



Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between Arctic charr (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids

Erik Jeppesen¹, Kirsten Christoffersen², Frank Landkildehus¹, Torben Lauridsen¹, Susanne L. Amsinck¹, Frank Riget³ & Martin Søndergaard¹

¹National Environmental Research Institute, Department of Lake and Estuarine Ecology, P.O. Box 314, DK-8600 Silkeborg, Denmark

²Freshwater Biological Laboratory, University of Copenhagen, Helsingørsgade 51, DK-3400 Hillerød, Denmark

³National Environmental Research Institute, Department of Arctic Research, Tagensvej 153 4th, DK-2200 Copenhagen N, Denmark

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Abstract

We studied the trophic structure in the pelagial and crustacean remains in the surface 1 cm of the sediment of 13 shallow, high arctic lakes in northeast Greenland (74° N). Seven lakes were fishless, while the remaining six hosted a dwarf form of Arctic charr (*Salvelinus alpinus*). In fishless lakes, *Daphnia pulex* was abundant, while no daphnids were found in the pelagial of lakes with fish. In fish lakes, the zooplankton community was dominated numerically by cyclopoid copepods and rotifers. Both lake sampling and analysis of remains in the top 1 cm of the sediment indicated that the phyllopod, *Lepidurus arcticus*, occurred in all fishless lakes, but was either absent or present in low densities from lakes with fish. Adult *Lepidurus* are mainly predators and forage in the top layer of the sediment. An analysis of surface sediment revealed low abundance of the benthic chydorids *Alona* sp. and *Macrothrix* sp. in lakes with *Lepidurus*, while they were abundant in lakes with fish. The low abundance in fishless lakes could not be explained by damage of crustacean remains caused by *Lepidurus* feeding in the sediment, because remains of the more soft-shelled, pelagic-living *Daphnia* were abundant in the sediment of these lakes. No significant differences between lakes with and without fish were found in chlorophyll *a*, total phosphorus, total nitrogen, conductivity or temperature, suggesting that the observed link between *Lepidurus arcticus* and the benthic crustacean community is causal. Consequently, remains of crustaceans in high arctic lake sediments may be useful for detecting the impact of past climate change on top-down control by fish. Not only remains of pelagic species, but also of *Lepidurus* and some benthic chydorids, may be used to detect changes in fish abundance and predation pressure in the past.

Introduction

Lakes in the arctic are often inhabited by few species and accordingly have simple pelagic food web structures (Rigler et al., 1974; Stross et al., 1980; Hobbie, 1984). Arctic charr (*Salvelinus alpinus*) is the only freshwater fish species found in high arctic (Hammar, 1989). Further south in subarctic continental freshwater lakes, sticklebacks (*Gasterosteus aculeatus*, *Pungitius pungitius*) and a number of salmonids, grayling (*Thymallus* spp.) and whitefish (*Coregonus* spp.) and

smelt (*Osmerus* spp.) may appear (Hammar, 1989). Zooplankton community structure in arctic lakes is also simple and highly influenced by fish (O'Brien, 1975; Hobbie, 1984). In the presence of fish, large-bodied cladocerans such as *Daphnia pulex* and *D. middendorffiana* are replaced by smaller species such as *D. longiremis* (if present in the area) and *Bosmina* spp., and the mean size of *Holopedium gibberum* declines (O'Brien, 1975). Likewise, only four species of copepods have been recorded in high arctic lakes (Halvorsen & Gullestad, 1976; Stross et al. 1980;

Hobbie, 1984). Except for large predacious species, both calanoid and cyclopoid copepods seem less affected by predation in these lakes (Rigler et al., 1974; O'Brien, 1975).

In northeast Greenland lakes, Arctic charr is the only fish species present, and depending on lake size and access to marine waters the forms occurring are anadromous and/or land-locked charr (Riget et al., 2000). In small lakes without access to the sea (<0.1 km²), only the dwarf land-locked form occurs, while lakes with a mean depth < 3 m are devoid of fish (Riget et al., 2000). The zooplankton community structure is also simple. So far, only one species of *Daphnia* (*D. pulex*) and one species of cyclopoids (*Cyclops abyssorum alpinus*) have been found. Two calanoids (*Diaptomus minutus*, *Limnocalanus macrurus*) have been recorded, but so far restricted to a single locality (Poulsen, 1940). The predacious calanoids *Heterocope septentrionalis* and *Hesperodiaptomus*, which play a key role in the food web in many fishless lakes in arctic Canada (O'Brien, 1975; Stross et al., 1980) and in high mountain lakes (Anderson, 1982; Paul et al., 1995), respectively, have not been found in northeast Greenland. In addition, *dystiscids* and branchiopods except *Lepidurus arcticus* are lacking (Poulsen, 1940; Røen, 1962). The food web structure is thus simpler than in most other high arctic lakes. Therefore, these northeast Greenland lakes are particularly well-suited for studies of food web interactions; however, so far nobody has studied the trophic interactions in the pelagial of these simple ecosystems.

L. arcticus appears all over the north Atlantic comprising northern Scandinavia, Svalbard, Iceland and Greenland (Poulsen, 1940). Besides fish predation, winter temperatures have been argued to restrict this species to cold climates, supposedly reflecting that winter eggs are unable to tolerate higher winter temperatures than those prevailing in arctic lakes (Aass, 1969). It co-occurs with fish only in deeper lakes (Borgstrøm et al., 1985). *Lepidurus* is pelagic until the 5th instar when it becomes benthic, preying primarily on other invertebrates (Arnold, 1967; Miller, 1980). Thus, by preying on *Lepidurus* fish may release predation on benthic invertebrates, including chydorids. Remains of *Lepidurus*, benthic chydorids and pelagic zooplankton accumulate in the sediment and may then potentially be used to assess fish predation pressure on zooplankton and benthic chydorids. Analysis of zooplankton remains has been used earlier to evaluate qualitatively the fish predation pressure in temperate lakes (Kerfoot, 1974; Kitchell and Kitchell, 1980) or

quantitative changes in fish abundance and predation pressure on zooplankton (Jeppesen et al., 1996).

We studied 13 oligotrophic high arctic lakes at Zackenberg in northeast Greenland to elucidate how fish predation on large-bodied zooplankton and *Lepidurus* affects the zooplankton and benthic chydorid community structure, respectively. Six lakes hosted Arctic charr and seven lakes were fishless. The study is the hitherto most comprehensive quantitative limnological investigation conducted in northeast Greenland.

Materials and methods

The study was conducted during July–August 1997 or 1998 in lakes near the coast in the valleys around Zackenberg and Store Sø of northeast Greenland (74° N, 21° W, altitude of 50–200 m). The lake area was determined from aerial photos and field measurements and the maximum depth was determined by echosounding in transects across and along the lakes.

Water samples were collected with a 5 l Patalas sampler at 0.5–1 m intervals in the deepest part of the lakes and mixed. For zooplankton analyses, 12–15 l subsamples were filtered on a 20 µm filter and fixed in acid Lugol's solution. For chemical analyses, a 250 ml subsample was frozen. For chlorophyll *a*, 1 l was filtered on a 0.45 µm GF/C filter and frozen until analysis.

To determine presence and absence of *Lepidurus*, we conducted vertical hauls with a 0.5 mm mesh-sized net (diameter 0.6 m) at 5 stations along a depth gradient running from the shore to the deepest part of the lake. Before each haul, the nets were placed on the sediment for 2 min to allow colonisation of *Lepidurus*. We also conducted visual surveys along the shoreline for at least 15 min in each lake.

We quantitatively assessed fish densities by setting (overnight, 18 h) multiple mesh-sized (height 1.5 m) gill nets with 14 randomly arranged sections of 3 m (6.25–75 mm mesh size). Three to nine nets were set in each lake depending on lake size. Equal number of nets were set in the littoral zone (benthic), in the benthic and in the pelagic habitats of the open water (Riget et al., 2000).

Lake water total phosphorus was determined as molybdate reactive phosphorus (Murphy & Riley, 1972) following persulphate digestion (Koroleff, 1970), and total nitrogen as nitrite + nitrate after potassium persulphate digestion (Solórzano & Sharp,

1980). Chlorophyll *a* was determined spectrophotometrically after ethanol extraction (Jespersen & Christoffersen, 1987). Zooplankton were counted at 40–100 × magnification.

Sediment samples were taken with a Kajak core sampler (50 cm, 5.2 cm diameter) in the deepest part of the lake. The upper 1 cm of the surface sediment of the core was sampled and wet weight, dry weight (90 °C, 24 h.) and loss on ignition (550 °C, 1 h.) determined on a 5 ml aliquot. Approximately 5 ml sediment were used for quantifying the zooplankton remains. Weighed subsamples were boiled for 20 min in 25 ml 10% KOH. Large crustacean remains and ephippia retained on a 140 µm nylon filter were counted with a stereomicroscope. Subsamples of smaller remains retained on an 80 µm filter were counted using an inverted microscope. We counted exoskeleton fragments (postabdominal claws, carapaces) and resting eggs of cladocerans and exoskeleton fragments (mandibles, furcal threads) of *Lepidurus*.

We used ANOVA to test for differences in physico-chemical variables in lakes with and without fish. Due to high variability, and a large proportion of zeroes, we used Wilcoxon non-parametric two sample tests (NPAR1WAY procedure; SAS, 1989) to test for differences in zooplankton abundance and microcrustaceans in the sediment. As we had pre-expectation of the effects of fish, we used a one-sided test.

Results

The 13 lakes were relatively small (surface area 0.4–17 ha), shallow (max depth 0.6–6.7 m) and nutrient-poor (Table 1). All lakes were oligotrophic (Table 1). Total phosphorus (TP) ranged from 2 to 22 µg P l⁻¹, total nitrogen from 80 to 430 µg N l⁻¹ and chlorophyll *a* from 0.6 to 3.3 µg l⁻¹. The oxygen concentration was close to saturation (78–101%) and the water temperature was low (6.3–10 °C). pH varied between 6.5 and 7.9 and with a single exception conductivity was low (7–18 µSi) (Table 1). While the mean depth of the lakes with fish was significantly higher than that of fishless lakes ($p < 0.003$), no significant differences were found for the other variables among lakes with and without fish ($p > 0.33$) (Table 1).

Dwarf Arctic charr were caught in gill nets in 6 lakes. However, CPUE was low (0.2–1.4 fish net⁻¹). Mean size of fish in the six lakes ranged between 8.4 and 12.5 cm. Sexually mature fish were 7–13.6 cm. Zooplankton community structure differed markedly

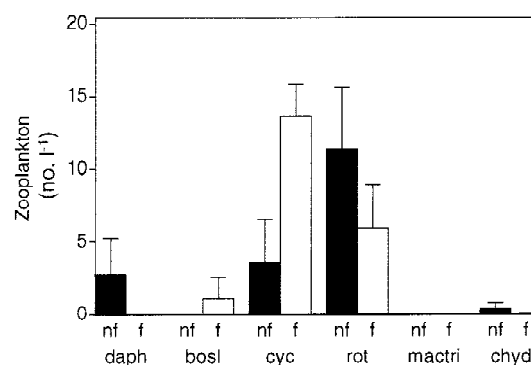


Figure 1. Abundance (mean ± 80% C.L., not 95% C.L. for visual reasons) of various zooplankton species in 7 shallow lakes without fish (black column) and 6 shallow lakes with landlocked dwarf forms of Arctic charr (*Salvelinus alpinus*, grey column). Rotifers are number × 0.25. daph = *Daphnia pulex*, bosl = *Bosmina longirostris*, cyc = cyclopoid copepods, rot = rotifers, mactri = *Macrothrix hirsuticornis*, chyd = *Chydorus sphaericus*. nf = no fish, f = fish present.

between lakes with and without fish (Fig. 1). *Daphnia pulex* occurred in all fishless lakes in densities up to 12 l⁻¹, but was absent from all lakes with fish. In contrast, *Bosmina longirostris* was found only in lakes with fish and was restricted to lakes in Store Sjø Valley. For the other two cladocerans observed (*Chydorus sphaericus* and *Macrothrix hirsuticornis*), no significant differences were found between lakes with or without fish ($p > 0.10$ and $p > 0.46$, respectively). However, their abundance tended to be higher in fishless lakes. The abundance of cyclopoid copepods was significantly higher ($p < 0.009$) in lakes with fish, while no significant ($p > 0.18$) differences between the two sets of lakes were found for rotifers. In terms of numbers, rotifer communities were most often dominated by *Polyarthra dolichoptera* (Table 2).

Lepidurus arcticus was not found in lakes with fish, but occurred in all lakes without fish. This pattern was in part corroborated by the sediment analysis. Remains of *Lepidurus* were abundant in the upper 1 cm of the sediment in the fishless lakes, but absent in most lakes with fish, except for two lakes in which they occurred in low concentrations (Fig. 2).

The remains of crustaceans in the surface sediment differed substantially between fish and fishless lakes (Fig. 2). The number of mandibles and furca threads of *Lepidurus* was significantly higher in lakes without fish when calculated both per unit of sediment dry weight (DW) ($p < 0.002$) and per unit of loss on ignition (LOI) ($p < 0.0001$). The same applied to *Daphnia ephippia* (DW: $p < 0.016$ and LOI: $p < 0.002$).

Table 1. Physico-chemical and fish data (mean \pm SD, (range)) for the 13 study lakes divided into 6 lakes with and 7 lakes without fish. Results from an ANOVA test of differences between the two sets of lakes are also shown. n.s. = not significant

	With fish	Without fish	$p <$
Max depth (m)	4.8 \pm 1.4 (3.3–6.7)	1.9 \pm 1.1 (0.6–3.3)	0.002
Total phosphorus ($\mu\text{g P l}^{-1}$)	10.2 \pm 5.9 (6–22)	10.2 \pm 5.9 (2–15)	n.s.
Total nitrogen ($\mu\text{g N l}^{-1}$)	197 \pm 94 (80–360)	290 \pm 88 (150–430)	n.s.
Chlorophyll <i>a</i> (chl <i>a</i> $\mu\text{g l}^{-1}$)	1.2 \pm 0.3 (0.8–1.5)	1.9 \pm 1.1 (0.6–3.3)	n.s.
Chla:TP	0.14 \pm 0.07 (0.06–0.22)	0.22 \pm 0.08 (0.13–0.33)	n.s.
Oxygen (percentage)	85 \pm 6 (78–89)	92 \pm 6 (84–101)	n.s.
Conductivity (μSi)	11 \pm 4 (7–18)	25 \pm 23 (10–77)	n.s.
pH	6.9 \pm 0.7 (6.5–7.9)	6.8 \pm 0.3 (6.5–7.3)	n.s.
Fish (CPUE, no. net $^{-1}$)	0.67 \pm 0.47 (0.17–1.4)	0	0.0001

Table 2. Number of lakes in which different zooplankton species were collected in the pelagial and in the upper 1 cm of the sediment. Six lakes were with and seven lakes without fish

	Pelagial		Sediment (remains)	
	With fish	Without fish	With fish	Without fish
Crustaceans				
<i>Lepidurus arcticus</i>	0	7	2 ^b	7
<i>Daphnia pulex</i>	0	7	1	7
<i>Chydorus sphaericus</i>	1	5	6	7
<i>Bosmina longirostris</i>	3 ^c	0	3 ^a	0
<i>Macrothrix hirsuticornis</i>	0	2	5	6
<i>Alona</i> sp.	0	0	5	5
<i>Cyclops abyssorum alpinus</i>	6	6	–	–
Harpacticidae	0	2	–	–
Rotifers				
<i>Polyarthra dolichoptera</i>	6	7	–	–
<i>Keratella quadrata</i>	5	2	–	–
<i>Conochilus unicornis</i>	2	3	–	–
<i>Notholca labis</i>	0	2	–	–
<i>Colurella</i> spp.	0	3	–	–
<i>Lepadella</i> sp.	0	1	–	–
<i>Collotheca</i> sp.	0	1	–	–
<i>Lecane</i> sp.	0	2	–	–
<i>Cephalodella</i> sp.	0	2	–	–
<i>Trichocerca</i> sp.	1	2	–	–
<i>Mytilina ventralis</i>	0	1	–	–

^aAll lakes with fish in Store Sjø Valley, ^bIn low numbers, however (see Fig. 2). – not determined, ^cNot found in the Zackenberg Valley.

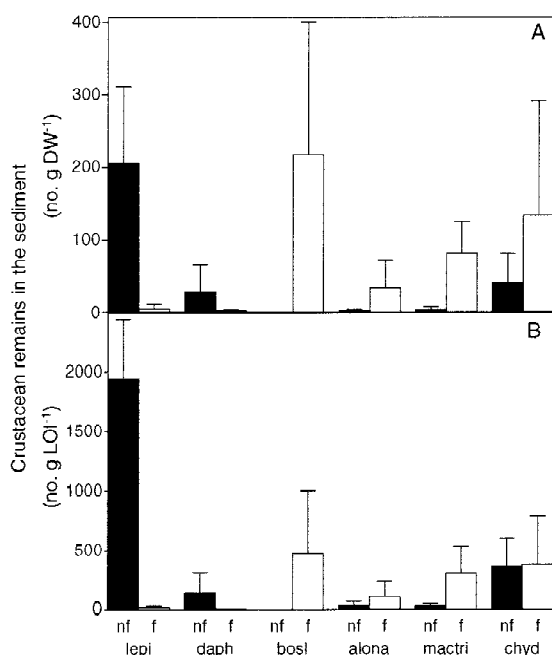


Figure 2. Abundance (mean \pm 80% C.L.) of various remains of microcrustaceans per unit of sediment dry weight (A) and organic dry weight (LOI) (B). *alona* = *Alona* sp., *lepi* = *Lepidurus arcticus*. See also legend of Figure 1.

Conversely, carapaces of *B. longirostris* tended to be higher in lakes with fish (DW, LOI: $p < 0.07$). The lack of significance in this case may reflect that *Bosmina* was restricted to lakes in Store Sødal, where it occurred in the sediment of all lakes with fish, but not in lakes without fish. No significant difference in the number of *Chydorus* carapaces in the sediment was found between fish and fishless lakes (DW: $p > 0.37$, LOI: $p > 0.22$), while the number of carapaces of *Macrothrix* was significantly higher in lakes with fish (DW, LOI: $p < 0.05$). Lakes with fish also hosted significantly ($p < 0.038$) higher densities of *Alona* sp. per unit of DW, while the density was only marginally significant per unit of LOI ($p < 0.096$). If the carapaces of *Macrothrix* and *Alona* are pooled (they tended to alternate somewhat between lakes) the difference in numbers becomes more significant (DW: $p < 0.007$ and LOI: $p < 0.04$) than for each of the genera.

Discussion

Arctic charr was the only fish species caught in the lakes and appeared only in a dwarf form that became sexually mature at a length down to 7 cm. Charr

were found in all lakes > 3 m deep, but were absent from shallower lakes, probably reflecting that shallow lakes either freeze solid during winter (if depth is below 2–2.5 m) or that oxygen in the remaining water volume is exhausted during the 8–9 months with ice cover. Welch & Bergmann (1985) argue that winter kill generally occurs in lakes that have a maximum depth below 4.5 m and a mean depth of 1.8 m. The lower threshold found in our study may reflect the ultra-oligotrophic state of the lakes and the cold high arctic climate, two factors that most likely result in low phytoplankton production and accordingly low oxygen consumption under ice during winter. Deeper lakes in northeast Greenland with landlocked charr also host a large-sized piscivorous form (Riget et al., 2000), and anadromous charr may appear as well if the lakes are interconnected with fjords (Riget et al., 2000).

The zooplankton communities were species-poor. In all the lakes, rotifers were exclusively dominated by *Polyarthra dolichoptera* as also seen in other high arctic lakes (Halvorsen & Gullestad, 1976). In the pelagic samples, we occasionally found benthic rotifers (Ruttner-Kolisko, 1972), such as *Lecane*, *Colurella* and *Lepadella*, which may reflect the shallowness of the lakes. We only found one species of *Daphnia* (*D. pulex*) which is widespread in small lakes and ponds throughout the arctic, including Greenland (Røen, 1962; Moore, 1978), and only few species of other cladocerans (Table 2). The occurrence of *B. longirostris* in lakes with fish in Store Sødal and not in similar lakes in the Zackenberg Valley, 5–10 km away, may indicate poor dispersal of species in the area. We found no calanoid copepods, although two species have been reported to occur in Sælsøen in northeast Greenland at 77° N lat (Brehm, 1912). The low species richness of crustaceans is in accordance with earlier studies in northeast Greenland lakes (Poulsen, 1940).

The differences in the crustacean community in lakes with and without fish suggest considerable predation pressure from fish. While *Daphnia pulex* in the pelagial was abundant in all lakes without fish, cyclopoid copepods were the most abundant crustacean in lakes with fish, and in these lakes no *Daphnia* were found in the pelagial though a few remains occurred in the surface sediment in one of the lakes. The low abundance of *D. pulex* in arctic lakes with Arctic charr corresponds with the findings of other studies (Stross et al., 1980) and may be interpreted as a result of size-selective predation (Brooks & Dodson, 1965;

Langeland, 1982; Dahl-Hansen, 1995). The predation risk of *Daphnia* is supposedly particularly strong in high arctic lakes in which large-bodied *D. pulex* is the only *Daphnia* species present. In other arctic and subarctic lakes, small-bodied *Daphnia* species like *D. longiremis* and *D. longispina* may co-exist with fish if fish densities are low (O'Brien, 1975; Adalsteinsson, 1979b; Dahl-Hansen, 1995). In our study, *Lepidurus* occurred in all fishless lakes, but not in lakes with charr. Similarly, Aass (1969) found that *Lepidurus* was absent from lakes with high densities of trout and charr. However, charr and *Lepidurus* coexist in deep reservoirs and deep lakes (Aass, 1969; Adalsteinsson, 1979b; Borgstrøm et al., 1985), where they may constitute an important food source for fish (Borgstrøm et al., 1985). As the depth was higher in those of our study lakes that hosted fish, it could be argued that the difference in zooplankton community structure reflected variations in depth. However, recently updated data from 42 lakes with contrasting maximum depths in west Greenland provided support for the predation hypothesis (Jeppesen et al., unpublished).

Only few fish (CPUE down to 0.2 net⁻¹) were needed to change the zooplankton community from *Daphnia* to cyclopoid dominance in our study lakes. A similar shift would require CPUE values of 200–400 fish net⁻¹ in shallow eutrophic temperate Danish lakes (Jeppesen et al., 1997b). Higher CPUE is needed in eutrophic lakes to maintain a predation pressure comparable to that in oligotrophic lakes, because higher productivity leads to higher zooplankton growth rate. However, if we standardize CPUE to phosphorus (CPUE:TP) to account for differences in lake productivity, up to 10 times as many fish are needed to gain the same effect on zooplankton community structure in nutrient-rich as in oligotrophic lakes (see Fig. 2 and Table 1; Jeppesen et al., 1997b). Though a comparison between Danish and Greenland lakes is hampered by differences in the species present, net selectivity of the species involved, and most likely also in activity due to temperature differences, there are several arguments in favour of a higher predation risk in oligotrophic arctic lakes than in morphometrically comparable eutrophic temperate lakes. First, the zooplankton is exposed to fish predation for a longer period before reproduction because the growth rate is low due to low temperature and food concentration (Dahl-Hansen, 1995). Second, the high water clarity in the arctic improves the foraging success of visually hunting fish. Third, high water clarity enhances the ratio of benthic–pelagic primary and thus second-

ary production, implying that benthic–pelagic feeding fish by feeding benthic invertebrates when zooplankton is scarce may maintain densities high enough to be continuously able to control large-bodied pelagic zooplankton. Fourth, *Daphnia* in northeast Greenland are represented by large *D. pulex* only, while smaller, less vulnerable *Daphnia* species as mentioned above occur in the temperate lakes and some arctic lakes on the larger continents (O'Brien, 1975; Moore, 1978). Fifth, *Daphnia* often show higher pigmentation in arctic lakes, making them more vulnerable to predation by fish, including charr (Sægrov et al., 1996). High vulnerability of large-bodied zooplankton to predation in oligotrophic lakes is not restricted to the arctic, but is also found in clearwater high mountain lakes (Anderson, 1982; Paul et al., 1995) as well as in clearwater lowland temperate lakes (Jeppesen et al., 2000).

The cascading effect of fish on large-bodied cladocerans and *Lepidurus* is probably enhanced by the shallowness of the study lakes. Thus, coexistence of Arctic charr with *Daphnia* spp. (e.g. Nilsson & Pejler, 1973) in deep but not in shallow lakes, and as discussed above also with *L. arcticus* (Aass, 1969), has been recorded. Data from subarctic Lake Myvatn, Iceland, also support this view. Here, the zooplankton community was dominated by cyclopoid copepods and rotifers in the shallow north basin, while *Daphnia longispina* was abundant in the deeper south basin (Adalsteinsson, 1979a). He ascribed this pattern to differences in the risk of fish predation (mainly Arctic charr and three-spined sticklebacks). The difference in the effects of depth corresponds with observations from temperate lakes where evidence has been given for a generally higher fish predation pressure on large-bodied zooplankton in shallow lakes (Keller & Conlon, 1994; Jeppesen et al., 1997a). The effects of fish on zooplankton did not appear to cascade to the phytoplankton, as no significant differences were found in chlorophyll *a* (chl_a) and the chl_a:TP ratio among lakes with and without fish. This agrees with results from other oligotrophic lakes (Currie et al., 1990; but see McQueen et al., 1986), but contrasts results from eutrophic lakes (Leibold, 1989; Jeppesen et al., 1997a).

We also found significant differences in the abundance and composition of crustacean remains in lakes with and without fish. Corresponding with observations from the pelagial, *Lepidurus* and *Daphnia* remains were either absent or found in low numbers in lakes with fish, while they were abundant in all fishless lakes. In contrast, the abundance of *Alona* and

Macrothrix remains was lower in lakes without fish (but with *Lepidurus*). *Lepidurus* are primarily benthic feeders when reaching a size of 2–3 mm (5th instar) (Miller, 1980). Experiments in Alaskan ponds showed that *Lepidurus* population mixed each m² of the upper 0.5 cm sediment surface daily during late summer (Miller, 1980). We may, therefore, assume that lower abundance of *Alona* and *Macrothrix* is caused by *Lepidurus* predation. An alternative explanation is that *Lepidurus* damage these chydorid remains when searching for food at the lake bottom. However, the more soft-shelled *Daphnia* were well-preserved in the sediment, making the predation hypothesis more feasible. Although higher densities of benthic chydorids might reflect differences in environmental conditions in lakes with and without fish, only depth differed significantly between the two sets of lakes (Table 1). It is unlikely that variations in depth are the cause as we would rather expect higher densities of benthic chydorids in the more shallow lakes seeing that benthic primary production was higher here than in the deeper lakes in the area (Vadeboncoeur, unpubl.) and most likely then also benthic chydorid production. However, the highest abundances of *Macrothrix* and *Alona* were observed in deep lakes with fish but without *Lepidurus*. Further support for the view of a predation effect of *Lepidurus* on *Alona* comes from the study of the Holocene development of Lake Tugtulligssuaq, northwestern Greenland. Here, Fredskild (1984) observed a major increase in abundance of *Alona* remains in the upper sediment coinciding with the disappearance of *Lepidurus* remains. Fredskild, in fact, interpreted the increase in abundance of *Alona* and also of *Acroperus harpae* to the disappearance of one of their predators. Also data from Nuusuaq Lake, Greenland, (Bennike, 2000) suggest an inverse relationship. Here, a major decline in the concentration of *Alona* remains in the upper 1 m of the sediment coincided with the appearance of *Lepidurus* remains.

In contrast to the other chydorids, we found no significant effects of fish on *Chydorus* remains in the sediment, which may be explained by the fact that *Chydorus* is more pelagic than the two other chydorids and thus less vulnerable to predation by the primarily benthic-feeding *Lepidurus*. *Chydorus* occurred in the pelagial of 5 of the 7 lakes without fish (but with *Lepidurus*) present (Table 2), while *Macrothrix* was observed in the pelagial in only two lakes and *Alona* not at all. Data from several hundred Greenland lakes and a number of lakes in Svalbard also revealed a large overlap in the distribution of *Daphnia pulex* and

Chydorus sphaericus in the pelagial, suggesting that *Chydorus* frequently occurs in the pelagial in fishless lakes (Røen, 1962; Husmann et al., 1978). If the hypothesis of a causal predation effect of *Lepidurus* on *Macrothrix/Alona* is correct, we are facing a significant pelagic-benthic coupling, where charr predation on *Lepidurus* indirectly enhances the abundance of these chydorids in the sediment. Field experiments are needed to clarify the impact of *Lepidurus* on benthic chydorids.

For a number of years, zooplankton sediment remains have been used for qualitative estimation of the historical development in fish predation (Kerfoot, 1974; Kitchell and Kitchell, 1980; Leavitt et al., 1994) and most recently also for quantitative descriptions of changes in fish predation pressure (Jeppesen et al., 1996). Due to the simple pelagic food web structure (Anderson, 1982; Paul et al., 1995), sediment remains of arctic and high altitude lakes are useful for studying historical changes in fish predation. Moreover, the fish signal in the sediment seems to be enhanced by the cascading effect of fish on some benthic chydorids. As mentioned above, it must be presumed that the strength of this signal decreases with increasing lake depth as the predation pressure by fish most likely declines. Therefore, the sediment of shallow lakes is well-suited for evaluating how anthropogenically induced changes in, for example, global warming affect fish abundance and fish predation in arctic lakes. This is emphasised by the strong link between fish and their prey in shallow lakes. Moreover, only minor changes in temperature may have a substantial effect on trophic structure in shallow lakes if, for example, the lakes reach a state of winter fish kill due to oxygen depletion under ice.

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