observed between DO, conductivity, and Cl ions. This may be why we found a correlation between DO and species richness, but it may also be why the correlation does not actually occur. Table 2 shows that DO values do not change much and fluctuate in the range of 7.98–9.17, especially in lakes such as TSL-1, AL-2, and BDL, located at altitudes above 2900 m. However, the results of bioindication confirm an increase in the number of indicators requiring increased oxygen content in water. At the same time, we do not forget that chemical analyses of oxygen content were carried out in the laboratory; therefore, they are subject to changes during transportation from the inaccessible research area, where sampling was carried out simultaneously. But the presence of certain indicator species is not instantaneous but is the result of the development of a biological system in given living conditions, and therefore integrates the chemical parameters inherent in lake waters over a long period. Thus, bioindicators confirm the connection between the saturation of lake water with oxygen and the altitude of the lake and the species composition of its communities, even though these changes are not statistically significant. Thus, bioindicator analysis allows us to conclude that the lakes of the park were clean, mesotrophic, and of class 2 water quality. The aquatic inhabitants of the lakes developed in well-oxygenated waters of moderate temperature, and the number of benthic species increased slightly with altitude.

With increasing lake altitude, an increase in the proportion of autotrophic species in communities was observed. At the same time, the number of indicators of slightly alkaline waters decreased slightly with altitude. The low degree of the studied lakes' diatom endemism and rarity [15,23,49] was revealed for this first study, which proved to be an insufficient study in the park, on the one hand, and stimulates future research on the other.

5. Conclusions

The species composition, dominant species, and prominent families and genera determined in this study are characteristic of the benthic diatom composition of high mountain lakes. Very frequent (VF) species comprised only 8.33% of the species composition, while very rare (VR) species comprised 57.14%. The composition of very frequent (VF) species is not rich (seven species).

The data we obtained from the research show that the physico-chemical properties of the waters, environmental conditions, and the lake altitude are effective in shaping the benthic diatom flora and in the distribution of diatoms. Future research in the Kaçkar Mountains National Park should include a greater number of high mountain lakes, so that deeper information about the distribution of diatoms within the park should be obtained. Continued research is all the more important, as our analysis reveals a trend for diatom diversity to increase in high mountain lakes if research is expanded. This study is the first on the benthic diatom flora of the high mountain lakes in Kaçkar Mountains National Park and therefore constitutes a starting point for the creation of diatom-based biomonitoring programs for further investigation on diatom–environment relationships and implementation of sustainable management plans.

High mountain lakes (especially oligotrophic lakes), which are a very fragile ecosystem type, are under the influence of local (road construction) and global (climatic warming) threats. They will be among the ecosystems that will be strongly affected by species loss, especially when it comes to climatic warming [5]. In order to protect these high mountain lakes, their ecological conditions must be constantly monitored in the Kaçkar Mountains National Park.

Author Contributions: Conceptualization, B.Ş. and S.B.; methodology, B.Ş. and S.B.; software, S.B.; validation, B.Ş. and S.B.; formal analysis, B.Ş. and S.B.; investigation, B.Ş.; resources, B.Ş.; data curation, B.Ş.; writing—original draft preparation, B.Ş. and S.B.; writing—review and editing, B.Ş. and S.B.; visualization, B.Ş. and S.B.; supervision, B.Ş.; project administration, B.Ş.; funding acquisition, B.Ş. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A

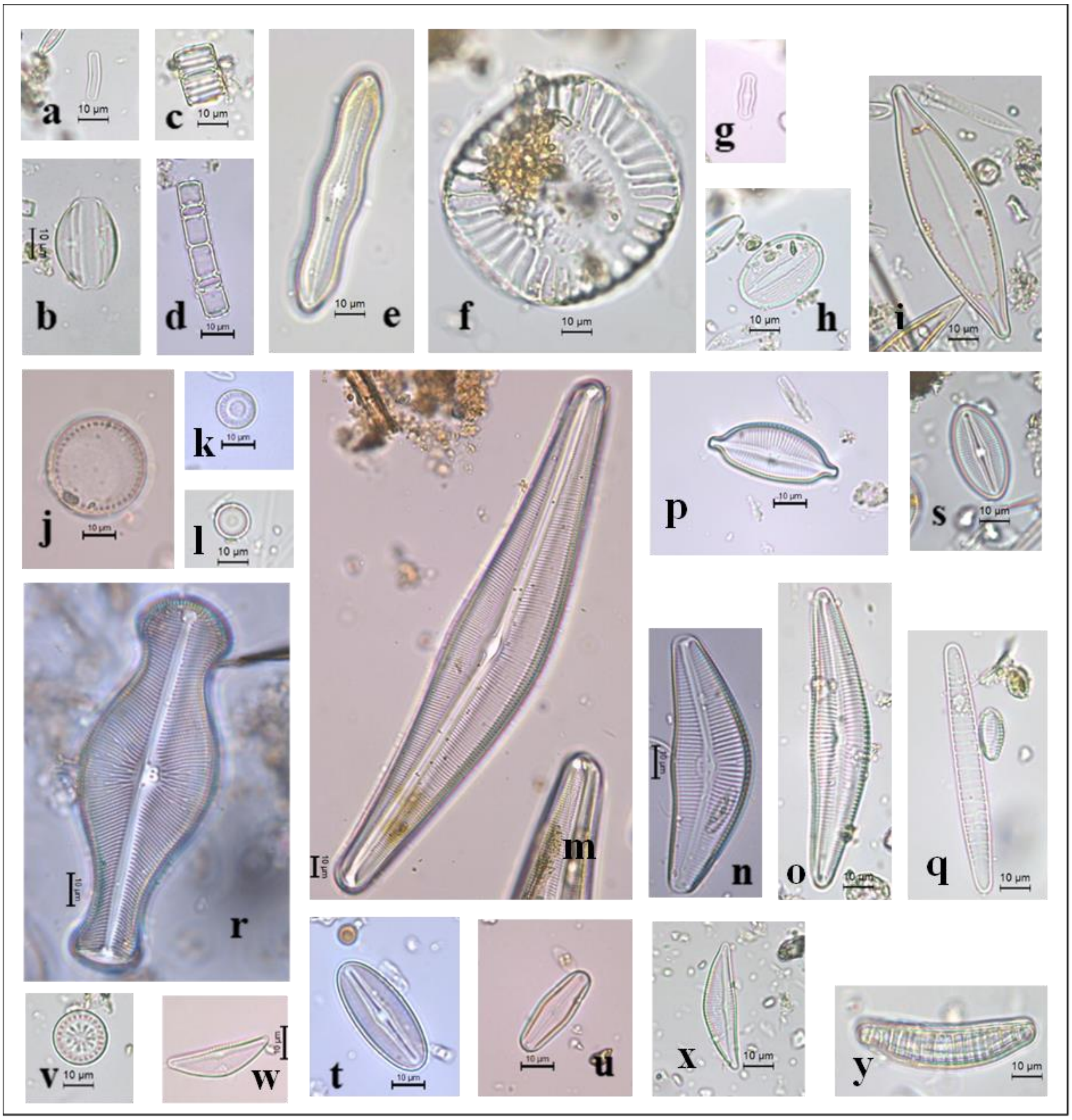

Figure A1. (**a**) *Achnanthidium minutissimum*, (**b**) *Amphora ovalis*, (**c**) *Aulacoseira ambigua*, (**d**) *A. valida*, (**e**) *Caloneis silicula*, (**f**) *Campylodiscus bicostatus*, (**g**) *Chamaepinnularia hassiaca*, (**h**) *Cocconeis lineata*, (**i**) *Craticula cuspidata*, (**j**) *Cyclotella bodanica* var. *lemanica*, (**k**) *C. distinguenda*, (**l**) *C. meneghiniana*, (**m**) *Cymbella aspera*, (**n**) *C. cistula*, (**o**) *C. cymbiformis*, (**p**) *Cymbopleura naviculiformis*, (**q**) *Diatoma vulgaris*, (**r**) *Didymosphenia geminata*, (**s**) *Diploneis elliptica*, (**t**) *D. oblongella*, (**u**) *D. petersenii*, (**v**) *Discostella stelligera*, (**w**) *Encyonema minutum*, (**x**) *E. silesiacum*, (**y**) *Epithemia adnata.* Scale bar: 10 µm.

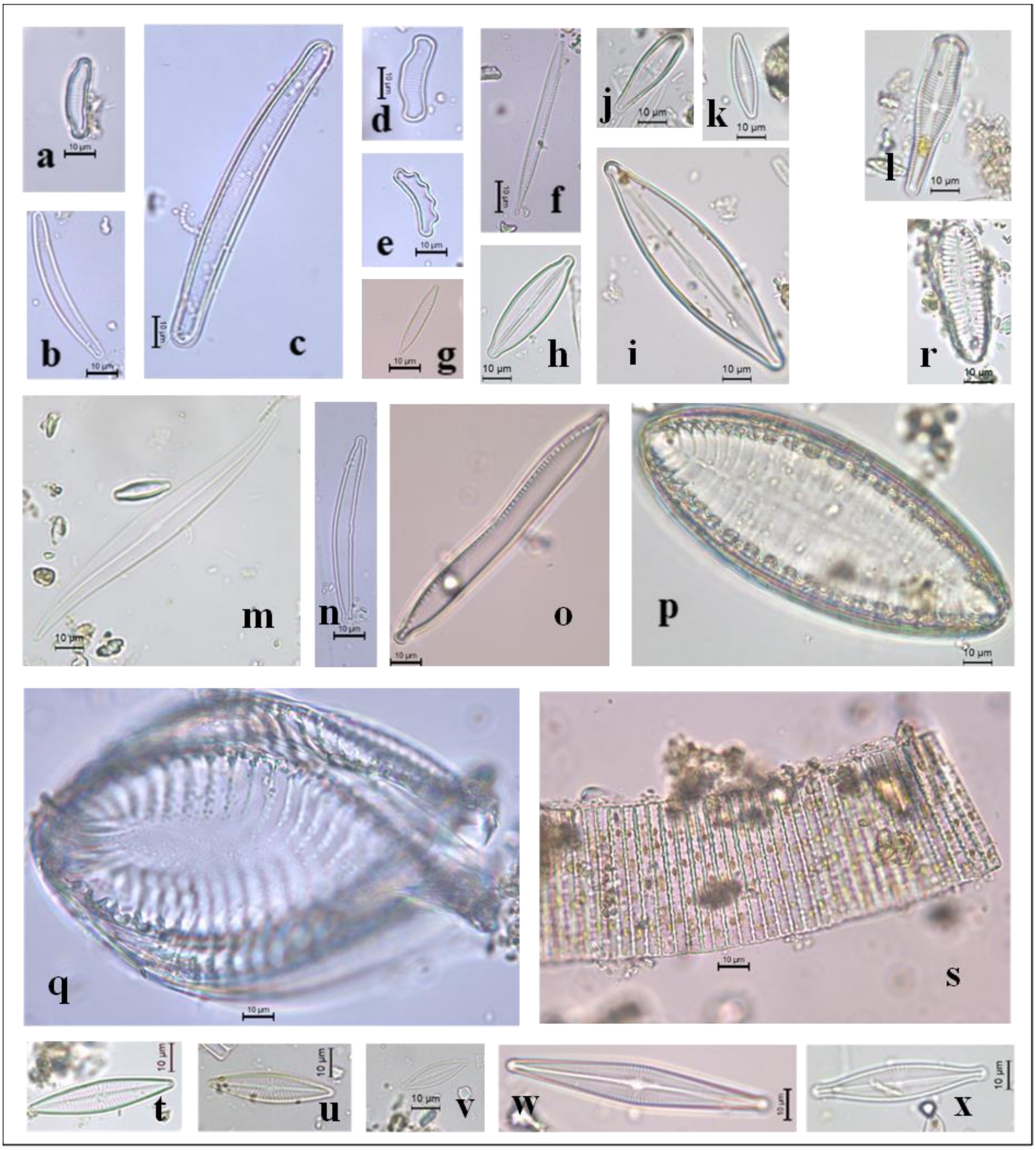

Figure A2. (**a**) *Eunotia arcus*, (**b**) *E. mucophila*, (**c**) *E. paludosa*, (**d**) *E. praerupta*, (**e**) *E. cristagalli*, (**f**) *Fragilaria gracilis*, (**g**) *F. rumpens*, (**h**) *Frustulia crassinervia*, (**i**) *F. saxonica*, (**j**) *Gomphonella olivacea*, (**k**) *Gomphonema parvulum*, (**l**) *G. truncatum*, (**m**) *Gyrosigma acuminatum*, (**n**) *Hannaea arcus*, (**o**) *Hantzschia amphioxys*, (**p**) *Iconella capronii*, (**q**) *I. spiralis*, (**r**) *I. tenera*, (**s**) *Meridion circulare*, (**t**) *Navicula cryptocephala*, (**u**) *N. cryptotenella*, (**v**) *N. phyllepta*, (**w**) *N. radiosa*, (**x**) *N. rhynchocephala*. Scale bar: 10 µm.

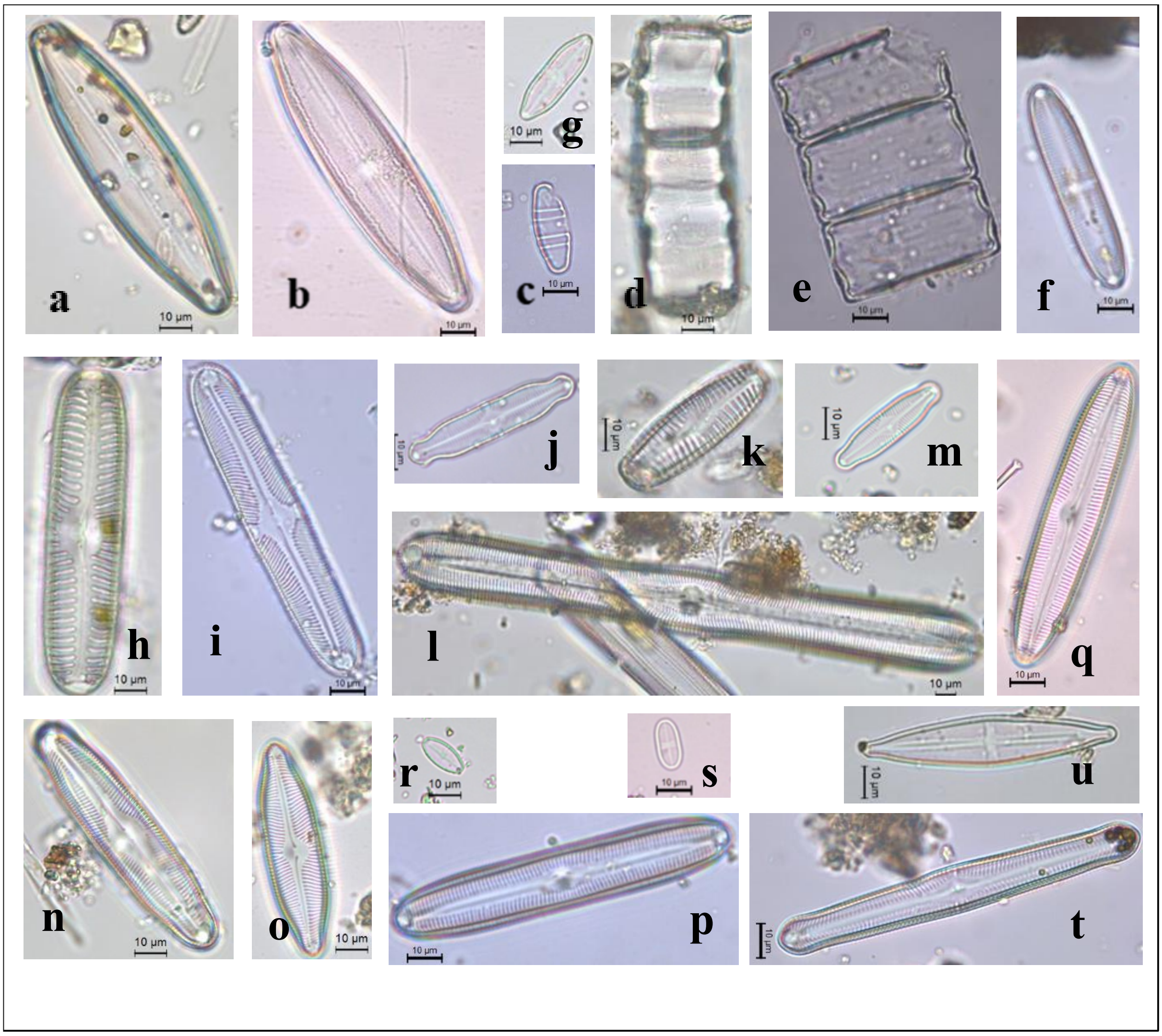

Figure A3. (**a**) *Neidium ampliatum*, (**b**) *N. iridis*, (**c**) *Odontidium mesodon*, (**d**) *Orthoseira dendroteres*, (**e**) *O. roeseana*, (**f**) *Pinnularia aestuarii*, (**g**) *P. balatoni* (**h**) *P. borealis*, (**i**) *P. brebissonii*, (**j**) *P. interrupta*, (**k**) *P. lata*, (**l**) *P. major*, (**m**) *P. mesogongyla*, (**n**) *P. microstauron*, (**o**) *P. microstauron* var. *nonfasciata*, (**p**) *P. rupestris*, (**q**) *P. viridis*, (**r**) *Planothidium distinctum*, (**s**) *Psammothidium helveticum*, (**t**) *Rhopalodia gibba*, (**u**) *Stauroneis anceps.* Scale bar: 10 µm.

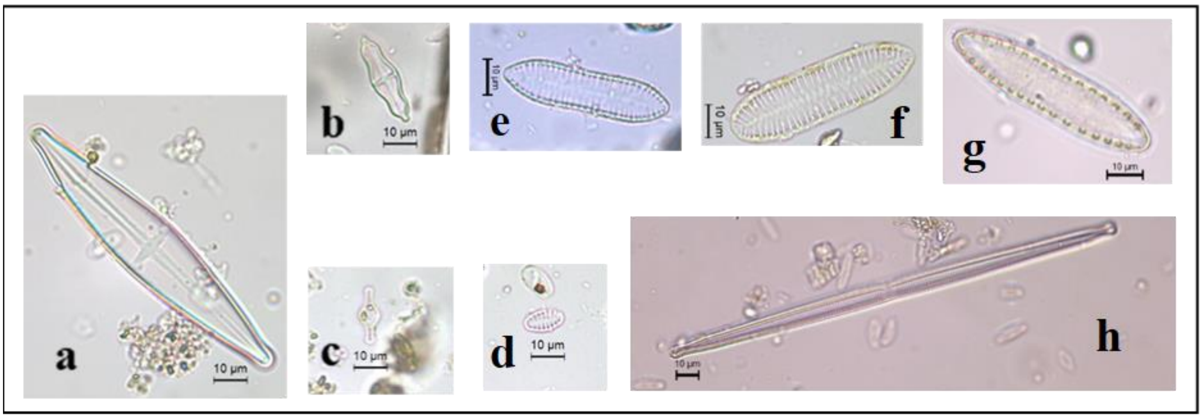

Figure A4. (**a**) *Stauroneis phoenicenteron*, (**b**) *S. smithii*, (**c**) *Staurosira construens*, (**d**) *Staurosirella pinnata*, (**e**) *Surirella angusta*, (**f**) *S. minuta*, (**g**) *S. roba*, (**h**) *Ulnaria ulna.* Scale bar: 10 µm.

Table A1. The list of benthic diatom species of 14 lakes and the pond in the Kaçkar Mountains National Park with frequencies of algal taxa, in summer and autumn of 2020.

Taxa	F	KPL-1	KPL-2	KPL-3	KPL-4	KPL-5	VKL	KRDL	KVL	BDL	AL-1	AL-2	ML	TSL-1	TSL-2	AP
Achnanthes sp.	VR	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Achnanthidium minutissimum (Kützing) Czarnecki	R	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0
Amphora ovalis (Kützing) Kützing	C	1	0	0	0	1	1	1	0	1	0	1	1	0	1	1
Aulacoseira ambigua (Grunow) Simonsen	VR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacoseira valida (Grunow) Krammer	VR	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
Caloneis silicula (Ehrenberg) Cleve	VF	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1
Campylodiscus bicostatus W. Smith ex Roper	VR	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Chamaepinnularia hassiaca (Krasske) Cantonati and Lange-Bertalot	VR	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Cocconeis lineata Ehrenberg	VR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Craticula cuspidata (Kutzing) D.G. Mann	VR	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cyclotella bodanica var. *lemanica* (O. Müller ex Schroter) Bachmann	VR	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cyclotella distinguenda Hustedt	VR	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cyclotella meneghiniana Kützing	VR	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Cymbella aspera (Ehrenberg) Cleve	VR	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cymbella cistula (Ehrenberg) O. Kirchner	C	1	1	1	0	0	1	1	0	1	0	0	1	1	1	0
Cymbella cymbiformis C. Agardh	VR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cymbopleura naviculiformis (Auerswald ex Heiberg) Krammer	F	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1
Diatoma vulgaris Bory	C	0	1	0	0	1	1	1	0	0	1	0	1	1	1	0
Didymosphenia geminata (Lyngbye) Mart.Schmidt	VF	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Diploneis elliptica (Kützing) Cleve	F	0	0	1	1	1	1	1	0	1	1	1	0	1	1	0
Diploneis oblongella (Nägeli ex Kützing) A. Cleve	VR	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Diploneis petersenii Hustedt	VR	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Table A1. *Cont.*

Taxa	F	KPL-1	KPL-2	KPL-3	KPL-4	KPL-5	VKL	KRDL	KVL	BDL	AL-1	AL-2	ML	TSL-1	TSL-2	AP
Discostella stelligera (Cleve and Grunow) Houk and Klee	R	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Encyonema minutum (Hilse) D.G. Mann	VF	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Encyonema silesiacum (Bleisch) D.G. Mann	R	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0
Epithemia adnata (Kützing) Brébisson	VR	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eunotia arcus Ehrenberg	VR	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
**Eunotia cristagalli* Cleve	VR	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Eunotia mucophila (Lange-Bertalot, Nörpel-Schempp and Alles) Lange-Bertalot	C	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1
Eunotia paludosa Grunow	VR	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Eunotia praerupta Ehrenberg	F	1	0	0	0	0	1	1	1	0	1	1	1	1	1	1
Fragilaria gracilis Østrup	VR	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Fragilaria rumpens (Kützing) G.W.F. Carlson	VR	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Frustulia crassinervia (Brébisson ex W. Smith) Lange-Bertalot and Krammer	R	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Frustulia saxonica Rabenhorst	VR	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Frustulia vulgaris (Thwaites) De Toni	VR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Frustulia sp.	VR	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gomphonella olivacea (Hornemann) Rabenhorst	F	1	1	0	0	1	1	1	0	1	0	1	0	1	1	1
Gomphonema parvulum (Kützing) Kützing	R	1	0	0	0	0	0	1	0	0	1	0	0	1	1	1
Gomphonema truncatum Ehrenberg	R	1	1	0	0	0	1	0	0	1	0	0	0	1	1	0
Gyrosigma acuminatum (Kützing) Rabenhorst	F	1	0	1	1	1	1	1	1	1	1	0	0	0	1	0
Hannaea arcus (Ehrenberg) R.M. Patrick	C	0	1	0	0	0	1	1	0	1	1	1	0	1	1	0
Hantzschia amphioxys (Ehrenberg) Grunow	R	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1
Iconella capronii (Brébisson and Kitton) Ruck and Nakov	VF	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A1. *Cont.*

Taxa	F	KPL-1	KPL-2	KPL-3	KPL-4	KPL-5	VKL	KRDL	KVL	BDL	AL-1	AL-2	ML	TSL-1	TSL-2	AP
Iconella spiralis (Kützing) E.C. Ruck and T. Nakov	VR	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Iconella tenera (W. Gregory) Ruck and Nakov	VR	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Meridion circulare (Greville) C. Agardh	VR	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Navicula cryptocephala Kützing	VF	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0
Navicula cryptotenella Lange-Bertalot	VR	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Navicula phyllepta Kützing	VR	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Navicula radiosa Kützing	F	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1
Navicula rhynchocephala Kützing	VR	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Neidium ampliatum (Ehrenberg) Krammer	R	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0
Neidium bisulcatum (Lagerstedt) Cleve	VR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neidium iridis (Ehrenberg) Cleve	VR	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Odontidium mesodon (Kützing) Kützing	R	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0
Orthoseira dendroteres (Ehrenberg) Genkal and Kulikovskiy	C	0	1	0	0	1	1	1	0	0	0	1	0	1	1	0
Orthoseira roeseana (Rabenhorst) Pfitzer	VR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pinnularia aestuarii Cleve	VR	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Pinnularia appendiculata (C. Agardh) Schaarschmidt	VR	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pinnularia balatonis (Pantocsek) F.W. Mills	VR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pinnularia borealis Ehrenberg	C	0	1	0	1	0	1	1	1	0	0	0	0	0	1	1
Pinnularia brebissonii (Kützing) Rabenhorst	VR	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
Pinnularia interrupta W. Smith	VF	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1
Pinnularia lata (Brébisson) W. Smith	VR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnularia major (Kützing) Rabenhorst	VF	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1
Pinnularia mesogongyla Ehrenberg	VR	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnularia microstauron (Ehrenberg) Cleve	VR	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A1. *Cont.*

Taxa	F	KPL-1	KPL-2	KPL-3	KPL-4	KPL-5	VKL	KRDL	KVL	BDL	AL-1	AL-2	ML	TSL-1	TSL-2	AP
Pinnularia microstauron var. *nonfasciata* Krammer	VR	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0
Pinnularia rupestris Hantzsch	VR	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pinnularia viridis (Nitzsch) Ehrenberg	C	1	0	1	1	1	1	1	1	0	0	0	1	0	0	1
Planothidium distinctum (Messikommer) Lange-Bertalot	VR	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Psammothidium helveticum (Hustedt) Bukhtiyarova and Round	R	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Rhopalodia gibba (Ehrenberg) O. Müller	R	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1
Stauroneis anceps Ehrenberg	F	0	1	1	1	0	1	1	1	1	0	0	1	0	1	1
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	VR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stauroneis smithii Grunow	VR	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Staurosira construens Ehrenberg	VR	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Staurosirella pinnata (Ehrenberg) D.M. Williams	VR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Surirella angusta Kützing	F	1	1	1	0	0	1	1	0	0	0	1	1	1	1	1
Surirella minuta Brébisson ex Kützing	VR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Surirella roba Leclercq	VR	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tabellaria flocculosa (Roth) Kützing	R	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0
Ulnaria ulna (Nitzsch) Compère	R	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0

Note: "1", present, "0", not found. Frequencies of algal taxa were determined according to the following scale based on the number of lakes studied in the Kaçkar Mountains Natural Park. Very rare (VR): taxa recorded in 1–20% of investigated lakes; rare (R): taxa recorded in 21–40% of investigated lakes; common (C): taxa recorded in 41–60% of investigated lakes; frequent (F): taxa recorded in 61–80% of investigated lakes; very frequent (VF): taxa recorded in 81–100% of investigated lakes [37].

Table A2. Indicator properties of diatom species in the lakes of the Kaçkar Mountains National Park, in summer and autumun of 2020.

Taxa	Hab	T	Oxy	Sal	pH	D	S	Aut-Het	Tro
Achnanthes sp.	-	-	-	-	-	-	-	-	-
Achnanthidium minutissimum (Kützing) Czarnecki	P-B	eterm	st-str	i	ind	es	0.95	ate	e
Amphora ovalis (Kützing) Kützing	B	temp	st-str	i	alf	sx	1.50	ate	e
Aulacoseira ambigua (Grunow) Simonsen	P	temp	st-str	i	alf	sp	1.70	ate	om
Aulacoseira valida (Grunow) Krammer	P-B	-	-	i	alf	es	1.30	ate	om
Caloneis silicula (Ehrenberg) Cleve	B	warm	st	i	ind	sp	1.30	ats	om
Campylodiscus bicostatus W. Smith ex Roper	B	-	-	mh	alb	-	-	ats	e
Chamaepinnularia hassiaca (Krasske) Cantonati and Lange-Bertalot	B	temp	st-str	hb	acf	es	1.00	ats	ot
Cocconeis lineata Ehrenberg	P-B	temp	st-str	i	alf	sx	1.20	ate	e
Craticula cuspidata (Kutzing) D.G. Mann	B	temp	st-str	i	alf	es	2.45	-	me
Cyclotella bodanica var. *lemanica* (O. Müller ex Schroter) Bachmann	P	-	-	i	ind	-	-	-	-
Cyclotella distinguenda Hustedt	P	-	str	hl	alf	-	1.30	-	om
Cyclotella meneghiniana Kützing	P-B	temp	st-str	hl	alf	sp	2.80	hne	e
Cymbella aspera (Ehrenberg) Cleve	B	-	st-str	i	neu	es	0.30	ats	e
Cymbella cistula (Ehrenberg) O. Kirchner	B	-	st-str	i	alf	sx	1.20	ats	e
Cymbella cymbiformis C. Agardh	B	temp	st-str	i	alf	sx	2.00	ats	om
Cymbopleura naviculiformis (Auerswald ex Heiberg) Krammer	B	temp	st-str	i	ind	-	-	-	-
Diatoma vulgaris Bory	P-B	temp	st-str	i	alf	-	2.40	-	-
Didymosphenia geminata (Lyngbye) Mart.Schmidt	B	-	st-str	i	ind	-	2.00	-	-
Diploneis elliptica (Kützing) Cleve	B	temp	str	i	alf	es	-	-	-
Diploneis oblongella (Nägeli ex Kützing) A. Cleve	B	-	st-str	i	ind	-	-	-	-
Diploneis petersenii Hustedt	B	-	str	i	ind	-	-	-	-
Discostella stelligera (Cleve and Grunow) Houk and Klee	P-B	temp	st-str	i	ind	-	-	-	-
Encyonema minutum (Hilse) D.G. Mann	B	temp	st-str	i	ind	sx	1.50	ats	-
Encyonema silesiacum (Bleisch) D.G. Mann	B	temp	st-str	i	ind	-	-	-	-
Epithemia adnata (Kützing) Brébisson	B	temp	st-str	i	alb	-	1.20	-	-
Eunotia arcus Ehrenberg	B	temp	st-str	i	acf	sx	0.40	ats	ot
**Eunotia cristagalli* Cleve	P-B	-	st-str	i	acf	-	1.00	-	ot
Eunotia mucophila (Lange-Bertalot, Nörpel-Schempp and Alles) Lange-Bertalot	P-B	temp	st-str	hb	acf	-	-	-	-
Eunotia paludosa Grunow	B	-	str	hb	acf	sx	0.50	ats	ot
Eunotia praerupta Ehrenberg	P-B	cool	st-str	hb	acf	-	0.30	-	-
Fragilaria gracilis Østrup	P-B	temp	str	i	ind	es	1.55	hne	-
Fragilaria rumpens (Kützing) G.W.F. Carlson	P-B	eterm	st-str	i	ind	-	2.00	ats	e
Frustulia crassinervia (Brébisson ex W. Smith) Lange-Bertalot and Krammer	B	-	str	hb	acf	sx	0.50	ats	ot
Frustulia saxonica Rabenhorst	B	temp	st-str	hb	acf	-	-	ate	-
Frustulia vulgaris (Thwaites) De Toni	P-B	temp	st-str	i	alf	-	1.00	-	-
Frustulia sp.	-	-	-	-	-	-	-	-	-
Gomphonella olivacea (Hornemann) Rabenhorst	B	temp	st-str	i	alf	-	2.30	ate	om
Gomphonema parvulum (Kützing) Kützing	B	temp	st-str	i	ind	-	0.70	ats	ot

Table A2. *Cont.*

Taxa	Hab	T	Oxy	Sal	pH	D	S	Aut-Het	Tro
Gomphonema truncatum Ehrenberg	B	temp	st-str	i	ind	-	2.00	-	-
Gyrosigma acuminatum (Kützing) Rabenhorst	B	temp	st-str	i	alf	-	-	-	-
Hannaea arcus (Ehrenberg) R.M. Patrick	B	temp	str	i	alf	-	-	-	-
Hantzschia amphioxys (Ehrenberg) Grunow	B,aer	temp	st-str	i	ind	-	3.00	-	me
Iconella capronii (Brébisson and Kitton) Ruck and Nakov	P-B,S	-	st	i	ind	sx	1.00	ats	e
Iconella spiralis (Kützing) E.C. Ruck and T. Nakov	B	-	str	i	alf	-	1.10	-	-
Iconella tenera (W. Gregory) Ruck and Nakov	P-B	temp	st	i	alf	-	0.20	ats	ot
Meridion circulare (Greville) C. Agardh	P-B	temp	st-str	i	ind	-	-	-	-
Navicula cryptocephala Kützing	P-B	temp	st-str	i	ind	-	2.40	-	-
Navicula cryptotenella Lange-Bertalot	P-B	temp	st-str	i	ind	-	-	-	-
Navicula phyllepta Kützing	B	-	-	hl	-	-	-	-	-
Navicula radiosa Kützing	B	temp	st-str	i	ind	sx	-	-	-
Navicula rhynchocephala Kützing	B	temp	st-str	hl	alf	-	1.30	-	-
Neidium ampliatum (Ehrenberg) Krammer	B	temp	st	i	ind	-	-	-	-
Neidium bisulcatum (Lagerstedt) Cleve	B	-	st-str	i	ind	-	1.00	-	-
Neidium iridis (Ehrenberg) Cleve	B	temp	st-str	hb	ind	-	-	-	-
Odontidium mesodon (Kützing) Kützing	B	cool	st-str	hb	ind	-	0.90	-	-
Orthoseira dendroteres (Ehrenberg) Genkal and Kulikovskiy	B,aer	-	-	i	-	es	1.80	-	-
Orthoseira roeseana (Rabenhorst) Pfitzer	P-B	warm	-	i	ind	-	-	-	om
Pinnularia aestuarii Cleve	B	-	-	mh	alf	-	-	-	-
Pinnularia appendiculata (C. Agardh) Schaarschmidt	B	-	st-str	i	ind	-	1.00	-	ot
Pinnularia balatonis (Pantocsek) F.W. Mills	-	-	-	-	-	-	0.80	-	-
Pinnularia borealis Ehrenberg	B,aer	-	st-str,aer	i	ind	-	1.00	-	ot
Pinnularia brebissonii (Kützing) Rabenhorst	B	temp	st-str	i	ind	-	1.00	-	-
Pinnularia interrupta W. Smith	B	-	st-str	i	ind	-	-	-	-
Pinnularia lata (Brébisson) W. Smith	P-B	-	str	i	acf	-	0.30	-	-
Pinnularia major (Kützing) Rabenhorst	B	temp	st-str	i	ind	-	1.00	ats	m
Pinnularia mesogongyla Ehrenberg	B	-	st	i	ind	sx	0.20	ats	ot
Pinnularia microstauron (Ehrenberg) Cleve	P-B	temp	st-str	i	ind	-	0.30	ats	ot
Pinnularia microstauron var. *nonfasciata* Krammer	B	-	-	-	-	-	-	-	ot
Pinnularia rupestris Hantzsch	B	temp	str	i	acf	-	-	-	-
Pinnularia viridis (Nitzsch) Ehrenberg	P-B	temp	st-str	i	ind	-	0.90	-	ot
Planothidium distinctum (Messikommer) Lange-Bertalot	B	-	-	-	-	-	2.00	-	o-e
Psammothidium helveticum (Hustedt) Bukhtiyarova and Round	B	temp	st-str	hb	alf	es	2.40	ate	m
Rhopalodia gibba (Ehrenberg) O. Müller	P-B	temp	st-str	i	alf	es	1.40	ate	om
Stauroneis anceps Ehrenberg	P-B	temp	st-str	i	ind	sx	1.30	ats	om
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	P-B	temp	st-str	i	ind	-	-	-	-
Stauroneis smithii Grunow	P-B	-	st-str	i	alf	-	1.00	-	om
Staurosira construens Ehrenberg	P-B	temp	st-str	i	alf	-	1.00	-	-

Table A2. *Cont.*

Taxa	Hab	T	Oxy	Sal	pH	D	S	Aut-Het	Tro
Staurosirella pinnata (Ehrenberg) D.M. Williams	P-B	temp	st-str	hl	alf	es	1.10	ats	om
Surirella angusta Kützing	P-B	temp	st-str	i	alf	-	-	-	-
Surirella minuta Brébisson ex Kützing	B	temp	st-str	i	alf	-	-	-	-
Surirella roba Leclercq	B	-	str	i	acf	-	-	-	-
Tabellaria flocculosa (Roth) Kützing	P-B	eterm	st-str	i	acf	-	0.30	-	-
Ulnaria ulna (Nitzsch) Compère	P-B	temp	st-str	i	alf	es	2.40	ate	e

Note: "-", not found. Abbreviations: habitat (Hab) (P-B—plankto-benthic, B—benthic); temperature (T) preferences (cool—cool water, temp—temperate, eterm—eurythermic, warm—warm water); oxygenation and streaming (Oxy) (str—streaming water, st-str—low streaming water); pH preference groups (pH) according to [57] (alb—alkalibiontes; alf—alkaliphiles, ind—indifferent; neu—neutrophiles as a part of indifferent group; acf—acidophiles); salinity ecological groups (Sal) according to [58] (hb—oligohalobes/halophobes, i—oligohalobes/indifferent, hl—halophiles; mh—mesohalobes); Index S, species-specific index saprobity according to [44]; organic pollution indicators according to [45] (D): sx—saproxenes; es—eurysaprobes; sp—saprophiles; nitrogen uptake metabolism (Aut-Het) [46]: ats—nitrogen-autotrophic taxa, tolerating very small concentrations of organically bound nitrogen; ate—nitrogen-autotrophic taxa, tolerating elevated concentrations of organically bound nitrogen; trophic state indicators (Tro) [46]: (ot—oligotraphentic; om—oligomesotraphentic; m—mesotraphentic; me—mesoeutraphentic; e—eutraphentic).

Table A3. Number of bioindicator taxa in the ecological groups in the diatom communities of the lakes in the Kaçkar Mountains National Park, in summer and autumun of 2020.

Indicator Group	AL-1	KPL-3	KPL-4	KPL-1	TSL-1	KPL-2	ML	TSL-2	KPL-5	BDL	KVL	AL-2	VKL	KRDL	AP
Habitat															
B	11	12	9	19	16	18	18	22	12	16	10	14	19	23	14
P-B	5	6	6	12	9	10	12	12	6	8	9	6	10	13	9
P	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0
Temperature															
cool	1	0	0	1	1	1	2	2	0	0	1	1	1	2	1
temp	10	11	9	22	17	16	17	21	13	16	11	13	18	24	15
eterm	0	0	1	0	1	0	3	0	0	2	0	0	1	1	0
warm	1	1	1	1	0	1	1	1	1	1	0	1	1	1	2
Oxygen															
st	2	2	2	3	1	3	2	3	3	2	2	3	2	3	2
st-str	11	13	12	26	19	21	26	25	13	18	12	14	22	29	20
str	2	1	1	3	5	1	1	4	1	4	2	2	3	2	0
Salinity															
hb	1	1	1	4	2	4	5	3	1	1	3	2	2	4	2
i	14	15	14	26	23	23	24	29	16	24	14	18	26	29	21
hl	0	0	0	2	1	0	0	2	1	0	0	0	1	2	0
mh	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0

Table A3. *Cont.*

Indicator Group	AL-1	KPL-3	KPL-4	KPL-1	TSL-1	KPL-2	ML	TSL-2	KPL-5	BDL	KVL	AL-2	VKL	KRDL	AP
pH groups															
acf	1	1	2	4	3	2	3	3	1	3	4	2	3	1	2
ind	10	11	11	17	12	16	20	17	10	14	10	10	13	18	16
alf	4	4	2	12	10	9	6	13	6	8	4	7	10	15	5
alb	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Watanabe															
sx	3	5	3	6	5	5	6	6	3	7	4	4	7	7	5
es	1	1	1	2	5	3	3	6	2	4	3	4	4	5	2
sp	1	1	1	3	0	1	1	2	2	1	0	1	1	1	1
Autotrophy–Heterotrophy															
ats	5	7	5	9	6	8	8	8	4	7	4	6	6	8	7
ate	0	0	0	5	4	4	3	4	2	5	2	3	3	5	3
hne	0	0	0	1	0	0	0	2	1	0	1	0	0	0	0
Trophic state															
ot	1	2	2	4	2	3	2	3	1	1	5	3	3	4	3
om	1	2	2	5	3	5	3	4	2	4	3	3	3	5	5
m	1	1	1	2	1	2	2	1	1	1	0	1	1	2	1
me	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1
e	1	3	1	5	4	2	5	6	3	5	1	2	4	5	3
o-e	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Class of Water Quality															
Class 1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Class 2	4	4	6	10	9	10	11	13	3	9	7	8	9	17	5
Class 3	4	3	2	8	7	7	5	8	5	5	2	4	7	6	2
Class 4	0	0	0	1	0	1	1	1	1	1	0	0	1	4	1
No. of Species	16	18	15	33	26	28	31	34	18	25	19	21	29	37	23
Sum of Scores	17	18	15	35	26	30	31	34	19	25	19	21	29	38	23
Index S	1.46	1.40	1.27	1.43	1.45	1.55	1.38	1.45	1.72	1.53	1.09	1.34	1.49	1.34	1.26

Note: "0", not found. Abbreviations: habitat (P-B—plankto-benthic, B—benthic); temperature preferences (cool—cool water, temp—temperate, eterm—eurythermic, warm—warm water); oxygenation and streaming (str—streaming water, st-str—low streaming water, st—standing water); pH preference groups according to [57] (alb—alkalibiontes; alf—alkaliphiles, ind—indifferent; acf—acidophiles); salinity ecological groups according to [58] (hb—oligohalobes/halophobes, i—oligohalobes/indifferent, hl—halophiles; mh—mesohalobes); Index S, species-specific index saprobity according to [41]; organic pollution indicators according to [40]: sx—saproxenes; es—eurysaprobes; sp—saprophiles; nitrogen uptake metabolism (Aut-Het) [46]: ats—nitrogen-autotrophic taxa, tolerating very small concentrations of organically bound nitrogen; ate—nitrogen-autotrophic taxa, tolerating elevated concentrations of organically bound nitrogen, hne—facultatively nitrogen-heterotrophic taxa, needing periodically elevated concentrations of organically bound nitrogen; trophic state indicators [46]: (ot—oligotraphentic; om—oligomesotraphentic; m—mesotraphentic; me—mesoeutraphentic; e—eutraphentic; o-e—oligo- to eutraphentic). The water quality class is determined as the sum of indicators whose species-specific index saprobity S from Appendix A Table A2 is within the range of each class.

Table A4. RDA correlation matrix for biological and environmental variable relationships of diatom communities in 14 lakes of the Kaçkar Mountains National Park.

SPEC AX1	1							
SPEC AX2	−0.1781	1						
SPEC AX3	0.315	0.0259	1					
SPEC AX4	0.1273	0.0221	0.316	1				
ENVI AX1	0.7153	0	0	0	1			
ENVI AX2	0	0.929	0	0	0	1		
ENVI AX3	0	0	0.6911	0	0	0	1	
ENVI AX4	0	0	0	0.7989	0	0	0	1
Cond	−0.3171	−0.4283	0.2503	−0.0255	−0.4433	−0.461	0.3622	−0.032
DO	−0.4333	0.0885	0.0443	−0.2701	−0.6058	0.0952	0.064	−0.338
pH	0.2282	0.0814	0.338	−0.445	0.319	0.0876	0.4891	−0.557
TDS	−0.1979	−0.3548	0.3495	0.1693	−0.2767	−0.3819	0.5057	0.2119
NH4	0.326	0.0381	0.2189	−0.0178	0.4558	0.041	0.3167	−0.0223
Cl	−0.4506	0.0902	−0.1177	−0.2943	−0.6299	0.0971	−0.1703	−0.3683
Temp	0.0593	0.118	0.1559	−0.0454	0.0829	0.127	0.2255	−0.0569
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4
Cond	1							
DO	0.6378	1						
pH	−0.3399	−0.1507	1					
TDS	0.9313	0.4196	−0.3814	1				
NH4	0.1539	−0.2901	0.0166	0.2938	1			
Cl	0.3683	0.8533	−0.1426	0.1453	−0.6628	1		
Temp	−0.5696	−0.6078	0.5679	−0.5259	0.1558	−0.5729	1	
	Cond	DO	pH	TDS	NH4	Cl	Temp	

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