

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

Lucy R. Roberts¹, Suzanne McGowan^{2,3}, Amanda Burson⁴, Jonathan A. Holmes¹, David J. Horne⁵

¹ Environmental Change Research Centre, Department of Geography, University College London, Gower Street, London, WC1E 6BT, UK.

² Department of Aquatic Ecology, Netherlands Institute of Ecology, Droevendaalsesteeg 10, 6708PB Wageningen, The Netherlands.

³ Departments of Biology and Physical Geography, University of Utrecht, Postbus 80125, 3508 TC Utrecht, The Netherlands

⁴ British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

⁵ School of Geography, Queen Mary University of London, Mile End Road, London, E1 4NS

Correspondence to: Lucy R Roberts (lucy.roberts@ucl.ac.uk)

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. Twenty-four lakes (<16 m deep) were surveyed in July 2021 in a SW-NE gradient from the Greenland Ice Sheet. Electrical conductivity in the lakes ranged from 0.01 to 4.1 mS cm⁻¹. All lakes were ultra-oligotrophic to mesotrophic; soluble reactive phosphorus ranged from 1.9 to 49.7 µg L⁻¹ and nitrate concentrations from below detection limit to 12.3 µg L⁻¹. In total, thirteen species of ostracods were recorded across the study lakes. *Candona candida* is a generalist species in the Kangerlussuaq region, being present in deeper lakes and at the higher end of the bioavailable

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 per decade (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.*, 2022). 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 as heat is transferred deeper into the water column (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.*,
75 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
80 crustaceans) can be a significant contributor to the benthic biomass (e.g. Geiger, 1998;
Rodríguez-Pérez and Baltanás, 2008). As both consumers and secondary 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),
85 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
90 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
95 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
100 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
105 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
110 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, 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
<i>Cypris pubera</i> O.F. Müller, 1776	Haberbosch, 1916
<i>Eucypris affinis hirsuta</i> (Fischer, 1851) = <i>Bradleystrandesia reticulata</i> (Zaddach, 1844)	Haberbosch, 1916
<i>Eucypris virens</i> (Jurine, 1820)	Alm, 1914
<i>Cypris incongruens</i> Ramdohr, 1808 = <i>Heterocypris incongruens</i> (Ramdohr, 1808)	Alm, 1914
<i>Prionocypris glacialis</i> Sars, 1890 = <i>Tonnacypris glacialis</i> (Sars, 1890)	Brehm, 1911
<i>Prionocypris glacialis</i> var. <i>albida</i> (Alm, 1914) = <i>Tonnacypris glacialis</i> var. <i>albida</i> (Alm, 1914)	Poulsen, 1940
<i>Candona candida</i> (O.F. Müller, 1776)	Alm, 1914
<i>Candona lapponica</i> Ekman, 1908 = <i>Fabaeformiscandona lapponica</i> (Ekman, 1908)	Haberbosch, 1916
<i>Candona groenlandica</i> Brehm, 1911 = <i>Fabaeformiscandona groenlandica</i> (Brehm, 1911)	Brehm, 1911
<i>Candona rectangula</i> (misspelling of <i>rectangulata</i>) Alm, 1914 = <i>Fabaeformiscandona harmsworthi</i> (Scott, 1899)	Alm, 1914
<i>Candona subgibba</i> Sars, 1926	Røen, 1962
<i>Candona falcata</i> Alm, 1914	Røen, 1962
<i>Cypridopsis vidua</i> (O.F. Müller, 1776)	Røen, 1962
<i>Limnocythere sanctipatricii</i> Brady & Robertson, 1869	Røen, 1962
<i>Potamocypris parva</i> Schmidt, 1976	Schmidt, 1976
<i>Ilyocypris bradyi</i> Sars, 1890	Bennike, 2000
<i>Sarscypridopsis aculeata</i> (Costa, 1847)	Bennike <i>et al.</i> , 2000

2. Methods

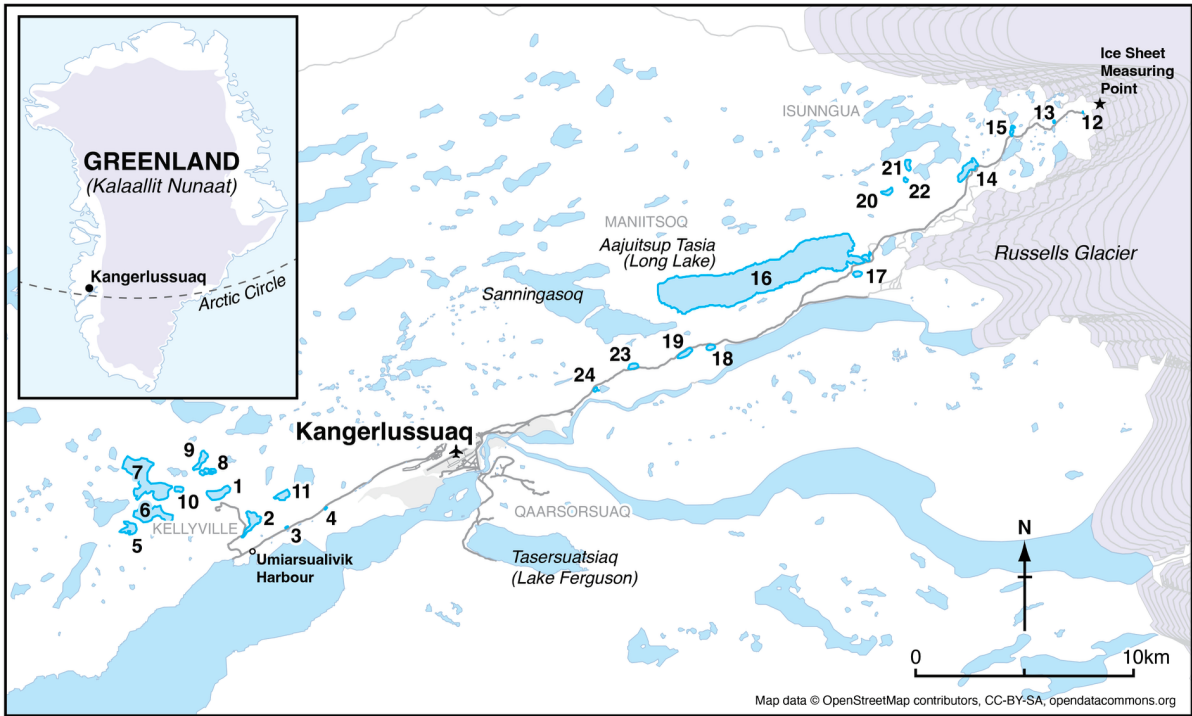
2.1 Study area

120 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
125 conditions (e.g. glacial inflow versus aridity, depth, size) in the region. The bedrock of the area
is Precambrian gneiss. 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 oligohaline due
130 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 between 1961 to 1990 was -5.7 °C (DMI, 2026). For the period July
2020 to July 2021, mean annual temperature was -2.2 °C with a maximum of 21 °C and a
minimum of -34.6 °C. Mean January air temperatures in 2021 were -16.5 °C and mean July
135 temperatures were 11.1 °C (DMI, 2026). Conditions close to the ice sheet, at higher elevations,
are on average 2-3 °C cooler and with at least 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
140 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, EC 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
145 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 by sampling the top ~1 cm of sediment. Where submerged macrophytes
150 were present, samples were collected with the net 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, clear/green,

155 green/brown and brown. According to the Nutrient Colour Paradigm, nutrient concentrations in the lakes are too low for colour to be classified as green. However, to visually distinguish between low nutrient clear water and more turbid water of 'green' colour, these lakes have been visually classified as 'clear/green Lake area was calculated at a later date using the polygon function in Google Earth.



160

Figure 1. Location of the study lakes in Kangerlussuaq, Greenland, showing the 24 study lakes in a SW-NE gradient. Coordinates of each lake are given in Table 2. The numbers indicate lake ID and distance from the ice sheet has been calculated from the location denoted with a star.

165

170

175

180

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

Lake ID	Scientific name in Anderson <i>et al.</i> ,(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		Clear/green
2	SS1 (Lake Helen)	66.981583, -50.930833	5.8	357041	43.1	132	Sandy silt	<i>Hippuris</i>	Clear/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	<i>Charophytes</i>	Clear
5	SS85	66.983111, -51.056388	11.9	278847	48.26	178	Gyttja		Clear/green
6	SS4 (Braya Sø)	66.986388, -51.016666	9.4	794644	47.14	170	Sandy silt	Elodeids	Clear/green
7	SS3 (Hunde Sø)	66.994222, -51.025611	12.1	1963022	46.85	175	Sandy silt	Isoetids	Clear/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	SS903	66.995555, -50.89688	1.5	180272	41.29	198	Organic lake mud	<i>Menyanthes</i>	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	<i>Hippuris</i>	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		Clear/green
17		67.086694, -50.290527	3.9	17594	13.32	235	Organic lake mud	Filamentous algae	Clear/green
18	SS906	67.056416, -50.442388	2.4	80643	20.68	169	Silty clay	<i>Hippuris</i>	Clear/green
19		67.055055, -50.464805	10.7	153816	21.8	180	Organic lake mud		Brown/Green
20		67.119694, -50.255666	15.7	93240	9.97	405	Organic lake mud		Clear/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	SS901	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

Samples for dissolved nutrients were passed through 0.7- μ m GF/F filters and analysed colorimetrically by the molybdate blue method for soluble reactive phosphorus (SRP), azo dye

method for nitrite (NO₂-N), which included a cadmium reduction step for nitrate (NO₃-N), the indophenol blue method for ammonium (NH₄-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).

200 **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 (i.e. carapaces and valves) 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).

220 **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 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.

235

3. Results

3.1 Limnology

For the 24 lakes, the dominant substrate was organic lake mud with low growing isoetid form macrophytes being the most common macrophytes. In seven lakes, no aquatic plants were observed. Water colour was categorised through observations as clear in four lakes, clear/green in nine lakes, brown in seven lakes and brown/green in three lakes (Table 2).

The electrical conductivity (EC) of the lakes ranged from 0.01 to 4.1 mS cm⁻¹, with the highest EC in lake 7 and lowest in lake 15 (Table 3). Water temperature ranged from 9.5 to 10.5 °C at lake 1 and lake 24. Total Alkalinity ranged from 0.2 meq L⁻¹ in lake 15 to 20.9 meq L⁻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 µg L⁻¹ from lake 9 to lake 3 and nitrate (NO₃-N) concentrations were highest in lake 12 at 12.3 µg L⁻¹. The concentrations were below detection limit in lakes 1, 2, 7, 14 and 16. Chlorophyll-*a* ranged from 0.06 µg L⁻¹ in lake 22 to 2.65 µg L⁻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).

260

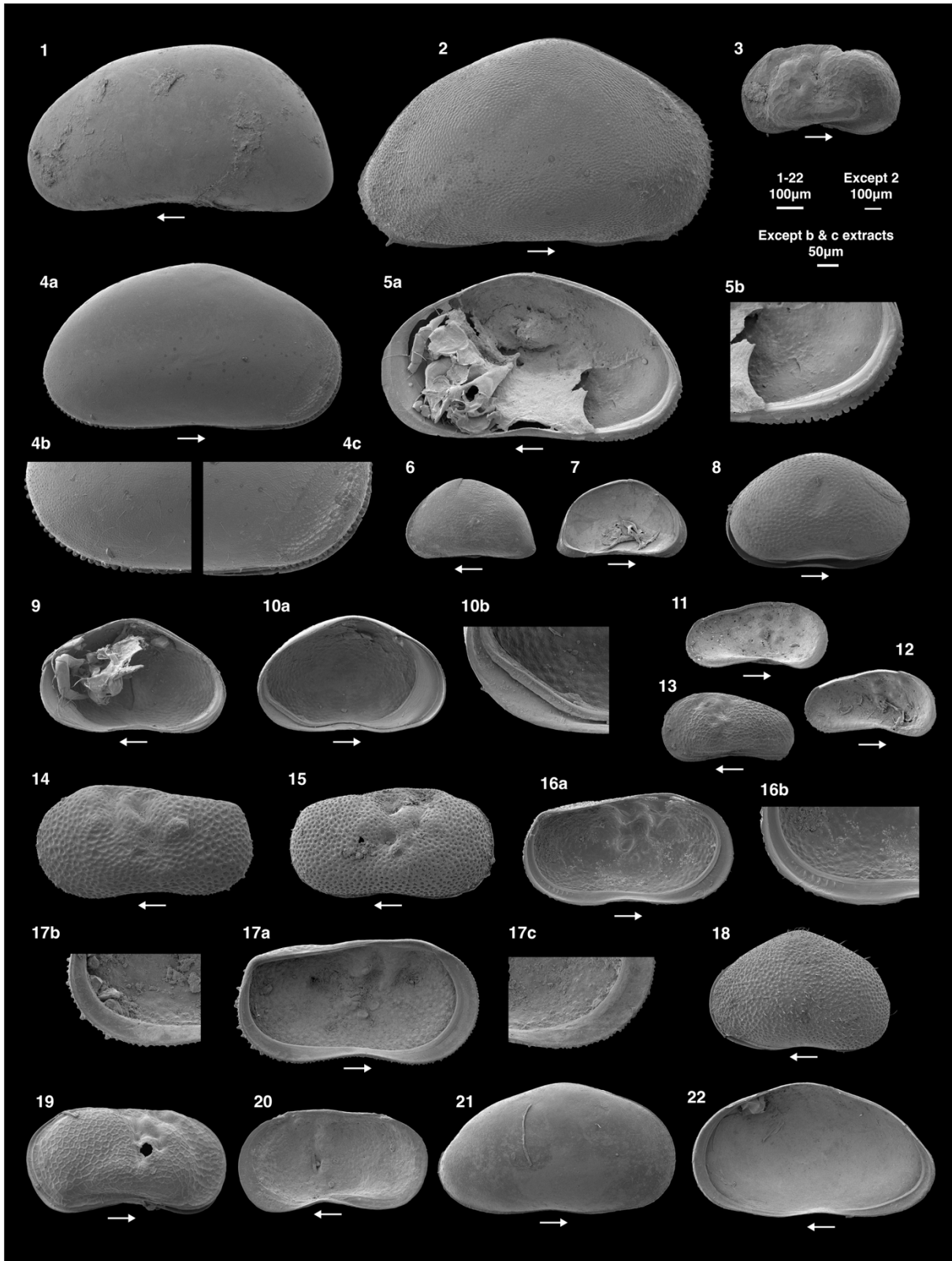
Table 3. Water composition and chemistry recorded in July 2021 in the 24 study lakes

Lake ID	Electrical conductivity (mS cm ⁻¹)	SRP (µg L ⁻¹)	NO ₃ -N (µg L ⁻¹)	Chlorophyll-a (µg L ⁻¹)	Total alkalinity (meq L ⁻¹)	pH
1	0.40	5.73	BDL	0.31	3.00	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	4.60	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	5.20	8.2
11	0.15	BDL	2.55	0.37	1.10	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	1.70	8.2
15	0.01	4.96	1.75	0.34	0.20	8.3
16	0.11	BDL	BDL	0.11	1.05	8.2
17	0.70	3.61	1.75	0.51	5.40	8.0
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	0.50	8.1
21	0.10	2.45	2.59	0.23	0.80	8.0
22	0.09	2.45	2.59	0.59	0.80	8.4
23	0.51	2.43	4.24	2.36	3.70	8.9
24	0.16	1.94	2.12	0.89	1.10	8.8

3.2 Ostracod fauna

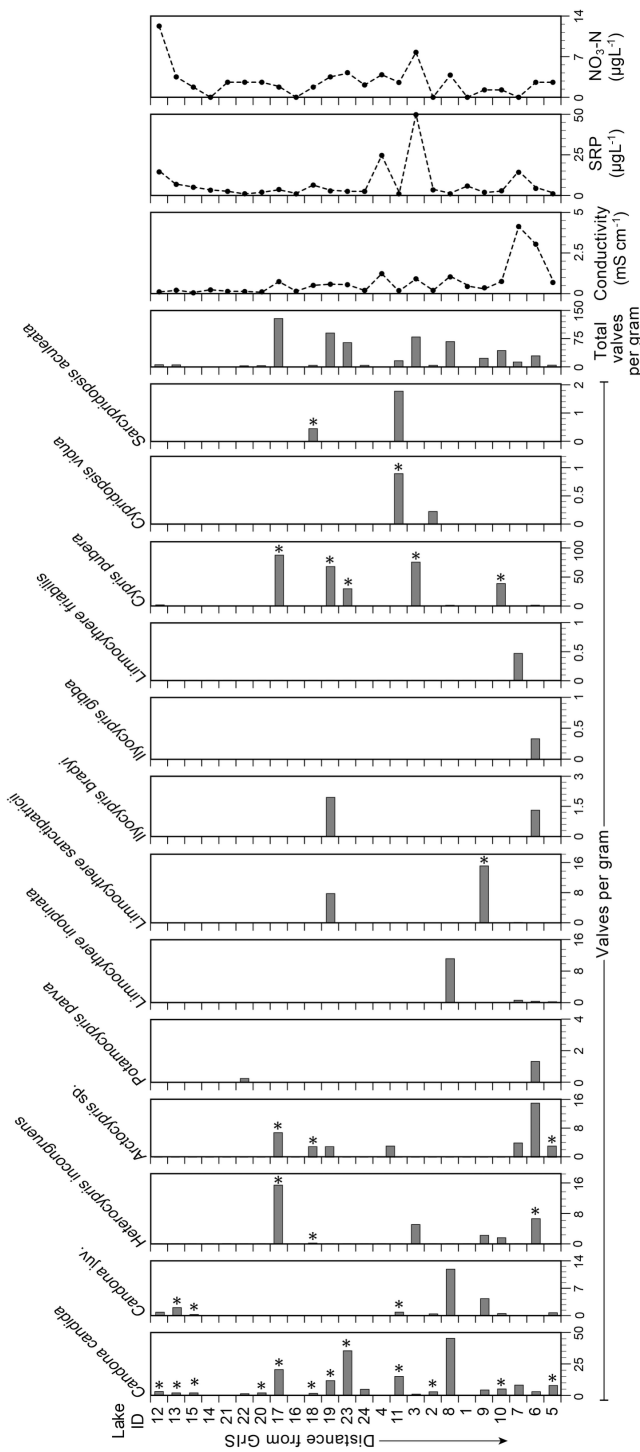
270 Thirteen species of ostracods were recorded across the study lakes (Fig. 2; Fig. 3). Other than
Limnocythere friabilis Benson & MacDonald, 1963 and species of *Ilyocypris*, some individuals
with soft parts were collected (Table S2) and so were assumed to be living at the time of
collection. The most 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
275 present in the most sites (n = 20) with *Ilyocypris gibba* (Ramdohr, 1808) present in the fewest
(n = 1). Shells (carapaces and valves) of *Candona* juveniles were present in ten 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

280 *Potamocypris parva* Schmidt, 1976 were rarely recorded, occurring in one to six 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 and 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 four to seven sites. Ostracods were not recorded
in three sites (lake 1, 4 and 16). The highest diversity of eight species was recorded in lake 6.
285 Lowest diversity of one species was recorded in lakes 13, 14, 20 and 24. At each of these
lakes, the only species recorded was *C. candida*.



290 **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. LV refers to left valve and RV to right valve. 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 ripples 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 ripples on the inner lamella. Images 15 and 17a,b are of the same individual; 18. *Sarocypris 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.



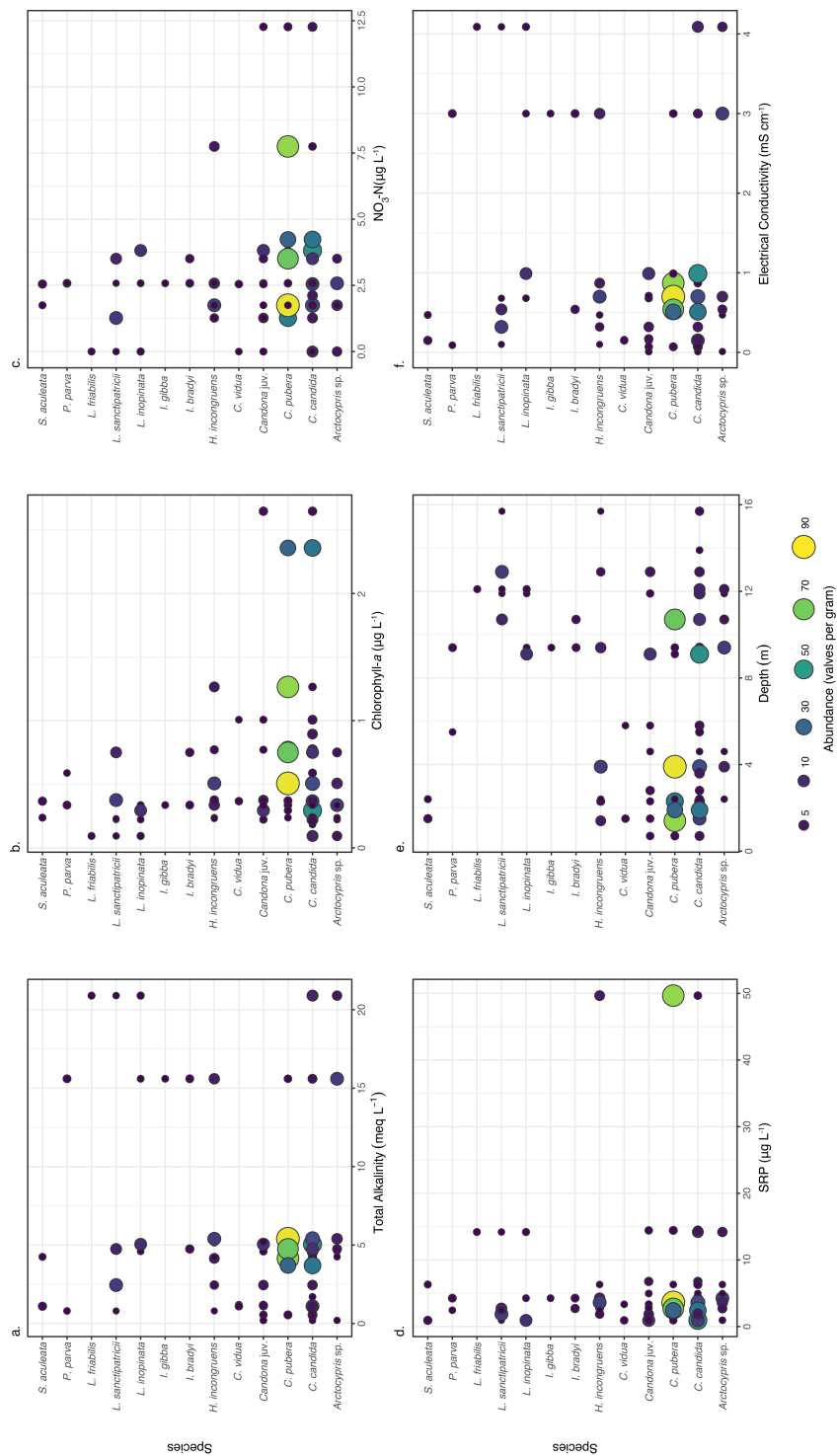
315

320

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 [NO₃-N]). The stars indicate the occurrence of individuals with soft parts, suggesting that they were collected alive. Table S2 provides a detailed breakdown of valves, carapaces and individuals with soft parts. Lakes are ordered in the distance from the 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 meq L⁻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 $\mu\text{g L}^{-1}$, with only *Candona* juveniles also present (Fig. 4b). *Heterocypris incongruens* and *Candona* juveniles were abundant between 0.2 and 0.8 $\mu\text{g Chl-a L}^{-1}$. *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 $\mu\text{g L}^{-1}$. *Candona candida* and *C. pubera* were most abundant at NO₃-N concentration between 1.3 and 4.2 $\mu\text{g L}^{-1}$ (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 $\mu\text{g L}^{-1}$, all species were most abundant at SRP concentrations of $< 6.8 \mu\text{g L}^{-1}$ (Fig. 4d). Only three species were present at the highest SRP concentration of 49.7 $\mu\text{g L}^{-1}$ 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 < 6 m and *C. pubera* was most abundant at depths < 4 m. 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 ECs above this. *Cypridopsis vidua* was only present at ECs 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 > 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 of 4.09 mS cm⁻¹. At the lowest EC of 0.01 mS cm⁻¹, only *C. candida*, *Candona* juveniles and *Arctocypris* sp. were present. Both species of *Ilyocypris* were only present at ECs above 0.54 mS cm⁻¹ and *L. inopinata* and *L. sanctipatricii* at concentrations > 0.32 mS cm⁻¹ (Fig. 4f).



350

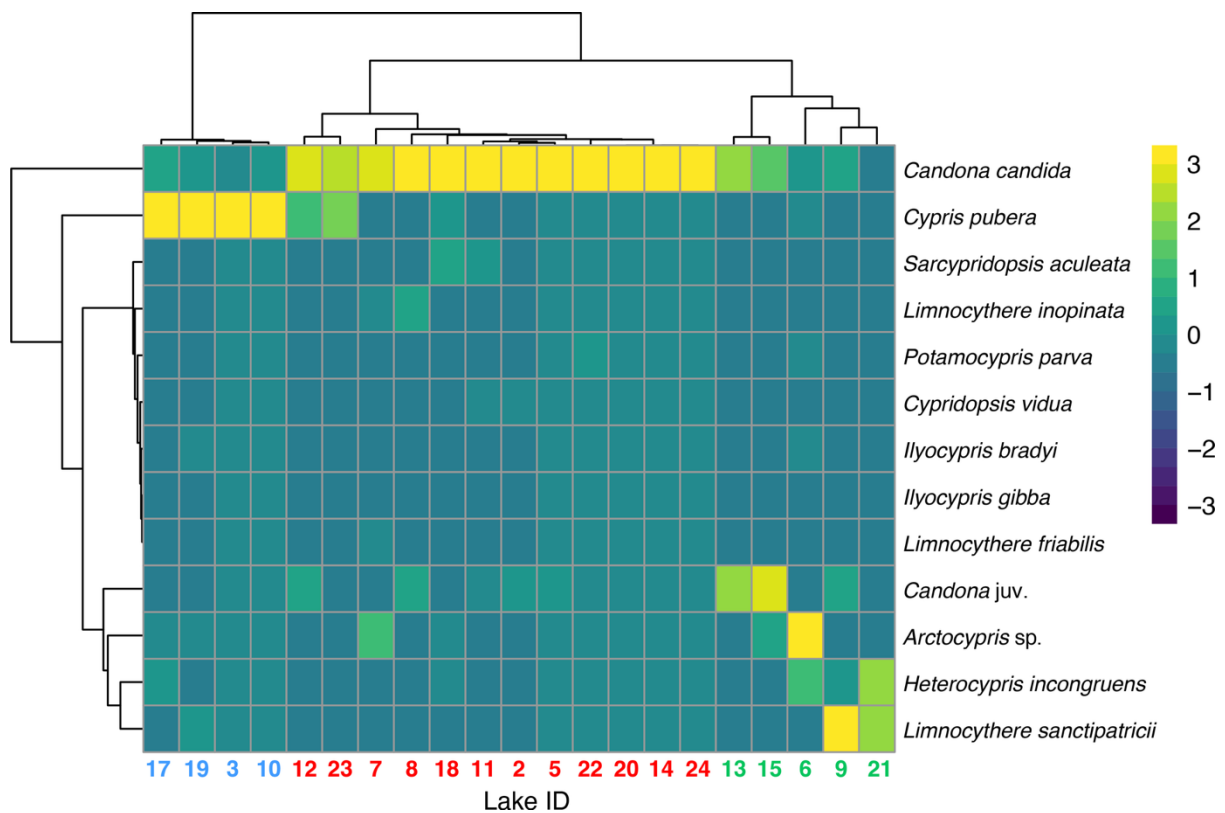
Figure 4. Abundance of ostracod species along gradients of a) total alkalinity, b) chlorophyll-a concentration, c) nitrate ($\text{NO}_3\text{-N}$) concentration, d) soluble reactive phosphorus (SRP) concentration, e) water depth and f) electrical conductivity. Ostracod abundance is given in valves per gram and includes all specimens collected. Table S2 provides a detailed breakdown of valves, carapaces and individuals with soft parts.

355

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 (twelve lakes) is characterised by high abundance of *C. candida*. Cluster 3 (five 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 (three lakes – 1, 4 and 16), not depicted on Fig. 5, is characterised by the absence of ostracods.

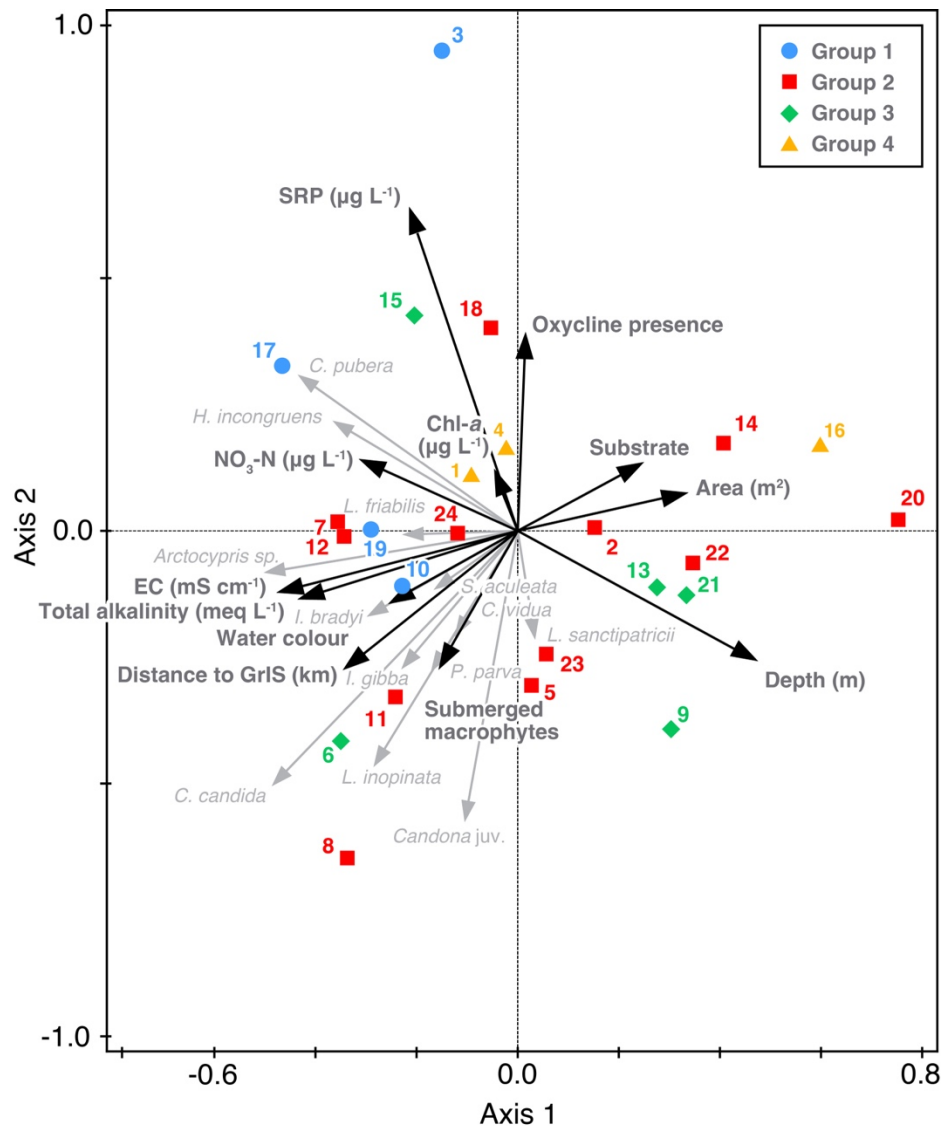
365



370

Figure 5. Identification of three clusters (cluster 1 N=4, cluster 2 N=12, cluster 3 N=5) based on ostracod assemblages Ward's method hierarchical 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. The analysis includes all specimens collected. Table S2 provides a detailed breakdown of valves, carapaces and individuals with soft parts.

375 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
380 m), higher SRP (mean 14.7 $\mu\text{g L}^{-1}$, ranging from 2.7 to 49.7 $\mu\text{g L}^{-1}$), higher $\text{NO}_3\text{-N}$ (mean 3.6
 $\mu\text{g L}^{-1}$, ranging from 1.3 to 7.8 $\mu\text{g L}^{-1}$) and higher chlorophyll-*a* (mean 0.82 $\mu\text{g L}^{-1}$, ranging from
0.51 to 1.27 $\mu\text{g L}^{-1}$). Cluster 2 lakes, on the other hand, are characterised by lowest mean
chlorophyll-*a* (0.50 $\mu\text{g L}^{-1}$, ranging from 0.09 to 2.36 $\mu\text{g L}^{-1}$) 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 9.1 m,
385 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 $\mu\text{g L}^{-1}$, ranging from 1.9
to 5.0 $\mu\text{g L}^{-1}$) 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
390 average $\text{NO}_3\text{-N}$ (1.29 $\mu\text{g L}^{-1}$, ranging from BDL to 3.88 $\mu\text{g L}^{-1}$) and lowest total alkalinity (3.1
 meq L^{-1} , ranging from 1.1 to 3.0 meq L^{-1}). There were also no macrophytes present in cluster
4 lakes other than the presence of filamentous algae in lake 3.



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

4. Discussion

400 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). Responses 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,
405 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

410 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).

415 **4.1 Controls on ostracod species distribution in Kangerlussuaq**

415

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 of SRP and NO₃-N. Total phosphorus (TP) and NO₃-N 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 being further from the source of dust and 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 NO₃-N concentrations (12.27 µg L⁻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 µg L⁻¹. Lake 15 (GL6 in Grider *et al.*, 2025) is located 3.71 km from the GrIS but has relatively low NO₃-N concentrations (1.75 µg L⁻¹) with high SRP concentrations (4.96 µg L⁻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, 430 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 µg L⁻¹, ranging from 2.7 to 49.7 µg L⁻¹), NO₃-N (mean 3.57 µg L⁻¹, ranging from 1.3 to 7.8 µg L⁻¹), and chlorophyll-*a* (mean 435 0.82 µg L⁻¹, ranging from 0.51 to 1.27 µg L⁻¹) are likely to become more dominant in the Kangerlussuaq landscape in the future. Higher nitrate concentration in lakes is associated with visual water colour (brown and brown/green) and higher chlorophyll-*a* concentrations (0.51 to 1.27 µg L⁻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 440 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 higher 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; 2010). Whilst *C. pubera* is considered abundant in our study, *C. pubera*

445 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, 450 *C. pubera* was most abundant in the pond with highest TP of 121.4 $\mu\text{g L}^{-1}$ (Coviaga *et al.*, 2015), 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 455 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 460 ostracod species that are abundant in deeper lakes are not present above $\text{NO}_3\text{-N}$ concentrations of 4.24 $\mu\text{g L}^{-1}$ (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 465 (Meisch, 2000). Both are also found in lakes across a range of salinities. Depth and EC 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 meq L^{-1} . As suggested by Jungwirth (1979), *L. inopinata* is also not present in lakes with clay or gravel substrates. In the Canadian 470 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 $\mu\text{g L}^{-1}$ and is most abundant in Cluster 2 lake 8.

Cluster 2 lakes are characterised by the lowest mean chlorophyll-*a* concentrations (0.50 $\mu\text{g L}^{-1}$, ranging from 0.09 to 2.36 $\mu\text{g L}^{-1}$) and an abundance of *C. candida*. *Candona candida* is 475 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; indeed, 480 it has been shown to be abundant at higher latitudes (Alkalaj *et al.*, 2019). Increasing

temperatures are, however, likely to affect the life cycle and abundance, but not presence of this species.

485 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
490 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*.

495 It may be considered surprising that variance partitioning analysis (VPA) of nutrients (SRP, NO₃-N, Chl-*a*), 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 R² = 0.035) but, overall, the variation is not explained by these three categories of variables (residuals = 1.01; Fig. S2). However, for
500 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 variables 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
505 *et al.*, 2018). Our results also provide a time-averaged "present day" living ostracod fauna, which is not an unreasonable approach in these remote environments, but it is likely that different ostracod species will be abundant in different seasons and that the measured parameters do not reflect the full range of habitat and environmental preferences.

510 Our record of *Limnocythere friabilis* is the only published occurrence of recent to living individuals outside North America. The North American species *Limnocythere friabilis*, considered to be a senior synonym of the extinct European species *Limnocythere suessenbornensis* (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
515 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.

520 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
525 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.

530 *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 lakes with lower EC but is most abundant (40 valves per gram) at EC up to 4.09 mS cm⁻¹.
535 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.
540 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 higher conductivity 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
545 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 years BP) before going
550 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.

555 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). Higher temperatures 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 increases in precipitation will also increase N in lakes. Previous $\delta^{15}\text{N}$ of NO_3^- -N in lakes from the Kangerlussuaq region suggest an addition from direct atmospheric N deposition (Anderson *et al.*, 2017). In ice core records this has been 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 the macrophyte species present, including sparse low form isoetids, do not offer the same habitat structure as species with leaves distributed 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.

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.

Data Availability

All data is available in the supplementary information.

Competing Interests

The authors declare that they have no conflict of interest.

630 **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

640 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.

645 **References**

- Aebly, F.A. and Fritz, S.C., 2009. Palaeohydrology of Kangerlussuaq (Søndre Strømfjord), west Greenland during the last~ 8000 years. *The Holocene*, 19(1), pp.91-104.
- Alkalaj, J., Hrafnisdottir, T.K., Ingimarsson, F., Smith, R.J., Kreiling, A.-K., Mischke, S., 2019. Distribution of Recent non-marine ostracods in Icelandic lakes, springs, and cave pools. *Journal of Crustacean Biology*, 39: 202-212.
- Alm, 1914. Beitrage zur Kentniss der nördlichen und arktischen Ostracodenfauna. *Arkiv for Zoologi.*, 9:5
- AMAP, 2017. Snow, Water, Ice and Permafrost. Summary for Policy-makers. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. 20 pp.
- 655 Anderson, N.J. and Brodersen, K.P., 2001. Determining the date of ice-melt for low Arctic lakes along Søndre Strømfjord, southern West Greenland. *Geology of Greenland Survey Bulletin*, 189, pp.54-59.
- Anderson, N.J., D'andrea, W. and Fritz, S.C., 2009. Holocene carbon burial by lakes in SW Greenland. *Global Change Biology*, 15(11), pp.2590-2598.
- 660 Anderson, N.J., Liversidge, A.C., McGowan, S. and Jones, M.D., 2012. Lake and catchment response to Holocene environmental change: spatial variability along a climate gradient in southwest Greenland. *Journal of Paleolimnology*, 48(1), pp.209-222.
- Anderson, N.J., Saros, J.E., Bullard, J.E., Cahoon, S.M., McGowan, S., Bagshaw, E.A., Barry, C.D., Bindler, R., Burpee, B.T., Carrivick, J.L. and Fowler, R.A., 2017. The
- 665

- Arctic in the twenty-first century: Changing biogeochemical linkages across a paraglacial landscape of Greenland. *BioScience*, 67(2), pp.118-133.
- Benardout, G., 2015. Ostracod-based palaeotemperature reconstructions for MIS 11 human occupation at Beeches Pit, West Stow, Suffolk, UK. *Journal of Archaeological Science*, 54, pp.421-425.
- 670 Bennike, O., 2000. Palaeoecological studies of Holocene lake sediments from west Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 155(3-4), pp.285-304.
- Bennike, O., Anderson, N.J. and McGowan, S., 2010. Holocene palaeoecology of southwest Greenland inferred from macrofossils in sediments of an oligosaline lake. *Journal of Paleolimnology*, 43(4), pp.787-798.
- 675 Bennike, O., Björck, S., Böcher, J. and Walker, I.R., 2000. The Quaternary arthropod fauna of Greenland: a review with new data. *Bulletin of the Geological Society of Denmark*, 47, pp.111-134.
- Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.J.W., Brown, R., Bhatt, U.S., Euskirchen, E.S., Romanovsky, V.E. and Walsh, J.E., 2019. Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, 14(4), p.045010.
- 680 Box, J.E., Nielsen, K.P., Yang, X., Niwano, M., Wehrlé, A., Van As, D., Fettweis, X., Køltzow, M.A., Palmason, B., Fausto, R.S. and van den Broeke, M.R., 2023. Greenland ice sheet rainfall climatology, extremes and atmospheric river rapids. *Meteorological Applications*, 30(4), p.e2134.
- 685 Brehm, V., 1911. Die Entomotraken der Danmark Expedition. *Meddelelser om Grønland*, 45(5), 12pp.
- Bullard, J.E. and Mockford, T., 2018. Seasonal and decadal variability of dust observations in the Kangerlussuaq area, west Greenland. *Arctic, Antarctic, and Alpine Research*, 50(1), p.S100011.
- 690 Burpee, B., Saros, J.E., Northington, R.M. and Simon, K.S., 2016. Microbial nutrient limitation in Arctic lakes in a permafrost landscape of southwest Greenland. *Biogeosciences*, 13(2), pp.365-374.
- 695 Burpee, B.T. and Saros, J.E., 2020. Cross-ecosystem nutrient subsidies in Arctic and alpine lakes: implications of global change for remote lakes. *Environmental Science: Processes & Impacts*, 22(5), pp.1166-1189.
- Burpee, B.T. and Saros, J.E., 2020. Cross-ecosystem nutrient subsidies in Arctic and alpine lakes: implications of global change for remote lakes. *Environmental Science: Processes & Impacts*, 22(5), pp.1166-1189.
- 700

- Burpee, B.T., Anderson, D. and Saros, J.E., 2018. Assessing ecological effects of glacial meltwater on lakes fed by the Greenland Ice Sheet: The role of nutrient subsidies and turbidity. *Arctic, Antarctic, and Alpine Research*, 50(1), p.S100019.
- 705 Burpee, B.T., Anderson, D. and Saros, J.E., 2018. Assessing ecological effects of glacial meltwater on lakes fed by the Greenland Ice Sheet: The role of nutrient subsidies and turbidity. *Arctic, Antarctic, and Alpine Research*, 50(1), p.S100019.
- Coviaga, C.A., Perez, A.P., Ramos, L.Y., Alvear, P. and Cusminsky, G.C., 2018. On two species of *Riocypris* (Crustacea, Ostracoda) from northern Patagonia and their relation to *Eucypris fontana*: implications in paleoenvironmental
- 710 reconstructions. *Canadian Journal of Zoology*, 96(8), pp.801-817.
- Danielopol, D.L., Handl, M., and Yin, Y., 1993. *Benthic ostracods in the pre-alpine deep lake Mondsee: Notes on the origin and distribution*. In K.G. McKenzie & P.J. Jones, (Eds): *Ostracoda in the Earth and Life Sciences. Proceedings of the 11th International Symposium on ostracoda*, Warrnambool, Victoria, Australia: 465-480. A.A. Balkema,
- 715 Rotterdam.
- Danish Meteorological Institute (DMI), 2026. Mittarfik Kangerlussuaq vejrdata. Available at: <https://www.dmi.dk/friedata/observationer> (accessed 20/03/26)
- Fowler, R.A., Osburn, C.L. and Saros, J.E., 2020. Climate-driven changes in dissolved organic carbon and water clarity in Arctic lakes of West Greenland. *Journal of Geophysical Research: Biogeosciences*, 125(2), p.e2019JG005170.
- 720 Frenzel, P., Henkel, D., Siccha, M. and Tschendel, L., 2005. Do ostracod associations reflect macrophyte communities? A case study from the brackish water of the southern Baltic Sea coast. *Aquatic Sciences*, 67(2), pp.142-155.
- Fuhrmann, R. 2012. *Atlas quartärer und rezenter Ostrakoden Mitteldeutschlands*,
- 725 Altenburger Naturwissenschaftliche Forschungen, 15, 1–320, 2012.
- Geiger, W., 1998. Population dynamics, life histories and reproductive modes. *Sex and Parthenogenesis. Evolutionary Ecology of Reproductive Modes in Non-Marine Ostracods*. Backhuys, Leiden, 215, p.228.
- Greenway, H., Holmes, J. and Burn, M., 2024. The response of ostracod faunal
- 730 assemblages to hydrology, lake level, and carbon cycling in a Jamaican marl lake: a palaeolimnological investigation. *Journal of Micropalaeontology*, 43(1), pp.81-91.
- Grider, A., Saros, J., Northington, R. and Yde, J.C., 2025. Glacially-fed lakes of West Greenland have elevated metal and nutrient concentrations and serve as regional repositories of these materials. *Science of The Total Environment*, 967, p.178744.
- 735 Haberbosch, P., 1916. Über Arktischen Süßwassercrustaceen. *Zool. Anz. Leipzig*. 47.
- Hartmann, G. and Hiller, D., 1977. Beitrag zur Kenntnis der Ostracodenfauna des Harzes und seines nördlichen Vorlandes (unter besonderer Berücksichtigung des

Männchens von *Candona candida*) 125 Jahre Naturwissenschaftlicher Verein Goslar: 99-116.

- 740 Hastings, M.G., Jarvis, J.C. and Steig, E.J., 2009. Anthropogenic impacts on nitrogen isotopes of ice-core nitrate. *Science*, 324(5932), pp.1288-1288.
- Hawkings, J., Wadham, J., Tranter, M., Telling, J., Bagshaw, E., Beaton, A., Simmons, S.L., Chandler, D., Tedstone, A. and Nienow, P., 2016. The Greenland Ice Sheet as a hot spot of phosphorus weathering and export in the Arctic. *Global Biogeochemical*
- 745 *Cycles*, 30(2), pp.191-210.
- Hazuková, V., Burpee, B.T., Northington, R.M., Anderson, N.J. and Saros, J.E., 2024. Earlier ice melt increases hypolimnetic oxygen despite regional warming in small Arctic lakes. *Limnology and Oceanography Letters*, 9(3), pp.258-267.
- Heinemann, G., 1999. The KABEG'97 field experiment: An aircraft-based study of katabatic wind dynamics over the Greenland ice sheet. *Boundary-Layer Meteorology*, 93(1),
- 750 pp.75-116.
- Higuti, J., Declerck, S.A., Lansac-Tôha, F.A., Velho, L.F.M. and Martens, K., 2010. Variation in ostracod (Crustacea, Ostracoda) communities in the alluvial valley of the upper Paraná River (Brazil) in relation to substrate. *Hydrobiologia*, 644(1), pp.261-278.
- 755 Horne, D.J., 2007. A mutual temperature range method for Quaternary palaeoclimatic analysis using European nonmarine Ostracoda. *Quaternary Science Reviews*, 26(9-10), pp.1398-1415.
- Horne, D.J., Ashton, N., Benardout, G., Brooks, S.J., Coope, G.R., Holmes, J.A., Lewis, S.G., Parfitt, S.A., White, T.S., Whitehouse, N.J. and Whittaker, J.E., 2023. A
- 760 terrestrial record of climate variation during MIS 11 through multiproxy palaeotemperature reconstructions from Hoxne, UK. *Quaternary Research*, 111, pp.21-52.
- Hu, X.M., Ma, J.R., Ying, J., Cai, M. and Kong, Y.Q., 2021. Inferring future warming in the Arctic from the observed global warming trend and CMIP6 simulations. *Advances in*
- 765 *Climate Change Research*, 12(4), pp.499-507.
- Huai, B., Ding, M., van den Broeke, M.R., Reijmer, C.H., Noël, B., Sun, W. and Wang, Y., 2025. Future large-scale atmospheric circulation changes and Greenland precipitation. *Climate and Atmospheric Science*, 8(1), p.10.
- Jeffrey, S.W. and Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophyll a, b, c1 and c2 in higher plants, algae and natural
- 770 phytoplankton. *Biochemie und Physiologie der Pflanzen*, 167: 191–194.
- Johansson, E., Berglund, S., Lindborg, T., Petrone, J., Van As, D., Gustafsson, L.G., Näslund, J.O. and Laudon, H., 2015. Hydrological and meteorological investigations

- 775 in a periglacial lake catchment near Kangerlussuaq, west Greenland—presentation of
a new multi-parameter data set. *Earth System Science Data*, 7(1), pp.93-108.
- Jungwirth, W., 1979. *Limnocythere inopinata* (Baird) (Cytheridae, Ostracoda): Its distribution
pattern and relation to the superficial sediments of Neusiedlersee. In Löffler, H (Ed):
Neusiedlersee: The limnology of a shallow lake in central Europe. Monographiae
Biologicae 37: 385-388. Dr. W. Junk Publishers, The Hague.
- 780 Kolde R., (2025). *pheatmap: Pretty Heatmaps*. R package version
1.0.13, <https://github.com/raivokolde/pheatmap>.
- Löffler, H., 1959. Zur Limnologie, Entomotraken- und Rotatorienfauna des Seewinkel-
Gebietes. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften,*
mathematischnaturwissenschaftliche Klasse, Abt. 1, 168: 315-362.
- 785 Mackereth F.J.H., Heron J. and Talling J.F., 1989. *Water analysis: some revised methods for*
limnologists, 2nd edn. Titus Wilson, Kendal (Freshwater Biological Association
Scientific Publication No. 36)
- Marchegiano, M., Francke, A., Gliozzi, E. and Ariztegui, D. 2018. Arid and humid phases in
central Italy during the Late Pleistocene revealed by the Lake Trasimeno ostracod
790 record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 490, 55–69
- Marchegiano, M., Horne, D.J., Gliozzi, E., Francke, A., Wagner, B. and Ariztegui, D., 2020.
Rapid Late Pleistocene climate change reconstructed from a lacustrine ostracod
record in central Italy (Lake Trasimeno, Umbria). *Boreas*, 49(4), pp.739-750.
- McCormack, J., Viehberg, F., Akdemir, D., Immenhauser, A. and Kwiecien, O., 2019.
795 Ostracods as ecological and isotopic indicators of lake water salinity changes: the
Lake Van example. *Biogeosciences*, 16(10), pp.2095-2114.
- McCrystall, M.R., Stroeve, J., Serreze, M., Forbes, B.C. and Screen, J.A., 2021. New climate
models reveal faster and larger increases in Arctic precipitation than previously
projected. *Nature Communications*, 12(1), p.6765.
- 800 McGoff, E., Aroviita, J., Pilotto, F., Miler, O., Solimini, A.G., Porst, G., Jurca, T., Donohue, L.
and Sandin, L., 2013. Assessing the relationship between the Lake Habitat Survey
and littoral macroinvertebrate communities in European lakes. *Ecological*
Indicators, 25, pp.205-214.
- McGowan, S., Gunn, H.V., Whiteford, E.J., John Anderson, N., Jones, V.J. and Law, A.C.,
805 2018. Functional attributes of epilithic diatoms for palaeoenvironmental
interpretations in South-West Greenland lakes. *Journal of Paleolimnology*, 60(2),
pp.273-298.
- Meisch, C. 2000. *Freshwater Ostracoda of western and central Europe*, Stuttgart: Spektrum
Akademischer Verlag. Gustav Fischer.

- 810 Meisch, C., Smith, R.J. and Martens, K., 2024. An updated subjective global checklist of the
extant non-marine Ostracoda (Crustacea). *European journal of taxonomy*, 974, pp.1-
144.
- Mernild, S.H., Liston, G.E., van As, D., Hasholt, B. and Yde, J.C., 2018. High-resolution ice
sheet surface mass-balance and spatiotemporal runoff simulations: Kangerlussuaq,
815 west Greenland. *Arctic, Antarctic, and Alpine Research*, 50(1), p.S100008.
- Nelligan, C., Sorichetti, R.J., Yousif, M., Thomas, J.L., Wellen, C.C., Parsons, C.T. and
Mohamed, M.N., 2021. Then and now: revisiting nutrient export in agricultural
watersheds within southern Ontario's lower Great Lakes basin. *Journal of Great
Lakes Research*, 47(6), pp.1689-1701.
- 820 O'Reilly, C.M., Sharma, S., Gray, D.K., Hampton, S.E., Read, J.S., Rowley, R.J., Schneider,
P., Lenters, J.D., McIntyre, P.B., Kraemer, B.M. and Weyhenmeyer, G.A., 2015. Rapid
and highly variable warming of lake surface waters around the globe. *Geophysical
Research Letters*, 42(24), pp.10-773.
- Olsen, J., Anderson, N.J. and Knudsen, M.F., 2012. Variability of the North Atlantic Oscillation
825 over the past 5,200 years. *Nature Geoscience*, 5(11), pp.808-812.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.,
Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker,
B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., Durand, S.,
Evangelista, H., Fitz, J.R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L.,
830 Martino, C., McGlinn, D., Ouellette, M., Ribeiro, C.E., Smith, T., Stier, A., Ter Braak,
C., Weedon, J. (2025). *Vegan: Community Ecology Package*. R package version 2.8-
0, <https://vegandevs.github.io/vegan/>.
- Paltan, H., Dash, J. and Edwards, M., 2015. A refined mapping of Arctic lakes using Landsat
imagery. *International Journal of Remote Sensing*, 36(23), pp.5970-5982.
- 835 Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling,
B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T. and Ims, R.A., 2009. Ecological dynamics
across the Arctic associated with recent climate change. *Science*, 325(5946), pp.1355-
1358.
- Poulsen, E.M. 1940. The Zoology of East Greenland. Freshwater Entomostraca. *Meddelelser
840 om Grønland*, 121 (4), 335pp.
- Prater, C., Bullard, J.E., Osburn, C.L., Martin, S.L., Watts, M.J. and Anderson, N.J., 2022.
Landscape controls on nutrient stoichiometry regulate lake primary production at the
margin of the Greenland Ice Sheet. *Ecosystems*, 25(4), pp.931-947.
- Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K.,
845 Vihma, T. and Laaksonen, A., 2022. The Arctic has warmed nearly four times faster
than the globe since 1979. *Communications Earth & Environment*, 3(1), p.168.

- Reuss, N.S., Hamerlík, L., Velle, G., Michelsen, A., Pedersen, O. and Brodersen, K.P., 2014. Microhabitat influence on chironomid community structure and stable isotope signatures in West Greenland lakes. *Hydrobiologia*, 730(1), pp.59-77.
- 850 Rodriguez-Perez, H. and Baltanas, A., 2008. Ecology and production of *Heterocypris exigua* and *Plesiocypridopsis newtoni* (Crustacea, Ostracoda) in an oligohaline hypertrophic shallow lake. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 172 (1), pp. 13-26
- Røen., U. 1962. Studies on freshwater Entomostraca in Greenland II. Localities, ecology, and
855 geographical distribution of the species. *Meddelelser om Grønland*, 170 (2), 249pp, 9 pls, 6 tables.
- Røen., U. 1968. Studies on freshwater Entomostraca in Greenland III. Entomostraca from Peary Land with notes on their biology. *Meddelelser om Grønland*, 184 (4), 59pp.
- Røen., U. 1970. Studies on freshwater Entomostraca in Greenland IV. A collection from
860 Angmagssalik, East Greenland. *Meddelelser om Grønland*, 184 (10), 18pp.
- Røen., U. 1981. Studies on the freshwater Entomostraca in Greenland V. The fauna of the Hazen camp study area, Ellesmere Island, N.WT., Canada compared to that of the Thule area, Greenland. *Steenstrupia* 7, 321–335.
- Saros, J.E., Anderson, N.J., Juggins, S., McGowan, S., Yde, J.C., Telling, J., Bullard, J.E.,
865 Yallop, M.L., Heathcote, A.J., Burpee, B.T. and Fowler, R.A., 2019. Arctic climate shifts drive rapid ecosystem responses across the West Greenland landscape. *Environmental Research Letters*, 14(7), p.074027.
- Saros, J.E., Arp, C.D., Bouchard, F., Comte, J., Couture, R.M., Dean, J.F., Lafrenière, M., MacIntyre, S., McGowan, S., Rautio, M. and Prater, C., 2022. Sentinel responses of
870 Arctic freshwater systems to climate: linkages, evidence, and a roadmap for future research. *Arctic Science*, 9(2), pp.356-392.
- Saros, J.E., Hazuková, V., Northington, R.M., Huston, G.P., Lamb, A., Birkel, S., Pereira, R., Bourdin, G., Jiang, B. and McGowan, S., 2025. Abrupt transformation of West
875 Greenland lakes following compound climate extremes associated with atmospheric rivers. *Proceedings of the National Academy of Sciences*, 122(4), p.e2413855122.
- Scharf, B.W. (1981) Zur rezenten Muschelkrebsfauna der Eifelmaare (Crustacea: Ostracoda) *Mitteilungen der Pollichia*, 69(1980): 185-204.
- Schmidt, P.P., 1976. Recent and subfossil finds of a new species of ostracod, *Potamocypris parva*, in Greenland (Crustacea, Ostracoda, Cyprididae). *Astarte; norvege*; vol. 9; no
880 1; pp. 13-17.
- Schneider, A., Wetterich, S., Schirrmeister, L., Herzsuh, U., Meyer, H. and Pestryakova, L.A., 2016. Freshwater ostracods (Crustacea) and environmental variability of

- polygon ponds in the tundra of the Indigirka Lowland, north-east Siberia. *Polar Research*, 35(1), p.25225.
- 885 Smith A.J. & Horne D.J. 2016. Class Ostracoda. In: Thorp J.H. & Covich A.P. (Eds) *Ecology and General Biology: Thorp and Covich's Freshwater Invertebrates, Volume 2*. Academic Press (Elsevier), Burlington
- Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S., Jones, V.J., Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D. and Brooks, S.J., 2005. Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences*, 102(12), pp.4397-4402.
- 890 Stephanides, T. (1948): A survey of the fresh-water biology of Corfu and of certain other regions of Greece. *Praktika of the Hellenic Hydrobiological Institute 2 (part 2): 1-263*.
- Taiyun Wei and Viliam Simko (2024). R package 'corrplot': Visualization of a Correlation Matrix (Version 0.95). Available from <https://github.com/taiyun/corrplot>
- 895 Vadeboncoeur, Y., Vander Zanden, M.J. and Lodge, D.M., 2002. Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models: Lake ecologists tend to focus their research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral part of lake food webs. *Bioscience*, 52(1), pp.44-54.
- 900 Van As, D., Hasholt, B., Ahlstrøm, A.P., Box, J.E., Cappelen, J., Colgan, W., Fausto, R.S., Mernild, S.H., Mikkelsen, A.B., Noël, B.P. and Petersen, D., 2018. Reconstructing Greenland ice sheet meltwater discharge through the Watson River (1949–2017). *Arctic, Antarctic, and Alpine Research*, 50(1), p.S100010.
- 905 Vesper, B., 1975. Ein Beitrag zur Ostracodenfauna Schleswig-Holsteins. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut* 72: 97-108.
- Viehberg, F.A. and Pienitz, R., 2017. Trends in Ostracoda and Cladocera distribution and water chemistry in subarctic Canada: Churchill (Manitoba) lakes and ponds revisited. *Journal of Limnology*, 76(3).
- 910 Wang, C., Zhao, D., Zhou, Z. and Yuan, C., 2025. Ostracod-based transfer function shifting to a broad prospect in palaeolimnology and palaeoclimate. *Science of The Total Environment*, 958, p.177894.
- Wetterich, S., Schirrmeister, L., Meyer, H., Viehberg, F.A. and Mackensen, A., 2008. Arctic freshwater ostracods from modern periglacial environments in the Lena River Delta (Siberian Arctic, Russia): geochemical applications for palaeoenvironmental reconstructions. *Journal of Paleolimnology*, 39(4), pp.427-449.
- 915 Whiteford, E.J., McGowan, S., Barry, C.D. and Anderson, N.J., 2016. Seasonal and regional controls of phytoplankton production along a climate gradient in South-West

920 Greenland during ice-cover and ice-free conditions. *Arctic, Antarctic, and Alpine Research*, 48(1), pp.139-159.

Woolway, R.I., Sharma, S. and Smol, J.P., 2022. Lakes in hot water: the impacts of a changing climate on aquatic ecosystems. *Bioscience*, 72(11), pp.1050-1061.