

New and previously known species of Copepoda and Cladocera (Crustacea) from Svalbard, Norway – who are they and where do they come from?

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Arctic landscapes are characterised by an immense number of fresh and brackish water habitats – lakes, ponds and puddles. Due to a rather harsh environment, there is a limited number of species inhabiting these ecosystems. Recent climate-driven regime shifts impact and change Arctic biological communities. New species may appear, and existing communities may become suppressed or even disappear, depending on how ongoing changes match their ecological needs. This study provides data on presently existing and probably recently arrived fresh and brackish water microcrustacean species in the Norwegian High Arctic - Svalbard archipelago. The study focused on two taxonomic groups, Cladocera and Copepoda and altogether we found seven taxa new for Svalbard: *Alona werestschagini*, *Polyphemus pediculus*, *Diatomus* sp., *Diacyclops abyssicola*, *Nitokra spinipes*, *Epactophanes richardi* and *Geeopsis incisipes*. Compared with an existing overview for the area, our study increased the number of species by more than 20 %, and some of the new species have never been found that far north. Finally, we present a complete and critically updated revised species list of fresh and brackish water cladocerans and copepods for Svalbard.

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INTRODUCTION

Svalbard is a remote high Arctic archipelago located in the Arctic Ocean north of mainland Norway. It is known as an internationally valuable, sensitive ecosystem with a number of inland waters. Most of them are small and shallow, exposed to a harsh, Arctic climate. The growing season is short, and many waterbodies may dry out in the summer and freeze solid during the winter. Further, they are exposed to ultraviolet radiation and characterised by low nutrient and food levels. Still, these habitats contribute significantly to the Arctic biodiversity,

as during the summer, before they eventually dry out, there is an extensive development of microinvertebrates, mostly microcrustaceans (Hebert & Hann 1986, Coulson 2007, Rautio *et al.* 2011, Coulson *et al.* 2014). Since their survival demands special adaptations, a limited number of species can inhabit these ecosystems. In general, Arctic freshwaters are species-poor, but both species richness and composition may vary regionally (Hebert & Hann 1986). One important reason for this is the glaciation history. Crustacean communities in the Arctic are greatly influenced by Pleistocene glaciations (Weider & Hobæk

2003). Svalbard, Greenland, Canadian and Russian northern archipelagos, as a largely glaciated area, have a relatively low diversity compared to Arctic areas that were unglaciated 10 000 years ago (Hebert & Hann 1986, Samchyshyna *et al.* 2008, Rautio *et al.* 2011). Landvik *et al.* (2003) proposed a scenario that refugia existed in Svalbard during the last glaciation and this could explain the occurrence of some microcrustacean species as relict species (Samchyshyna *et al.* 2008).

Increasing temperature and related environmental changes as well as species dispersal from the south are also important factors for species communities (McBean *et al.* 2005). During the last decades, Svalbard exhibits a positive linear trend in annual temperatures and strong winter warming. Førland *et al.* (2011) reported that there is an increase in mean annual temperature of 2.5°C during the latest 100 years in the Svalbard Airport/Longyearbyen area. This is about three times the estimated global warming during the same period. Similar trends in temperature increase are observed from other parts of Svalbard (Førland *et al.* 2011). A reconstruction of growing season intensity at Svalbard's Airport showed that the growing season has become more intense from the early 1960 onward (Weijers *et al.* 2013). Such changes in temperatures and length of the growing season will strongly affect life in freshwater habitats, including microcrustacean communities. Meanwhile, reduced snow cover and thawing of permafrost make new areas available for species to inhabit (McBean *et al.* 2005).

Svalbard is one of the best-studied regions in the Arctic and has become an increasingly important area for Arctic research, especially during the last decades (Misund 2017). Despite extensive studies, the diversity is concluded to be low and recent surveys still uncover new species (Dimante-Deimantovica *et al.* 2016). As the temperature rises, we can expect warmth-demanding species to appear (recent dispersal). Some species may also have been present in refugia in Svalbard since the early Holocene (past dispersal), and these species may earlier have been overlooked.

Knowledge about present species and shifts in their communities are necessary to evaluate ecosystem state and its

future development. However, it has been slow to accumulate new knowledge on invertebrate groups in Arctic habitats due to the region's inaccessibility and harsh climate conditions (Bartsch 2007, Borutsky 1952, Makarova 2015, Novichkova & Azovsky 2016). The aim of the present study is therefore to contribute to this knowledge with new data. Further, we wanted to prepare a critically reviewed updated species list and to analyse the zoogeographical position of recently appearing microcrustacean species in a global context. Our study focused on two microcrustacean groups – Cladocera and Copepoda, inhabiting Svalbard's fresh and brackish waters. We also assess the origin of new species and whether they can be considered as permanent or temporary populations.

MATERIAL AND METHODS

Study site

The Svalbard archipelago is a group of small islands in the High Arctic located from 74° to 81° N and from 10° to 35° E. Largest islands are Spitsbergen, Nordaustlandet and Edgeøya. The southernmost island of the archipelago is Bear Island. Spitsbergen is the only permanently populated island. Glaciers cover more than 60% of the land area (the total area is 61 022 km²). We collected original material from the central and western part of Spitsbergen, in various parts along Isfjorden (Longyearbyen, Aldegondabreen, Grønfjordbreen, Randvika, Barentsburg, Ymerbukta, Pyramiden, Kapp Napier, Diabasodden) and Kongsfjorden (Ny-Ålesund) (Figure 1). Altogether, we took 84 samples from 79 localities in 2014 and 2015. The waterbodies were categorized in four classes according to their size and approximate average depths. These categories were based on an already existing concept presented by CAFF (Conservation of Arctic Flora and Fauna) Freshwater Expert Monitoring Group for Pan-Arctic Monitoring Program and from other literature sources (Culp *et al.* 2012, Rautio *et al.* 2011). For sampling site classification, see Table 1, for sampling sites coordinates and ordering numbers further in the text, see Table 2. With a few exceptions, all ponds were shallow and less than 2 m deep. Depth estimates for the lakes are somewhat rough, since they had to be performed without the use of a boat for logistic reasons. Many of surveyed freshwater habitats are influenced by sea aerosols and conductivity therefore varied from < 0,01 µS/cm (in pure freshwaters) to > 10000 µS/cm (in mesohaline ponds located along the sea shore).

Table 1. Classification of sampling sites.

Sampling locality class	Number of localities	Area (ha)	Average depth (m)
Puddles	22	< 0.01	≤ 0.25
Small ponds	23	≥ 0.01 - ≤ 0.1	0.25 - 1
Large ponds	20	> 0.1 - ≤ 1	1 - 2
Lakes	14	> 1	2, usually more

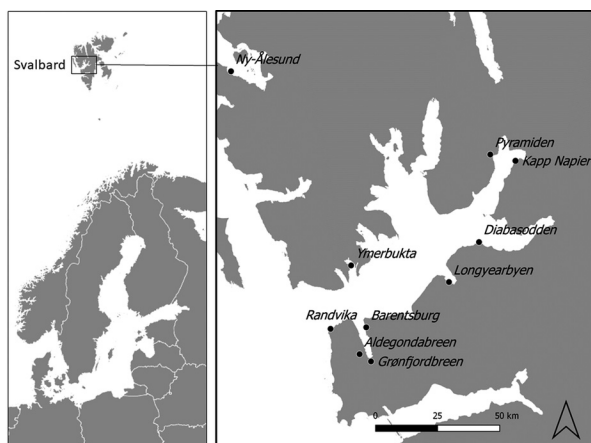


Figure 1. Sampling sites in Svalbard.

Table 2. Coordinates of sampling sites.

	Locality	Habitat type	Coordinates North	Coordinates East		Locality	Habitat type	Coordinates North	Coordinates East
1	Longyearbyen	puddle	78.2038	15.7625	43	Kapp Napier	small pond	78.6375	16.7424
2	Longyearbyen	small pond	78.2178	15.7060	44	Kapp Napier	large pond	78.6359	16.7331
3	Aldegondabreen	puddle	77.9908	14.1856	45	Kapp Napier	puddle	78.6344	16.7371
4	Aldegondabreen	puddle	77.9902	14.1838	46	Kapp Napier	small pond	78.6321	16.7373
5	Aldegondabreen	puddle	77.9910	14.1798	47	Kapp Napier	puddle	78.6356	16.7438
6	Aldegondabreen	lake	77.9898	14.1685	48	Pyramiden	puddle	78.6518	16.3415
7	Aldegondabreen	large pond	77.9922	14.1937	49	Diabassoden	small pond	78.3609	16.1082
8	Aldegondabreen	puddle	77.9922	14.1945	50	Diabassoden	small pond	78.3583	16.1683
9	Aldegondabreen	puddle	77.9874	14.1769	51	Ny-Ålesund	lake	78.9235	11.8775
10	Aldegondabreen	puddle	77.9863	14.1531	52	Ny-Ålesund	lake	78.9144	12.0591
11	Aldegondabreen	puddle	77.9864	14.1501	53	Ny-Ålesund	small pond	78.9049	12.0711
12	Aldegondabreen	puddle	77.9855	14.1466	54	Ny-Ålesund	large pond	78.9041	12.0635
13	Aldegondabreen	puddle	77.9815	14.1456	55	Ny-Ålesund	large pond	78.9003	12.0670
14	Aldegondabreen	lake	77.9846	14.1764	56	Ny-Ålesund	large pond	78.8988	12.0623
15	Aldegondabreen	large pond	77.9855	14.1869	57	Ny-Ålesund	small pond	78.9055	12.0791
16	Aldegondabreen	large pond	77.9705	14.2325	58	Ny-Ålesund	lake	78.9164	11.8636
17	Aldegondabreen	small pond	77.9643	14.2420	59	Ny-Ålesund	small pond	78.9178	11.9252
18	Aldegondabreen	large pond	77.9598	14.2491	60	Ny-Ålesund	lake	78.9251	11.9385
19	Randvika	small pond	78.0827	13.7915	61	Ny-Ålesund	small pond	78.9257	11.9233
20	Randvika	small pond	78.0811	13.7939	62	Ny-Ålesund	puddle	78.9207	11.9537
21	Randvika	large pond	78.0808	13.8040	63	Ny-Ålesund	puddle	78.9186	11.9621
22	Randvika	large pond	78.0826	13.7991	64	Ny-Ålesund	puddle	78.9157	11.9755
23	Randvika	large pond	78.0738	13.8128	65	Ny-Ålesund	small pond	78.9159	11.9772
24	Randvika	large pond	78.0686	13.8075	66	Ny-Ålesund	small pond	78.9235	11.9537
25	Randvika	lake	78.0658	13.7830	67	Ny-Ålesund	small pond	78.9356	11.7992
26	Randvika	lake	78.0704	13.7950	68	Ny-Ålesund	large pond	78.9343	11.8164
27	Randvika	lake	78.0717	13.7982	69	Grønfjordbreen	large pond	77.9595	14.2506
28	Randvika	large pond	78.0745	13.7981	70	Grønfjordbreen	puddle	77.9561	14.2595
29	Randvika	small pond	78.0757	13.7991	71	Grønfjordbreen	puddle	77.9561	14.2595
30	Randvika	large pond	78.0733	13.7845	72	Grønfjordbreen	large pond	77.9544	14.2634
31	Barentsburg	small pond	78.0707	14.2161	73	Grønfjordbreen	puddle	77.9540	14.2669
32	Barentsburg	small pond	78.0952	14.1928	74	Grønfjordbreen	lake	77.9551	14.2812
33	Ymerbukta	large pond	78.2802	14.0775	75	Grønfjordbreen	puddle	77.9536	14.2811
34	Ymerbukta	large pond	78.2795	14.0921	76	Grønfjordbreen	puddle	77.9504	14.2606
35	Ymerbukta	large pond	78.2831	14.1174	77	Grønfjordbreen	lake	77.9404	14.2604
36	Ymerbukta	small pond	78.2814	14.1154	78	Grønfjordbreen	small pond	77.9425	14.2502
37	Pyramiden	lake	78.6561	16.1835	79	Grønfjordbreen	puddle	77.9637	14.2606
38	Pyramiden	lake	78.6549	16.1901	80	Aldegondabreen	puddle	77.9863	14.1531
39	Pyramiden	small pond	78.6544	16.2088	81	Aldegondabreen	puddle	77.9863	14.1505
40	Pyramiden	small pond	78.6527	16.2037	82	Aldegondabreen	puddle	77.9910	14.1798
41	Pyramiden	lake	78.6397	16.1182	83	Aldegondabreen	large pond	77.9922	14.1945
42	Kapp Napier	large pond	78.6381	16.7342	84	Aldegondabreen	small pond	78.0012	14.1710

Large area (> 1 ha) flooded waterbodies belong to large ponds class. Two large lakes in the coastal zone, Lake Linné and Lake Bretjörna (surface areas 4.6 km² and 1.3 km², respectively), were also included in the survey (both belong to the Lake class in Table 1).

Sampling, species identification and fauna analysis

Samples were collected during the periods 18 – 24 August 2014 (Isfjorden area only) and 17 – 22 August 2015 (Isfjorden and Kongsfjorden area). Crustaceans were sampled from four habitats: the open water, the littoral zone, the near-sediment layer and the upper sediment layer. Different methods were used. A zooplankton net (100 mm diameter, 50 µm mesh) was thrown and hauled at low speed through the water. When this method was impossible due to the small size of the water body or stones, water was collected in a bucket and then filtered for animals. In the littoral zone, samples were taken with a small net having a long handle. Meiobenthic samples were taken with a plastic tube (diameter 2 cm). A column of the upper sediment layer (3–4 cm) was pushed out from the tube with a plunger.

The following literature was used for species identification: Smirnov (1971, 1996), Lieder (1996), Sinev (1999, 2002), Flösner (2000) for Cladocera and Sars (1911), Lang (1948), Dussart (1967) and Einsle (1993, 1996) for Copepoda. To analyse the dispersal and colonization of the Svalbard crustacean fauna in a wider context, we used available literature to generate a checklist and figures for the global distribution of species and their appearance in the archipelago (Table 4). In this paper we focus on records of new species for Svalbard, the complete species list of the study is included in Table 4 (cf. Walseng et al. 2018).

RESULTS

Original data results

From our study, seven fresh and brackish water Crustacea species (two Cladocera and five Copepoda), turned out to be new for Svalbard (Table 3).

Alona werestschagini has a Palearctic distribution (Figure 2). According to Sinev (2002), its patchy spread is an exception among Chydoridae species and rather indicates that this

is a cold-adapted postglacial relict, which survived in the mountain lakes of Central Asia. The species is also found in paleolimnological samples from Lake Värddoajávri (northern Finland), where it constituted a significant part of the chydorid fauna deposits of the early Holocene (Sarmaja-Korjonen & Sinev 2008). In Svalbard it was found in three puddles (loc. 70, 71, 73) close to Grønfjordbreen. The species is closely related to *A. guttata*, hence we cannot rule out that some of the previous *A. guttata* records from Svalbard belong to *A. werestschagini*.

Polyphemus pediculus has an entire Holarctic/circumpolar distribution (Xu et al. 2009, Novichkova & Azovsky 2016) with a northern limit between latitudes 70° and 73° (records by Røen (1962) from Greenland). The species is absent in Franz Josef Land, Novaya Zemlya, Severnaya Zemlya, New Siberian Islands, Bering Island, Ellesmere Island and Wrangel Island (Figure 3) (Novichkova & Azovsky 2016). Our record from Ny-Ålesund at latitude 78° has extended its range towards the north. It was found in two small ponds, respectively in Pyramiden (loc. 39) and Ny-Ålesund (loc. 59).

Species belonging to the family Diaptomidae have not been found in Svalbard before. A few young specimens (*Diaptomus* sp.) were found in a puddle close to the Aldegondabreen (loc. 6). There are three *Diaptomus* species represented in the Arctic (Dussart & Defaye 2002): *D. (D.) castor* (Jurine, 1820), *D. (Chaetodiaptomus) glacialis* Lilljeborg, 1889 and *D. (C.) rostripes* (Herbst, 1955) (Figure 3). In general, the genus has a Holarctic distribution (Dussart & Defaye 2002, Novichkova & Azovsky 2016). *Diaptomus (C.) glacialis* can be considered as a typical Arctic species that might have originated from Northern Europe/Siberia and later migrated to North America over Beringian connections. *Diaptomus (C.) rostripes* is close to the previously mentioned species, with a sporadic distribution, pending revision and verification.

Diacyclops abyssicola was found in two relatively deep lakes in Randvika: Lake Borgdammen (loc. 24) and an unnamed lake (loc. 26). It has a circum-Arctic/Subarctic scattered distribution and has never been found south of latitude 45° (Figure 4). It is mainly Palearctic, with records also from Ontario, Canada (Lilljeborg 1901, Rylov 1948, Walseng et al. 2008, Schaburova 2011, Fefilova 2015, Novichkova & Chertoprud 2015, Karpowicz 2017, Chertoprud unpubl.). *Diacyclops abyssicola* is a typical benthic species, inhabiting

Table 3. Crustacea species new for Svalbard. Brackish water species are marked with asterisk (*).

Subclass	Order/Suborder	Family	Species
Phyllopoda	Cladocera	Chydoridae	<i>Alona werestschagini</i> Sinev, 1999
		Polyphemidae	<i>Polyphemus pediculus</i> (Linnaeus, 1761)
Copepoda	Calanoida	Diaptomidae	<i>Diaptomus</i> sp.
	Cyclopoida	Cyclopidae	<i>Diacyclops abyssicola</i> (Lilljeborg, 1901)
	Harpacticoida	Ameiridae	<i>Nitokra spinipes</i> Boeck, 1865 *
		Canthocamptidae	<i>Epactophanes richardi</i> Mrazek, 1893
		Tachidiidae	<i>Geeopsis incisipes</i> (Klie, 1913) *

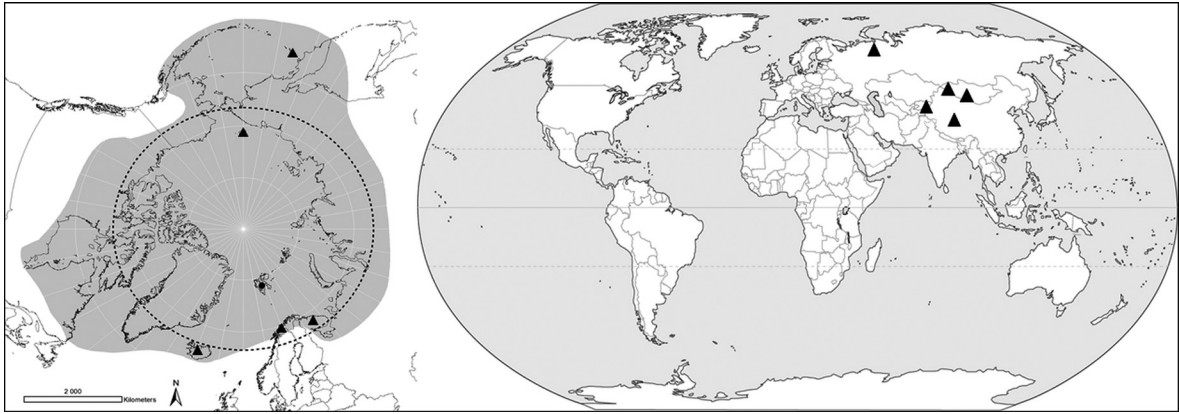


Figure 2. Arctic and global (apart from Arctic) distribution of *Alona werestschagini* Sinev 1999. Circle – first record from Svalbard, triangle – existing records, dotted line – Arctic circle, highlighted grey area – Arctic boundary. Source: Sinev 1999, Sinev 2002, Sarmaja-Korjonen & Sinev 2008, Novichkova & Chertoprud 2015, Novichkova & Azovsky 2016.

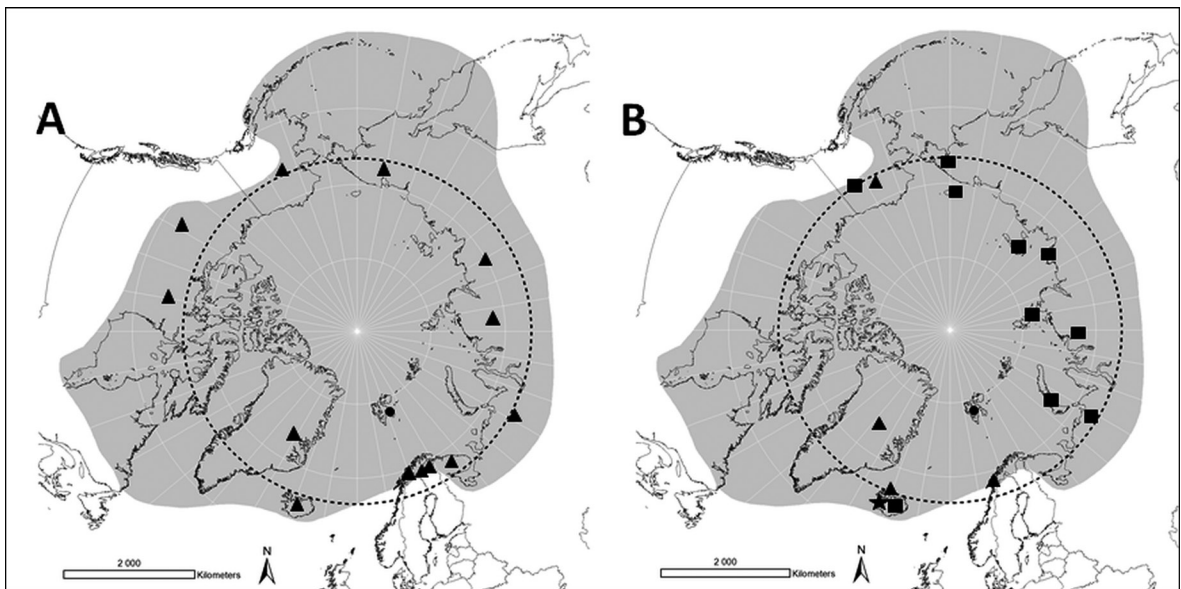


Figure 3. Arctic distribution of A – *Polyphemus pediculus* (Linnaeus, 1761), B – *Diaptomus* sp. Circle – first record from Svalbard, triangle – existing records, dotted line – Arctic circle, highlighted grey area – Arctic boundary. For *Diaptomus* sp. triangle – *D. (Diaptomus) castor* (Jurine, 1820), square – *D. (Chaetodiaptomus) glacialis* Lilljeborg, 1889, star – *D. (Chaetodiaptomus) rostripes* Herbst, 1955. Source: Røen 1962, Dussart & Defaye 2002, Xu et al 2009, Novichkova & Azovsky 2016.

the bottom substrate in the littoral zone down to the depth of more than 40 m (Rylov 1948). It is truly overlooked, and its distribution most likely represents the sampling effort rather than the species zoogeography.

Nitokra spinipes Boeck, 1865, which was found in a brackish lake near the shore (loc. 52) and in a brackish pond (loc. 66) close to the Ny-Ålesund settlement, is presumably a cosmopolitan species (Defaye & Dussart 2011). It inhabits muddy sediments of estuaries and lagoons characterized by a high content of marine salts (Lang 1948, Borutsky 1952). Findings from Sub- to High Arctic are rather sporadic (Figure 5), and the chance to find it decreases towards the north. In North America, for instance, High Arctic records are only from

Alaska, all other know records are more southwards (Reid & Williamson 2010). In Svalbard, *N. spinipes* has been mentioned from Svalbard lacustrine environments before in non-peer reviewed publication – in a dissertation by Spitzenberger (1996).

Epaetophanes richardi Mrazek, 1893 is a cosmopolitan species recorded from Afro-tropical, Palearctic, Nearctic, Neotropical, Australian, Oriental, Arctic (Figure 5) and Antarctic regions (Defaye & Dussart 2011, de Jong et al. 2014). In Svalbard, *E. richardi* was found in 18 water bodies of different size and type: Longyearbyen (loc. 1), Randvika area (loc. 26, 27, 28, 29), Kapp Napier (loc. 42) Aldegondabreen (loc. 9, 14, 16, 80, 81, 84), Grønfjordbreen glaciers (loc. 69, 73), Pyramiden (loc. 38) and Ny-Ålesund (loc. 57, 58, 68).

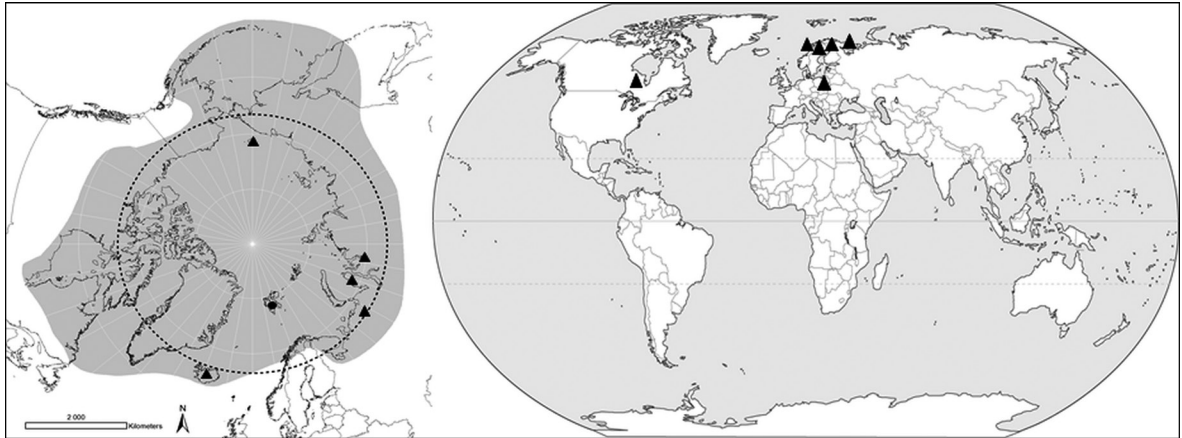


Figure 4. Arctic and global (apart from Arctic) distribution of *Diacyclops abyssicola* (Lilljeborg, 1901). Circle – first report from Svalbard, triangle – existing records, dotted line – Arctic circle, highlighted grey area – Arctic boundary. Source: Lilljeborg 1901, Rylov 1948, Dussart & Defaye 2006, Walseng et al 2008, Schaburova 2011, de Jong et al. 2014, Fefilova 2015, Novichkova & Chertoprud 2015, Novichkova & Azovsky 2016, Karpowicz 2017, Chertoprud unpubl.

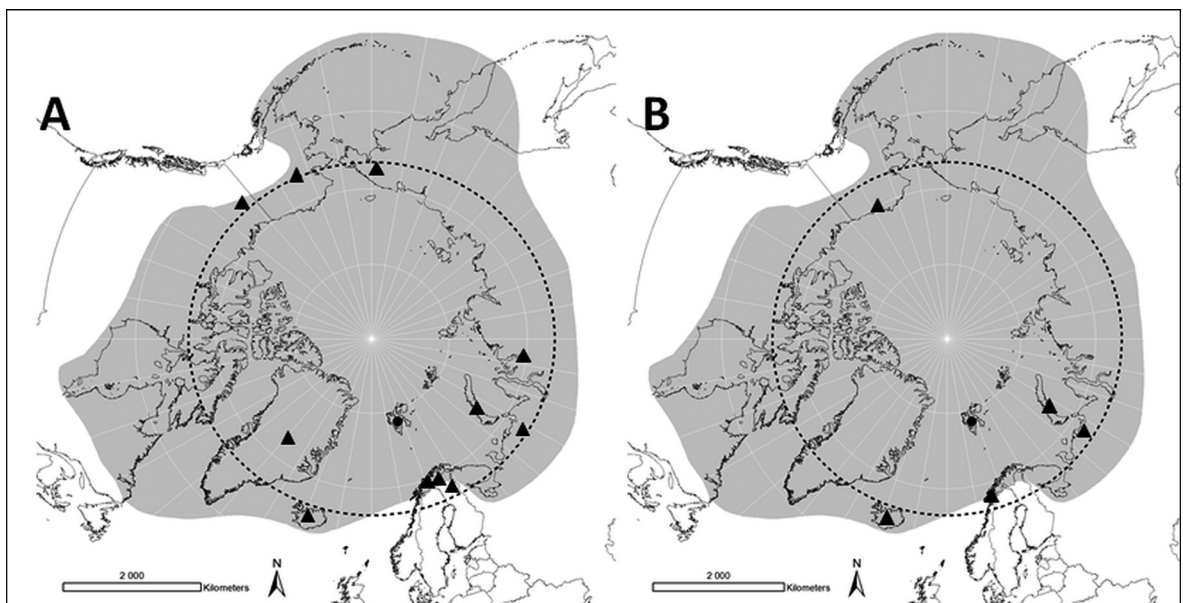


Figure 5. Arctic distribution of A – *Epactophanes richardi* Mrazek, 1893, B – *Nitokra spinipes* Boeck, 1865. Circle – first report from Svalbard, triangle – existing records, dotted line – Arctic circle, highlighted grey area – Arctic boundary. Source: Lang 1948, Borutsky 1952, Røen 1962, Spitzberger 1996, Reid & Williamson 2010, Defaye & Dussart 2011, de Jong et al. 2014, Evtimova & Pandourski 2016, Novichkova & Azovsky 2016, Dimante-Deimantovica unpubl.

Geeopsis incisipes (Klie, 1913) has a Holarctic distribution (Figure 6), and records are mostly from the circum-Arctic region. However, there is also record from Australian region (New Zealand) pending verification (Defaye & Dussart 2011). The species is typical for brackish waters, inhabiting soft sediments of estuaries and lagoons close to the sea (Lang 1948, Borutsky 1952, Chertoprud et al. 2014, Fefilova 2015). In Svalbard, *G. incisipes* was found in a puddle along the sea shore in the Grønfjordbreen area and in a brackish pond along the sea shore near the Ny-Ålesund settlement (loc. 79 and 66, respectively).

DISCUSSION

General overview of Svalbard Archipelago fresh and brackish water microcystaceans

After a critical review of available data in the literature (Table 4) and including new records from our survey, we conclude that 31 fresh and brackish water microcystacean species (13 Cladocera and 18 Copepoda) have been found in Svalbard (Table 4). Our study increases the total number of species with more than 20%. Of all the species, 68% are freshwater and 26%

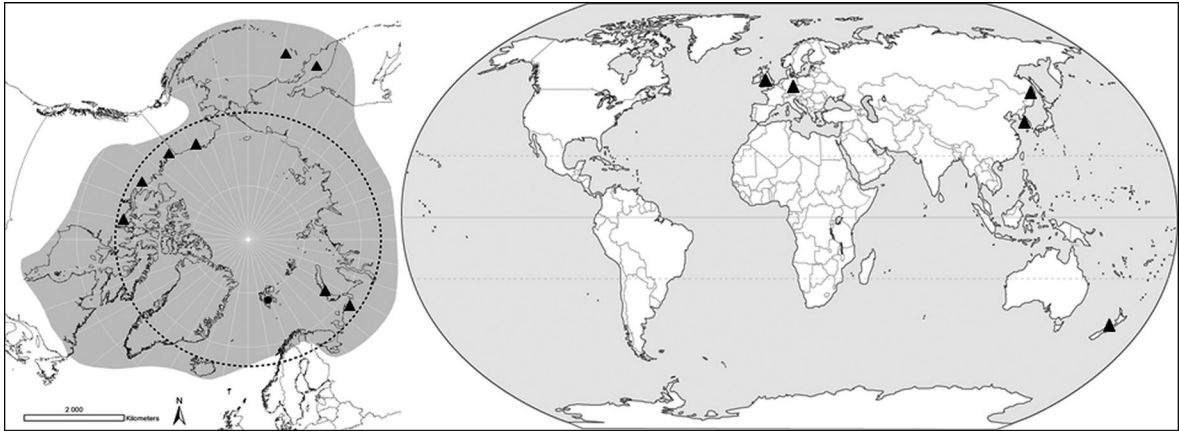


Figure 6. Arctic and global (apart from Arctic) distribution of *Geeopsis incisipes* (Klie, 1913). Circle – first report from Svalbard, triangle – existing records, dotted line – Arctic circle, highlighted grey area – Arctic boundary. Source: Lang 1948, Borutsky 1952, Chang 2008, Reid & Williamson 2010, Defaye & Dussart 2011, Chertoprud et al 2014, Fefilova 2015, Novichkova & Azovsky 2016.

are fresh and brackish water species, only 6% are true brackish water species. Most of the represented freshwater species in Svalbard are known for being able to tolerate at least slightly brackish water conditions (Aladin 1991).

The following species are not included in the species list since identification is uncertain: *Diacyclops bisetosus* (Rehberg, 1880) and *D. bicuspidatus* (Claus, 1857) – Richard (1897, 1898), Scourfield (1897), based on copepodites; *Megacyclops viridis* (Jurine, 1820) – Richard (1898), the species is probably mixed up with a close relative; *Paralona pigra* (G. O. Sars, 1862) – Spitzenberger (1996), verification and peer review publication is missing; *Coronatella rectangula* (G. O. Sars, 1862) – Lilljeborg (1900b), original reference is not clear. Nor have we included species with fossil records only, e.g. *Pleuroxus* sp. and *Daphnia* (*D.*) *longispina* (O. F. Müller, 1776) for Spitsbergen (Guilizzoni et al. 2006).

Nannopus palustris Brady, 1880 is mentioned for Svalbard in Wojtasik & Kur (2007). They found differences in the morphological characteristics of two populations from Svalbard. The original description of this species is poor (Brady 1880). Recent studies based on molecular-genetic analysis (Garlitska et al. 2012) recognised separate species. Several have been described: *N. didelphis* Fiers & Kotwicki 2013, *N. scaldicola* Fiers & Kotwicki 2013, *N. procerus* Fiers & Kotwicki 2013 and *N. hirsutus* Fiers & Kotwicki 2013, although, of these only *N. didelphis* is found in Svalbard.

Olofsson (1917) has described several new species for science within the family Tachidiidae – *Tachidius spitzbergensis*, *T. arcticus* and *Geeopsis longicornis*. Later the validity of the two *Tachidius* species has not been confirmed and is reduced to one species *T. discipes* Giesbrecht, 1881. The validity of the *G. longicornis*, which was first reduced (Lang 1948), was later restored by Huys (2009). The harpacticoid *E. richardi* displays high ecological and morphological variability. Attempts to identify varieties (Borutzky 1952, 1964) have been made, however, presently all have been synonymized with the nominal

species (Huys 2009). The species is pending revision and verification. For *N. spinipes* several possible species are recognized (Lang 1965), hence the worldwide geographical distribution should be revised.

About one third of the total fauna consist of cosmopolitan species, while 45% and 22% are considered to have their origin from the Holarctic and Palearctic region, respectively. So far, no endemic species have been described from Svalbard. However, in the last decade the global understanding of cosmopolitanism in species has changed. Many species are assumed to be endemic to their zoogeographical region (Boxshall & Defaye 2008) and a cryptic genetic variation may occur (Hamrová et al. 2012). Phenotypical differences may hardly be visible although there are biological, ecological and evolutionary differences.

Where do the species come from?

Svalbard's fauna, both its composition and low diversity, is a result of geographical isolation and the fact that this area was covered by ice during the last glaciation (Hebert & Hann 1986). However, the species composition is relatively stable. Thirteen species have been regularly found from the very first studies in the late 1890s until recent time (Table 4 – basic species). Some of these species may be glacial relicts (including possible relic clades and cryptic lineages), e.g. *Daphnia* (*D.*) cf. *pulex* complex, *Daphnia* (*D.*) *longispina* complex, *Chydorus* cf. *sphaericus*, *Cyclops* sp., *Diacyclops crassicaudis*, *Eurytemora raboti*, *Limnocalanus grimaldi* (Rylov 1948, Weider & Hobæk 2003, Samchyshyna et al. 2008, Hamrová et al. 2012, Kotov et al. 2016). Nunataks in the north-west, the northernmost part of Spitsbergen, King Karl's Land and Bear Island may have served as ice-free refugia (Dahl 1946 and references therein, Landvik et al. 2003).

Besides the refugia hypothesis, smaller animals inhabiting shallow water bodies (*D. crassicaudis*) or semi-aquatic habitats (*Maraenobiotus brucei*) may have survived under the ice (Lewis & Reid 2007). Cladocerans may hatch from diapausing

Table 4. Presently known fresh and brackish water Cladocera and Copepoda species from Svalbard. Bear Island records are represented by the last column only. Shaded lines – species found mostly likely on Bear Island only.

Species	Thor 1930	Records 1930 - 2000	Records >2000 and/or our records	Bear Island (first record)
<i>Macrothrix hirsuticornis</i> Norman & Brady, 1867	X	X	X	X (Richard 1898)
<i>Daphnia</i> (<i>Daphnia</i>) cf. <i>pulex</i> Leydig, 1860	X	X	X	X (Bertram 1933)
<i>Chydorus</i> cf. <i>sphaericus</i> (O. F. Müller, 1776)	X	X	X	X (Richard 1898)
<i>Alona guttata</i> G. O. Sars, 1862	X	X	X	
<i>Limnocalanus grimaldi</i> (de Guerne, 1886)	X	X		
<i>Eurytemora raboti</i> (Richard, 1897)	X	X	X	
<i>Cyclops abyssorum</i> G. O. Sars, 1863	X	X	X	X (Lilljeborg 1900a)
<i>Tachidius discipes</i> Giesbrecht, 1881	X		X	
<i>Diacyclops crassicaudis</i> G. O. Sars, 1863	X	X	X	X (Thor 1930)
<i>Maraenobiotus brucei</i> Richard, 1898	X	X	X	X (Richard 1898)
<i>Daphnia</i> (<i>Daphnia</i>) <i>longispina</i> group				X (Richard 1898)
<i>Cyclops vicinus vicinus</i> Ulyanin, 1875		?		X (Lilljeborg 1900a)
<i>Megacyclops gigas</i> (Claus, 1857)				X (Richard 1898)*
<i>Sida crystallina</i> (O. F. Müller, 1776)		X		X (Bertram 1933)
<i>Bosmina</i> (<i>B.</i>) <i>longirostris</i> (O. F. Müller, 1776)		X		
<i>Acroperus harpae</i> (Baird, 1834)	X**		X	X (Bertram 1933)
<i>Eucyclops</i> sp. / <i>E. serrulatus serrulatus</i> (Fischer, 1851)		X	X	
<i>Geeopsis longicornis</i> (Olofsson, 1917)	X			
<i>Geeopsis incisipes</i> (Klie, 1913)			X	
<i>Harpacticus uniremis</i> (Krøyer, 1842)		X		
<i>Nitokra spinipes</i> Boeck, 1865		X	X	
<i>Parastenocaris glacialis</i> Noodt, 1954		X		
<i>Bosmina</i> (<i>E.</i>) <i>longispina</i> (Leydig, 1860)			X	
<i>Ophryoxus gracilis</i> (G. O. Sars, 1862)			X	
<i>Polyphemus pediculus</i> (Linnaeus, 1761)			X	
<i>Eurycercus</i> sp.			X	
<i>Alona werestschagini</i> Sinev, 1999			X	
<i>Diaptomus</i> sp.			X	
<i>Diacyclops abyssicola</i> (Lilljeborg, 1901)			X	
<i>Nannopus didelphis</i> Fiers & Kotwicki, 2013			X	
<i>Epactophanes richardi</i> Mrazek, 1893			X	

*Originally as *M. viridis*, ? needs verification, mentioned from Spitsbergen by Thomasson 1961, Spitzberger 1996.

** Summerhayes & Elton 1923.

References: Richard (1897, 1898), Guerne & Richard (1889), Scourfield (1897), Lilljeborg (1900a, b), Ekman (1904), Brehm (1917), Olofsson (1917, 1918), Thor (1930), Bertram (1933), Amren (1964a, b), Halvorsen & Gullestad (1976), Husman et al (1978), Jacobi & Meijering (1978), Meijering & Jacobi (1981), Jørgensen & Eie (1993), Sywula et al (1994), Spitzberger (1996), Coulson (2007), Skaugrud (2009), Zawisza & Szeroczyńska (2011), Coulson & Refseth (2004), Novichkova & Azovsky (2016), Walseng et al (2018).

eggs that have been frozen for many years (Meijering 2003). Other species may have appeared by dispersal. Svalbard's remote location and fragmented ice-free landscape reduces the possibility for active dispersal. Long-range passive dispersal agents in the environment like wind, water, animals and humans can contribute significantly to species post-glacial colonization. Wind (anemochory) can move dry sediments with zooplankton resting stages (Bennike 1999, Incagnone et al. 2015). The efficiency of this vector is linked to the distance among sites and size of the transportable entity (Incagnone et al. 2015). Ocean currents (hydrochory) may also serve as a dispersal agent by carrying species directly on the sea surface or indirectly - concealed in cracks in the driftwood or other material, or frozen in ice (Bennike 1999). Experiments on long-distance dispersal confirmed that survival times in soil-dwelling arthropods are sufficient to permit ocean current transport from northern Norway to Svalbard (Coulson et al. 2002). Finally, birds (zoochory) and man (antropochory) may have contributed to the dispersal of new species to Svalbard. Water birds mediated dispersal including eggs and/or entire animals have been observed for several Cladocera and Copepoda species (Coughlan et al. 2017, Frisch et al. 2007, Figuerola et al. 2003, Figuerola & Green 2002). Copepods can be easily carried in moist soil or plant parts due to human activities. Ballast water, fish farming, transportation of goods, food, ecotourism, industrial and scientific field-work etc. are also examples that may have spread new species to Arctic regions included Svalbard (Reid 2001, Waterkeyn et al. 2010, Incagnone et al. 2015).

Both, favourable climate conditions, new alternatives for dispersal and more intensive studies may explain why many new species have been discovered during the last decades. Whether a newcomer will settle on a permanent basis or disappear, may vary. The abundance of individuals in the found populations and their distribution patterns within this study, suggest that at least some of the newly discovered species have settled permanently. *Epactophanes richardi* – common and abundant – is such an example. *Alona werestschagini* was found in three localities (n=10 individuals). *Nitokra spinipes* is rather abundant, found in few localities. However, species disappearance may also occur. Species records derived from cores proved that *Alona* cf. *bergi* Røen 1992 in Nordaustlandet (Svalbard) was replaced by *Chydorus* cf. *sphaericus* at approximately 8000 cal year BP (Nevalainen et al. 2012).

Species distribution data throughout the archipelago are rather heterogeneous, there is still a lack of comprehensive sampling campaigns. Many locations have been sampled only once and many areas are not investigated at all. The faunistic difference between Svalbard regions can be remarkable. An example is the Bear Island, located in the western part of the Barents Sea, approximately halfway between Spitsbergen and Norwegian mainland. Some species were found particularly here (Table 4). Due to the North Atlantic warm water current there is a warmer climate here than in other areas at similar

latitude and milder winters than in Spitsbergen. All Bear Island exclusive species are relatively large, especially copepods, and therefore with limited ability for dispersal. For some species, this could be a natural distribution border since the present dispersal picture suggests that these species are restricted to the Low Arctic (Novichkova & Azovsky 2016). The affinity of the fauna between northern Europe, Novaya Zemlya, Jan Mayen, Greenland and Svalbard can be also explained by timber carried down the large Siberian rivers to the sea and further by westerly Arctic currents. The driftwood is by-passing Bear Island, hence not all species reaching Spitsbergen spread to Bear Island (Bristowe 1925).

In conclusion, the present fresh and brackish water microcrustacean fauna of Svalbard is relatively young, and species poor, and it has not reached its maximum richness yet. We expect that the combination of higher temperature and new active dispersal agents will increase the diversity faster than in a more undisturbed situation. We will experience new warmth-demanding species to be more common at the cost of cold-adapted species. Hence, data on fresh and brackish water microcrustacean species in Svalbard may provide valuable information for the monitoring of changes in Arctic biodiversity and ecosystems.

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