

# Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake, Norway

Per-Arne Amundsen · Rune Knudsen

Received: 21 May 2009 / Accepted: 25 June 2009 / Published online: 11 July 2009  
© Springer Science+Business Media B.V. 2009

**Abstract** We studied habitat choice, diet, food consumption and somatic growth of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) during the ice-covered winter period of a subarctic lake in northern Norway. Both Arctic charr and brown trout predominantly used the littoral zone during winter time. Despite very cold winter conditions (water temperature  $<1^{\circ}\text{C}$ ) and poor light conditions, both fish species fed continuously during the ice-covered period, although at a much lower rate than during the summer season. No somatic growth could be detected during the ice-covered winter period and the condition factor of both species significantly declined, suggesting that the winter feeding rates were similar to or below the maintenance requirements. Also, the species richness and diversity of ingested prey largely decreased from summer to winter for both fish species. The winter diet of Arctic charr  $<20$  cm was dominated by benthic insect larvae, chironomids in particular, and *Gammarus lacustris*, but zooplankton was also important in December. *G. lacustris* was the dominant prey of charr  $>20$  cm. The winter diet of brown trout  $<20$  cm was dominated by insect larvae, whereas large-sized trout mainly was piscivorous,

feeding on juvenile Arctic charr. Piscivorous feeding behaviour of trout was in contrast rarely seen during the summer months when their encounter with potential fish prey was rare as the small-sized charr mainly inhabited the profundal. The study demonstrated large differences in the ecology and interactions of Arctic charr and brown trout between the winter and summer seasons.

**Keywords** Fish · Feeding · Habitat choice · Ice · Interactions · Winter

## Introduction

The winter season in subarctic and Arctic lakes is considered to be a challenging period for many lacustrine fishes due to low temperatures and poor light conditions under ice cover and snow. The lakes are often ice bound for more than half of the year, which offers logistic difficulties associated with under ice sampling of fish. Consequently, few studies have been conducted on the winter ecology of high latitude fish. The few lake studies that exist are mainly related to resource use (e.g., Knudsen et al. 1996, 1997, 2006; Klemetsen et al. 1997, 2003a, b; Svenning et al. 2007) and growth performance (e.g., Finstad et al. 2003; Byström et al. 2006) of single fish species. Our knowledge of the winter ecology of

---

P.-A. Amundsen (✉) · R. Knudsen  
Department of Aquatic BioSciences, Norwegian College  
of Fishery Science, University of Tromsø, 9037 Tromsø,  
Norway  
e-mail: Per-Arne.Amundsen@uit.no

lacustrine fish communities at high latitudes is thus limited as potential interactions between co-occurring fish species have rarely been investigated, even though the transition from summer to winter is likely to induce large changes in the ecology and behaviour of sympatric species. Low temperatures and poor light conditions may for instance influence spatial requirements, leading to different resource use during winter and summer periods. Furthermore, low temperatures are known to influence digestion rates, metabolic requirements and appetite of fish (Jobling 1994; Sæther et al. 1996), and poor light conditions are challenging for successful search and capture of prey (e.g., Mazur and Beauchamp 2003; Turesson and Brönmark 2007). Combining these factors with the assumed lower productivity and reduced prey availability during winter time, leads to the expectation that both diet composition and feeding rates and energetic status and growth rates should highly differ between winter and summer seasons.

Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) are common fish species in northern lakes (Klemetsen et al. 2003a). When living in sympatry, these species may engage in several ecological interactions both as competitors (e.g., Nilsson 1967; Langeland et al. 1991; Jansen et al. 2002; Gregersen et al. 2006) and as predators and prey (e.g., Byström 2006; Finstad et al. 2006; Persson et al. 2007). During summer, the two species appear to have similar habitat and dietary preferences, and brown trout is, due to its more aggressive behaviour, being the dominant species in the littoral zone (Nilsson 1967; Langeland et al. 1991). The cold winter conditions may reduce these interactions as salmonids are known to become less aggressive (Huusko et al. 2007) and the food requirements decrease at low temperatures (Jobling 1994). The brown trout is also described as a visual predator relying on good light conditions for efficient predation (Langeland et al. 1991; Jansen et al. 2002; Rader et al. 2007) and has been assumed to eat very little during winter (Hammar 1998). The Arctic charr appears in contrast to be able to feed quite intensively also during wintertime (Brännäs and Wiklund 1992; Hammar 1998; Klemetsen et al. 2003b; Knudsen et al. 2006; Svenning et al. 2007). The ecological interactions between these two species are thus expected to differ between the winter and summer seasons.

In the present study, we compare the winter ecology of Arctic charr and brown trout living in sympatry as the only two fish species present in a subarctic lake, Fjellfrøsvatn, situated at 69°N in northern Norway. The lake is covered by ice for 6–7 months, and there are nearly 2 months (approx. November 25 to January 15) of polar night at this latitude. The study lake harbours two different morphs of Arctic charr, one littoral spawning morph (L-morph) and one profundal spawning, dwarf-like morph (P-morph) that differ distinctly in their ecology, morphology and genetics (Klemetsen et al. 1997, 2002, 2006; Westgaard et al. 2004; Knudsen et al. 2006, 2007; Amundsen et al. 2008). The L-morph charr resemble the Arctic charr populations found in other lakes in the region (Klemetsen et al. 1997; Knudsen et al. 2006), whereas the dwarfed P-morph charr appear to be confined to a rare and untypical ecological niche for the species, residing their whole life in the profundal zone and feeding on typical profundal prey from the soft-bottom sediments (Klemetsen et al. 1997, 2002, 2003a, 2006; Knudsen et al. 2006; Amundsen et al. 2008). The P-morph charr have therefore not been included in our interspecific comparison of Arctic charr and brown trout.

We explored habitat choice, feeding, somatic growth and conditions of the L-morph Arctic charr and brown trout during the winter period and contrasted the results with comparable findings from the summer season. We hypothesised that the habitat and diet utilisation of the two species differ between the ice-covered and ice-free seasons. Furthermore, we predicted that the Arctic charr would feed more actively than brown trout during winter, although for both species the consumption rates were expected to be poor and the winter diets to be less diverse than the summer diets. Finally, we predicted that somatic growth would be insignificant during the winter period and that the condition factor of the fish would decrease.

## Materials and methods

### Study site

Lake Fjellfrøsvatn is situated at 125 m a.s.l. in northern Norway (69°05'N, 19°20'E); it is 6.5 km<sup>2</sup>

in area, has a maximum depth of 88 m deep, and is oligotrophic. The littoral zone extends down to about 15 m depth (see Klemetsen et al. 2003b) and comprises about 30% of the lake area. The shore regions are mostly sandy or stony with little emergent vegetation. The catchment area of the lake is about 90 km<sup>2</sup>, consisting of treeless mountains and woodland with birch (*Betula pubescens*) and pine (*Pinus silvestris*), and with a few small farms and some cottages located around the lake. The lake is dimictic with ice cover for 6–7 months, usually from November to May. During the ice-free period in 1992–1993, the temperature in the littoral and upper pelagic zones approached a maximum of 12°C in August (Fig. 1), whereas the profundal temperature ranged between 4.5 and 8.0°C. During wintertime the littoral temperature in the lake was 0.6–0.7°C, and the profundal temperature 2.0–2.1°C. At this latitude, there are nearly 2 months of polar night around winter solstice, and nearly 2 months of midnight sun around summer solstice. Arctic charr and brown trout are the only fish species in the lake.

#### Sampling and analyses

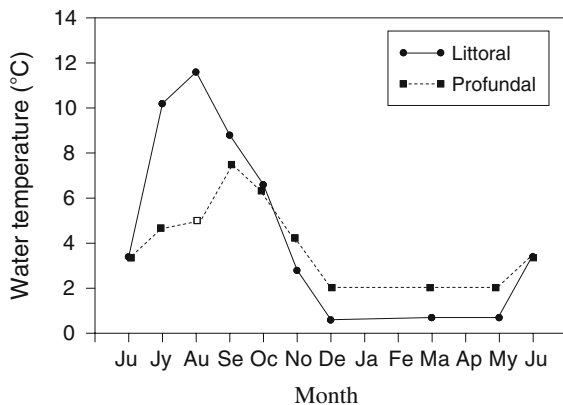
Samples were collected monthly during the ice-free period (June–November) and three times under ice during winter (December, March, May) in 1992–1993. The ice thickness was about 30 cm in December, 80 cm in March and 60 cm in May. There was clear ice and practically no snow in December, about half a metre of snow on top of the ice in March, and

opaque ice and little snow in May. Fish were sampled in littoral, profundal and pelagic habitats using 40 m long survey gillnets having eight randomly distributed 5-m panels of 10, 12.5, 15, 18, 22, 26, 35 and 45 mm bar mesh sizes. In the littoral and profundal, we used 1.5 m deep bottom nets and in the pelagic zone 6 m deep floating nets. Sampling in the pelagic zone was not done during wintertime as studies in the nearby lake Takvatn have shown that Arctic charr rarely use this habitat during the ice-covered period (Klemetsen et al. 2003b). The littoral nets were set from the shore down to 15 m depths, whereas the profundal sampling was done at 25–40 m depths. The gill nets were randomly positioned within the different habitats. The habitat use of the Arctic charr and brown trout was compared by estimating the per cent habitat distribution of each species at each sampling occasion from area-adjusted catch per unit effort data (number of fish per survey gillnet per night) from the littoral, profundal and pelagic habitats, respectively. The total number of fish caught during study period comprised 1924 Arctic charr and 244 brown trout, including 350 charr and 20 brown trout caught during the ice-covered period. As habitat and diet utilisation are often influenced by the size of the fish, we split the results for both Arctic charr and brown trout into two sizes: small-sized (<20 cm) and large-sized fish (>20 cm). A further division into sizes was infeasible because of limited sample sizes for brown trout during some months. For both species, the small-sized group was dominated by fish up to 4 years of age, and the large-sized group by fish older than 4 years.

The fish were measured (fork length) and weighed. Fulton's condition factor ( $K$ ) was calculated as:

$$K = 100 \times WL^{-3}, \quad (1)$$

where  $W$  is the wet weight in grams and  $L$  the fork length in centimetre. Stomach contents and otoliths were sampled and preserved in 96% ethanol until later analysed in the laboratory. Ageing of fish was performed by surface reading of otoliths under a binocular microscope. The stomachs were opened and the total fullness was visually determined in the range from empty (0%) to full (100%). The prey items were identified and their contribution to the total fullness was estimated (Amundsen 1995). The proportion of each diet category was expressed as per cent prey abundance ( $A_i$ ):



**Fig. 1** Water temperatures in the littoral (5 m depth; solid line) and the profundal (30 m depth; dotted line) zones of lake Fjellfrøsvatn at the sampling occasions in 1992 and 1993

$$A_i = (\sum S_i / S_t) \times 100, \quad (2)$$

where  $S_i$  is the stomach fullness of prey  $i$  and  $S_t$  the total stomach fullness of all prey categories (Amundsen et al. 1996). The prey items were mainly identified to the species, genus or family level, and a total of 32 taxa were recorded. Prey diversity was calculated from Simpson's reciprocal diversity index ( $D$ ):

$$D = 1 / \sum p_i^2, \quad (3)$$

where  $p_i$  is the proportion of each prey type  $i$  in the diet and equals  $A_i$  expressed as fraction rather than percentage. The dietary overlap between Arctic charr and brown trout was calculated as per cent overlap (Krebs 1999):

$$P_{jk} = \left[ \sum_1^n (\text{minimum } p_{ij}, p_{ik}) \right] \times 100, \quad (4)$$

where  $P_{jk}$  is the percentage overlap between species  $j$  and species  $k$ ,  $p_{ij}$  and  $p_{ik}$  are the proportions of fish prey  $i$  used by species  $j$  and  $k$ , and  $n$  the total number of diet categories (Krebs 1999). In the graphical presentation of the dietary results (see Fig. 3), the prey taxa have been sorted in eight functional diet categories: (a) zooplankton (planktonic cladocerans and copepods), (b) surface insects (adult terrestrial and aquatic insects), (c) chironomid pupae, (d) the chydorid *Eurycercus lamellatus*, (e) insect larvae, (f) snail, mainly *Lymnaea peregra*, and mussels (*Pisidium* sp.), (g) *Gammarus lacustris*, and (h) fish (Arctic charr).

After the diet analysis, the dry weight (65°C for >48 h) and ash weight (540°C for >12 h) were determined and the stomach contents weight was expressed as milligram organic ash-free dry weight (AFDW) per gram fresh weight of fish. The feeding rate of the Arctic charr was estimated in terms of daily food consumption ( $C_{24}$ ) using the Baikov/Eggers method (Eggers 1979):

$$C_{24} = 24SR, \quad (5)$$

where  $S$  is the mean weight of stomach contents for the 24-h period and  $R$  is the instantaneous gastric evacuation rate. The method is known to provide a robust field estimate of food consumption rates in fish (Amundsen and Klemetsen 1986; Richter et al. 2004). Estimates of gastric evacuation rates were obtained from Amundsen and Klemetsen (1988) and Elliott

(1972) for Arctic charr and brown trout, respectively. Because the arithmetic means are very sensitive to a few high values due to skewed distributions of the weights of stomach contents (Amundsen and Klemetsen 1986), we used a logarithmic transformation to derive geometric means.

## Results

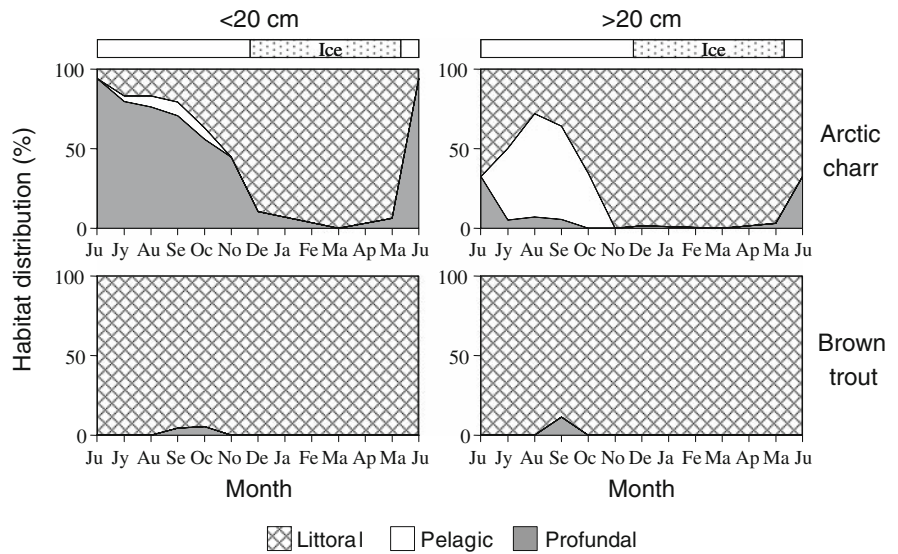
### Habitat choice

During wintertime most of the Arctic charr (97%) and all brown trout (100%) were caught in the littoral zone (Fig. 2). Also, during the ice-free period the brown trout were almost exclusively found in the littoral, whereas the Arctic charr used all three habitats: the littoral, pelagic and profundal. Large-sized charr (>20 cm) predominantly utilised the littoral and pelagic habitats during the ice-free season. In contrast, the small-sized Arctic charr (<20 cm) mainly inhabited the profundal zone during this period, whereas after ice cover they were almost exclusively caught in the littoral habitat, co-occurring with large-sized charr and brown trout.

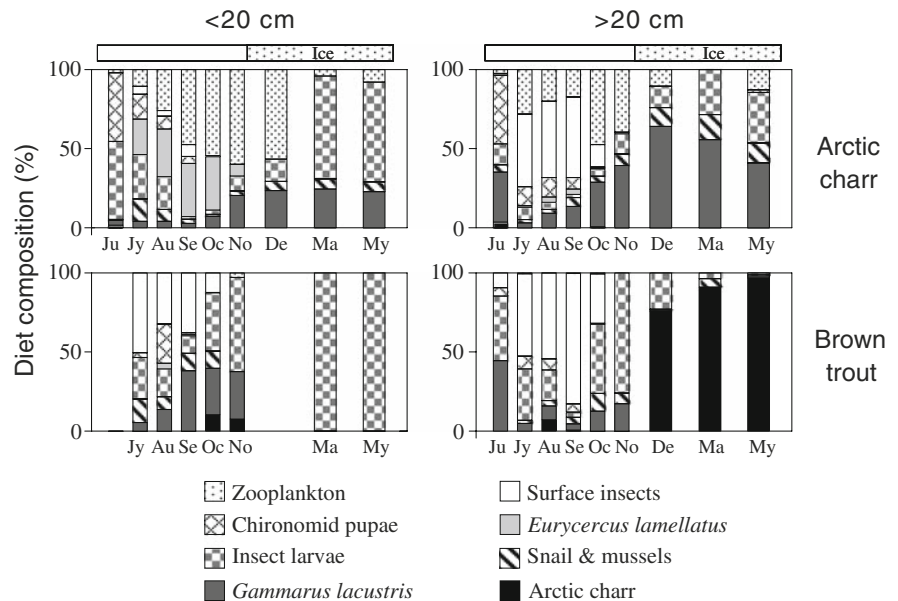
### Diet and food consumption

A total of 32 prey taxa were recorded in the stomach contents of Arctic charr and brown trout. Arctic charr, irrespective of its size, fed on a large variety of prey types during the ice-free period, whereas a few prey types, mainly insect larvae and the amphipod *G. lacustris*, dominated their diets during winter time (Fig. 3). Zooplankton, mainly cladocerans, and the benthic cladoceran *E. lamellatus*, were important prey categories for charr <20 cm during the summer. Planktonic cladocerans, in particular *Bosmina longispina*, were also important contributors to the charr diet in December, whereas *Daphnia galeata* was encountered in some stomach contents during March and May. Insect larvae (mainly chironomids) and *G. lacustris* were, however, the most important prey types for charr <20 cm during winter. For charr >20 cm, surface insects and zooplankton were dominant prey during summer. *G. lacustris* increased in dietary importance towards autumn and was the dominant prey during the whole winter. The species richness and diversity of prey decreased from

**Fig. 2** Seasonal habitat distribution of small (<20 cm) and large-sized (>20 cm) Arctic charr (upper panel) and brown trout (lower panel) in lake Fjellfrøsvatn from June 1992 to May 1993. The ice-covered period is indicated at the top of the figure



**Fig. 3** Seasonal diet composition (% prey abundance) of small (<20 cm) and large-sized (>20 cm) Arctic charr (upper panels) and brown trout (lower panels) in lake Fjellfrøsvatn from June 1992 to May 1993. The ice-covered period is indicated at the top of the figure panels

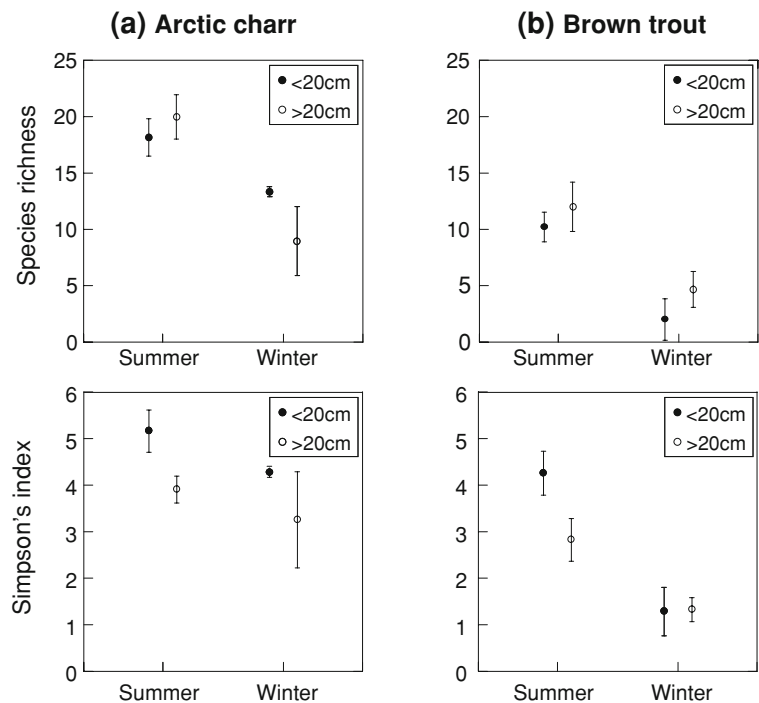


summer to winter for both size groups of Arctic charr (Fig. 4a).

A similar pattern was also seen for the diet of brown trout but both species richness and diversity of prey were lower than for Arctic charr, and the trout also exhibited a distinct and more pronounced decrease in these diet parameters from summer to winter (Fig. 4b). The winter diet of brown trout <20 cm was dominated by insect larvae, mainly Plecoptera and Megaloptera, whereas the diet was more diverse during the ice-free period, including also surface insects, *Gammarus*,

chironomid pupae, snails and fish eggs. In winter, brown trout >20 cm fed predominantly on Arctic charr. In contrast, such a piscivorous feeding was rare during the ice-free period, when surface insects and large-sized insect larvae like Trichoptera and Tipulidae dominated the diet of trout >20 cm (Fig. 3). Throughout the winter and summer periods, the diets of small sized (<20 cm) Arctic charr and brown trout distinctly differed, with the diet overlap generally <30% (Table 1). Also, for large-sized fish (>20 cm) the diet overlap was negligible during the ice-covered

**Fig. 4** Mean species richness and prey diversity (Simpson's reciprocal index) in small (<20 cm) and large (>20 cm) **a** Arctic charr and **b** brown trout during the summer (*ice-free*) and winter (*ice-covered*) seasons from June 1992 to May 1993 in lake Fjellfrøsvatn. Vertical bars indicate standard error (SE)



period. In contrast, during summer, the dietary overlap between large-sized charr and trout was pronounced and exceeded 60% during July–September (Table 1).

Arctic charr and brown trout had a similar seasonal pattern in food consumption rates (Fig. 5). Both species continued to feed during the whole winter period, but at a much lower rate than during summer time. During the ice-covered period the feeding rates of the two species generally ranged from 0.3 to 0.5 mg AFDW  $g^{-1}$  fish  $day^{-1}$ , compared with the

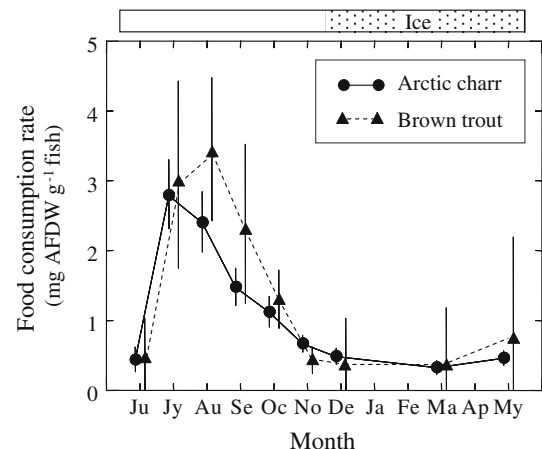
highest observed rates that ranged from 2.8 to 3.4 mg AFDW  $g^{-1}$  fish  $day^{-1}$  during summer.

#### Winter growth and condition factor

Mean body mass of all age classes of Arctic charr (1+ to 6+) increased significantly during the ice-free

**Table 1** Per cent diet overlap between Arctic charr and brown trout in different sampling months during the time period from June 1992 to May 1993 in lake Fjellfrøsvatn, Norway

Month	Size groups with % diet overlap	
	<20 cm	>20 cm
June	–	49
July	19	65
August	24	68
September	14	64
October	10	32
November	33	24
December	–	12
March	24	2
May	8	3



**Fig. 5** Seasonal variations in daily food consumption rates (mean,  $\pm 95\%$  confidence limits) of Arctic charr and brown trout (all size groups combined) from June 1992 to May 1993 in Fjellfrøsvatn. The *ice-covered period* is indicated at the top of the figure

period (Fig. 6a; ANOVA,  $P < 0.01$ ). During the ice-covered period (November–June), however, there were no significant changes in mean body mass of charr (age classes 1+, 2+, 3+ and 6+; ANOVA,  $P > 0.05$ ). For analysis of the somatic growth of brown trout, only 4+ fish were sufficiently represented in the winter samples. The mean body mass of the 4+ fish increased during the ice-free period, but not significantly (Fig. 6b; ANOVA,  $P > 0.05$ ). During wintertime no significant changes in the mean body mass of the brown trout could be observed (ANOVA,  $P > 0.05$ ).

Over the ice-covered period the condition factor of all age groups of both Arctic charr and brown trout significantly declined (Fig. 7; ANOVA,  $P < 0.05$ ). In Arctic charr, there was an increase in condition factor between consecutive age groups from 1+ to 4+ (ANCOVA;  $P < 0.001$ ), whereas age groups 4+ to 6+ showed no significant differences (ANCOVA;  $P > 0.05$ ) and were compiled in the analyses.

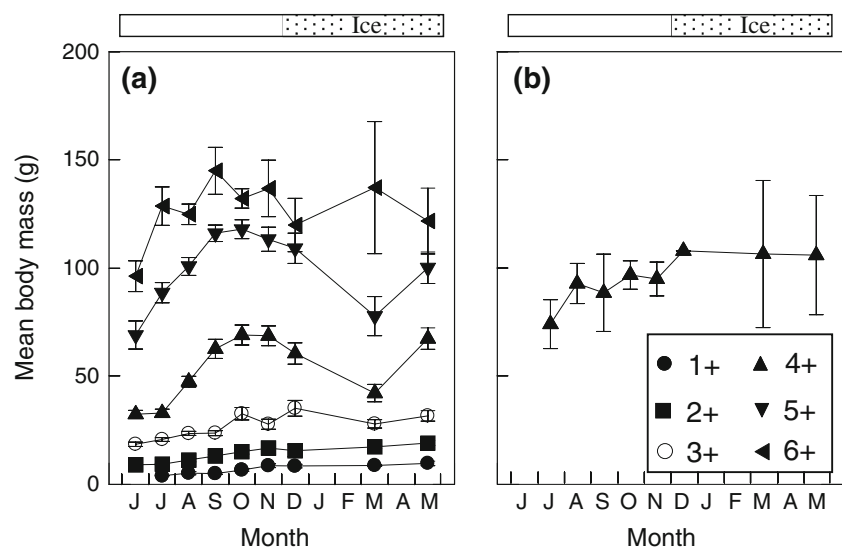
## Discussion

The winter conditions in subarctic lakes appear to present a challenging environment for fish and other biota in several respects due mainly to low temperatures and darkness. Fish are ectotherms and most life processes are therefore decelerated when the temperatures become low (Jobling 1994). Furthermore, since salmonids like Arctic charr and brown trout

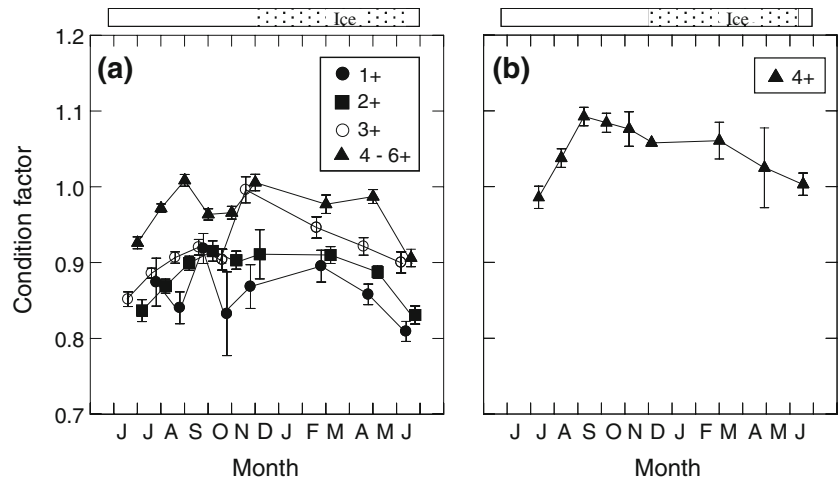
are visual predators, their foraging success may rely heavily upon the ambient light conditions (Mazur and Beauchamp 2003; Rader et al. 2007). Consequently, salmonids and most other fish are assumed to reduce their swimming activity and aggressive feeding behaviour during wintertime (Huusko et al. 2007). Because a marked decline in body temperatures during winter results in reduced metabolism and energy costs (Jobling 1994), fish may even become dormant, stop feeding, and rely solely on their energy reserves to survive the winter (Crawshaw 1984; Garvey et al. 2004). Interestingly, however, we observed that both Arctic charr and brown trout remain active during wintertime and feed actively, despite the fact that both species mainly inhabit the cold littoral zone with water temperatures constantly  $< 1^{\circ}\text{C}$ .

Notwithstanding their age and size differences, both fish species inhabited the littoral habitat during the winter period. Brown trout also resided mainly in this habitat during the summer season. This is in contrast with Arctic charr which exhibits ontogenetic differences in habitat use during the ice-free season, and exploits all main habitats of the lake. The habitat transition between summer and winter appears to be most pronounced for small-sized charr, which mainly reside in the profundal during the ice-free period, but moves to the littoral before and at the time of ice formation and stays there during the whole winter. This habitat shift may increase the general intra- and inter-specific resource competitions for littoral prey,

**Fig. 6** Growth in terms of changes in mean body mass ( $\pm$ SE) of different age groups of **a** Arctic charr (age groups 1–6 year) and **b** brown trout (age group 4 year) during the period from June 1992 to May 1993 in Fjellfrøsvatn. The ice-covered period is indicated at the top of the figure panels



**Fig. 7** Mean condition factor ( $\pm$ SE) in different age groups of **a** Arctic charr and **b** brown trout during the period from June 1992 to May 1993 in Fjellfrøsvatn. The ice-covered period is indicated at the top of the figure panels



but simultaneously also alter the predation risk for small-sized charr. High predation risk in the littoral zone during summer time is suggested as the main reason why small charr tend to reside in the profundal at this time of the year (Klemetsen et al. 1989, 2003a). Potential predators in the littoral of the study lake include piscivorous brown trout, cannibalistic Arctic charr and predatory birds, e.g., divers *Gavia* spp. and red-breasted mergansers *Mergus serrator*. Predatory birds are obviously absent from frozen lakes, and piscivorous fish are assumed to be less efficient predators under winter conditions (e.g., Hammar 1998; Huusko et al. 2007). The littoral may therefore be considered a less dangerous habitat for small-sized charr during winter. However, our diet studies show that Arctic charr dominate the diet of brown trout in winter, implying that the trout can catch their fish prey also under the dark and cold winter conditions. Thus, the use of the littoral as a habitat by small-sized Arctic charr in winter involves an enhanced predation risk, and suggests that shifting of the juvenile charr into the littoral zone during winter is a trade-off to offset their food demand that apparently is more critical than the predation threats from the trout. This may be related to the observation that small charr are likely to starve to death during winter if they are unable to feed (Byström et al. 2006), and the availability of food resources is therefore a critical factor for their survival during this period. Zooplankton, which is an important food resource for juvenile charr during the ice-free period (Klemetsen et al. 1992, 2003a; Amundsen et al. 2008), is generally low in abundance during winter.

Juvenile charr are thus likely to suffer from food limitations if they continue to reside in the profundal and pelagic habitat during winter. This may thus be the principal reason for their habitat shift to the colder but more food-rich littoral at the start of the winter season, even though the predation rate is higher there.

The two species appear to have a low dietary overlap in winter, regardless of their sizes. The study shows that the small-sized charr mainly feed upon chironomid larvae, whereas small trout chiefly utilise other taxa of insect larvae like Plecoptera and Megaloptera. For large-sized fish the diet overlap is even lower as the charr predominantly feed on *G. lacustris*, whereas the trout mainly prey upon small Arctic charr. *Gammarus* is an important macroinvertebrate prey for many fish species (MacNeil et al. 1999), but it is also an important intermediate host for several parasite species, including the cestode *Cyathocephalus truncatus* that can parasitize both Arctic charr and brown trout (Amundsen et al. 2003; Knudsen et al. 2008). This cestode can manipulate the behaviour of their *Gammarus* hosts in order to increase transmission rates (Knudsen et al. 2001). Altered host behaviour may increase predation rates as predators often appear to take prey that act peculiarly or are otherwise conspicuous (Lafferty 1992, 1999), and the presence of *C. truncatus* in *Gammarus* may thus facilitate and enhance the predation rates of *Gammarus* by the fish. The infection rates of *C. truncatus* in *Gammarus* consumed by fish were highest in November and December (Amundsen et al. 2003), and this coincides largely with the time period when *Gammarus* dominated the diet of Arctic charr.



As expected, the diet of the two fish species was less diverse during winter than in the summer when surface insects were absent and zooplankton was less important. For Arctic charr, also the benthos diet was less diverse during winter when *Gammarus* and chironomid larvae dominated, whereas several other insect taxa were less important than in the ice-free season. For the large-sized brown trout there was a particularly large reduction in prey richness and prey diversity from summer to winter, as Arctic charr was a very dominant prey during wintertime. A similar reduction in prey diversity was also found for the small-sized brown trout, but this may partly also be related to low sample sizes during winter.

Arctic charr is known as a species that is more adapted to coldwater than brown trout (Klemetsen et al. 2003a) and able to feed during wintertime (e.g., Parker and Johnson 1991; Hammar 1998; Klemetsen et al. 2003b; Svenning et al. 2007; Amundsen et al. 2008). The feeding of brown trout in winter is more surprising as the brown trout is known as a typical visual predator requiring good light conditions for efficient feeding (Langeland et al. 1991; Mazur and Beauchamp 2003). The observed feeding on fish prey under ice cover and in the darkest period of winter demonstrates that the trout can predate on difficult prey even in virtual darkness. Potentially the trout is capable of using some other senses than vision during their predation in darkness, but it also seems that the sensitivity to light increases in salmonids in winter as the ratio of retinal porphyropsin to rhodopsin increases (Tsin and Beatty 1997). Contrary to our present results, Hammar (1998) found that the brown trout hardly was feeding during wintertime. These differences may be related to local adaptations, but further studies are needed as the number of observation on feeding of brown trout during wintertime is low in both of these studies. It should also be emphasised that the food consumption rates of both for Arctic charr and brown trout are low during winter and do not facilitate allocation of energy to somatic growth or body condition during this period. Thus, even though both species feed in winter, the winter may represent a serious bottleneck for resource acquisition, possibly resulting in a depletion of energy reserves.

In conclusion, both Arctic charr (L-morph) and brown trout use the littoral zone as their principal winter habitat, and both species feed actively during the ice-covered period. The species have low dietary

overlap during winter, even though the prey diversity in winter is lower than in summer. In our study lake, *G. lacustris* is an important winter prey for Arctic charr, whereas large brown trout mainly are piscivorous, feeding on juvenile Arctic charr. As expected, the Arctic charr as the northernmost freshwater fish in the World appears to be befittingly adapted to a long winter period. More surprisingly, also the brown trout seems to be quite well adapted to the harsh winter conditions with low water temperatures and light levels. However, for both species the food consumption rates are much lower in winter than during summer, which explains lack of somatic growth and decline in body condition during the ice-covered period. The winter ecology of the two species in high latitude lakes with harsh winters thus differs in several important aspects from the summer situation. The species interactions apparently also changed, particularly with respect to the predation of juvenile charr by brown trout. Hence, the winter period appears to be important in the population and community ecology of these salmonids, and in future studies of subarctic lakes more emphasis should be allocated to the winter situation.

**Acknowledgments** Many people have contributed to this study, but we especially like to thank Laina Dalsbø and Jan Evjen for their skilled assistance in the field and laboratory work. We also like to thank two anonymous referees and K. Salonen and R. D. Gulati for helpful comments on the manuscript.

## References

- Amundsen P-A (1995) Feeding strategy of Arctic charr (*Salvelinus alpinus*): general opportunist but individual specialist. Nord J Freshw Res 71:150–156
- Amundsen P-A, Klemetsen A (1986) Within-sample variabilities in stomach contents weight of fish—implications for field studies of consumption rate. In: Simenstad CA, Cailliet GM (eds) Contemporary studies on fish feeding. Junk, The Hague, pp 307–314
- Amundsen P-A, Klemetsen A (1988) Diet, gastric evacuation rates and food consumption in a stunted population of Arctic charr, *Salvelinus alpinus* (L.), in Takvatn, northern Norway. J Fish Biol 33:697–709
- Amundsen P-A, Gabler H-M, Staldivik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. J Fish Biol 48:607–614
- Amundsen P-A, Knudsen R, Kuris AM, Kristofferesen R (2003) Seasonal and ontogenetic dynamics in trophic transmission of parasites. Oikos 102:285–293

- Amundsen P-A, Knudsen R, Klemetsen A (2008) Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. *Environ Biol Fish* 83:45–55
- Brännäs E, Wiklund B-S (1992) Low temperature growth potential of Arctic char and rainbow trout. *Nord J Freshw Res* 67:77–81
- Byström P (2006) Recruitment pulses induce cannibalistic giants in Arctic char. *J Anim Ecol* 75:434–444
- Byström P, Anderson J, Kiessling A, Eriksson L-O (2006) Size and temperature dependent foraging capacities and metabolism: consequences for winter starvation mortality in fish. *Oikos* 115:43–52
- Crawshaw LI (1984) Low temperature dormancy in fish. *Am J Physiol* 246:479–486
- Eggers DM (1979) Comment on some recent methods for estimating food consumption by fish. *J Fish Res Board Can* 36:1018–1019
- Elliott JM (1972) Rates of gastric evacuation in brown trout (*Salmo trutta* L.). *Freshw Biol* 2:1–18
- Finstad AG, Berg OK, Lohrmann A (2003) Seasonal variation in body composition of Arctic charr, *Salvelinus alpinus*, from an ultraoligotrophic alpine lake. *Ecol Freshw Fish* 12:228–235
- Finstad AG, Ugedal O, Berg OK (2006) Growing large in a low grade environment: size dependent foraging gain and niche shifts to cannibalism in Arctic char. *Oikos* 112:73–82
- Garvey JE, Ostrand KG, Wahl DH (2004) Energetics, predation, and ration affect size-dependent growth and mortality of fish during winter. *Ecology* 85:2860–2871
- Gregersen F, Aass P, Vollestad LA, L'Abée-Lund JH (2006) Long-term variation in diet of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*: effects of changes in fish density and food availability. *Fish Manag Ecol* 13:243–250
- Hammar J (1998) Interactive asymmetry and seasonal niche shifts in sympatric Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): evidence from winter diet and accumulation of radioecesium. *Nord J Freshw Res* 74:33–64
- Huusko A, Greenberg L, Stickler M, Linnansaari T, Nykänen M, Vehanen T, Louhi P, Alfredsen K (2007) Life in the ice lane: the winter ecology of stream salmonids. *River Res Appl* 23:469–491
- Jansen PA, Slettovold H, Finstad AG, Langeland A (2002) Niche segregation between Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms. *Can J Fish Aquat Sci* 59:6–11
- Jobling M (1994) *Fish bioenergetics*. Chapman & Hall, London
- Klemetsen A, Amundsen P-A, Muladal H, Rubach S, Solbakken JI (1989) Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. *Physiol Ecol Japan* 1: 187–200
- Klemetsen A, Muladal H, Amundsen P-A (1992) Diet and food consumption of young, profundal Takvatn charr (*Salvelinus alpinus*). *Nord J Freshw Res* 67:34–43
- Klemetsen A, Amundsen PA, Knudsen R, Hermansen B (1997) A profundal winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in Lake Fjellfrøsvatn, northern Norway. *Nord J Freshw Res* 73:13–23
- Klemetsen A, Elliott JM, Knudsen R, Sørensen P (2002) Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. *J Fish Biol* 60:933–950
- Klemetsen A, Amundsen P-A, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003a) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol Freshw Fish* 12:1–59
- Klemetsen A, Knudsen R, Staldvik FJ, Amundsen P-A (2003b) Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. *J Fish Biol* 62: 1082–1098
- Klemetsen A, Knudsen R, Primicerio R, Amundsen PA (2006) Divergent, genetically based feeding behaviour of two sympatric Arctic charr, *Salvelinus alpinus* (L.), morphs. *Ecol Freshw Fish* 15:350–355
- Knudsen R, Klemetsen A, Staldvik F (1996) Parasites as indicators of individual feeding specialization in Arctic charr during winter in northern Norway. *J Fish Biol* 48:1256–1265
- Knudsen R, Kristoffersen R, Amundsen P-A (1997) Parasite communities in two sympatric morphs of Arctic charr, *Salvelinus alpinus* (L.), in northern Norway. *Can J Zool* 75:2003–2009
- Knudsen R, Gabler H-M, Kuris AM, Amundsen P-A (2001) Selective predation on parasitized prey—a comparison between two helminth species with different life-history strategies. *J Parasitol* 87:941–945
- Knudsen R, Klemetsen A, Amundsen P-A, Hermansen B (2006) Incipient speciation through niche expansion: an example from the Arctic charr in a subarctic lake. *Proc R Soc Lond Ser B* 273:2291–2298
- Knudsen R, Amundsen P-A, Primicerio R, Klemetsen A, Sørensen P (2007) Contrasting niche-based selection in trophic morphology of two neighbouring Arctic charr populations. *Evol Ecol Res* 9:1005–1021
- Knudsen R, Amundsen P-A, Nilsen R, Kristoffersen R, Klemetsen A (2008) Food borne parasites as indicators of trophic segregation between Arctic charr and brown trout. *Environ Biol Fish* 83:107–116
- Krebs CJ (1999) *Ecological methodology*, 2nd edn. Addison-Wesley, Reading
- Lafferty KD (1992) Foraging on prey that are modified by parasites. *Am Nat* 140:854–867
- Lafferty KD (1999) The evolution of trophic transmission. *Parasitol Today* 15:111–115
- Langeland A, Abeelund JH, Jonsson B, Jonsson N (1991) Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *J Anim Ecol* 60:895–912
- MacNeil C, Dick JTA, Elwood R (1999) The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biol Rev* 74:375–395
- Mazur MM, Beauchamp DA (2003) A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environ Biol Fish* 67: 397–405
- Nilsson N-A (1967) Interactive segregation between fish species. In: Gerking SD (ed) *The biological basis of freshwater fish production*. Blackwell, Oxford, pp 295–313
- Parker HH, Johnson L (1991) Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L.), in 4 unexploited lakes in the Canadian high Arctic. *J Fish Biol* 38:123–147

- Persson L, Amundsen P-A, De Roos AM, Klemetsen A, Knudsen R, Primicerio R (2007) Culling prey promotes predator recovery—alternative states in a whole-lake experiment. *Science* 316:1743–1746
- Rader RB, Belish T, Young MK, Rothlisberger J (2007) The scotopic visual sensitivity of four species of trout: a comparative study. *West North Am Nat* 67:524–537
- Richter H, Luckstadt C, Focken U, Becker K (2004) Some mathematical considerations in estimating daily ration in fish using food consumption models. *Ecol Model* 171:381–393
- Sæther B-S, Johnsen HK, Jobling M (1996) Seasonal changes in food consumption and growth of Arctic charr exposed to either simulated natural or a 12:12 LD photoperiod at constant water temperature. *J Fish Biol* 48:1113–1122
- Svenning M-A, Klemetsen A, Olsen T (2007) Habitat and food choice of Arctic charr in Linnévatn on Spitsbergen, Svalbard: the first year-round investigation in high Arctic lake. *Ecol Freshw Fish* 16:70–77
- Tsin AT, Beatty DD (1997) Visual pigment changes in rainbow trout in response to temperature. *Science* 195:1358–1359
- Turesson H, Brönmark C (2007) Predator-prey encounter rates in freshwater piscivores: effects of prey density and water transparency. *Oecologia* 153:281–290
- Westgaard JI, Klemetsen A, Knudsen R (2004) Genetic differences between two sympatric morphs of Arctic charr confirmed by microsatellite DNA. *J Fish Biol* 65:1185–1191