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Ecotonic Communities of Diatoms in the Southeastern Part of the Kamchatka Peninsula

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Abstract: Data about the ecotonic diatom communities of the Kamchatka Peninsula, a unique territory with strong volcanic activity, are very limited. We aimed to investigate diatom algae of the ecotones in the southeastern part of Kamchatka, including the Paratunka river valley, at the foot of the Vachkazhets volcano, and the bank of the Bystraya river. In total, 55 taxa were identified. The most diverse were the flora of the Paratunka river, with 31 taxa. Near the Bystraya river, 26 taxa were identified. Near the Vachkazhets volcano, 18 taxa were identified. *Fragilariforma virescens*, *Planothidium lanceolatum*, *Pinnularia* cf. *subcapitata*, *Halamphora normanii*, *Nitzschia palea*, and *Eunotia exigua* were the dominant species in the studied ecosystems, with the maximum abundance score. *Pinnularia* cf. *subcapitata* and *Planothidium lanceolatum* were found in all ecotones. In the studied habitats, small indifferent alkaliphilic cosmopolitan species prevailed. Our study revealed that the diatom species composition of the Kamchatka ecotones reflects their adaptability to survive in the extreme conditions of volcanic substrates. The results contribute to our knowledge of the ecology and biogeography of a number of diatom taxa.

Keywords: communities; cosmopolitans; diversity; Bystraya river; Paratunka river; Vachkazhets volcano; *Eunotia exigua*; *Fragilariforma virescens*; *Pinnularia* cf. *subcapitata*; *Planothidium lanceolatum*

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1. Introduction

The Kamchatka Peninsula is a unique region that is characterized by a number of features. The first is the specificity of soils due to the following combination of a number of factors of soil formation: the cold, excessively humid climate in the coastal areas; the variety of relief; the vegetation features; and the special soil-forming rocks of volcanic origin [1–7]. The composition of the soil-forming rocks of Kamchatka includes volcanogenic deposits. There are three zones of ashfall influence on the peninsula. The central Kamchatka depression is located in the zone of moderate ashfall. The southern half of the West Kamchatka Lowland is located in the zone of moderate ashfall, a subzone of weakened ashfall. The northern half of the West Kamchatka Lowland is in the zone of weak ashfall [6]. In the first two zones, volcanic deposits are represented by volcanic sands and ash; in the third zone, volcanic deposits are represented by volcanic dust [8].

The second peculiarity is the climate. The great originality of the climate of the region is associated with its physical and geographical location. The difficult terrain leads to climate differences, even between closely located areas. The peninsula is dominated by strong winds, hurricanes, and storms and produces a significant amount of precipitation, depending on the large extent of the peninsula from north to south, the terrain, the proximity of large water spaces and the movements of cyclones [8,9]. There is frequent variability in the weather in all seasons of the year, especially in winter. In the central regions of Kamchatka, some winter months can be almost 10 °C colder or warmer than usual. On the coasts, in some years, the average temperature in winter can be higher than the long-term average by almost 15 °C. A sharp warming or cooling period can occur not only from winter to winter or from summer to summer; they also often occur during the day. In most of the territory, there is a long, snowy winter and negative average annual temperatures, as well as a short cloudy summer. Snow falls early, and a stable snow cover is formed almost immediately. This time of year lasts about five months throughout the peninsula, and it reaches up to seven months in the far north [9].

A significant role in the transformation of the relief of the Kamchatka Peninsula belongs to earthquakes and volcanic activity [10–12]. In this regard, the next feature of the region is its high seismic activity. Lava flows of different ages cover more than one third of the peninsula's territory. In particular, there are many volcanoes in the southern and eastern parts, as well as in the middle ridge. During earthquakes, numerous rock collapses and landslides occur. Deep cracks are formed that dissect the surface of the earth. Earthquakes, the epicenters of which are located in the sea, often give rise to tsunamis, producing significant destruction along the coastal strip on the eastern coast of Kamchatka [13]. In the soils of Kamchatka, relatively high concentrations of some elements, such as Na, Ca, Mg, Cd, Mn, Co, and Cu, have been observed [14,15].

The peculiarity of the natural and climatic conditions of the peninsula contributes to the formation of various natural ecosystems in its territory, especially in its southeastern part, characterized by abnormally high heat flow, the widespread development of modern volcanism, and the manifestation of numerous hydrothermal systems [16,17]. For a long time, special algae communities with species with a high degree of resistance to such unusual environmental conditions have developed here.

Kamchatka has significant freshwater reservoirs, the formation of which occurred in very diverse geological–structural, hydrogeological, geochemical, and geothermal conditions. IN the territory of the peninsula, there are 139 thousand rivers, with a total length of 359.8 thousand km. There are also more than 112 thousand lakes in the territory of the region, with a total water surface area of more than 5.8 thousand km^2, which is 1.2% of the area of Kamchatka [18]. The species richness and the structural and functional parameters of the diatom algae complexes of transitional territories—ecotones—are interesting objects of study that depend on many factors.

Ecotones are widely distributed in nature. Special ecotonic biotic communities and corresponding ecotonic systems are formed in ecotone zones. They have special compositions, structures, and mechanisms of stability [19]. Such communities differ from zonal communities. One of the main features of ecotonic territories is the increased fluctuation activity of environmental factors [20]. Ecotones reflect the continuity of the biogeocenotic cover and perform the function of connecting various natural communities. At the same time, they perform a buffer function and function as refugia for a number of organisms [21].

Algae are the most important component of the biotic communities of ecotonic systems, and their role in aquatic–terrestrial ecotones is especially significant. However, algological studies of ecotones are insufficient [22–25], and our knowledge of the compositions, structures, and patterns of growth in ecotonic systems lags significantly behind the degree of study of higher vegetation. Meanwhile, the study of the role of algae as a component of aquatic and aquatic–terrestrial ecotones will allow us to more fully reveal the patterns of life activity in ecotonic communities. It is especially interesting to study the diatoms of ecotonic communities because this group of algae is known as indicators of environmental conditions [26–28]. The analysis of diatom species composition and quantitative abundance provides an integral assessment of the results of natural and anthropogenic processes.

Despite the existing information about the diatoms of some Kamchatka ecosystems, including freshwater bodies [29–32], thermal springs [33–35], and volcanic soils [36,37], the data concerning the diatoms of the ecotonic assemblage, including the diatoms of the coastal zone, are very limited and need further investigation.

The aim of this work was to study the biodiversity of the diatoms of some ecotones in the coastal zones of the southeastern part of the Kamchatka Peninsula.

2. Materials and Methods

2.1. Studied Area

The environmental conditions of the territory of the Kamchatka Peninsula are characterized by a high level of heterogeneity, which was taken into account during the research. We analyzed the following three sites: the valley of the Paratunka river near the village of Paratunka; the foot of the Vachkazhets volcano near the village of Malki; and the bank of the Bystraya river in the village of Malki (Figure 1).

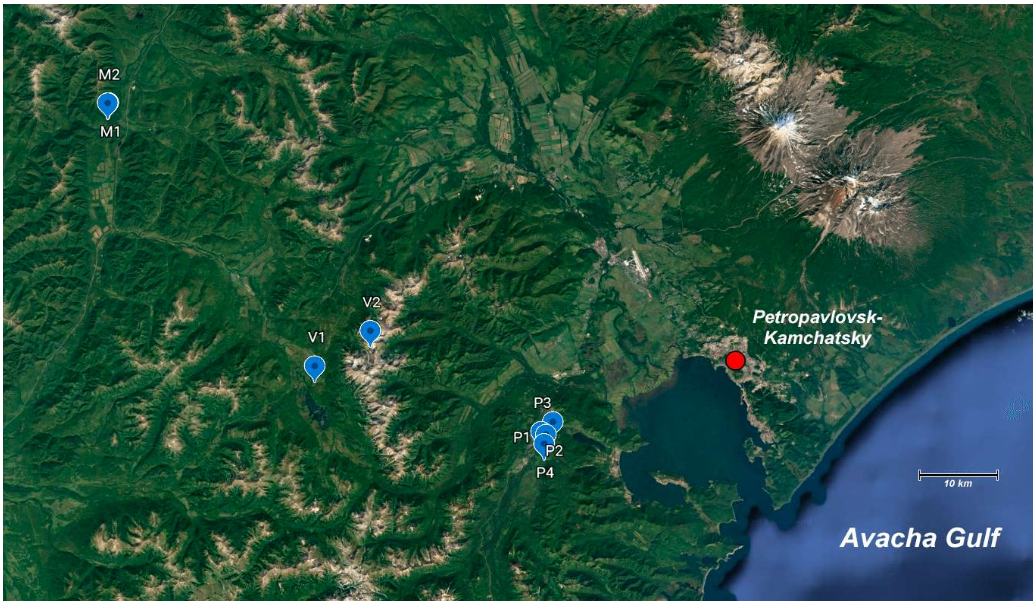

Figure 1. Study area. The red circle indicates Petropavlovsk-Kamchatsky. Sites P1–P4, V1–V2, and M1–M2 are numbered according to Table 1.

Table 1. Sampling sites.

Site Number	Site Description	Site Name	GPS	The Name of the Area	Sample Description
1	Central part of the Paratunka river valley	P1	52°56′59.0″ N 158°16′18.0″ E	Paratunka river	Soil from a swampy area
2	Abandoned pioneer camp (on the lake shore 500 m from the highway in the forest)	P2	52°57′53.0″ N 158°17′07.0″ E	Paratunka river	Soil 0.3 m from the water's edge
3	Paratunka village	P3	52°57′09.0″ N 158°16′08.0″ E	Paratunka river	Soil from a dried-up swamp
4	Paratunka river (2 km from the village of Paratunka)	P4	52°57′07.0″ N 158°16′10.0″ E	Paratunka river	Soil 0.2 m from the water's edge
5	The foot of the Vachkazhets volcano (3 km from the volcano)	V1	53°02′54.0″ N 157°52′57.0″ E	Vachkazhets volcano	Soil 10 m from the lake
6	"Veronica's Hair" Waterfall	V2	53°04′07.0″ N 157°56′28.0″ E	Vachkazhets volcano	Soil at the base of the waterfall bowl
7	Village Malki (the bank of the Bystraya river)	M1	53°19′43.0″ N 157°27′55.0″ E	Bystraya river	Soil 0.3 m from the river bank
8	Village Malki (the bank of the Bystraya river)	M2	53°19′43.0″ N 157°27′55.0″ E	Bystraya river	Soil 15 m from the river bank

According to the soil zoning of Kamchatka [7,38], the studied region belongs to the southeastern soil province. The surface organogenic horizon within the province was formed on the andesite–basalt gray coarse-grained ash of the 1907 eruption of the Ksudach volcano. All ash horizons, except the near-surface layer, have a predominantly acidic composition. The soil pH is acidic or slightly acidic.

Paratunka village geographically belongs to the Yelizovsky district of the Kamchatka Territory. It is located along the upper reaches of the Paratunka river, 25 km southwest of the city of Petropavlovsk-Kamchatsky. A river of the same name flows through the village, originating in the foothills of the Vilyuchinskaya Sopka volcano [39].

The Vachkazhets mountain range is located in the south of the Kamchatka Peninsula, the highest point of which is Mount Vachkazhets, with a height of 1556 m above sea level, which is located 80 km west of Petropavlovsk-Kamchatsky. Vachkazhets is an ancient volcano that was divided into three main parts as a result of a strong eruption [40].

Village Malki is situated on the Bystraya river, which flows along the southern part of the median ridge. Its length is 180 km, its depth ranges from 1 to 3 m, its width in the lower reaches is 50–100 m, and its width in the middle reaches is 20–40 m [41].

2.2. Sample Collection and Data Analysis

Eight soil samples were collected in August 2009 according to previously described methods [35,42] from the Paratunka river valley (four samples), the foot of the Vachkazhets volcano (two samples), and the bank of the Bystrica River (two samples). Small amounts of wet soil (50–100 g) from several random points at each studied site were taken with a metal cylinder and put into plastic bags. Thus, the sample from each site was a composite sample. In the laboratory, the samples were dried in the shade [43]. Thus, the diatom communities were studied along transects crossing the interface between the aquatic and terrestrial environments. In the laboratory, the samples were investigated using the standard procedure to study soil diatoms [43]. The samples were rinsed in deionized water and nitric acid, boiled in nitric acid, and washed in deionized water again. The diatoms were mounted on permanent slides in Naphrax [35].

For the identification of diatom algae, Zeiss Axio Imager A2 light microscopes (Carl Zeiss, Jena, Germany) with differential interference contrast at 1000× magnification and oil immersion were used. Valve images were taken using an AxioCam MRc camera and Axio Vision 4.9.1 software. The permanent diatom slides were placed in the Collection of Algae and Cyanobacteria (BCAC). For species identification, basic key books [44–48] and recent publications [47–51] were used. For the estimation of the ecology of species, the relevant literature was used [49–53].

For the estimation of the floristic similarities between ecotones, the Sørensen–Czekanowski coefficient was used, as follows:

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

where K is the coefficient of the floristic similarity, 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 [54].

For a demonstration of the similarities between the diatom communities from the ecotones near the Paratunka river, the Vachkazhets volcano, and the Bystraya river, a Venn diagram was used [55,56]. It was created online using the web-based tool InteractiVenn [57] and edited manually using Microsoft Visio 2019.

The species abundance was calculated on a coverslip according to previously described methods [35,58]. The abundance of diatoms was estimated on a 15-point scale on a slide, where the minimum abundance corresponded to 1 point and the maximum abundance was 15 points.

A map of the study area was created using the online tool Google Earth [59].

3. Results

In our investigations, 55 species and infraspecific taxa of diatom algae from the genera *Achnanthes* Bory, *Aulacoseira* Thwaites, *Diatoma* Bory, *Diploneis* Ehrenberg ex Cleve, *Encyonema* Kützing, *Epithemia* Kützing, *Eunotia* Ehrenberg, *Fragilaria* Lyngbye, *Fragilariforma* D.M. Williams and Round, *Frustulia* Rabenhorst, *Gomphonema* Ehrenberg, *Halamphora* (Cleve) Levkov, *Hannaea* Patrick in Patrick and Reimer, *Hantzschia* Grunow, Luticola D.G. Mann, *Mayamaea* Lange-Bertalot, Navicula Bory, *Neidium* Pfitzer, *Nitzschia* Hass, *Pinnularia* Ehrenberg, *Planothidium* Round and L. Bukhtiyarova, *Pseudostaurosira* D.M. Williams and Round, *Rhopalodia* O. Muller, *Sellaphora* Mereschowsky, *Staurosira* Ehrenberg, *Staurosirella* D.M. Wiliams and Round, *Surirella* Tyrpin, *Synedra* Ehrenberg, and *Tabellaria* Ehrenberg ex Kützing were detected (Table 2 and Figure 2A–I).

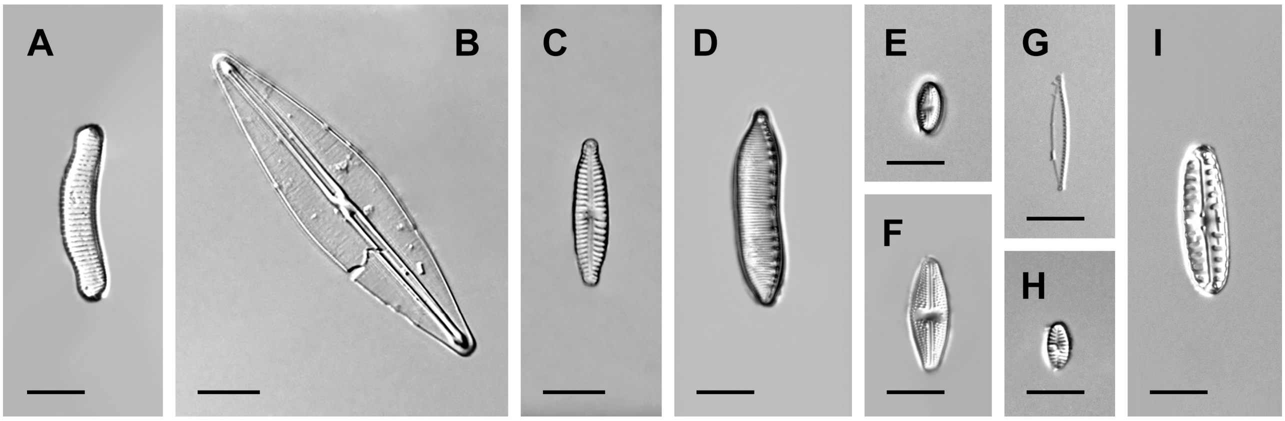

Figure 2. Species of diatoms in the ecotones of the Paratunka river valley, the Vachkazhets volcano, and the Bystraya river. (**A**) *Eunotia arcus* var. *fallax*; (**B**) *Frustulia krammeri*; (**C**) *Gomphonema parvulum*; (**D**) *Hantzschia* cf. *abundans*; (**E**) *Mayamaea atomus*; (**F**) *Luticola mutica*; (**G**) *Nitzschia palea*; (**H**) *Planothidium lanceolatum*; (**I**) *Pinnularia borealis.* Scale bar: 10 µm.

The genera *Gomphonema* and *Pinnularia* (six species each); *Eunotia* (five species); and *Encyonema*, *Navicula*, and *Sellaphora* (three species each) had the largest numbers of species (Table 2).

The diatom communities of ecotones in the Paratunka river valley were the most diverse and accounted for 31 taxa (Table 2 and Figure 3). In the ecotones near the Bystraya river, 26 taxa were detected. In the ecotones near the Vachkazhets volcano, 18 taxa were detected (Table 2 and Figure 3). In sample P1 from the central part of the Paratunka river valley, 31 species were identified. This was the highest number of species in a sample. The lowest number of taxa (14) was found in sample V1, which was collected 3 km from the Vachkajec volcano (Table 2). An average of 6.9 species were identified in the samples. Five species (*Encyonema silesiacum*, *Navicula cincta*, *Pinnularia* cf. *subcapitata*, *Planothidium lanceolatum* (Figure 2H), and *Synedra ulna*) were found in all of the studied ecotones (Figure 3). This indicated the low level of similarity between the studied diatom communities. The similarities between ecotones obtained with a pairwise comparison were also low (Figure 3); only 3–4 common species were detected. The diatom communities of the Paratunka river valley and the territory near the Vachkazhets volcano were the most similar (Figure 3). The value of the Czekanowski–Sørensen coefficient was 16.3%. The similarity between the Paratunka river valley and the bank of the Bystraya river was 14.1%, and the similarity between the territory near the Vachkazhets volcano and the Bystraya river was 13.6%.

Fragilariforma virescens, *Planothidium lanceolatum*, *Pinnularia* cf. *subcapitata*, *Halamphora normanii*, *Nitzschia palea*, and *Eunotia exigua* were the dominant species in the studied ecosystems, with the maximum abundance score (15 points).

Fragilariforma virescens was a dominant species in the diatom communities in the Malki and Upper Paratunka hot springs [23]. *Planothidium lanceolatum* also dominated in the Kamchatcan hot springs [23]. *Fragilariforma virescens* and *Planothidium lanceolatum* were dominant species in the ecotones of the Paratunka river valley and the Vachkazhets volcano (Table 2 and Figure 3). *Planothidium lanceolatum* was also detected in the samples from the Bystraya river bank (Table 2). *Pinnularia* cf. *subcapitata* prevailed in several samples from all of the studied ecotones (Table 2 and Figure 3). *Halamphora normanii* and *Nitzschia palea* dominated in the ecotones in the Paratunka river valley (Table 2). *Eunotia exigua* dominated in the communities of the Bystraya river bank (Table 2).

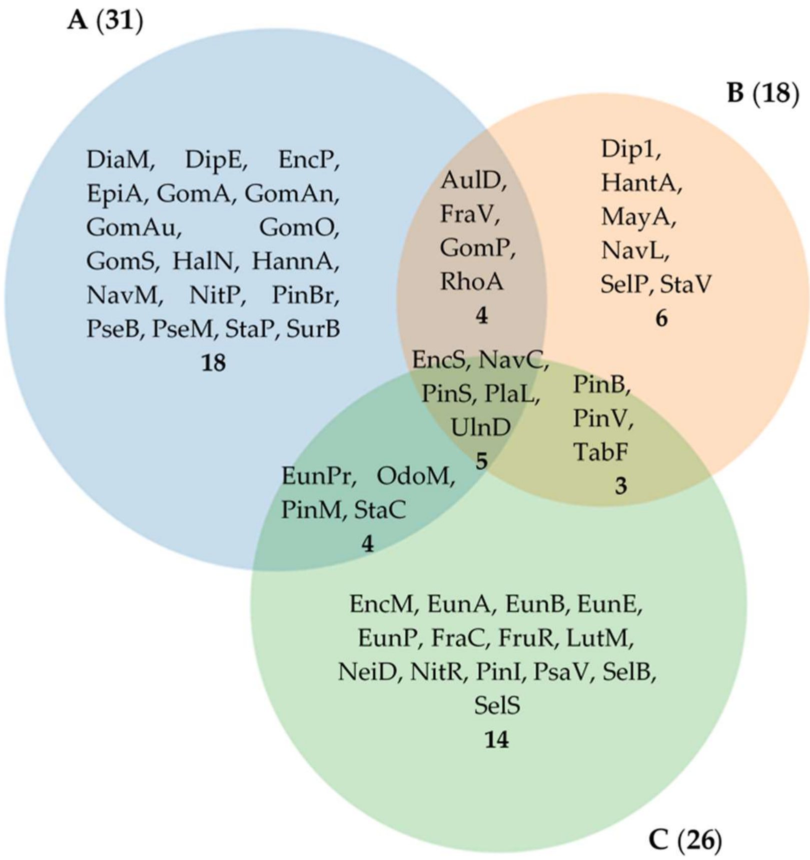

Figure 3. (**A**) (blue circle)—ecotones in the Paratunka river valley, (**B**) (beige circle)—ecotones near the Vachkazhets volcano, (**C**) (green circle)—ecotones near the Bystraya river. Numbers in brackets indicate the numbers of species in the communities. Species abbreviations: AulD—*Aulacoseira distans*; DiaM—*Diatoma moniliformis*; DipE—*Diploneis elliptica*; *Diploneis* sp.1—Dip1; EncM—*Encyonema minutum*; EncP—*E. perpusillum*; EncS—*E. silesiacum*; EpiA—*Epithemia adnata*; EunA—*Eunotia arcus* var. *fallax*; EunB—*Eunotia bilunaris*; EunE—*E. exigua*; EunP—*E. paratridentula*; EunPr—*Eunotia praerupta*; FraC—*Fragilaria capucina*; FraV—*Fragilariforma virescens*; FruR—*Frustulia rhomboides*; GomA—*Gomphonema acuminatum*; GomAn—*Gomphonema angustatum*; GomAu—*Gomphonema augur*; GomC—*Gomphonema clavatum*; GomP—*Gomphonema parvulum*; GomS—*Gomphonema subclavatum*; HalN—*Halamphora normanii*; HannA—*Hannaea arcus*; HantA—*Hantzschia* cf. *abundans*; LutM—*Luticola mutica*; MayA—*Mayamaea atomus*; NavC—*Navicula cincta*; NavL—*N. leptostriata*; NavM—*N. minima*; NeiD—*Neidium dubium*; NitP—*Nitzschia palea*; NitR—*N. recta*; OdoM—*Odontidium mesodon*; PinBr—*Pinnularia brevicostata*; PinB—*P. borealis*; PinI—*Pinnularia intermedia*; PinM—*P. microstauron*; PinS—*P.*cf. *subcapitata*; PinV—*Pinnularia viridis*; PlaL—*Planothidium lanceolatum*; PsaV—*Psammothidium ventrale*; PseB—*Pseudostaurosira brevistriata*; PseM—*Pseudostaurosira medliniae*; RhoA—*Rhopalodia acuminata*; SelB—*Sellaphora bacillum*; SelP—*Sellaphora pupula*; SelS—*S. seminulum*; StaC—*Staurosira construens*; StaV—*Staurosira venter*; StaP—*Staurosirella pinnata*; SurB—*Surirella brebissonii*; TabF—*Tabellaria flocculosa*; TabF—*Tabellaria fenestrate*; UlnD—*Ulnaria danica*.

Table 2. Floristic list of diatom taxa, with relative abundance and ecological preferences, in the ecotones of the Paratunka river valley, the Vachkazhets volcano, and the Bystraya river. The abundances of the species are expressed on a scale from 1 to 15 according to Kabirov and Safiulina [58].

Taxon	A				B		C		Habitat *	Salinity Tolerance *	pH *	Distribution *	Typical Environment *
	P1	P2	P3	P4	V1	V2	M1	M2					
Aulacoseira distans (Ehrenberg) Simonsen	8		4	4		2			P B	i	ac	b	Marine, freshwater
Diatoma moniliformis (Kützing) D.M. Williams	6			5					P B	hl	al	c	Marine, freshwater
Diploneis elliptica (Kützing) Cleve	2	6	1	2					B	i	al	c	Freshwater
Diploneis sp.1						1			B	i	al	c	Freshwater
Encyonema minutum (Hilse) D.G. Mann							4	4	B Ep	i	al	c	Marine, freshwater
Encyonema perpusillum (A. Cleve) D.G. Mann	5	7							B Ep	hb	ac	c	Freshwater
Encyonema silesiacum (Bleisch) D.G. Mann	3	5	4		3	2	3	1	B Ep	i	al	b	Freshwater, terrestrial
Epithemia adnata (Kützing) Brébisson	10	12		8					Ep	i	al	c	Freshwater, terrestrial
Eunotia arcus var. *fallax* Hustedt							4		Ep	hb	i	c	Freshwater
Eunotia bilunaris (Ehrenberg) Schaarschmidt							6	8	L Ep	hb	ac	c	Freshwater
Eunotia exigua (Brébisson ex Kützing) Rabenhorst							15	15	L Ep	hb	ac	c	Freshwater
Eunotia paratridentula Lange-Bertalot and Kulikovskiy							2	4	L Ep	hb	ac	c	Freshwater
Eunotia praerupta Ehrenberg	12	5	3	8			8	10	L Ep	hb	ac	c	Freshwater
Fragilaria capucina Desmazières							2	1	L P	i	al	c	Marine, freshwater
Fragilariforma virescens (Ralfs) D.M. Williams and Round	15	15	15	15	15	15			L Ep	i	i	aa	Freshwater
Frustulia rhomboides (Ehrenberg) De Toni							3		B	hb	ac	aa	Freshwater, terrestrial
Gomphonema acuminatum Ehrenberg	13	10	6	4					Ep	i	i	c	Freshwater
Gomphonema angustatum (Kützing) Rabenhorst	10	8							Ep	i	al	c	Freshwater
Gomphonema augur Ehrenberg	1		1						Ep	i	i	c	Freshwater
Gomphonema olivaceum (Hornemann) Ehrenberg	7		5	4					Ep	i	al	c	Freshwater
Gomphonema parvulum (Kützing) Kützing	8	13	10	8	5	4			Ep	i	i	c	Freshwater
Gomphonema subclavatum (Grunow) Grunow	7		6	9					Ep	i	al	c	Freshwater
Halamphora normanii (Rabenhorst) Levkov	15	15	15						B	i	al	c	Freshwater, terrestrial

Table 2. *Cont.*

Taxon	A				B		C		Habitat *	Salinity Tolerance *	pH *	Distribution *	Typical Environment *
	P1	P2	P3	P4	V1	V2	M1	M2					
Hannaea arcus (Ehrenberg) R.M. Patrick	3		1	1					L	hb	al	aa	Freshwater
Hantzschia cf. *abundans* Lange-Bertalot					4	2			B	i	al	c	Freshwater
Luticola mutica (Kützing) D.G. Mann							10	13	B Ep	hl	al	c	Marine, brackish, freshwater, terrestrial
Mayamaea atomus (Kützing) Lange-Bertalot					10	8			B Ep	i	al	c	Marine, brackish, freshwater, terrestrial
Navicula cincta (Ehrenberg) Ralfs	3	7	5		4	5	5	2	B Ep	hl	al	c	Marine, brackish, freshwater, terrestrial
Navicula leptostriata Jørgensen						3			B	hb	ac	c	Freshwater
Navicula minima Grunow	10	12	5						B Ep	i	al	c	Freshwater
Neidium dubium (Ehenberg) Cleve							3		B	i	al	c	Marine
Nitzschia palea (Kützing) W. Smith	15	15	15						B	i	al	c	Freshwater
N. recta Hantzsch ex Rabenhorst							2		B	i	al	c	Freshwater
Odontidium mesodon Kützing (Ehrenberg)	3			1			1		B Ep	hb	al	aa	Freshwater
Pinnularia brevicostata Cleve	12	3							B	hb	i	b	Freshwater, terrestrial
Pinnularia borealis Ehrenberg					6		8	10	B	i	ac	c	Freshwater, terrestrial
Pinnularia intermedia (Lagerstedt) Cleve							3	12	B	i	i	aa	Freshwater
Pinnularia microstauron (Ehrenberg) Cleve	10	6	6	4			6		B	i	i	c	Freshwater, terrestrial
Pinnularia cf. *subcapitata* W. Gregory	15	15		15	8		15	14	B	hb	ac	c	Freshwater, terrestrial
Pinnularia viridis (Nitzsch) Ehrenberg					2		4		B	i	i	c	Freshwater, terrestrial
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot	15	15		15	15	15	10	8	Ep	i	al	c	Freshwater
Psammothidium ventrale (Krasske) Bukhtiyarova and Round							3	1	Ep	hb	ac	aa	Freshwater
Pseudostaurosira brevistriata (Grunow) D.M. Williams and Round	5	7	1						L Ep	i	al	c	Freshwater

Table 2. *Cont.*

Taxon	A				B		C		Habitat *	Salinity Tolerance *	pH *	Distribution *	Typical Environment *
	P1	P2	P3	P4	V1	V2	M1	M2					
Pseudostaurosira medliniae D.M. Williams and E.A Morales	1		1						L Ep	i	al	c	Freshwater
Rhopalodia acuminata Krammer in Lange-Bertalot and Krammer	4			2	15	15			Ep	i	al	b	Freshwater
Sellaphora bacillum (Ehrenberg) D.G. Mann							5	3	B	i	al	c	Freshwater
Sellaphora pupula (Kützing) Mereschkovsky					3	6			B	hl	i	c	Freshwater
Sellaphora seminulum (Grunow) D.G. Mann							5	2	B Ep	i	ac	c	Freshwater
Staurosira construens Ehrenberg	8	10	10	5			8	6	L Ep	i	al	c	Freshwater
Staurosira venter (Ehrenberg) Cleve and J.D. Möller						3			L Ep	i	al	c	Freshwater
Staurosirella pinnata (Ehrenberg) D.M. Williams and Round	2		2	2					L	hl	al	c	Marine, freshwater
Surirella brebissonii Krammer and Lange-Bertalot	4			1					B	i	al	c	Freshwater
Tabellaria flocculosa (Roth) Kützing					5	2			P Ep	hb	ac	aa	Freshwater, terrestrial
Tabellaria fenestrata (Lyngbye) Kützing							4	8	P	i	i	b	Freshwater
Ulnaria danica (Kützing) Compère and Bukhtiyarova	1	3		2	2	1	1		Ep L	i	al	c	Freshwater
Total number: 55	31	20	20	20	14	15	26	18					

Notes. (A) Ecotones in the Paratunka river valley: P1—central part of the Paratunka river valley, P2—abandoned pioneer camp (on the lake shore 500 m from the highway in the forest), P3—Paratunka village; P4—Paratunka river (2 km from the village of Paratunka). (B) Ecotones near the Vachkazhets volcano: V1—the foot of the Vachkajec volcano (3 km from the volcano); V2—"Veronica's Hair" Waterfall. (C) Ecotones near the Bystraya river: M1—Village Malki (the bank of the Bystraya river); M2—Village Malki (the bank of the Bystraya river). 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 are from the literature.

Our study revealed the existence of a wide range of ecological groups in the studied ecotonic communities of diatoms. They belonged to benthic, littoral, planktonic, epiphytic–littoral, littoral–planktonic, benthic–planktonic, epiphytic–planktonic, benthic–epiphytic, and epiphytic algae (Table 2). Typical benthic (18 taxa, 33%) and epiphytic (11 taxa, 20%) diatoms were the most diverse groups. Epiphytic–littoral algae accounted for 10 species. The benthic–epiphytic group was represented by nine taxa. The remaining groups were individually represented (1–2 species).

The most numerous were indifferent (36 taxa, 65%) and halophobic (14 taxa, 25%) species (Table 2). Halophilic taxa accounted for only five species, including *Diatoma moniliformis*, *Luticola mutica* (Figure 2F), *Navicula cincta*, *Sellaphora pupula*, and *Staurosirella pinnata*.

The studied habitats were dominated by alkaliphilic species (31 taxa, 56%), such as *Encyonema silesiacum*, *Hannaea arcus*, *Hantzschia* cf. *abundans* (Figure 2B), *Navicula cincta*, *Planothidium lanceolatum*, *Rhopalodia acuminata*, *Sellaphora bacillum*, and others (Table 2). In total, 13 taxa (24%), such as *Aulacoseira distans*, *Encyonema perpusillum*, *Eunotia bilunaris*, *Pinnularia borealis*, and *Sellaphora seminulum*, were acidophilic algae. Taxa that were indifferent to pH were the third largest group, with 11 species (20%). This group included *Odontidium hyemale*, *Diploneis calcilacustris*, *Encyonema silesiacum*, *Epithemia operculata*, *Luticola acidoclinata*, and *Staurosirella pinnata* (Table 2).

Regarding the geographic distribution of the studied diatom communities, the prevalence of cosmopolitan species (43, 78.2%) was a characteristic feature (Table 2). This group included *Diatoma moniliformis*, *Diploneis elliptica*, *Encyonema minutum*, *E. perpusillum*, *Epithemia adnata*, and other taxa. The arcto-alpine group was represented by seven species (12.7%), including *Fragilariforma virescens*, *Frustulia rhomboids*, *Hannaea arcus*, *Odontidium mesodon*, *Pinnularia intermedia*, *Psammothidium ventrale*, and *Tabellaria flocculosa.* Boreal species included only five taxa (9.1%), including *Aulacoseira distans*, *Encyonema silesiacum*, *Pinnularia brevicostata*, *Rhopalodia acuminata*, and *Tabellaria fenestrate* (Table 2).

In the studied diatom communities, freshwater species prevailed (Table 2). There were 10 freshwater and terrestrial taxa, including *Encyonema silesiacum*, *Epithemia adnate*, *Frustulia rhomboides*, and others. Five species, such as *Aulacoseira distans*, *Diatoma moniliformis*, and *Fragilaria capucina*, belonged to marine and freshwater taxa. Three species, *Luticola mutica* (Figure 2F), *Mayamaea atomus* (Figure 2E), and *Navicula cincta*, were marine, brackish, freshwater, and terrestrial algae. Only one species, *Neidium dubium*, belonged to the marine algae category (Table 2).

4. Discussion

In the studied diatom communities, a characteristic feature was the predominance of cold-loving species that are common in temperate zones, which had adapted to living in the conditions of highly mineralized substrates. The predominance of cold-loving species of diatoms is probably explained by the specifics of the studied ecotones. It has been established that plain shrub tundras are often located within the territories of the valleys of large rivers, in floodplains, and on upper floodplain terraces. These communities are situated in the floodplain of the lower reaches of the Bystraya river [13].

As noted above, the dominant complex of the diatoms of the studied territories was represented by the following five species: *Fragilariforma virescens*, *Halamphora normanii*, *Nitzschia palea*, *Pinnularia* cf. *subcapitata*, and *Planothidium lanceolatum*. *Encionema silesiacum*, *Navicula cincta*, *Pinnularia* cf. *subcapitata*, *Planothidium lanceolatum*, and *Synedra ulna* were common to all three habitat groups. These taxa are abundant in both soil substrates and aquatic ecosystems [33,34,60], which corresponds to the formation of the species diversity of ecotonic communities.

Species diversity is the result of the formation of sustainable ecosystems. In stable habitat conditions, more species can exist. On volcanoes, the substrates are not formed and are loose, which negatively affects biodiversity. Therefore, in soil samples near the Vachkazhets volcano, less species were found than near the Paratunka and Bystraya rivers. The climate of the southern volcanic district of Kamchatka, near which the ecotonic communities of the

Paratunka river are located, is characterized by intense cyclonic activity and a high level of precipitation [13], which probably affects the rich species diversity of diatoms.

According to the results of previous studies of diatom algae of the Kamchatka Peninsula [35], the species composition of the studied ecosystems was similar to the diatom complexes of the Malki, Upper Paratunka, and Dachnie thermal springs. In both ecotonic communities and in soils near hot springs, representatives of the genera *Encyonema*, *Navicula*, and *Pinnularia* prevailed. A number of local "spots of life", associated with the edge effect, could be distinguished. These "spots" include, among other things, the ecosystems of hot springs, lakes, and floodplains of rivers that are periodically flooded. Previous studies have shown that life in aquatic systems is concentrated and most active in the water layers adjacent to the external and internal sections with active surfaces [61].

It should be noted that the communities of diatoms in ecotones near water significantly differed from similar communities of previously studied soils of the Mutnovsky and Gorely volcanoes [37]. These differences were especially pronounced in the composition of the diatoms. In contrast to the studied ecotonic communities of Kamchatka diatoms, the soils of Mutnovsky and Gorely were dominated by *Pinnularia borealis* and *Humidophila contenta*, which are often detected in terrestrial habitats [62,63]. *Caloneis bacillum* and *Encyonema sudetica*, which were absent in the well-moistened substrates of ecotones, were found in volcanic soils.

The similarity of the diatom communities of the soils of the Mutnovsky and Gorely volcanoes and the studied ecotones consisted of the frequent occurrence of various representatives of the genus *Pinnularia*.

Pinnularia cf. *subcapitata* and *Planothidium lanceolatum* were found in all studied habitats, including ecotones in the Paratunka river valley, near the Vachkazhets volcano, and near the Bystraya river; in the soils near the Malki, Upper Paratunka and Dachnie thermal springs [35]; and in the soils of the Mutnovsky and Gorely volcanoes [37]. These taxa are widely distributed in different ecosystems around the world [49,60,64,65]. These data once again confirmed that in the terrestrial ecosystems of Kamchatka, the main part of the diatom algae community is represented by small cosmopolitan benthic forms. The same results were obtained in previous studies [35,37].

Most of the identified taxa belong to species that are recognized as freshwater species. This does not fully reflect their ecological characteristics. For example, at least some taxa, such as *Fragilariforma virescens*, *Eunotia exigua*, *Planothidium lanceolatum*, and *Nitzschia palea*, should be considered not only freshwater but also terrestrial species.

Thus, our studies of the communities of diatoms of the Kamchatka Peninsula have shown that the species composition of these communities reflects their adaptability to living in the conditions of organically poor volcanic substrates with sharp pH fluctuations, high concentrations of some elements, and a cold climate. In such conditions, the selection of the most resistant species with high adaptability to extreme environmental conditions is underway. The results of this research allow us to expand our knowledge about the ecology and biogeography of a number of diatom genera and species and will contribute to the more intensive study of these organisms in volcanic habitats around the world.

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