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Distribution of Recent non-marine ostracods in Icelandic lakes, springs, and cave pools

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ABSTRACT

Ostracods in Icelandic freshwaters have seldom been researched, with the most comprehensive record from the 1930s. There is a need to update our knowledge of the distribution of ostracods in Iceland as they are an important link in these ecosystems as well as good candidates for biomonitoring. We analysed 25,005 ostracods from 44 lakes, 14 springs, and 10 cave pools. A total of 16 taxa were found, of which seven are new to Iceland. *Candona candida* (Müller, 1776) is the most widespread species, whereas *Cytherissa lacustris* (Sars, 1863) and *Cypria ophtalmica* (Jurine, 1820) are the most abundant, showing great numbers in lakes. *Potamocypris fulva* (Brady, 1868) is the dominant species in springs. While the fauna of lakes and springs are relatively distinct from each other, cave pools host species that are common in both lakes and springs. Icelandic non-marine ostracods include mostly generalist species, as well as species adapted to cold climates and resemble those of other north European countries while sharing very few species with the North American Arctic. Iceland is experiencing impacts from climate change and a booming tourism. It is possible to use selected freshwater ostracods as biomonitoring tools by constructing a detailed database of these species.

Key Words: Arctic region, biodiversity, biogeography, ecology, freshwater environment

EIGHTEENTH INTERNATIONAL SYMPOSIUM ON OSTRACODA

INTRODUCTION

Ostracods inhabit almost all aquatic environments. One of their major defining features is their hard, bivalve, calcitic shell, dorsally connected and encasing the entire non-mineralized parts of the body, with only the tips of their appendages occasionally protruding. Both the carapace and the soft body parts can have taxonomically distinguishing characteristics, which are the basis of accurate taxonomic identification (Meisch, 2000).

Ostracods constitute one of the most diverse crustacean groups, with 62,000 described nominal freshwater and marine, extant and fossil species (Kempf, 1980), of which the estimated number of living species is around 10,000 to 15,000 (Meisch, 2000). Based on the knowledge of ecology and biology of the living species, it is possible to apply palaeoecological and palaeoclimatological reconstructions from the fossilised ostracod shells found in sediments (Horne *et al*., 2012). It is thus important to fully understand the ecology of extant species as well as their current distributions.

Approximately 2,330 freshwater ostracod species have been described worldwide (Meisch *et al*., 2019), of which 47 have been found to inhabit Arctic non-marine water bodies, four of them endemic to the region (Hodkinson *et al*., 2013).

Few studies have dealt with the existence and distribution of ostracods in Iceland, and none in a systematic way and within the past few decades. The first collection of Icelandic freshwater crustaceans was undertaken by the French explorer Charles Rabot in 1891 (De Guerne & Richard, 1892). He reported two freshwater species of ostracods, *Cypris pubera* Müller, 1776 and *Sarscypridopsis aculeata* (Costa, 1847) (recorded by Rabot as *Cypris aculeata*). Haberbosch (1916) published a list of crustaceans collected by

A. G. Böving from the Zoological Museum of Copenhagen, adding one more freshwater ostracod species, *Bradleystrandesia affinis* (Fischer, 1851) (listed as *Eucypris affinis hirsuta)*. In 1936, Schwabe (1936) recorded four more species from thermal waters, *Herpetocypris chevreuxi* (Sars, 1896), *Heterocypris incongruens* (Ramdohr, 1808) (as *Cyprinotus incongruens*), *Cyprideis torosa* (Jones, 1850) (as *Cyprideis littoralis*), and *Heterocypris salina* (Brady, 1868) (as *Cyprinotus salina*). The first (and last) comprehensive study of Icelandic non-marine ostracods was conducted by the Danish zoologist Erik M. Poulsen (1939), who added another eight species and compared Iceland to other high-latitude regions, such as Greenland, the Faroe Islands, and Sweden. He found, in addition to those mentioned above, *Eucypris pigra* (Fischer, 1851), *Tonnacypris glacialis* (Sars, 1890) (as *Eucypris glacialis*), *Potamocypris pallida* Alm, 1914, *Cyclocypris ovum* (Jurine, 1820), *Cypria ophtalmica* (Jurine, 1820), *Candona candida* (Müller, 1776), *Cytherissa lacustris* (Sars, 1863) (as *Cytheroidea lacustris*), and *Limnocytherina sanctipatricii* (Brady & Robertson, 1869) (as *Limnocythere sanctipatricii*). Since then, most research of the Icelandic freshwater fauna excluded ostracods entirely (i.e., Lindegaard, 1979) or relied on Poulsen (1939). Ólafsdóttir (2015) recorded six ostracod taxa, of which *Potamocypris zschokkei* (Kaufmann, 1900) was the only species not previously found in Iceland. A specimen of *P. zschokkei* was re-examined during the current study.

As ostracods are an important component of many ecosystems, acting as predators and prey, this absence from faunal listings has left a prominent gap in the knowledge of the Icelandic fauna. Taking into consideration the disjointed ostracod records available so far, a systematic and comprehensive database of freshwater ostracod species found in Iceland requires a clean start. With the tourist boom of the past decade as well as the effects of climate change, it is unwise to ignore the potential of ostracods as biomonitoring tools. Certain ostracod species might be especially sensitive to the changes in nutrient availability and oxygen content, water temperature, and other parameters (Geiger, 1990), and if they are to be used effectively, it is important to map their current distribution so that they could be compared with future collections. This study explores the Icelandic ostracod fauna and its distribution in lakes, springs, and cave pools, and aims to provide a comprehensive overview of these species.

STUDY SITES

Iceland is a volcanic island in the North Atlantic Ocean on the Mid-Atlantic Ridge marking the boundary between the Eurasian and North American tectonic plates. As such, Iceland is geologically active, with numerous active volcanoes, geysers, and hot springs. The island has an area of 103,125 km^2 of which about 11% is covered by glaciers and 2.8% by water (Statistics Iceland, 2015), including approximately 1,850 freshwater lakes larger than 0.1 km^2 and about 200 lakes larger than 1 km^2 (Aðalsteinsson *et al.*, 1989).

Despite lying just below the Arctic Circle, the Icelandic climate is considered subarctic and generally more temperate than that of other regions located at the same latitude. This is due to the effect of the warm North Atlantic Current that keeps the coasts ice-free throughout the year. The weather is also affected by the East Greenland Polar Current, mainly in the northeastern region. The clash of the mild Atlantic air and colder Arctic air causes the weather to be very variable. Much of Iceland is covered by tundra and the central region is dominated by a highland plateau (the central highlands) that has a rough climate and is not inhabited by people. Vegetation is mostly subarctic and only covers around 23% of the land, compared to 63% covered by wastelands.

The active Mid-Atlantic Ridge crosses Iceland in a southwest-northeast direction, causing new oceanic crust to emerge and form. Thus, the bedrock age increases with increasing distance from the ridge (Fig. 1). The topography, geology and soil characteristics of the catchment area influence the aquatic ecosystem; waters formed in younger bedrock have a higher biodiversity than those formed in

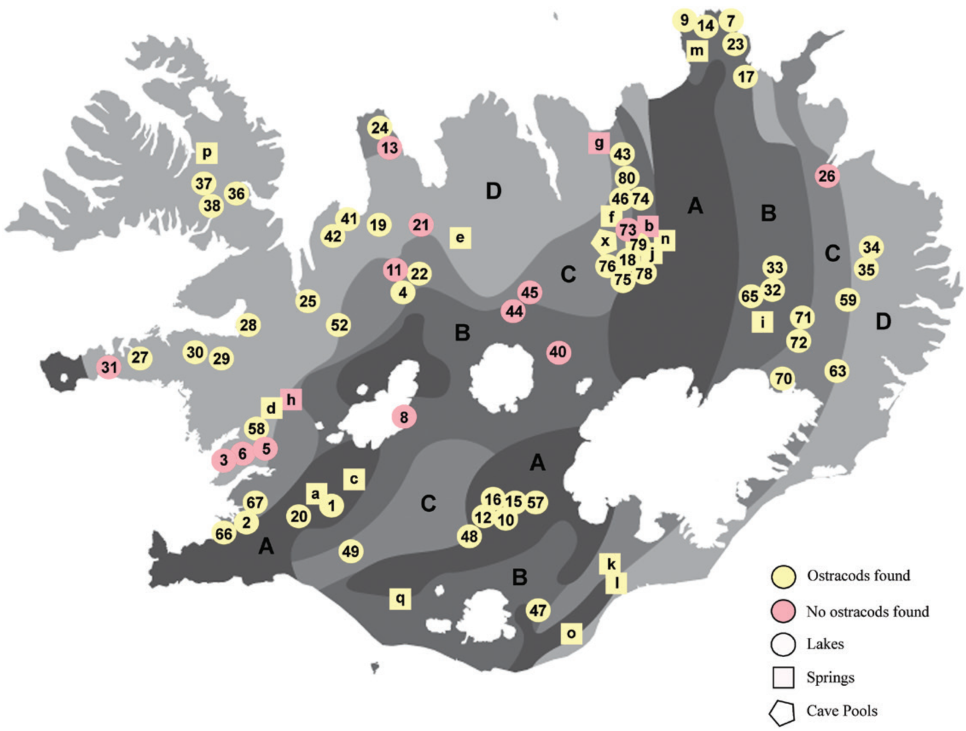

Figure 1. Map of Iceland showing sampled locations (numbers and letters correspond to names of locations given in Supplementary material Table S1) and zonation of four major bedrock classes in Iceland (modified from Jóhannesson & Saemundsson, 1998; different coloured zones are marked by letters A to D): Historical (< 0.0011 Ma) and postglacial prehistoric (0.0011–0.01 Ma) basic and intermediate lavas (**A**); late and middle Pleistocene (0.01–0.8 Ma) basic and intermediate hyaloclastite pillow lavas, interglacial and supraglacial lavas (**B**); early Pleistocene and upper Pliocene (0.8–3.3 Ma) basic and intermediate extrusive rocks (**C**); and upper Neogene (> 3.3 Ma) basic and intermediate extrusive rocks (**D**). The caves are put in one cluster and marked with ×.

older bedrock (Malmquist *et al.*, 2000, Ólafsson *et al.*, 2001). Iceland's two biggest lakes, Lakes Þingvallavatn and Þórisvatn, are mostly of tectonic origin, which is also the case for many other lakes. Some lakes were formed by the deepening of valleys by glacial erosion, or damming by lava flows (Lake Mývatn), glacial deposits, and rock slides. Volcano craters can also fill up with water and form lakes, such as Lake Öskjuvatn, the deepest crater lake in Iceland (217 m). Lagoon lakes are also formed on the sandy shores, the largest being Lake Hóp [http://web.archive.org/web/20090216142035/http://www.iceland.is:80/country-and-nature/nature/RiversandLakes/].

MATERIALS AND METHODS

Ostracods from 44 lakes, 14 springs, and 10 cave pools were identified (Fig. 1, Supplementary material Table S1). Their locations were widely distributed across the country.

Lakes

A total of 38 studied lakes were sampled between 1993 and 1998 as part of the Ecological Survey of Icelandic Lakes (ESIL), a standardised database of biological, limnological, hydrological, and geological information on the main types of Icelandic lakes (Malmquist *et al.*, 2000); the remaining six were sampled in 2004 as part of the Euro-limpacs project to evaluate impacts of global change on European freshwater ecosystems. The samples were taken between July and early September from stones within the littoral zone of lakes, as well as by using a Kajak corer (~5 cm in diameter) for samples retrieved from the soft sediment bottom. Stone samples were taken from four to six stations per location, dispersed evenly around the littoral zones of lakes. Five stones, 10–15 cm in diameter, were taken in each station from depths of 20–50 cm and brushed clean in a bucket of water before sieving the water. Similarly, Kajak samples were taken from two to six stations across the lake, with five samples per station. Samples were sieved through a 250 µm mesh sieve and fixed and stored in 4% formaldehyde (samples taken between 1992 and 1994), 70% isopropanol (1997–1998), or 80% ethanol (2004). The samples were washed and the organisms sorted into higher taxonomic groups, including ostracods.

Additional information on geology and hydrology (coordinates, lake area, depth, volume, altitude, type of bedrock in catchment), chemical and physical parameters (temperature, pH, conductivity, nutrients, alkalinity), aquatic vegetation and fishes was collected for each location. Also recorded was water temperature, conductivity, and pH at the water surface at 3 or 4 sites (depending on lake size) at the date of sampling. Air temperature data were collected from the meteorological stations nearest to the lake, supplied by the Icelandic Meteorological Office (www.vedur.is).

Springs

All but one of the sampled springs are limnocrene. One spring, Nauteyri, in the West Fjords, is a hot spring with temperatures of 25.5°C and 29.8°C at two sampled stations. The only rheocrene spring is Skarðslækur in southern Iceland. Spring samples were taken between June and August 2015, except for Nauteyri and Skarðslækur which were sampled in June and July 2016.

All spring samples were sampled at the substrate 23 m downstream of the source, using a Surber sampler and at the source by electrobugging (Kreiling *et al.* 2018). The samples were then sieved through a 63 µm mesh sieve and fixed in 70% ethanol. Water temperature, pH, oxygen content, and conductivity were measured once at the time of sampling with a multi-probe sonde (DS5; Hydrolab, Sheffield, UK).

Cave pools

The cave samples come from groundwater-fed limnocrene cave pools. All ten caves are made of basaltic lava rock and lie adjacent to Lake Mývatn, northeast Iceland. Sampling was conducted in June and July 2014 using modified crustacean traps (Örnólfsdóttir & Einarsson, 2004) placed into the cave pools 30 mm above the bottom. The traps were laid in such a way as to allow crustaceans to enter and remain trapped until collection. There could have been a certain amount of bias in the species collected as burrowing species are less likely to get trapped than swimming ones. The traps were collected after 12 h and the contents fixed in 70% ethanol (Combot, 2018).

Laboratory identifications

Identifications were based on the carapaces as well as on the dissections of soft parts, relying mostly on the identification keys of Meisch (2000). The descriptions and SEMs of Fuhrmann (2012) were also used. Some specimens kept in formaldehyde had decalcified shells and a reddish-brown colour. This hindered the identification based only on the carapace, most notably for *Candona candida*, *Limnocytherina sanctipatricii*, and *Limnocythere inopinata* (Baird, 1843). Only certain specimens were chosen for dissection as means of confirmation for species with carapaces less affected by formaldehyde. Identifications based on the soft body almost always corresponded to the initial carapace-based identifications. Specimens were dissected to avoid misidentification in species recorded by only a single specimen. Juveniles were ignored unless they were the only representatives of their taxa in each location. The soft parts were mounted on glass slides and embedded in glycerol for microscopic examination. A dissected specimen of each species was chosen, and taxonomically relevant body parts from each of these specimens were drawn by hand using a drawing tube mounted on a microscope. The drawings were then scanned and redrawn digitally in Adobe Photoshop CC 2014.

RESULTS

A total of 24,541 ostracod specimens were identified from lakes, 449 from springs, and 15 from cave pools, totalling at 25,005 individuals. Sixteen taxa were identified from these samples (Table 1, Supplementary material Table S2), of which four were found at only one location. Seven of the species were newly recorded for Iceland. Six of these were identified to species level: *Cryptocandona reducta* (Alm, 1914), *Ilyocypris bradyi* Sars, 1890, *Ilyocypris decipiens* Masi, 1905, *Limnocythere inopinata*, *Potamocypris fulva* (Brady, 1868) and *Potamocypris villosa* (Jurine, 1820); one, *Fabaeformiscandona* sp., was identified to genus level.

Candona candida was the most widespread species, found in all types of sampled habitats (Table 1). The most abundant species were *Cytherissa lacustris* and *Cypria ophtalmica*, which have been found in large numbers in Icelandic lakes but are rare, or absent, from springs and cave pools. *Potamocypris fulva* dominated the spring samples, but was scarcely found in lakes. *Heterocypris incongruens* was found only in the hot spring samples from Nauteyri. Only two species were found at the deepest sampled station (80.6 m) in Lake Langisjór: *Candona candida*, represented by a single specimen, and *Cytherissa lacustris*, which was abundant. Certain species were only found in shallow waters in springs, cave pools, and on stones in the littoral zone of lakes (Fig. 2A). *Potamocypris fulva* was found in many locations and in great abundance (Supplementary material Table S2, Supplementary material Fig. S3), but was not found in waters deeper than 1 m.

Four species were found in the location with the highest measured specific conductivity, Lake Kötluvatn, 4,950 µS cm^{-1} (Fig. 2B). The most abundant species in this lake were *Limnocythere inopinata* and *Candona candida*. *Cyclocypris ovum* and *Cypria ophtalmica* were also found, while *Cytherissa lacustris*, which seems almost ubiquitous in Icelandic lakes (Supplementary material Fig. S3, Supplementary material Table S1), was absent. Lake Hóp is the second largest lake, 29.8 km^2 and the second highest specific conductivity, 1131 µS cm^{-1}. The location with the lowest specific conductivity was the Miðhúsaskógur Spring, 36 µS/cm^{-1}, which contained only one species, *Potamocypris pallida*.

Table 1. Sampled habitats and number of occurrences of ostracod species; * hot spring.

Species	Number of occurrences	Number of lakes	Number of springs	Number of cave pools
Bradleystrandesia affinis	1	0	1	0
Candona candida	51	43	7	1
Cryptocandona reducta	2	1	1	0
Cyclocypris ovum	15	13	0	2
Cypria ophtalmica	34	32	0	2
Cytherissa lacustris	37	35	1	1
Fabaeformiscandona sp.	1	0	1	0
Heterocypris incongruens	1	0	1*	0
Ilyocypris bradyi	2	2	0	0
Ilyocypris decipiens	1	1	0	0
Limnocythere inopinata	16	12	1	3
Limnocytherina sanctipatricii	13	13	0	0
Potamocypris fulva	16	3	11	2
Potamocypris pallida	8	0	8	0
Potamocypris villosa	3	1	1	1
Tonnacypris glacialis	1	1	0	0

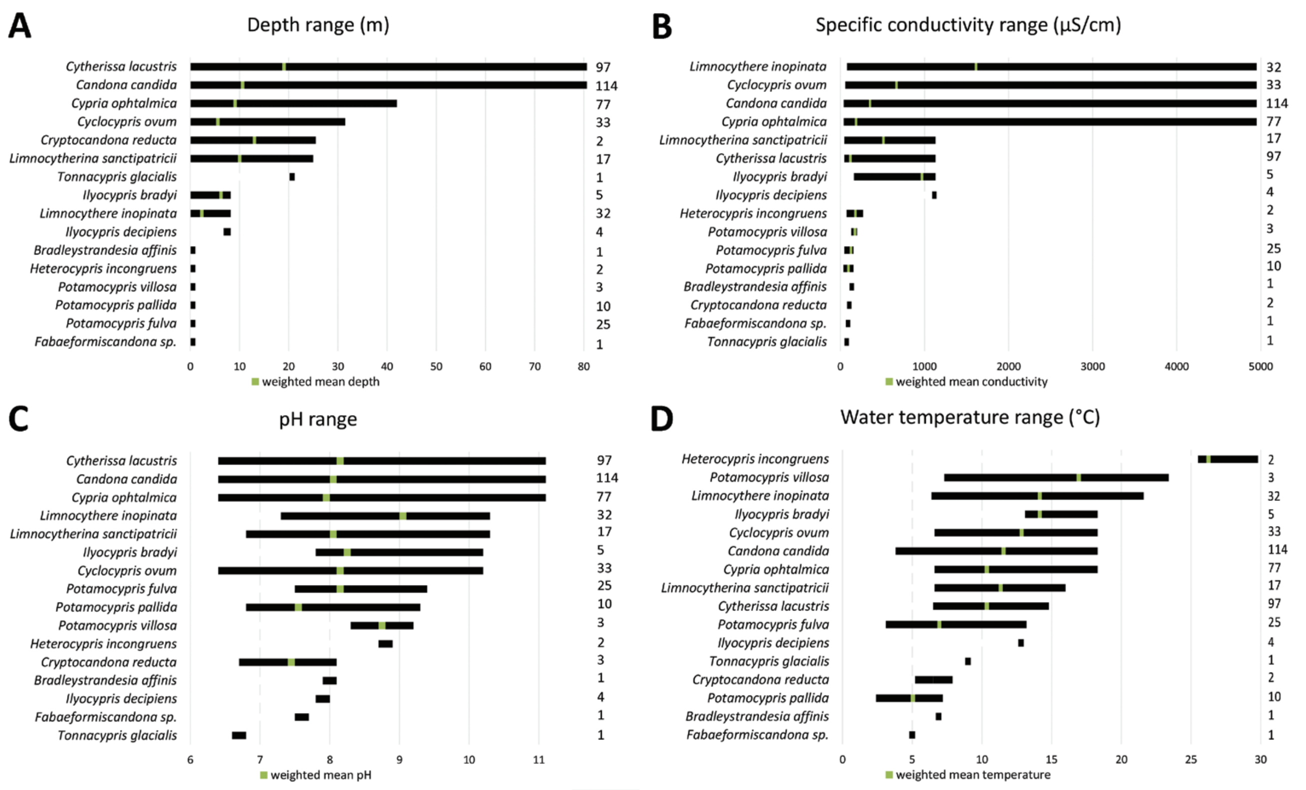

Figure 2. Recorded depth range (**A**), specific conductivity range (**B**), pH range (**C**), and water temperature range (**D**) of ostracod species, with a weighted mean indicated where possible. Numbers to the right represent the number of data points.

The measured pH varied 6.4–11.1 (Fig. 2C). Three species were found throughout this range, *Candona candida*, *Cypria ophtalmica*, and *Cytherissa lacustris*, while others, such as *Limnocythere inopinata* and *Potamocypris fulva*, have a narrower range, although they were recorded at many locations (Supplementary material Fig. S3).

The measured water temperature in lakes ranged from 6.6 °C in Lake Skálavatn, where *Cytherissa lacustris*, *Candona candida*, *Cypria ophtalmica*, *Limnocythere inopinata* and *Limnocytherina sanctipatricii* were present, to 18.3°C in Stakhólstjörn, where *Candona candida*, *Cypria ophtalmica*, *Limnocythere inopinata*, *Cyclocypris ovum* and *Ilyocypris bradyi* were recorded (Fig. 2D). Cave waters were generally cooler, ranging 6.0–7.2 °C. Springs show greatest variability with temperatures as low as 2.4 °C or as high as 29.8 °C. The hottest spring, Nauteyri, contained one species, *Heterocypris incongruens*, found only in this location throughout the study (Supplementary material Table S1, Supplementary material Fig. S4). The coldest spring, Miðhúsaskógur, with a temperature of 2.4 °C, also only contained one species, *Potamocypris pallida* (Fig. 2D).

The location with the highest number of recorded ostracod taxa, eight species, was Lake Hóp, north Iceland. *Cypria ophtalmica* comprised over 40% of the assemblage. *Ilyocypris bradyi* and *I. decipiens* were also recorded, the latter only in Hóp. Springs and cave pools generally exhibit a lower species richness, with several springs containing up to four species and only two cave pools were found to host two species; all others contained only one.

SPECIES RECORDED

Candona candida (Müller, 1776)

Candona candida (Figs. 3A, 3C, 4, Supplementary material Fig. S5) was present in most sampled locations (Table 1, Supplementary material Fig. S3), including large, deep lakes, lava cave pools, and springs across Iceland. Even though found in all lakes but Eiðavatn, the species was rarely the dominant one. Even in lakes where it comprised the majority, it was found in fairly low numbers, especially the adults. It was the only species found in Lake Ónefnt vatn. It does not seem to have a depth preference and was usually found relatively evenly distributed between stations of various depths, though rarely in the stone samples from the littoral zone (Fig. 2A). One specimen was found at 80.6 m in the deepest station in Lake Langisjór, but it was also found in other stations deeper than 30 m (Supplementary material Table S1).

Juvenile specimens outnumbered adults and comprised the bulk of the assemblage in the majority of samples. Males (Figs. 3A, 4) are seldom reported but they were found at three locations in Iceland: lakes Sænautavatn (21.5 m), Langavatn (1.5 m and 7.5 m) and Stóra-Fossvatn (11.0 m).

***Fabaeformiscandona* sp.**

Only one specimen was found (Fig. 5A, 5C, Supplementary material Fig. S6) in a surface sample from Þverá limnocrene spring in south Iceland (Supplementary material Fig. S4). The male specimen was still in a juvenile instar phase, and as such it could not be identified to species.

Cryptocandona reducta (Alm, 1914)

Two female specimens of *C. reducta* were found (Fig. 3D, Supplementary material Fig. S7), one from Lake Stóra-Viðarvatn

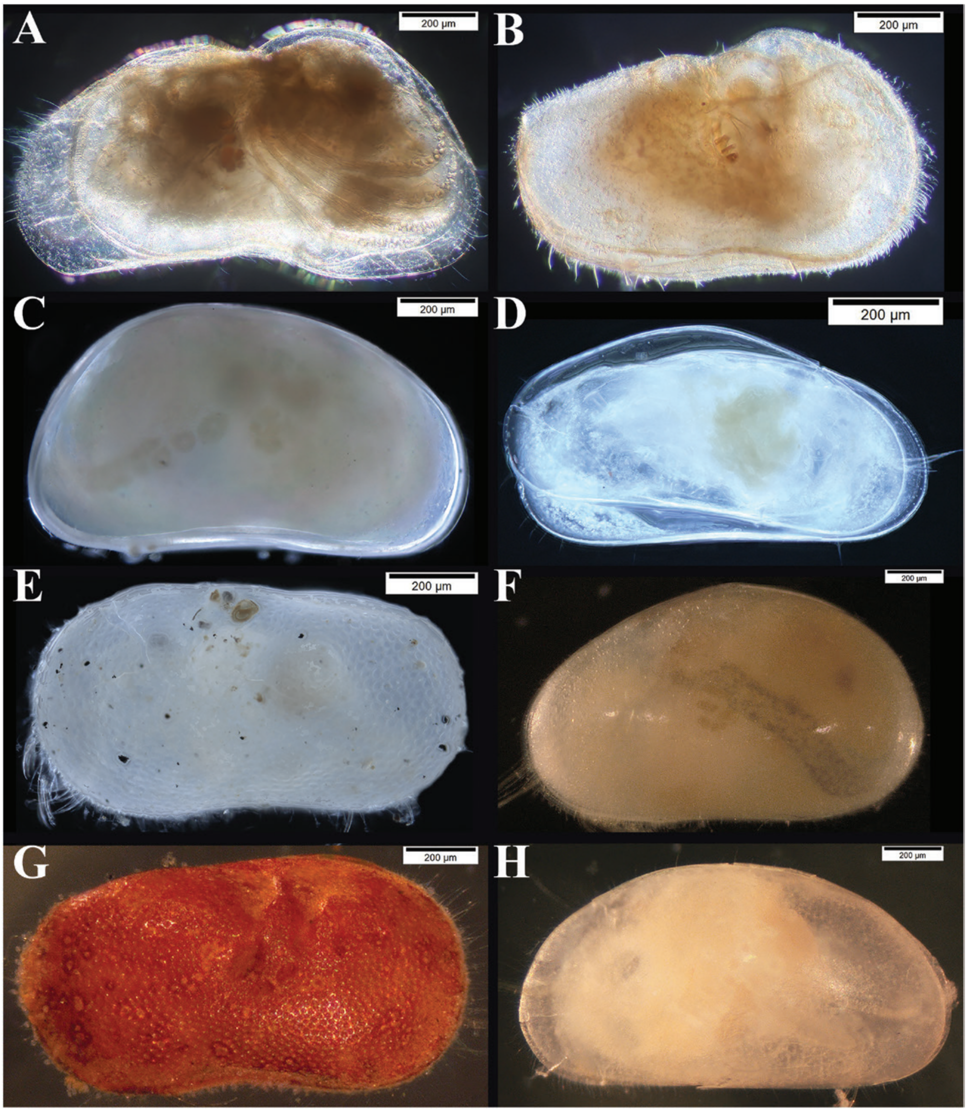

Figure 3. *Candona candida* (male, left lateral view of decalcified carapace) from Lake Langavatn (**A**); *Cytherissa lacustris* (right lateral view) from Lake Þríhyrningsvatn (**B**); *Candona candida* (female, right lateral view) from lava pool in Cave 20 (**C**); *Cryptocandona reducta* (female, right lateral view) from Skarðslækur Spring (**D**); *Ilyocypris bradyi* (left lateral view) from Lake Stakhólstjörn (**E**); *Heterocypris incongruens* (left lateral view) from Nauteyri hot spring (**F**); *Ilyocypris decipiens* (right lateral view) from Lake Hópið (**G**); *Tonnacypris glacialis* (female, juvenile, left lateral view) from Lake Langisjór (**H**).

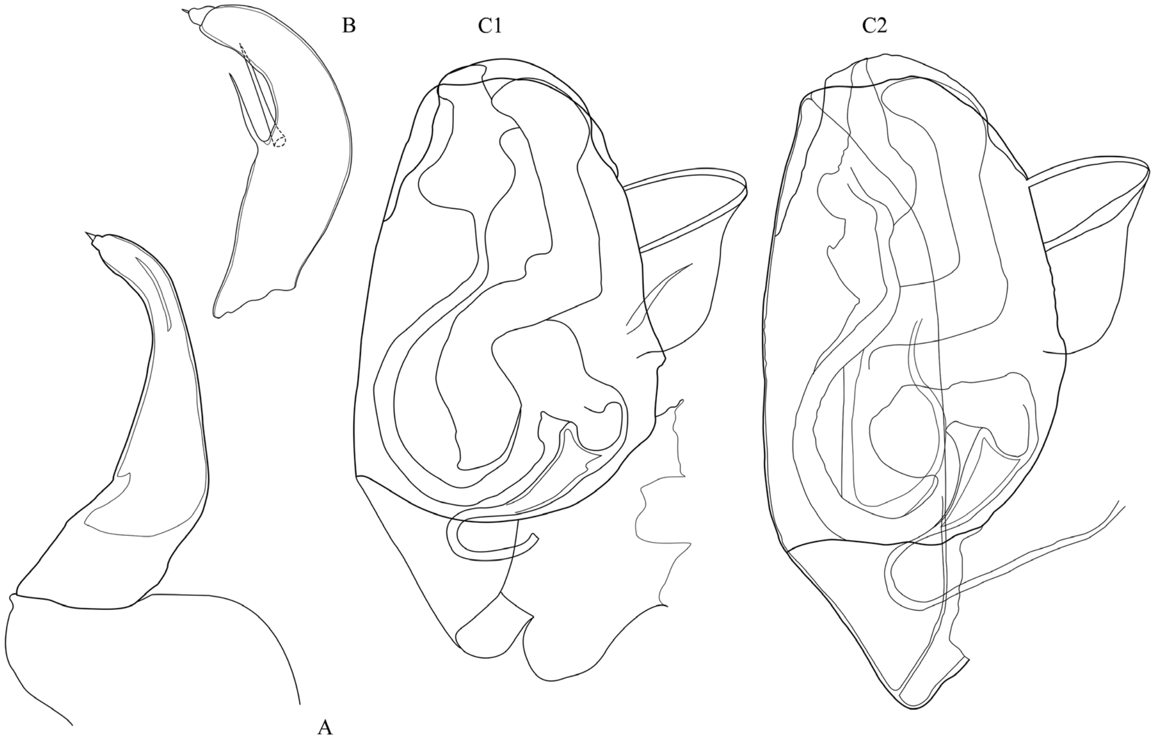

Figure 4. *Candona candida* (male). Left and right male clasping organs (**A**, **B**); the two hemipenes (**C1**, **C2**)

(25.5 m depth), in northeastern Iceland and one from Skarðslækur, the rheocrene spring in the south (Supplementary material Table S1, Supplementary material Fig. S4).

Cypria ophtalmica (Jurine, 1820)

Cypria ophtalmica (Fig. 6A, 6B, 6D, Supplementary material Fig. S8) is, together with *Cytherissa lacustris*, one of the two most abundant species in Icelandic lakes, found in 34 locations (Table 1, Supplementary material Table S1, Supplementary material Fig. S3). It was not found in any of the springs, nor was it found in the deepest sampled station in Lake Langisjór. It was the dominant species in nine of the lakes and was the only species found in two lava cave pools (C10 and C25). The species showed tolerance to a wide range of temperatures, pH, and conductivities (Fig. 2).

Two forms are known. *Cypria ophtalmica* forma *ophtalmica* (Fig. 6D) tends to be smaller, more distinctly pigmented, and have two female genital processes, whereas *C. ophtalmica* forma *lacustris* (Fig. 6A) seems to be slightly larger, paler, and with only one genital process (Meisch, 2000). The two distinct forms as well as individuals with transitional characters of the carapaces were found in the study. Because the two forms can only be reliably distinguished after examining the female genital processes, they were pooled together as *C. ophtalmica*. Specimens of the forma *lacustris* seem to prefer the deeper zone. Males were found in most locations.

Cyclocypris ovum (Jurine, 1820)

Cyclocypris ovum (Fig. 6C, Supplementary material Fig. S9) was found in 15 locations, mostly in lakes in western and northern Iceland (Supplementary material Table S1, Supplementary material Fig. S3). It was usually found in small numbers, but it was the dominant species in Lake Sandvatn, even if only 22 individuals were collected. It was commonly found in littoral stone samples and at various depths of the lake basins, with the deepest recorded depth of 31.5 m (Fig. 2A). The species was not found in any of the sampled springs, but it was recorded in two of the lava cave pools (C22 and C23) where it was the only species recorded. *Cyclocypris ovum* is known to be able to tolerate a wide range of conditions (Meisch, 2000), and we found it in waters with varying pH, conductivities, and temperatures (Fig. 2). Three of the dissected individuals were female and one was a male.

Ilyocypris bradyi Sars, 1890

Ilyocypris bradyi (Fig. 3E, Supplementary material Fig. S10) was found at only two locations, lakes Hóp and Stakhólstjörn (Supplementary material Table S1, Supplementary material Fig. S4). In Lake Hóp, which is a slightly brackish lake in northern Iceland, 41 individuals were found throughout the lake, all female, comprising 2.9% of the ostracods sampled in the lake. They were found in all stations at depths of 6.8–8.2 m (Fig. 2A).

Ilyocypris decipiens Masi, 1905

Ilyocypris decipiens (Fig. 3G, Supplementary material Fig. S11) was only found in Lake Hóp in relatively small numbers (12 individuals, all female, less than 1% of the ostracods collected from the lake) (Supplementary material Table S1, Supplementary material Fig. S4). It was, however, found in all four stations from the lake at depths of 6.8–8.2 m (Fig. 2A).

Cytherissa lacustris (Sars, 1863)

The species (Fig. 3B, Supplementary material Fig. S12) was recorded in 37 locations throughout Iceland, of which 35 were lakes (Table 1, Supplementary material Table S1, Supplementary material Fig. S3). It was the dominant species in 17 lakes, with a relative abundance of over 80%, and is the other most abundant species in Icelandic lakes beside *C. ophtalmica*. All dissected specimens were female.

Cytherissa lacustris was very abundant at depths of 20 m or more, where it was often the only recorded species. It was nevertheless found in abundance at various depths throughout lakes, although

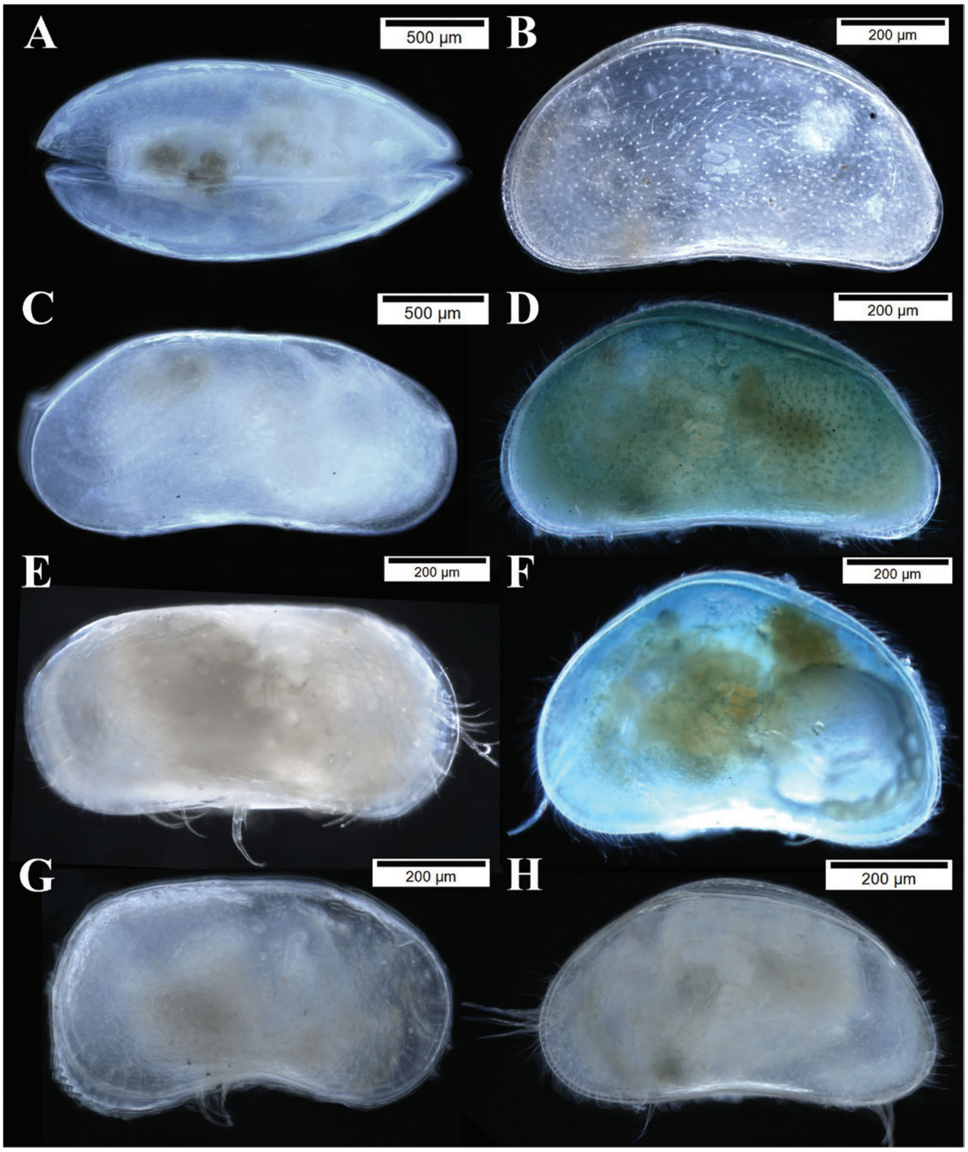

Figure 5. *Fabaeformiscandona* sp. (male, juvenile), dorsal view (**A**); right lateral view (**C**) from Þverá spring; *Potamocypris fulva* (white, left lateral view) from Grænavatn Norður Spring (**B**); *P. fulva* (green, left lateral view) from Hruni 2 Spring (**D**); *Limnocytherina sanctipatricii* (female, right lateral view) from Lake Lagarfljót (**E**); *Potamocypris villosa* (female, left lateral view) from Mælifellslaug Spring (**F**); *Limnocythere inopinata* (female, right lateral view) from Lake Stakhólstjörn (**G**); *Potamocypris pallida* (left lateral view) from Hruni 2 Spring (**H**).

it was mostly absent from littoral stone samples (Fig. 2A). Very few specimens were found in springs and cave pools.

Tonnacypris glacialis (Sars, 1890)

Only two specimens of *T. glacialis* (Figs. 3H, 7) were found in a single station in Lake Langisjór in the central highlands (Fig. 1, Supplementary material Fig. S4) at 20.2 m depth (Fig. 2A). Previous Iceland records also came only from the central highlands (Poulsen, 1939). The two specimens were female and light yellow in colour.

Bradleystrandesia affinis (Fischer, 1851)

Only one specimen of *B. affinis* (Supplementary material Fig. S13) was found in a surface sample of the limnocrene Botnar II Spring, southern Iceland (Fig. 1, Supplementary material Fig. S4). The specimen was female.

Heterocypris incongruens (Ramdohr, 1808)

This species (Fig. 3F, Supplementary material Fig. S14) was only found in one location, Nauteyri, a hot spring in the West Fjords (Fig. 1, Supplementary material Fig. S4), with water temperature ranging 25.5 °C–29.8 °C (Fig. 2D). Juveniles in various instar phases and adults were abundant in both source and surface samples. The two dissected specimens were female.

Potamocypris fulva (Brady, 1868)

This stygophilic species was found across Iceland (Fig. 1, Supplementary material Table S1, Supplementary material Fig. S3). In lakes, it was only found in the littoral zone, where it was usually the dominant species. It was also found in springs and cave pools (Table 1). It was the dominant species in the rheocrene Skarðslækur Spring, constituting almost 84% of the ostracods. It was the dominant species in six limnocrene springs and it was the only species in two cave pools (C17 and C21). Its absence in

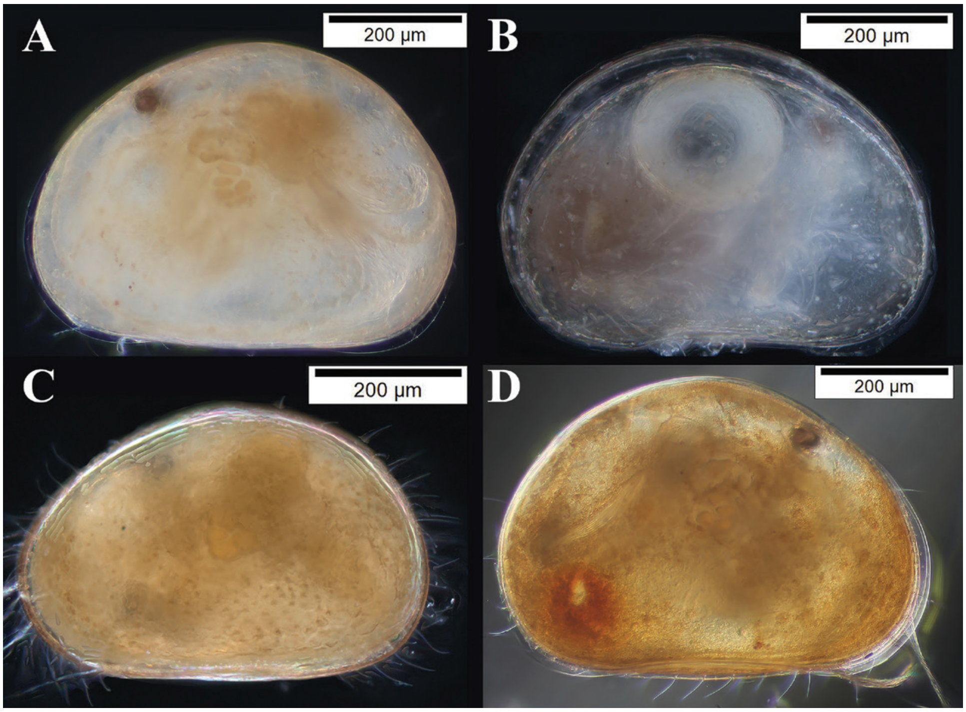

Figure 6. *Cypria ophtalmica* forma *lacustris* (male, left lateral view) from Lake Frostastaðavatn (**A**); *Cypria ophtalmica* (male) with the sperm coil visible from Lake Eystra-Gíslholtsvatn (**B**); *Cyclocypris ovum* (female, left lateral view) from Lake Hraunhafnarvatn (**C**); *Cypria ophtalmica* forma *ophtalmica* (male, right lateral view) from Lake Skálavatn (**D**).

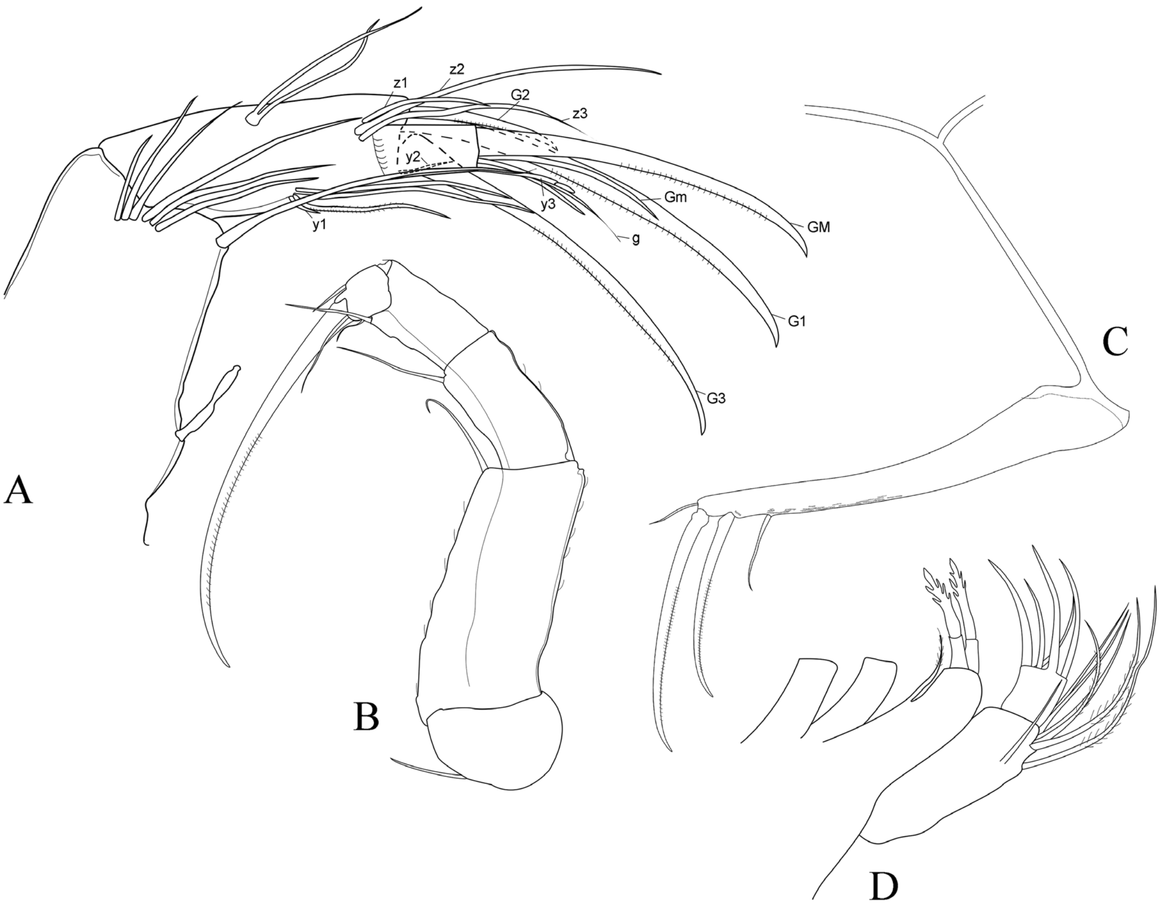

Figure 7. *Tonnacypris glacialis* (female). Antenna (**A**); walking leg (**B**); uropod (**C**); maxillula (**D**) from Lake Langisjór.

samples from the profundal zones of lakes and its presence in other habitats indicates its preference for shallow, constantly moving waters (Fig. 2A). The coloration varied between white, blue-green, and dark green (Figs. 5B, 5D), variants that were commonly seen in the spring samples. Only white specimens were found in lake samples, and green in cave pools. All eight dissected specimens were female (Supplementary material Fig. S15).

The examination of one of the specimens identified as *Potamocypris zschokkei* by Ólafsdóttir (2015) revealed that it belonged, based on shell morphology, to *Potamocypris fulva*.

Potamocypris pallida Alm, 1914

Potamocypris pallida (Fig. 5H, Supplementary material Fig. S16) was not found in any of the lakes or cave pools sampled but it was relatively abundant in springs, where it was found at 8 of 14 locations, mostly in the north and south, sometimes as the only species (Fig. 1, Supplementary material Table S1, Supplementary material Fig. S3). This species showed an affinity to cooler springs and was not found in waters with a temperature higher than 7.2 °C. It was the only species found in the coolest Miðhúsaskógur spring at the temperature of 2.4 °C (Fig. 2D). All three dissected specimens were female.

Potamocypris villosa (Jurine, 1820)

Potamocypris villosa (Fig. 5F, Supplementary material Fig. S17) was collected at three locations, a lake, one spring, and one cave pool, all in northern Iceland (Fig. 1, Table 1, Supplementary material Table S1, Supplementary material Fig. S4). It was only found in the samples from the littoral zone at Lake Grænavatn. Only four specimens were collected, all female.

Limnocythere inopinata (Baird, 1843)

Limnocythere inopinata (Fig. 5G, Supplementary material Fig. S18) was found at 16 locations, mostly in the north (Supplementary material Table S1, Supplementary material Fig. S3). It was found in lakes, though usually represented by only a few individuals, a few dozen at most. Notable exceptions were lakes Stakhólstjörn, Kötluvatn, and Mývatn, where it was found in large numbers and was the dominant species. It was also found in springs and it was the only species found in one of the cave pools (C7). Only females were found among the eight dissected specimens, but because of the effects of formaldehyde, it was impossible to tell sexes apart without dissection. The species tolerated a wide range of environmental conditions, and out of all the species collected, it thrived in more saline waters (Fig. 2B). It also tolerated a wide range of water temperatures (Fig. 2D). It was not found at depths below 8.2 m and generally preferred waters to 7 m depth (Fig. 2A).

Limnocytherina sanctipatricii (Brady and Robertson, 1869)

Limnocytherina sanctipatricii (Fig. 5E, Supplementary material Fig. S19) was found at 13 locations, all of which were lakes across the country (Supplementary material Table S1, Supplementary material Fig. S3). The numbers were always low, especially in proportion to other species, and their percentage did not exceed 5%, except in Grænavatn, where the species represented ~24% of the ostracods. The species was mostly collected from stations at 6–13 m depth, but also at 25 m in Lake Lagarfljót (Fig. 2A). All 12 dissected specimens were female.

DISCUSSION

The two species collected by Rabot (De Guerne & Richard, 1892), *Cypris pubera* and *Sarscypridopsis aculeata*, were absent among the 16 recorded species. The species reported by Haberbosch (1916), *Bradleystrandesia affinis*, which Poulsen (1939) described as the "most common of the Icelandic Ostracoda" was found at only one location (Supplementary material Table S1, Supplementary material Fig. S4). This could be due to the limited types of habitats we explored, although *B. affinis* was found in various locations, such as ditches, ponds, streams, and rivers (Poulsen, 1939).

As *Candona candida* is one of the most common freshwater ostracods throughout Eurasia and North America, commonly recorded in a wide range of aquatic habitats (Meisch, 2000) it is not surprising that it is widespread across Iceland as well. It is generally tolerant of various conditions, confirmed by its wide coverage in Iceland. *Cypria ophtalmica* is similarly a widespread and resilient species tolerant to a wide range of environmental factors including high organic pollution (Meisch, 2000). Like *C. candida*, it is omnipresent in Iceland. *Cytherissa lacustris* is generally considered a cold stenothermal species that has a preference for sublittoral and profundal zones of cold, deep lakes (Meisch, 2000). This holds true for Iceland too, as previously it has been found only in bottom samples of lakes (Poulsen, 1939), and although we found it in shallower waters, including springs, its affinity for profundal zones of lakes is clear. This species is also considered a bioindicator with regards to oxygen content due to its preference for well-oxygenated waters (Geiger, 1990), and considering its abundance in Iceland, at least during the 1990s, it could be a valuable proxy for future research. *Heterocypris incongruens* was previously found to inhabit Icelandic thermal waters (Schwabe, 1936), as well as colder waters (Poulsen, 1939). We found this species in one location, a hot spring, the only hot spring sampled.

The species composition of Icelandic freshwater ostracods represents assemblages typical of other Arctic and subarctic regions. Most of the Icelandic species, such as *Candona candida*, *Cyclocypris ovum*, and *Bradleystrandesia affinis* have also been found in northern Sweden, Norway and Finland (Poulsen, 1939; Iglikowska & Namiotko, 2012). Faroe Islands species are all also found in Iceland (Poulsen, 1929). Despite lying between Europe and North America, it is clear that the Icelandic species correspond more closely to the European fauna, as Iceland shares very few species with North America (Sars, 1926; Bunbury and Gajewsky, 2008). This is in agreement with the Icelandic biota in general showing Palaearctic affinities (Downes, 1988; Gíslason, 2005). *Cytherissa lacustris*, *Heterocypris incongruens* and *Tonnacypris glacialis* are examples of species found on both continents. Greenland, which shows a mix of European and North American ostracods, shares some species with Iceland, mainly those found in Northern Europe such as *Candona candida* and *Limnocytherina sanctipatricii* (Bennike *et al.*, 2000). Iceland also shares a number of species with Siberia, such as *Limnocythere inopinata*, *Cypria ophtalmica*, *Candona candida* and *Tonnacypris glacialis* (Wetterich *et al.*, 2008; Schneider *et al.*, 2016). Of the Arctic endemics, only *Tonnacypris glacialis*, a relatively widespread species (Griffiths *et al.*, 1998), was found in Iceland. There are, however, a few species that seem atypical in these regions but are found in Iceland. The only previous report of *Ilyocypris bradyi* from the Arctic was of subfossil valves from West Greenland sediments, and this species was considered to have gone extinct in the region after the end of the Holocene thermal maximum (Anderson & Bennike, 1997). *Potamocypris fulva* has similarly not been reported from other Arctic locations.

The ostracod fauna of Iceland, with 21 species reported here and in other studies, so far is clearly less species-rich than in regions such as Scandinavia, Siberia, or Canada, which could be a result of Iceland's smaller size and remoteness. The distance from other land masses means that it is much harder for new species to colonise Iceland, and the relatively harsh climatic conditions do not promote the establishment of consistent populations. Iceland nevertheless hosts an apparently above-average species richness when compared to remote islands such as Greenland, with 16 species (e.g., Jensen, 2003), Svalbard with 10 species (Hodkinson *et al.*, 2013), and the Faroe Islands with three species (Poulsen, 1929).

Because many ostracod species have a clear preference for particular habitats, we focused only on those species that inhabit fairly large, permanent, still-water bodies. Even by comparing the results from the lake dataset with springs and cave pools (Table 1), obvious differences in species distribution hint that the species list is not exhaustive. Species such as *Cypria ophtalmica*, *Cyclocypris ovum*, and *Limnocytherina sanctipatricii* found in many lakes were absent in any of the sampled springs. Conversely, *Potamocypris pallida* was exclusively found in springs. Some of the species found in both habitats nevertheless prefer a specific habitat. Such is the case of *Cytherissa lacustris*, recorded from only one spring but is one of the most common lake species, and *Potamocypris fulva*, the most common spring species, that was only collected from the littoral zone of lakes. Data from cave pools are more difficult to analyse due to the limited number of adult individuals collected. Samples usually contained a single adult specimen, both species typically found in springs and those typically found in lakes. Because the samples were collected at the entrance of caves, the specimens probably represent opportunistic occurrences rather than true cave species.

The majority of lake samples were taken during the 1990s. It is thus possible that ecological conditions in certain lakes might have changed since sampling so that new sampling could detect anthropogenic changes. The narrow parameter ranges of some species described in Figure 2 correspond with the low number of records. *Candona candida*, *Cytherissa lacustris*, and *Cypria ophtalmica* seem to have widest tolerance ranges with respect to most examined parameters but this could be the result of these species being by far the most abundant, while certain species, such as *Bradleystrandesia affinis* and *Ilyocypris decipiens*, have only been found at one location each. The data derived for the distribution of the latter are thus poorly represented and more detailed collections are required to understand their ecological requirements.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Table S1. Names of lakes and springs corresponding to numbers and letters indicated in Figure 1.

Table S2. List of species reported from Iceland during 1892–2017.

Figure S3. Distributional map of *Candona candida*, *Cytherissa lacustris*, *Cypria ophtalmica*, *Limnocythere inopinata*, *Potamocypris fulva*, *Cyclocypris ovum*, *Limnocytherina sanctipatricii*, and *Potamocypris pallida*.

Figure S4. Distributional map of *Potamocypris villosa*, *Cryptocandona reducta*, *Ilyocypris bradyi*, *Ilyocypris decipiens*, *Bradleystrandesia affinis*, *Heterocypris incongruens*, *Tonnacypris glacialis*, and *Fabaeformiscandona* sp.

Figure S5. *Candona candida* female.

Figure S6. *Fabaeformiscandona* sp. male juvenile.

Figure S7. *Cryptocandona reducta* female.

Figure S8. *Cypria ophtalmica* male and female.

Figure S9. *Cyclocypris ovum* male.

Figure S10. *Ilyocypris bradyi* female.

Figure S11. *Ilyocypris decipiens* female.

Figure S12. *Cytherissa lacustris* female.

Figure S13. *Bradleystrandesia affinis* female.

Figure S14. *Heterocypris incongruens* female.

Figure S15. *Potamocypris fulva* female.

Figure S16. *Potamocypris pallida* female.

Figure S17. *Potamocypris villosa* female.

Figure S18. *Limnocythere inopinata* female.

Figure S19. *Limnocytherina sanctipatricii* female.

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