https://doi.org/10.5194/egusphere-2025-6147
Preprint. Discussion started: 6 January 2026

Environmental and habitat controls on non-marine ostracod distribution in Arctic lakes

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Abstract

The Arctic is warming almost four times faster than the global average. Lakes in the Arctic are a prominent feature of the landscape and are consequently undergoing limnological and ecological change such as shifts in algal productivity, water column mixing depths, and ice persistence. Most recently, the nutrient-colour paradigm has been associated with extensive loss of benthic habitat. Ostracods (small aquatic crustaceans) are a significant contributor to the benthic biomass of shallow to mid-depth lakes (<20 m) and there is great potential to use fossil ostracods to reconstruct past environmental change and predict future ecosystem states in these lake-rich regions. However, relative to mid-latitude regions, little is known of the ecological traits of ostracods in the Arctic. Here we present the first systematic survey of ostracod species and ecological preferences for the Kangerlussuaq region of southwest Greenland, the largest ice-free margin of Greenland. *Candona candida* is a generalist species in the Kangerlussuaq region, being present in deeper lakes and at the higher end of the bioavailable soluble reactive phosphorus and nitrate gradients. These traits suggest that *C. candida* will become abundant in the Greenlandic ostracod fauna, and potentially across the Arctic. For some species, particularly *Cypris pubera,* bioavailable nutrient concentrations are a dominant control on distribution. Nutrient status of water appears to be a significant control

on ostracod presence and abundance and should be included in future ecological studies globally.

1. Introduction

Since 1979 CE, the Arctic has warmed almost four times faster than the global average (Rantanen *et al*., 2022). Changes to the physical environment are marked and ongoing, including permafrost thaw, retreating glaciers, reduced seasonal snow cover, increased river run off, longer ice-free periods both at sea and on lakes, and altered nutrient availability (Post *et al.,* 2009; Box *et al.,* 2019). Globally, in areas where temperature and solar radiation are increasing, and cloud cover is decreasing, seasonally ice-covered lakes are warming at an average summer surface temperature rate of 0.72 °C decade^{-1} (compared to an average lake warming of 0.34 °C decade^{-1}; O'Reilly *et al*., 2015).

Lakes in the Arctic are, therefore, particularly at risk of ecological and limnological transformations (Woolway *et al*., 022). With >3.5 million lakes in the Arctic, they are prominent features in the landscape (Paltan *et al*., 2015). There are still significant knowledge gaps for many aspects of Arctic freshwater biodiversity (Saros *et al.,* 2022) with much previous work focused on shifts in algal productivity related to increased and altered growing seasons owing to longer ice-free periods (e.g. Smol *et al*., 2005; Burpee and Saros, 2020). Longer periods of light penetration rapidly alter habitat structure, increasing primary productivity and lake mixing depths (Olsen *et al.,* 2012). With greater mixing depths, there is a consequent expansion of the lake littoral zone to deeper areas of the lake and 'benthification', i.e the increase of benthic productivity (Saros *et al*., 2019). Recent studies, however, have demonstrated that lakes have shifted from blue to brown (under the nutrient-colour paradigm) with higher nutrient concentrations (nitrogen [N] and phosphorus [P]) and a consequent extensive loss of benthic habitat due to light reduction (Saros *et al*., 2025).

Viable benthic habitat in lakes has important implications for whole lake productivity and functioning. Benthic primary productivity is often equal to or greater than phytoplankton productivity in the pelagic zone, particularly in low productivity Arctic lakes, and zoobenthos productivity accounts for 42 % of whole-lake secondary productivity (Vadeboncoeur *et al*., 2002). In addition, the sublittoral zone, where there is high benthic biodiversity, is particularly vulnerable to changes in temperature, oxygen availability and light penetration (McGoff *et al*., 2013). Consequently, this might ultimately favour organisms with wide ecological and environmental tolerances. More pertinent, however, is that shifts in diversity of benthic organisms are most likely to record and characterise environmental changes.

In shallow and mid-depth lakes (<20 m), ostracods (small benthic or nektobenthic aquatic crustaceans) can be a significant contributor to the benthic biomass (e.g. Geiger, 1998; Rodríguez-Pérez and Baltanás, 2008). As both consumers and producers, ostracods are an important component of the aquatic food web (Mesquita-Joanes *et al*., 2012). In addition to playing a vital role in the lake food web, non-marine ostracods are sensitive to a range of climatic and environmental conditions, including temperature (e.g. Horne, 2007), salinity (e.g. McCormack *et al*., 2019), pH (e.g. Wang *et al*., 2022), substrate (e.g. Higuti *et al*., 2010) and aquatic plant diversity and abundance (e.g. Frenzel *et al*., 2005). Consequently, fossil ostracod shells in lacustrine sediments are a commonly used indicator of climatic and environmental change in the Quaternary. However, insufficient knowledge of ecological preferences of species can lead to speculative or poorly constrained paleolimnological reconstructions (Greenway *et al*., 2024). This is of particular concern for studies in the Arctic since much of the ecological information known about ostracod species is based on present and past occurrence in mid-latitude regions. The difference in seasonality, ice persistence and occurrence, and daylight hours between the regions raises questions about the viability of transferring ecological traits. In Arctic environments the ecological niches and diversity of ostracods remain largely unknown (Schneider *et al*., 2016), particularly in Greenland (Smith and Horne, 2016). However, the Arctic, and particularly the benthic environment (e.g. Saros *et al*., 2025), is entering a new ecosystem state, which will not return to the previous state(s) within the next 100 years (AMAP, 2017). There is great potential to use palaeolimnology, and particularly ostracods, to reconstruct past environmental change and predict future ecosystem states in these lake-rich regions. There is, therefore, a pressing need to understand and characterise current environmental and habitat preferences of Arctic ostracod species to understand and interpret current, future and past change.

Previous surveys of freshwater cladoceran, copepod and ostracod crustaceans in Greenland have sampled around 300 waterbodies (Poulsen, 1940; Røen, 1962, 1968, 1970, 1981) recording 13 ostracod species and one variety (Table 1). Palaeolimnological studies (Bennike, 2000) and Bennike *et al*. (2000; 2010) have recorded a further three species (Table 1), giving 16 species recorded in total. Here, we provide the first systematic survey of ostracod species and ecological preferences for the Kangerlussuaq region of southwest Greenland, the largest ice-free margin of Greenland with a landscape comprising ~20,000 glacially-derived lakes, accounting for ~15% of the land area (Anderson *et al*, 2009). This density of lakes extending a range of environmental conditions allows a space-for-time approach in determining the ecological preferences of ostracod species.

Table 1. List of freshwater ostracods recorded in Greenland by Poulsen (1940), Røen (1962, 110 1968, 1970, 1981), Bennike (2000) and Bennike *et al*. (2000; 2010) with updated nomenclature following Meisch *et al.* (2024).

Ostracod species	**First recorded in Greenland by**
Cypris pubera O.F. Müller, 1776	Haberbosch, 1916
Eucypris affinis hirsuta (Fischer, 1851) = *Bradleystrandesia reticulata* (Zaddach, 1844)	Haberbosch, 1916
Eucypris virens (Jurine, 1820)	Alm, 1914
Cypris incongruens Ramdohr, 1808 = *Heterocypris incongruens* (Ramdohr, 1808)	Alm, 1914
Prionocypris glacialis Sars, 1890 = *Tonnacypris glacialis* (Sars, 1890)	Brehm, 1911
Prionocypris glacialis var. *albida* (Alm, 1914) = *Tonnacypris glacialis* var. *albida* (Alm, 1914)	Poulsen, 1940
Candona candida (O.F. Müller, 1776)	Alm, 1914
Candona lapponica Ekman, 1908 = *Fabaeformiscandona lapponica* (Ekman, 1908)	Haberbosch, 1916
Candona groenlandica Brehm, 1911 = *Fabaeformiscandona groenlandica* (Brehm, 1911)	Brehm, 1911
Candona rectangula (misspelling of *rectangulata*) Alm, 1914 = *Fabaeformiscandona harmsworthi* (Scott, 1899)	Alm, 1914
Candona subgibba Sars, 1926	Røen, 1962
Candona falcata Alm, 1914	Røen, 1962
Cypridopsis vidua (O.F. Müller, 1776)	Røen, 1962
Limnocythere sanctipatricii Brady & Robertson, 1869	Røen, 1962
Potamocypris parva Schmidt, 1976	Schmidt, 1976
Ilyocypris bradyi Sars, 1890	Bennike, 2000
Sarscypridopsis aculeata (Costa, 1847)	Bennike *et al*., 2000

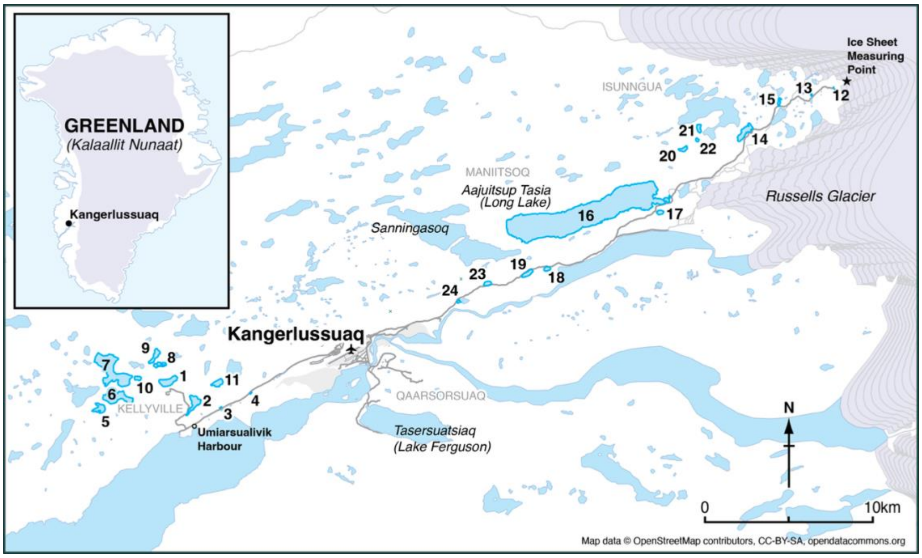
2. Methods

2.1 Study area

Twenty-four lakes (Table 2) <16 m deep in the Kangerlussuaq (67°00′N, 50°43′20″W) region located 0.4 to 48.3 km from the Greenland ice sheet (GrIS; Fig. 1) were sampled in July 2021. The transect characterised expected spatial trends in environmental and limnological conditions (e.g. glacial inflow versus aridity, depth, size) in the region. The study lakes are predominantly hydrologically isolated with no inflows and negligible input from groundwater or snowmelt (Anderson *et al*., 2001; Johansson *et al*., 2015), except those close to the GrIS, which are, in some circumstances, glacially fed (Burpee *et al*., 2018). The lakes furthest from the GrIS in Kellyville (Fig. 1) are oligosaline due to low precipitation, high rates of evaporation and locally derived salts (primarily an aeolian input). Annual precipitation is low (< 250 mm y^{-1}; Mernild *et al*., 2015; Box *et al*., 2023) and the mean annual temperature is -6 °C (Anderson *et al*., 2012). Conditions close to the ice sheet, at higher elevations, are on average 2-3 °C cooler and with >10 mm more precipitation per month (Fowler *et al*., 2020).

2.2 Field methods

Water column profiles of chlorophyll-*a*, dissolved oxygen (DO), pH, temperature and electrical conductivity (EC) at the deepest point of the lakes were measured using a YSI EXO2 multiparameter probe, which was set to log at 2 second intervals. The presence of an oxycline was assessed by subtracting the DO of bottom waters from the DO of surface waters. For pH, temperature, salinity and chlorophyll-*a*, an average value for the top 2 m was calculated to represent values for the surface mixed layer and where ostracods were sampled. Secchi depth to determine water clarity was measured using a Secchi disk. Water samples for the determination of nutrient concentrations were collected from the same location using HCl-washed bottles. Samples were filtered with Whatman GF/F 0.7 µm filters, or with 0.4 µm polypropylene filters for silicate. Ostracods were collected in a 250 µm mesh zooplankton net from the littoral zone. Where submerged macrophytes were present, samples were collected from amongst the vegetation and included sampling the top ~1 cm of sediment. Water colour, substrate and the dominant vegetation were noted from the littoral zone. Benthic images and videos were taken using an underwater camera and used to identify if submerged macrophyte cover was evident across the littoral zone. These videos were also used to visually determine water colour as clear, green, green/brown and brown. Lake area was calculated at a later date using the polygon function in Google Earth.



Map data © OpenStreetMap contributors, CC-BY-SA, opendatacommons.org

Figure 1. Location of the study lakes in Kangerlussuaq, Greenland, showing the 24 study lakes in a SW-NE gradient. The numbers indicate lake ID and distance from the ice sheet has been calculated from the location denoted with a star.

https://doi.org/10.5194/egusphere-2025-6147
Preprint. Discussion started: 6 January 2026

Table 2. Physical and habitat characteristics of the 24 study lakes

Lake ID	Scientific name in Anderson *et al.* (2001)	Location	Depth (m)	Area (m^2)	Distance to ice sheet (km)	Altitude (m)	Substrate	Dominant Macrophyte	Water colour
1	SS2	66.995222, -50.968638	11.8	376628	44.03	187	Sandy silt		Green
2	SS1 (Lake Helen)	66.981583, -50.930833	5.8	357041	43.1	132	Sandy silt	Hippuris	Green
3		66.981694, -50.89100	1.4	2262	41.9	136	Organic lake mud	Filamentous algae	Clear
4		66.990027, -50.849416	1.7	6215	39.81	103	Organic lake mud	Charophytes	Clear
5	SS85	66.983111, -51.056388	11.9	278847	48.26	178	Gyttja		Green
6	SS4 (Braya Sø)	66.986388, -51.016666	9.4	794644	47.14	170	Sandy silt	Elodeids	Green
7	SS3 (Hunde Sø)	66.994222, -51.025611	12.1	1963022	46.85	175	Sandy silt	Isoetids	Green
8		67.005722, -50.98002	9.1	189529	43.98	200	Sandy silt	Elodeids	Brown
9	SS1590	67.007944, -50.987916	12.9	234911	44.35	199	Gyttja	Elodeids	Brown
10		66.997702, -51.003833	2.3	84145	45.51	194	Gyttja	Isoetids	Brown
11		66.995555, -50.89688	1.5	180272	41.29	198	Organic lake mud	Menyanthes	Brown
12		67.152694, -50.049861	0.7	619	0.37	516	Silty clay		Brown/Green
13		67.149083, -50.080388	2.8	8279	1.77	439	Organic lake mud	Hippuris	Brown
14	SS903	67.126611, -50.174333	13.9	359590	6.27	337	Sandy silt	Isoetids	Clear
15		67.144222, -50.125694	4.6	51861	3.71	400	Sandy silt		Brown/Green
16	Aajuitsup Tasia (Long Lake)	67.093027, -50.302000	13.2	12832147	17.43	250	Coarse gravel sand		Green
17		67.086694, -50.290527	3.9	17594	13.32	235	Organic lake mud	Filamentous algae	Green
18		67.056416, -50.442388	2.4	80643	20.68	169	Silty clay	Hippuris	Green
19		67.055055, -50.464805	10.7	153816	21.8	180	Organic lake mud		Brown/Green
20	SS906	67.119694, -50.255666	15.7	93240	9.97	405	Organic lake mud		Green
21	SS901	67.130361, -50.233500	15.7	121336	8.7	399	Organic lake mud	Isoetids	Clear
22		67.125861, -50.239472	5.5	27703	9.07	400	Sandy silt		Brown
23		67.048469, -50.523258	1.9	45513	24.13	401	Organic lake mud	Isoetids	Brown
24		67.039277, -50.563944	3.6	27341	26.24	177	Organic lake mud	Filamentous algae	Brown

2.3 Laboratory methods

2.3.1 Water chemistry

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Samples for dissolved nutrients were passed through 0.7-μm GF/F filters and analysed colorimetrically by the molybdate blue method for soluble reactive phosphorus (SRP), azo dye method for nitrite (NO_2-N), which included a cadmium reduction step for nitrate (NO_3-N), the indophenol blue method for ammonium (NH_4-N), and the molybdenum yellow method for silicate (Mackereth et al. 1989). The dissolved inorganic nitrogen forms were summed to give total dissolved inorganic nitrogen (TDIN). Bicarbonate and carbonate alkalinity (summed to total alkalinity) were determined through titrations with 0.1N hydrochloric acid (Mackereth et al. 1989). Chlorophyll *a* (Chl-*a*) was measured by filtering a known volume of water through a GF/F filter, extraction of the filtered residue and trichromatic analysis on a spectrophotometer (Jeffrey and Humphrey 1975).

2.3.2 Ostracod identification

Sediment samples were wet-sieved at 250 μm, to remove any remaining fine sediment. Sample residue was dried in an oven at 40 °C and weighed to calculate dry weight. Ostracod shells were picked under low-power stereo microscope using a 0000-paintbrush. A total of 100 ostracods were picked or the whole sample, depending on which limit was reached first. Using the dry weight, or, where 100 ostracods were picked, the picked fraction, the number of individuals per gram dry weight was calculated.

Although ostracods comprise two valves, it is not possible to determine paired valves once they become disarticulated, which can occur naturally or during sample processing. Therefore carapaces, single valves and fragments >half a valve (allowing identification but also ensuring fragments of the same valve were not duplicated in the count) were treated as one individual. The number of carapaces with soft parts was noted and used as an indicator of individuals that were living at the time of collection.

Ostracod specimens were sorted and mounted on standard micropalaeontological slides, and identified using Meisch (2000) and Fuhrmann (2012) together with other literature as appropriate. Selected specimens were imaged using a Jeol JSM-6480LV Scanning Electron Microscope at University College London. Ostracods were mounted on double-sided carbon tape on aluminium stubs and coated with gold palladium before examination. Figured specimens are to be deposited in the Natural History Museum (catalogue numbers will be allocated once the paper has been accepted for publication).

2.4 Statistical methods

Spatial patterns in species composition were determined by grouping the 24 lakes into clusters according to their similarity in ostracod assemblages based on Ward's method hierarchical

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clustering using the Pheatmap package in R version 4.4.1 (Kolde, 2025). The Corrplot package in R version 4.4.1 (Wei and Simko, 2024) was used to test for any statistically significant correlations between environmental variables. Any variables that were significantly correlated were excluded from further analysis. Multivariate correlations between ostracod species and environmental variables were examined using Redundancy Analysis (RDA). Variance partitioning analysis (VPA) was undertaken using the Vegan package in R version 4.4.1 (Okasen *et al*. 2025). For inclusion in statistical tests, the dominant submerged macrophytes, presence of an oxycline, water colour and substrate were converted from categorical data to numeric.

3. Results

3.1 Limnology

For the twenty-four lakes, the dominant substrate was organic lake mud with low growing isoetid form macrophytes being the most common macrophytes. In 7 lakes, no aquatic plants were observed. Water colour was categorised through observations as green in 9 lakes, brown in 8 lakes and brown/green in 3 lakes (Table 2).

The electrical conductivity (EC) of the lakes ranged from 0.9 to 4.1 mS cm^{-1}, with the highest EC in lake 7 and lowest in lake 15 (Table 3). Water temperature ranged from 9.50 to 10.49 °C at lake 1 and lake 24. Total Alkalinity ranged from 0.2 meqL^{-1} in lake 15 to 20.9 meqL^{-1} in lake 7. pH ranged from 7.7 in lake 13 to 9.7 in lake 19. All lakes were ultra-oligotrophic to mesotrophic; soluble reactive phosphorus (SRP) ranged 1.9 to 49.7 µgL^{-1} from lake 9 to lake 3 and nitrate (NO_3-N) concentrations were highest in lake 12 at 12.3 µgL^{-1}. The concentrations were below detection limit in lakes 1, 2, 7, 14 and 16. Chlorophyll-*a* ranged from 0.06 µgL^{-1} in lake 22 to 2.65 µgL^{-1} in lake 13.

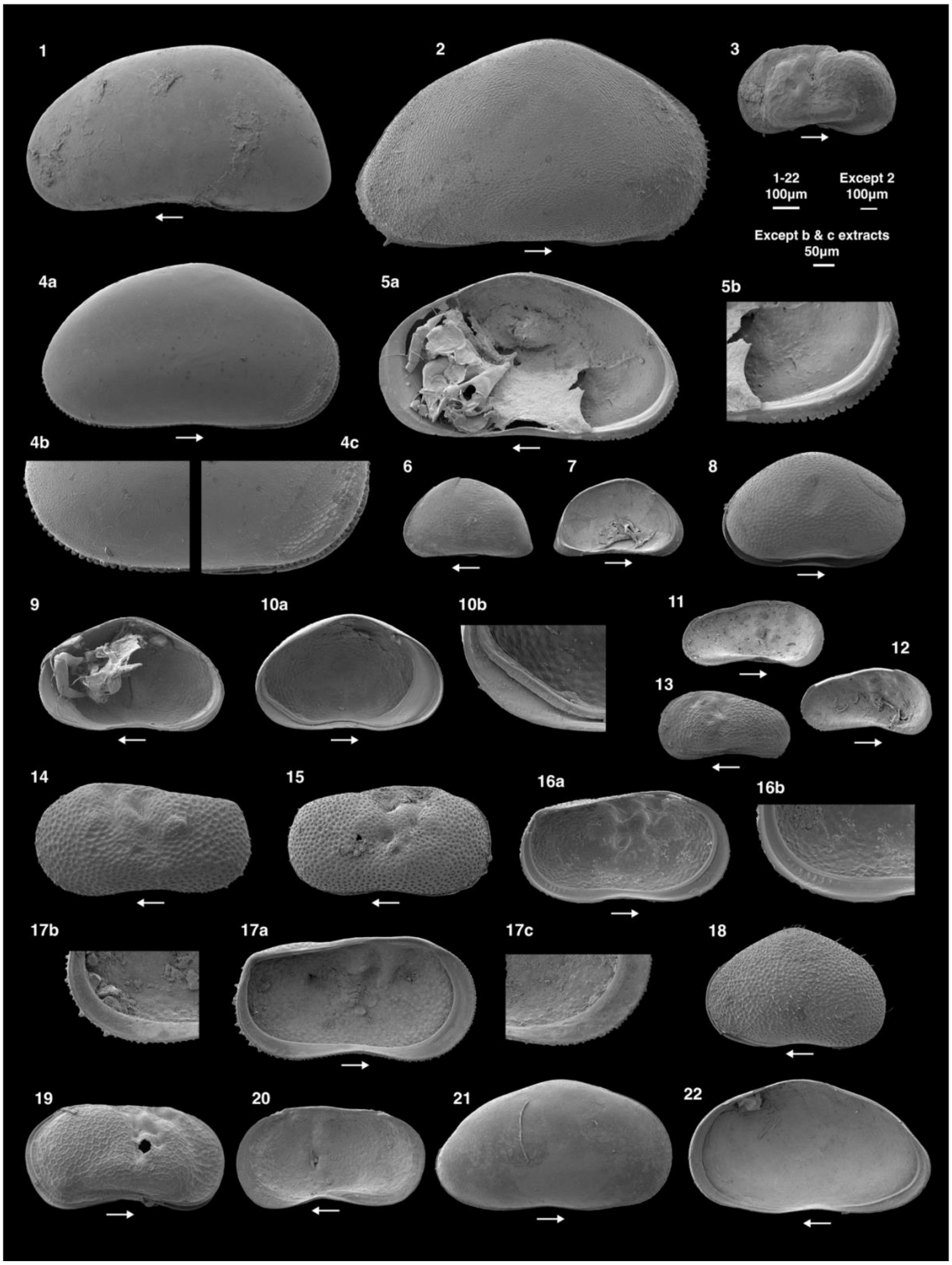
Secchi depth, altitude, silicate, total dissolved inorganic nitrogen, nitrite, ammonium, water temperature and the macrophyte cover were all significantly correlated (at $p < 0.001$ or $p < 0.01$ and an $r > 0.42$) with at least two other variables (Table S1; Fig. S1).

Table 3. Water composition and chemistry recorded in July 2021 in the 24 study lakes

Lake ID	Electrical conductivity (mS cm^{-1})	SRP (µgL^{-1})	NO_3^- (µgL^{-1})	Chlorophyll-*a* (µgL^{-1})	Total alkalinity (mgL^{-1})	pH
1	0.4	5.73	BDL	0.31	3	8.5
2	0.16	3.34	BDL	1.01	1.2	8.6
3	0.87	49.66	7.75	1.27	4.15	8.1
4	1.19	24.59	3.88	1.27	5.15	8.6
5	0.68	BDL	2.58	0.22	4.6	8.6
6	3.00	4.26	2.58	0.34	15.6	8.4
7	4.09	14.19	BDL	0.09	20.9	9.1
8	0.99	BDL	3.82	0.29	5.05	9.2
9	0.32	1.87	1.27	0.38	2.45	8.8
10	0.71	2.8	1.27	0.77	5.2	8.2
11	0.15	BDL	2.55	0.37	1.1	9.3
12	0.07	14.43	12.27	0.37	0.55	8.8
13	0.17	6.77	3.51	2.65	1.15	7.7
14	0.19	3.16	BDL	0.18	1.7	8.2
15	0.01	4.96	1.75	0.34	0.2	8.3
16	0.11	BDL	BDL	0.11	1.05	8.2
17	0.7	3.61	1.75	0.51	5.4	8
18	0.47	6.31	1.75	0.24	4.25	9.3
19	0.54	2.71	3.51	0.75	4.75	9.7
20	0.07	1.96	2.59	0.21	0.5	8.1
21	0.1	2.45	2.59	0.23	0.8	8.0
22	0.09	2.45	2.59	0.59	0.8	8.4
23	0.51	2.43	4.24	2.36	3.7	8.9
24	0.16	1.94	2.12	0.89	1.1	8.8

3.2 Ostracod fauna

Thirteen species of ostracods were recorded across the study lakes (Fig 2; Fig 3). Other than *Limnocythere friabilis* Benson & MacDonald, 1963 and species of *Ilyocypris*, some individuals with soft parts were collected (Table S2) and so were assumed to be living at the time of collection. The most abundant species was *Cypris pubera* O.F. Müller, 1776, with a maximum abundance of 87 valves per gram in lake 17. *Candona candida* (O.F. Müller, 1776) was present in the most sites (n = 20) with *Ilyocypris gibba* (Ramdohr, 1808) present in the fewest (n = 1). Shells of *Candona* juveniles were present in 10 sites, all of which also had adult *C. candida* individuals present. *Cypridopsis vidua* (O.F. Müller, 1776), *Ilyocypris bradyi* Sars, 1890, *Ilyocypris gibba*, *Sarscypridopsis aculeata* (Costa, 1847) and *Potamocypris parva* Schmidt, 1976 were rarely recorded, occurring at 1 to 6 sites at an abundance of no more than 3, 2, 2 and 2 valves per gram respectively. *Arctocypris* sp., *Heterocypris incongruens* (Ramdohr, 1808)., *L. sanctipatricii* (Brady & Robertson, 1869) and *L. inopinata* (Baird, 1843) were somewhat abundant with maximum abundances of 7, 15, 15 and 11 valves per gram, and occurring in 4 to 7 sites. Ostracods were not recorded in 3 sites (lake 1, 4 and 16). The highest diversity of eight species was recorded in lake 6. Lowest diversity of 1 species was recorded in lakes 13, 14, 20 and 24. At each of these lakes, the only species recorded was *C. candida*.



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Preprint. Discussion started: 6 January 2026

Figure 2. Scanning electron microscope images of ostracod species collected from the 24 study lakes. The 100 µm scale bar applies to images 1-20, the 200 µm scale bar to image 2 and the 50 µm scale bar to the b and c extracts. The lake in brackets represents where the specimen was collected. 1. *Candona candida*, female, LV (Lake 7); 2. *Cypris pubera*, female, RV, (Lake 17); 3. *Limnocythere inopinata*, female, RV (Lake 7); 4a. *Heterocypris incongruens*, female, RV external; 4b. extract of the posterior margin of 4a; 4c. extract of the anterior margin of 4a (Lake 17); 5a. *Heterocypris incongruens* with evidence of soft parts, female, RV internal; 5b. extract of the posterior margin of 5a. The flange on the anterior margin is visible in 5a (Lake 17). Images 4a,b,c, and 5a,b are of the same individual; 6. *Potamocypris parva*, assumed female since males are not known, LV (Lake 7); 7. *Potamocypris parva*, assumed female since males are not known, LV internal (Lake 7). Images 6 and 7 are of the same individual; 8. *Cypridopsis vidua*, female, carapace (Lake 18); 9. *Cypridopsis vidua*, female, RV (Lake 18); 10a. *Cypridopsis vidua*, female, LV (Lake 18); 10b. extract of the posterior margin of 10a. Images 8, 9, 10a and 10b are of the same individual; 11. *Limnocythere friabilis*, female, LV internal (Lake 7); 12. *Limnocythere friabilis*, female, juvenile, LV internal (Lake 7); 13. *Limnocythere friabilis*, female, juvenile, LV (Lake 7). Images 12 and 13 are of the same individual; 14. *Ilyocypris bradyi*, female, LV (Lake 6); 15. *Ilyocypris gibba*, female, LV (Lake 6); 16a. *Ilyocypris bradyi*, female, LV internal (Lake 7); 16b. extract of the posterior margin of 16a with no ripplets on the inner lamella; 16c. extract of the anterior margin of 16a. Images 14 and 16a,b,c are of the same individual; 17a. *Ilyocypris gibba*, female, LV internal (Lake 7); 17b. extract of the posterior margin of 16a with six visible ripplets on the inner lamella. Images 15 and 17a,b are of the same individual; 18. *Sarcypridopsis aculeata,* female, adult, LV (Lake 6; N.B this individual was not collected during the July 2023 survey). 19. *Limnocythere sanctipatricii*, female, carapace (Lake 9); 20. *Limnocythere sanctipatricii*, female, RV (Lake 9); 21. *Arctocypris* sp., A-1, RV (Lake 7); 22. *Arctocypris* sp., A-1, RV internal (Lake 7). Images 21 and 22 are of the same individual.

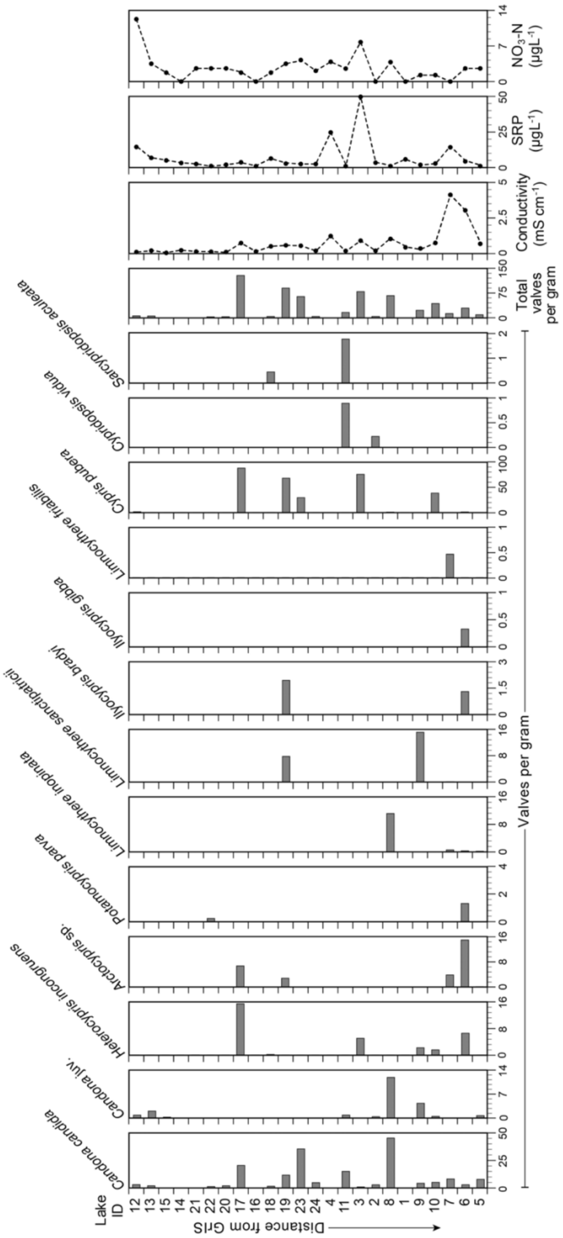

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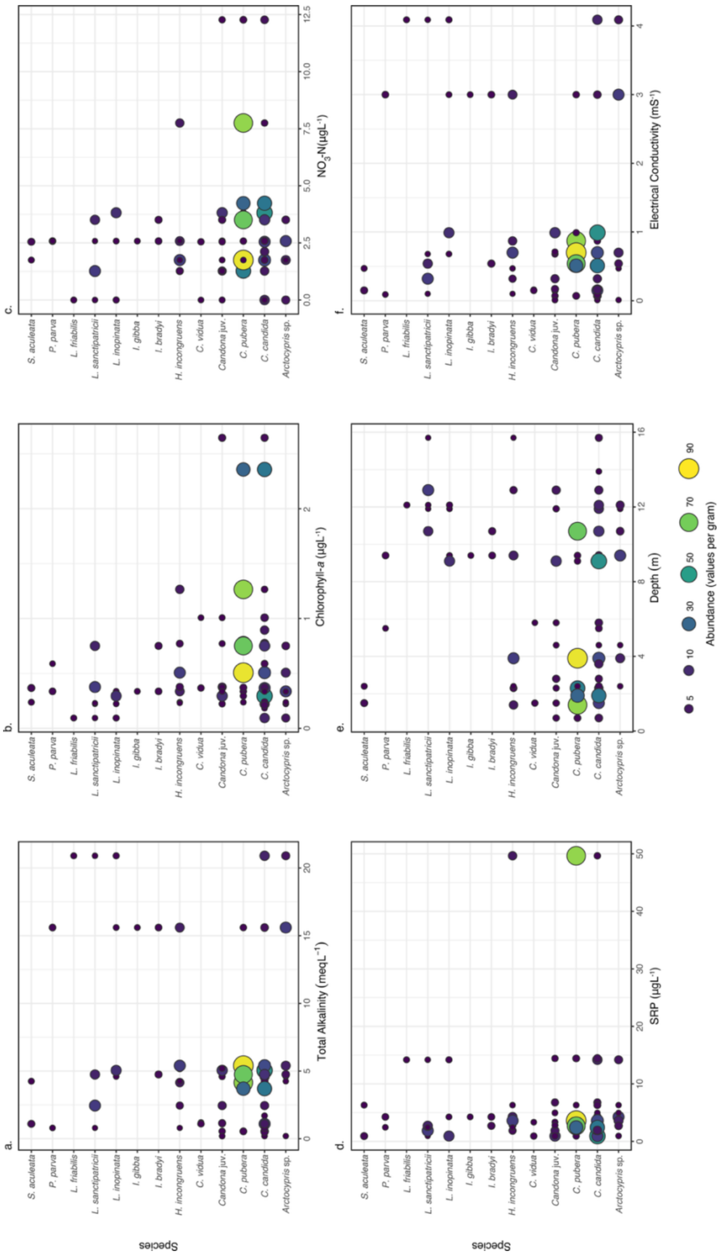
Figure 3. Ostracod species abundance as valves per gram in each of the 24 study lakes alongside selected recorded environmental variables (electrical conductivity, soluble reactive phosphorus [SRP] and nitrate [NO_3-N]). Lakes are ordered in the distance from the

300 Greenland Ice Sheet.

3.3 Abundance of ostracod species along environmental gradients

All ostracod species except *Arctocypris* sp. were most abundant at low total alkalinity (≤5.4 meqL^{-1}; Fig. 4a). *Cypridopsis* sp. and *S. aculeata* were not present at total alkalinity values above this. *Cypris pubera* and *C. candida* were the only ostracod species abundant above chlorophyll-*a* concentrations of 2 µgL^{-1}, with only *Candona* juveniles also present (Fig. 4b). *Heterocypris incongruens* and *Candona* juveniles were abundant between 0.2 and 0.8 µg Chl-*a* L^{-1}. *Heterocypris incongruens*, *Cypridopsis vidua*, *Cypris pubera, S. aculeata, I. bradyi, I. gibba, P. parva* and *Candona* juveniles were not present below Chlorophyll-*a* concentrations of 0.2 µgL^{-1}. *Candona candida* and *C. pubera* were most abundant at NO_3-N concentration between 1.3 and 4.2 µgL^{-1} (Fig. 4c). Only *C. pubera*, *H. incongruens, C. candida* and *Candona* juveniles were present at concentrations above this. Other than *L. friabilis*, which was most abundant at concentrations of 14.2 µgL^{-1}, all species were most abundant at SRP concentrations of <6.8 µgL^{-1} (Fig. 4d). Only three species were present at the highest SRP concentration of 49.7 µgL^{-1} namely *C. pubera*, which was very abundant (at 75 valves per gram), *C. candida* and *H. incongruens*. *Potamocypris parva, L. friabilis, L. inopinata L. sanctipatricii, I. bradyi, I. gibba., C. candida* and *Candona* juveniles are most abundant at depths >9 m (Fig. 4e). *Cypridopsis vidua* was only present at depths <6m and *C. pubera* was most abundant at depths <4m. All ostracod species were most abundant at EC <1 mS cm^{-1}, other than *Arctocypris* sp. (Fig 4f). *Cypris pubera*, *Cypridopsis vidua* and *S. aculeata* were not present at EC concentrations above this. *Cypridopsis* vidua. was only present at EC concentrations between 0.15 and 0.16 mS cm^{-1}. Lakes 5, 6, 7, 8, 9 and 10 are oligohaline and nine species were present at EC concentrations >3 mS cm^{-1}; of these *L. friabilis L. sanctipatricii, L. inopinata*, *I. bradyi, I. gibba, C. candida* and *Arctocypris* sp. were present at the EC concentration of 4.09 mS cm^{-1}. At the lowest EC concentration of 0.01 mS cm^{-1}, only *C. candida*, *Candona* juveniles and *Arctocypris* sp. were present. Both species of *Ilyocypris* were only present at EC concentrations above 0.54 mS cm^{-1} and *L. inopinata* and *L. sanctipatricii* at concentrations >0.32 mS cm^{-1} (Fig. 4f).



330 **Figure 4.** Abundance of ostracod species along gradients of a) total alkalinity, b) chlorophyll-*a* concentration, c) nitrate (NO_3-N) concentration, d) soluble reactive phosphorus (SRP) concentration, e) water depth and f) electrical conductivity.

https://doi.org/10.5194/egusphere-2025-6147
Preprint. Discussion started: 6 January 2026

3.4 Lake clusters

Based on ostracod assemblages, three clusters of lakes were identified (Fig. 5). Cluster 1 (4 lakes – 17, 19, 3, 10) is characterised by high abundance of *C. pubera*. Cluster 2 (12 lakes) is characterised by high abundance of *C. candida*. Cluster 3 (5 lakes – 13, 15, 21, 6, 9) is characterised by a more diverse ostracod fauna with high abundances of *Candona* juv, *H. incongruens.*, *Arctocypris* sp., *L. inopinata, L. sanctipatricii* and *P. parva* with intermediate abundance of *C. candida.* Cluster 3 lakes also have the lowest abundances of *C. pubera* and *Cypridopsis* vidua. A fourth cluster (3 lakes – 1, 4 and 16), not depicted on Fig. 5, is characterised by the absence of ostracods.

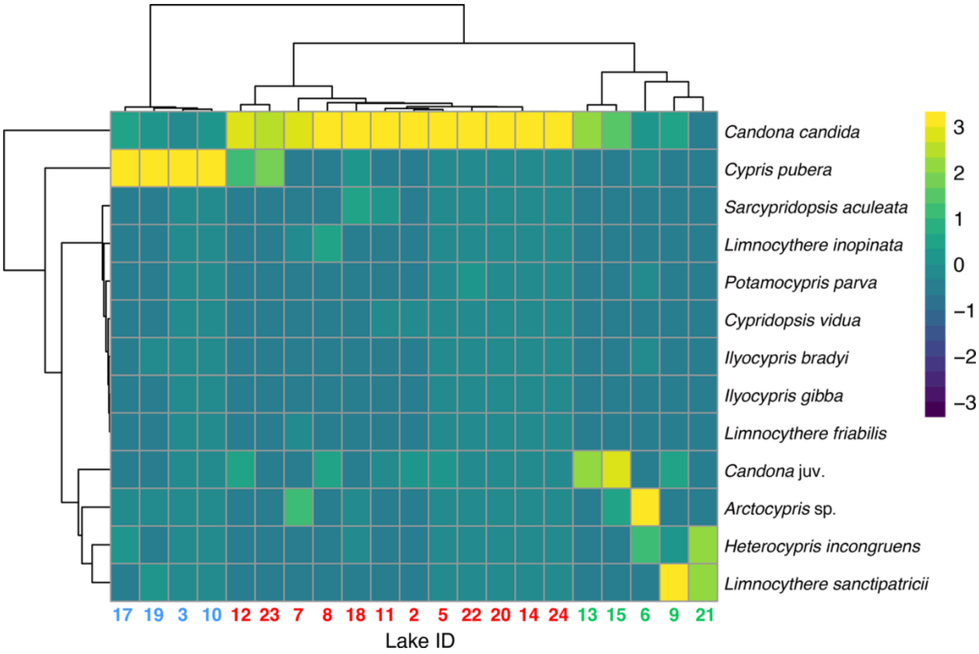


Figure 5. Identification of 3 clusters (cluster 1 N=4, cluster 2 N=12, cluster 3 N=5) based on ostracod assemblages Ward's method hierarchal clustering. A fourth cluster (N=3) is not depicted as no ostracod species were recorded in these lakes. Clusters are colour coded on the x-axis (Group 1 in blue, Group 2 in red, Group 3 in green and Group 4 in yellow). These colours correspond to grouping in Figure 6.

RDA axis 1 is negatively correlated with EC and positively correlated with lake area and substrate and explains 16.23% of variation (Fig. 6). Axis 2 is positively correlated with presence of an oxycline and nutrients and is negatively correlated with the presence of submerged macrophytes and depth. Axes 1 and 2 together explain 28.94 % of variation. Cluster 1 lakes are characterised by the lowest depths (mean 4.6 m, ranging from 1.4 to 10.7

m), higher SRP (mean 14.7 µgL^{-1}, ranging from 2.7 to 49.7 µgL^{-1}), higher NO_3-N (mean 3.6 µgL^{-1}, ranging from 1.3 to 7.8 µgL^{-1}) and higher chlorophyll-*a* (mean 0.82 µgL^{-1}, ranging from 0.51 to 1.27 µgL^{-1}). Cluster 2 lakes, on the other hand, are characterised by lowest mean chlorophyll-*a* (0.50 µgL^{-1}, ranging from 0.09 to 2.36 µgL^{-1}) and, although still high for lakes, the lowest pH (8.7, ranging from 8.0 to 9.3). Cluster 3 lakes are the deepest (mean 9.08 m, ranging from 2.8 to 15.7 m), encompass the oligohaline lakes 6 and 9 so have the highest EC (0.72 mS cm^{-1}, ranging from 0.01 to 3.00 mS cm^{-1}), lowest SRP (4.1 µgL^{-1}, ranging from 1.9 to 5.0 µgL^{-1}) and the majority of lakes (3 of 5 lakes) are within 10 km of the GrIS. In contrast, the majority of lakes in cluster 4 (2 of 3) are ≤40 km from the GrIS and have the largest average area (4.4 km^2, ranging from 0.01 km^2 to 12.8 km^2). Lakes in cluster 4 also have the lowest average NO_3-N (1.29 µgL^{-1}, ranging from BDL to 3.88 µgL^{-1}) and lowest total alkalinity (3.1 meqL^{-1}, ranging from 1.1 to 3.0 meqL^{-1}). There were also no macrophytes present in cluster 4 lakes other than the presence of filamentous algae in lake 3.

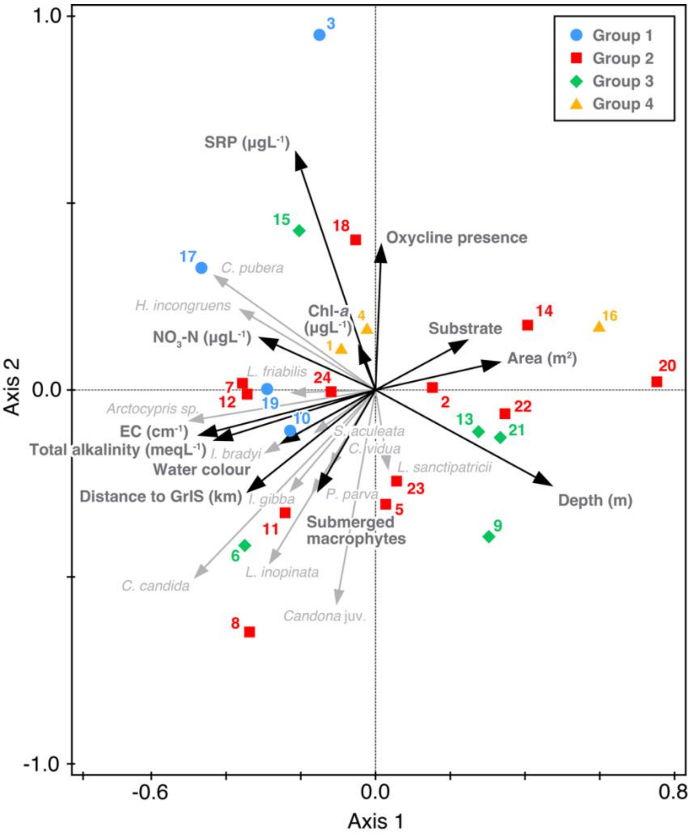


Figure 6. Redundancy analysis of ostracod species and selected environmental variables for the 24 study lakes

4. Discussion

Over recent decades, mean June air temperatures have increased by 2.2 °C and mean winter precipitation has doubled with continued predicted increased precipitation in SW Greenland (Saros *et al*., 2019; Huai *et al*., 2025). Reponses to recent warming have been non-linear but include increasing ice sheet discharge (van As *et al*., 2018), increasing dust deposition (Bullard and Mockford, 2018), and earlier ice out (Hazuková *et al*., 2024). It is, therefore, expected for lakes to become more nutrient rich due to wind-driven P in dust (Prater *et al*., 2022) and snowmelt-derived N (Whiteford *et al*., 2016), water colour to be more brown from increased dissolved organic material, mixing regimes and growing seasons to be altered from longer ice-out periods, and benthic productivity to decline (Saros *et al*., 2025). Spatial controls on water chemistry, particularly distance from the GrIS, have previously been documented and include increases in EC with distance from the GrIS, due to increases in aridity (Aebly and Fritz, 2009; Fig. 3), and higher nutrient concentrations in lakes close to the GrIS (Prater *et al*., 2022), particularly in those lakes that are glacially fed (Grider *et al*., 2025).

4.1 Controls on ostracod species distribution in Kangerlussuaq

Our results indicate a more complex pattern of nutrient distribution with lakes close to the GrIS and a spatial cluster of lakes (3 and 4) having higher concentrations in SRP and NO_3^-. Total phosphorus (TP) and NO_3^- concentrations in glacially fed lakes have been shown to be three times higher than in snowmelt fed lakes (Grider *et al*., 2025). Lower bioavailable nutrient concentrations in Kellyville lakes (those located furthest from the GrIS; Fig. 1) could be related to the reduced wind speed at >10 km from the GrIS (Heinemann, 1999) therefore decreasing dust derived P (Burpee *et* al., 2016; Prater *et al*., 2022). As expected, therefore, highest NO_3^- N concentrations (12.27 μgL^{-1}) were in lake 12, which is glacially fed and located 0.37 km from the GrIS. After lakes 3 and 4, lake 12 had the third highest SRP concentrations of 14.43 μgL^{-1}. Lake 15 (GL6 in Grider *et al*., 2025) is located 3.71 km from the GrIS but has relatively low NO_3-N concentrations (1.75 μgL^{-1}) with high SRP concentrations (4.96 μgL^{-1}). Meltwater is therefore likely a dominant source of nutrients with N concentrations derived from atmospheric deposition on the ice sheet and P derived from geological weathering of the glacial bed (Hawkings *et al*., 2016). However, previous work has suggested that most of this mineralogically-derived P is not biologically available (Burpee *et al*., 2018).

Consequently, cluster 1 lakes, which have high SRP (mean 14.7 μgL^{-1}, ranging from 2.7 to 49.7 μgL^{-1}), NO_3-N (mean 3.57 μgL^{-1}, ranging from 1.3 to 7.8 μgL^{-1}), and chlorophyll-*a* (mean 0.82 μgL^{-1}, ranging from 0.51 to 1.27 μgL^{-1}) are likely to become more dominant in the

Kangerlussuaq landscape in the future. Higher nitrate concentration in lakes is associated with water colour (brown and brown/green) and higher chlorophyll-*a* concentrations (0.51 to 1.27 µgL^{-1}; Fig. 6). Cluster 1 lakes are characterised by a high abundance of *C. pubera* (Fig. 5), which is most abundant at depths <4 m but present and still relatively abundant between 8 and 12 m. Here the species is only present in lakes with an EC <1 mS cm^{-1} but reportedly found at salinity up to 4 ‰ (~7.3 mS cm^{-1}; Stephanides, 1948). In paleolimnological records of high salinity lakes in the region (SS6, Lille Saltsø and Store Saltsø), *C. pubera* has been considered rare, being only recorded in two lake basins across Greenland (Bennike, 2000; Bennike *et al.,* 2000; Bennike *et al*., 2010). Whilst *C. pubera* is considered abundant in our study, *C. pubera* was not present in the Kellyville 'salt' lakes, suggesting high salinity significantly limits distribution in the Kangerlussuaq region.

In general, information on nutrient status of lakes is often not included when documenting ostracod species presence and abundance. In a study of three ponds in Patagonia, however, *C. pubera* was most abundant in the pond with highest TP of 121. 4 µgL^{-1}, suggesting an ecological preference for higher nutrient availability. A preference for waters with higher nutrient concentrations may be related to food source. *Cypris pubera* is omnivorous, feeding on algae, bacteria and daphnia (Meisch, 2000; Coviaga *et al*., 2015). In lakes 3, 10 and 19, *C. pubera* was present in very high numbers (75, 38 and 67 valves per gram respectively). These lakes have high coverage of filamentous algae or large *Nostoc* cyanobacteria balls, colloquially named sea tomatoes. It is likely, therefore, that *C. pubera* is present in large numbers in these lakes due to a dietary preference.

Cluster 1 lakes are typically shallower (<4.6 m) than those belonging to other clusters. Most ostracod species that are abundant in deeper lakes are not present above NO_3-N concentrations of 4.24 µgL^{-1} (Fig. 4c,e). Cluster 3 lakes are on average the deepest and are characterised by a diverse ostracod fauna including *L. inopinata, H. incongruens*, *Arctocypris* sp., *P. parva, L. sanctipatricii, I. bradyi* and *C. candida*. *Limnocythere inopinata* and *C. candida* are known to inhabit deep lakes, but both are also present in shallow lakes across Europe (Meisch, 2000). Both are also found in lakes across a range of salinities. Depth and salinity are therefore likely not the controls on distribution for *L. inopinata* in this region. Total alkalinity has also been suggested as a control on *L. inopinata* abundance (Löffler, 1959). Indeed lakes 6 and 7 have the highest alkalinities of 20.9 and 15.6 meqL^{-1}. As suggested by Jungwirth (1979), *L. inopinata* is also not present in lakes with clay or gravel substrates. In the Canadian Arctic, the abundance of *L. inopinata* is negatively correlated with chlorophyll-*a* concentrations (Viehberg and Pienitz, 2017). Our results suggest *L. inopinata* is not present at concentrations above 0.8 µgL^{-1} and is most abundant in Cluster 2 lake 8.

Cluster 2 lakes are characterised by the lowest mean chlorophyll-a concentrations (0.50 µgL^{-1}, ranging from 0.09 to 2.36 µgL^{-1}) and an abundance of *C. candida*. *Candona candida* is considered to be oligothermophilic (Vesper, 1975), preferring low nutrient concentrations and adults are present throughout the year in waters where the water temperature does not exceed 18°C in the summer (Hartmann and Hiller, 1977), suggesting an upper temperature limit on adult life stage persistence. The species has a known Holarctic distribution and its life cycle preference for cooler summers would suggest abundance of the species in the Arctic. Increasing temperatures are, however, likely to affect the life cycle and abundance, but not presence of this species.

Nutrient concentration has also been suggested as a control on *L. sanctipatricii*, which shows a preference for oligotrophic habitats (Scharf, 1981). The species is documented to have disappeared from Lake Mondsee, Austria, following anthropogenically-derived eutrophication (Danielopol *et al*., 1985). It is considered to be a cold-water indicator and has been found previously in Greenland (Table 1) as well as in Arctic Siberia (Wetterich et al., 2008). The presence of *L sanctipatricii* is characteristic of Cluster 3 lakes 9 and 21 (Fig. 5), which are relatively deep, large lakes with relatively low nutrient concentrations (Fig. 6). Future increased water temperatures and nutrient concentrations in the region, may therefore limit the abundance and distribution *of L. sanctipatricii*.

It may be considered surprising that variance partitioning analysis (VPA) of nutrients (SRP, NO_3-N, Chl-*a*), salinity (EC), and habitat (the dominant submerged macrophytes and macrophyte cover), explained little of the overall variation in ostracod species composition (~2.5%). EC contributed the largest unique contribution (adjusted $R^2 = 0.035$) but, overall, the variation is not explained by these three variables (residuals = 1.01; Fig. S2). However, for some species that are nektobenthic and large (e.g. *C. pubera*), provision of food and protection from predation offered by macrophyte cover may be a larger contributor to its presence and abundance than can be determined from this dataset. Due to the sampling strategy, it is also likely that variable such as pH, Chl-*a*, macrophyte cover and bioavailable nutrients vary within and between seasons, particularly in the late summer with longer ice-free periods (McGowan *et al*., 2018).

Our record of *Limnocythere friabilis* is the only published occurrence of recent to living individuals outside North America. The N. American species *Limnocythere friabilis,* considered to be a senior synonym of the extinct European species *Limnocythere suessenbornensis* (see Horne et al., 2023), is unique to cluster 3 and only recorded in lake 7. *Limnocythere friabilis* is common in the Great Lakes region, which shares limnological features, which may favour *L. friabilis,* with the Kangerlussuaq region such as seasonal ice cover, increasing anthropogenic N and P enrichment since the 1970s CE (Nelligan *et al*., 2021) and are deep with an average depth of 19 m in Lake Erie. *Candona candida, L. inopinata*, and *L. suessenbornensis* occur together in interglacial records in Europe (e.g. Benardout, 2015; Marchegiano *et al*., 2020; Horne *et al*., 2023), with *L. suessenbornensis* regarded as a cold-water species. *Limnocythere suessenbornensis* is present during warm interglacial periods when, at least, UK summer temperatures are suggested to be similar or slightly warmer than today, but winter temperatures were up to 10 °C cooler (Benardout, 2015; Horne *et al*., 2023). There is, therefore, likely a significant winter temperature control on its life cycle and hence distribution. Our record would corroborate the requirement for significantly cooler average winter temperatures. Increased temperature and earlier ice out in western Greenland may therefore have an adverse impact on the distribution and abundance of *L. friabilis.*

Potamocypris parva is, to our knowledge, only recorded in the Kangerlussuaq area. It is considered to be endemic to Greenland, and specifically the oligohaline lakes within the Kangerlussuaq region. The species was first described from lakes close to Kellyville (Schmidt, 1976) and since then, it has been recorded in other saline lakes including Store Saltsø and SS6 (Bennike, 2000; Bennike *et al*., 2010). Our results suggest that *P. parva* is also present in lower salinity lakes but is most abundant (40 valves per gram) at higher salinity up to 4.09 mS cm^{-1}. In carapace morphology it is closely similar to an African species, *Potamocypris paludum* Gauthier, 1939, which has been found in European Pleistocene ostracod assemblages (Fuhrmann, 2012; Marchegiano et al., 2018). However, while *P. parva* has long antennal swimming setae, those of *P. paludum* are relatively short, suggesting that these are two distinct species (C. Meisch, Musée national d'histoire naturelle, Luxembourg, pers. com. 22/09/2025); we have not found any specimens with preserved antennae in our material.

Sarscypridopsis aculeata is considered an indicator of saline waters. Here, the species is not present in the more saline waters but is found in lakes with an EC of <0.47 mS cm^{-1}. However, it has previously been collected from lake 6 with an EC of 3 mS cm^{-1} (L. Roberts unpublished data) and is therefore likely still an indicator of more saline waters in this region. Previously, the species was not thought to be extant in Greenland (Bennike, 2000) with the only previous record in isolation basins formed during the Early Holocene. *Ilyocypris bradyi* was also not considered to be extant in Greenland with the last recorded occurrence in Store Saltsø in Kangerlussuaq during the Holocene warm period (~7000 BP) before going extinct in the region (Bennike, 2000). The recording of these species in the modern fauna suggests that increasing average temperature are now placing the region within the temperature tolerance of these species and they will continue to thrive.

4.2 Implications for future distribution of ostracod species

Predictions for the Arctic are for temperature and precipitation to continue to increase in the 21st century (Hu *et al*., 2021; McCrystall *et al*., 2021). Increased temperature in the Arctic will increase P and N loading into lakes by reactivating hydrological flows transporting soil- and dust-borne nutrients into lakes. For the limited number of glacially-fed lakes (e.g lakes 12 and 15) meltwater discharge into lakes will likely increase P and N loading associated with the release of ice-locked atmospheric deposition of N and P from glacial bed erosion (Hawkings *et al*., 2016). Predicted increased precipitation itself will also increase N with previous δ^{15}N of NO_3^- in lakes from the Kangerlussuaq region suggesting an addition from direct atmospheric N deposition (Anderson *et al*., 2017), which records from ice cores has shown to have increased over the last 50–100 years (Hastings *et al.,* 2009). Future trends of N deposition, however, are reliant on policies to control emissions. Conversely, increased precipitation and meltwater may reduce P derived from dust by increasing the fluvial area, consequently reducing the effectiveness of aeolian erosion and transportation.

Increased NO_3-N concentrations in lakes is likely to favour *C. pubera, C. candida,* and *H. incongruens* occurrence, abundance and distribution (Fig. 4c; Fig. 6). With warmer temperatures, earlier ice out will alter the timing of, and support longer, growing seasons for phytoplankton and macrophytes, which may reduce bioavailable N due to N-uptake and denitrification (McGown *et al.,* 2018). During this process, P concentrations may increase due to internal loading. Increases in SRP concentrations would favour the same ostracod species (*C. pubera, C. candida,* and *H. incongruens*; Fig 4d). The results presented here do not suggest a strong association between dominant macrophyte taxa and ostracod species distribution or abundance (Fig. 6) despite previous studies linking macrophyte cover and ostracod species occurrences (e.g. Roca and Danielopol 1991; Roca *et al*., 1993; Frenzel *et al*., 2005), perhaps due to the macrophyte species present, including sparse low form isoetids that do not offer the same habitat structure as species with leaves throughout the water column (e.g. Potamogeton). However, a more systematic macrophyte survey would be needed to verify this; notwithstanding a lower diversity and abundance in the oligohaline lakes, a more diverse flora, including Potamogeton has been described in the freshwater lakes in Kangerlussuaq (Reuss *et al*., 2014). The implications of macrophyte persistence and diversity for future ostracod distribution are, therefore, currently uncertain.

https://doi.org/10.5194/egusphere-2025-6147
Preprint. Discussion started: 6 January 2026

With increased temperatures, precipitation is more likely to occur as rainfall, rather than snow. Coupled Model Intercomparison Project Phase 6 (CMIP6) experiments suggest that, across most of the Arctic, precipitation in winter will continue to have snowfall as the dominant type but with some rainfall and increasing in amount. However, in summer and autumn the dominant precipitation will be rainfall (McCrystall *et al*., 2021). By 2100, relative to the year 2000, there is a 422% increase in CMIP6 predicted rainfall in winter, 261% in spring, 71% in summer, and 268% in autumn. Greenland is predicted to have rainfall-dominated precipitation with 1.5 °C warming in CMIP6 (McCrystall *et al*., 2021). Currently, precipitation-evapotranspiration (P-E) patterns in the region are paced by ice and snowmelt-derived freshwater pulses. Increased rainfall will alter this seasonal pattern and could result in lower evaporation from lakes in Kellyville, with increased seasonal outflow already reported since 2023 from lake 6. *Potamocypris parva* and *L. friabilis* are most abundant at high EC (Fig. 4f) and therefore alterations to the P-E balance may affect the future distribution of these species, potentially restricting their distribution to coastal lakes.

5. Conclusions

Sixteen species had previously been documented from Greenland of which only five have been recorded living or in recent sediments from Kangerlussuaq (Bennike *et al*., 2000). Eight (*C. candida*, *C. vidua*, *L. sanctipatricii, I. bradyi, C. pubera, P. parva, H. incongruens*, and *S. aculeata*) of the sixteen species are present in this study, the other species presented here are new records for Greenland. Furthermore, two species (*I. bradyi* and *S. aculeata*) were considered to be extinct in Greenland, neither being recorded since the early Holocene. *Candona candida* has previously been recorded in the Siberian and Canadian Arctic (Wetterich *et al*., 2008; Viehberg and Pienitz, 2017) with *C. pubera*, and *L. inopinata* also recorded in Canada (Viehberg and Pienitz, 2017). *Candona candida* is a generalist species in the Kangerlussuaq region, being present in deeper lakes, higher SRP concentrations and higher nitrate concentrations. These traits suggest that *C. candida* will become abundant in the Greenlandic ostracod fauna, and potentially across the Arctic. For some species, particularly *C. pubera,* nutrient concentrations are a dominant control on distribution. As Arctic warming increases, nutrient sources are predicted to increase. However, currently there is little understanding of the direct and indirect nutrient controls on ostracod fauna. Nutrient status of water appears, however, to be a significant control on ostracod presence and abundance and should be included in future ecological studies globally.

Author Contributions

Lucy Roberts: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Visualization. **Suzanne McGowan:** Methodology, Validation, Investigation, Resources, Writing – original draft. **Amanda Burson:** Investigation, Resources, Writing – Review & Editing. **Jonathan Holmes**: Investigation, Writing – Review & Editing. **David Horne**: Investigation, Writing – Review & Editing,

Acknowledgements

The authors thank: Chris Sørensen at Kangerlussuaq International Science Support (KISS); Mathi Woolford for assistance with ostracod picking; Miles Irving for help with editing figures; and Jim Davy for SEM operation. Travel to Greenland was funded by NWO Rubicon grant 019.183EN.018 awarded to AB.

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