Fauna norvegica 2025 Vol. 44: 9–27.

Review paper

Ecology and distribution of the Arctic Tadpole Shrimp *Lepidurus arcticus* (Branchiopoda, Notostraca) in the Fennoscandian Mountain Range and on the Svalbard Archipelago

Tore Qvenild[1], Arne Fjellheim[2], Trygve Hesthagen[3] and Hanna-Kaisa Lakka[4,5,6]

Qvenild T, Fjellheim A, Hesthagen T and Lakka H-K. 2025. Ecology and distribution of the Arctic Tadpole Shrimp *Lepidurus arcticus* (Branchiopoda, Notostraca) in the Fennoscandian Mountain Range and on the Svalbard Archipelago. Fauna norvegica 44: 9–27.

Lepidurus arcticus is frequently found at sea level in the Svalbard archipelago, extending further south from 80°N into the tundra zone and at increasing altitudes in the Fennoscandian Mountain Range (Scandes) down to 59°N, spanning 2300 km. In this region, there are records of *Lepidurus arcticus* in at least 686 locations. In Svalbard, it is noted in 87 fishless ponds and two rivers with anadromous Arctic charr. In Bear Island, it inhabits 103 fishless ponds, eight lakes, and three rivers containing resident Arctic charr. In the Scandes, it is found in 483 locations, predominantly in deep, large lakes with fish. This demonstrates a greater adaptability to various habitats than other notostracan species. The species' ability to withstand significant environmental changes since its emergence is attributed to its resilient eggs, which can endure both freezing and desiccation and remain viable for decades. Additionally, its reproductive flexibility, which creates egg banks of overlapping generations, helps buffer the population against environmental variability. While the embryonic phase may persist for decades in the Arctic, both the embryonic and postembryonic phases are typically completed within a year in the Scandes. *Lepidurus arcticus* can reproduce both sexually and asexually. Asexual reproduction enhances dispersal abilities, as single eggs or individuals can establish new populations. Predicted warming of freshwater habitats may significantly impact *Lepidurus arcticus*, as water temperature limits its distribution. With rising temperatures, *L. arcticus* will likely expand its range into the colder territories of Svalbard. In the Scandes, prolonged warmth could restrict its range, yet it may ascend in altitude in southern Scandes. In Svalbard, warmer water and prolonged open water seasons may boost production. This could make the lakes more similar to those in Bear Island, and thus, coexistence with fish could become more common. Therefore, baseline studies are needed for cold-adapted freshwater species such as *Lepidurus arcticus*.

ISSN: 1891-5396 (electronic). doi: https://doi.org/10.5324/fn.v44i0.5919.
Received: 2024-06-11. Accepted: 2025-06-10. Published online: 2025-06-24.

Keywords: *Lepidurus arcticus*, Bear Island, distribution, Arctic freshwater biodiversity, climate, ecological changes

1. Solhellinga 29 J, NO-2315 Hamar, Norway
2. Sandalsbakken 2, NO-4022 Stavanger, Norway
3. Lundavegen 330, NO-2690 Skjåk, Norway
4. Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland
5. The University Centre in Svalbard, P.O. Box 156, NO-9171 Longyearbyen, Norway
6. Kilpisjärvi Biological Station, University of Helsinki, Käsivarrentie 14622, FI-99490 Kilpisjärvi, Finland

Corresponding author: Tore Qvenild
E-mail: fmhetq@outlook.com

INTRODUCTION

The Branchiopoda class, except for the Cladocera, is often referred to as «large branchiopods», although this name lacks a phylogenetic or taxonomic foundation (Brendonck *et al.* 2008). Within the Branchiopoda, the order Notostraca includes the Triopsidae family, with the two genera *Triops* Schrank, 1803, and *Lepidurus* Leach, 1819, as well as extinct members of the stem lineage (Geyer *et al.* 2024). These crustaceans are notable for their evolutionary stasis, showing little to no morphological changes over extensive geological periods since their initial divergence. The term «living fossil» is often used for such species or genera. Historically, Notostraca fossils from the Lower Triassic Voltzia Sandstone Lagerstätte in northeastern France were linked to *Triops cancriformis* (Bosc 1801), claiming it as the oldest continuously existing animal species at 240 million years (Geyer *et al.* 2024). This assertion has been discredited due to the lack of molecular evidence supporting a relatively recent Cenozoic radiation (Vanschoenwinkel *et al.* 2012). Moreover, a re-evaluation classified these fossils as *Apudites antiquus*, an extinct stem lineage species (Geyer *et al.* 2024). Despite this, the concept of a «living fossil» can be defined as a taxon belonging to a group with a long evolutionary history, retaining several primitive characteristics, and having few living relatives (Vanschoenwinkel *et al.* 2012). By this definition, members of the order Notostraca can generally be considered living fossils.

Notostracan species are characterised by hypervariability in numerous morphological characters, despite their long-term stability in gross morphology. The taxonomic distinctions within the crown group remain unresolved. However, the genera *Triops* and *Lepidurus* can be differentiated by the presence of the supra-anal plate found in *Lepidurus* but absent in *Triops* (Longhurst 1955).

Morphological studies of the Arctic tadpole shrimp, *Lepidurus arcticus* (Pallas, 1793), have uncovered notable variations in the supra-anal plate's size, with Svalbard populations having significantly shorter plates (Lakka 2015). These populations exhibit greater phenotypic plasticity compared to those in Fennoscandia (Lakka 2013, 2015; Järvinen *et al.* 2014). Genetically, *L. arcticus* is distinctly different from other *Lepidurus* species (Hessen *et al.* 2004; Vanschoenwinkel *et al.* 2012). Research on 48 populations across a wide geographical range identified two haplogroups (A and B) with five haplotypes (A1-A3, B1-B2) (Hessen *et al.* 2004). A distinctive pattern is the separation of haplogroups between Bear Island (haplotype B1) and Svalbard (haplotype A1). Haplotype A1 is also found in Norway and Russia, suggesting possible dispersal by migratory birds. This is likely because it has been demonstrated that at least 57 bird species consume large branchiopods (Dolmans *et al.* 2025).

The Notostraca are cosmopolitan crustaceans whose ecology is closely connected with ephemeral waters in warm, arid regions (Longhurst 1955). In contrast, *L. arcticus* is found in the circum-Arctic regions. Adaptation to warm, arid desert pools, which demand rapid development and reproduction, has prepared this species for another distinct environment where favourable conditions for life emerge seasonally for brief durations. Consequently, the existence in temporary arid desert pools may have equipped this notostracan species to survive in Polar desert pools, where the growth period is similarly abbreviated. Except for *L. arcticus*, *Lepidurus couessi* Packard, 1875, the closest relative to *L. arcticus* (Hessen *et al.* 2004), held the distinction of being the northernmost species among the other Notostraca in both Canada where it is found north to 50°N (Hann & Loonsberry 1991), compared to 65°N in sub-arctic Europe (Brtek & Thiery 1995).

Figure 1. The Arctic tadpole shrimp *Lepidurus arcticus* is a large (<4 cm) cold-adapted Arctic species living in freshwater lakes and ponds. Photo: Hanna-Kaisa Lakka.

In general, notostracan species are restricted to ephemeral waters without fish (Brendonck *et al.* 2008; Vanschoenwinkel *et al.* 2012). Likewise, *L. arcticus* is restricted to temporal ponds without fish in the High Arctic, but further south, in Arctic and subarctic regions, it is also frequently found in permanent lakes with fish (Sømme 1934; Qvenild *et al.* 2021). Here, *L. arcticus* was first documented as fish prey by Huitfeldt-Kaas (1911) under the name *Apus glacialis* (Braem, 1893), with several synonyms used in early 20th-century literature (Rogers 2001).

The species' ecological sensitivity is pronounced in Arctic and alpine habitats, where baseline studies are crucial for predicting global warming impacts on cold-water-adapted species like *L. arcticus*. In general, a broader knowledge and attention on large branchiopods are needed (O´Brien & Helm 2025). This paper aims to compile updated knowledge and historical records of *L. arcticus* across its extensive range, from 80°N in Svalbard to 59°N in the Fennoscandian mountains, highlighting its environmental adaptability and resilience.

MATERIAL AND METHODS

Definitions

In this paper we distinguish between *regulated* and *natural lakes,* which are simply lakes without damming. For convenience, we use the term *Lepidurus lake* to refer to a lake or pond of any size hosting *L. arcticus,* including regulated lakes. In this paper the summer period is defined as July 1st to September 15th. The Svalbard archipelago consists of Spitsbergen and the islands nearby in the High Arctic (74–81°N, 10–35°E), hereafter called *Svalbard.* In addition, the archipelago includes the outlier Bear Island in the Low Arctic. The Fennoscandian mountain range, also known as the Scandes, spans from 59°N to 70°N and 8°E to 11°E, covering roughly 1700 kilometres and featuring a diverse terrain from subarctic to alpine regions.

Description of the area

Freshwater localities in Svalbard are typically found in coastal, lowland areas below 50 m (Lakka 2013). These locations can be significantly impacted by glacier runoff, which results in high sediment loads, irregular flows, and persistently low water temperatures even during summer months (Svenning 2015). In contrast, most permanent clear-water lakes achieve higher temperatures in summer. Ice break-up generally occurs from July to late August, allowing lakes to remain ice-free for up to three months, although some may remain partially or permanently ice-covered (Svenning 2015; Lakka 2013).

The absence of a comprehensive database for lake areas in Svalbard has necessitated the use of polygons from TopoSvalbard -

Norsk Polarinstitutt (https://npolar.no), leading to estimates of roughly 300 lakes, with only 82 exceeding 1 km^2 in area. In addition, there are numerous small puddles and ponds (≤ 1 ha) that may dry out in the summer and freeze solid during the winter.

Bear Island, lacking glaciers, experiences a longer ice-free period, typically starting in late June and lasting between 2.5 and 3.5 months. Of the approximately 740 freshwater localities in Bear Island, most are shallower than five metres, with only ten lakes reaching depths between five and ten metres (Klemetsen *et al.* 1985). The deepest lake, Lake Ellasjøen, spans 0.72 km^2 and reaches a maximum depth of 34 m. The largest lake, Lake Haussvatnet, covers 1.17 km^2. The northern plateau of Bear Island is flat, mostly below 50 m, and features numerous small lakes and ponds.

The High Arctic climate is characterised by extreme variations in photoperiod, with continuous daylight long before ice break-up and high ultraviolet radiation intensity. Even before the ice begins to melt, photosynthetically active radiation penetrates through the ice, and the extent of this under-ice radiation and UV exposure is regulated by the thickness of the ice and snow cover (Belzile *et al.* 2021; Brittain *et al.* 2020). At ice break-up, the sudden improvement in light conditions in the littoral zone can create an ‘illumination shock’ (see Svenning 2015).

In Svalbard, the summer air temperature, fairly constant due to oceanic influence, has seen a notable increase of 1.41°C during the period 2000–2020 compared to the 1961–1990 norm (estimated as a mean from the meteorological stations Bear Island, Hornsund, Isfjord radio, Svalbard airport, and Ny-Ålesund) (https://seklima.met.no). Coastal areas exposed to the open ocean experience higher yearly precipitation, ranging from 402 to 529 mm, while Longyearbyen has a mean yearly precipitation of only 204 mm (mean for the period 2017–2020).

The Scandes experiences longer ice-free summers lasting from three to five months. Of the 482 recorded *Lepidurus* lakes in the Scandes, almost 50% are larger than 1 km^2, and most are relatively deep and large. Most lakes reach higher surface temperatures in summer, aligning with observed air temperatures (Qvenild *et al.* 2021). In contrast to the High Arctic, *L. arcticus* coexists with fish in 97% of these lakes. Mid-summer days are mostly illuminated even at the southernmost localities (up to 18 hours at 59°N).

Temperature data from six meteorological stations in the Scandes indicate an increase of 1.26°C above normal in the period 2000–2019 (Qvenild *et al.* 2021). The range also creates a rain shadow, resulting in higher precipitation on the western side and drier conditions on the eastern side. Annual precipitation varies from over 2800 mm on the western side to less than 400 mm on the eastern fells. The Scandes, mostly situated above the treeline, are influenced by both marine and continental climates.

Sampling of *Lepidurus arcticus*

Multiple sampling techniques, such as bottom samplers (Lakka 2020), sieves (Halvorsen 1973), artificial substrates (Fjellheim *et al.* 2007), benthic littoral kick samples (Fjellheim *et al.* 2007), traps and density samplers such as ‘peltipelle-sampler’ (Lakka 2013), have been used. Visual observing is also frequently used (Lakka 2020). However, in lakes and ponds with fish, fish stomach analyses proved to be the most effective method, particularly when *L. arcticus* was present in low numbers or exhibited a patchy distribution (Fjellheim *et al.* 2007; Qvenild & Hesthagen 2019). The timing of sampling is crucial, as the abundance of *L. arcticus* varies throughout the season (Qvenild & Hesthagen 2019). Most fish investigations occur from August to October when *L. arcticus* is more abundant. In cold summers, *L. arcticus* may appear later and might not be visible until September, if at all. Detecting *L. arcticus* can be challenging, necessitating repeated investigations. Fish predation greatly diminishes *L. arcticus* populations, making detection difficult when fish are abundant. Moreover, in Arctic conditions, repeated sampling is essential, as a large portion of the population may be dormant in the egg bank.

DISTRIBUTION

Lepidurus arcticus has a circumpolar distribution in the northern hemisphere, spanning both North America and Siberia (Rogers 2001; Hessen *et al.* 2004). The species was first described following a Siberian expedition in 1768, which included Peter Simon Pallas.

Lepidurus arcticus is found as far north as 74°N in the eastern Novaya Semlya archipelago (Veckhof 1997) and extends to the Kuril Archipelago (Sayenko & Minakawa 1999). Rasshua Island (47°N) in the middle Kuril Islands is likely the southernmost limit of *L. arcticus* in Asia. These islands experience frequent summer fog and are snow-covered for much of the year. *Lepidurus arcticus* is also common in Iceland (Scher *et al.* 2000; Eiríksson *et al.* 2021) and Greenland (Sømme 1934; Røen 1962; Jeppesen *et al.* 2001). Dated sediment remains of *L. arcticus* show that the species once had a broader range, including Denmark (Økland & Økland 2003), Ireland, Scotland, and the Isle of Man (Mitchell 1957).

Distribution in Svalbard

The initial record of *L. arcticus* in the Svalbard archipelago dates back to 1878 in Advent Bay (Richard 1878, cited in Sømme 1934). By the 1930s, it had been documented in at least 16 locations (Sømme 1934). Due to logistical challenges in Svalbard, most records from Spitsbergen come from areas near Longyearbyen and Ny-Ålesund (Figure 2), although some findings are from more remote regions. A few observations are reported from the eastern islands, including a pond in Snaddvika, Murchison Bay on Nordaustlandet (80.0°N, 18.8°E), which might be the northernmost record in Svalbard, albeit lacking an exact date and position (Sømme 1934). There is also an unspecified record from Barentsøya (Richard 1898, cited in Sømme 1934). Bennike & Hedenås (1995) found sediment remains of *L. arcticus* at four locations in Visdalen on Edgeøya in 1991.

Jørgensen & Eie (1993) studied 17 locations on the Mosselhalvøya peninsula in 1977, recording *L. arcticus* in nine fishless ponds but not in eight lakes hosting Arctic charr (*Salvelinus alpinus* Linnaeus, 1758). The ponds near Polheim (79.89°N, 16.02°E) are the northernmost properly documented localities for *L. arcticus* in Spitsbergen, though Sømme (1934) noted a nearby finding in Sorgfjorden (at Treurenberg) at almost the same latitude, which is difficult to pinpoint. In 2010, Lakka (2013) found *L. arcticus* in one of the four ponds near Polheim. Further northern observations have been made from Reinsdyrflya (79.70°N) (Sømme 1934; Lakka 2013).

Recent studies have thoroughly investigated the *Lepidurus* localities in the vicinity of Ny-Ålesund. In 2010, Lakka (2013) examined nine locations, finding *L. arcticus* in seven ponds. In 2015, Dimante-Deimantovica *et al.* (2015) studied eleven locations, with only one record of *L. arcticus* (information provided by Bjørn Walseng, pers. comm.). Calizza *et al.* (2022) investigated 18 locations, recording *L. arcticus* in nine, including three new habitats not previously studied (Dimante-Deimantovica *et al.* 2015; Lakka 2013). At least four *L. arcticus* localities (Storvatnet, Solvatnet, Tvillingvatnet, and Trehyrdingene) and two ponds without *L. arcticus* (Gluudneset and Goose Pond) were studied in all three projects

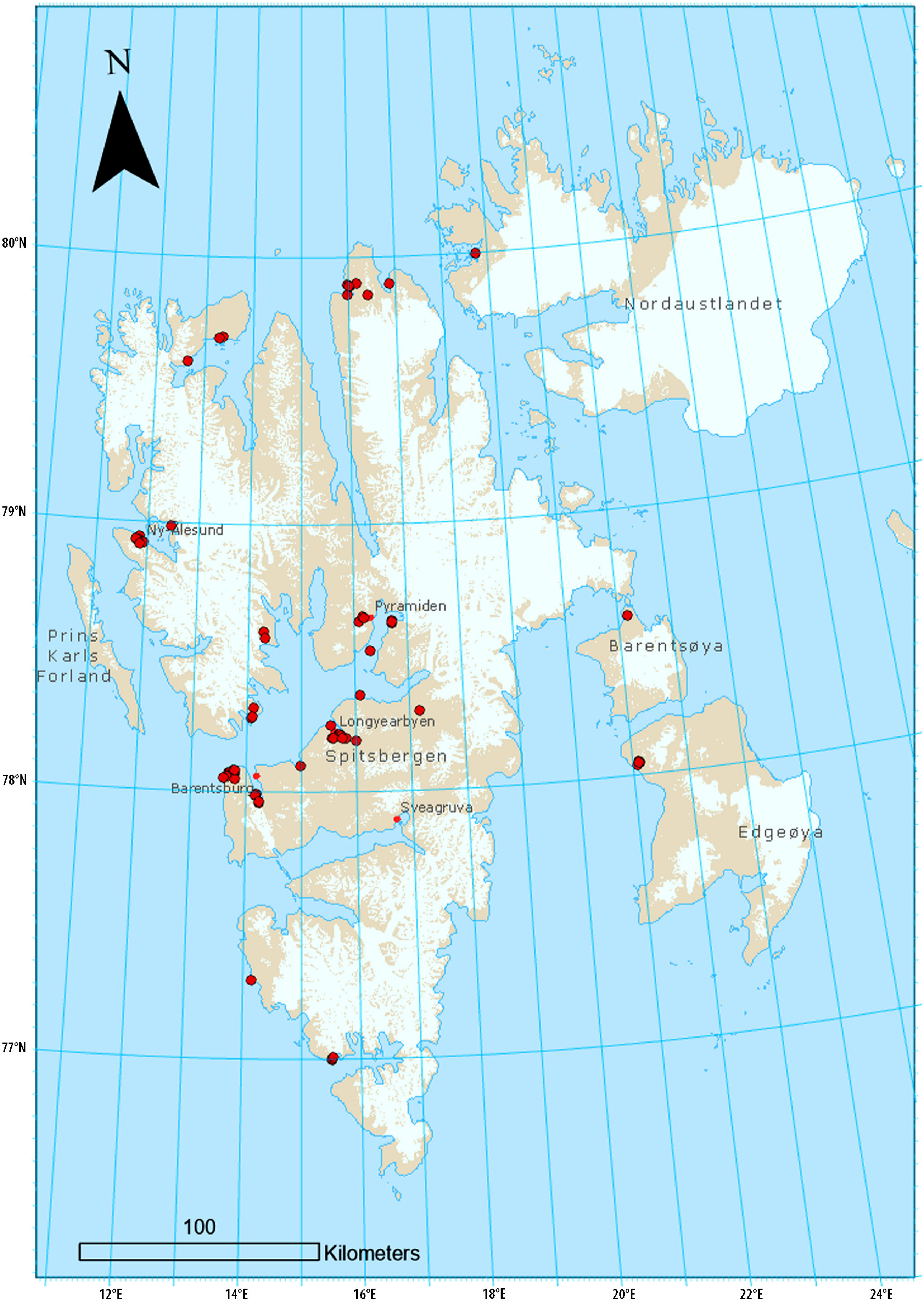

Figure 2. *Lepidurus arcticus* has been reported in 81 fishless puddles and ponds in Spitsbergen, in addition to the outlet rivers from Lake Straumsjøen and Lake Linnévatnet, which both host anadromous Arctic charr. In addition, *Lepidurus arcticus* is found in one locality at Nordaustlandet, one on Barents Island, and four localities with sediment remains on Edge Island. Norwegian Mapping Authority CC BY 4.0.

Figure 3. In Svalbard, a typical habitat for *Lepidurus arcticus* is a shallow pond. An example is this artificial pond situated near the old coal mines in Longyearbyen. The pond is dammed and gets its water from a glacier river. Photo: Hanna-Kaisa Lakka.

(Calizza *et al.* 2022; Dimante-Deimantovica *et al.* 2015; Lakka 2013). *Lepidurus arcticus* was also detected in Lake Storvatnet in 1980 (Økland & Økland 2003). Lake Solvatnet has been studied on multiple occasions, with *Lepidurus* eggs collected for laboratory experiments in 2014 and 2015 (Mancinelli & Pasquali 2016; Pasquali *et al.* 2019). Despite the lack of findings in many locations, *L. arcticus* appears to be very common in the area, with an early observation near the Conway glacier on Kongsfjorden's eastern shore (Sømme 1934).

Lepidurus arcticus has long been known from the Isfjorden area, with thorough studies by various authors. In Adventdalen, both Sars (1885–91) and Richard (1898) (cited in Sømme 1934) reported *L. arcticus* from small ponds sampled in 1878 and 1897, respectively. In 1910, Olofsson (1918) found it in a lake (Teich XXI), likely the same location investigated in 1928 by Thor (1930), which he referred to as Isdammane. Lakes and ponds in this area served as drinking water and ice supplies for Longyearbyen, later dammed into the present Isdammen in 1960. In recent years, *L. arcticus* has been sampled in many localities nearby Isdammen (Lakka 2013; Dimante-Deimantovica *et al.* 2015). A find was noted six kilometres further into the valley at 'Engelskhytta' (Thor 1930). Ponds in Longyeardalen also host *L. arcticus* (Lakka 2013), though it has not been observed annually in all city ponds since 2010 (Coulson, pers. comm.). On Diabasodden, northeast of Longyearbyen, a pond was positively investigated by both Olofsson (1918) and Dimante-Deimantovica *et al.* (2015).

Expeditions have visited both sides of the Billefjorden area. On Kapp Napier, Olofsson (1918) failed to find the species in six ponds in 1910, but positive findings were made in 1970 and 2014 (Artsdatabanken; Dimante-Deimantovica *et al.* 2015). In Mimerdalen, three well-defined lakes repeatedly examined as water supplies for Pyramiden's early settlement also yielded positive findings (Lakka 2013; Dimante-Deimantovica *et al.* 2015). In Lake Goluboye, two kilometres further into the valley, *L. arcticus* was found (Dimante-Deimantovica *et al.* 2015). Two ponds in this area also hosted *L. arcticus*.

Surveys in the outer Isfjorden area include both Ymerbukta in the north and southern banks (Colesbukta, Grønnfjorden, and Kapp Linné). No lakes with Arctic charr have yielded positive findings despite extensive stomach analyses, except for anadromous Arctic charr caught in the outlet rivers of Straumsjøen (Aas 2007; Borgstrøm *et al.* 2018) and Lake Linné (Ebne 2009). Large, shallow lakes of Flydammane on Erdmans Tundra in Ymerbukta all hosted *L. arcticus* (Olofsson 1918; Dimante-Deimantovica *et al.* 2015), as did most ponds in Randvika (Dimante-Deimantovica *et al.* 2015), Aldegondabreen (Dimante-Deimantovica *et al.* 2015), Coles Bay (Olofsson 1918), and all at Kapp Linné (Lakka 2013). Thus, *L. arcticus* seems prevalent in small, fishless water bodies in the Isfjorden area, though year-to-year variation is significant.

Further south, only three areas have been investigated. In Sveagruva, van Miejenfjorden, Olofsson (1918) found no records of *L. arcticus* in five freshwater locations. On the western coast, at Kapp Bruunodden, an old record exists (Sømme 1934). Some activity has occurred at the Polish station in Hornsund, with Janiec (1996) noting *L. arcticus* in three nearshore ponds in 1989. Genetic studies were conducted in two lakes at Fuglebergsletta by Wojtasik & Brylka-Wolk (2010), with a replicate in Fugledammen by Luoto *et al.* (2016). Wojtasik & Brylka-Wolk (2010) reported *L. arcticus* in 13 of 50 water bodies examined in Hornsund, though no further site details are provided. Thus, *L. arcticus* populations do exist in this area.

Lepidurus arcticus is commonly recorded in numerous fishless water bodies in Spitsbergen, ranging from a 6 m^2 pond in Nybyen (Lakka 2013) to the 15 ha Flydammane on Erdmans Tundra (Dimante-Deimantovica *et al.* 2015). In total, *L. arcticus* has been documented in at least 81 fishless puddles and ponds in Spitsbergen, plus one locality on Nordaustlandet, one on Barents Island, and four sediment remains sites on Edge Island. *Lepidurus arcticus* is also noted in two outlet rivers that host anadromous Arctic charr, totalling at least 89 documented localities in Svalbard.

Distribution in Bear Island

Lepidurus arcticus is frequently found in Bear Island (Klemetsen *et al.* 1985). In a survey conducted in 1998/1999, Hessen *et al.* (2004)

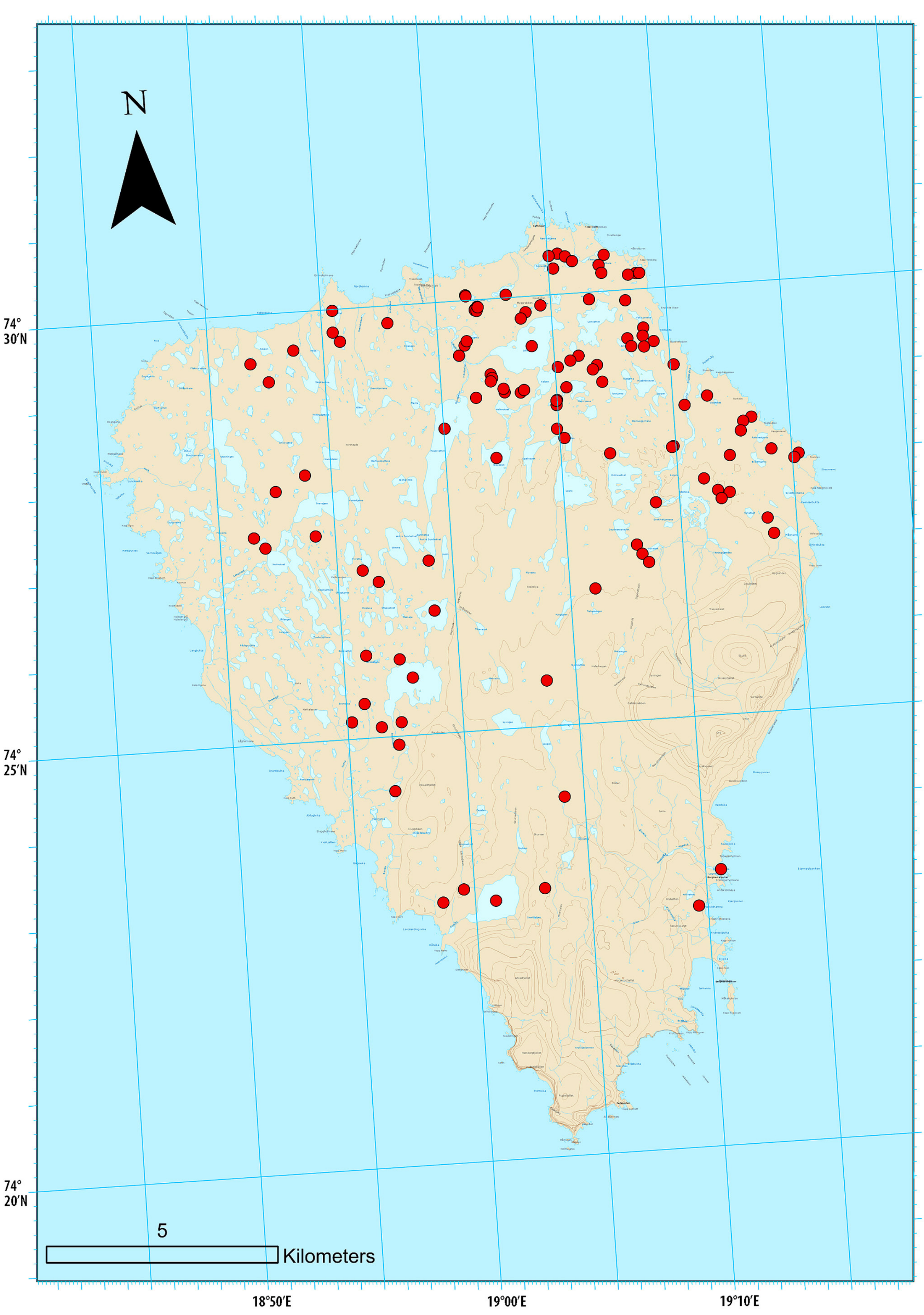

Figure 4. In Bear Island, *Lepidurus arcticus* is found in 114 localities, of which 103 are fishless ponds. At least eight of the 12 lakes that contain resident Arctic charr host *Lepidurus arcticus*. In addition, *Lepidurus arcticus* is recorded in three rivers, all with resident Arctic charr populations. Norwegian Mapping Authority, CC BY 4.0.

collected samples of *L. arcticus* from 29 ponds scattered across the island. Subsequently, in a more extensive survey of 109 ponds on the northeastern plateau, *L. arcticus* was detected in 71 (65%) of them (Klausen 2012) (coordinates provided by Sigurd Einum, pers. comm.). *Lepidurus arcticus* is abundant in three rivers – Engelskelva, Jordbruelva, and Lakselva – all of which support populations of resident Arctic charr (Klemetsen *et al.* 1985).

In Bear Island, *L. arcticus* is also present in lakes where it coexists with Arctic charr. Of the twelve lakes studied, all hosting Arctic charr, *L. arcticus* was found in eight (Klemetsen *et al.* 1985; Berg *et al.* 2010; Evenseth *et al.* 2005). Overall, *L. arcticus* is present in 114 locations: 103 fishless ponds, eight lakes, and three rivers with resident Arctic charr populations (Figure 4).

Distribution in the Scandes

The Scandes represent the southernmost limit of *L. arcticus* occurrences in Europe (Økland & Økland 2003; Qvenild *et al.* 2021). The species was first recorded in Norway by G.O. Sars during his mountain trip to Filefjell in 1863 (Sars 1864). In Sweden, an early record exists from the Sulitjelma area (Lilljeborg 1877, cited in Sømme 1934). By the early 20th century, *L. arcticus* had been reported from at least 37 localities: 29 in Norway and 8 in Sweden (Sømme 1934). The first Finnish observation was from a pond near the Halti fells in 1955 (Koli 1957). A summary of records for the Norwegian mainland was provided by Økland & Økland (2003).

A recent study from the Scandes reported *L. arcticus* in 391 natural and 88 regulated lakes, spanning latitudes from 59 to 71°N and elevations from 74 to 1524 m a.s.l (Qvenild *et al.* 2021). Norwegian localities extend further south and north than those in Sweden and Finland. On the Norwegian mainland, 315 natural lakes and 79 regulated lakes were recorded. Most Swedish records of *L. arcticus* were found in northern river systems, with 78 locations documented, including eight regulated lakes. In 2023, an additional record was made in a small pond (68.7024°N, 20.8518°E) with Arctic charr in Northern Sweden (Lakka, unpubl.). Finnish *Lepidurus* lakes in the Scandes are situated in the northwestern part of Finnish Lapland above 666 m a.s.l (Lakka 2020). Here, *L. arcticus* was found in seven localities, one of which is a regulated lake outside the Scandes (Lake Inarijärvi). Recently three more observations of *L. arcticus* are made: Lake Pitsusjärvi (69.2292°N, 21.2767°E), Lake Jápmajávri (69.1186°N, 21.4725°E), and Pond 'Luonnontutkija' (69.1598°N, 21.1606°E) (Lakka, unpubl.). In total, 686 localities hosting *L. arcticus* are known in the Scandes.

The distribution in the Scandes appears to be dichotomous, with a large northern area north of 64°N and a smaller southern 'island' south of 63°N. Southernmost records are at altitudes ranging from 489 to 1524 m a.s.l, while north of 70°N, only 11 natural lakes are located below 327 m a.s.l. In this region, mountains are low, with few reaching more than 400 m a.s.l. The altitudes of natural lakes with *L. arcticus* decline towards the north, and regulated lakes are often at lower altitudes than natural ones. Of natural *Lepidurus* lakes, 87% are situated above the treeline (Qvenild *et al.* 2021).

In contrast to Svalbard, *L. arcticus* normally coexists with fish in the Scandes. Fish status was obtained in 379 of 391 *Lepidurus* lakes (Qvenild *et al.* 2021), documenting ten fish species. Most lakes host brown trout (89%) and Arctic charr (>23%), particularly in the northern part. The invasive Eurasian minnow *Phoxinus phoxinus* (L., 1758) is now established in at least 9% of *Lepidurus* lakes. Other species include grayling *Thymallus thymallus* (L., 1758), burbot *Lota lota* (L., 1758), perch *Perca fluviatilis* L., 1758, whitefish *Coregonus lavaretus* (L., 1758), ninespine stickleback *Pungitius pungitius* (L., 1758), northern pike *Esox lucius* L., 1758, and non-native American brook trout *Salvelinus fontinalis* (Mitchill, 1814). In lake Inarijärvi, outside the Scandes, three more species are documented: salmon *Salmo salar* L., 1758, three-spine stickleback *Gasterosteus aculeatus* L., 1758, and non-native lake trout *Salvelinus namaycush* (Walbaum, 1792).

In a study of 124 natural lakes on Hardangervidda in southern Norway, *L. arcticus* was most frequently found at altitudes of 1100–1199 m a.s.l, with an occurrence rate of 80% (Qvenild & Hesthagen 2019). A thermal deficit may limit the species at high latitudes and altitudes. On Hardangervidda, the highest lake hosting *L. arcticus* is Lake Kolsnutgryslane at 1386 m a.s.l. They may exist at higher altitudes, as recorded in Lake Rygghøtjønne at 1524 m a.s.l further north (Økland & Økland 2003). Cold water also limits reproduction in Svalbard populations (Olofsson 2018; Lakka 2015).

LIFE HISTORY TRAITS

Reproduction and recruitment

For many species, there is a shift from facultative parthenogenesis in temperate regions to obligate parthenogenesis in the Arctic (Hessen *et al.* 2004). Asexuality enhances dispersal capabilities, as single eggs or individuals can establish new populations. *Lepidurus arcticus* exhibits both parthenogenesis and sexual reproduction (Wojtasik & Brylka-Wolk 2010; Lakka 2015).

Males are rarely found in studied populations. In Spitsbergen, males made up only 2.6% of the total sample (N = 789) from 19 ponds (Lakka 2015). In the six ponds where males were present, the male-to-female ratio averaged 1:16. Thus, sexual reproduction in *L. arcticus* may be more common than previously thought. Lakka (2015) documented males as far north as Reinsdyrflya (Kilneset at 79.70°N).

Selective pressures affect the sexes differently. Male fitness improves through successful mate searching, while female reproductive potential increases with larger body sizes (Lakka 2015). Smaller males searching for females face greater risks due to the increased chance of encounters with cannibalistic females. Cannibalism, a form of extreme sexual conflict, may explain the low number of males in populations. Injuries caused by birds and conspecifics, including cracks and holes in carapaces and broken cercopods, were observed in *L. arcticus* populations in Svalbard (Lakka 2013).

Maturity is determined by the carapace length when foot capsules (ovisacs) appear on the 11th pair of legs (Miller 1980). In Spitsbergen, *L. arcticus* reached maturity at 4.0 mm (range 4.0–9.1 mm) in carapace length (Lakka 2013). Temperature, growing season length, and salinity influence the size of maturing females. In other studies, females reached sexual maturity at 5.0 to 8.9 mm in carapace length (Sømme 1934; Arnold 1966; Borgstrøm 1970).

In Spitsbergen, egg size was studied in 14 populations (Lakka 2013). Sizes ranged from 0.2 to 1.1 mm, with the most common sizes being between 0.6 mm and 0.8 mm. Early in the season, small *L. arcticus* produced small to medium-sized eggs. When carapace length reached approximately 8 mm, they began producing eggs larger than 0.8 mm. Eggs sampled in some small ponds at Barrow in Alaska had a size of 0.71 mm (weight 33±0.5 µg C) (Miller 1980).

The number of developing eggs carried internally is linearly related to female length, with full-grown females (total length 25–30 mm) carrying up to 60–70 eggs in their lifetime (Miller 1980). Egg shape can be irregular before rounding inside the egg capsules (Lakka 2013). Externally, one to three eggs are carried at a time (Miller 1980), but in Svalbard, Lakka (2013) found females carrying up to

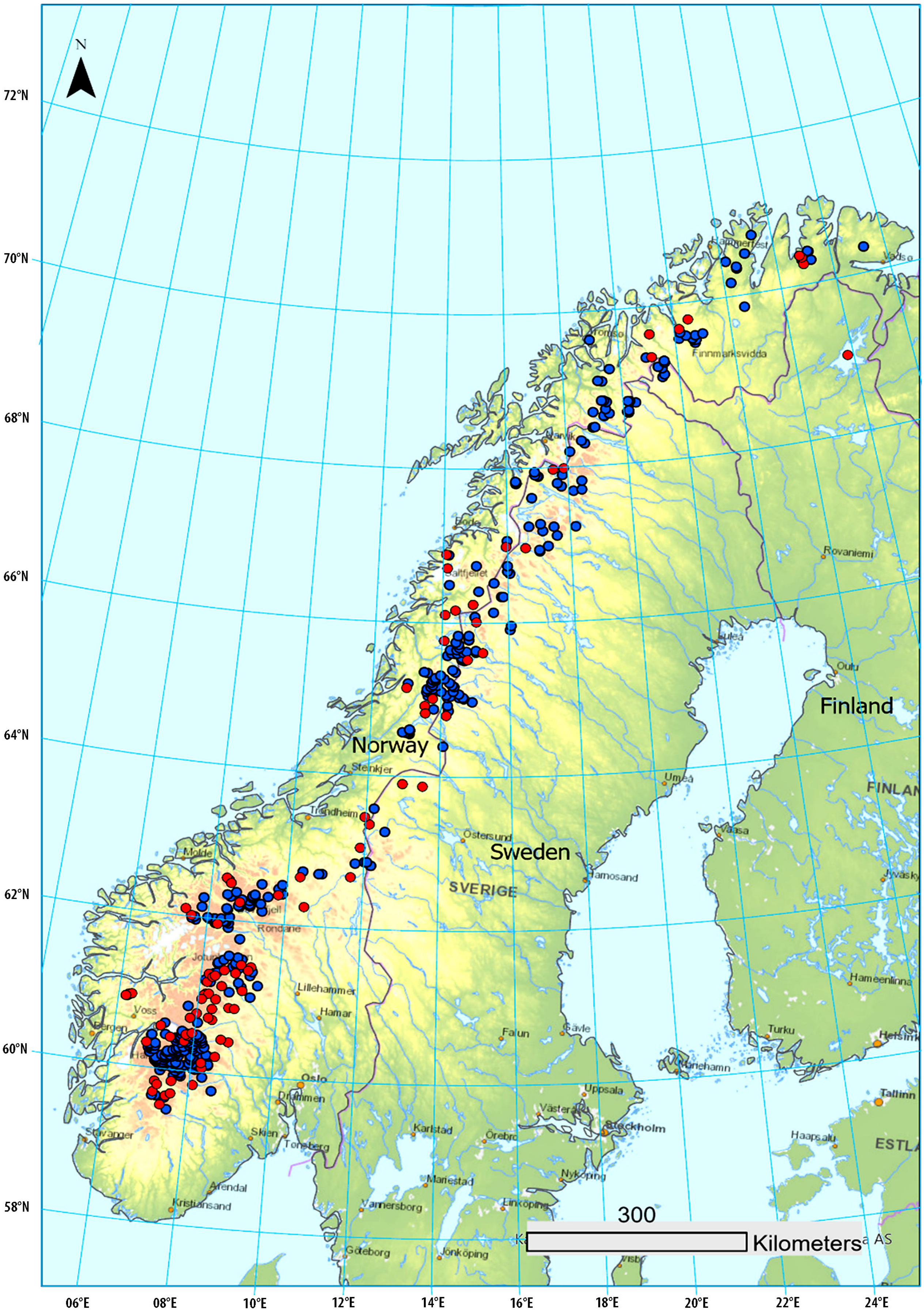

Figure 5. Distribution of 479 lakes hosting *Lepidurus arcticus* in the Scandes (Qvenild et al. 2021). Natural lakes (N = 391) are indicated by blue dots and regulated lakes (N = 88) with red dots. In addition, four new localities were recently mapped (not in the map). Norwegian Mapping Authority, CC BY 4.0.

twelve eggs. These eggs harden over a few days before release. In Spitsbergen, females mainly produced one egg when smaller than 8 mm in carapace length. On average, a single female produced 2.6 eggs (range 0–12 eggs), more than previously observed (Sømme 1934; Arnold 1966; Miller 1980; Vekhoff 1997).

Embryonic development: egg laying to hatch

Branchiopods have evolved various adaptations to endure the harsh and unpredictable conditions of both Arctic and arid temporary water bodies, which may freeze or dry out unexpectedly (Longhurst 1955). Their encysted embryos enable their progeny to survive periods of desiccation and freezing. These resting eggs, known for their remarkable longevity during dormancy, can withstand multi-year droughts, freezing temperatures, mechanical damage, oxygen deprivation, ultraviolet radiation, and digestion by predators (Rogacki & Brysiewicz 2021). When in a dry or frozen state, these eggs can remain viable for decades or even centuries without the need for rehydration (Brendonck *et al.* 2008; Hann & Lonsberry 1991).

Embryonic development within an egg capsule is affected by temperature. During this phase, embryos may enter dormancy if the cysts undergo desiccation or freezing. It is essential for any organism to receive a minimum amount of thermal input for embryonic development (Gillooly & Dodson 2000). Only a portion of the eggs hatch upon rehydration (Hann & Lonsberry 1991; Fryer 1996; Rogers 2014; Pasquali *et al.* 2019). This may be explained with egg banks containing eggs of varying ages, with embryos being at different developmental stages. Furthermore, the incomplete hatching of egg batches, even from individual females, might be an adaptation to the highly variable environments found in ephemeral water bodies (Hann & Loonsberry 1991).

Branchiopod eggs contain rhodopsin. When activated by water, this pigment reacts to light, stimulating the dormant embryo (Rogers 2014). In notostracan species, hatching is influenced by light, temperature, pH and salinity, as well as by some biotic parameters: nutrients, predators and population density (see Brendonck 1996; Schönbrunner & Eder 2006).

Branchiopods are known to produce both dormant and subitaneous embryos (Fryer 1988; Hann & Lonsberry 1991). This adaptation enables eggs to either endure dry or frozen conditions without progressing in development or to continue developing in water based on temperature (Borgstrøm & Larsson 1974).

Hatching in *L. arcticus* normally coincides with the melting of snow and ice break-up, leading to a rapid increase in water temperature followed by an illumination shock to the benthic eggs. From southern Norway, notable examples include larvae found in late June in Lake Stolsvatn (Borgstrøm 1970) and early August in Lake Litlosvatn (Simonsen & Valderhaug 1994), due to the rise in temperature and the illumination shock at ice break-up. Larvae have also been observed as late as August in newly ice-free locations on northern Hardangervidda (Halvorsen 1973).

Postembryonic phase: hatch to adult

Lepidurus arcticus hatches as a non-feeding nauplius, undergoing a virtual metamorphosis at the first moult (Fryer 1988). It hatches in the lake sediment or among vegetation and possibly does not leave the bottom since it rapidly changes to the second instar, the first larval stage found in plankton samples (Borgstrøm & Larsson 1974). The second instar swims but does not feed because its mandibles are incapable of handling food (Fryer 1988). The third instar is also pelagic, but after these three stages, the larvae become benthic,

Figure 6. On Hardangervidda, the occurrence of *Lepidurus arcticus* increased significantly with lake size. Lake Tinnhølen (1213 m a.s.l) is a large and shallow lake (4.54 km^2) with a high abundance of *Lepidurus arcticus* and a brown trout population of big-sized fish of excellent quality. Photo: Åsmund Tysse.

living on or digging in the sediments. When feeding begins at stage 3, the mechanism involved is already adult-like (Fryer 1988). Both *Lepidurus* and *Triops* have a developed carapace from the earliest free-swimming stage (Møller *et al.* 2003).

In a laboratory study by Miller (1980), growth was nearly continuous, with moults occurring every 48 to 60 hours at a constant temperature. Over the 60 days of the experiment, the animals underwent 24 to 30 moults. Adults typically eat their old cuticle after moulting (Lakka 2013).

The more southerly species of Notostraca exhibit a rapid growth rate (Longhurst 1955; Rogacki & Brysiewicz 2021). Most branchiopods need a dry period for cyst hatching and are progressively eliminated at higher latitudes where low temperatures slow embryonic development (Brtek & Thiery 1995). Species, such as *L. arcticus*, inhabiting northern ponds, have a growth rate closely linked to water temperature and utilise much of the summer months to reach sexual maturity. In Svalbard, *L. arcticus* typically matures in August (Lakka 2015). In the Scandes, adults are generally observed in late July or early August (Borgstrøm 2019; Qvenild *et al.* 2018). In this region, peak abundance is typically noted from late August to September, after which the population ceases and dies. On Hardangervidda, *L. arcticus* has been found in brown trout stomachs as late as December (Sømme, 1934).

Sars' studies (1896) documented the largest males and females from Svalbard to be 13 and 24 mm, respectively. In 2010, the mean total length of *L. arcticus* males was 11 mm in Spitsbergen (Lakka 2013). Males were generally smaller than females, but they could reach up to 27.5 mm in total length. The largest female recorded in this study measured 39.4 mm, the largest *L. arcticus* ever noted.

In a study in Lake Solvatnet in Spitsbergen, Mancinelli & Pasquali (2016) sampled adult *L. arcticus* early in August 2014. Adults with carapace lengths >4 mm were randomly selected on-site and held in the laboratory for a week. The individual dry mass averaged 4.75±0.22 mg (range 1.71–7.39 mg), corresponding to a total length of approximately 15 mm (range 9.5–18.5 mm), as estimated from TL = 0.015*DW2.12 (Miller, 1980).

DISPERSAL

Large Branchiopoda possess a remarkable ability to colonise new areas due to their dormant eggs within the egg banks (Longhurst 1955). Numerous studies have shown that branchiopod eggs are passively dispersed by mammals, birds, fish, amphibians, crayfish, insects, and wind (see Rogers 2014). When eggs are moved by predators like ducks and waders, which select similar habitats, this constitutes a 'directed' passive dispersal vector. Additionally, eggs, larvae, and adults drifting downstream can also be considered 'directed' passive dispersal, while wind acts as a 'random' passive dispersal vector.

Many branchiopods have developed the tactic of attaching their propagules to firm substrates, effectively reducing the likelihood of dispersal (Fryer 1996). This is also true in *L. arcticus* (Lakka 2013). This indicates that remaining in a favourable habitat may be more advantageous than risking the hazards of dispersal to other locations. An example of this is the slow colonisation of *L. arcticus* to newly established habitats near Aldegondabreen in Spitsbergen (Walseng *et al.* 2018).

In Svalbard, small ponds are closely linked to the nearby terrestrial landscape, which often is inundated by snowmelt and rainfall, with passive water dispersal being possible (Borgstrøm *et al.* 2018). In the Scandes, the drift of larvae from upstream lakes into a reservoir is well documented (Brabrand *et al.* 2015). Downstream dispersal of adults of *L. arcticus* from a fishless headwater pond has similarly been observed in the Tornionjoki catchment in northern Finland (Lakka, unpubl.). Consequently, the establishment of *L. arcticus* in reservoirs downstream from their natural lower limit may also result from passive drift from upstream lakes (Dahl 1932; Aass 1969).

Ponds and wetlands in Svalbard and lakes in the Scandes serve as important habitats for a diverse range of waterfowl and other bird species. At least 23 bird species are identified as potential dispersal vectors since they are frequently observed on or near water bodies (Lakka 2013, 2020; Håland 2012). Many of these birds prey on the adults, larvae and eggs of *L. arcticus*, thus serving as dispersal vectors. Water birds are more likely to travel directly between suitable habitats. Branchiopod eggs resist avian digestive enzymes, and passage through the alimentary canal can even enhance hatching (see Rogers 2014). Sticky eggs can be embedded in mud and attached to the fur of mammals or the feathers of birds (Neretina *et al.* 2020; Rogers *et al.* 2021). In Svalbard, eggs have been found at the foot of a ringed plover, *Charadrius hiaticula* Linneus, 1758 (see Lakka 2013). The distribution of similar haplotypes of *L. arcticus* across wide geographical ranges suggests high dispersal via migrating birds (Hessen *et al.* 2004). *Lepidurus arcticus* may also be actively dispersed by human stockings (Berg 1954; Aass 1969; Hesthagen 1979; Fjellheim *et al.* 2007).

PREY-PREDATION RELATIONSHIPS

Freshwater organisms play important ecosystem roles in linking terrestrial and aquatic detritus and periphytic algal production to higher trophic organisms such as fish. As an adult, *L. arcticus* is an omnivore species preying on detritus, bacteria, and different kinds of plants and algae, and it is also a predator of other crustacean species (Jeppesen *et al.* 2001), including conspecifics (Miller 1980; Lakka 2013, 2015). Evidence from a study of ten lakes on Hardangervidda conducted between 2000 and 2002, where the food web of brown trout was analysed using stable isotopes, revealed elevated δ^{15}N levels indicating *L. arcticus'* diverse diet in comparison with other invertebrates (Rognerud *et al.* 2003).

In Arctic freshwater communities, *L. arcticus* dominates in size and biomass (Klemetsen *et al.* 1985; Dimante-Deimantovica *et al.* 2015, 2018). As a predator of smaller crustaceans, it significantly impacts the planktonic food web, as demonstrated in a study of Greenland ponds and lakes (Cristoffersen 2001). However, research on 75 ponds and lakes in Svalbard showed no substantial difference in taxa numbers between locations with and without *L. arcticus* (Walseng *et al.* 2018).

Many lakes in the Scandes are renowned for their excellent fishing conditions, hosting large, high-quality brown trout (Figure 7). The abundance of crustacean food sources like *L. arcticus*, *Gammarus lacustris* G.O. Sars, 1863, and *Eurycercus lamellatus* (O.F. Müller, 1776) contributes to the brown trout's substantial growth, often reaching one to three kilos or more (Qvenild *et al.* 2021). Arctic charr also attain big-sized specimens of excellent quality in lakes with these crustaceans.

Lepidurus arcticus is highly sought for by fish. When this species is abundant, it positively influences the growth and production of the fish stocks, which are of considerable economic importance to Northern countries. In Lake Øvre Heimdalsvatn, *L. arcticus* accounted for 15% of the annual energy intake of the brown trout population (Lien 1978). Instances of heavy predation show more than 200–300 specimens in a single brown trout stomach (Aass 1969; Borgstrøm 1970). Lake Sylvetjønne, located at high altitude in the

Figure 7. A rich supply of crustacean food items such as *Lepidurus arcticus* and *Gammarus lacustris* is regarded as the main reason for big-sized brown trout of several kilos in many mountain lakes in the Scandes. Photo: Tore Qvenild.

Jotunheimen mountains, demonstrated remarkable yields of brown trout, primarily based on a diet of *L. arcticus* and *G. lacustris*, with total yields reaching 13 kg per hectare in 1941–1942 and individual specimens weighing up to 10–12 kg (Hesthagen 2005).

Brown trout selectively prey on *L. arcticus*, with its significance as a food source increasing with the size of the fish (Qvenild & Hesthagen 2020). Conversely, an overstocking of juvenile brown trout can negatively affect *L. arcticus* populations. For example, in Lake Vesle Øljusjø, excessive stocking led to the species' near-extinction, although it reappeared in brown trout diets after a decade without stocking (Aass 1969). In a comprehensive dietary analysis of brown trout populations across five lakes on Hardangervidda, the exceptionally strong 1997 year-class nearly eliminated *L. arcticus* and *G. lacustris* (Qvenild & Hesthagen 2020). The crustacean populations recovered once the brown trout numbers returned to normal levels. The absence of *L. arcticus* in High Arctic lakes is frequently attributed to the presence of Arctic charr, which is the only fish species present (Jeppesen *et al.* 2001; Presthus Heggen *et al.* 2010; Borgstrøm *et al.* 2018).

In the Scandes, the invasive Eurasian minnow has populated many lakes and reservoirs since the 1960s, thriving in habitats up to 1400 m a.s.l (Museth *et al.* 2007). As opportunistic foragers, minnows introduced to high-altitude lakes have been linked to reduced availability of brown trout prey (Museth *et al.* 2007; Borgstrøm *et al.* 2010). In Lake Øvre Heimdalsvatn, minnows appeared in 1969, leading to significant changes in the brown trout diet during the summer months between 1970–1972 and 1993–2005 (Lien 1978; Borgstrøm *et al.* 2010). Here, the Eurasian minnow has severely reduced *L. arcticus* populations, causing its virtual disappearance from the brown trout diet.

On Hardangervidda, the Eurasian minnow was first observed in Lake Ørteren in 1973 and has since spread to at least 42 lakes in the northeastern plateau (Qvenild & Hesthagen 2019). The expansion continued westward, eventually reaching the headwater lakes in the tributary Sevra in the Lågen catchment. Numerous lakes in the neighbouring catchments, where both *L. arcticus* and *G. lucustris* are staple food organisms for brown trout, are easily accessible from the flat terrain near Stigstuv. In August 1999, a rotenone treatment was carried out, followed by another in September 2000, effectively eradicating the minnows. This action also caused immediate mortality within the invertebrate community (Fjellheim 2004). Remarkably, the diversity was almost completely restored within just one year.

Lake Skjerja, formerly a prominent brown trout lake, experienced drastic declines in brown trout yield due to intense exploitation and subsequent minnow invasion, leading to a reduction in annual catches to only 32% of the initial values (Qvenild *et al.* 2024). Despite fishing efforts to control minnows, the competition for food has negatively impacted brown trout production. In Lake Skjerja, the two crustacean species, *G. lacustris* and *L. arcticus*, were the basic food items. Fishing with baited traps on the minnows and the presence of a large fraction of predatory brown trout feeding on minnows have reduced the predation pressure on these two crustacean species, and they are still a part of the brown trout diet. In contrast, *L. arcticus* and *G. lacustris* no longer seem to be important in the brown trout diet in the nearby Lake Skaupsjøen, where no systematic reduction of Eurasian minnow is performed (Borgstrøm 2009).

The balance of fish predation on *L. arcticus* is mainly determined by the abundance of fish and the availability of suitable refuges for the prey. Unlike other notostracan species that grow rapidly in temporary water bodies before they dry out or encounter increased predation (Longhurst 1955), this strategy is unfeasible in the High Arctic's permanent lakes, which are often inhabited by stunted populations of Arctic charr dwarfs (Jeppesen *et al.* 2001). In these cold environments with clear water, the growth and development of *L. arcticus* are slow, making them particularly vulnerable to fish predation. Fish density also acts as a limiting factor in the permanent lakes of Bear Island and the Scandes. Nevertheless, in lakes where optimal refuges are accessible and fish abundance is low, *L. arcticus* can thrive. Thus, *L. arcticus'* adaptability to various habitats seems to be broader compared to other notostracan species. Studies conducted on Hardangervidda and Northern Finland indicated a higher occurrence rate of *L. arcticus* populations in larger lakes with better access to refuges (Qvenild & Hesthagen 2019; Lakka 2021). Larger lakes also are generally colder than smaller ones.

Birds are significant predators of *L. arcticus*. In Spitsbergen and Bear Island, species such as the purple sandpiper *Calidris maritima* Brünnich, 1764, the dunlin *Calidris alpine* (Linneus, 1758), and the arctic tern *Sterna paradisaea* Pontoppidan, 1763, frequently prey on *L. arcticus* in the shallow tundra ponds (Summerhayes & Elton 1923; Lakka 2015). When faced with these avian predators, *L. arcticus* exhibit behavioural adaptations (Lakka 2013). Observations in a pond with a dense *L. arcticus* population in Kapp Linné in Svalbard revealed that *L. arcticus* sought the shallowest areas when a red phalarope, *Phalaropus fulicarius* (Linneus, 1758), visited. The shallow and muddy waters (5–15 cm deep) hindered the red phalarope from performing its typical hunting behaviour of swimming in circles. The variations in the colour morphs of *L. arcticus* are believed to be an adaptation to avoid bird predation in addition to harmful UV radiation (Lakka 2013).

In Lake Langavatnet on Hardangervidda, sea ducks, such as the black scoter *Melanitta n. nigra* (Linneus, 1758), have declined comparatively with the increase in brown trout abundance, which likely is a result of increased competition for their common food item, *L. arcticus* (Håland 2012). Simultaneously, piscivorous waterbird species like the Goosander (*Mergus merganser* Linnaeus, 1758), Red-breasted Merganser (*Mergus serrator* Linnaeus, 1758), Great Cormorant (*Phalacrocorax carbo* Linnaeus, 1758) and Black-throated Diver (*Gavia arctica* Linnaeus, 1758) grazing on the enhanced numbers of small brown trout increased.

ENVIRONMENTAL CONDITIONS

Lepidurus arcticus has demonstrated a remarkable ability to withstand significant environmental changes in the harsh alpine and Arctic environments since its emergence. Despite this, the species exhibits considerable sensitivity at various stages of its life cycle to numerous environmental stressors.

Critical temperatures and thermal thresholds

Temperature is a key environmental factor controlling the distribution of ectotherm species, including branchiopods. Typically, *Triops* species are more warmth demanding than *Lepidurus* (Fryer 1988). The cold-adapted *L. arcticus* can withstand water temperatures ranging from 1.8°C (Lakka 2013) to 19°C (Arnold 1966). Although *L. arcticus* can endure temperatures above 20°C for brief periods (Borgstrøm 2019), it is crucial that temperatures do not remain above 16.5°C (Lakka 2020). The ideal temperature for adult *L. arcticus* is around 10°C (Lakka 2013). In the Arctic, this optimal thermal condition is met for only short-duration periods, but it is more commonly encountered in Scandes lakes.

Every species has an optimal temperature range for hatching efficiency. In a laboratory experiment in Svalbard, the highest hatching rate for *L. arcticus* was noted at 10°C (Pasquali *et al.* 2019). There was no hatching observed at 15°C and 25°C, likely because these temperatures surpassed the eggs' physiological tolerance limits. Comparatively, the optimal hatching temperature of the more southerly distributed *L. couessi* was found to be 20°C (Hann & Loonsberry 1991). On the other hand, the more adaptable species, *T. cancriformis*, exhibited hatching within a broader range of 16–32°C, with an optimal range of 22–32°C (Kuller & Gasith 1996).

Elevated temperatures above 15°C during the juvenile phase negatively impact survival (Pasquali *et al.* 2019). Abrupt changes in water temperature during the initial hatching phase, following ice break-up, can frequently occur. For instance, Lake Øvre Heimdalsvatn experienced a rise in water temperature from 4 to 14°C within just ten days in 2018 (Sildre, https://sildre.nve.no). These temperature shocks are especially likely in small, shallow lakes and ponds, particularly in the Scandes region. During the moult stage, *L. arcticus* is also highly vulnerable (Thiéry 1997).

Warm, oxygen-poor water can trigger an 'oxygen search behaviour', where an adult swims to the surface, collects a small air bubble between their legs, and then swims back to the bottom (Lakka 2013). This behaviour exposes *L. arcticus* to predators such as birds and fish.

The lower thermal threshold

The time required for an organism to complete its life cycle can be measured in thermal units, known as degree-days. Laboratory experiments conducted with *L. arcticus* eggs collected in the autumn from lakes in southern Norway (Borgstrøm & Larsson 1974) and northern Finland (Lakka, unpubl.) suggest that a cumulative thermal energy of between 400 and 500 degree-days is necessary for the embryonic development to complete once the eggs are submerged in water. Fryer (1988) also noted that *L. arcticus* eggs could hatch without undergoing a drying or freezing period.

In dry or frozen conditions, embryonic development is halted. For example, the shallow Lake Solvatnet in Spitsbergen freezes solid during winter (Pasquali *et al.* 2019). Eggs collected after the ice melted and incubated at temperatures of 5.0°C and 10.0°C began hatching after 15 and 7 days, respectively. Thus, eggs incubated at 5.0°C in Lake Solvatnet hatched more quickly than those kept constantly wet (Borgstrøm & Larsson 1974). This indicates that part of the embryonic development must have occurred during the previous summer or earlier. Only 64% of the eggs in the Lake Solvatnet experiment hatched, highlighting the importance of the egg bank as a buffer against variable environmental conditions (Hann & Lonsberry 1991; Brendonck 1996).

Lepidurus arcticus can tolerate very low temperatures close to freezing. However, a minimum thermal input is essential for the organism to develop into adults. In a study of six lakes on Hardangervidda, no adult *L. arcticus* was found in brown trout stomachs until approximately 400 degree-days were achieved (Qvenild *et al.* 2018). This equates to a mean summer temperature of at least 5°C from July 1st to September 15th. In the High Arctic, only ponds tend to be warm enough to support *L. arcticus* (Nowiński & Wiśniewska-Wojtasik 2006; Lakka 2013) in at least some seasons, enabling the establishment of an egg bank. After hatching, the postembryonic phase must be completed, and new eggs laid before freezing. In particularly cold environments, females seem unable to produce eggs (Olofsson 1918; Lakka 2015), thus restricting their altitudinal and latitudinal range. The heat sum required may vary in different climatic regions since adaptation to colder habitats is likely, as is revealed in Arctic charr (Koops & Tallman 2004; Jeuthe *et al.* 2016). However, information is lacking for *L. arcticus*.

Late ice break-up and low water temperatures during a short growing season can significantly impede the growth and development of *L. arcticus*. This has been documented over several years on Hardangervidda (Halvorsen 1973; Pedersen & Scobie 1990; Simonsen & Valderhaug 1994; Borgstrøm 2016; Qvenild *et al.* 2018) and in ponds in Svalbard (Lakka 2013). *Lepidurus arcticus* was found to be smaller in colder ponds near glaciers compared to warmer ponds closer to the sea (Lakka 2013). In many ponds studied by Olofsson (1918), *L. arcticus* appeared to be absent, likely due to excessively low temperatures.

The upper thermal threshold

The lower altitude boundary for lakes containing *L. arcticus* in the Scandes signifies that beyond a certain thermal threshold, the conditions become unfavourable. Most *Lepidurus* lakes remain at mean air temperatures below the 10°C isotherm (Qvenild *et al.* 2021). This explains why the distribution appears to be dichotomous in the Scandes, splitting into northern and southern zones. The intermediate region is generally too warm to support *L. arcticus* populations. In the northernmost area, reaching up to 70°N, the 10°C isotherm falls below 250 m a.s.l, with few lakes situated above 300 metres in this region. Consequently, the likelihood of discovering new *L. arcticus* populations is minimal.

Few *Lepidurus* lakes have a mean lake air temperature higher than 11°C in summer (Qvenild *et al.* 2021). Lakes with lake air temperatures at this level tend to have mean summer water temperatures close to 14°C. Hence, the upper thermal threshold for *Lepidurus* lakes was assumed to be close to this level. Excessive accumulation of thermal energy during the initial embryonic phase can lead to life cycle mismatches, resulting in eggs hatching too early under completely dark conditions of winter.

In the Scandes, *L. arcticus* is rarely found in ponds, although it does occur (Berg 1954; Koli 1957; Halvorsen 1973; Hesthagen 1979; Blomkvist 1995; Walseng *et al.* 1996). Most small lakes and ponds have environmental conditions that are often too unstable for sustained survival. Fluctuating temperatures and acidic waters have adversely impacted these habitats (Blomkvist 1995; Fjellheim *et al.* 2002; Lakka 2013, 2020). *Lepidurus arcticus* populations are more commonly found in larger lakes where there is better access to refuges and colder water (Qvenild & Hesthagen 2019; Lakka 2021). Moreover, deeper lakes allow *L. arcticus* to evade warm surface layers by migrating to cooler depths.

Further north, including Bear Island and Spitsbergen, the species predominantly inhabits coastal zones (Klemetsen *et al.* 1985; Lakka 2013). In these northern islands, the mean air temperature during summer typically does not exceed 5°C, ensuring that elevated temperatures do not limit its distribution.

Water quality

Acid waters low in calcium

In addition to temperature, water quality plays a crucial role in determining distribution. These conditions are likely to interact with one another, as evidenced in *T. cancriformis* (Schönbrunner & Eder 2006). In a study on Hardangervidda, the absence of *L. arcticus* in the western region was attributed to low water temperature, a short growing season, and water that was low in pH and calcium (Qvenild & Hesthagen 2019).

The melting snow in spring usually leads to a drop in pH levels during ice break-up in Arctic and alpine lakes (Fjellheim *et al.* 2002; Lakka 2020), which can be detrimental or even lethal for *L. arcticus* larvae, as shown in a laboratory study by Borgstrøm & Hendrey (1976). Hence, the juvenile phase is crucial in evaluating extinction risks. For crustaceans, rapid calcification of their exoskeleton immediately after moulting is essential, but this process can be hampered in regions with low calcium levels and poor water quality (Rukke 2002). This problem is further exacerbated by low pH levels, which normally interfere with low calcium concentrations.

Multiple studies have shown that *L. arcticus* does not inhabit water bodies with pH levels below 6.1 (Borgstrøm & Larsson 1974; Borgstrøm & Hendrey 1976; Fjellheim *et al.* 2007; Lakka 2013). However, a recent analysis of 95 lakes on Hardangervidda, which host *L. arcticus*, revealed that pH levels ranged from 5.49 to 7.26, and calcium levels varied between 0.28 and 5.54 mg/L^{-1} (Qvenild & Hesthagen 2019). Ten of these lakes had pH levels under 6.0 and calcium levels below 0.84 mg/L^{-1}, conditions which are thought to be critical for *L. arcticus*. The two lakes with the lowest calcium levels, Lake Svartavasstjørni and Svartavatnet, have been monitored each year. In 1993–1994, the pH was approximately 5.5, and the calcium level was approximately 0.4 mg/L^{-1} (Tysse *et al.* 2022). An annual liming programme began in 1994, and the lost *L. arcticus* population was restocked over three consecutive years (1997–1999) (Fjellheim *et al.* 2007). The species has been observed nearly every year since then, despite the liming programme ending in 2013. Calcium levels have stabilised between 0.5 and 1.0 mg/L^{-1}, and pH values have been close to 6.0. Therefore, *L. arcticus* can survive in waters with calcium levels at approximately 0.5 mg/L^{-1} and low pH values near 6.0. Proximity to refugia with better water quality is crucial for mitigating harmful pH fluctuations (see Fjellheim *et al.* 2007), as close to non-lethal conditions may inadvertently impact functional traits like growth and reproduction.

Previous studies have indicated that *L. arcticus* likely became extinct in multiple regions, such as Finland (see Lakka 2020) and Northern Sweden (Lingdell & Engblom 2002). Recent research on the ponds examined by Koli (1957) suggests that the population has become extinct due to acidification (Lakka 2020). In the southernmost regions of the Scandes, specifically Setesdalsheiene, numerous populations of *L. arcticus* may have similarly faced decline and eventual extinction following the disappearance of brown trout populations observed in the mid-1880s (Enge *et al.* 2017).

Humic waters

The concentration of total organic carbon (TOC mg L^{-1}) in humic waters is an indicator of the runoff of external organic matter from surrounding areas. In shallow inland water bodies, carbon can accumulate at the bed of lakes or ponds, influencing the carbon flux. For lakes with clear water in the Scandes, TOC levels are typically low. On Hardangervidda, the TOC in nearly all *Lepidurus* lakes was less than 2.0 mg C L^{-1} (Qvenild & Hesthagen 2019). Research conducted by Lakka (2013) in Svalbard in 19 ponds revealed TOC levels ranging between 0.9 and 52.0 mg L^{-1}. Despite these conditions, thriving populations of *L. arcticus* were observed, demonstrating the species' tolerance to elevated TOC concentrations, at least temporarily.

Salinity

The hatching of many notostracan species is influenced by various environmental factors, including salinity (Brendonck 1996; Schönbrunner & Eder 2006). The salinity levels in water bodies where *L. arcticus* resides are typically very low. Salinity can exceed 30‰ in coastal regions of the Barents Sea. Research from Spitsbergen has shown that *L. arcticus* flourishes in ponds with salinities reaching up to 1.5‰ (Lakka 2013). Slightly saline water has been found to promote the growth of *L. arcticus*, an adaptation likely linked to survival in temporary ponds where salinity increases as they dry up. In these environments, *L. arcticus* must efficiently produce eggs before the pond desiccates. This assertion is backed by two observations from Lakka (2013). Firstly, faster growth to a larger size enhances reproductive success in *L. arcticus*, as larger individuals can produce more and bigger eggs. A low salt concentration (1‰) was found to significantly accelerate the second moulting process. Secondly, smaller individuals began producing more eggs in slightly saline temporary ponds compared to permanent ones. Arctic lowlands near the sea and river systems are generally former seabeds where sea spray is prevalent. This is also true for Svalbard, where populations of *L. arcticus* are located near the sea (Lakka 2013). The salinity tolerance of *L. arcticus* may have evolved in coastal seabed habitats where the primary water source was melting snow and glacier ice, with permafrost keeping pond bottom soil activity minimal.

Lepidurus arcticus in regulated lakes

In the Scandes, *L. arcticus* is frequently observed in regulated lakes. Out of 483 locations where *L. arcticus* is present, 88 are hydropower reservoirs, of which 25 are regulated more than 20 m, sometimes even 125 m (Qvenild *et al.* 2021). These reservoirs present highly variable environmental conditions that are often detrimental to many freshwater organisms. However, *L. arcticus* and another Branchiopoda, the Cladocera *Eurycercus lamellatus*, typically show an increase in abundance (Dahl 1933; Huitfeldt-Kaas 1935; Aass 1969). This is likely due to their drought- and freeze-resistant eggs, which may stay dormant in the dry drawdown zone.

The relative significance of these two species as food for brown trout was illustrated in the reservoir Lake Aursjøen in the Reinheimen area (Hesthagen 2018; Lakka *et al.* 2020). During the period 1985–1989, *L. arcticus* dominated in the brown trout diet. Following a change in the regulation regime, the abundance of *L. arcticus* collapsed. The reason remains largely unknown, but both climate- and hydropower-driven changes may be important. The alternative food source, *E. lamellatus*, did not appear to adequately compensate for the caloric deficit resulting from the decreased consumption of the larger *L. arcticus*. This likely contributed to the observed decline in the condition, growth, and delayed maturation of the brown trout.

The temperature of the water significantly affects the altitudinal distribution of *L. arcticus*, also in reservoirs (Qvenild *et al.* 2021). This was initially demonstrated through the impoundment history of Lake Pålsbufjorden in the Lågen catchment (Dahl 1932). This catchment drains numerous *Lepidurus* lakes located in the eastern fells of Hardangervidda. *Lepidurus arcticus* was not previously recorded in this downstream lake, but just a few years after the impoundment, it became established in the new reservoir. Dahl (1932) explained this phenomenon by the cooling of the drawdown zone, leading to an 'arctification' of the lake. Specifically, the 'arctification' might be attributed to the halted embryo development in the dry drawdown zone, which accumulates fewer degree-days than in the wetter zone below. This allowed *L. arcticus* to flourish in Lake Pålsbufjorden, a habitat that was initially too warm for this species. Comparable altitudinal shifts of *L. arcticus* have been observed in other lakes following the establishment of hydropower reservoirs (Aass 1969; Brabrand & Saltveit 1980).

The reproductive success of *L. arcticus* in regulated lakes is heavily influenced by the timing of reservoir refilling. In Lake Mårvatn on eastern Hardangervidda, increased lowering of the water level during the winter of 1969/70 without subsequent refilling resulted in poor condition and low brown trout catches (Borgstrøm 1973). In preceding years, *L. arcticus* was the main food source, but it almost disappeared from the diet in 1970 and 1971, likely because the eggs remained dormant in the dry drawdown zone. Moreover, siltation resulting from erosion adversely affected the production of algae, which serves as the primary food for *L. arcticus* larvae. During 2009–2010, Lake Mårvatn was again permanently lowered, resulting in a similar outcome (Rognerud & Fjeld 2014). Proper management practices are thus crucial to maintaining healthy populations of *L. arcticus* and supporting the ecosystems that depend on them.

In some reservoirs, the introduction of new fish species has caused *L. arcticus* to become a less significant food source. For instance, in Lake Stolsvatn in the Hallingdal mountains, *L. arcticus* was a primary food item for brown trout before the Eurasian minnow was introduced (Borgstrøm *et al.* 1985). The eggs, which are reddish or orange, are typically deposited in the littoral zone, and the sticky eggs are firmly glued to the bottom substrate. Upon hatching, the larvae are highly visible and exposed to predation from the schooling minnows. After several years, adult *L. arcticus* no longer constituted a significant part of the brown trout diet. Minnows did not replace *L. arcticus* in the diet, indicating that new fish species can cause increased food competition and diminish brown trout yields. Similar adverse effects have been observed in other hydropower reservoirs such as Lake Halnefjorden on Hardangervidda (Lehmann *et al.* 2008) and Lake Kaldfjorden in the eastern fells of Jotunheimen (Hesthagen 2022). In Lake Kaldfjorden, Eurasian minnow and whitefish were introduced in the 1970s, resulting in *L. arcticus* being excluded from the brown trout diet. The disappearance of *L. arcticus* in the fish diet may serve as an indicator of an impending decline in a fish population.

In some reservoirs, the Eurasian minnow seems to be less harmfull. Lake Vinsteren in Jotunheimen was impounded in the 1940s, and *L. arcticus* was the predominant food item for brown trout (Aass 1969). After the Eurasian minnow was introduced in the 1980s, the abundance of *L. arcticus* has differed. However, there has been no significant decrease in brown trout yield, likely because the minnows are more exposed to brown trout predation, given the absence of refuges in the drawdown zone (Hesthagen & Gran 2019).

CLIMATE CHANGE

Few regions on Earth have experienced more dramatic climate changes than the High Arctic, a trend that is projected to continue unabated. Over the last thirty years, temperatures in Svalbard have increased by at least 2°C above the 1961–1990 normal (Hanssen-Bauer *et al.* 2019). Of particular interest in this context is the rise in summer temperatures. In the Svalbard archipelago, data from five meteorological stations reveal that the summer air temperature has increased by 1.41°C in the first two decades of this century compared to the normal period (July 1st to September 15th). Similar data from six meteorological stations in the Scandes show a concurrent increase of 1.26°C, suggesting significant changes in summer temperatures in both Arctic and Alpine regions.

The Svalbard archipelago

The diversity of freshwater organisms in the still waters of Svalbard is notably low, even when compared to other High Arctic regions (Coulson *et al.* 2014). Climate change is causing glaciers to retreat, leading to the formation of new, untouched freshwater ecosystems. This rapid warming and lengthening of growing seasons may influence biodiversity and dispersal patterns, potentially attracting more warmth-demanding species. Currently, there are 31 documented crustacean species on the Svalbard archipelago, with at least seven being recent arrivals (Dimante-Deimantovica *et al.* 2018). This represents an increase of over 20% in the total number of known species on the island.

As water bodies warm, *L. arcticus* may extend its range into the colder regions of Svalbard, including new inland ice-free areas, and become more prevalent on the colder islands, such as Nordaustlandet and other eastern islands. Dry sediments in temporary ponds are susceptible to wind dispersal. Increased bird activity due to warming affects ponds and lakes (Walseng *et al.* 2018), and birds preying on *L. arcticus* may aid in egg dispersal. The eggs can adhere to fur and are resistant to avian digestive enzymes (see Rogers 2014). Similar haplotypes over large areas suggest significant bird-mediated dispersal (Hessen *et al.* 2004).

The distribution of freshwater fauna along a gradient from the glacier edge at Aldegondabreen in Grønfjorden to the coastline probably mirrors the colonisation history from the last 80 years of melting in Svalbard (Walseng *et al.* 2018). This study found *L. arcticus* in six of the 22 surveyed sites, all located in ‘older’ water ecosystems near the shoreline (Bjørn Walseng, pers. comm.). So far, these findings suggest a relatively low dispersal rate of *L. arcticus* over a short period.

Currently, *L. arcticus* exists below its optimal temperature in Spitsbergen and could thus benefit from warmer summer temperatures and prolonged growing seasons. Consequently, in the clear-water ponds in Spitsbergen, *L. arcticus* may experience accelerated growth and development. Notably, the size of *L. arcticus* has significantly increased since Sars’ studies in 1896 (Lakka 2013). The clear-water lakes may warm considerably and resemble those in Bear Island, potentially leading to coexistence with Arctic charr. Lakes such as Straumsjøen and Nordre Borgdam may reach temperatures conducive to developing such populations.

The Scandes

Sediment remains of *L. arcticus* indicate that it once had a much broader distribution across Europe (see Økland & Økland 2003), suggesting a later recolonisation of colder lakes formed its current presence in the Scandes.

In the Scandes, *L. arcticus* mainly inhabits the alpine zone, with 87% of its lakes located above the treeline (Qvenild *et al.* 2021). The early Holocene warm period (7800–7600 BP) serves as an early indicator of potential increased precipitation linked to ongoing greenhouse warming (Dahl & Nesje 1996). During this time, a notable rise in the treeline occurred, which could have resulted in a considerable range retraction if *L. arcticus* followed this treeline extension. Thus, prolonged warm periods might pose significant challenges for *L. arcticus* in the Scandes, which is the southernmost edge of its range in Europe. A retraction from the lower part of its distribution is documented for another cold-water adapted branchiopod, *Branchinecta palludosa* (O.F. Müller, 1788) (Lindholm *et* *al.* 2015). In the southern Scandes, *L. arcticus* extends its distribution slightly above 1500 m a.s.l. In a warmer climate, *L. arcticus* might potentially thrive some hundred metres higher than this.

Baseline studies and ongoing monitoring programmes are urgently needed (Qvenild 2022). The only long-term programme in the Scandes, involving repeated monitoring of environmental conditions and biota, is at Lake Øvre Heimdalsvatn (Brittain *et al.* 2019). Since 1993, *L. arcticus* has virtually been absent from the brown trout diet in this lake. Predation from brown trout and Eurasian minnow poses a significant risk to *L. arcticus*, compounded by notable warming since 1985 (Sildre, https://sildre.nve.no). The average summer temperature has nearly reached 14°C, a critical threshold (Qvenild *et al.* 2021). Consequently, further warming could be detrimental to *L. arcticus* in this lake. Updated surveys in *Lepidurus* lakes with observations older than ten years would be invaluable and might reveal extinct populations, particularly in the lowermost lakes.

Lepidurus arcticus as an indicator species

While *L. arcticus* is relatively common in Norway, and in national Red List assessments it has been assessed to *Near Threatened* in Sweden and *Endangered* in Finland. *Lepidurus arcticus* is vulnerable to acid precipitation, fish predation and the ongoing global warming, which all may lead to habitat reduction and range retraction, making *L. arcticus* a valuable indicator species.

The significance of this charismatic species has been acknowledged and included in the conservation guidelines for freshwater ecosystems (Lakka 2020). The Nordic countries have committed to the Kunming-Montreal Global Biodiversity Framework (CBD 2022), which sets a goal of conserving 30% of inland waters by 2030. As a result, Arctic nations have a unique obligation to protect genuine Arctic species and their habitats.

CONCLUDING REMARKS

1. The Notostraca are cosmopolitan crustaceans whose ecology is closely connected with ephemeral waters in arid regions. In contrast, *L. arcticus* is the only species found in the Arctic regions. Adaptation to warm, arid desert pools, which demand rapid development and reproduction, has prepared this species to survive in polar desert pools, where the growth period is similarly abbreviated.
2. The upper altitudinal and northern range of *L. arcticus* is constrained by low temperatures, while its lower altitudinal and southern range is restricted by elevated temperatures. Additionally, *L. arcticus* is sensitive to acidic water. These environmental sensitivities account for the distribution pattern observed across the large-scale gradient from 80°N to 59°N.
3. In some instances, *L. arcticus* has successfully established in lakes that were originally too warm for the species, following lake regulation—a process known as ‘arctification’. This occurrence may be attributed to the arrested development of embryos in the dry drawdown zone, which experiences fewer cumulative degree-days compared to embryos in the wetted zone below.
4. Most notostracan species, including *L. arcticus* in Svalbard, inhabit fishless ponds. Permanent lakes are usually too cold and pose high risks of predation. However, in the slightly warmer lakes in Bear Island, *L. arcticus* coexists with Arctic charr and is also present in many fishless ponds. In the Scandes, it primarily inhabits lakes with fish where the temperature conditions are relatively stable. This appears to demonstrate a wider adaptability to various habitats compared to other notostracan species.
5. The High Arctic has experienced significant climate change over the last decades. Summer temperatures since 2000 have increased by approximately 1.4°C, and a similar trend is observed in Alpine regions of the Scandes.
6. Climate change is expected to have significant impacts on the distribution of *L. arcticus*. With rising temperatures, it is likely that *L. arcticus* will extend its range into the colder territories of Svalbard, including new inland ice-free areas, and become more prevalent on the colder northern and eastern islands. In the Scandes, situated at the southernmost boundary of its European habitat, prolonged periods of warmth could create a range retraction from the lowermost parts and an altitudinal expansion of its current distribution.
7. The extraordinary capacity of this species to cope with environmental changes is attributed to the robustness of their eggs, which can remain dormant yet viable for years, ensuring the species’ survival. Furthermore, their reproductive adaptability creates egg banks with overlapping generations, providing a buffer against environmental fluctuations.
8. Branchiopods disperse their eggs through various means, including passive dispersal by wind and by birds, which significantly contribute to long-distance dispersal. In the short term, the species exhibits a slow rate of colonisation, as evidenced by recent observations in Svalbard.

ACKNOWLEDGEMENT

This research was made possible through the dedicated support of several organisations and individuals. Hanna-Kaisa Lakka’s work is funded by the Nordic Working Group for Biodiversity (NBM) under the auspices of the Nordic Council of Ministers, alongside grants from the Jorma and Martha Foundation, the Arctic Field Grant from the Norwegian Research Council (RiS ID 3622), the Finnish Ministry of the Environment, and the Research Council of Finland (#340901 and #346293). We will also thank Sigurd Einum and Bjørn Walseng for making available their unpublished records on *L. arcticus* in Bear Island.

REFERENCES

Aas M. 2007. Bestandsdynamikk og habitatbruk hos anadrom og stasjonær røye (*Salvelinus alpinus*) i Straumsjøen; en grunn innsjø på Svalbard. MSc thesis, University of Life Sciences, Ås. 80 pp. (In Norwegian).

Aass P. 1969. Crustacea, especially *Lepidurus arcticus* Pallas, as brown trout food in Norwegian mountain reservoirs. Report, Inst. Freshw. Res., Drottningholm, 49: 183–201.

Arnold GP. 1966. Observations on *Lepidurus arcticus* (Pallas) (Crustacea, Notostraca) in east Greenland. Annals and Magazine of Natural History 9: 599–617. https://doi.org/10.1080/00222936608651674

Belzile C, Vincent WF, Gibson JA, Hove PV. 2001. Bio-optical characteristics of the snow, ice, and water column of a perennially ice-covered lake in the High Arctic. Canadian Journal of Fisheries and Aquatic Sciences, 58(12): 2405–2418. https://doi.org/10.1139/f01-187

Bennike O, Hedenås L. 1995. Early Holocene land floras and faunas from Edgeøya, eastern Svalbard. Polar Research 14 (2): 205–214. https://doi.org/10.3402/polar.v14i2.6663

Berg M. 1954. New localities of *Lepidurus arcticus* Pallas in North-Norway. Astarte. No 9: 1–3.

Berg OK, Finstad AG, Olsen PH, Arnekleiv JV, Nilssen K. 2010. Dwarfs and cannibals in the Arctic: production of Arctic char (*Salvelinus alpinus* (L.)) at two trophic levels. Hydrobiologia 652: 337–347. https://doi.org/10.1007/s10750-010-0366-9

Blomkvist D. 1995. Bladfotingar som försurningsindikatorer i fjällen. Länsstyrelsen i Norrbottens län. Rapport nr. 3-1995. 30 pp. (In Swedish).

Borgstrøm R, Garnås E, Saltveit SJ. 1985. Interactions between brown trout, *Salmo trutta* L., and minnow, *Phoxinus phoxinus* (L.) for their common prey, *Lepidurus arcticus* (Pallas). Verhandlungen International Vereinigung für Limnologie 22: 2548–2552. https://doi.org/10.1080/03680770.1983.11897721

Borgstrøm R, Hendrey GR. 1976. pH tolerance of the first larval stages of *L. arcticus* (Pallas) and adult *Gammarus lacustris* G.O.Sars. The SNSF-project, Oslo-Ås, Norway. IR 22/76. 37 pp. (In Norwegian with an English summary).

Borgstrøm R, Larsson P. 1974. The first three instars of *Lepidurus arcticus* (Pallas) (Crustacea: Notostraca). Norw. J. Zool. 22: 45–52.

Borgstrøm R, Museth J, Brittain JE. 2010. The brown trout (*Salmo trutta*) in the lake Øvre Heimdalsvatn: long-term changes in population dynamics due to exploitation and the invasive species, European minnow (*Phoxinus phoxinus*). Hydrobiologia 642: 81–91. https://doi.org/10.1007/s10750-010-0161-7

Borgstrøm R, Aas M, Hegseth H, Dempson JB, Svenning M-A. 2018. *Lepidurus arcticus* (Crustacea: Notostraca); an unexpected prey of Arctic char (*Salvelinus alpinus*) in a High Arctic river. Boreal Env. Res. 23: 149–157.

Borgstrøm R. 1970. Skjoldkreps, *Lepidurus arcticus,* i Stolsvannsmagasinet i Hallingdal. Fauna 23: 12–20. (In Norwegian with an English summary).

Borgstrøm R. 1973. The effect of increased water level fluctuation upon the brown trout population of Mårvann, a Norwegian reservoir. Norwegian Journal of Zoology 21: 101–112.

Borgstrøm R. 2009. Aurebestanden i Skaupsjøen. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences. Fagrapport fiskeforvaltning i høgfjellet 1 (1): 11 pp. (In Norwegian).

Borgstrøm R. 2016. Auren på Hardangervidda er sterkt påverka av klimatilhøve. Naturen nr. 4-2016: 147–155. (In Norwegian). https://doi.org/10.18261/issn.1504-3118-2016-04-02

Borgstrøm R. 2019. Skjoldkreps – eit viktig næringsdyr i høgfjellsvatn som er sterkt påverka av miljøfaktorar. VANN 01-2019: 33–42. (In Norwegian with an English summary).

Brabrand Å, Bremnes T, Brittain JE, Saltveit SJ, Gjemlestad L, Haaland S. 2015. En vurdering av virkning på bunndyr og fisk ved økt senkning av Vinstern i Oppland. Naturhistorisk museum, Universitetet i Oslo, Rapport nr. 42, 31 pp. (In Norwegian).

Brabrand Å, Saltveit SJ. 1980. Skjoldkreps, *Lepidurus arcticus*, i Volbufjorden 434 m o.h. i Øystre Slidre, Oppland. Fauna 33: 105–108. (In Norwegian).

Brendonck L, Rogers DC, Olesen J, Weeks S, Hoeh WR. 2008. Global diversity of large branchiopods (Crustacea: Branchiopoda) in freshwater. Hydrobiologia 595: 167–176. https://doi.org/10.1007/s10750-007-9119-9

Brendonck L. 1996. Diapause, quiescence, hatching requirements: What we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). Hydrobiologia 320: 85–97. https://doi.org/10.1007/BF00016809

Brittain JE, Borgstrøm R, Bremnes T, Haaland S, Mjelde M, Nilssen JP, Skjelbred B. 2019. Øvre Heimdalsvatn – økologisk langtidsovervåking. Naturhistorisk museum, Universitetet i Oslo, Rapport nr. 84. 64 pp. (In Norwegian with an English summary).

Brittain JA, Schartau AK, Svenning M-A. 2020. Biologisk mangfold i ferskvann på Svalbard: kunnskapsgrunnlag, påvirkninger og forslag til framtidig overvåking. Norges vassdrags- og energidirektorat. NVE Rapport nr. 13/2020. 97 pp. (In Norwegian).

Brtek J, Thiéry A. 1995. The geographic distribution of the European Branchiopods (Anostraca, Notostraca, Spinicaudata, Laevicaudata). Hydrobiologia 298: 263–280. https://doi.org/10.1007/978-94-011-0291-9_25

Calizza E, Salvatori R, Rossi D, Pasquali V, Careddu G, Sporta Caputi S, Maccapan D, Santarelli L, Montemurro P, Rossi L, Costantini ML. 2022. Climate-related drivers of nutrient inputs and food web structure in shallow Arctic lake ecosystems. Scientific Reports, 12(1), 2125. https://doi.org/10.1038/s41598-022-06136-4

Christoffersen K. 2001. Predation on *Daphnia pulex* by *Lepidurus arcticus*. Hydrobiologia 442: 223–229. https://doi.org/10.1023/A:1017584928657

Coulson SJ, Convey P, Aakra K, Aarvik LL, Ávila-Jiménez ML, Babenko A, Biersma EM, Bostrom S, Brittain JE, Carlsson AM, Christoffersen KS, de Smet WH, Ekrem T, Fjellberg A, Füreder L, Gustafsson DR, Gwiazdowicz DJ, Hansen LO, Holmstrup M, Hullé M, Kaczmarek L, Kolicka M, Kuklin VV, Lakka H-K, Lebedeva N, Makarova OL, Maraldo K, Melekhina EN, Ødegaard F, Pilskog HE, Simon JC, Sohlenius B, Solhøy T, Søli GEE, Stur E, Tanasevitch AV, Taskaeva AA, Velle G, Zawierucha K, Zmudczyńska-Skarbek K. 2014. The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef land and Novaya Zemlya. Soil Biology & Biochemistry 68, 440–470. https://doi.org/10.1016/j.soilbio.2013.10.006

Dahl K. 1932. Influence of water storage of food conditions on trout in Lake Paalsbufjord. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse. 1931. No. 4. 53 pp.

Dahl K. 1933. Vassdragsreguleringers virkninger på fisket i innsjøer. J. W. Cappelens forlag, Oslo. (In Norwegian).

Dahl SO, Nesje A. 1996. A new approach to calculating Holocene winter precipitation by combining glacier equilibrium-line altitudes and pine-tree limits: a case study from Hardangerjøkulen, central southern Norway. The Holocene 6, 4: 381–398. https://doi.org/10.1177/095968369600600401

Dimante-Deimantovica I, Chertoprud M, Chertoprud E, Christoffersen KS, Novichkova A, Walseng B. 2015. FREMONEC: Effect of climate change and related stressors on fresh and brackish water ecosystems in Svalbard. A Norwegian and Russian joint scientific project. Norwegian Institute for Nature Research (NINA). Report 1218. 40 pp. http://hdl.handle.net/11250/2380592

Dimante-Deimantovica I, Walseng B, Chertoprud ES, Novichkova A. 2018. New and previously known species of Copepoda and Cladocera (Crustacea) from Svalbard, Norway – who are they and where do they come from? Fauna norvegica 38: 18–29. https://doi/10.5324/fn.v38i0.2502

Dolmans V, Partoens L, Deboelpaep E, Horváth Z, Vanschoenwinkel B. 2025. Dietary data suggest large branchiopods may be an underrecognised food resource for a wide range of waterbirds. Hydrobiologia: 1–17. https://doi.org/10.1007/s10750-025-05810-8

Ebne I. 2009. Anadrom røye (*Salvelinus alpinus*) i Linnévassdraget, Svalbard; Diett, oppvandring, bestandssammensetning og fangbarhet. MSc thesis, University of Life Sciences, Ås. 64 pp. (In Norwegian).

Eiríksson Þ, Þorleifsdóttir Þ, Sigurjónsdóttir H, Malmquist HJ. 2021. Huldudýr á heiðum uppi– útbreiðsla skötuorms á Íslandi. Náttúrufræðingurinn 91 (3–4): 146–165. (A rare animal in the Iceland Highland – the Arctic tadpole shrimp). (In Icelandic). https://rorum.is/files/skra/63/

Enge E, Qvenild T, Hesthagen T. 2017. Fish death in mountain lakes in southwestern Norway during 1800s and early 1900s – a review of historical data. Vann nr. 1-2017: 66–80.

Evenseth A, Christensen G, Kallenborn R. 2005. Selected chlorobornanes, polychlorinated naphthalenes and brominated flame retardants in Bjørnøya (Bear Island) freshwater. Environmental Pollution 136: 419–430. https://doi.org/10.1016/j.envpol.2005.01.018

Fjellheim A. 2004. Virkning av rotenonbehandling på bunndyrsamfunnene i et område ved Stigstu, Hardangervidda. Lab. Ferskv. Økol. Innlandsfiske. LFI-UNIFOB. Universitet i Bergen. Rapport nr. 122. 60 pp. (In Norwegian).

Fjellheim A, Tysse Å, Bjerknes V, Wright RF. 2002. Finprikkauren på Hardangervidda. DN-utredning 2002-1. 58 pp. (In Norwegian).

Fjellheim A, Tysse Å, Bjerknes W. 2007. Fish Stomachs as a Biomonitoring Tool in Studies of Invertebrate Recovery. Water, Air and Soil Pollution 7: 293–300. https://doi.org/10.1007/s11267-006-9074-x

Fryer G. 1988. Studies on the functional morphology and biology of the Notostraca (Crustacea: Branchiopoda). Philosophical Transactions of the Royal Society B. Vol. 321: 27–124. https://doi.org/10.1098/rstb.1988.0091

Fryer G. 1996. Diapause, a potent force in the evolution of freshwater crustaceans. Hydrobologia 320: 1–14. https://doi.org/10.1007/BF00016800

Geyer G, Hegna TA, Kelber KP. 2024. The end of the 'living fossil' tale? A new look at Triassic specimens assigned to the tadpole shrimp *Triops cancriformis* (Notostraca) and associated phyllopods from the Vosges region (eastern France). Papers in Palaeontology, Vol. 10, Part 5, e1589. https://doi.org/10.1002/spp2.1589

Gillooly JF, Dodson SI. 2000. The relationship of neonate mass and incubation temperature to embryonic development in a range of animal taxa. Journal of Zoology 251: 369–375. https://doi.org/10.1111/j.1469-7998.2000.tb01087.x

Halvorsen G. 1973. Crustacea from the High Mountain Area Hardangervidda, South Norway. Rapport fra Høyfjellsøkologisk Forskningssenter, Finse, Norge. 1973 (3). 17 pp.

Hann BJ, Lonsberry B. 1991. Influence of temperature on hatching of eggs of *Lepidurus couesii* (Crustacea, Notostraca). Hydrobiologia, 212: 61–66. https://doi.org/10.1007/BF00025987

Hanssen-Bauer I, Førland EJ, Hisdal H, Mayer S, Sandø AB, Sorteberg A. (Editors). 2019. Climate in Svalbard 2100 – a knowledge base for climate adaptation. Norwegian Environment Agency (Miljødirektoratet), Report 1/2019. 207 pp.

Hessen D, Rueness EK, Stabell M. 2004. Circumpolar analysis of morphological and genetic diversity in the Notostracan *Lepidurus arcticus*. Hydrobiologia 519: 73–84. https://doi.org/10.1023/B:HYDR.0000026486.16615.06

Hesthagen T, Gran R. 2019. Auren i Vinstre-magasinet: bestandstilhøve, fangst og utsettingar gjennom 40 år. Norwegian Institute for Nature Research (NINA). Report 1637. 53 pp. (In Norwegian).

Hesthagen T. 1979. Utbredelse av skjoldkreps *Lepidurus arcticus* i Lom kommune, Oppland. Fauna 33: 30–33. (In Norwegian).

Hesthagen T. 2018. Fangstutbyte og bestandstilhøva hjå auren i Aursjøen-magasinet i Skjåk kommune i søraustlege delen av Reinheimen i åra 1980–2017. Norwegian Institute for Nature Research (NINA). Report 1446. 35 pp. (In Norwegian).

Hesthagen T. 2022. Draggarnfisking i Gudbrandsdalen. Årbok for Gudbrandsdalen 90: 157–176. (In Norwegian).

Hesthagen T. 2005. Sylvetjønne – eit fiskevatn utanom det vanlege. Heim og bygd 13: 68–81. (In Norwegian).

Huitfeldt-Kaas H. 1911. Indberetning om Fiskeriforholdene paa Hardangervidden. I: Indstilling fra Fjeldbeitekomiteen om Harangviddens Utnyttelse. Landbruksdepartementet. (Centraltrykkeriet, Kristiania). 106 pp. (In Norwegian).

Huitfeldt-Kaas H. 1935. Der Einfluss der Gewässerregelungen auf den Fischbestand in Binnenseen. Oslo. 105 pp. (In Deutsh).

Håland A. 2012. Numbers, density and trends of breeding Black Scoters *Melanitta n. nigra* at the Hardangervidda plateau, southern Norway 1978–2012, in perspective of climate variations and varying density of Brown Trout *Salmo trutta*. Ornithology Studies 2012-1: 1–15.

Janiec K. 1996. The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). Polish Polar Research 17 (3–4): 173–202.

Jeppesen E, Christoffersen K, Landkildehus F, Lauridsen T, Amsinck SL, Riget F, Søndergaard M. 2001. Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between Arctic char (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids. Hydrobiologia 442: 329–337. https://doi.org/10.1023/A:1017508211819

Jeuthe H, Brännäs E, Nilsson J. 2016. Effects of variable egg incubation temperatures on the embryonic development in Arctic charr *Salvelinus alpinus*. Aquaculture Research, 47(12): 3753–3764. https://doi.org/10.1111/are.12825

Jørgensen I, Eie JA. 1993. Utbredelsen av fisk, bunndyr og fisk i innsjøer og dammer på Mosselhalvøya, Svalbard. Norwegian Institute for Nature Research (NINA). Research report 45. 25 pp. (In Norwegian).

Järvinen A, Lakka H-K, Sujala M. 2014. Arktinen Kilpikidusjalkainen, tunturivesien elävä fossiili, löydetty jälleen Suomesta. (The living fossil Arctic tadpole shrimp was found again in Finland). Luonnon Tutkija, 1: 19–24. (In Finnish).

Klausen TR. 2012. Population regulation in the tadpole shrimp *Lepidurus arcticus*. MSc-thesis, Norwegian University of Science and Technology, Department of Biology. 25 pp. http://hdl.handle.net/11250/245161

Klemetsen A, Grotnes PE, Holthe H, Kristoffersen K. 1985. Bear Island Charr. Report, Inst. Freshw. Res., Drottningholm, 62: 98–119.

Koli L. 1957. Beiträge zur Kenntnis der Euphyllopodenfauna Finnlands. Archiv Societatis Zoologicae Botanicae Fennica 'Vanamo'. 11, 2: 108–111. (In Deutsch).

Koops MA, Tallman RF. 2004. Adaptive variation in the development and mortality of Arctic char eggs. In Physiology of Fish Eggs and Larvae: Proc. Symp. Int. Congr. Biol. Fish, Manaus, Brazil, 1: 47–68.

Kuller Z, Gasith A. 1996. Comparison of the hatching process of the tadpole shrimps *Triops cancriformis* and *Lepidurus apus lubbocki* (Notostraca) and its relation to their distribution in rain-pools in Israel. Hydrobiologia 335: 147–157. https://doi.org/10.1007/BF00015276

Lakka H-K, Eloranta AP, Hesthagen T, Saksgård R, Power M. 2020. Impacts of reduced *Lepidurus arcticus* availability on brown trout life history traits in a mountain reservoir. Aquatic Sciences 82:78. 11 pp. https://doi.org/10.1007/s00027-020-00751-x

Lakka H-K. 2013. The ecology of a freshwater crustacean: *Lepidurus arcticus* (Branchiopoda, Notostraca) in a high Arctic region. The University Centre in Svalbard, Department of High Arctic Biology. MSc thesis. The University Centre in Svalbard/ University of Helsinki. 151 pp. http://hdl.handle.net/10138/41586

Lakka H-K. 2015. Description of the male *Lepidurus arcticus* (Branchiopoda: Notostraca) and the potential role of cannibalism in defining male form and population sex ratio. Journal of Crustacean Biology 35(3): 319–329. https://doi.org/10.1163/1937240X-00002324

Lakka H-K. 2020. Environmental Changes in Arctic Freshwaters. The Response of Indicator Species to Global Warming and Acidification in the Arctic. PhD-thesis, University of Jyväskylä, 2020: 51 pp. https://jyx.jyu.fi/jyx/Record/jyx_123456789_72134

Lakka H-K. 2021. Haussa tunturivesien äyriäisiä – ilmoita havaintosi! (Looking for crustaceans from mountain waters – report your observations). Suomen Luonto. (In Finnish).

Lehmann GB, Gabrielsen S-E, Wiers T, Sandven OR. 2008. Fiskeribiologiske undersøkelser i Halnefjorden, Store og Vesle Krækkja, Krækjungen, Heinungen og Øvre og Nedre Hein august 2007. LFI-Unifob. Report 152. 62 pp. (In Norwegian).

Lien L. 1978. The energy budget of the brown trout population of Øvre Heimdalsvatn. Holarctic Ecology 1: 279–300. https://doi.org/10.1111/j.1600-0587.1978.tb00963.x

Lindholm M, Hessen DO, Færøvig PJ, Rognerud B, Andersen T, Stordal F. 2015. Is distribution of cold stenotherms constrained by temperature? The case of the Arctic fairy shrimp (*Branchinecta palludosa* O.F.Müller 1788). Journal of Thermal Biology 53: 46–52. https://doi.org/10.1016/j.jtherbio.2015.08.005

Lingdell P-E, Engblom E. 2002. Bottendjur som indikator på kalkningseffekter. Report 5235, Naturvårdsverket. 191 pp. (In Swedish).

Longhurst AR. 1955. Evolution in the Notostraca. Evolution 9: 84–86. https://doi.org/10.2307/2405360

Luoto T, Oksman M, Ojala AEK. 2016. Invertebrate communities of the High Arctic ponds in Hornsund. Polish Polar Research, 37(1): 105–119. https://doi.org/10.1515/popore-2016-0003

Mancinelli G, Pasquali V. 2016. Body size-related constraints on the movement behaviour of the arctic notostracan *Lepidurus arcticus* (Pallas, 1793) under laboratory conditions. Environment changes in Arctic. https://doi.org/10.1007/s12210-016-0512-z

Miller MC. 1980. Tadpole shrimp. In Hobbie, J.E (ed.). Limnology of Tundra Ponds. Barrow, Alaska. US/IBP Synthesis Series 13: 323–335.

Mitchell GF. 1957. Late-glacial finds of *Lepidurus arcticus* (Pallas) in the British Isles. Nature 180: 153. https://doi.org/10.1038/180513a0

Møller OS, Olesen J, Høeg JT. 2003. SEM studies on the early larval development of *Triops cancriformis* (Bosc) (Crustacea: Branchiopoda, Notostraca). Acta Zoologica 84: 267–284. https://doi.org/10.1046/j.1463-6395.2003.00146.x

Museth J, Hesthagen T, Sandlund OT, Thorstad EB, Ugedal O. 2007. The history of the minnow *Phoxinus phoxinus* (L.) in Norway: from harmless species to pest. Journal of Fish Biology 71 (Supplement D): 184–195. https://doi.org/10.1111/j.1095-8649.2007.01673.x

Neretina AN, Gololobova MA, Neplyukhina AA, Zharov AA, Rogers CD, Horne DJ, Protopopov AV, Kotov AA. 2020. Crustacean remains from the Yuka mammoth raise questions about non-analogue freshwater communities in the Beringian region during the Pleistocene. Sci. Report 10, 859. https://doi.org/10.1038/s41598-020-57604-8

Nowiński K, Wiśniewska-Wojtasik B. 2006. Diversity of abiotic properties of water in shallow lakes in Hornsund area (SW Spitsbergen). Limnological Review 6: 215–222.

O'Brien SM, Helm B. 2025. First record of *Lepidurus lemmoni* (Holmes 1894) (Crustacea: Notostraca) in California's Central Valley. California Fish and Wildlife journal, 111, e1. https://doi.org/10.51492/cfwj.111.1

Olofsson O. 1918. Studien über die Süsswasserfauna Spitzbergens. Beitrag zur Systematik, Biologie und Thiergeographie der Crustaceen und Rotatorien. Zoologiska Bidrag från Uppsala, Bd 6. 468 pp. (In German).

Pasquali V, Calizza E, Setini A, Hazzlerigg D, Christoffersen KS. 2019. Preliminary observations on the effect of light and temperature on the hatching success and rate of *Lepidurus arcticus* eggs. Ethology, Ecology & Evolution 31–4: 348–357. https://doi.org/10.1080/03949370.2019.1609093

Pedersen K, Scobie L. 1990. Dynamikk, habitatbruk og redskapsseleksjon for ørretbestanden i Kollsvatn, en innsjø på Hardangervidda. MSc thesis, University of Life Sciences, Ås. 59 pp. (In Norwegian).

Presthus Heggen M, Birks HH, Anderson NJ. 2010. Long-term ecosystem dynamics of a small lake and its catchment in west Greenland. The Holocene 20(8): 1207–1222. https://doi.org/10.1177/0959683610371995

Qvenild T, Fjeld E, Fjellheim A, Hammar J, Hesthagen T, Lakka H-K. 2021. Upper thermal threshold of *Lepidurus arcticus* (Branchiopoda, Notostraca) in lakes on the southern outreach of its distribution range. Fauna norvegica 41: 50–88. https://doi.org/10.5324/fn.v41i0.3832

Qvenild T, Fjeld E, Fjellheim A, Hesthagen T, Lakka H-K, Rognerud S, Tysse Å. 2021. Ørretens viktigste næringsdyr på Hardangervidda. NATUREN nr. 4: 202–212. (In Norwegian). https://doi.org/10.18261/issn.1504-3118-2021-04-06

Qvenild T, Fjeld E, Fjellheim A, Rognerud S, Tysse Å. 2018. Climatic effects on a cold stenotherm species *Lepidurus arcticus* (Branchiopoda, Notostraca) on the southern outreach of its distribution range. Fauna norvegica 38: 37–53. https://doi.org/10.5324/fn.v38i0.2598

Qvenild T, Hesthagen T, Museth J. 2024. A long-term study of the impact of the invasive species Eurasian minnow *Phoxinus phoxinus*, on brown trout *Salmo trutta* production in a high mountain lake, Southern Norway. Fauna norvegica 43: 1–11. https://doi.org/10.5324/fn.v43i0.5826

Qvenild T, Hesthagen T. 2019. Environmental conditions limit the distribution of *Lepidurus arcticus* (Branchiopoda, Notostraca) on the Hardangervidda mountain plateau, Southern Norway. Fauna norvegica 39: 77–110. https://doi.org/10.5324/fn.v39i0.2687

Qvenild T, Hesthagen T. 2020. The viability of the crustacean *Eurycercus lamellatus* (Branciopoda, Cladocera) in a high mountain area in southern Norway. Fauna norvegica 40: 22–42. https://doi.org/10.5324/fn.v40i0.3340

Qvenild T. 2022. Climatic impact on the crustacean species *Lepidurus arcticus*, *Gammarus lacustris* and *Eurycercus lamellatus* on brown trout *Salmo trutta* production in a high mountain area in Southern Norway. Doctoral thesis, Faculty of Mathematics and Natural Sciences, University in Oslo. 227 pp. http://urn.nb.no/URN:NBN:no-93328

Røen UI. 1962. Studies on Freshwater Entomostraca in Greenland. II. Locations, Ecology and Geographical Distribution of the Species. Meddelser om Grønland, Bd. 170, No. 2. 149 pp.

Rogacki M, Brysiewicz A. 2021. Tadpole shrimps – A general review of the little known crustaceans of ephemeral waterbodies. Research in Ecology, Vol. 03(02): 18–24. https://doi.org/10.30564/re.v3i2.2910

Rogers DC. 2001. Revision of the Nearctic *Lepidurus* (Notostraca). Journal of crustacean biology, 21(4): 991–1006. https://doi.org/10.1163/20021975-99990192

Rogers DC. 2014. Larger hatching fractions in avian dispersed anostracan eggs (Branchiopoda). Journal of Crustacean Biology. 34(2): 135–143. https://doi.org/10.1163/1937240X-00002220

Rogers DC, Zharov AA, Neretina AN, Kuzmina SA, Kotov AA. 2021. A Review of Recently Discovered Remains of the Pleistocene Branchiopods (Anostraca, Notostraca) from NE Siberia and Arctic Canada. Water 13, 280. https://doi.org/10.3390/w13030280

Rognerud S, Borgstrøm R, Qvenild T, Tysse Å. 2003. Ørreten på Hardangervidda. Norwegian Institute for Water Research (NIVA), Report L.NR. 4712–2003. 68 pp. (In Norwegian).

Rognerud S, Fjeld E. 2014. Undersøkelser av fisk og næringsdyr i Mår og Ringedalsvatnet 2011–2013. Norwegian Institute for Water Research (NIVA), Report L.NR. 6682-2014. 52 pp. (In Norwegian).

Rukke NA. 2002. Effects of low calcium concentrations on two common freshwater crustaceans, *Gammarus lacustris* and *Astacus astacus*. Freshwater Ecology 16: 357–366. https://doi.org/10.1046/j.1365-2435.2002.00637.x

Sars GO. 1864. Beretning om en i Sommeren 1863 foretagen zoologisk reise i Christiania Stift. Nyt Mag. Naturvid. 13: 225–260.

Sayenko E, Minakawa N. 1999. Occurrence of two crustacean species, *Branchinecta palludosa* (O.F. Müller, 1788) (Anostraca) and *Lepidurus arcticus* (Pallas, 1793) (Notostraca), on the Kuril Archipelago. Crustaceana 72(7): 710–712.

Scher O, Defaye D, Korovchinsky NM, Thiéry A. 2000. The Crustacean fauna (Branchiopoda, Copepoda) of shallow freshwater bodies in Iceland. Vestnik zoologii, 34(6): 11–25.

Schönbrunner IM, Eder E. 2006. pH-related hatching success of *Triops cancriformis* (Crustacea: Branchiopoda: Notostraca). Hydrobiologia. 563: 515–520. https://doi.org/10.1007/s10750-006-0018-2

Simonsen TA, Valderhaug NA. 1994. Bestandsdynamikk, habitatbruk og ernæring for aure i Litlosvatn – en innsjø på Hardangervidda. MSc thesis, University of Life Sciences, Ås. 65 pp. (In Norwegian).

Sømme S. 1934. Contributions to the biology of Norwegian fish food animals. I. *Lepidurus arcticus* Pallas. Avh. Norske Vidensk Akad 6: 1–36.

Summerhayes VS, Elton CS. 1923. Contributions to the ecology of Spitzbergen and Bear Island. Journal of Ecology 11: 214–286.

Svenning M-A. 2015. Miljøvariable i innsjøer på Svalbard; vanntemperatur, lys- og isforhold. Norwegian Institute for Nature Research (NINA). Minireport 575. 37 pp. (In Norwegian).

Thiéry A. 1997. Horizontal distribution and abundance of cysts of several large branchiopods in temporary pool and ditch sediments. Hydrobiologia, 259: 177–189. doi.org/10.1023/A:1003124617897

Thor SA. 1930. Beiträge zur Kenntnis der Invertebraten Fauna von Svalbard. Skrifter om Svalbard og Ishavet nr. 27. 145 pp. (In Deutsch).

Tysse Å, Fjellheim A, Stakseng H, Gåsdal O, Aasland E, Elnan G. 2022. Finprikkauren på Hardangervidda. Årsrapport 2022. 19 pp. (In Norwegian).

Vanschoenwinkel B, Pinceel T, Vanhove MPM, Denis C, Jocque M, Timms BV, Brendonck L. 2012. Toward a global phylogeny of the «living fossil» crustacean order Notostraca. PLoS One, 7, e34998. https://doi.org/10.1371/journal.pone.0034998

Vekhoff NV. 1997. Large branchiopod Crustacea (Anostraca, Notostraca, Spinicaudata) of the Barents region of Russia. Hydrobiologia 359: 69–74. https://doi.org/10.1023/A:1003116432010

Walseng B, Raddum G, Saksgård R, Schartau AKL. 1996. Ferskvannsbiologiske undersøkelser i Kvenna 1995, med fokus på indikatorarter som redskap i forsuringsovervåkingen. Norwegian Institute for Nature Research (NINA). Oppdragsmelding 433. 36 pp. (In Norwegian).

Walseng B, Jensen T, Dimante-Deimantovica I, Christofersen KS, Chertoprud M, Chertoprud E, Novichkova A, Hessen DO. 2018. Freshwater diversity in Svalbard: providing baseline data for ecosystems in change. Polar Biology 41: 1995–2005. https://doi.org/10.1007/s00300-018-2340-3

Wojtasik B, Brylka-Wolk M. 2010. Reproduction and genetic structure of a freshwater crustacean *Lepidurus arcticus* from Spitsbergen. Polish Polar Research 31 (1): 33–44. https://doi.org/10.4202:ppres.2010.03

Økland KA, Økland J. 2003. Skjoldkrepsen *Lepidurus arcticus* i Norge. Fauna nr. 1-2003: 2–12. (In Norwegian with an English summary).

Editorial responsibility: Anne Helene Tandberg.