

Article

Diatoms in Kamchatka's Hot Spring Soils

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Abstract: Diatoms inhabiting terrestrial habitats that are affected by thermal activity remain poorly studied, despite significant interest in the biodiversity of hot springs. The Kamchatka peninsula is characterized by the presence of 30 active volcanoes associated with hydrotherms. Our study involved a survey of diatom diversity in soils around the Malki, Upper Paratunka, and Dachnie thermal springs on the Kamchatka peninsula. A total of 49 diatom taxa were found. The genera *Pinnularia*, *Planothidium*, *Fragilariforma*, *Epithemia*, *Halamphora*, *Gomphonema*, *Nitzschia*, *Aulocoseira*, *Sellaphora*, *Surirella*, and *Navicula* were the most common. *Pinnularia* cf. *subcapitata* and *Planothidium lanceolatum* were dominant in all springs. Diatom communities in the soils near the thermal springs included both aquatic and terrestrial species, which may reflect the transitional nature of habitats at the borders of hot springs and soils. To gain a better understanding of the diversity of diatom communities in soils near thermal springs, broader worldwide studies are necessary.

Keywords: cosmopolitan taxa; ecotone; extreme habitats; diversity; hydrothermal ecosystems; Kuril-Kamchatka Island Arc

1. Introduction

The ecology and biodiversity of microorganisms inhabiting extreme habitats have attracted significant attention in recent years because they may shed light on the origins of life on Earth and potentially on other planets [1–10]. Terrestrial hydrothermal systems (including hot or thermal springs heated by geothermal groundwater discharging at the land surface) are of particular interest and likely represent the oldest ecosystems on the Earth's surface [11,12].

Hot spring water is characterized by constantly elevated water temperatures that exceed ambient ground temperatures and sometimes reach boiling point. In addition to its high temperature, the water in these springs is rich in minerals; therefore, such springs are often regarded as mineral springs [1]. Only limited groups of organisms can survive in such harsh environments, and diatoms are one of these groups. Some researchers have investigated the biodiversity of diatom algae in hot springs [13–17]. *Achnantheidium exiguum* (Grunow) Czarnecki and *Achnantheidium saprophilum* (H.Kobayashi & Mayama) Round & Bukhtiyarova are the most distributed species in diatom communities in the thermo-mineral springs of Galicia, NW Spain [15]. *Diatomella balfouriana* Greville, *Achnantheidium exiguum*, and *Anomoeoneis sphaerophora* Pfitzer are the dominant species in hot springs in northern Thailand [17]. *Pinnularia* Ehrenberg was commonly found in hot springs in New Zealand, with *Navicula* Bory and *Anomoeoneis* Pfitzer being the distributed taxa common to Kenyan hot springs [13]. However, very little is known about diatoms inhabiting the soils surrounding the

springs, which are almost equally affected by high temperature and salinity. Previous research has described the combination of extreme factors such as high temperature, alkaline substrate, and poor nutrient contents of the soil near thermal springs that represents an unusual habitat for microbial communities [18]. These ecotone microorganism assemblages could be distinct from those in hot springs. For example, previous research has suggested that communities of nonthermophilic Crenarchaeota in soils surrounding the Great Basin Hot Springs are distinct from those in the springs themselves [19].

The Kamchatka peninsula is of particular interest for exploring the biodiversity of algae associated with hot springs in general and diatoms in particular. The species composition of diatoms in these hot springs has been studied previously [20,21]; however, there are no data on algae inhabiting the surrounding soils. In this study we investigated the biodiversity of diatoms in soils around the Malki, Upper Paratunka, and Dachnie thermal springs and surrounding areas.

2. Materials and Methods

2.1. Studied Area

Kamchatka is part of the Kuril–Kamchatka volcanic arc that is characterized by high volcanic activity [22,23]. Numerous thermal fields containing hot springs are situated in this territory [24]. Among these are the Malki, Upper Paratunka, and Dachnie thermal springs (Figures 1 and 2A–D).



Figure 1. Study area. Red dot indicate the Kamchatka peninsula and red circles indicate the springs investigated. Area 1—Malki thermal springs (sites 1–2); Area 2—Upper Paratunka thermal springs (sites 3–5); Area 3—Dachnie thermal springs (sites 6–8).

The Malki thermal springs (area 1) are situated on the left bank of the river Kluchevka (N 53°19'20" E 157°32'18"). There are six groups of vents at the small thermal site, which is covered by gravel [25].

The Upper Paratunka thermal springs (area 2) (N 52°49'20" E 158°09'28") are situated on the left slope of the Paratunka river valley, 2.5 km above the river Karimshina confluence and ca. 16 km south-west of Paratunka and the village Paratunka. The springs are located at an 80 m altitude in a small fold of the hill of Goriachaya's slope that separates the valleys of Paratunka and Karimshina [25].

The Dachnie thermal springs (area 3) comprise the largest group in the Mutnovskie springs, which are situated in the Mutnovski volcano valley. The Mutnovski geothermal deposit is one of the largest in the world [20]. The Dachnie hot springs are located in the fumarole field, with discharging gases heating the cold stream waters. The physical and chemical characteristics of the hot springs studied are summarized in Table 1 [20,21,26,27].

Table 1. Physical and chemical characteristics of the hot springs studied [20,21,26,27].

Studied Area	Temperature, °C	pH	Total Mineralization, g/L
1	65.9	3.5	0.70
2	39.5	8.3	1.00
3	30.0–50.0	3.2–9.4	0.12–0.70

2.2. Samples Collections

Eight composite wet soil samples (each from five 5 cm³ soil blocks) were collected in August 2009 from eight sites (Table 2). Samples were taken from soil near the springs with metal cylinders according to the standard method for sampling terrestrial diatoms [28], and then were dried in the shade and put into sterile plastic bags. The soil samples were treated according to previously described methods [28]. In one case (site 6), mud samples from the thermal bath were collected. In the laboratory, diatom cells were extracted from 1 g of each sample by rinsing the soil with 10 mL of deionized water and 10 mL of nitric acid. This mixture was boiled to a double volume reduction for water evaporation and, after cooling to room temperature, was washed four times with deionized water.

Table 2. Characteristics of the studied sites.

Number	Description	Name	GPS	Area	Sample Description
1	River Kluchevka bank (village Malki)	K1	53°19'15.0'' N 157°31'55.7'' E	Malki	Soil sample near the spring vent
2	Village Malki	K2	53°19'21.6'' N 157°32'12.7'' E	Malki	Soil sample near hot spring vent
3	Hot springs in Upper Raratunka valley, 19 km from Thermalni village	K3	52°45'46.7'' N 158°10'52.9'' E	Upper Paratunka	Soil sample 0.2 m from the thermal bath
4	River Paratunka valley, Paratunka village	K4	52°45'33.7'' N 158°11'02.8'' E	Upper Paratunka	Soil sample near a small swamp close to the vent
5	Hot springs in Upper Raratunka valley	K5	52°45'39.1'' N 158°11'00.4'' E	Upper Paratunka	Soil sample 0.2 m from the spring vent
6	Small geysers on the plateau on Mutnovski volcano valley	K6	52°22'22.4'' N 158°04'31.5'' E	Dachnie	Mud sample from the thermal bath
7	Small geysers on the plateau on Mutnovski volcano valley, fumaroles	K7	52°22'10.8'' N 158°04'33.0'' E	Dachnie	Soil sample near small boiling mud pool
8	Small geysers on the plateau near Mutnovski volcano	K8	52°22'31.5'' N 158°04'28.5'' E	Dachnie	Soil sample near the geyser

To minimize damage during acid removal and washing of the diatom frustules, they were settled by sedimentation instead of centrifugation. Suspensions of cleaned frustules were dried on glass coverslips and mounted on permanent slides using Naphrax following standard procedures [29]. Valves were examined in a bright field (BF) at × 1000 magnification using Ergaval and Zeiss Axio Imager A2 light microscopes (Carl Zeiss, Jena, Germany) equipped with oil immersion objectives with differential interference contrast (DIC) and Axio Cam MRccameras. Soil samples and permanent slides were deposited in the Bashkortostan Collection of Algae and Cyanobacteria (BCAC) (WDCM 1023, Ufa, Russia). For species identification, relevant references [30–34] and recent publications [35–39] were used. For descriptions of the ecology of species, standard flora and related literature were used [40–47].

For floristic similarity estimation purposes, the Sørensen–Czekanowski coefficient was used:

$$K = 2c \times 100\% / (a + b) \quad (1)$$

where K is the floristic similarity coefficient, c is the number of species common to the two floras, a is the number of species in the flora of the first area, and b is the number of species in the flora of the second area [48].

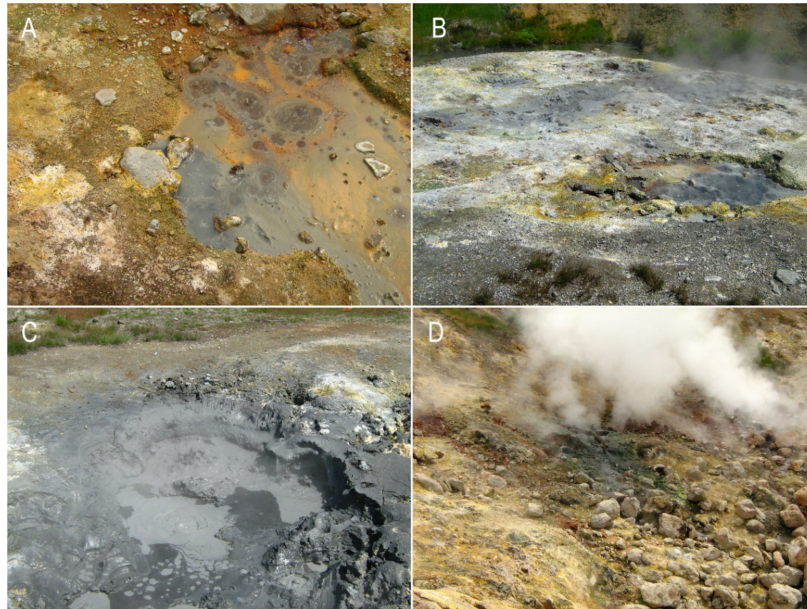


Figure 2. Study sites: (A)—K1, the River Kluchevka bank, the spring vent (area 1); (B)—K2, the Village Malki, hot spring vent (area 1); (C)—K7, small geysers on the plateau on Mutnovski volcano valley, fumaroles, and small boiling mud pool (area 3); (D)—K8, small geysers on the plateau near Mutnovski volcano (area 3).

For the comparison and visualization of the similarities between diatom communities from the Malki, Upper Paratunka, and Dachnie thermal springs, we used a Venn diagram [49,50]. The Venn diagram was created using the web-based InteractiVenn tool [51].

The abundance of species was estimated on a coverslip according to the method of R.R. Kabirov [52]. During microscopic observation, five transects were examined: four along the perimeter and one through the center. The abundance of algae was assessed on a 15-point scale on a slide: 1 point, 1–3 diatom valves found on the transect (1–15 on a slide); 2 points, 4–10 diatom valves (4–80 on a slide); 3 points, more than 10 diatom valves (more than 50 on a slide). After observation of five transects, the sum of the abundance points was calculated. Thus, the minimum abundance was 1 point (1–15 on a slide) and the maximum was 15 points (more than 50 on a slide).

3. Results

During the study, a total of 49 diatom taxa from the genera *Aulacoseira* Thwaites, *Caloneis* Cleve, *Diatoma* Bory, *Diploneis* Ehrenberg ex Cleve, *Decussiphycus* Guiry & Gandhi, *Encyonema* Kützing, *Epithemia* Kützing, *Eunotia* Ehrenberg, *Fragilariforma* D.M. Williams & Round, *Frustulia* Rabenhorst, *Gomphonella* Rabenhorst, *Gomphonema* Ehrenberg, *Halamphora* (Cleve) Levkov, *Hannaea* Patrick in Patrick & Reimer, *Hantzschia* Grunow, *Luticola* D.G.Mann, *Navicula*, *Nitzschia* Hass, *Odontidium* Kützing, *Pinnularia*, *Planothidium* Round & L.Bukhtiyarova, *Psammothidium* L.Bukhtiyarova & Round, *Pseudostaurosira* D.M.Williams & Round, *Sellaphora* Mereschowsky, *Staurosira* Ehrenberg, *Staurosirella* D.M.Williams & Round, *Surirella* Tyrpin, *Synedra* Ehrenberg, and *Tabellaria* Ehrenberg ex Kützing were identified (Table 3), (Figure 3A–AD).

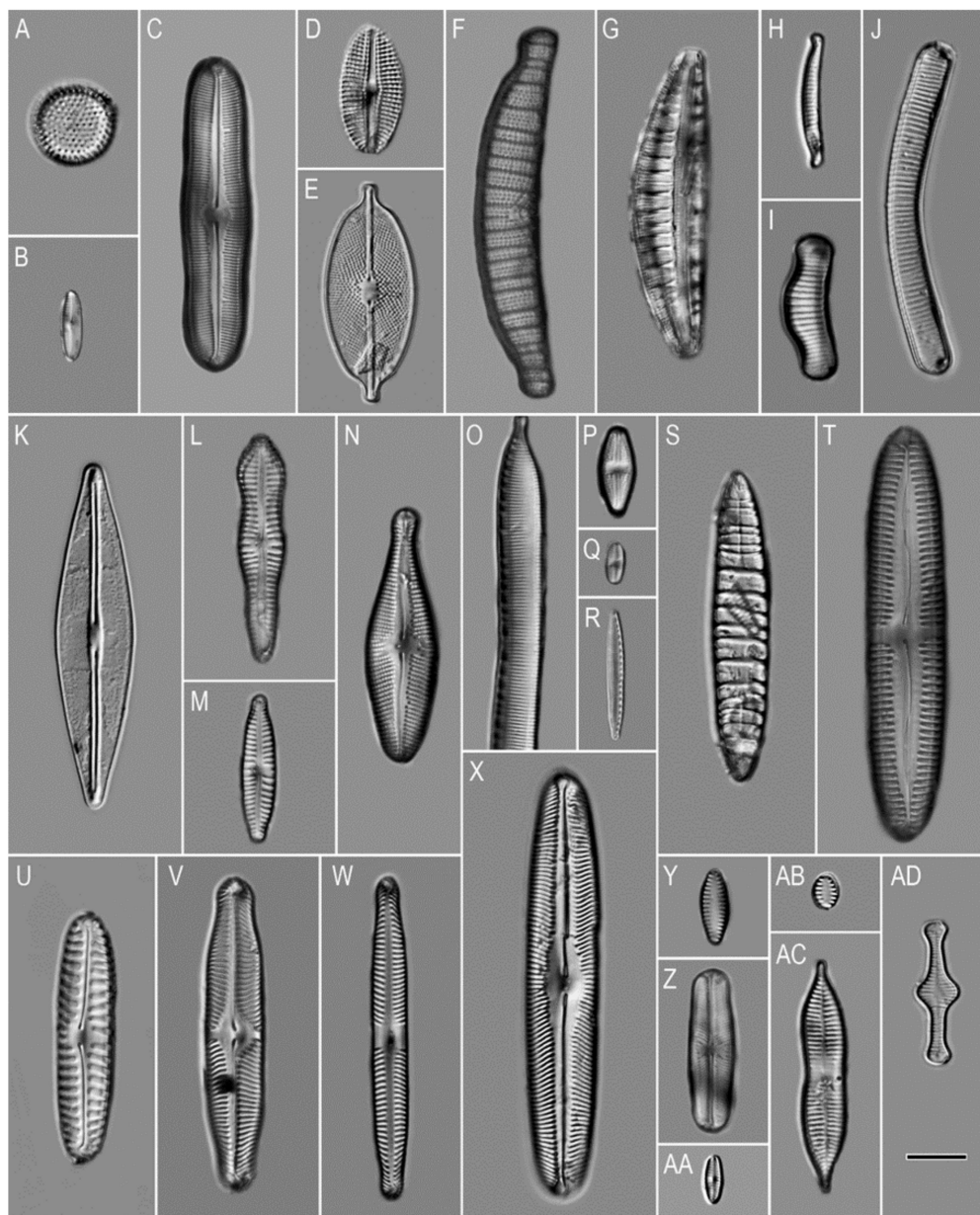


Figure 3. Species of diatoms from soils near the Malki, Upper Paratunka and Dachnie thermal springs. (A)—*Aulacoseira distans*; (B)—*Caloneis lancettula*; (C)—*Caloneis silicula*; (D)—*Diploneis calcilacustris*; (E)—*Decussiphycus placenta*; (F)—*Epithemia adnata*; (G)—*Epithemia operculata*; (H)—*Eunotia arcus* var. *fallax*; (I)—*Eunotia curtagrunowii*; (J)—*Eunotia* sp.; (K)—*Frustulia krammeri*; (L)—*Gomphonema brebissonii*; (M)—*Gomphonema* sp.; (N)—*G. ventricosum*; (O)—*Hantzschia* cf. *abundans*; (P)—*Luticola acidoclinata*; (Q)—*Navicula minima*; (R)—*Nitzschia hantzschiana*; (S)—*Odontidium hyemale*; (T)—*Pinnularia substreptoraphe*; (U)—*P. borealis*; (V)—*P. microstauron*; (W)—*P. cf. subcapitata*; (X)—*P. cf. subrupestris*; (Y)—*Pseudostaurosira brevistriata*; (Z)—*Sellaphora rectangularis*; (AA)—*S. seminulum*; (AB)—*Staurosira venter*; (AC)—*Synedra goulardii*; (AD)—*Tabellaria flocculosa*. Scale bar—10 μ m.

Table 3. List of diatom taxa with the relative abundance and ecological preferences * [40–47] in the Malki Upper Paratunka and Dachnie thermal springs.

Taxon	1	2	3	Habitat *	Salinity Tolerance *	pH *	Distribution *	Ecological Group *
<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	12	10		P B	i	ac	b	marine, freshwater
<i>Caloneis lancettula</i> (Schulz) Lange-Bertalot & Witkowski			8	B	i	al	c	freshwater
<i>C. silicula</i> (Ehrenberg) Cleve	5			B Ep	i	ac	c	freshwater
<i>Diatoma moniliformis</i> (Kützing) D.M. Williams	9			P B	hl	al	c	marine, freshwater
<i>Diploneis calcilacustris</i> Lange-Bertalot & Fuhrmann	3			B	i	al	c	freshwater
<i>Decussiphycus placenta</i> (Ehrenberg) Guiry & Gandhi		3		B	i	i	c	freshwater, terrestrial
<i>Encyonema minutum</i> (Hilse) D.G. Mann			4	B Ep	i	al	c	marine, freshwater
<i>E. perpusillum</i> (Cleve-Euler) D.G. Mann	6			B Ep	hb	ac	c	freshwater
<i>E. silesiacum</i> (Bleisch) D.G. Mann	3	1	7	B Ep	i	al	b	freshwater, terrestrial
<i>Epithemia adnata</i> (Kützing) Brébisson	2			Ep	i	al	c	freshwater, terrestrial
<i>E. operculata</i> (C. Agardh) Ruck & Nakov	14	15		Ep	i	al	c	freshwater
<i>Eunotia arcus</i> var. <i>fallax</i> Hustedt			4	Ep	hb	i	c	freshwater
<i>E. curtagrunowii</i> Nörpel-Schempp & Lange-Bertalot	6		10	L Ep	hb	ac	aa	freshwater
<i>E. exigua</i> (Brébisson ex Kützing) Rabenhorst			15	L Ep	hb	ac	c	freshwater
<i>E. paratridentula</i> Lange-Bertalot & Kulikovskiy			2	L Ep	hb	ac	c	freshwater
<i>Eunotia</i> sp.			6	L Ep	hb	ac	c	freshwater
<i>Fragilariforma virescens</i> (Ralfs) D.M. Williams & Round	15	15		L Ep	i	i	aa	freshwater
<i>Frustulia krammeri</i> Lange-Bertalot & Metzeltin			9	B	hb	ac	aa	freshwater, terrestrial
<i>Gomphonella olivacea</i> (Hornemann) Rabenhorst	5			Ep	i	i	c	freshwater
<i>Gomphonema brebissonii</i> Kützing	4			Ep	i	al	c	freshwater
<i>G. ventricosum</i> W. Gregory	4			Ep	i	i	aa	freshwater

Table 3. Cont.

Taxon	1	2	3	Habitat *	Salinity Tolerance *	pH *	Distribution *	Ecological Group *
<i>Gomphonema</i> sp.	13	10		Ep	i	i	c	marine, freshwater
<i>Halamphora normanii</i> (Rabenhorst) Levkov	14			B	i	al	c	freshwater, terrestrial
<i>Hannaea arcus</i> (Ehrenberg) R.M.Patrick	2			L	hb	al	aa	freshwater
<i>Hantzschia</i> cf. <i>abundans</i> Lange-Bertalot		5		B	i	al	c	freshwater
<i>Luticola acidoclinata</i> Lange-Bertalot			4	B	hl	al	c	freshwater
<i>Navicula cincta</i> (Ehrenberg) Ralfs	2	5	1	B Ep	hl	al	c	marine, brackish, freshwater, terrestrial
<i>N. leptostriata</i> Jørgensen		8		B	hb	ac	c	freshwater
<i>N. minima</i> Grunow	6			B Ep	i	al	c	freshwater
<i>Neidium dubium</i> (Ehrenberg) Cleve			8	B	i	al	c	marine
<i>Nitzschia hantzschiana</i> Rabenhorst	15			B	i	al	b	freshwater, terrestrial
<i>N. recta</i> Hantzsch ex Rabenhorst			4	B	i	al	c	freshwater
<i>Odontidium hyemale</i> (Roth) Kützing	6		6	B Ep	hb	i	aa	freshwater
<i>Pinnularia substreptorapha</i> Krammer			2	B	i	i	c	freshwater
<i>P. borealis</i> Ehrenberg		6	10	B	i	ac	c	freshwater, terrestrial
<i>P. microstauron</i> (Ehrenberg) Cleve	9	7	6	B	i	i	c	freshwater, terrestrial
<i>P. cf. subcapitata</i> W.Gregory	14	15	15	B	hb	ac	c	freshwater, terrestrial
<i>P. cf. subrupestris</i> Krammer		2	3	B	i	i	c	freshwater, terrestrial
<i>Planothidium lanceolatum</i> (Brébisson ex Kützing) Lange-Bertalot	15	14	15	Ep	i	al	c	freshwater
<i>Psammothidium ventrale</i> (Krasske) Bukhtiyarova & Round			1	Ep	hb	ac	aa	freshwater
<i>Pseudostaurosira brevistriata</i> (Grunow) D.M.Williams & Round	1			L Ep	i	al	c	freshwater
<i>P. medliniae</i> D.M.Williams & E.A Morales	2			L Ep	i	al	c	freshwater

Table 3. Cont.

Taxon	1	2	3	Habitat *	Salinity Tolerance *	pH *	Distribution *	Ecological Group *
<i>Sellaphora rectangularis</i> (W.Gregory) Lange-Bertalot & Metzeltin		10		B	hl	i	c	freshwater
<i>S. seminulum</i> (Grunow) D.G.Mann		3	4	B Ep	i	ac	c	freshwater
<i>Staurosira venter</i> (Ehrenberg) Cleve & J.D.Möller	4		9	L Ep	i	al	c	freshwater
<i>Staurosirella pinnata</i> (Ehrenberg) D.M.Williams & Round	5			L	hl	al	c	marine, freshwater
<i>Surirella brebissonii</i> Krammer & Lange-Bertalot	9			B	i	al	c	freshwater
<i>Synedra gouldardii</i> Brébisson ex Cleve & Grunow			3	L Ep	i	al	c	marine, freshwater
<i>Tabellaria flocculosa</i> (Roth) Kützing			6	P Ep	hb	ac	aa	freshwater, terrestrial
Total number 49	27	16	25					

Notes. 1—Malki thermal springs, 2—Upper Paratunka thermal springs, 3—Dachnie thermal springs; Habitat: P—planktonic, B—benthic, L—littoral, Ep—epiphytic; salinity tolerance: i—indifferent, hb—halophobic, hl—halophilic; pH (relation to pH): ac—acidophilic, al—alkaliphilic, aa—arcto-alpine, b—boreal, c—cosmopolitan. * means the data from the literature.

Representatives from the class Bacillariophyceae were the most diverse and accounted for 48 diatom taxa (98% of the total). The genera *Pinnularia* and *Eunotia* (5 species/taxa each), *Navicula* (4 species), and *Encyonema* and *Gomphonema* (3 species/taxa each) contributed the most assemblages. The majority of the taxa identified have been described in the literature as benthic (18 species, 37% of the total species), indifferent to salinity (31 species, 63%), and alkaliphilic (24 species, 49%). Widely distributed and cosmopolitan species prevailed (38 species, 78%).

In all samples studied, we found representatives of the genera *Encyonema*, *Navicula*, *Pinnularia*, and *Planothidium*. The number of species ranged from 3 to 12. The highest number of species (12) was identified in sample 2 collected from the Malki thermal springs soils, and the lowest (3) was found in sample 3 from the Upper Paratunka thermal springs. An average of ± 3 species were identified in the samples. The diatom flora of the Malki hot springs soils (27 taxa, 55%) was the most diverse, while at Dachnie thermal springs, 25 taxa (51%) were found, and 16 taxa (32%) were found in the soils from the Upper Paratunka springs. Only five species (*Encyonema silesiacum*, *Navicula cincta*, *Pinnularia microstauron* (Figure 3V), *P. cf. subcapitata* (Figure 3W), and *Planothidium lanceolatum*) were found in all three hot spring systems (Table 3, Figure 4), which resulted in low similarities between the local flora. The samples from Malki and Upper Paratunka thermal springs showed maximum similarities (Figure 4) and values of the Czekanowski–Sørensen coefficient (41.9%). The similarity between the Dachnie and Upper Paratunka thermal springs was 39.0% (Figure 4). The Malki and Dachnie hot springs were less similar (26.9%) (Figure 4).

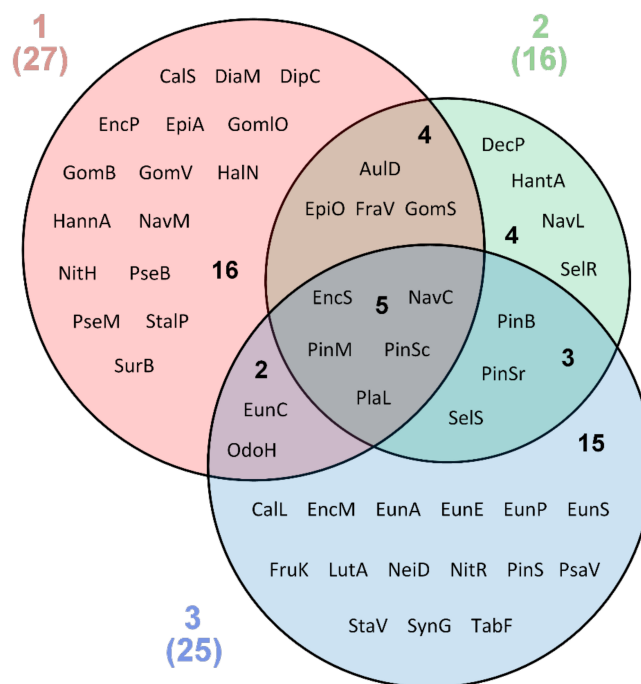


Figure 4. The similarities between diatom communities from the thermal springs studied. 1 (pink circle)—Malki hot springs community, 2 (green circle)—Upper Paratunka thermal springs, 3 (blue circle)—Dachnie thermal springs. Numbers in brackets indicates the numbers of species in communities. Species abbreviations: AulD—*Aulacoseira distans*; CalL—*Caloneis lancettula*; CalS—*C. silicula*; DiaM—*Diatoma moniliformis*; DipC—*Diploneis calcilacustris*; DecP—*Decussiphycus placenta*; EncM—*Encyonema minutum*; EncP—*E. perpusillum*; EncS—*E. silesiacum*; EpiA—*Epithemia adnata*; EpiO—*E. operculata*; EunA—*Eunotia arcus* var. *fallax*; EunC—*E. curtagrunowii*; EunE—*E. exigua*; EunP—*E. paratridentula*; EunS—*Eunotia* sp.; FraV—*Fragilariforma virescens*; FruK—*Frustulia krammeri*; GomIO—*Gomphonella olivacea*; GomB—*Gomphonema brebissonii*; GomS—*Gomphonema* sp.; GomV—*G. ventricosum*; HalN—*Halamphora normanii*; HannA—*Hannaea arcus*; HantA—*Hantzschia abundans*; LutA—*Luticola acidoclinata*; NavC—*Navicula cincta*; NavL—*N. leptostriata*; NavM—*N. minima*; NeiD—*Neidium dubium*; NitH—*Nitzschia hantzschiana*; NitR—*N. recta*; OdoH—*Odontidium hyemale*; PinS—*Pinnularia substreptoraphe*; PinB—*P. borealis*; PinM—*P. microstauron*; PinSc—*P. cf. subcapitata*; PinSr—*P. cf. subrupestris*; PlaL—*Planothidium lanceolatum*; PsaV—*Psammothidium ventrale*; PseB—*Pseudostaurosira brevisstriata*; PseM—*P. medliniae*; SelR—*Sellaphora rectangularis*; SelS—*S. seminulum*; StaV—*S. venter*; StalP—*Staurosirella pinnata*; SurB—*Surirella brebissonii*; SynG—*Synedra goulardii*; TabF—*T. flocculosa*.

Epithemia operculata (Figure 3G), *Fragilariforma virescens*, *Halamphora normanii*, *Nitzschia hantzschiana* (Figure 3R), *Pinnularia* cf. *subcapitata* and *Planothidium lanceolatum* were the most abundant in the diatom communities in soils associated with hot springs. These species had the maximum abundance scores (14–15 points) (Table 3).

Species that were indifferent to salinity changes (31 taxa, 63%), and halophobic (13 taxa, 27%) were the most numerous (Table 3). Halophilic taxa accounted for only five species: *Diatoma moniliformis*, *Luticola acidoclinata* (Figure 3P), *Navicula cincta*, *Sellaphora rectangularis* (Figure 3Z), and *Staurosirella pinnata*.

Representatives from almost all ecological groups of algae (benthic, littoral, planktonic, epiphytic–littoral, benthic–planktonic, epiphytic–planktonic, benthic–epiphytic, and epiphytic) were found in the samples (Table 3). Most species were typical benthic (18 taxa). The epiphytic and littoral–epiphytic groups were represented by nine species. Eight taxa were benthic–epiphytic.

The dominance of alkaliphilic species (24 taxa, 49%), such as *Encyonema silesiacum*, *Hannaea arcus*, *Hantzschia* cf. *abundans* (Figure 3O), *Luticola acidoclinata*, *Navicula cincta*, *Nitzschia hantzschiana*,

and *Sellaphora rectangularis*, characterized the soils associated with the hot springs (Table 3). Acidophilic species like *Aulacoseira distans* (Figure 3A), *Encyonema perpusillum*, *Eunotia* sp. (Figure 3J), *Frustulia krammeri* (Figure 3K), *Pinnularia borealis* (Figure 3U), and *Psammothidium ventrale* were represented by fourteen taxa (Table 3). Eleven species were indifferent to pH (for example, *Odontidium hyemale* (Figure 3S), *Diploneis calcilacustris* (Figure 3D), *Encyonema silesiacum*, *Epithemia operculata*, *Luticola acidoclinata*, *Nitzschia hantzschiana*, and *Staurosirella pinnata*) (Table 3).

Cosmopolitan taxa—*Decussiphycus placenta* (Figure 3E), *Epithemia adnata* (Figure 3F), *Gomphonella olivacea*, *Luticola acidoclinata*, *Navicula cincta*, *Pinnularia borealis*, *Sellaphora rectangularis*, *S. seminulum* (Figure 3AA), *Staurosira venter* (Figure 3AB), and *Surirella brebissonii*—comprised the bulk of the list (38 diatom taxa, 78%). Only eight arcto-alpine species (16%) were found. Three of these taxa (6%) are regarded as boreal species: *Aulacoseira distans*, *Encyonema silesiacum*, and *Nitzschia hantzschiana* (Table 3).

4. Discussion

In the diatom communities of the Malki, Upper Paratunka, and Dachnie thermal springs, representatives of the genera and species common to such environments were identified (Table 3).

The wide distribution of the genus *Pinnularia* (Table 3) in the thermal springs has been discussed in previous studies [13]. *Pinnularia* is abundant in slightly acidic freshwater bodies [42], and also was typical for diatom communities in terrestrial ecosystems [40].

In all of the springs studied, at pH levels from 3.5 to 9.4, *Pinnularia* cf. *subcapitata* dominated (Table 3). *Pinnularia subcapitata* belongs to acidophilic group of species (Table 3), and *Pinnularia subcapitata* var. *elongata* has been identified in samples from Bekanbeushi Wetland (Eastern Hokkaido, Japan) in a territory of the Kuril–Kamchatka island arc [53]. Like most cosmopolitan species, this taxon is possibly adapted for life in a wide range of ecological conditions.

Another representative of genus *Pinnularia*—*P. microstauron*, which was abundant in all springs studied (Table 3), has been recorded at pH 6.7–7.0 and temperature 40 °C in Stolbchaty Cape hydrothermal springs (Kunashir Island) [54]. Thus, our results indicate that *P. microstauron* exists in wider ranges of pH and temperature than has been reported previously for the thermal springs of the Kuril–Kamchatka island arc.

The results of our study confirm that *P. borealis* also belongs to the ecologically resistant taxa. In the samples we obtained from the Upper Paratunka and Dachnie springs, this diatom was found at pH 3.2–9.4 and temperature 30.0–69.5 °C. In a previous study of diatoms from hydrothermal springs on Kunashir Island, *P. borealis* was identified in Stolbchaty Cape springs and in Alekhin Bay springs at pH 4–5, 50–55° C [54]. This taxon has also been found in the sulfidic Cuntis hot springs in Galicia (NW Spain), which are characterized by deep hydrothermal flows and temperatures of 48–54 °C [15].

The wide distribution of *P. borealis*, *P. subcapitata*, and *P. microstauron* in terrestrial habitats [40] confirms the ecological resistance of these species and explains their frequency in thermal spring ecotones.

Planothidium lanceolatum, which dominated in all of the springs we investigated, belongs to the most common and abundant species of diatoms in the springs and streams of Türkmen Mt., Turkey [36]. This species was found as a dominant or abundant species in ten Sakhalin and Kuril Islands hot springs at temperatures from 24 to 71 °C, and has been characterized as indifferent to the salinity rheophilic diatom in the Sakhalin hydrothermal springs [54]. *Planothidium lanceolatum* was previously found to be dominant in alpine springs with cold water, low conductivity, and slightly alkaline pH, and also in the Font de Bleix thermo-mineral spring in Auvergne, France, which has high concentrations of nitrates and calcium [17]. In addition, this diatom has been identified in hot spring diatoms in northern Thailand. A number of ecological factors, such as concentration of silicon dioxide, pH, conductivity, water temperature, and total hardness influence the relative abundance of *P. lanceolatum* [16].

We discovered that *Encyonema silesiacum* was relatively frequent in diatom communities in the Malki, Upper Paratunka, and Dachnie thermal springs. This species has been found in the Stolbchaty

Cape springs at pH 6.7–7.0 and temperature 40 °C (Kunashir Island) [54]. *Encyonema silesiacum* has also been observed in Sardinia, Italy, in the San Saturnino thermo-mineral spring, which has a medium–high conductivity and low nutrient content [17]. Our findings indicate a greater thermal and pH amplitude for *E. silesiacum* than has previously been recorded [54]. Similar to representatives of the genus *Pinnularia*, this taxon is cosmopolitan in terrestrial ecosystems [40].

Another species that was found in all of the thermal springs we studied was *Navicula cincta*. *Navicula* is one of the most common genera in springs [55–58]. *Navicula* species related to *N. cincta* are rare in springs, but many new species from this group have been described [58]. *Navicula* is a benthic–epiphytic, alkaliphilous species with cosmopolitan distribution [46], and is also common in thermo-mineral springs [15,17]. *Navicula cincta* prefers mostly eutrophic, electrolyte-rich waters and periodically wet habitats [58], and it is widely distributed in soils [40], so the discovery of this species in soils near hot springs was expected.

The dominance of *Fragilariforma virescens* and *Epithemia operculata* in the diatom communities in the Malki and Upper Paratunka hot springs at 39.5–69.5 °C and pH 3.5–8.3 indicates the environmental plasticity of these species. *Fragilariforma virescens* prefers freshwater littoral–benthic habitats and is distributed in arcto-alpine regions [46]. This diatom belongs to the characteristic species found in algal communities in an ephemeral sandstone stream in the Bohemian Switzerland National Park, Czech Republic [59]. *Epithemia operculata* has been recorded in both freshwater [60] and terrestrial habitats [40].

Of particular interest in this investigation is our finding of the typical freshwater taxa *Aulacoseira distans*. This may indicate the transitional characters of the studied habitats between aquatic and terrestrial environments. *Aulacoseira* is one of the most distributed freshwater-centric diatom genera [44]. In previous studies of Kunashir Island, *A. distans* var. *distans* was recorded in Alekhin Bay hydrothermal springs [55].

The abundance of *Nitzschia hantzschiana*, *Halamphora normanii*, and *Gomphonema* sp. found in our study confirms existing data regarding the distribution these taxa in thermo-mineral springs [15,17,54].

The *Gomphonema* species were abundant in the sulfurous spring on the coast of Alekhin Bay on Kunashir Island [54]. *Gomphonema* is also member of diatom communities in the Outariz thermo-mineral springs in Galicia, NW Spain [15], and have frequently been found in thermo-mineral springs in Auvergne and Sardinia [17].

Nitzschia hantzschiana has been recorded in Guitiriz thermo-mineral springs in Galicia, NW Spain, in conditions of lower conductivity and temperature [15]. *Halamphora normanii* is a common species in the Auvergne and Sardinia thermo-mineral springs [17]. Both taxa are common in terrestrial ecosystems [40].

In this work, *Diatoma moniliformis* and *Surirella brebissonii* were abundant in the Malki hot springs in low pH conditions (Table 3, Figure 4), but according to existing literature, these taxa are alkaliphilic. However, we studied soil and mud samples, the pH of which could differ from the pH of water in the thermal springs. *Diatoma moniliformis* has been recorded in the alluvial Middle Fork Flathead River within the Nyack Flood Plain, Montana, at downwelling and neutral exchange sites [61]. *Surirella brebissonii* has been recorded in hydrothermal springs on Sakhalin Island [54].

In our study, *Eunotia curtagrunowii* and *Odontidium hyemale* were recorded in the Malki and Dachnie thermal springs at 30–65.9 °C and pH 3.2–8.3. The diatoms from the genus *Eunotia* prefer soft and acidic water bodies [41]. *Eunotia curtagrunowii* has also been recorded in soils in the Low Beskids, Poland [47], and it may inhabit the soils near the thermal springs that we studied. *Odontidium hyemale* has been found in the Tovare rheocrenic spring in the Brenta mountain range in the Western Dolomites [62].

Sellaphora rectangularis and *Navicula leptostriata* are abundant in the Upper Paratunka thermal springs diatom communities at 39.5 °C and pH 8.3 [41]. According to published data, *Sellaphora* is a widespread genus in alkaline waters and brackish waters close to a neutral pH. *Navicula leptostriata* has been recorded in freshwater bodies on Bering Island at pH 5.2–9.6 (Kamchatka) [38].

In the present work, *Eunotia exigua*, *Frustulia krammeri*, *Caloneis lancettula*, and *Neidium dubium* were recorded in the Dachnie thermal springs at 30.0–50.0 °C and pH 3.2–9.4. *Eunotia exigua* is typical in hot springs with a low pH [54,63]. *Frustulia krammeri*, like *Navicula leptostriata*, has been found in Bering Island freshwater habitats at neutral and alkaline pH [38]. *Caloneis lancettula* is a common diatom in freshwater bodies and is a good indicator of an elevated trophic level [34]. It has been found in streams and springs in the territory of Turkey [36]. The genus *Neidium* is common in neutral and slightly acidic waters, and this genus is characterized by a low abundance [42].

The species composition of diatoms that we found in soils associated with the Malki, Upper Paratunka, and Dachnie thermal springs of Kamchatka was similar to the species composition of periphyton communities described in the same springs in previous studies [20,21]. In these habitats, boreal species that are adapted to high temperatures prevail [21]. Surprisingly, in the aquatic and terrestrial habitats of the studied area, thermophilic species did not play significant roles in this work. *Hannaea arcus*, *Encyonema silesiacum*, *Gomphonema* sp., *Planothidium lanceolatum*, *Frustulia krammeri*, and others appear to be well adapted to a wide range of temperatures and habitats, as they have been recorded in a wide range of cold water habitats and hot springs in Kamchatka, Kuril, and Sakhalin Islands in previous works [54] and in our study.

In our study, dominance of cosmopolitan diatom taxa was the basic feature of the soils near the Malki, Upper Paratunka, and Dachnie thermal springs. The same results were obtained for diatom flora of the Malki, Upper Paratunka [21], and Dachnie thermal springs [20] in previous studies. The springs we investigated are characterized by a range of abiotic factors such as high temperature, mineralization, and soil moisture, which affect the species diversity of diatoms. The prevalence of diatom species that are benthic, indifferent to salinity, or alkaliphilic in the soils near the Malki, Upper Paratunka, and Dachnie thermal springs might be a consequence of environmental conditions. The diatom flora of the hot springs in Sakhalin Island have the same characteristics [54]. The diatoms were characterized by predominance of taxa that are benthic, indifferent to salinity, or acidophilic. These features may reflect the peculiarities of the ecological conditions in the thermal springs of the Kuril–Kamchatka volcanic arc.

The territory that we studied is a kind of ecotone between aquatic and terrestrial habitats; therefore, typical terrestrial species should be expected in soils associated with the hot springs. We found numerous soil taxa such as *Gomphonema brebissonii*, *Gomphonema* sp., *Hantzschia* cf. *abundans*, *Navicula cincta*, *N. minima*, *Pinnularia borealis*, *P. cf. subcapitata*, and *Tabellaria flocculosa*, together with typical aquatic species like *Aulacoseira distans*, *Decussiphycus placenta*, *Hannaea arcus*, *Nitzschia recta*, *Odontidium hyemale*, *Surirella brebissonii*, and others. Such aerophilic diatoms, which are also regarded as common in soil like *Pinnularia borealis*, have also been observed in water samples from the Malki, Upper Paratunka [21], and Dachnie thermal springs [20]. In soil samples, however, the number of terrestrial species is more numerous. This phenomenon can be explained by the transitional nature of the habitat at the border of the hot springs and soils. To gain a better understanding of the diversity of diatom communities in soils near thermal springs, broader worldwide studies are necessary.

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