



Differences in food web structure and composition between new and nearby older lakes in West Greenland suggest succession trajectories driven by glacier retreat

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Abstract With the retreat of glaciers, new ponds and lakes are often formed. These are gradually colonised and become more productive as vegetation develops in their catchments, creating more complex food webs. Near the Jakobshavn Isbræ in West Greenland, we studied trophic structure and food web complexity using stable isotopes in 26 lakes

belonging to two different age groups (19 new lakes and 7 nearby older (> 150 years) ones). The older lakes had significantly higher total nitrogen and pelagic chlorophyll-*a* concentrations, as well as a higher organic matter content in the surface sediment. The biomass and richness of cladocerans, copepods and rotifers were higher in the older lakes and so was the zooplankton:phytoplankton biomass ratio. Multi-variate analyses showed a marked difference between the zooplankton communities of new and older lakes. Layman food web metrics indicated higher food chain

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length and width of invertebrates (zooplankton and benthic macroinvertebrates) in the older lakes, being significantly higher in lakes with fish. Our findings highlight a potential sequence of succession occurring in lakes created by glacial retreat in the Arctic, implying an increase in food web complexity and higher taxonomic (and likely also functional) diversity following ageing and increased nutrient state.

Keywords Climate change · Arctic · Glacier-fed lakes · Richness · Zooplankton · Food webs · Stable isotopes

Introduction

Climate change is affecting the ecosystem structure and community composition of lakes world-wide (Adrian et al., 2009; Moss et al., 2011), with the largest effects foreseen in the Arctic (IPCC, 2007, 2021). However, the ecological consequences of climate change in the Arctic remain comparatively underreported even though the magnitude of abiotic changes here are larger than in temperate, tropical and montane biomes (Wrona et al., 2005). Massive glacier retreat is ongoing, creating new habitats available for colonisation (Young et al., 2011; Shugar et al., 2020). A notable example is Greenland, which has been subjected to major deglaciation throughout the last 200 years (Weidick et al., 1990; Cuzzone et al. 2019), particularly since the mid-1990s when the rate of ice loss accelerated due to rising atmosphere and ocean temperatures as well as reconfiguration of the ice margin (Moon et al. 2020; IPCC, 2021).

Lakes of glacial origin are probably the most numerous on Earth (Wetzel, 2001), but surprisingly, little is

known about their ecology in the early stages of succession (Sommaruga, 2015). Newly created lakes by ice melting in the glacier foreland (i.e. proglacial lakes) usually go through a succession from a state of high inorganic turbidity to clear water conditions when their hydrological connection to the glacier or ice sheet decreases or is lost (Sommaruga, 2015; Peter et al., 2018). Paleoecological analyses reveal that past periods with glacial meltwater input to lakes have led to a reduction in the species richness of zoo- and phytoplankton (e.g., Birks et al., 2000; Karabanov et al., 2004) and in some cases to the absence of cladocerans (Pawłowski et al., 2013). When the new lakes are turbid due to high concentrations of suspended inorganic particles resulting from glacier abrasion on the underlying rock or sediment (so-called glacial or rock flour), they represent a particular challenge for generalist filter-feeding organisms such as *Daphnia*. This is because these organisms will largely fill their gut with inorganic particles or be forced to invest more energy in finding a suitable food item (Koenings et al., 1990). For example, interference of glacial flour in the submicron range with bacteria causes a significant reduction of clearance rates in heterotrophic protists as observed in experiments with fluorescently labelled prey surrogates (Sommaruga & Kandolf, 2014).

As the water clears after sedimentation of the glacial flour, the lakes gradually become less light-limited and more productive, which coincides with the development of terrestrial vegetation in the surrounding landscape and the expected associated N_2 fixation (Rousk et al., 2018). Further, ageing likely leads to higher in-lake accumulation of nutrients such as inorganic nitrogen and organic carbon but an initial reduction in phosphorus when glacial flour settles (Elser et al., 2020), although the magnitude of those changes may be different among newly deglaciated regions. In mountain lakes, it has been shown that these environmental changes result in more complex food webs (Tiberti et al., 2020). However, food webs, nutrient dynamics and successions, as well as energy pathways, are far from being understood in other types of deglaciated areas. In general, there are three factors interacting with each other: ageing can lead to the accumulation of species that need to reach the habitat to establish, ageing leads to changes in abiotic environmental conditions, and ageing can lead to strongly changed dynamics due to the arrival of

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specific taxa. As an example of the latter, fish can colonise deglaciated areas such as in Greenland as long as migration is not hampered by physical barriers (Jeppesen et al., 2017). Fish arrival is expected to have strong trophic cascading effects on prey items, such as macroinvertebrates and large-bodied zooplankton but insignificant cascading effects on phytoplankton biomass due to nutrient limitation, as judged from a study of 87 lakes in Northwest and East Greenland (Jeppesen et al., 2017).

One of the most prominent examples of rapid ice sheet retreat is the Jakobshavn Isbræ in western Greenland, whose recent development (past 200 years) has been well documented (Weidick et al., 1990; Sohn et al., 1998; Young et al., 2011; Shugar et al., 2020). The area has been under continuous recession since 1850, with rapid acceleration in the past few decades leading to exposure of new land and the creation of new lakes and ponds (Sohn et al., 1998).

Here, we tested the idea that richness of the biota and biomass of consumers, as well as the complexity of the food web including the occurrence of fish in lakes, increase with lake age and associated higher productivity. For this purpose, we compared selected environmental variables

to characterise the lakes and sampled the littoral, planktonic and benthic regions, as well as fish to analyse the food web by stable isotopes in a set of relatively recently formed lakes of contrasting age in the foreland of the Jakobshavn Isbræ.

Materials and methods

Study area and sampling

The sampling was done during July and August 2012 in 27 lakes located on the western coast of Greenland ($69^{\circ} 5' 27''$ N, $49^{\circ} 47' 4''$ W, 200 km south of the polar Arctic circle) (Fig. 1). The lakes were classified into “new” (N) systems ($n=20$, later reduced to 19, see below, with 9 formed less than 62 years ago) and “old” (O) systems (formed > 150 years ago; $n=7$). Age was determined by analysing aerial photographs and comparing old and current maps (Hailese-lasie et al., 2016a) (Fig. 1). Terrestrial vegetation was scarce or absent in the catchments of the new systems but abundant in the old systems (see Fig. 1). Estimation of surface area was based on aerial photographs. Maximum depth was recorded in situ with an echosounder. Water pH, temperature ($^{\circ}$ C) and

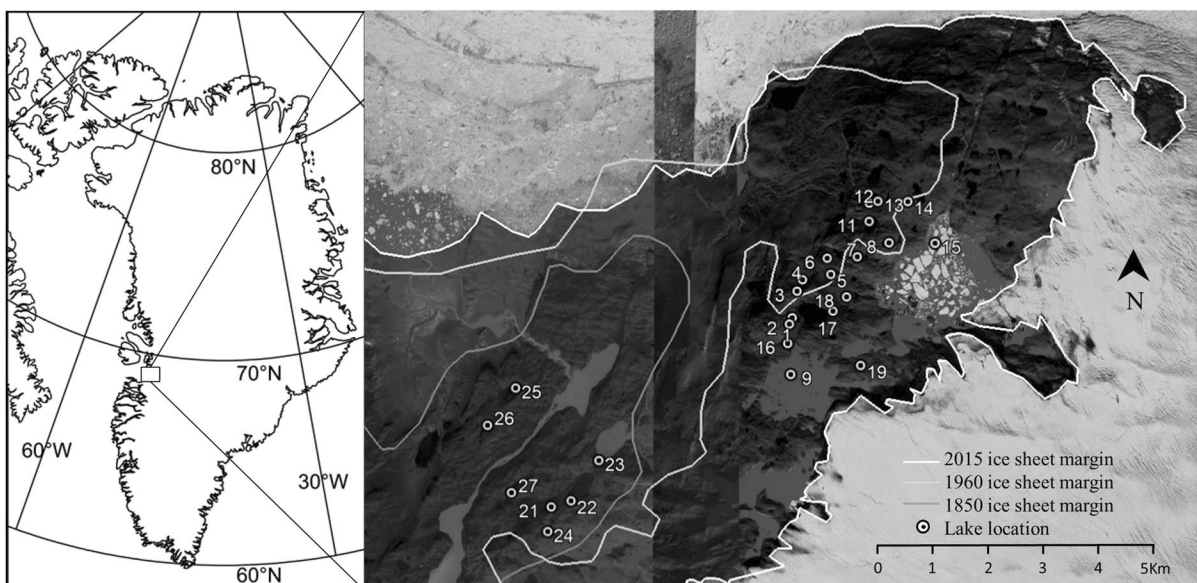


Fig. 1 The glacial terminus at Jakobshavn Isbrae near Ilulissat in 1850, 1960 and 2015 shown on Google Map. Position of lines is adopted from Weidick et al. (1990) and Csatho et al. (2008). Position of the lakes sampled is also shown

conductivity ($\mu\text{Si cm}^{-1}$) were measured with a YSI 6600 multi parameter probe at maximum depth.

Composite samples were collected with a 5-l Schindler sampler at 0.5–3-m intervals (depending on lake depth) from the surface to 0.5 m above the bottom in the deepest part of each lake and then pooled. For zooplankton analyses, 12–20 l subsamples of the pooled sample were filtered onto a 20- μm mesh size filter and fixed in acid Lugol's solution (4%). For chemical analyses, a subsample of 250 ml was frozen, and for chlorophyll-*a* (Chl-*a*) duplicate 1-l subsample was filtered on a GF/C filter (Whatman) and was frozen until analysis.

Fish sampling consisted of overnight catches using multiple mesh size (height 1.5 m) gill nets with 14 randomly distributed sections of 3 m (mesh sizes: 6.25–75.0 mm). Depending on lake size, 2–6 nets were used in each lake. The nets were set parallel to the shore at ca. 2 m depth and in the larger lakes also at a mid-lake station. In lakes deeper than 10 m, both benthic (placed at the bottom) and pelagic nets (positioned at half the maximum depth) were used at the mid-lake station. In one deep and large lake, only littoral nets were set due to time constraints. For each net section, all fish (i.e., Arctic charr, *Salvelinus alpinus* (Linnaeus, 1758), the only species present in the area) were counted and weighed, and fork length was measured. For stable isotope analyses, we used flank muscle of 20 to 60 individuals of Arctic Charr, 20 individuals being randomly selected from each of the habitats (littoral, benthic and pelagic zones) sampled (4 lakes with fish). The samples were kept in cooling boxes and frozen as soon as possible (-18°C) until analysis.

For stable isotope analysis, we further collected (1) mid-lake samples of zooplankton using vertical nets with two (140 μm and 500 μm) mesh sizes (the latter only including large-sized zooplankton) and (2) littoral and benthic macroinvertebrates using a sweep net (1000 μm mesh size). Furthermore, we collected benthic macroinvertebrates from the deep zone and in the littoral zone using an Ockelman epibenthic sledge (KC Denmark A/S Research Equipment, Silkeborg, Denmark). A standardised sampling effort was made spending at least 2 h on sampling and collection in each lake. We assume that nearly all taxa present in these species-poor lakes were collected, allowing us to calculate richness. From these bulk samples, 5–100 individuals of each taxon were taken and stored

frozen before analysis. No quantitative samples for macroinvertebrates were collected.

Analyses

Lake water total phosphorus (TP, mg l^{-1}) was determined as molybdate reactive phosphorus (Murphy & Riley, 1972) following persulphate digestion (Koroleff, 1970) and total nitrogen (TN, mg l^{-1}) as nitrite + nitrate after potassium persulphate digestion (Solórzano & Sharp, 1980). Chlorophyll *a* (Chl-*a*, $\mu\text{g l}^{-1}$) concentration was determined spectrophotometrically after ethanol extraction (Jespersen & Christoffersen, 1987). We further sampled surface sediment, taking three to five cores with a Kajak sampler in the deepest part of the lakes or at a mid-lake station in uniform shallow lakes. From each core, the upper 0–1 cm was sampled and pooled and frozen until analyses. Dry weight (DW) and ash-free dry weight (AFDW) were determined in the lab on a 5 ml aliquot, and we calculated the weight loss on ignition (LOI) percentage as $(\text{DW}-\text{AFDW})/\text{DW}\times 100$.

Zooplankton were identified to genus/species level and counted at 40–100 \times magnification (Olympus). Richness was defined as taxa/genera of the lowest identifiable level. Rotifer biomass was calculated using taxa-specific standard dry weights (Dumont et al., 1975; Bottrell et al., 1976), while cladoceran and copepod biomasses were calculated based on published length–weight relationships (Dumont et al., 1975; Bottrell et al., 1976) determined from measurements of 25 individuals of each species (when possible). The zooplankton:phytoplankton biomass ratio was calculated after converting Chl-*a* according to Jeppesen et al. (2003a).

Samples for stable isotope analyses were thawed in the laboratory and cleaned using distilled water. We separated and identified macroinvertebrates to family level. The processed samples were freeze-dried, fine-powdered and kept in glass vials and then weighed using a precision balance (0.01 mg, Sartorius Genius), loaded into tin capsules and analysed at UC Davis Stable Isotope Facility (University of California, USA) for stable isotopes of carbon (^{12}C : ^{13}C , $\delta^{13}\text{C}$) and nitrogen (^{14}N : ^{15}N , $\delta^{15}\text{N}$). We expressed stable isotope data in parts per thousand (‰) deviations from international standards (Vienna Pee Dee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) using the following equation: $\delta X = (\text{Rsample}/$

$R_{\text{standard}} - 1) \times 1000$ where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$ and R = ratio of heavy/light isotope content (${}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$). Internal precision was $< 0.2\%$.

Data analysis

We first divided the lakes into two categories, old (O) and new (N) lakes, identified based on the retreat of the glacial terminus at Jakobshavn Isbræ near Ilu since 1850 AD (Weidick et al., 1990; Csatho et al., 2008) and corresponded clearly in the field and on maps to vegetated and bare soil, respectively (Fig. 1). We then divided the lakes into four categories. Based on the fish studies, we divided the old lakes into lakes with (O+F, $n=4$) and without fish (O-F, $n=3$) and the new lakes, all without fish, were divided into turbid (NT, $n=4$) and clear lakes (NC) ($n=16$). One of the turbid lakes was, however, later excluded from the analyses (see the reason for the division and exclusion below under PCA results).

For the comparison of new and old lakes, we used Kruskal–Wallis non-parametric tests (NPARIWAY procedure, SAS Institute, 1989). We applied a one-sided test as we had an a priori expectation of the direction of changes of the variables, as presented in the introduction. Exceptions were for the maximum lake depth and lake area, where a two-sided test was used. For the comparison of the four categories, we used the Kruskal–Wallis multiple test followed by post hoc tests for pairwise comparison (Wilcoxon Z score test, two-sided).

Principal components analysis (PCA) was used to characterise the variation in the zooplankton biomass data, and redundancy analysis (RDA) was applied to determine which environmental variables correlated best with the variation in zooplankton biomass data. The zooplankton biomass data were Hellinger-transformed prior to analysis as this has been shown to be an appropriate transformation of ecological data when using methods based on Euclidean distance, such as PCA and RDA (Legendre & Gallagher, 2001). All ordination analyses were carried out in R version 3.1.3 (R Development Core Team, 2015), with the vegan package (version 2.3–4, Oksanen et al., 2022).

Food web metrics as defined by Layman et al. (2007) were calculated using the ‘SIBER package’ in ‘R’ (Jackson et al., 2011). We used the range of $\delta^{13}\text{C}$ (CR), representing the width of the food web and thus the range of trophic channels exploited, and the range

of $\delta^{15}\text{N}$ (NR), which indicates the range of trophic levels within a food web or trophic niche space. Both ranges were calculated as the difference between the maximum and minimum values recorded. We also calculated the total area (TA) in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot and the standard ellipses area (SEAc), which englobes 40% of isotopic data and is a robust analysis even at low n to represent the isotopic niche width (Batschelet, 1981), while TA is sensitive to variation in sample numbers (Jackson et al., 2014). We mainly focused on SEAc but also used TA in the comparison among the four lake categories as SEAc could not be calculated for the turbid glacial-fed lakes. We did not include isotope values of primary producers since they are highly variable, and their use for calculating Layman’s metrics has been criticised (Hoeinghaus & Zeug, 2008). Instead we used stable isotope values of the primary consumers (benthic macroinvertebrates plus zooplankton) as the base of the food web as they better integrate the natural variation in space and time of these basal resources (Layman et al., 2007). For testing the differences in the metrics among the lake categories, we use the NPARIWAY procedure (two-sided test) as described above.

Results

The new lakes were positioned at rather similar elevations (about 300 m a.s.l.), but closer to the Greenland ice sheet than the old ones (Fig. 1; Table 1). The lakes varied markedly in size and maximum depth (Table 1). No significant differences were, however, found in lake area, maximum depth and water temperature among the new and old lakes (Table 1). Minimum temperature tended to be lower in the new lakes (Table 1) as some lakes were glacial-fed. The mean nutrient concentrations (TN and TP) were overall low, with TP mostly below 0.01 mg l^{-1} , except for the glacial-fed lakes that had about 3 times higher concentrations, while TN was below 0.6 mg l^{-1} (Fig. 2), and Chl-*a* was low ($< 2 \mu\text{g l}^{-1}$). The old lakes had significantly higher TN and Chl-*a* concentrations and significantly higher organic content in the surface sediment (i.e. LOI) than new lakes, but lower pH and conductivity (Fig. 2, left). No difference emerged for TP concentrations (Fig. 2, left).

When dividing the lakes into the four categories (Fig. 2, right), we found significantly lower TN

Table 1 Main, standard deviation (STD) and range of lake morphometrical characteristics and water temperature according to age class

	New lakes (20) Mean (STD) (range)	Old lakes (7) Mean (STD) (range)	Two samples test	
			<i>z</i>	<i>P</i> (<i>z</i>)
Elevation (m)	315 (31) (275–389)	287 (21) (254–312)	– 1.73	> 0.09
Lake area (ha)	21.5 (60) (0.05–247)	10.7 (11.7) (0.3–29)	0.96	> 0.34
Lake depth (m)	9.4 (9.1) (1.9–26)	18.7 (16,2) (4.8–50)	1.62	> 0.10
Distance to ice sheet (km)	1.5 (0.7) (0.2–2.5)	3.4 (1.0) (2.2–4.3)	3.64	< 0.001
Water temperature (°C)	9.8 (2.7) (0.7–12.1)	11.0 (0.8) (9.4–11.6)	1.56	> 0.06

Also shown are the test values using Kruskal–Wallis non-parametric 2 samples test (Wilcoxon Z Score) – 1-sided for distance to the ice and water temperature and 2-sided for the other variables (see text)

concentrations and higher TP and conductivity in the new turbid lakes than in the other three lake categories. Chl-*a* was significantly lower in the new clear lakes than in the two old lake categories. The new clear lakes had a higher pH than the old lakes with fish, but otherwise, no significant differences in pH were observed among the lake categories. LOI in the surface sediment was significantly lower in the new lakes, both clear and turbid, than in the old lakes without fish. Overall, the new lakes had lower LOI than the old lakes—being particularly low in the new turbid lakes—although differences were not significant, likely reflecting the low sample size for the new turbid lakes (Fig. 2, right).

Zooplankton taxa richness differed significantly between the new and old lakes (Fig. 3, left). Total taxon richness averaged 4.9 (STD 2.2) in the new lakes and 13.9 (2.3) in the old lakes. The corresponding figures for rotifers were 3.2 (1.4) and 8.7 (2.4), respectively, and for crustaceans, 1.6 and 5.1. When using again the four lake categories, all three zooplankton groups had significantly higher richness in both of the old lake categories (with and without fish) than in the two new lake categories (clear and turbid) (Fig. 3, right). Among the crustaceans, *Leptodiptomus minutus* (Lilljeborg in Guerne & Richard, 1889), *Holopedium gibberum* Zaddach, 1855, *Macrothrix* sp., *Bosmina longirostris* (O.F. Müller, 1776), *Euryercus lamellatus* (O.F. Müller, 1776), *Simocephalus vetulus* (O.F. Müller, 1776) and *Polyphe-mus pediculus* (L. 1761) were only found in the old lakes. The latter three, being relatively large-sized and fish predation-vulnerable species, occurred only in lakes without fish. *Daphnia* (*Daphnia pulex* Leydig, 1860) were recorded in both old and new clear

lakes. Calanoid copepods (represented by *L. minutus*) were exclusively found and were ubiquitous in the old lakes, while cyclopid copepods were recorded in 60% of the new lakes and in all the old lakes. Among the rotifers, *Conochilus* sp., *Colloctheca* sp., *Gastropus* sp., *Ascomorpha* sp., *Asplanchna priodonta* Gosse, 1850, *Kellicotia longispina* (Kellicott, 1879) and *Tricocerca* sp. only occurred in the old lakes. By contrast, the rotifers *Colurella* sp., *Not-holca squamula* (Müller, 1896), *Cephalodella* sp. and *Monommata* sp. were only found in the new lakes. *Asplanchna priodonta* Gosse 1850 were found in both lake types.

The PCA and RDA analyses of the zooplankton community showed an overall marked difference between the new and the old lakes, but no clear separation of old lakes with and without fish. The RDA suggested that four variables shaped the composition of the zooplankton community, namely fish abundance, Chl-*a*, TN and lake area (Fig. 4, right). Among the new lakes, three of the four turbid lakes were well separated from the clear ones. One of the new turbid lakes was associated with the new clear ones. While the other three were true glacial-fed lakes (on the river), this lake received only glacial river water (backwater) at high water level, which may explain why the zooplankton community was more associated with the NC lakes. This lake was, therefore excluded from the comparison of the four lake categories because it belongs to a 5th category with only one system.

We found significantly higher biomasses of total zooplankton, as well as of cladocerans, copepods and rotifers in the old lakes than in the new ones despite high variability among lakes. The

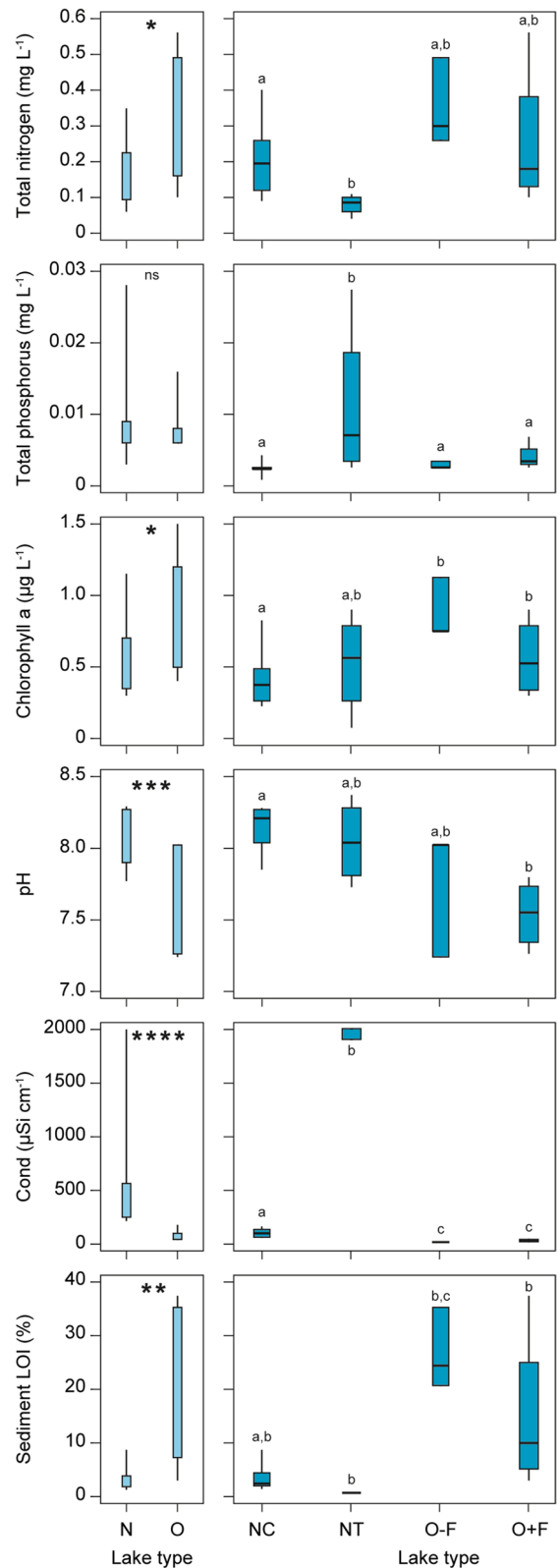
Fig. 2 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of environmental variables for lakes divided into new (N) and old (O) (left-hand side) and into four categories (new lakes with clear water (NC) and turbid water (NT), respectively, and old systems with (O+F) and without fish (O-F) (right-hand side). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b and c show significant differences in pairwise comparisons (at $P < 0.05$ level). LOI is weight loss of ignition

zooplankton:phytoplankton biomass ratio was also higher in the old lakes (Fig. 5, left). When dividing the lakes into the four categories, the results became less clear. Total zooplankton and copepod biomasses were significantly higher in the old lakes without fish than in than in the new clear ones while none of the other pairwise comparisons were significant (Fig. 5, right).

Whereas the mean body size (body weight) of both copepods and cladocerans (and thus total crustaceans) was significantly higher in the new lakes, the mean body size of rotifers was largest in the old ones (Fig. 6). However, as rotifers were by far the most abundant zooplankton in the old lakes and proportionally more abundant than in the new lakes, the mean body size of all zooplankton pooled was lower in the old lakes (Fig. 6, left). When dividing the lakes into the four groups, no significant differences emerged, although zooplankton (all groups) in the old lakes tended to have a smaller mean body size in lakes with than without fish (Fig. 6, right). Among the new lakes, the mean body size of cladocerans tended to be lower in the new turbid lakes than in the new clear ones (Fig. 6, right).

The number of macroinvertebrate taxa sampled for the SIA analysis averaged 7.4 (SD 0.5) in the old lakes (7 in lakes with and 8 in lakes without fish), and it was significantly lower in the new lakes, averaging 4.3 (0.9) in the new clear lakes and 2.8 (1.0) in the new turbid ones (Fig. 7). Whereas the community in the new lakes mainly consisted of the chironomids Tanipodinae, Tanitarsini, Diamesinae, and Orthocla-diinae, as well as of the beetle *Colymbetes dolabratus* (Paykull, 1798), the more diverse fauna in the old lakes also included more taxa of Chironominae, oligochaetes, caddisflies and the mussel *Pisidium* sp.

The Layman food web metrics NR, CR, SEAc and TA for invertebrates (zooplankton plus benthic macroinvertebrates) were significantly higher in the old lakes than in the new lakes (Fig. 8, left). When



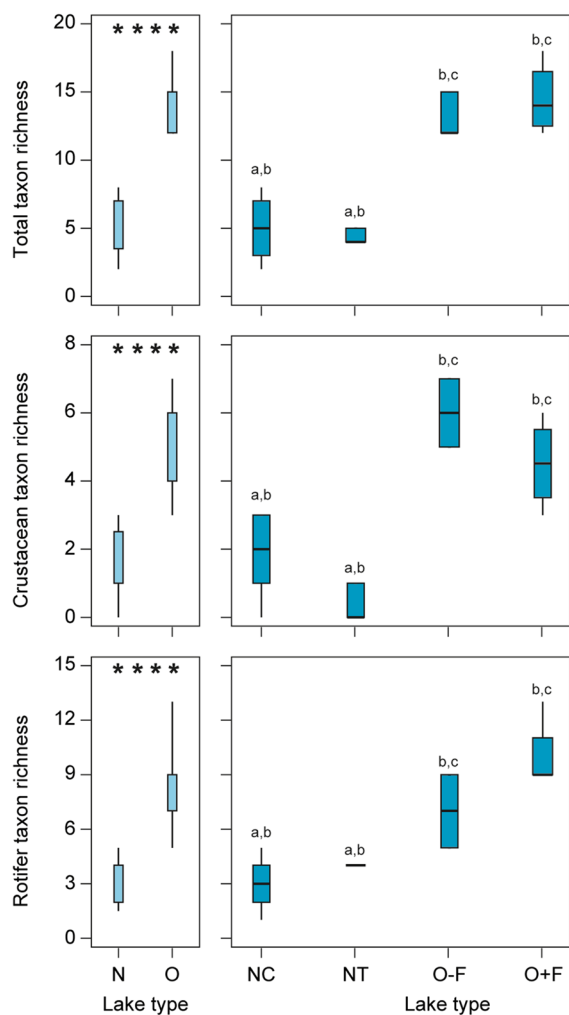


Fig. 3 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of the total zooplankton taxon richness and the taxon richness of microcrustaceans and rotifers in lakes divided into new lakes (N) and old lakes (O) (left-hand side) and into four categories (new systems with clear water (NC) and turbid water (NT), respectively, and old systems with (O+F) and without fish (O-F) (right-hand side). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b and c show significant differences in pairwise comparisons (at $P < 0.05$ level)

including the four groups, no significant differences were found, although the new turbid lakes tended to have lower metric values than the other three lake categories.

When including fish, however, all Layman metrics were significantly higher in the old lakes with fish (see new category called O+F2 in Fig. 8) than in both the old ones without fish and the new clear ones (also without fish) but not higher than in new turbid

lakes, obviously because of a low number of lakes in this category as the average values in these lakes appeared lowest for all metrics.

The variation in the complexity of the lake food web is illustrated in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplots (Fig. 9), including one of the lakes from each of the four categories selected to match as much as possible the lake size and depth of the different lake types. An exception was the turbid glacier-fed lake that was deeper and larger at the time of sampling (due to summer melting) as no proper match was available. The complexity of the food web increased from the new turbid Lake 9, over the new clear Lake 18, to the old lakes without (Lake 24) and with fish (Lake 27), with a gradually enhanced carbon range ($\delta^{13}\text{C}$) and increasing food web length ($\delta^{15}\text{N}$). The beetle *C. dolabratus* was the top predator in Lake 18, *C. dolabratus* and the caddisfly *Polycentropus* sp. in Lake 24 and Arctic charr in Lake 27.

Discussion

The results support our expectation that the older lakes would support higher taxonomic and functional diversity and more complex food webs in lakes created by glacial retreat in Greenland. The finding that TN and Chl-*a*, but not TP, were significantly higher in the old lakes compared with the new ones may reflect that the more vegetated catchments (Rousk et al., 2018) of the old lakes potentially enriched the lakes with dissolved organic nitrogen (DON) due to N_2 fixation, making the older systems indeed more productive. No difference was found in TP between the new and old lakes when combined, but TP was significantly higher in those of the new lakes that were turbid. It is well established that glacier outlets can have high TP (Tockner et al., 2002; Saros et al., 2010; Slemmons & Saros, 2012; Kammerlander et al., 2016). Studies of glacial meltwater in West Greenland have also shown high concentrations of P, most of the dissolved P being derived from the dissolution of P-containing rocks (Hawkings et al., 2016). Physical erosion of bedrock by glacier action exposes finely ground apatite in this area to biogeochemical weathering, thereby liberating phosphate (Hawkings et al., 2016). Furthermore, Hawkings et al. (2016) found elevated electrical conductivity and pH in the meltwater. This may in part explain the higher values

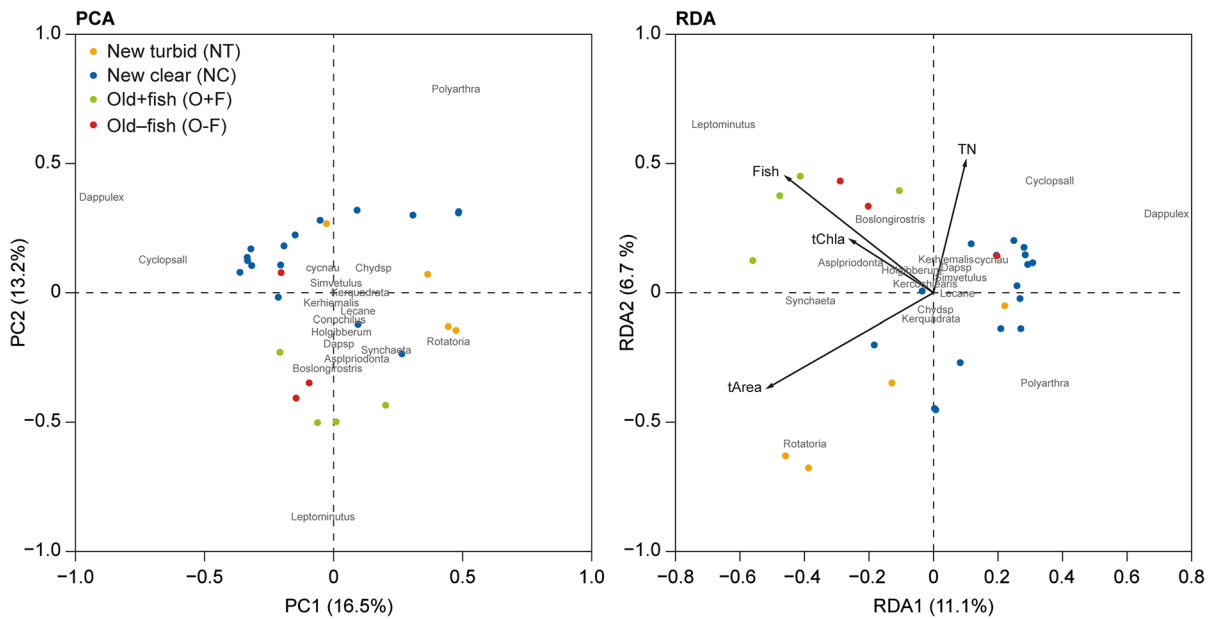


Fig. 4 PCA (left) and RDA (right) biplots on Hellinger-transformed biomass data showing the location of the sites on the first two axes of variation. The environmental variables shown are those chosen by forward selection. cynau=nauplii of cyclopoid copepods; Cyclopall=advanced stages of cyclopoids; D. pulex=*Daphnia pulex*; Dapsp=*Daphnia* sp.; Kerhiemalis=*Keratella hiemalis*; Kercochlearis=*Keratella*

cochlearis; Kerquadrata=*Keratella quadrata*; Chydsp=*Chydorus sphaericus*; Boslongirostris=*Bosmina longirostris*; Leptominutus=*Leptodiatomus minutus*; Asplpriodonta=*Asplanchna priodonta*; Holgibberum=*Holopedium gibberum*; Simvetulus=*Simoccephalus vetulus*. Other names are rotifers with their full genus name

of these variables in the new lakes, particularly in the turbid ones. However, those lakes had lower TN, which concurs with some, but not all studies of glacier-fed lake systems (Burpee & Saros, 2020).

As expected from the lower water TN and Chl-*a* concentrations, the organic content in the surface sediment was significantly lower in the new lakes than in the old ones, and especially low in the new turbid lakes. Autochthonous organic accumulation in the sediment in many clear Arctic lakes is a result of benthic production rather than being derived from settled phytoplankton, as primary production is typically higher on the sediment surface than in the water in Arctic and sub-Arctic nutrient-poor lakes (Vadeboncoeur et al., 2003; Rautio & Vincent, 2006). Low phytoplankton production in the water in our study lakes is indicated by the generally low Chl-*a* levels in all lakes, with slightly higher levels, though, in the old ones. Organic matter input from the surrounding landscape likely also contributed to the higher LOI in the surface sediment in the old lakes. The particularly low values of LOI in the turbid lakes were expected

from dilution of organic matter by the silt entering these lakes and low productivity levels (low light and low temperature).

The taxonomic richness of total zooplankton, rotifers and crustaceans was substantially higher in the old lakes, irrespective of the presence or absence of fish. The larger richness of species in the more productive systems was expected (Odum, 1963; Rosenzweig & Abramsky, 1993), but, in our case, lake age itself may also have played a role, allowing longer time for colonisation. The positive influence of lake age/nutrient state on taxonomic richness has also been documented for clones of *Daphnia* spp. in a series of ponds and lakes in the study area (including some of the lakes of our study) (Haileselasie et al., 2016a, b). Calanoid copepods were exclusively found and were ubiquitous in the old lakes, while cyclopoid copepods were found in many of the new lakes and in all the old ones. The lack of calanoids in the new lakes might reflect their comparatively more limited dispersal capacity as evidenced by their absence in most lakes in East Greenland (Jeppesen et al., 2017)

Fig. 5 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of the total zooplankton biomass, the biomass of various zooplankton groups and the zooplankton:phytoplankton biomass ratio for lakes divided into new lakes (N) and old lakes (O) (left) and into four categories (new systems with clear water (NC) and turbid water (NT), respectively, and old systems with (O+F) and without fish (O-F) (right). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b and c show differences in pairwise comparisons (at $P < 0.05$ level)

and, for instance, lakes in the Faroe Islands (Lauridsen & Hansson, 2002).

In agreement with existing literature on glacier-fed lakes elsewhere (Sommaruga & Kandolf, 2014; Sommaruga, 2015; Tiberti et al., 2020), we found that glacial runoff seems to limit the development of invertebrate communities also in Greenland. Zooplankton richness was generally low in the turbid lakes, and cladoceran filter-feeding taxa, such as *Daphnia*, *Bosmina* and *Holopedium* spp., were absent or present in low abundances in the new turbid (glacier-fed) lakes, as seen in similar Alaskan and alpine lakes (Koenings et al., 1990; Sommaruga & Kandolf, 2014). Moreover, only few groups of macroinvertebrates were found in those lakes (Fig. 8).

As expected (e.g., Hanson & Peters, 1984; Jeppesen et al., 1997), the biomasses of total zooplankton, copepods, cladocerans and rotifers were higher in the old lakes than in the new ones and were particularly low in the new turbid lakes. Higher dominance of rotifers might reflect more diverse food resources in the old lakes. In a comparative study of glacier-fed and non-glacier-fed alpine lakes, Tiberti et al. (2020) also found lower densities of both cladocerans and copepods in the former category and observed that the influence of glaciers was negatively associated with several functional groups (e.g., eukaryotic phytoplankton, copepods and gatherer-collector macroinvertebrates). Interestingly, the zooplankton:phytoplankton ratio was also higher in old lakes, independent of the presence of fish, which may reflect fuelling of zooplankton by benthic-produced organic matter (Rautio & Vincent 2006, 2007; Mariash et al., 2011; Cazzanelli et al., 2012) and by allochthonous-derived organic matter (Cole et al., 2011). The organic matter and nutrient (particularly nitrogen) input would be higher in these lakes due to the more developed terrestrial vegetation in the

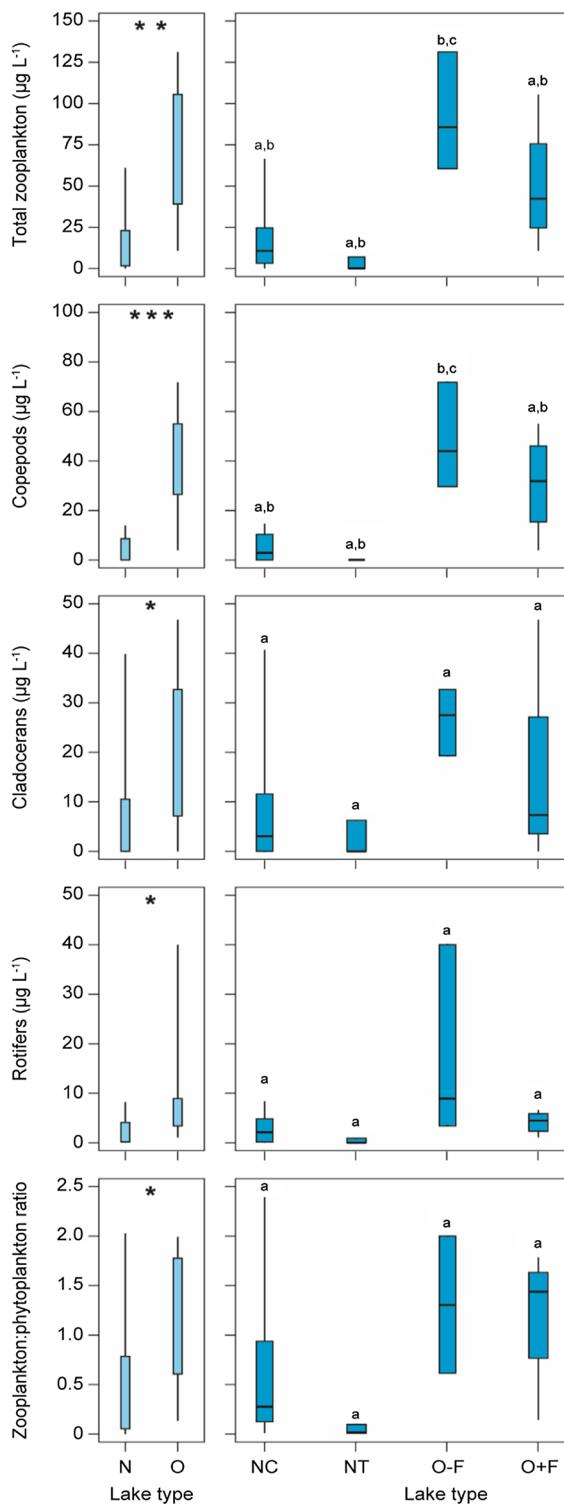
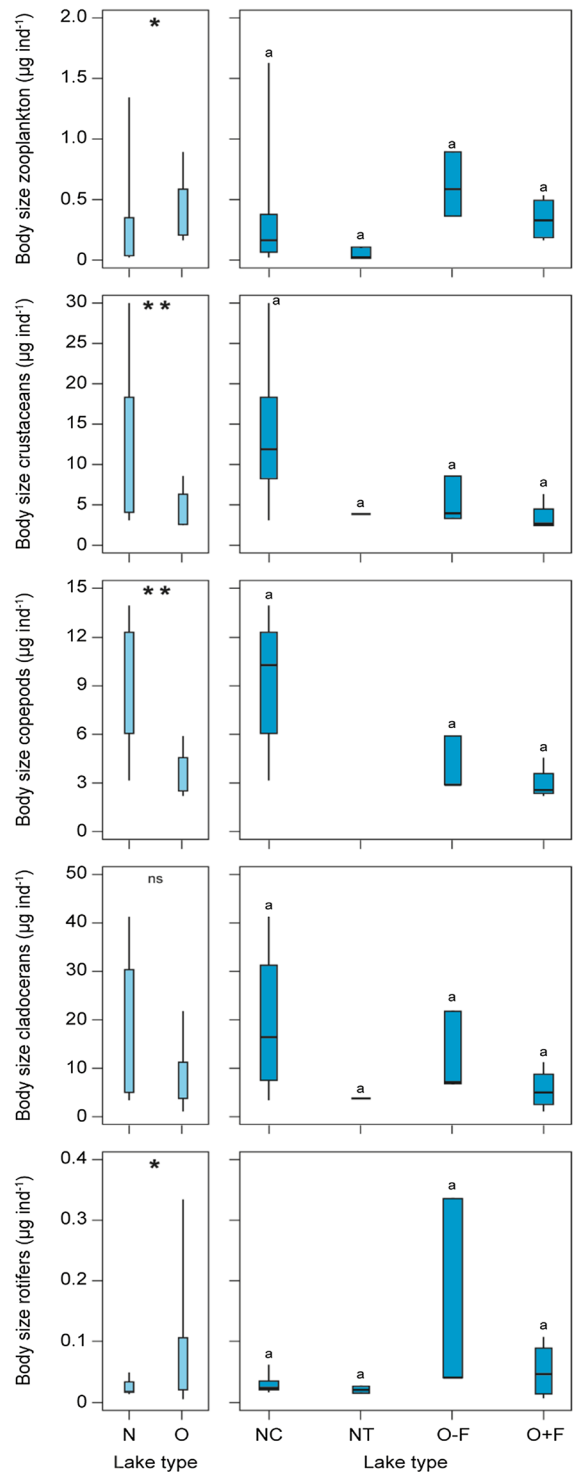


Fig. 6 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of the body mass of all zooplankton and various sub-groups for lakes divided into new lakes (N) and old lakes (O) (left-hand side) and into four categories (new systems with clear water (NC) and turbid water (NT), respectively, and old systems with (O+F) and without fish (O-F) (right-hand side). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b and c show differences in pairwise comparisons (at $P < 0.05$ level)

watersheds as also indicated by the higher TN concentrations in these lakes.

In a study of 87 lakes in West and East Greenland, Jeppesen et al. (2017) examined zooplankton in the water and their remains in the surface sediment along with benthic invertebrates and found that both the biomass and body size of zooplankton, and the abundance and composition of benthic invertebrates showed strong top-down control by fish. In contrast to the study by Jeppesen et al. (2017) which found fish caused lower zooplankton:phytoplankton ratios and an absence of *Daphnia*, we did not detect significant differences in the zooplankton:phytoplankton ratio or the absence of *Daphnia* when fish were present. These findings may indicate a relatively low predation pressure from fish (Jeppesen et al., 2011) in our study lakes. However, this cannot be explained by a low density of Arctic Charr because numbers were comparable with those in lakes in other parts of Greenland where high predation on large-bodied crustacean plankton has been observed (Jeppesen et al., 2017; Arranz et al., 2022). These findings are based both on snap-shot contemporary samples in summer (as in our study) and on the sedimentary remains of cladocerans (Jeppesen et al., 2003a, b; Davidson et al., 2011). Davidson et al. (2011), analysing surface sediment remains of cladocerans from 53 lakes in Greenland, found that besides fish, also lake depth had significant effects on the cladoceran community structure. While three of the four lakes with fish were deep (20.4–49.7 m in maximum depth) of which 2 had *Daphnia*, the fourth one was only 5.4 m deep, but also with *Daphnia*, indicating that depth, which potentially provides a refuge from predation, was not a key factor for the presence of *Daphnia*. Nevertheless, we found that the body size of cladocerans, copepods and rotifers (and thus of total zooplankton) tended to be lower in the old lakes with fish than in those without fish, indicating some, albeit a weak, effect of fish. Whether this weak predation



effect reflects that part of the fish population is anadromous and thus just arrived prior to the sampling remains to be evaluated. As in the study of Jeppesen

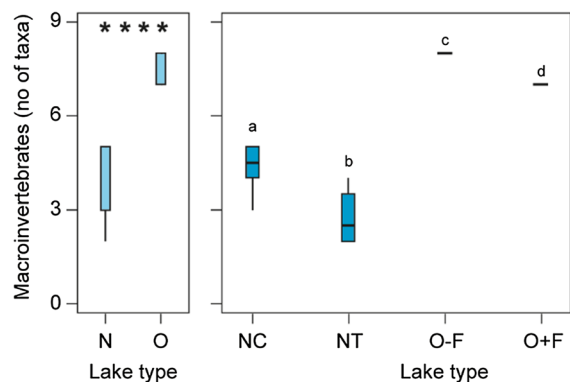


Fig. 7 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of the number of taxa of benthic invertebrates collected in the littoral zone using nets and a benthic sledge and the profundal zone with a benthic sledge for lakes divided into new lakes (N) and old lakes (O) (left-hand side) and into four categories (new systems with clear water (NC) and turbid water (NT), respectively, and old systems with (O+F) and without fish (O-F) (right-hand side). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b, c and d show significant differences in pairwise comparisons (at $P < 0.05$ level)

et al. (2017), we found no cascading effect of fish on phytoplankton biomass as Chl-*a* did not differ between the old lakes with and without fish, likely reflecting both severe nutrient limitation and, in our study, also a weak fish effect on zooplankton.

We found that the mean zooplankton body size was smaller in the old lakes, which reflects the higher degree of dominance of rotifers in these lakes as copepods and cladocerans overall had larger body sizes in the new ones, while the rotifer sizes were smaller in these lakes. The smaller sizes of crustaceans might reflect higher predation by invertebrate predators, as suggested by the presence of more predator species, in the old lakes without fish and potentially also by fish, although we did not observe significant differences in body size between lakes with and without fish. Higher predation on crustaceans in the old lakes may also explain why the body size of rotifers was larger than in the new ones, particularly if they were released from crustacean predation pressure and competition. However, as we have no data on the abundance of predacious invertebrates, this question remains unresolved. A potential effect of water temperature as a driver of changes in body size seems less likely. The larger body size of crustaceans in the new lakes could be a result of the (insignificant) lower temperature in the lakes closer to or associated

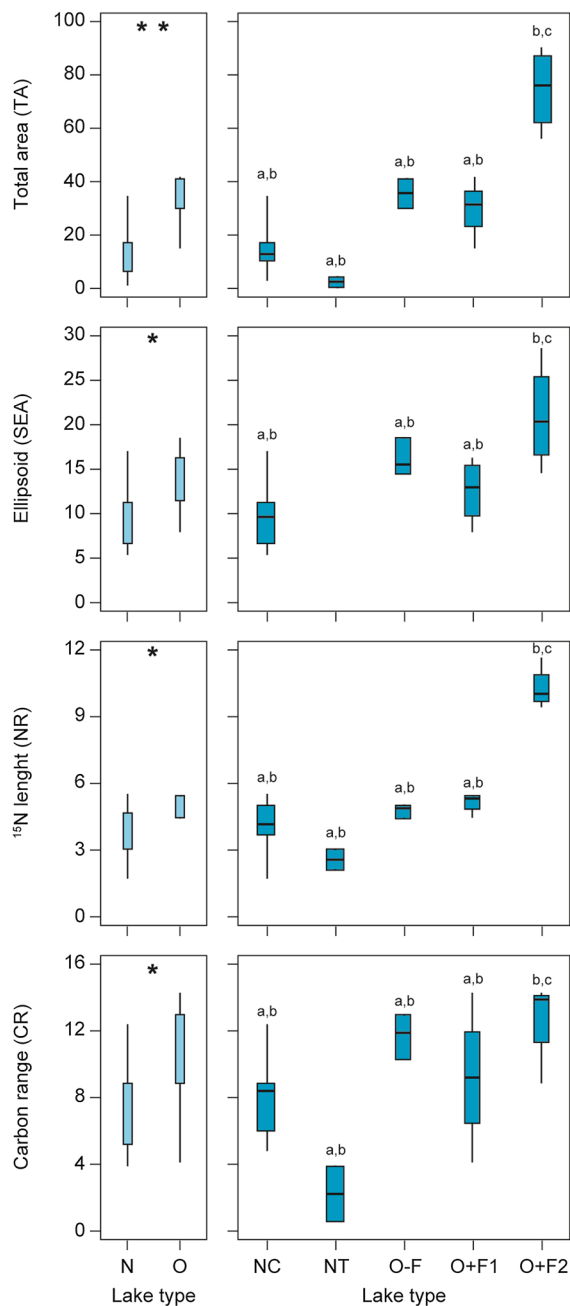


Fig. 8 Box plot (showing the 10th, 25th, 75th and 90th percentiles) of various Layman food web metrics for invertebrates (zooplankton and macroinvertebrates) in lakes divided into new lakes and old lakes (left-hand side, a line through the median) and into five categories (in new systems with clear water (NC) and turbid water (NT), respectively, and old systems without (O-F) and with fish (O+F1) (right). An extra fifth column is here added, which includes fish in the metrics (O+F2) (right-hand side). Stars indicate significant differences ($P < 0.05$ to $P < 0.0001$), and a, b and c show significant differences in pairwise comparisons (at $P < 0.05$ level). SEA (SEAc) is the best ellipsoid that can be drawn through the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot

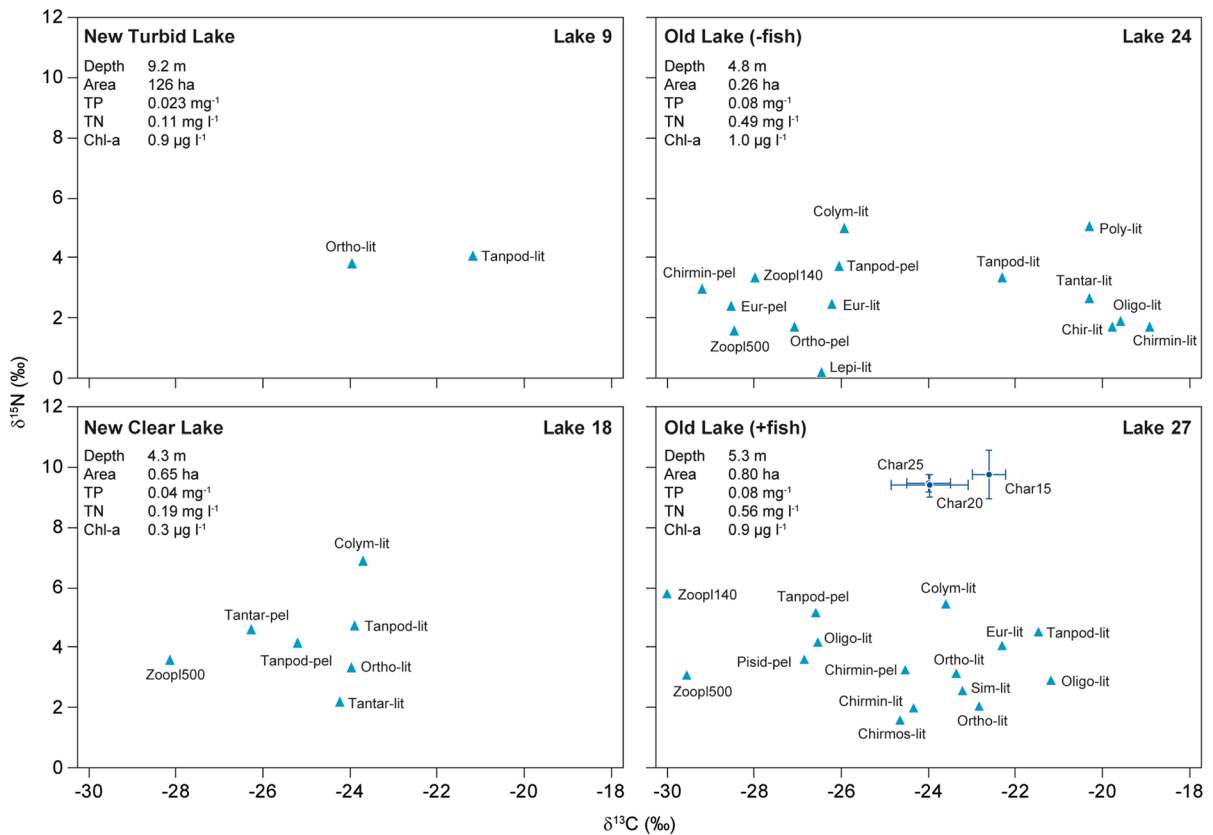


Fig. 9 $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot for four lakes representing the different lake categories (lake position, see Fig. 1). Included are macroinvertebrates, zooplankton and, when present, fish (Arctic charr). Char15 = Arctic charr < 15 cm; Char20 = same in the range 15–20 cm; Char25 = same > 25 cm; Zoopl140 = Zooplankton > 140 μm ; Zoopl500 = Zooplankton > 500 μm ; Eur = *Eurycerus lamellatus*; Sim = *Simocephalus vetulus*;

Lepi = *Lepidurus arcticus* (Pallas, 1793); Colym = *Colymbetes dolabratus*; Poly = *Polycentropus* sp.; Pisisid = *Pisidium* sp.; Oligo = Oligochaeta; Chir = Chironomid unidentified; Chirmin = Chironominae, Chirmos = *Chironomus* sp.; Tanpod = Tanipodinae; Tantar = Tanitarsini; Ortho = Orthocladinae. Pel is taken in the open water zone and Lit in the littoral zone

with the glacier (runoff) as mean body size overall decreases with increasing temperature (Atkinson, 1994; Daufresne et al., 2009; Havens et al., 2015). However, the temperature difference was only 1.2 °C, which is unlikely to explain the major differences in the size of crustaceans between the old and new lakes and cannot explain a smaller body size of rotifers in the old lakes.

The food web structure differed substantially between the new and the old lakes. The Layman food web metrics NR, CR, TA and SEAc (used as proxies for trophic diversity) of invertebrates (zooplankton and benthic macroinvertebrates) were all higher in the old lakes. These results clearly indicate a more complex and developed food web in the old lakes, which is

supported also by the higher species richness in these lakes. In nutrient-poor ecosystems, the length of the trophic web is expected to correlate positively with productivity (MacArthur, 1955; Post, 2002). Accordingly, we found NR to be higher in the old lakes. In a related study, López-Rodríguez et al. (unpublished data) analysed the gut content of zooplankton and macroinvertebrates to elucidate the trophic network in 16 fishless ponds in the same area. They found that in the new ponds, TN and Chl-*a* were significantly related to connectance, trophic niche overlap and the maximum trophic level (this also related to surface area), while the trophic network in the old ponds was not significantly related to environmental factors, suggesting that the older ecosystems are more

stable. Accordingly, Haileselesie et al. (2016b) found that *Daphnia* metapopulations in the new lakes and ponds were far from in equilibrium. A study of the food web in glacial and non-glacial alpine lakes by Tiberti et al. (2020) similarly showed less nodes and trophic links in the food web and lower link densities in the glacier-fed lakes than in clear water ones in the same area.

When dividing the results into the four categories, we found no significant differences among the lake types for any of the food web metrics applied to the invertebrate food webs. The new turbid lakes tended, though, to have lower metric values, which can be attributed to both the lower productivity (Chl-*a* in the water as well as lower LOI% in the surface sediment) and to the low richness of zooplankton and macroinvertebrates. If fish were also considered in the food webs as an extra food chain link in the lakes, all metrics would become substantially higher in the old lakes with fish than in the new clear ones (all without fish) and in the old lakes without fish. This pattern suggests a broader use of resources when fish are present. Even without including the fish, our results indicate an increasing ecosystem complexity from new turbid lakes to new clear ones followed by old lakes without and finally old lakes with fish, respectively (Fig. 8), as evidenced also by the four lake examples (Fig. 9).

Our study has some weaknesses. Due to logistical constraints in this remote area, the number of lakes included was limited. While the comparison between new and old lakes was robust (a reasonably large number of lakes) and yielded clear results and differences, the division into four categories left us with few lakes in three of the four categories and thus less clear results (apart from the clear differences recorded between the glacier-fed lakes and the other three categories). Real differences may have gone unnoticed and can only be identified when the number of lakes is increased.

Our findings highlight a potential sequence of succession occurring in lakes created by glacial retreat, as depicted by Sommaruga (2015), with exception of the effects of fish presence. Despite the fact that our study had just two age classes, the “intermediate phase” seen in our database is expected to occur, namely the decrease in water turbidity in new lakes after an initial turbid phase and the arrival of fish once the lakes and watersheds become more productive

after a longer isolation time. Artic Charr was the only fish species occurring in lakes connected to the sea by a large river. They were, however, only found in the old lakes and not in the new turbid lakes upstream connected to the glacial river or in the clear lakes partly connected to this river. We hypothesise that this potential succession implies an increase in food web complexity and higher taxonomic (and likely functional) diversity, but likely moderate cascading effects until productivity becomes high enough to support at least a moderate biomass of predators.

As we can expect a further substantial retreat of glaciers in the future, not least in Greenland, we encourage the establishment of (high frequency) monitoring in the glacial foreland to fully understand the changes during lake ontogeny in such areas.

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Author contributions EJ contributed to conceptualisation, methodology, funding formal analysis, investigation, data curation and writing—original draft; TAD contributed to conceptualisation, methodology, formal analysis and data curation, review and editing; ST data curation, review and editing; TLL contributed to conceptualisation, methodology, review and editing; MM, LDM, IG, NV, HA, KJ, RS, and KÖ investigation, review and editing.

Data availability The data are available from the authors upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval Not applicable.

Consent to participate All the authors consent to participate in this manuscript.

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