



Preliminary study of the benthic fauna in lakes of the Novaya Zemlya Archipelago and Vaigach Island (the Russian Arctic)

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Abstract

The biodiversity of freshwater fauna of the Arctic Islands of the Russian Federation is currently poorly studied and to date there are insufficient molecular genetic data concerning most of the taxa. This study presents the new data on species composition and distribution of freshwater benthic invertebrates in lakes of the Novaya Zemlya Archipelago and Vaigach Island based on both the published and the original records. A total of 29 species of invertebrates in 4 classes and 14 orders were found. Considering the published data, the list of species expands to 136 species. The copepod *Mesocyclops leuckarti*, the pontoporeid amphipod *Monoporeia affinis*, the ostracod *Leucocythere mirabilis*, and the mollusk *Euglesa globularis* were recorded for the first time from the Novaya Zemlya Archipelago. The oligochaete *Rhyacodrilus coccineus*, the stonefly *Nemoura sahlbergi*, the caddisflies *Agrypnia obsoleta*, *Micrasema gelidum* and *Philarctus bergrothi* were registered for the first time from Vaigach Island; *P. bergrothi* was also recorded for the first time from Europe. The crane fly larvae of *Tipula (Arctotipula)* were recorded as inhabitants of the bottom layer of Arctic lakes for the first time. The obtained molecular data are in accordance with the tabula rasa hypothesis that the invertebrate fauna of the Novaya Zemlya Archipelago and Vaigach Island are the result of recent species immigration after the Last Glacial Maximum. Our data can be used in further ecological studies and conservation management. The molecular data are of considerable interest for the taxonomy and biogeography of the fauna of the Arctic islands during the Pleistocene.

Keywords Freshwater invertebrates · Vaigach Island · Novaya Zemlya Archipelago · Distribution · Biogeography · Biodiversity

Introduction

Freshwater invertebrates serve as important contributors to ecosystem functioning which includes detritus decomposition, self-purification, animal-microbial interactions,

herbivory and energy transfer to the consumers at higher trophic levels (Heino 2005; Novichkova and Azovsky 2016). Although the ecological studies of the Arctic islands began in the early nineteenth century, the biodiversity of freshwater invertebrates is still poorly known (Kuiper et al. 1989;

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Bespalaya 2015; Loskutova and Kononova 2015). The first data on the fauna of freshwater invertebrates of the Novaya Zemlya were obtained by Nordenskiöld during the Swedish expedition in 1875 (Vekhoff 1998). After that, data were received in 1887 during the Danish expedition (Hansen 1887). Further studies were conducted in 1921 by the Norwegian Expedition to the Novaya Zemlya Archipelago (Holtedahl 1928) the results of which were published in a series of articles (Kieffer 1922; Lenz and Thienemann 1922; Morton 1923; Odhner 1923; Ulmer 1925; Smith 1928; and others). To date, the collected papers under the title “Report of the scientific results of the Norwegian Expedition to Novaya Zemlya in 1921” (Holtedahl 1928) still constitute the largest review of the invertebrate fauna of the Novaya Zemlya Archipelago, including the first checklist and zoogeographic analysis (Økland 1928). During the periods of 1923–1927 and 1930–1931, studies of the freshwater fauna of the Novaya Zemlya Archipelago were carried out by the Northern Scientific and Commercial Expedition (Gorbunov 1929) and the expedition of the Floating Marine Scientific Institute (Sidorov 1925). Later, the research was continued within the framework of the Marine Arctic Complex Expedition (MACE) of the Russian Research Institute for Cultural and Natural Heritage (1986–1998).

The data on freshwater mollusks of the Novaya Zemlya Archipelago are limited to a few publications (Odhner 1923; Sidorov 1925; Bespalaya et al. 2017). The species diversity, ecology and reproduction of freshwater mollusks from the lakes of Vaigach Island were investigated by Bespalaya (2015) and Bespalaya et al. (2015a, 2015b, 2019). The fauna and distributions of crustaceans (Anostraca, Notostraca, Cladocera, Copepoda, Ostracoda, Amphipoda) of Vaigach Island and the Novaya Zemlya Archipelago were summarized by Vekhoff (1998, 2000a, 1997a, b) and Semenova (2003). Currently, there is scant data on many important benthic taxa such as Oligochaeta, Plecoptera, Trichoptera and Ephemeroptera of the Arctic Islands (Coulson et al. 2014). There is scant recent literature on freshwater aquatic insects of Vaigach Island and the Novaya Zemlya Archipelago which largely cover Diptera (see Discussion section for further details).

Leshko (2008) and Leshko et al. (2008) described benthic communities in lakes and rivers of the southern part of Vaigach Island. Przhiboro (2016, 2018) published the preliminary data on the communities of immature Diptera in semiaquatic shoreline and shallow aquatic habitats of standing and running freshwaters of Vaigach Island and Northern Island of the Novaya Zemlya Archipelago. The biogeography of freshwater biota from the Arctic islands has been investigated intensively (Hessen et al. 2004; Coulson et al. 2014; Kotov et al. 2016; Bolotov et al. 2017; Bespalaya et al. 2017; Bekker et al. 2018). Despite the high level of interest regarding the points noted above, the data based on

molecular genetic studies are still absent for most of the taxa from this area (Coulson et al. 2014).

In the summers of 2010 and 2015–2017 the Federal Center for Integrated Arctic Research, Russian Academy of Sciences, and Northern (Arctic) Federal University organized the complex research of freshwater invertebrates on Vaigach Island and the Novaya Zemlya Archipelago. Although these expeditions focused on the investigation of freshwater mollusks, we were able to collect representative material of other invertebrate taxa. A part of the material was collected by A. Przhiboro during an expedition of the Arctic Floating University in 2016.

The main aims of the present study were to evaluate the species diversity of freshwater invertebrates in the lakes of Vaigach Island and the Novaya Zemlya (Southern Island) and to analyze their distribution and biogeography within the Arctic region.

Materials and methods

Study lakes

This study was conducted in two areas of Vaigach Island and the Novaya Zemlya Archipelago in Arctic Russia (Fig. 1). The islands are located in the Arctic Ocean between the Kara Sea and the Barents Sea.

Novaya Zemlya is the largest European Arctic Archipelago with an area of 81,280 km² and it is characterized by a rugged mountain terrain (maximum elevation: 1547 m above sea level) and with large parts of the coastline incised by fjords (Grant et al. 2009; Stokes 2011) which in terms of the geology are a northern extension of the Ural Mountains (Stokes 2011). The archipelago has an Arctic climate and the winter months are very cold with the temperature in the coldest months (December to January) being $-15\text{ }^{\circ}\text{C}$, and the temperature in the warmest months (July to August) being $+6\text{ }^{\circ}\text{C}$ (Coulson et al. 2014).

In total, 15 freshwater lakes of the Novaya Zemlya Archipelago and Vaigach Island were investigated. The detailed data on the abiotic factors of the lakes are given in Online Resource 1 Table 1.

The lakes of the Novaya Zemlya Archipelago differ in their genesis, nutrient type, and chemical composition. Lakes on the plain are relict and thermokarst, lakes situated along the sea coast are lagoons, and lakes in the mountains are glacial (Vekhoff 1997a). The freshwater lakes of the Novaya Zemlya Archipelago are located mainly on the Southern Island, which belongs to the Arctic tundra zone (Vekhoff 1997b). The studied lakes, Svyatoye Lake and Krugloe Lake, of the Novaya Zemlya Archipelago are of glacial origin. Lakes No. 1 to No. 6 are small and likely glacial or thermokarstic (Vekhoff 1997a) (Online Resource 2, Fig. 1).

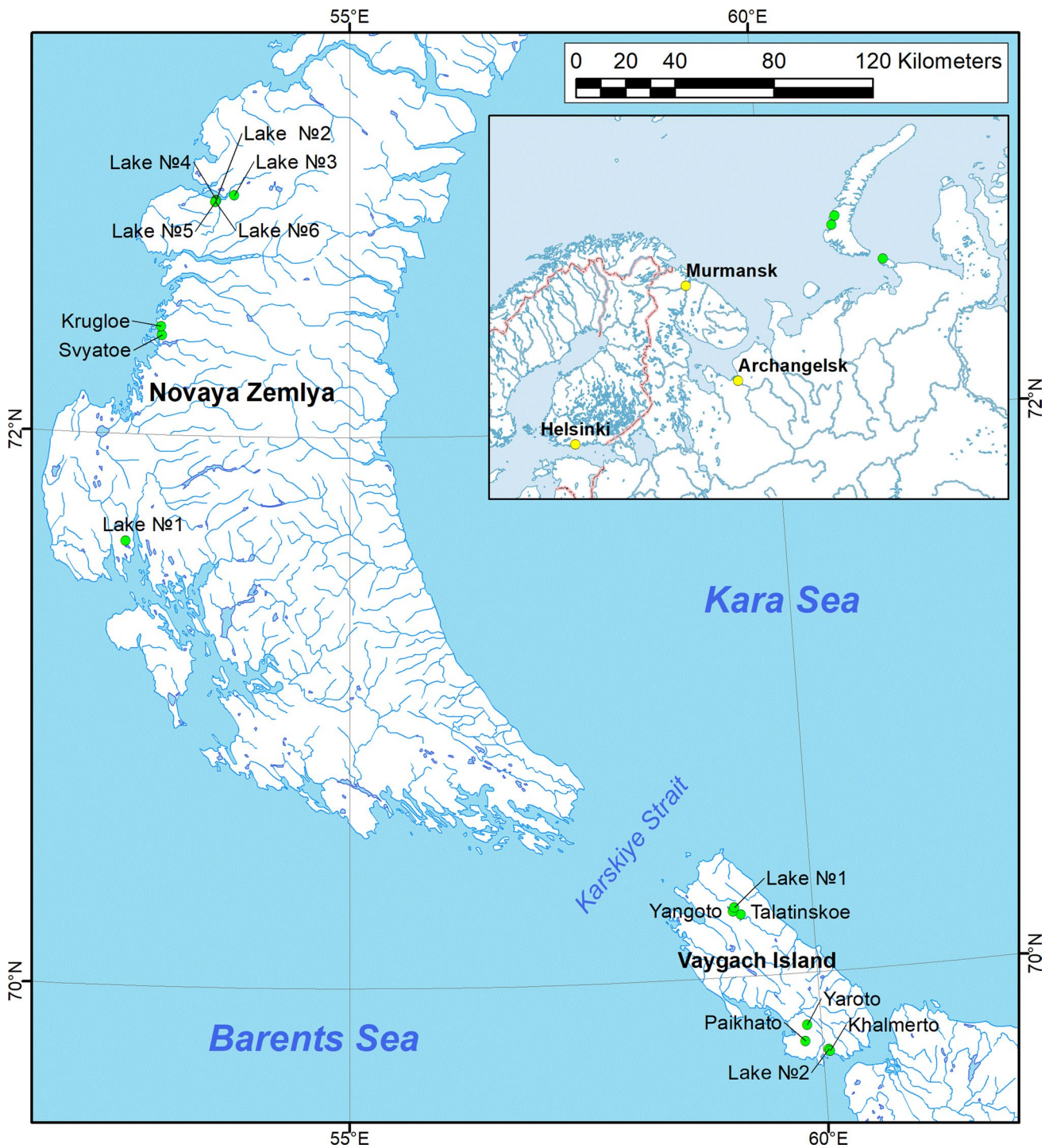


Fig. 1 Map of the study area. The green circle indicates the location of investigated lakes of Vaygach Island and Novaya Zemlya Archipelago

Vaygach Island is separated from the mainland by the Yugorsky Shar Strait and from the Southern Island of the Novaya Zemlya Archipelago by the Karskie Vorota Strait. The average temperature of the warmest month (August) is 5 °C and of the coldest month (February) is – 18.5 °C (Koreisha 2000).

Topographically, the island has a coastal plain and ridge hills, of which Osmininsky and Vaigachsky Ridge are the most prominent (Vekhoff 2000a, b). Lake Talatinskoe is a shallow, thermokarstic lake of 1 m average depth and 1.5 m maximum depth (Vekhoff 2000a; Badukov 2011). Lake Yangoto is a relatively deep glacial-tectonic lake of 10 m average

Table 1 List of species of freshwater invertebrates recorded from freshwater lakes of Vaigach Island and the Novaya Zemlya Archipelago in our study and in previous publications

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
Oligochaeta				
1	<i>Rhyacodrilus coccineus</i> (Vejdovský, 1875)	H, Australia, Antarctic islands	Present study	–
2	<i>Lumbriculus variegatus</i> (Müller, 1774)	H (introduced in some countries of Southern Hemisphere)	Present study; Leshko et al. (2008)	–
	<i>Lumbriculus</i> sp.	–	Present study	–
3	<i>Tubifex tubifex</i> (Müller, 1774)	C (except tropics)	Leshko et al. (2008)	–
	Tubificidae gen. sp.	–	Present study	–
4	<i>Nais barbata</i> Müller, 1774	H, Sino-Indian Region, Australia	Leshko et al. (2008)	–
5	<i>Nais communis</i> Pignet, 1906	C	Leshko et al. (2008)	–
6	<i>Nais elinguis</i> Müller, 1774	C	Leshko et al. (2008)	–
7	<i>Nais parvialis</i> Pignet, 1906	H, Southern Asia, South America	Leshko et al. (2008)	–
8	<i>Nais alpina</i> Sperber, 1948	E, Great Lakes of NA	Leshko et al. (2008)	–
9	<i>Chaetogaster diaphanus</i> (Cruithuisen, 1828)	C	Leshko et al. (2008)	–
10	<i>Pristina amphibiotica</i> Lastočkin, 1927	C	Leshko et al. (2008)	–
11	<i>Pristina rosea</i> (Pignet, 1906)	PA, Antilles	Leshko et al. (2008)	–
12	<i>Limnodrilus hoffmeisteri</i> Claparède, 1862	C	Leshko et al. (2008)	–
13	<i>Cognettia</i> sp.	–	Leshko et al. (2008)	–
	Enchytraeidae gen. sp.	–	Leshko et al. (2008)	–
Anostraca				
14	<i>Branchinecta paludosa</i> (O. F. Müller, 1788)	H	Present study; Vekhoff (1987, 1997a, 2000a)	Present study; Vekhoff (1997a, 1998, 2000b)
15	<i>Polyartemia forcipata</i> Fischer, 1851	PA	Vekhoff (1987, 1997a, 2000a)	Vekhoff (1997a, b, 1998)
16	<i>Artemiopsis bungei plovomorni</i> Jaschnov, 1925	PA	Vekhoff (1997a, 2000a)	Vekhoff (1997a, b, 1998)
17	<i>Branchinectella media</i> (Schmankewitsch, 1873)	PA	–	Vekhoff (1997a, b, 1998)
Notostraca				
18	<i>Lepidurus arcticus</i> (Pallas, 1776)	H	Present study; Vekhoff (1997a, 2000a)	Vekhoff (1997a, b, 1998)
19	<i>Caenestheria propinqua</i> (Sars, 1901)	PA	–	Coulson et al. (2014)
20	<i>Caenestheria sahlbergi</i> (Simon, 1886)	H	–	Coulson et al. (2014)
Cladocera				
21	<i>Acroperus harpae</i> (Baird, 1834)	C	Leshko et al. (2008)	–
22	<i>Alona guttata</i> G.O. Sars, 1862	PA	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
23	<i>Coronatella rectangularis</i> (G.O. Sars, 1862)	PA and Paleotropics	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
24	<i>Bosmina obtusirostris</i> G.O. Sars, 1862	EWS	Vekhoff (2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998)
25	<i>Camptocercus fennicus</i> Stenroos, 1898	ES	Vekhoff (1997a)	Vekhoff (1997a)
26	<i>Chydorus sphaericus</i> (O.F. Müller, 1785)	C	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Present study, Vekhoff (1998, 2000b, 1997a)
27	<i>Daphnia middendorffiana</i> Fischer, 1851	H	Present study; Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998)
28	<i>Daphnia longiremis</i> G.O. Sars, 1862	H	–	Vekhoff (1997a, 1998)

Table 1 (continued)

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
29	<i>Daphnia pulex</i> Leydig, 1860	H	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
30	<i>Eurycerus glacialis</i> Lilljeborg, 1887	E	Vekhoff (1997a, 2000a)	Present study and Vekhoff (1997a, 1998)
31	<i>Eurycerus lamellatus</i> (O.F. Müller, 1776)	H	Leshko et al. (2008)	–
32	<i>Macrothrix hirsuticornis</i> Norman & Brady, 1867	H	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1998, 2000b, 1997a)
33	<i>Tretoccephala ambigua</i> (Lilljeborg, 1900)	ES	–	Vekhoff (1998)
Copepoda				
Calanoida				
34	<i>Arctodiaptomus bacillifer</i> (Koelbel, 1885)	ES	Present study and Vekhoff (1988, 1997a, 2000a) and Leshko et al. (2008)	Present study and Vekhoff (1998, 2000b, 1997a)
35	<i>Arctodiaptomus wierzejskii</i> (Richard, 1888)	EWS, Central Asia	Vekhoff (1988, 2000a)	–
36	<i>Diaptomus glacialis</i> Lilljeborg, 1889	PA	Present study, Vekhoff (1988, 1997a, 2000a) and Leshko et al. (2008)	Present study, Vekhoff (1997a, 1998)
37	<i>Eurytemora affinis</i> (Poppe, 1880)	H	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
38	<i>Eurytemora raboti</i> Richard, 1897	PA (the coastal Arctic)	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998), Coulson et al. (2014)
39	<i>Eurytemora canadensis</i> Marsh, 1920	H	Vekhoff (2000a)	–
40	<i>Hetercope borealis</i> (Fischer, 1851)	PA	Present study and Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998)
41	<i>Hetercope saliens</i> Lilljeborg, 1863	PA	Leshko et al. (2008)	–
42	<i>Limnocalanus grimaldii macrurus</i> G.O. Sars, 1863	H	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
43	<i>Mixodiaptomus theeli</i> (Lilljeborg, 1889)	ES	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
Cyclopoida				
44	<i>Acanthocyclops capillatus</i> (G.O. Sars, 1863)	H	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
45	<i>Acanthocyclops venustus venustus</i> (Norman & Scott, 1906)	–	Leshko et al. (2008)	–
46	<i>Acanthocyclops vernalis</i> (Fischer, 1853)	H	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1998, 2000b, 1997a)
47	<i>Cyclops abyssorum</i> G.O. Sars, 1863	H	Vekhoff (1997a)	Vekhoff (1997a, 1998)
48	<i>Cyclops scutifer</i> G.O. Sars, 1863	H	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
49	<i>Cyclops strenuus</i> Fischer, 1851	H	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
50	<i>Cyclops vicinus</i> Uljanin, 1875	C	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
51	<i>Diatyclops crassicaudis crassicaudis</i> (G.O. Sars, 1863)	E	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
52	<i>Diatyclops languidus</i> (G.O. Sars, 1863)	–	Leshko et al. (2008)	–
53	<i>Eucyclops serrulatus</i> (Fischer, 1851)	PA	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998)
54	<i>Eucyclops speratus</i> (Lilljeborg, 1901)	–	Vekhoff (1997a)	Vekhoff (1997a, 1998)

Table 1 (continued)

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
55	<i>Mesocyclops leuckarti</i> (Claus, 1857)	C	–	Present study
56	<i>Megacyclops viridis</i> (Jurine, 1820)	H	Vekhoff (1997a) and Leshko et al. (2008)	Vekhoff (1997a, 1998)
Harpacticoida				
57	<i>Canthocamptus glacialis</i> Lilljeborg, 1902	S	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
58	<i>Canthocamptus staphylinus</i> (Jurine, 1820)	PA	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998)
59	<i>Maranobiotus brucei</i> (Richard, 1898)	PA	Leshko et al. (2008)	–
60	<i>Mesochra lilljeborgi</i> Boeck, 1864	ES, Africa, NA	Vekhoff (2000a)	Vekhoff (2000b)
61	<i>Mesochra pygmaea</i> (Claus, 1863)	ES, Africa, NA	Vekhoff (2000a)	–
62	<i>Morarita duthiei</i> (Scott & Scott, 1896)	PA	Leshko et al. (2008)	–
63	<i>Morarita schmeili</i> Van Douwe, 1903	PA	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
64	<i>Microarthridion littorale</i> (Poppe, 1881)	H	Vekhoff (1997a, 2000a)	Vekhoff (1997a, 1998, 2000b)
65	<i>Nannopus palustris</i> Brady, 1880	–	Leshko et al. (2008)	–
66	<i>Nitocra spinipes</i> Boeck, 1864	E, NA	Vekhoff (2000a)	–
67	<i>Nitocra typica</i> Boeck, 1864	H	Vekhoff (2000a) and Leshko et al. (2008)	Vekhoff (2000b)
68	<i>Neomrazekiella (Atheyella) nordenskjöldi nordenskjöldi</i> (Lilljeborg, 1902)	PA	Vekhoff (1997a, 2000a) and Leshko et al. (2008)	Vekhoff (1997a, 1998, 2000b)
69	<i>Orychocamptus mohammed</i> (Blanchard & Richard, 1891)	C	Leshko et al. (2008)	–
70	<i>Tachidius discipes</i> Giesbrecht, 1881	H	Leshko et al. (2008)	–
71	<i>Tachidius longicornis</i> Olofsson, 1918	EWS	Vekhoff (1997a, 2000a)	Vekhoff (1998, 2000b, 1997a)
Ostracoda				
72	<i>Tonnacypris glacialis</i> (G.O. Sars, 1890)	H	Present study, Aim (1914), Sars (1925), Bronstein (1947), Vekhoff (2000a) and Semenova (2003)	Present study, Aim (1914), Sars (1925), Bronstein (1947), Vekhoff (1998, 2000b, 1997a) and Semenova (2003)
73	<i>Eucypris pigra</i> (Fischer, 1851)	PA	–	Vekhoff (1997a, 2000b) and Semenova (2003)
74	<i>Leucocythere mirabilis</i> Kaufmann, 1892	PA	–	Present study
	<i>Leucocythere</i> sp.		–	Vekhoff (1997a)
75	<i>Limnocytherina sanctipatricii</i> Negadaev-Nikonov, 1967	H	Vekhoff (2000a) and Semenova (2003)	Semenova (2003) and Vekhoff (2000b)
76	<i>Limnocythere inopinata</i> (Baird, 1843)	H	Semenova (2003)	Semenova (2003)
77	<i>Candona candida</i> Baird, 1845	H	Semenova (2003)	Vekhoff (1998, 2000b, 1997a) and Semenova (2003)
78	<i>Candona candida humilis</i> Ekman, 1914	EWS	–	Vekhoff (1997a) and Semenova (2003)
79	<i>Fabaformiscandona groenlandica</i> (Brehm, 1911)	H	Semenova (2003)	Vekhoff (1998, 2000b, 1997a) and Semenova (2003)
80	<i>Candona lapponica arctica</i> Alm, 1914	H	Semenova (2003)	Vekhoff (1998, 2000b, 1997a) and Semenova (2003)

Table 1 (continued)

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
81	<i>Fabaeformiscandona pedata</i> Alm, 1914	S	Semenova (2003)	Vekhoff (1997a, 1998) and Semenova (2003)
82	<i>Candona rectangularis</i> Alm, 1914	H	Vekhoff (2000a) and Semenova (2003)	Vekhoff (1997a, 1998) and Semenova (2003)
83	<i>Fabaeformiscandona acuminata</i> (Fischer, 1851)	H	Semenova (2003)	Semenova (2003) and Vekhoff (2000b)
84	<i>Candona sibirica</i> G.W. Muller, 1912	PA	–	Semenova (2003) and Vekhoff (2000b)
85	<i>Cypridocypris vidua</i> (O.F. Muller, 1776)	C	Semenova (2003)	Vekhoff (1997a) and Semenova (2003)
86	<i>Cypridopsis</i> sp.	–	Semenova (2003)	Semenova (2003)
87	<i>Cyclocypris globosa</i> (Sars, 1863)	H	–	Vekhoff (1997a)
88	<i>Cyclocypris globosa ovoides</i> Alm, 1914	H	–	Semenova (2003)
	<i>Cyclocypris</i> sp.	–	–	Vekhoff (1997a) and Semenova (2003)
89	<i>Cyclocypris ovum</i> (Jurine, 1820)	H	Vekhoff (2000a) and Semenova (2003)	Semenova (2003)
90	<i>Cyclocypris laevis</i> (O.F. Muller, 1776)	H	Vekhoff (2000a) and Semenova (2003)	Semenova (2003)
91	<i>Cyclocypris serena</i> (Koch, 1838)	H	Semenova (2003)	Semenova (2003)
92	<i>Cypris marginata</i> (Straus, 1821)	H	–	Semenova (2003)
	<i>Cypria</i> sp.	–	Semenova (2003)	Semenova (2003)
Amphipoda				
93	<i>Monoporeia affinis</i> (Lindström, 1855)	A, PA	Present study	Present study
94	<i>Gammarus lacustris</i> Sars, 1863	H	Present study; Vekhoff (2000a)	–
95	<i>Gammarus pellucidus</i> Gurjanova, 1930	WPA	Vekhoff (2000a)	–
96	<i>Gammarus pulex</i> (Linnaeus, 1758)	WPA	Vekhoff (2000a)	–
Ephemeroptera				
97	<i>Baetis (Acentrella) lapponicus</i> (Bengtsson, 1912)*	E (A-B)	–	Ulmer (1925, 1932), Økland (1928), Bauernfeind and Soldan (2012) and Coulson et al. (2014)
	<i>Baetis</i> sp. [larvae]	–	Present study	–
Plecoptera				
	Perlodidae gen. sp. [larvae]	–	Present study	–
98	<i>Capnia zaitcevi</i> (Klapálek, 1914)*	ES (A-B)	–	Morton (1923) and Økland (1928), Ulmer (1932), Brinck (1958), Zhiltsova (2003) and Coulson et al. (2014)
99	<i>Mesocapnia variabilis</i> (Klapálek, 1920)*	H (A-B)	Zhiltsova (1966, 2003)	Zhiltsova (1966, 2003)
100	<i>Nemoura arctica</i> Esben-Petersen, 1910	H (A-B-M)	–	Morton (1923), Økland (1928), Brinck (1958) and Coulson et al. (2014)
101	<i>Nemoura sahlbergi</i> Morton, 1896	H (A-B-M)	Present study	–
Trichoptera				
102	<i>Hydropsyche</i> sp. (? <i>H. pellucidula</i> (Curtis, 1834)*)	–	–	Ujjanin (1872), Økland (1928) and Ulmer (1932)
103	<i>Agrypnia obsoleta</i> (Hagen, 1864)	H	Present study	–

Table 1 (continued)

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
104	<i>Brachycentrus subnubilus</i> Curtis, 1834*	PA	–	Uljain (1872) and Økland (1928)
105	<i>Micrasema gelidum</i> McLachlan, 1876	H (A-B in Europe)	Present study	–
106	<i>Apatania zonella</i> (Zetterstedt, 1840)	H (A-B in Europe)	–	Ulmer (1925, 1932), Økland (1928) and Coulson et al. (2014)
107	<i>Limnephilus lunatus</i> Curtis, 1834	WPA	–	Ulmer (1932)
108	<i>Philarctus bergrothi</i> McLachlan, 1880	EPA, NA: Siberia, Far East	Present study	–
109	Limnephilidae: ? <i>Chaetopteryx sahlbergi</i> McLachlan, 1876 [larvae of instars 2–3]	E—for <i>C. sahlbergi</i>	Present study	–
Coleoptera				
110	<i>Hydroporus acutangulus</i> Thomson, 1856*	PA (A-B)	–	Poppius (1910), Økland (1928) and Coulson et al. (2014)
111	<i>Hydroporus lapponum</i> (Gyllenhal, 1808)*	H (A-B-M)	Prokin et al. (2017)	–
112	<i>Hydroporus morio</i> Aubé, 1838*	H (A-T)	Prokin et al. (2017)	Munster (1925) and Økland (1928)
113	<i>Agabus adpressus</i> Aubé, 1837*	H (A-B-M)	Prokin et al. (2017)	–
114	<i>Agabus infuscatus</i> Aubé, 1838*	H (A-B)	Prokin et al. (2017)	–
115	<i>Agabus lapponicus</i> (C.G. Thomson, 1867)*	PA (A-B-M)	Prokin et al. (2017)	–
116	<i>Agabus moestus</i> (Curtis, 1835)*	H (A)	Munster (1925) and Prokin et al. (2017)	Jacobson (1898), Munster (1925) and Økland (1928)
117	<i>Agabus thomsoni</i> (J. Sahlberg, 1871)*	H (A-B-M)	Prokin et al. (2017)	–
	<i>Agabus</i> sp. [larvae]	–	Present study	–
118	<i>Ilybius angustior</i> (Gyllenhal, 1808)*	H (A-B-M)	Chernov et al. (2014), Prokin et al. (2017)	–
119	<i>Colymbetes dolabratus</i> (Paykull, 1798)	H	Prokin et al. (2017) and present study	–
120	<i>Helophorus niger</i> J. Sahlberg, 1880*	EPA	–	Munster (1925) and Økland (1928)
Diptera				
121	<i>Prionocera</i> sp.	–	Present study	–
122	<i>Tipula (Arctotipula) oklandi</i> Alexander, 1922*	EPA (A-M)	–	Alexander (1922) and Savchenko (1961)
123	<i>Tipula (Arctotipula) salicetorum</i> Siebke, 1870*	H (A-M)	Savchenko (1961) and Lantsov and Chernov (1987)	Lantsov and Chernov (1987)
	<i>Tipula (Arctotipula)</i> sp. [larvae]	–	Present study	Present study
Mollusca				
124	<i>Euglesa globularis</i> (Clessin in Westerlund, 1873)	EWS	Bespalaya (2015)	Present study
125	<i>Odhneripsoidium conventus</i> (Clessin, 1877)	H	–	Odhner (1923) and Bespalaya et al. (2017)
126	<i>Euglesa waldeni</i> (Kuiper, 1975)	PA	–	Bespalaya et al. (2017)
127	<i>Euglesa casertana</i> (Poli, 1791)	C	Bespalaya (2015) and Bespalaya et al. (2015b, 2019)	–
128	<i>Euglesa subtruncata</i> (Malm, 1855)	H	Bespalaya (2015)	–

Table 1 (continued)

No.	Species	Geographic distribution	Vaigach Island	Novaya Zemlya Archipelago
129	<i>Pisidium dilatatum</i> Westerlund, 1897	PA	Bespalaya (2015)	—
130	<i>Euglesa liljeborgii</i> (Clessin in Esmark & Hoyer, 1886)	H	Bespalaya (2015)	—
131	<i>Sphaerium cf. nitidum</i> Clessin in Westerlund, 1876	H	Bespalaya (2015) and Bespalaya et al. (2015a)	—
132	<i>Stagnicola palustris</i> (O. F. Müller, 1774)	EWS	Leshko et al. (2008)	—
133	<i>Armiger crista</i> (Linnaeus, 1758)	EWS	Leshko et al. (2008)	—
134	<i>Gyraulus albus</i> (O.F. Müller, 1774)	PA	Leshko et al. (2008)	—
135	<i>Gyraulus acronicus</i> (Ferussac, 1807)	ES	Bespalaya et al. (2019)	—
136	<i>Anisus leucostoma</i> (Millet, 1813)	ES	Leshko et al. (2008)	—

Chironomidae are not considered in the table (see "Discussion" for further details)

Geographic distribution, longitudinal aspect: PA—Palearctic, WPA—West Palearctic, EPA—East Palearctic; NA—Nearctic; H—Holarctic; C—Cosmopolitan, EWS—Europe and West Siberia, ES—Europe and Siberia (in parentheses, latitudinal aspect: A—Arctic, B—Boreal, M—Montane south of Boreal zone, T—temperate)

Taxa of amphibiotic insects marked with asterisk (*) are probable lake inhabitants previously recorded from the study region. They were recorded in publications either as terrestrial adults or without precise habitats. We included these species in the list taking into account their bionomics in other regions

depth and 22 m maximum depth. Vaigach Lake No. 1 is a very small lake, which likely has a glacial or glacial-tectonic origin. Vaigach Lake No. 2 and Lake Kholmerto are very small lakes close to the coast; these lakes are most likely of glacial or thermokarstic origin. Lake Yaroto is located in the area of the Osmininsky mountain range and has a tectonic or glacial origin. Lake Paikhato, which likely has a glacial or mixed origin, has an average depth of 1.5 m and estimates of its maximum depth are in the range of 7–13 m (Aleynikov et al. 2014) (Online Resource 3, Fig. 2). All lakes on Vaigach Island receive atmospheric nutrients delivered through intensive snowmelt (Vekhoff 2000a).

The duration of the ice-free period on Vaigach Island and Southern Island of the Novaya Zemlya Archipelago is 2.5–3 months, from the end of June, that is early July to late September (Vekhoff 1997a; Badyukov 2011).

Sampling localities of Talatinskoe Lake of Vaigach Island (mean depth 0.6 ± 0.2 m) were characterized by silty-sand, silty and clay sediments. Those in Yangoto Lake (2.5 ± 2.3 m) and Lake No. 1 (0.27 ± 0.03 m) had silty-sand, gravel and clay bottom substrates with vegetation remnants; mosses and macroalgae (*Nostoc*) were present. In the other shallow lakes of Vaigach Island (Yaroto, Paykhato, Kholmerto, and Lake No. 2), sampling localities had silty-sand and gravel bottom substrates vegetated by mosses and higher macrophytes. The average depth was 0.28 ± 0.17 m.

Sampling localities on lakes of the Southern Island of the Novaya Zemlya (lakes Svyatoye and Krugloe) were characterized by gravel substrates. The mean depth in Svyatoye Lake ranged between 2 and 4 m and in Krugloe Lake between 3 and 4 m. In the Novaya Zemlya Lakes No. 1–No. 6, the substrates were silty-gravel and the depth varied between 0.1 and 1.0 m.

Field sampling and laboratory procedures

Samples of benthic invertebrates from the lakes of Vaigach Island were collected in August 2010 (Talatinskoe Lake, Yangoto Lake, Lake No. 1) and June 2016 (Yaroto, Paykhato, Kholmerto, and Lake No. 2), and from Southern Island of the Novaya Zemlya Archipelago in July 2015 (Lakes Svyatoye and Krugloe) and in July 2017 (Lake No. 1–Lake No. 6) (Fig. 1, Online Resource 4, Table 2). The samples were taken using a rectangular hand net (dimensions $0.28 \text{ m} \times 0.5 \text{ m}$, mesh size $200 \mu\text{m}$) in shallow areas, and using a Petersen grab (0.024 m^2) in deeper waters. Samples were washed with clean water using a benthic sieve (0.4 mm) and then fixed with 96% ethanol. We collected 306 benthic samples at 45 stations in the 15 studied lakes of Vaigach Island and the Southern Island of the Novaya Zemlya Archipelago (Online Resource 4, Table 2). Despite the fact that the samples were taken from the bottoms of lakes, many species

usually considered as planktonic were found in the samples and were included in the analysis.

Many samples taken from the lakes of both islands contained the larvae and pupae of Chironomidae (Diptera). The chironomids were not identified in the scope of this study. The parasitic forms have not been studied.

In the laboratory, all invertebrates were identified to the lowest relevant taxonomic group and counted. The identification of most taxa was based on the guide for zooplankton and zoobenthos by Alekseev and Tsalolikhin (2010, 2016). The identification of oligochaetes was based on the analysis of external and internal morphological characters (Chekanovskaja 1962; Popchenko 1988; Timm 2009). Worms were observed in a whole glycerin mount. A stereomicroscope (MSP-2; LOMO, Russia) and a microscope (Micmed-6; LOMO, Russia) were used. The identification of freshwater bivalves was based on the integrative taxonomic approach together with morphological, anatomical (Korniushin 1996; Glöer and Meier-Brook 2003) and molecular data. The shell morphology was analyzed based on the shape and structure of the cardinal teeth, shell shape, umbo position and characteristics of the distribution of pores on the shell inner surface. Shell photographs were obtained using a stereomicroscope (M165C; Leica, Germany and AxioZoomV16; Carl Zeiss, Germany), and photographs of the teeth and pore details were obtained using a microscope (Lab.A1; Carl Zeiss, Germany) with a digital camera (AxioCam ICc 5; Carl Zeiss, Germany). The ostracods were identified with the help of the manuals by Bronstein (1947), Meisch (2000) and Kurashov (2012). The amphipod body length was measured from the tip of the rostrum to the end of the telson with an accuracy of 0.1 mm. The sex was determined according to the presence of the oostegites in females and the penis-papillae in males. Most of the insects were identified using the following keys: Kluge (1997) for Ephemeroptera; Teslenko and Zhiltsova (2009) for Plecoptera; Ivanov et al. (2001) for Trichoptera; Kirejtshuk and Shaverdo (2011) for Coleoptera (Dytiscidae); and Lantsov (1999) for Diptera (Tipulidae).

Differences in total length (cephalothorax, abdomen and caudal ramae) of *Branchinecta paludosa* were estimated using the Mann–Whitney *U* test with the PAST program (Hammer et al. 2001).

The material of Oligochaeta was mounted, identified and analyzed by I.G. Tsiplenkina; Anostraca, Notostraca, Cladocera and Copepoda by L.F. Litvinchuk; Ostracoda by E.A. Kurashov; Amphipoda by N.A. Berezina; Insecta by A.A. Przhiboro; Mollusca by O.V. Aksenova and Y.V. Bespalaya.

Most of the identified material is stored in the collections of the Russian Museum of Biodiversity Hotspots of the N. Laverov Federal Center for Integrated Arctic

Research of Russian Academy of Sciences, Arkhangelsk. A part of the material is deposited at the Zoological Institute of Russian Academy of Sciences, St Petersburg, Russia.

This work includes the data on the fauna of freshwater mollusks from the Southern Island of the Novaya Zemlya Archipelago but only for Lake 1 to Lake 6, while the data on this group for other lakes have already been published (Bespalaya 2015; Bespalaya et al. 2015a, b, 2017, 2019).

DNA isolation, PCR, and sequencing

Total DNA was extracted from twenty-three specimens of *Euglesa globularis* (Clessin, 1873) and two specimens of *Lepidurus arcticus* (Pallas, 1776) according to standard phenol/chloroform procedures (Sambrook et al. 1989) (Online Resource 5, Table3). For molecular analyses, we obtained sequences of the 16S large subunit ribosomal RNA (16S) (partial sequence of 505 and 506 bp) for *E. globularis* and the cytochrome oxidase subunit I (COI) (partial sequence of 660 bp) for *L. arcticus*, respectively. The targets were amplified and sequenced using primer pairs 16Sar and 16Sbr (Palumbi 1996) for 16S and LoboF1 and LoboR1 (Lobo et al. 2013) for COI. The PCR mix contained approximately 200 ng of total cellular DNA, 10 pmol of each primer, 200 μ mol of each dNTP, 2.5 μ l of PCR buffer (with 10×2 mmol $MgCl_2$), 0.8 units of Taq DNA polymerase (SibEnzyme Ltd., Russia), and H_2O which was added up to a final volume of 25 μ l. Thermocycling included one cycle at 95 °C (4 min), followed by 29–33 cycles of 95 °C (50 s), 48–50 °C (50 s), and 72 °C (50 s) and a final extension at 72 °C (5 min). Forward and reverse sequencing were performed on an automatic sequencer (ABI PRISM3730, Applied Biosystems) using the ABI PRISM BigDye Terminator v.3.1 reagent kit. The resulting sequences were checked using a sequence alignment editor (BioEdit version 7.2.5; Hall 1999). In addition, eight sequences were obtained from NCBI GenBank (Online Resource 6 Table4).

Sequence alignment and phylogeographic analyses

The alignment of 16S sequences was performed using the MUSCLE algorithm implemented in MEGA6 (Tamura et al. 2013). Each 16S sequence of the aligned datasets was trimmed, leaving a 407-bp fragment. The phylogeographic analyses were performed based on a median-joining network approach using Network version 4.6.1.3 software with default settings (Bandelt et al. 1999).

Results

Altogether, 1380 specimens of freshwater invertebrates were collected from the lakes under study. Twenty-eight species in 4 classes and 14 orders were identified during this study. One oligochaete species, one crustacean species and four insect species were recorded for the first time from Vaigach Island, and four crustacean and one bivalve species were recorded for the first time from Novaya Zemlya Archipelago. One of the insect species was recorded for the first time from European Russia. Taking into account the reliable data from previous publications, the list of invertebrates inhabiting the lakes in the study area expands to around 136 species (Table 1, Online Resource 7 Fig. 3).

In all investigated lakes of the Novaya Zemlya Archipelago and Vaigach Island the benthic fauna inhabits shallow areas of lakes with the exception of Lakes Svyatoye, Krugloe (Novaya Zemlya Archipelago) and Yangoto Lake (Vaigach Island). Some species have been found both in shallow- and in deepwater areas of lakes. Hence, in Lakes Svyatoye and Krugloe amphipods *Monoporeia affinis*, *Gammarus lacustris*, anostracan *Branchinecta paludosa*, cladoceran *Chydorus sphaericus*, *Eurycercus glacialis*, *Daphnia middendorffiana*, copepods *Arctodiaptomus bacillifer*, *Diaptomus glacialis*, *Heterocope borealis*, *Mesocyclops leuckartii*, ephemeropteran *Baetis* sp., Perlodidae gen. sp. and, dipteran *Tipula* (*Arctotipula*) were found at depths of 3.0–3.5 m. In Yangoto Lake amphipod *Gammarus lacustris* and freshwater bivalves *E. casertana*, *E. supina*, *E. globularis* (Bespalaya et al. 2019) were discovered in deepwater areas of the lake (2.2–6.4 m).

Oligochaeta

In total, we examined 21 specimens of oligochaetes from the lakes of Vaigach Island. Four taxa were identified: *Rhyacodrilus coccineus*, *Lumbriculus variegatus*, *Lumbriculus* sp. and Tubificidae gen. sp. (Online Resource 7, Figs3a, 3b). The most abundant species was *L. variegatus* at 67% (from the total sample $N=21$). One specimen of Tubificidae was infected by a parasite (Cestoda: Caryophyllaeidae).

Anostraca

In total, 116 specimens of *Branchinecta paludosa* were found in the lakes of the islands under study (Online Resource 7, Fig. 3c) and the species is distributed throughout the Holarctic area. The lengths of specimens from Vaigach Island were greater than the lengths of specimens from the Novaya Zemlya Archipelago. Mean total length (cephalothorax, abdomen and caudal ramae) of *B. paludosa* in the lakes of Novaya Zemlya Archipelago was 12.5 ± 2.1 mm, min–max

8.0–18.0 mm, which is less compared with the lakes of Vaigach Island (15.7 ± 3.04 mm, min–max 11.6–20.1 mm) (Mann–Whitney U test: $P=0.0002$).

Notostraca

We examined 51 specimens of the crustacean *Lepidurus arcticus* (Pallas, 1776) from the lakes of Vaigach Island (Online Resource 7, Fig. 3d). The analysis of COI sequences of Notostraca samples from Vaigach Island showed that they belong to the species *L. arcticus*.

Cladocera

We examined 5 specimens of *Chydorus sphaericus* and 28 specimens of *Eurycercus glacialis* that were recorded in the studied lakes of the Novaya Zemlya Archipelago (Online Resource 7, Figs3e, 3f). In the lakes of Vaigach Island 70 specimens of *Daphnia middendorffiana* were found (Online Resource 7, Fig3g).

Copepoda

We examined 650 specimens of copepod crustaceans *Arctodiaptomus bacillifer* and 34 specimens of *Diaptomus glacialis* from the lakes of both islands (Online Resource 7, Figs3h, 3j). Two individuals of *Mesocyclops leuckartii* were found only on the Novaya Zemlya Archipelago. In total, 59 specimens of *Heterocope borealis* were found in the lakes of Vaigach Island (Online Resource 7, Fig3k). The body length of Copepods from Novaya Zemlya Archipelago and Vaigach Island lakes are presented in Online Resource 8, Table5.

Ostracoda

In the lakes of Novaya Zemlya and Vaigach Island 18 specimens of ostracods were found. *Tonnacypris glacialis* was found in the lakes of both islands, *Leucocythere mirabilis* was found in the lakes of the Novaya Zemlya Archipelago.

Amphipoda

In the lakes under study, 120 specimens of two species of amphipods were collected, the pontoporeid amphipod *Monoporeia affinis* and the gammaridean amphipod *Gammarus lacustris* (Online Resource 7, Figs 3l, 3m). *M. affinis* was recorded in Svyatoye Lake and Krugloe Lake on the Novaya Zemlya Archipelago and its body size was in the

range of 7–10 mm. *G. lacustris* was found in seven of lakes under study on Vaigach Island and the Novaya Zemlya Archipelago. Around 70% of males of *G. lacustris* that were found in Talatinskoe Lake, Yangoto Lake, Lake No. 1, and Paikhato Lake (August 2010) on Vaigach Island were greater than 20 mm in body length (max 27 mm).

Ephemeroptera

Nymphs of *Baetis* were common in Lake Talatinskoe, Vaigach Island. This is the first record of mayflies from Vaigach Island. Possibly, they are conspecific with *Baetis lapponicus*, the only mayfly species known from the Novaya Zemlya Archipelago (Ulmer 1925, etc.; see Table 1).

Plecoptera

The nymphs of two taxa were collected on Vaigach Island, the abundant *Nemoura sahlbergi* (Nemouridae) from Kholmerto Lake and one specimen of undetermined Perlodidae from Talatinskoe Lake; *N. sahlbergi* is a new species for Vaigach Island.

Trichoptera

Larvae of four species were collected on Vaigach Island and all were from Kholmerto Lake: *Argynnia obsoleta* was common on the lake bottom, whereas the other three taxa were collected from (semi)aquatic vegetation along the shoreline: *Micrasema gelidum* and *Philarctus bergrothi* were scant, Limnephilidae larvae of instars 2–3 (possibly, *Chaetopteryx sahlbergi*) were abundant. *A. obsoleta*, *M. gelidum* and *Ph. bergrothi* were registered as new records for Vaigach Island; *P. bergrothi* is also recorded for the first time from European Russia and from Europe.

Coleoptera

Two specimens of Dytiscidae were collected from Vaigach Island, an adult *Colymbetes dolabratus* from Talatinskoe Lake and a larva of *Agabus* sp. from Kholmerto Lake.

Diptera

Non-chironomid dipterans in the study lakes were represented only by the larvae of craneflies (Tipulidae). All specimens but one belonged to the subgenus *Arctotipula* of the genus *Tipula*. The different-aged *Arctotipula* larvae were collected from most of the lakes on Vaigach Island (Lake No 1, Yangoto Lake and Talatinskoe Lake in August 2010, Paikhato Lake in June 2016). One larva was collected from Lake No. 1 of Novaya Zemlya Archipelago. The larvae can

belong to at least two species known from the region as adults (see Table 1 for details). Here, the larvae of *Arctotipula* are recorded as inhabitants of the bottom layer of Arctic lakes for the first time. In addition, one larva of *Prionocera* was collected from Yaroto Lake on Vaigach Island.

Mollusca

Only in Lake No. 1 in the Novaya Zemlya Archipelago from six investigated lakes, 26 specimens of the freshwater bivalve *E. globularis* were found (Online Resource 9, Fig4). The five sequenced specimens from the Novaya Zemlya Archipelago share a single 16S rRNA haplotype, which is identical to the *E. globularis* specimen of Vaigach Island and most closely related to the *E. globularis* specimens from Arctic Russia, Germany and the USA (Colorado) with p-distances not exceeding 1.6% (Online Resource 10, Fig5).

Discussion

The oligochaetes were found only in the lakes of Vaigach Island. In general, based on our study and on previous studies (Leshko et al. 2008), the Oligochaeta fauna of Vaigach Island includes 13 species. All these are widespread in the Holarctic (Popchenko 1988; Timm 2009). *Rhyacodrilus coccineus* was registered from Vaigach Island for the first time. *R. coccineus* is a common and widespread species in the Holarctic, but it was also recorded in Australia and in the Antarctic Islands (Baturina et al. 2020). *R. coccineus* inhabits lakes and streams and is found in sand and mud at depths of up to 25.5 m (Timm 2009).

In all of the studied lakes, only the anostracan, *Branchinecta paludosa*, was found. The body lengths of specimens from the Novaya Zemlya Archipelago were less than those of the specimens from Vaigach Island. Our results are in accordance with the observation of Vekhoff (1987a), who recorded that in harsher environments the body size and growth rate of *B. paludosa* were reduced.

Although widely distributed in tundra waterbodies of Eurasia (Smirnov 1936), the anostracan species *Polyartemia forcipata* was not found in our samples. However, according to Vekhoff (1987b, 1997a,b, 1998, 2000a) this species was recorded on Vaigach Island and the Novaya Zemlya Archipelago.

Three species of Notostraca are known from the study region (see Table 1). In our research, only *Lepidurus arcticus* was registered on Vaigach Island. *L. arcticus* is distributed by way of a circumpolar areal, includes the areas of continuous permafrost in the Arctic and Subarctic regions (Rogers 2001). This species has been recorded in multiple

sites on Novaya Zemlya Archipelago, Spitsbergen, Bjørnøya, and Franz Josef Land (Coulson et al. 2014).

According to previously published data, 13 species of Cladocera were recorded from Vaigach Island and the Novaya Zemlya Archipelago (Vekhoff 1997a, 1998, 2000a, b; Leshko et al. 2008). In our research, only three cladoceran species were registered. Such poor species composition is explained by sampling focused on benthic organisms. The species are widespread in northern regions of the European part of Russia (Tiberti 2011; Bekker and Kotov 2016). Besides *Eurycercus glacialis* was also detected in shallow waterbodies of Bering Island, and Iceland (Novichkova 2015). *Chydorus sphaericus* is known from Wrangel Island (Novichkova 2015), Bering Island (Novichkova 2015), Iceland (De Guerne 1892; Novichkova 2015; Scher et al. 2000), and Svalbard (Novichkova 2015).

The copepod *Mesocyclops leuckarti* was found for the first time on Novaya Zemlya Archipelago. This species has a very wide geographical distribution and is well adapted to a cold environment (Gophen 1976; Frolova et al. 2013). According to literature data, *Mesocyclops leuckarti* was found in the lakes of Wrangel Island (Novichkova 2015), Bering Island (Novichkova 2015), and in the lakes in the north of Krasnoyarsk Territory (Fefilova et al. 2013). At the same time this species was not found in the waterbodies of Iceland and Svalbard (De Guerne 1892; Scher et al. 2000; Novichkova 2015). According to Fefilova et al. (2013), *Mesocyclops leuckarti* was not observed in the Kharbei lakes and small thermokarst waterbodies of the Bol'shezemelskaya tundra.

Taking into account our own data and the data from the available literature, the ostracod fauna of Vaigach Island and the Novaya Zemlya Archipelago includes 21 species (Table 1). *Leucocythere mirabilis* was recorded for the first time for the Novaya Zemlya Archipelago. *L. mirabilis* mostly inhabits oligotrophic lakes (Danielopol et al. 1989; Scharf 1993). The species are widespread in the Palearctic (Griffiths et al. 1998; Meisch 2000; Martens and Savatzenalinton 2011). At the same time, according to Külköylüoğlu et al. (2012), the ecological characteristics of *L. mirabilis* are probably much broader than previously thought. *L. mirabilis* has been reported from Switzerland, Sweden, Finland, north-eastern Poland, Corfu, China, Turkey, and northern India (Danielopol et al. 1989; Meisch 2000; Altınışıl and Griffiths 2001; Mischke et al. 2007; Zhu et al. 2007; Kramer et al. 2014) and also in brackish waters (Gulf of Bothnia, Baltic Sea) (Savolainen and Valtonen 1983). According to paleodata, *L. mirabilis* was discovered in Mongolia, Austria, and Germany (Scharf 1993; Poberezhnaya et al. 2006).

The amphipod *M. affinis* was found for the first time in the Novaya Zemlya Archipelago. *M. affinis* belongs to a small geographical group, the so-called “glacial relicts” (Segerstråle 1957; Spikkeland et al. 2016). The size range of the

adult *M. affinis* (7–10 mm) which was recorded in the lakes under study is typical for freshwater populations in northern lakes (Berezina and Maximov 2016). The maximum length of *M. affinis* is known from marine habitats (near the Sakhalin Island) and was recorded at around 15.2 mm (Demchenko 2010).

G. lacustris belongs to the Holarctic group of species and is widely distributed in the Northern Hemisphere on both continents (Takhteev et al. 2015). It is unusual that in most of the studied lakes on Vaigach Island we found a notable number of very large gammarid individuals (20–27 mm) with discriminating characters of the species *lacustris*. The maximum body length described for *G. lacustris* from a mountain region (Lake Abant, Turkey) was 25 mm (Karaman and Pinkster 1977). Usually, the males of *Gammarus* are larger than the females and reach 16–22 mm. The species status needs further clarification using molecular methods, and it is very likely that the form from Vaigach Island may be separated as a new subspecies.

Another species, *Pallasea laevis* Ekman 1923, was recorded earlier in lakes from the Novaya Zemlya Archipelago (Ekman 1923). According to WoRMS database (<http://www.marinespecies.org/>) *P. laevis* is a junior synonym of *Pallaseopsis quadrispinosa*. No other representatives of family Pallaseidae were confirmed during the present study hence the status of this species on the Novaya Zemlya Archipelago requires further studies.

Gammarus pellucidus was known mainly from the lower course of the Yenisei River and the Ob River (Gurjanova 1951). Vekhoff (2000a) reported this species from two freshwater lakes on Vaigach Island with a low frequency of occurrence (5%). The findings of *G. pellucidus* in some mountain lakes of the Altai-Sayan region (proximal to where Russia, China, Mongolia and Kazakhstan meet) are not confirmed, since it was shown that the species was identified incorrectly (Kuzmenkin and Yanygina 2018). Due to the scarcity of records, the distribution range of this species is difficult to recognize, and it is most probable that *G. pellucidus* may belong to the West Palearctic group of species that spreads no farther east than the Lena River basin.

According to our data and data from the literature, the faunas of freshwater mollusks of the Novaya Zemlya Archipelago include 3 species, and on Vaigach Island include 11 species (Leshko et al. 2008; Bespalaya et al. 2017, 2019) (Table 1). The present study provides the first record of *E. globularis* on the Novaya Zemlya Archipelago. Previously, this archipelago had only two species, *P. conventus* and *P. waldeni* (Odhner 1923; Sidorov 1925; Bespalaya et al. 2017). *E. globularis* used to be synonymized with *E. casertana* for a long period of time. Furthermore, based on conchological, anatomical and ecological differences between species, *E. globularis* is considered to be a distinct species (Glöer and Meier-Brook 2003; Horsák and Neumanová

2004; Horsák 2006; Glöer et al. 2014) (Online Resource 8, Fig4d). *E. globularis* is widespread from Europe to Western Siberia (Korniushin 1996). Recent studies have shown that the populations of *E. globularis* are abundant in the lakes and rivers of the Arctic (Dolgin 2001; Bespalaya et al. 2018, 2019, 2020). The northernmost archipelagoes are completely lacking in mollusks (Vinarski et al. 2020). Novaya Zemlya Archipelago is the northernmost record for *Euglesa* in the Palearctic Region (Ashworth and Preece 2003; Bespalaya et al. 2017).

In the lakes of Vaigach Island and Novaya Zemlya Archipelago, aquatic and amphibiotic insects are represented by no less than 27 species in five orders (see Table 1; chironomids not taken into account).

Five species of Plecoptera in three families (Nemouridae, Perlodidae, Capniidae) are reliably known from the study region (see Table 1). We consider the published records of three more species from the Novaya Zemlya Archipelago, *Capnia pygmaea*, *C. vidua* and *Capnopsis schilleri* (Jacobson 1898; Morton 1923; Økland 1928; Ulmer 1932; etc.) as doubtful, following the opinions of Brinck (1958) and Zhiltsova (1966), hence we do not include these three species in the list.

Trichoptera of Vaigach Island and the Novaya Zemlya Archipelago now include eight species in five families, Hydropsychidae, Phryganeidae, Brachycentridae, Apataniidae and Limnephilidae (see Table 1). In addition, three more species, *Agrypnia pagetana* (Phryganeidae), *Asynarchus lapponicus* and *Grammotaulius signatipennis* (Limnephilidae), were recently collected in the sea near Vaigach Island thus presenting the possibility to find them in the lakes on the islands (Melnitsky and Ivanov 2019). This study provides the first record of *P. bergrothi* from European Russia; however, it was known from Siberia, Russian Far East, Mongolia and the USA (Ivanov 2011; Morse 2020). It is also the first reliable record of *P. bergrothi* from Europe: although the species was included in a checklist for Europe by Malicky (2005), but we found no published records of *P. bergrothi* from Europe.

Aquatic Coleoptera are represented by 10 species of Dytiscidae (of these, 9 species are known from Vaigach Island and only 3 are known from Novaya Zemlya Archipelago) and one species of Helophoridae known only from Novaya Zemlya Archipelago (see Table 1).

Amphibiotic Diptera, known from the freshwaters of Vaigach Island and Novaya Zemlya Archipelago, are represented by eight families: Tipulidae, Limoniidae, Pediciidae, Simuliidae, Chironomidae, Ceratopogonidae, Culicidae, and Empididae (Økland 1928; Przhiboro 2016, 2018 and unpublished data). Only two of these families, Tipulidae and Chironomidae, are now known to be associated with truly aquatic (not semiaquatic) habitats in the lakes of the region under study.

Chironomidae, the most species-rich group of freshwater aquatic/semiaquatic macroinvertebrates in the Arctic, are not considered in this paper. Recently, Makarchenko et al. (1998) and Zelentsov (2007a) contributed to the fauna of Chironomidae (Diptera) of the Novaya Zemlya Archipelago largely based on the material of larvae and adults, respectively. Zelentsov also described two new chironomid species from the archipelago (Zelentsov 2006, 2007b, 2007c). Krasheninnikov (2013) reviewed the published data on Chironomidae of the Novaya Zemlya Archipelago and compiled a preliminary checklist, which included 68 taxa. The checklist mostly includes freshwater aquatic and semiaquatic species, many of which can be associated with lakes. However, direct data on chironomid taxa in the lakes of this region are almost absent. Økland (1928) recorded several taxa of chironomids from the lakes of the Novaya Zemlya Archipelago, and Leshko et al. (2008) recorded two taxa from the lakes of Vaigach Island (no precise identifications are given in both cases).

Crane fly larvae of the subgenus *Arctotipula* of the genus *Tipula* are the only non-chironomid dipterans which undoubtedly inhabit the lakes under study. Apparently, these are the largest free-living invertebrates (3–4 cm in length) in the lakes of the study region. Two species of *Arctotipula* are known in the region as adults, *T. (Arctotipula) oklandi* Alexander 1922 and *T. (Arctotipula) salicetorum* Siebke, 1870 (Alexander 1922; Savchenko 1961; Lantsov and Chernov 1987; Oosterbroek 2020; see also Table 1). Typically, *Arctotipula* larvae inhabit running waters in many cold or mountain areas, preferring stony and gravel bottoms; they can live in both bottom aquatic and shoreline semiaquatic habitats (Lantsov and Chernov 1987; Podeniene et al. 2006; Saaya 2010; Przhiboro, unpublished data). They are abundant in the fast-running streams and rivers of Vaigach Island and the Novaya Zemlya Archipelago (Przhiboro 2016, 2018). There are very few registrations of *Arctotipula* from lakes and mainly they are from Norway (Hofsvang 1979) and the Altai Mountains in Southern Siberia (Przhiboro unpubl data). Our data have demonstrated that *Arctotipula* larvae are a common component of the benthos in shallow Arctic lakes.

Among the aquatic and amphibiotic insects recorded from Vaigach Island and Novaya Zemlya Archipelago, only species with broad geographical ranges were found (24 spp.). Most of these species are Holarctic (15) and some are broadly Palearctic (4), West Palearctic (2) or East Palearctic (2); one species is distributed from the East Palearctic to the West Nearctic (see Table 1 for more details). At the same time, 16 of the 24 species are characterized by relatively narrow latitudinal distribution and are confined to zones with cold or cool climate (Arcto-boreal, Arcto-boreo-montane and similar ranges). However, only one species, *Agabus moestus*, has a more narrow Arctic range.

According to our data, freshwater benthic fauna in the lakes of Novaya Zemlya are taxonomically poor in comparison with Vaigach Island (Bespalaya et al. 2017, present data). Freshwater biodiversity in Svalbard and Franz Josef Land are low in comparison with Novaya Zemlya due to isolation of the archipelagoes, distance to the mainland, its more northerly location, and zonal features of climate (Vekhoff 1997b, 2000b; Coulson et al. 2014). A decrease in species diversity is typical for freshwater communities at high latitudes (Callaghan et al. 2004). In general, the freshwater invertebrate fauna of the studied lakes are cold-adapted species that are widely distributed in the Holarctic and Palearctic (Table 1). The shallow lakes of the Novaya Zemlya Archipelago and Vaigach Island freeze to the bottom (Badyukov 2011; Vekhov 1997). Consequently, some benthic species of the studied lakes can be frozen into winter ice and recover after ice melting. This strategy is widely used by invertebrates for survival in extreme environment (Olsson 1981; Mekhanikova et al. 2009; Coulson et al. 2014; Vinarski et al. 2020).

In this study, we also provide, to the best of our knowledge, the first molecular data of *E. globularis* from the Novaya Zemlya Archipelago and *L. arcticus* from Vaigach Island. In the high alpine lakes of Colorado (USA) samples of *Pisidium* sp. were collected by Guralnick (2005) (GenBank acc. nos. AY957859, AY957860), which have from 98.6 to 99.6% similarity with specimens that were collected from Vaigach Island and the Yamal Peninsula, Russian Arctic, being defined as *E. globularis*. This indicates that *E. globularis* possibly has a wider distribution (Holarctic). However, this would require additional molecular and morphological studies.

Biogeography of the fauna of the High Arctic islands during the Pleistocene is controversial (Coulson et al. 2014; Bolotov et al. 2017). From one perspective, a number of recent studies indicate that the fauna of Arctic islands is the result of recent immigration (*tabula rasa* hypothesis) (Brochmann et al. 2003; Coulson et al. 2014; Lindholm et al. 2016; Bolotov et al. 2017; Bespalaya et al. 2017), but other authors assume that some organisms survived the last glaciation in ice-free refugia (Provan and Bennett 2008; Samchyshyna et al. 2008; Bespalaya et al. 2015a; Potapov et al. 2017).

Our molecular data are in accordance with the *tabula rasa* hypothesis that the invertebrate fauna of Novaya Zemlya Archipelago and Vaigach Island observed today are the result of recent immigration after the retreat of the ice. According to our data, the endemic species are absent in the fauna of the Novaya Zemlya Archipelago and Vaigach Island. Records of the close relationship of *E. globularis* 16S rRNA haplotypes from the Novaya Zemlya Archipelago, Vaigach Island, Kolguev Island, Yamal Peninsula and Gydan Peninsula support these suggestions (Online

Resource 10). The same result was obtained for *L. arcticus* from Vaigach Island, whose COI sequences differ from specimens collected in Norway (GenBank acc. nos. HF911403, HF911404) by only two nucleotide substitutions.

Conclusion

The present study has provided additional data on the species diversity of poorly studied taxa of freshwater invertebrate of the Novaya Zemlya Archipelago and Vaigach Island, which can be used in future ecological and conservation studies. Of the 29 species of invertebrates in 4 classes and 14 orders that were found, ten species are recorded for the first time. Taking into account the data in the literature, the list of species has increased to around 136 species. Species with Holarctic and Palearctic distributions are dominant in the lakes. Our molecular data are of interest for taxonomic, biogeographic and phylogeographic studies.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no known conflict of interest.

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