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ORIGINAL PAPER

Population structure, biomass, and diet of landlocked Arctic charr (*Salvelinus alpinus*) in a small, shallow High Arctic lake

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Abstract Although landlocked Arctic charr, *Salvelinus alpinus*, occur in a large number of High Arctic lakes and often as the only fish species, knowledge of densities and resource use is limited. An allopatric landlocked population of Arctic charr in the 1.47 ha Lake Nordre Borgdam on Svalbard (78°3′N, 13°5′E) was studied during the period 1998–2004. Population abundance was estimated by mark–recapture in July–August 2001. The population was dominated by small individuals with lengths below 16 cm. In 2001, the total number of charr in the length-class 6.0–15.9 cm corresponded to 1,920 individuals/ha or 20.7 kg ha^{-1}. They were mostly feeding on chironomid and trichopteran larvae. The few larger charr seem to feed mainly on smaller conspecifics, and these cannibals probably control the population structure and the abundance of smaller fish. Due to low total number of prey fish in the lake, few individuals are likely to become piscivores.

Keywords Landlocked Arctic charr · High Arctic · Svalbard · Biomass · Diet · Cannibalism

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Introduction

In the High Arctic, fish communities in fresh water are simple, often with Arctic charr as the only fish species (Hammar 1985). Due to the marked seasonality and generally low productivity of High Arctic lakes (Svenning et al. 2007), cannibalism may be more pronounced in such systems than in lakes at lower latitudes (Hammar 2000). The length distribution of freshwater resident Arctic charr is frequently bimodal (Hammar 1989; Parker and Johnson 1991), with increasing frequency of bimodality with increasing latitude (Griffiths 1994). This population structure seems to be very stable, and even after perturbations caused by fishing, the population may return to its original size structure (Johnson 1983, 1994). Furthermore, the size differences between the morphs and the frequency of cannibalism also increase with latitude (Griffiths 1994). According to Claessen et al. (2002), a prerequisite for a bimodal fish population size distribution is "the combination of (1) stagnation of the growth rate near the maximum length in the planktivorous niche and (2) rapid increase in the growth rate beyond this size". This may be true for Svalbard Arctic charr populations as well, although the planktivorous niche in the very harsh Svalbard lakes is often replaced by the littoral benthic niche, i.e. strongly dominated by chironomid larvae (see Svenning et al. 2007).

Aspects of the life history conditions of Arctic charr are described for several populations on Svalbard and the nearby Bear Island (see Klemetsen et al. 1985; Svenning and Borgstrøm 1995; Hammar 2000; Svenning and Gullestad 2002; Svenning et al. 2007; Berg et al. 2010), but in general, little information exists concerning population numbers of resident Arctic charr in this area. Commonly, the trophic ecology of High Arctic populations of Arctic charr demonstrates a narrow food base with chironomids, Trichoptera and small crustaceans as the main food sources throughout the

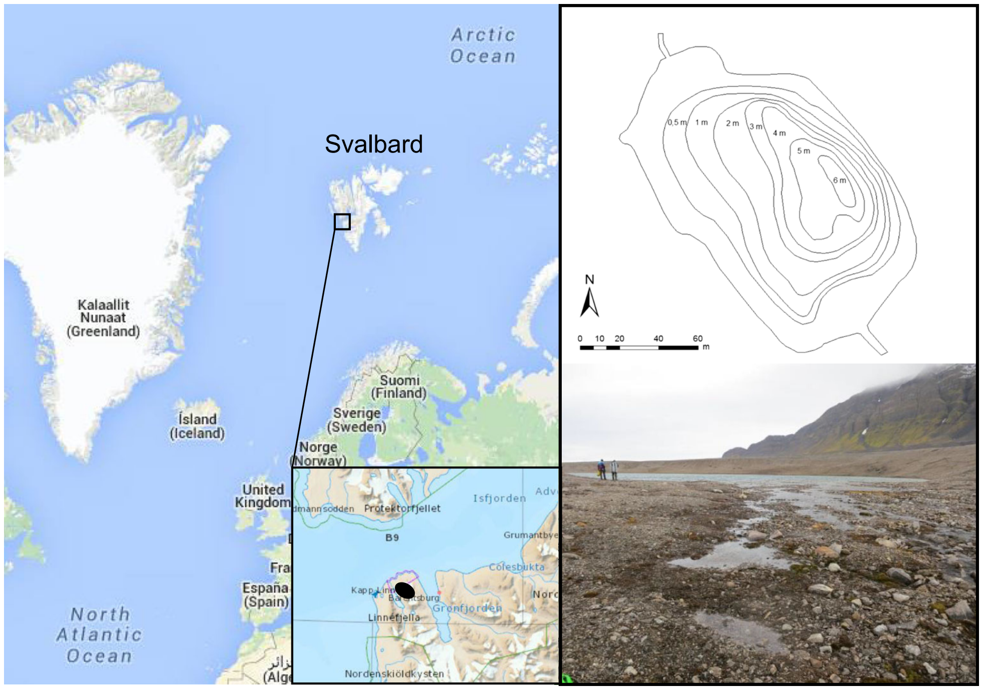

Fig. 1 Location, contour map, and photo of Lake Nordre Borgdam (Photo: M-A Svenning)

year, and with fish as an additional food item for large individuals (Guiguer et al. 2002; Svenning et al. 2007). Annual growth rate of dwarf landlocked Arctic charr in High Arctic lakes is very low, with individuals in length-class 10–15 cm commonly being up to 15 years old (Hammar 2000). The low annual growth of the small Arctic charr may reflect both low temperature and low food intake. Conversely, the shift in diet from invertebrates to fish results in a much faster growth rate of larger individuals (Hammar 1989; Svenning and Borgstrøm 1995; Berg et al. 2010), suggesting that food availability may be the most limiting factor for growth. In some anadromous populations of Arctic charr on Svalbard, the number of ascending individuals from the sea to rivers/lakes has been recorded (Gulseth and Nilssen 2000; Svenning and Gullestad 2002; Borgstrøm et al. 2010), while to our knowledge, number of fish and biomass of resident Arctic charr in lakes on Svalbard have not previously been studied. The purpose of the present study was therefore to estimate population density of Arctic charr in a small, shallow High Arctic lake, where we expect few invertebrate groups forming the diet of small fish, and small conspecifics being part of the diet of larger individuals.

Materials and methods

Study area

The study was carried out in Lake Nordre Borgdam, situated on the southern side of the Ice Fjord on the west coast of Spitsbergen (78°3′N, 13°5′E) (Fig. 1). The lake is 1.47 ha in surface area, with maximum depth 6.3 m, and average depth 1.8 m. An allopatric population of landlocked Arctic charr inhabits the lake. In the deepest area of the lake, the substratum is black gyttja, while the more shallow parts are dominated by small stony ridges. Precipitation at the nearby Isfjord Radio (Kapp Linné) is <300 mm year^{-1}, and the average monthly air temperature exceeds 2.0 °C only in July and August (Svenning et al. 2007). In 2010, the average water temperature during the ice free period in Nordre Borgdam, i.e. between early July and the end of September, was 5.5 °C, while the average water temperature from September 2010 to June 2011 was 0.4 °C (Svenning, unpublished). All temperature recordings are obtained by a logger which was placed at 3 m depth. In the nearby Lake Linne, ice-break has been in middle of August in some years (Bøyum and Kjensmo 1978).

During four winter and five summer visits, we have never seen other people in the area, and due to the small size of the lake, its remote location, and the fact that gill-netting is not allowed, it is unlikely that the Arctic charr population has been exploited before our study. This was also the reason why we selected this lake for our study. A small number of charr have, however, been captured in connection with different surveys in a freshwater course given by The University Centre in Svalbard (UNIS) during the period 1998–2004 (led by M-A. Svenning). Some data concerning fish size, age, diet, and parasite infection from these surveys are included in the present study. During the

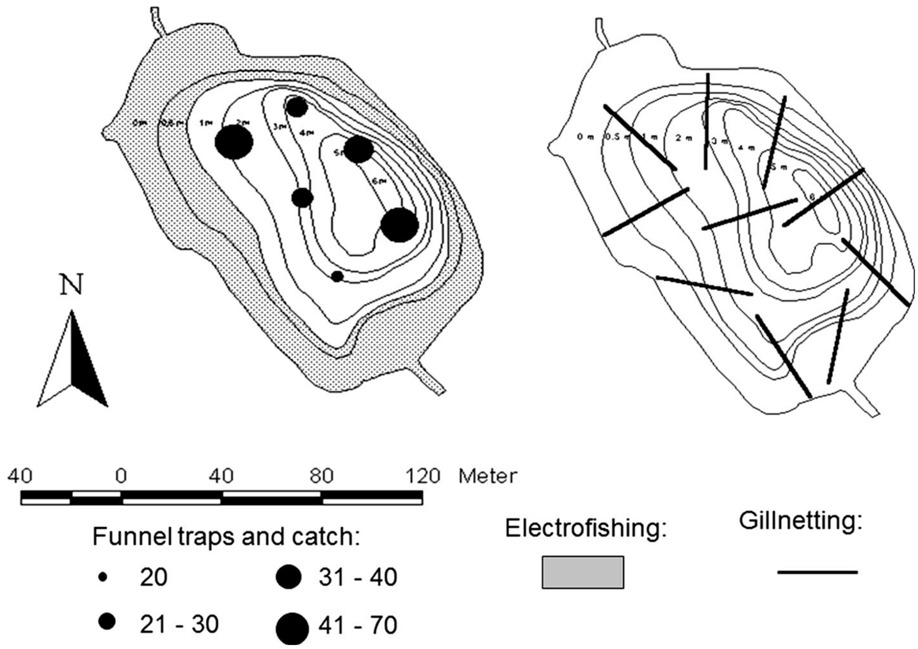

Fig. 2 Locations and catch by funnel traps, area covered by electro fishing (*left*), and gillnet locations (*right*) at Lake Nordre Borgdam

field work, Arctic tern (*Sterna paradisaea*) and red-throated diver (*Gavia stellata*) were occasionally seen predating charr. Divers (*Gavia* spp.) may serve as final hosts for the cestode *Dihyllobothrium ditremum*, with the plerocercoid larvae occurring in salmonid species (Halvorsen 1970; Bylund 1973).

Estimation of population number and biomass

In summer 2001, the total number of charr between 6.0 and 15.9 cm fork length was estimated by multiple mark–recapture, using the Schumacher and Eschmeyer's estimate (Ricker 1975):

$$\frac{1}{N} = \frac{\sum (M_t R_t)}{\sum (C_t M_t^2)}$$

where N = estimated number of charr in the population, M_t = total number of marked charr at the start of day t, C_t total number of charr caught at day t, and R_t number of recaptures of marked charr in the catch on day t.

Both funnel traps and electrofishing were used for capture of live fish for marking and control, with sampling occurring between 27 July and 29 August. No individuals with fork length ≥16.0 cm were captured by these gears. The funnel traps were set at depths 1–6 m (Fig. 2). The traps, made of mink farm wire, were 90 cm long, with diameter 50 cm, and mesh size 12.5 × 12.5 mm. The diameter of the two entrances of the trap was adjusted to c. 6 cm. The traps were baited with cod eggs, emptied every 1–3 days, and with a total effort of 70 trap days. Electrofishing was used in all areas with depths <1 m, covering approximately one half of the lake area (Fig. 2). The total electrofishing effort was divided into eight intervals of mark and recapture during a 20-day period beginning in late July. Arctic charr captured both by funnel traps and by electrofishing were anaesthetised using benzocaine (12 ml of 5 g benzocaine l^{-1} ethanol mixed in 1 l of water), marked by cutting a small section of the lower or upper part of the caudal fin, and released after being held in a closed trap for 3 h for inspections. Separate estimates were carried out for individuals in the three length-classes, 6.0–9.9, 10.0–12.9, and 13.0–15.9 cm.

When funnel trap and electrofishing sampling were completed, ten 40-m-long gillnets with 5 m panels of the mesh sizes 10, 12.5, 15, 18.5, 22, 26, 35, 45 mm (knot to knot) were set in both the deeper areas and shallow parts of the lake (Fig. 2). The gillnetting continued for a period of 24 h, with hourly inspections to reduce the potential risk of catching more than a few larger fish. Fork length (in mm) and fish weight (to nearest 0.1 g) were measured for all captured fish. In 2001, a total of 185 charr were killed for determination of age and sex, as well as for analyses of diet and the infection with the cestode *D. ditremum*. In addition, 45 charr captured in April–May 2000, 2001, and 2004 were also used for *D. ditremum* analyses. Sexual maturity was examined following the description of Dahl (1917). Otoliths were used for age determination. The otoliths were cleared in alcohol and then placed in propandiol on a black plate under a stereo microscope. Whole otoliths with age >7 winters were also divided through the centre, and thereafter burnt before the age determination (Christensen 1964; Power 1978), but no difference in age was observed between whole and cut otoliths.

Table 1 Number of Arctic charr captured by electrofishing, funnel traps, and gillnetting in Nordre Borgdam, Svalbard, over a 20-day period from July–August 2001

Length-classes (mm)	Electrofishing	Funnel traps	Gillnets	Total
<60	25	0	0	25
60–99	224	0	3	227
100–129	349	155	7	511
130–159	121	104	4	229
>450	0	0	1	1
Total	719	259	15	993

A more detailed length distribution is given in Fig. 3

In order to calculate the biomass of cohorts represented in the length-class 6.0–15.9 cm, the total number of individuals within each cm-class was apportioned according to the frequency of each cohort within each cm-class. Thus, the total number of individuals within each cohort (N_j) was calculated by summing the numbers from all cm-classes between 6 and 15 cm (Borgstrøm 1992). Based on the estimated number (N_j) and mean weight (W_j) of charr within the cohorts 1–15 winters, the biomass of each cohort was calculated as $B_j = \mathrm{N}_j \times W_j$, and total biomass ($B$) of the population was obtained by summing the biomass of all cohorts. The biomass of the length-classes 6.0–9,9, 10.0–12.9, and 13.0–15.9 cm was additionally calculated as $N_i \times W_i$, where N_i is the estimated number and W_i is the mean weight of captured fish in length-class i, respectively.

In all treatments of captured and handled fish, the national guidelines for the care and use of animals was followed.

Results

Estimated number and length distribution

A total of 993 charr were captured (Table 1), of which 857 were untagged individuals. In the deepest part of the lake, Arctic charr were captured both by gillnets and funnel traps, while in more shallow water, most fish were captured by electrofishing ($n = 719$), with individuals varying in lengths from 2.6 to 15.9 cm. Fish caught in funnel traps ($n = 259$) varied from 10.1 to 15.9 cm, while 15 charr caught by gillnets were between 8.0 and 47.7 cm in length (Fig. 3a).

A fairly similar length distribution was recorded during the restricted gillnet sampling between April and May (below 1.7 m ice cover) in the years 1998, 2000, and 2004 (Fig. 3b). During these samplings, six charr with length >15.9 cm (16.8, 21.9, 21.9, 23.2, 24.3, and 43.9 cm in length, respectively) were captured. The Schumacher–

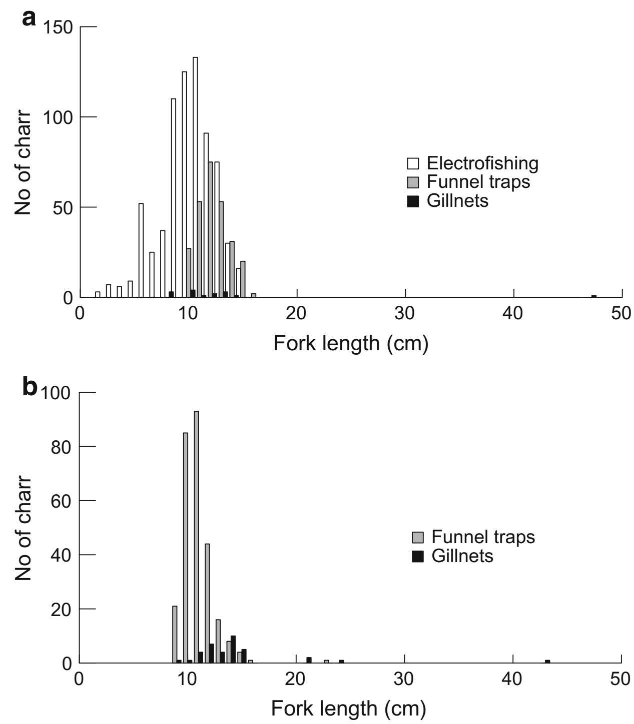

Fig. 3 **a** Length distribution of Arctic charr captured by gillnets, electrofishing, and funnel traps in Lake Nordre Borgdam during July and August 2001. **b** Length distribution of Arctic charr captured by gillnetting and funnel traps in Lake Nordre Borgdam in April–May 1998–2004

Eschmeyer estimation gives a total number of charr in length-class 6.0–15.9 cm to be 2,823 in 2001, corresponding to 1,920 fish ha^{-1}, but with relatively large confidence limits for each of the three length-classes (Table 2). According to the number of fish captured in each cm-class within each of the three estimated length-classes, length-class 9.0–9.9 cm was the most abundant. All samplings indicate that the population consists of small individuals, with very few larger fish (Fig. 3a, b).

Age composition, annual growth, and maturation

Age-classes up to 24 winters were represented in the 2001 sample, but few fish seem to be older than about 19 winters. The estimated age composition indicates considerable variation in year-class strength (Table 3). The majority of the population consists of individuals with age below eight winters and with age-class seven winters being the most abundant. The summer old individuals are, however, not included in these estimates.

Mean length of 1+ in August was 63 mm (±SD 3), and the age specific length increment decreased with increasing age (Fig. 4). At age 5+, the mean length was only 105 mm (±SD 13), giving an annual growth increment of <20 mm, and from age 5+ to 18+, the total mean increment was

Table 2 Summary statistics for computation of Schumacher and Eschmeyer estimates of three length-classes of Arctic charr in Lake Nordre Borgdam, Svalbard, from multiple trap and electrofishing recaptures during August 2001

Length-class, cm	Number caught C_t	Number recaptured R_t	Number marked	Marked fish at large M_t	C_tM_t	M_tR_t	$C_tM_t^2$	R_t^2/C_t	Estimated number N	Confidence limits (0.95)
6.0–9.9	224	13	148	466	19,314	1,659	2,230,796	1.32	1,345	1,083–1,774
10.0–12.9	503	90	320	1,476	93,240	18,712	22,922,460	27.49	1,225	772–2,963
13.0–15.9	227	78	146	916	17,694	7,340	1,855,272	40.71	253	179–433

Table 3 Biomass of the cohorts from age 1 to 19 years of Arctic charr in Lake Nordre Borgvatn, based on estimated number of individuals in each cohort from age 1 to 19 years in August 2001, and mean individual weight ± Standard deviation

Cohort (age yrs)	Number of sampled individuals	Estimated number in population	Mean individual weight (g)	Estimated biomass (kg)
1	13	292	2.6 ± 0.4	0.76
2	15	269	4.8 ± 1.0	1.29
3	25	399	6.5 ± 1.5	2.59
4	15	263	9.2 ± 2.3	2.42
5	11	196	11.7 ± 4.6	2.29
6	22	331	11.9 ± 3.3	3.93
7	39	527	13.6 ± 4.6	7.17
8	9	121	15.7 ± 5.4	1.90
9	3	33	18.3 ± 6.3	0.61
10	7	96	16.5 ± 6.3	1.58
11	5	51	21.5 ± 6.1	1.09
12	6	65	19.8 ± 4.4	1.30
13	3	45	20.7 ± 8.0	0.94
14	2	31	18.2	0.56
15	3	66	16.0 ± 0.9	1.06
18	1	30	26.6	0.68
19	1	9	25.1	0.22
Sum	180	2,823		30.39

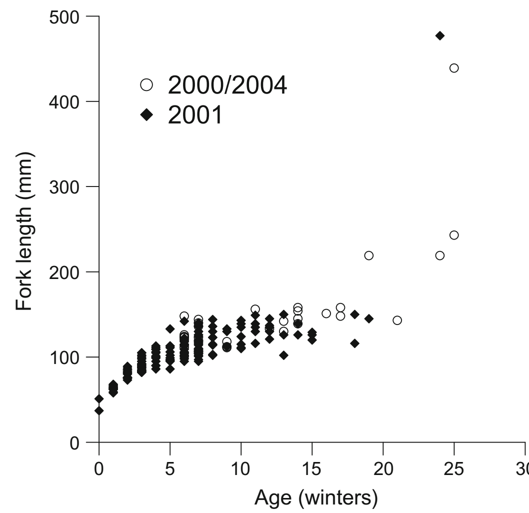

Fig. 4 Empiric length (mm) and age (winters) of 0–24 winter old Arctic charr from the Lake Nordre Borgdam, captured in August 2001, and in April–May 2000 and 2004

only 28 mm, i.e. growth in length has nearly stagnated. The 24 years old, gillnetted individual with fork length 477 mm, indicates a fast mean annual growth rate during the last 5–10 years (Fig. 4). The female charr reached sexual maturity at a minimum length of 102 mm and an age of 5 years. Male charr were found to be sexually mature from an age of 3 years and 95 mm in length.

Biomass

The total biomass of the age-classes 1–19 years was calculated to 30.4 kg, corresponding to 20.7 kg ha^{-1} (Table 3). According to the mean weight of captured fish within the three length-classes 6.0–9.9 cm, 10.0–12.9 cm, and 13.0–15.9 cm, the calculated biomass was 6.9, 15.4, and 5.6 kg, respectively, giving a total biomass of 27.9 kg or 19.0 kg ha^{-1}. Fish below 6.0 cm and above 15.9 cm are not included in the population estimation, and the calculated biomasses are thus minimum values. When including the large gillnetted individual, with age 24 years and weight 1,059 g, the minimum biomass become 19.7 and 21.4 kg ha^{-1}, according to the two different calculations.

Diet and infection with plerocercoids of *D. ditremum*

Larvae and pupae of chironomids and the trichopteran, *Apatania zonella,* were the only food items found in the stomach contents of sampled Arctic charr in August 2001. Of the 184 stomachs analysed, 34 (18.5 %) were empty. Chironomids occurred in 94 of 150 stomachs with content, while *A. zonella* was found in 26 stomachs. By weight, chironomids were the dominant food item of both length-class 6.0–9.9 cm and 10.0–15.9 cm in August 2001. During sampling in winter (April), the diet of length-class 10.0–15.9 cm was more diverse, including both Ostracoda, Copepoda, *A. zonella,* and plant material, but with chironomid larvae still being the dominant group (Fig. 5). The large charr (47.7 cm) captured in August 2001 had an

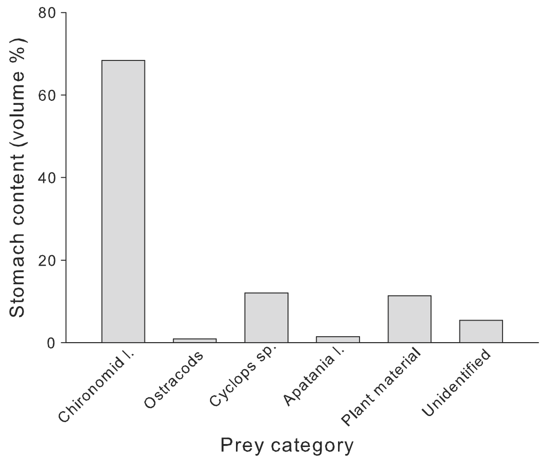

Fig. 5 Stomach content (volume%) of Arctic charr in length-class 10.0–15.9 cm (*n* = 19) captured in the Lake Nordre Borgdam in April 2000

empty stomach, while of four larger charr (21.9–43.9 cm) sampled in 2000 and 2004, three had stomach contents, with Arctic charr making up more than 98 % of the stomach volume. The preyed individuals of which fork length could be measured were approximately 5.0, 6.0, 7.0, 8.5, 9.5, and 10 cm in length.

In all length-classes <16 cm, the majority of charr (92.4 %) was uninfected with plerocercoids of *D. ditremum*. The number of infected charr increased with fish length. In length-class 5.0–9.9 cm (*n* = 74), only one individual was infected (with three plerocercoids), while in length-class 10.0–15.9 cm (*n* = 151), 16.6 % of the individuals were infected, with mean abundance 6.2 plerocercoids. Four of the five individuals between 21 and 47 cm were infected, with a mean abundance of 720 plerocercoids, and *c*. 2,000 plerocercoids as maximum in one fish.

Discussion

The length-frequency distribution of charr in Nordre Borgdam, with the majority of individuals <16 cm in length, demonstrates that many fish stagnate in growth at a small length. The most obvious explanation for this is low food intake. The capture of five individuals which had small charr in their stomachs indicates that some charr manage to pass the length interval in which the majority stagnate, probably due to a shift in feeding from mainly invertebrates to piscivory (Claessen et al. 2002). Similar changes have been described from other Arctic charr populations, especially in the High Arctic, with large fish becoming cannibals usually at a length above 15–17 cm, followed by a marked increase in annual length increment (Klemetsen et al. 1985; Griffiths 1994; Svenning and Borgstrøm 1995; Svenning et al. 2007; Berg et al. 2010).

The forage base of piscivorous Arctic charr in allopatric populations is, however, restricted, especially in low productivity lakes, resulting in a prey fish biomass not allowing for more than a few specialised piscivores per hectare (Sandlund and Forseth 1995). Probably, annual recruitment may vary considerably, as indicated in our results, and years with strong recruiting cohorts, like the year-class 1994 (cohort 7), may enhance emergence of cannibals, as analysed by Byström (2006) for an allopatric Arctic charr population in a small lake in northern Sweden. Annual variations in year-class strength may be related to number of spawners (i.e. number of eggs), but also to conditions during the incubation period until hatching (for example annual variations in ice thickness) and growth of YOY charr due to varying temperatures, as also seen for brown trout in high mountain lakes (Borgstrøm and Museth 2005). We have no data on consumption of Arctic charr by the birds foraging in the lake, but this foraging activity may possibly also show annual variations. Since growth of the majority of the individuals in Nordre Borgdam more or less stagnates early, the annual production of Arctic charr in the lake is probably only a fraction of the biomass, i.e. very low, in accordance with estimates from other Arctic charr populations in the Arctic (Saunders and Power 1969; Rigler 1975; Berg et al. 2010). A low total production may indicate that the food base for cannibals is very restricted, especially when the bird predation on charrs is taken into account as well. A pair of common loon *Gavia immer* with two chicks may require 220 kg fish (Kerekes 1990). Although the red-throated diver (*G. stellata*) occasionally observed in the lake is smaller than the common loon, one pair may require much more food than is produced in the small Lake Nordre Borgdam, and most probably, the fish eating birds mainly feed in the nearby Lake Linnè or in the fjord.

The calculated minimum density of Arctic charr <16.0 cm in length (19.0–20.7 kg ha^{-1}) was higher than that found for instance in the lake Trestikkelen (dwarf charr = 10.1 kg ha^{-1}) on Bear Island (74°30′N) (Berg et al. 2010), and 9.2 kg ha^{-1} measured in Char Lake in the Arctic region of Canada (74°47′N) (MacCallum 1972), probably due to the depths of these lakes (>20 m). Char Lake (52.6 ha) has more than 35 times the surface area of Nordre Borgdam and has a large volume of water that probably gives little contribution to the productivity. In lake Trestikkelen, the biomass relation between dwarf and piscivore Arctic charr was about 20:1 (Berg et al. 2010). A similar result was obtained in a small alpine lake in mid Norway, with estimated biomass of charr in length-class 60–150 mm to be 7.93 kg ha^{-1}, while biomass of cannibalistic charr was estimated to be 0.62 kg ha^{-1} (Finstad et al. 2001). Given the same relationship in biomass between prey fish and piscivores in Nordre Borgdam as in these studies, the total biomass of piscivores may be around 2 kg. The low ratio of captured piscivores to small-sized individuals in the current study may therefore give a realistic picture of the population composition. A similar length-frequency distribution of unexploited Arctic charr was found in lake B (4 ha), situated at the head of Oobloyah Bay on Ellesmere Island (Parker and Johnson 1991). Most of the captured Arctic charr in this lake were in the length range below 18 cm, but a few individuals were in the range 34–42 cm. A continuous gillnetting may be destructive to the large fish component, as pointed out by Svärdson (1976), resulting in loss of piscivores and stunting of Arctic charr populations in Sweden after introduction of nylon gillnets. Accordingly, the removal of some large piscivores from Lake Nordre Borgdam during the years 1998–2004 might have had an immediate effect on the mortality of small charr due to a reduced predation pressure and thus temporarily changed the population structure towards smaller fish. Johnson (1983) found, however, a remarkable stability of Arctic charr in Arctic lakes, with return to the original population structure even after severe perturbation, i.e. removal of a significant fraction of the initial population (in Keyhole lake) by intensive gillnetting during a short time interval (3 years). Our brief removal of some cannibals from Lake Nordre Borgdam may therefore hardly have any long-term effect on the population structure.

Primary production and zooplankton biomass are generally low in Arctic lakes (Hammar 1989), and according to the $\delta^{13}C$ signatures, benthic algae may be the main source of carbon for fish in clear Arctic lakes (Sierszen et al. 2003). The shape of the Nordre Borgdam with a maximum depth of only 6 m, allows light to penetrate through the whole water column 24 h a day during the open water season, probably increasing the primary production of benthic algae compared to a deeper lake, and thereby also increasing the benthic invertebrate production. Temperature was recorded at 3 m depth, but due to the wind exposure, the temperature is most probably the same throughout the water column during the open water season. In very shallow water, however, where small fish find shelter, temperature is probably higher. By staying in the shallow, stony littoral zone, the YOY and smaller individuals in general may be less prone to predation, as well as experience higher temperatures and thus better growth. In a study of YOY Arctic charr from the Dieset watercourse on Svalbard, otolith-derived water temperatures were significantly higher than temperatures recorded in the outlet river, but were consistent with temperatures previously recorded in shallow littoral areas of other Svalbard lakes where YOY charr are commonly found (Godiksen et al. 2011), also indicating that the small individuals use much of their time in very shallow water. Still the growth rate is slow, since the mean size of 1+ charr captured in Nordre Borgdam was only 63 mm in August.

In a year-round investigation in the nearby Lake Linné (Svenning et al. 2007), copepods (*Cyclops abyssorum*) occurred in the charr diet only in October. They had a high frequency of occurrence in stomach contents of small Arctic charr and were also common in individuals ≥15 cm. In another year-round study of brown trout diet in the subalpine lake Øvre Heimdalsvatn (1,088 m.a.s.l.) in southern Norway, copepods were likewise found as trout food in winter, from November to May (Lien 1978). A similar feeding pattern was observed in Nordre Borgdam, with copepods (*Cyclops* sp.) found as part of the charr diet in April–May when the lakes was ice-covered, but not in August. However, in Nordre Borgdam, small charr seem to have a very restricted zooplankton feeding, since the majority of the fish studied were uninfected by plerocercoids of *D. ditremum*. The life cycle of this cestode includes cyclopoid copepods as first intermediate host, Arctic charr commonly being the second intermediate host, and the red-throated loon as the likely main final host on Svalbard (Hammar 2000, and references therein). Although length-class 5.0–9.9 cm was practically uninfected, and length-class 10–15.9 cm had an average infection intensity at 6.2 plerocercoids per fish, the two large charr, with length 43.9 and 47.7 cm, had a total burden of c. 3,000 plerocercoids. The high parasite burden of the cannibals is in line with the findings of Hammar (2000) from other Arctic charr populations in northern Svalbard and is probably a result of descrete ontogenetic niche shifts. Furthermore, the parasite burden of charr with length >20 cm in Nordre Borgdam is far higher than found in a charr population in southern Norway (Halvorsen and Andersen 1984). In this population, fish was not recorded in the diet of Arctic charr, and infection must have been due to consumption of infected copepods. The plerocercoid number had a trend towards over-dispersion up to age 5+ and a dominating trend towards under-dispersion after this age, suggesting that plerocercoids of *D. ditremum* alone may cause mortality of individuals with high plerocercoid burdens (Halvorsen and Andersen 1984). The large charr in Nordre Borgdam had, however, a plerocercoid burden around ten times higher than the most infected fish in Lake Røyetjern. Due to the faster growth rate of the large charr in Nordre Borgdam and the occurrence of small Arctic charr in their diet, it is most likely that this heavy parasite burden is due to transfer of plerocercoids from the prey fish to the piscivore. Assuming that the large individuals mainly attain plerocercoids by feeding on small, infected charrs in the same length range as found in the stomach contents, the total plerocercoid burden of the two large individuals indicate a consumption corresponding to more than 3,000 individuals of small charr. Although the parasite burden may have been attained over several years, there were additional cannibals in the lake, and our simplified calculation may demonstrate that even a low number of cannibals may totally control the number of prey fish. Such effect of piscivores was observed after stocking with large Arctic charr (weighting 0.9–3.9 kg) in a small lake in northern Norway inhabited by allopatric, small-sized Arctic charr. The native charr population was subsequently reduced from around 9,500 to 3,000 individuals in less than 16 months (Svenning and Borgstrøm 2005), but without any change in annual growth rate of the remaining, native individuals (Svenning, unpublished). All stocked fish became cannibals, but the frequency of cannibals with prey fish in their stomachs decreased during the second year, probably as a result of the reduced density of native fish, i.e. leading to a highly reduced availability of prey fish (Svenning and Borgstrøm 2005).

Especially in shallow lakes like Nordre Borgdam, the presence of some large fish may force the smaller individuals to reduce their foraging activity to a minimum during the summer period (see Svenning and Borgstrøm 2005) and seek refuge in the stony, shallow part of the lake with a complex bottom substrate, as also observed by Dick et al. (2009). This behaviour, with a cryptic existence in between the loose stony littoral substrate, reduces the predation risk, but at the same time gives little foraging reward, probably explaining the very slow annual growth increments, and the dominance of small chironomids in the diet. Deep lakes may offer an additional refuge for small Arctic charr in the profundal zone (Kristoffersen et al. 1994; O'Connell and Dempson 2002), but the use of this habitat may also be at the expense of growth rate due to both low temperatures and low food availability. Optimal temperature for growth of Arctic charr may be in a temperature range around 15 °C (Larsson and Berglund 2005), while the temperature in most Svalbard lakes is far below this (see Godiksen et al. 2011) and in Nordre Borgdam usually exceeding 5–6 °C for only 2–3 weeks during the open water period (Svenning, unpublished data).

In conclusion, cannibalism may be the major force in structuring age and length-class distribution in the Arctic charr population in Lake Nordre Borgdam. Low temperature and short open water season may contribute to low invertebrate prey availability, but both primary productivity and invertebrate prey availability may increase as a result of a future climate change with increased temperatures. Nevertheless, the presence of a few cannibalistic charr may prevent the small-sized charr from taking advantage of such a potential increase in food availability. The population structure, with a high density of small charr and a few large individuals, may therefore persist even after a marked climate change, due to an effective population control by the large cannibals.

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