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Abstract – Fry of the Arctic charr, *Salvelinus alpinus*, were experimentally stocked into a small fish-free lake to test the hypothesis that the size-dependent habitat shift from the epibenthic to the pelagic habitat is genetically determined. The charr originated from a nearby lake inhabiting predatory brown trout *Salmo trutta*. The cohort of stocked charr was investigated for three years. The Arctic charr started to exploit the pelagic habitat in their first summer at a size of 7–9 cm in contrast to about 15 cm in the donor lake. In the next two summers, the pelagic fraction of the cohort increased. The main fraction lived in epibenthic areas, utilizing the same prey as pelagic charr. Water temperature moderated the habitat use of juveniles such that they avoided warm (>16°C) waters and resided in cool, deep areas. The result was consistent with the hypothesis of a trade-off between feeding benefit and the predation risk producing spatial segregation of Arctic charr and demonstrated that the fish can facultatively respond to predation risk and adjust the size at which they migrate to the pelagic zone to feed on zooplankton.

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Key words: Arctic charr; habitat; genetics

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

By necessity, fish live highly flexible lives. Diets, habitat use and growth rates often change dramatically with ontogeny and may also vary between environments. Differences in diet may be due to size-specific foraging tactics and prey abundance (Werner & Hall 1976; Werner et al. 1983; Holbrook & Schmitt 1988) and can have significant consequences for species interactions (Werner & Gilliam 1984). Recent work has shown that ontogenetic changes in diet or habitat also may be mediated by predation risk (Mittelbach & Chesson 1987; He & Kitchell 1990).

In experimental studies, fish have been shown to respond to predators by moving to protective habitats (Cerri & Fraser 1983; Werner et al. 1983), reducing foraging distances (Dill & Fraser 1984) and limiting feeding time and intake (Milinski & Heller 1978). Laboratory experiments have dem-

onstrated that prey fish balance foraging and risk of predation when exposed to a simulated predator (reviewed by Milinski 1993). A similar trade-off between feeding possibilities and risk of predation has been demonstrated in a field study of natural populations of Arctic charr, *Salvelinus alpinus* (L'Abée-Lund et al. 1993). They found that juvenile charr used the pelagic habitat in accordance with food availability and risk of predation. The length of the smallest charr recorded in the pelagic habitat was positively correlated with the body size of the largest predatory brown trout, *Salmo trutta*, present. However, they could not determine whether the length when this habitat shift occurred was genetically or environmentally determined. In their study of ontogenetic habitat shift in bluegill sunfish, *Lepomis macrochirus*, Werner & Hall (1988) demonstrated a complex pattern of migration mechanisms. The bluegill fry migrated to the pelagic zone to feed on zooplankton and re-

turned to littoral areas in four lakes at a length of ≈ 12.5 mm. After some years in the littoral zone they reentered the pelagic zone at a specific body length that varied among lakes. This length was positively correlated with the density of large-mouth bass, *Micropterus salmoides*, a major bluegill predator. This interlake variation was explained by a genetic component (Werner & Hall 1988).

The Arctic charr is a coldwater species commonly distributed in arctic and temperate areas with a highly variable habitat use and feeding habits (Johnson 1980). In general they exploit littoral areas and feed on littoral zoobenthos and crustacean zooplankton in allopatry, whereas they are confined to deep epibenthic and pelagic areas in sympatry with brown trout (Nilsson 1965; Langeland et al. 1991).

In this study we test the hypothesis whether the body size when juvenile Arctic charr migrate from epibenthic areas to pelagic habitat has a genetic component. If this is true, we predict that the lake specific length when becoming pelagic is maintained when the stock is transplanted into a new environment. An alternative hypothesis saying that the size of pelagic Arctic charr differ between the donor and the new environment, is based on the plasticity of Arctic charr in optimizing habitats and diet. This was tested by experimentally stocking a fish-free lake with fry of hatchery reared Arctic charr from a nearby lake. In the donor lake, charr live in sympatry with predatory brown trout and demonstrate a habitat shift from epibenthic to pelagic areas at a body size larger than 15 cm (L'Abée-Lund et al. 1993). We studied the habitat use and food of one single cohort of charr over a three-year period.

Methods

The experimental lake, Ellingtjern, is small (surface area 3 ha) and situated 453 m a.s.l. close to

Lake Songsjøen, Central Norway, where the fish populations have been well studied (Langeland et al. 1991; L'Abée-Lund et al. 1993; Langeland & L'Abée-Lund 1996). The fish species in Lake Songsjøen (Arctic charr and brown trout) are exploited only for scientific purpose (op.cit.). Ellingtjern had a small population of introduced brown trout which were eliminated using the toxin rotenone in the spring of 1992. This was to ensure that the lake was complete free of predators before the stocking of charr fry. Survival tests with young charr in small cages during summer of 1992 showed that the fish died after few days. Very low density of zooplankton in 1992, only a few rotifers and cyclopid copepodids were recorded, also indicated the toxicity of the lake water. In 1993, the common cladocerans reappeared, however, the density was very low and less than 20 mg dry weight/m². The stocking of charr was therefore postponed to the spring of 1994. Apart from the lack of fish, the aquatic ecosystem had fully recovered by spring 1994 when our experiment started. This was indicated by the recovery of zooplankton and high survival of charr fry after stocking in 1994.

Lake Ellingtjern is 15 m deep, oligotrophic and with a total phosphorous content of 5 µg per liter. It is strongly influenced by humic substances in the watershed resulting in a brown color of 40 mg Pt/L and water transparency of 3.0–3.5 m (Secchi depth). Commercial fertilizers were added to the lake in 1993 and the year of stocking (1994) to increase and recover the zooplankton. As a result the phosphorous content increased four fold in the epilimnion and doubled in the hypolimnion. The increase in phytoplankton biomass only slightly reduced the water transparency from ca. 3.8 m to ca. 3.3 m, mainly due to a 3- to 4-fold increase in herbivorous zooplankton such as *Holopedium gibberum*.

Table 1. Total catch of Arctic charr in benthic and pelagic gill nets, temperature (°C) at 1 m depth, bar mesh size of gill nets used and number of stomach samples analyzed in Lake Ellingtjern in 1994, 1995 and 1996 and Lake Songsjøen in 1985–1994. In Songsjøen the six mesh sizes were used in both periods in each year. In Ellingtjern the increase in mesh sizes corresponded to the increase in length of the stocked fish.

Period	Habitat		Temperature	Mesh size	Stomachs number
	Benthic	Pelagic			
Ellingtjern					
1994 28 July	53	4	19.7	6, 8, 10 mm	20
8 Sept.	190	12	11.2	6, 8, 10 mm	24
1995 13 July	666	279	16.0	8, 10, 12.5 mm	49
31 Aug.	208	64	9.7	10, 12.5, 16 mm	67
1996 19 July	203	72	11.0	12.5, 16, 19.5 mm	44
6 Sept.	146	72	12.3	12.5, 16, 19.5 mm	52
Songsjøen					
1985–1994 July	704	329		12.5, 16, 19.5,	
Sept.	238	159		24, 29, 35 mm	

In the autumn of 1993, eggs of Arctic charr from the nearby Lake Songsjøen were fertilized by hand and incubated in a nearby conventional hatchery. The alevins were fed artificial food until stocking on June 7 1994, when a total of 3500 fry (mean length 6.0 cm, SE=0.45 cm) were released.

Sampling was performed in six periods during 1994–1996 using gill nets of bar mesh sizes 6–19.5 mm (Table 1). The mesh size was increased according to increased body size as growth proceeded. The pelagic nets were set over the deepest area of the lake from the surface down to 6 m depth for one night each sampling period. The benthic nets were set perpendicular to the shore at two deep (1–10 m deep) and one shallow (<1.5 m) station. Nets were set at 1600–1800 hours and emptied the next day at 0900–1200 hours. Three pelagic gill nets (each 25 m×6 m, total net area 450 m²) were used in all sampling periods. Six benthic gill nets (each 25 m×1.5 m, total net area 225 m²) were used in the three first sampling periods and three gill nets (total net area 112.5 m²) in the last three samplings. In Lake Songsjøen, similar benthic and pelagic gill nets of bar mesh sizes 12.5–35 mm were used in the years 1985–94 (Langeland & L'Abée-Lund 1996). This study demonstrated small interyear variation in habitat use, and thus the lack of temporal pseudoreplicates in our experimental lake are supposed not to be a problem. The catches of Arctic charr in gill nets with mesh sizes 12.5–19.5 mm in Lake Songsjøen were selected for comparison of the size distributions of fish between the two lakes in the pelagic zones.

In total, 1969 charr (58%) were recaptured in Lake Ellingtjern. The position in the gill nets and depth of capture was recorded for each fish, as was total fish length (to 0.1 cm) and weight. In each period of netting a subsample of recaptured charr was taken for stomach analysis (Table 1). As all charr in the experimental lake originated from one cohort, otoliths for age determination were not sampled. Stomach contents were identified to species level in the case of zooplankton and littoral crustaceans, while other food items were classified as chironomids, snails, aquatic insect larvae, adult terrestrial insects, coleoptera and unidentified items.

Two replicate samples of zooplankton was taken each period using a plankton net (mesh size 95 µm, net diameter 30 cm) from 10 m depth to surface in the years 1992–1996.

Water temperature were recorded at surface and down to 10 m with one meter interval in the evening. In July 1996 temperature was measured down to 2 m depth.

All statistical tests were performed with the SPSS/PC computer package (Norusis 1986). Dif-

ferences in mean size were tested by analysis of variance (ANOVA).

Results

Spatial distribution

The stocked charr demonstrated a change in habitat use throughout the study. About one month after release most (53 out of 57) recaptured charr were caught in epibenthic areas, close to the bottom in the lower 10 cm of the gill nets. One month thereafter, the charr were more evenly distributed in the bottom nets, indicating increased activity and a change from a cryptic behaviour close to the bottom. Moreover, the charr exhibited an increased tendency to use the pelagic habitat through the study in terms of both number caught and in their spatial location (Fig. 1).

The use of epibenthic areas in summer was similar in 1994 and 1995; fish were chiefly using depths between 4 and 10 m (Fig. 1). Maximum densities were registered at 6–8 m, i.e., 2.5 times the Secchi depth. In July 1996, however, juvenile charr used the shallow littoral area (<1.5 m) as well as deeper areas. This was in contrast to July 1994 and 1995 when only a few charr were caught in the shallow littoral waters (<1.5 m).

The charr exhibited a similar use of pelagic habitat in 1995 and 1996, irrespective of the period of the year and water temperature (Fig. 1). Only a few charr were caught in the pelagic zone in 1994.

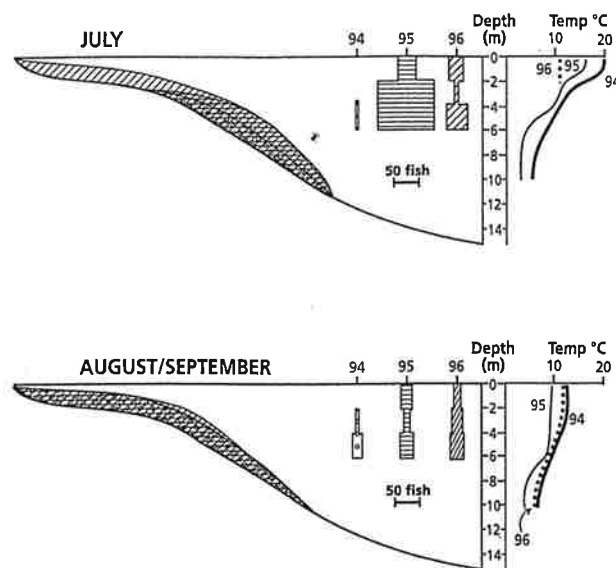


Fig. 1. Pattern of spatial distribution of Arctic charr in benthic and pelagic habitats and temperature (°C) in Lake Ellingtjern during the period 1994–1996. The left hand-side is a profile indicating spatial locations of fish caught in benthic nets, while centre shows depth from surface of fish caught in pelagic nets. Total catches are given in Table 1.

The temperature stratification in July was similar in 1994 and 1995, whereas 1996 was considerably (ca. 5–8°C) cooler (Fig. 1). There were only small differences in water temperatures between years in August/September with maximum temperatures of 11–12°C.

Fish length and food

The charr more than doubled their length during the study (Fig. 2). Up until July 1995, charr recaptured in epibenthic areas had a tendency to be larger than their pelagic conspecifics, but after this date pelagic charr were significantly (ANOVA; $P < 0.001$) larger than epibenthic individuals. The small difference in length between habitats in July 1995 was statistically significant due to large sample sizes, and were probably of little ecological importance. The charr started exploiting the pelagic areas soon after release, and the smallest charr recaptured by pelagic nets was 6.2 cm in length. The length distribution of charr recaptured in pelagic waters (mean = 12.5 cm, S.D. = 2.0 cm, all years 1994–1996) was significantly (ANOVA; $P < 0.001$) skewed to the left compared to the donor strain in Lake Songsjøen (mean = 20.0 cm, S.D. = 2.4 cm, 1985–1994). Fig. 3 shows the size distribution of charr caught on the same mesh sizes (12.5–19.5 mm) in both lakes in the pelagic zones. In Lake

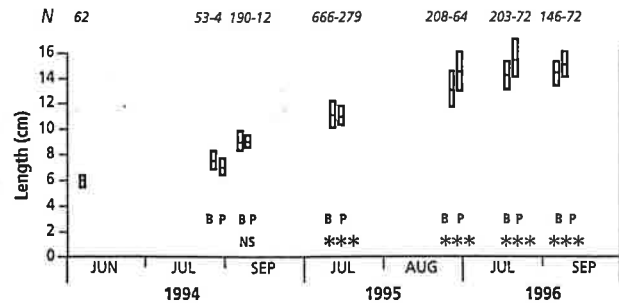


Fig. 2. Length (cm) of Arctic charr stocked in Lake Ellingtjern in June 1994 and during the investigation period 1994–1996 caught in benthic (B) and pelagic (P) habitats. Fish length in June 1994 is fry size at stocking. Data are plotted as means ± SD. N = number of observations. Asterisks indicate significant differences (ANOVA) between habitats, NS = not significant.

Songsjøen the smallest charr caught in the pelagic habitat was 10.8 cm. The dominating size classes of pelagic charr caught by identical mesh sizes in the lakes Ellingtjern and Songsjøen were 11–12 cm and 19–21 cm, respectively (Fig. 3). Comparison of charr size in July showed that growth of 2+ fish was similar in both lakes; 14.5 cm and 14.4 cm in Ellingtjern and Songsjøen, respectively. The dominating age classes of pelagic charr in Songsjøen were 3 to 6 years. Thus the pelagic charr caught in Ellingtjern was both smaller (11–12 cm) and

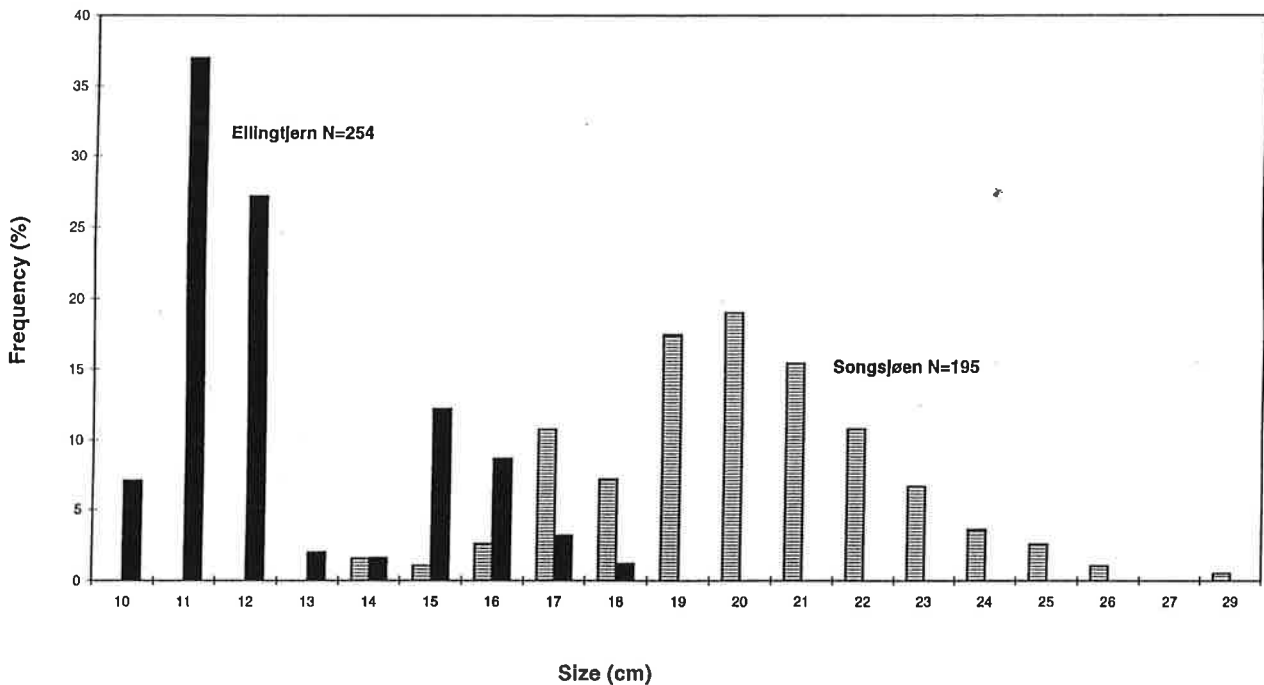
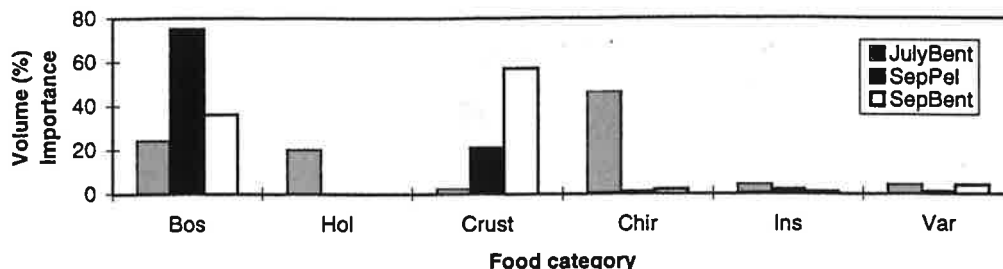
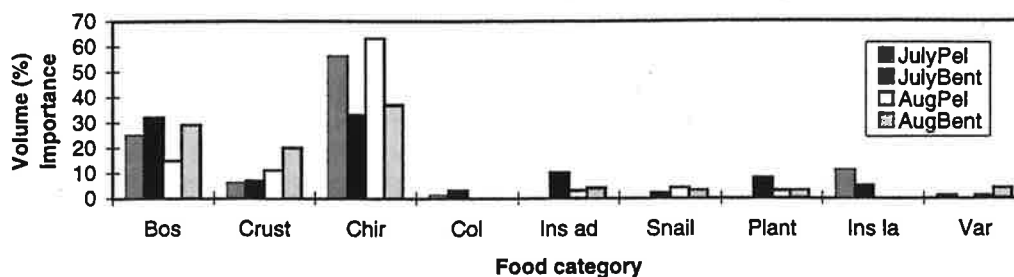


Fig. 3. Size (cm) distribution (%) of Arctic charr caught in pelagic areas with gill nets of bar mesh size 12.5–19.5 mm in July and September 1994–1996 in Lake Ellingtjern (without brown trout) and July–September 1985–1994 in the donor Lake Songsjøen with piscivorous brown trout.

1994 (0+)



1995 (1+)



1996 (2+)

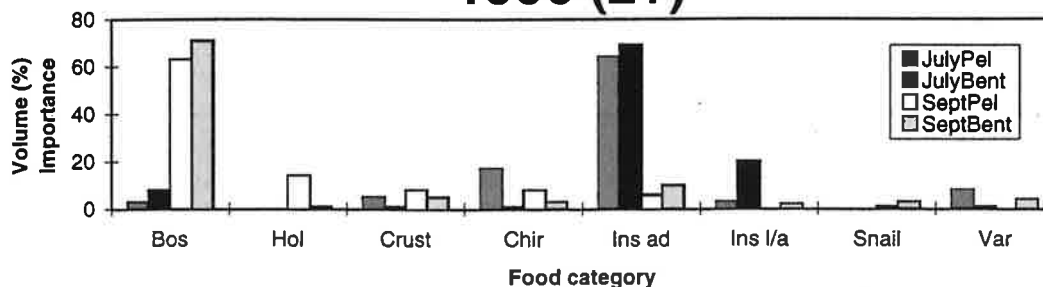


Fig. 4. Food of one cohort of Arctic charr in Lake Ellingtjern caught in benthic and pelagic habitats in July-September 1994-1996. Bos=*Bosmina longispina*, Hol=*Holopedium gibberum*, Crust=littoral crustacean, Chir=Chironomidae larvae and pupae, Ins ad=adult insects caught on surface, Ins la=water living insect larvae, Var=various. Pel=pelagic gillnet, Bent=benthic gillnet.

younger (1+) compared to Songsjøen (19-21 cm, 3-6 years).

The fertilization of the lake in 1994 increased the zooplankton biomass (360 mg dry weight/m²) three-to-four-fold compared to the following years mainly due to high densities of *Holopedium gibberum*. In the pre-stocking years, 1992-1993, the zooplankton density was very low, due to the poisoning in 1992 which killed most of the crustacean. *Bosmina longispina* was the overall dominating zooplankton in 1995 and 1996 (total zooplankton biomass about 100 mg dry weight/m²), and only single individuals of a few other zooplankton species were recorded during the investigation. The

zooplankton results indicate that the benefit of feeding in pelagic waters was low in all years. The zooplankton biomass in Lake Songsjøen (ca 100 mg dry weight/m² in 1985-89) was similar to that of Lake Ellingtjern in 1995 and 1996.

There were small differences in food intake among charr caught in the epibenthic and pelagic zones (Fig. 4). The food choice of charr in both zones consisted of up to eight different food items. *B. longispina*, chironomids, adult insects and *Eurycerus lamellatus* were important prey items in most years, although their relative ranking changed among years, but not among habitats. In general, the size of the food items increased with

increasing fish length, although *B. longispina* maintained its importance as a food item independent of fish size. The dominating zooplankton species in 1994, *H. gibberum*, was of low importance as food (Fig. 4).

Discussion

These results show clearly that juvenile Arctic charr demonstrate plasticity in the length at which they migrate into pelagic waters. This shift from epibenthic to pelagic areas mostly occurred at a small size of 10 cm during their second summer of life in Lake Ellingtjern, although a few charr were recaptured in the pelagic waters in their first summer at a length of about 6 cm. This was at a significantly smaller size than their conspecifics in the donor lake, Songsjøen. The main difference in the two lakes is that the donor lake contains brown trout in addition to Arctic charr. Brown trout are in general an important predator on small Arctic charr (L'Abée-Lund et al. 1992). If juvenile charr entered the pelagic zone in Lake Songsjøen at a small size and were eaten by brown trout, this could affect the probability of catching small charr relative to the larger individuals. However, only eight brown trout (0.5 %) out of a total catch of 1725 trout had Arctic charr in their stomachs (L'Abée-Lund et al. 1992). In other respects the lakes are comparable – water transparency is almost identical (ca. 3–4 m), the biomass of pelagic cladocera was low (ca. 100 mg dry weight /m²), the dominating species and most important prey for charr is *Bosmina longispina* in both lakes (Langeland & L'Abée-Lund 1996; this study).

The minimum size at which charr exhibit ontogenetic habitat shift during their first and second summer of life was about 8 cm in Lake Ellingtjern, which is the preferred prey size of brown trout of 25–35 cm in length (L'Abée-Lund et al. 1992). This length interval of the predator is common in Lake Songsjøen (Langeland & L'Abée-Lund 1996). In contrast, charr attain pelagic behavior by about 15 cm and 2–3 years old in Lake Songsjøen (L'Abée-Lund et al. 1993). Thus, our results demonstrate that there is no genetic threshold determining when the juvenile Arctic charr attain pelagic behavior. If the ontogenetic habitat shift from epibenthic to pelagic habitat was genetically determined, we should have found similar length when juvenile Arctic charr became pelagic in our fishless experimental lake and in the donor lake that contained a piscivorous fish species. The length distributions were, however, significantly different – and skewed to the left in the fish-free lake. We consider our results consistent with the hypothesis of a trade off between food demand and

presence of predators in spatial distribution of juvenile Arctic charr (L'Abée-Lund et al. 1993), and that Arctic charr demonstrate an opportunistic habitat or resource use. The predator-dependent size at habitat shift in Arctic charr fits the model presented by Werner & Gilliam (1984) and Werner (1986). A decreased risk of predation in the pelagic habitat should result in a decreased size at the habitat shift. Werner & Hall (1988) demonstrated that the length of bluegill sunfish at the time of habitat shift between littoral and pelagic habitat was directly correlated with the density of the major predator of the bluegill in the lakes studied.

The biomass of cladocera in the pelagic habitat was low in our lake but almost identical to the donor lake. Compared with the habitat use of Arctic charr in several other lakes investigated (Langeland et al. 1991), we consider the foraging benefit in the pelagic zone to be less than in littoral areas. Despite this, a considerable number of the stocked charr were recaptured at a small size in the pelagic habitat. The density (as CPUE) of Arctic charr, was 10–20 times higher in epibenthic zone and 10 times higher in pelagic zone in Lake Ellingtjern than in Lake Songsjøen. This may indicate a strong intra-cohort competition for food in Lake Ellingtjern. Moreover, this may have affected the habitat shift in Lake Ellingtjern. However, if the fish density was important in regulating the fraction being pelagic, we would have expected a higher fraction of pelagic charr in Lake Ellingtjern compared to Lake Songsjøen than recorded. Thus, we consider the fish density being of minor importance affecting the ontogenetic habitat shift in Arctic charr. The cessation in growth in 1996 occurred simultaneously with sexual maturation of males and indicate that food availability in all habitats was too low to maintain both growth and production of gonads. The low growth rate and small size attained after three years is a typical result of food limitation when compared to the growth potential of Arctic charr (Vøllestad & L'Abée-Lund 1994; Ugedal et al. 1994).

Our study revealed the effect of water temperature in structuring the habitat use of juvenile Arctic charr. The Arctic charr avoided shallow littoral waters in July when the water temperature was about 16–20°C. The habitat use in July 1994 and 1995 (warm) and 1996 (cool) demonstrate the temperature effect. Thus, all other factors being unchanged, the juvenile Arctic charr avoided warm waters in both epibenthic and pelagic areas. One reason for this may be that the optimum temperature range for growth of Arctic charr is 11–14°C (Jobling 1983; Jensen 1985).

How do fish evaluate the risk of predation in the pelagic zone? We can think of two explanations –

vision and chemical cues. Chemosensory mechanisms are important for many salmonids during their migratory periods. Under laboratory conditions chemical cues have also been demonstrated to be important in kinship recognition (reviewed by Brown & Brown 1996). Thus, it is reasonable to believe that prey species are able to detect the presence of a predator by olfaction. Laboratory experiments with pike, *Esox lucius*, and minnow, *Phoxinus phoxinus*, showed that minnow alter their behaviour being less likely to take risks in the presence of pike-odours in the water (Magurran 1990). However, this mechanism can not explain the significant, linear relationship between size of the smallest pelagic prey fishes and the size of the largest predators recorded among lakes (L'Abée-Lund et al. 1993). Thus, an additional sensory cue must take part in the evaluation of the predation risk in juvenile Arctic charr. This could be vision as charr are known to feed successfully under poor light conditions (Ali & Wagner 1980), and thus be able to detect a predator over distances under poor light conditions.

To conclude, our experimental study demonstrates that the size when Arctic charr attain a pelagic behavior is under environmental control and not direct under genetical control. Moreover, water temperature has a strong effect on habitat use in juvenile Arctic charr restricting the use of warm (>16°C) waters.

Resumen

1. Para determinar si el cambio en el uso de hábitat dependiente del tamaño desde zonas epibénticas a pelágicas está determinado genéticamente, realizamos un experimento consistente en introducir juveniles de *Salvelinus alpinus* en un pequeño lago libre de peces, donde fueron investigados durante tres años consecutivos. Los juveniles procedieron de un lago cercano habitado por *Salmo trutta*.
2. Los juveniles de *S. alpinus* comenzaron a explotar la zona pelágica durante el primer verano de vida, cuando tenían unos 7–9 cm de longitud, mientras que en el lago original, lo hacen a los 15 cm. Durante los dos veranos siguientes, la fracción pelágica de la cohorte aumentó aunque la mayor parte de la población utilizó la zona epibéntica predando sobre las mismas presas que los individuos pelágicos. La temperatura del agua también influyó en el uso del hábitat de los juveniles, de manera que éstos evitan las aguas de temperaturas >16°C, seleccionando zonas más profundas y frías.
3. Nuestros resultados son consistentes con la hipótesis relativa a un trade-off entre beneficio alimenticio y riesgo de predación, que tiene como resultado una segregación de la especie. Además, los peces pueden responder de forma facultativa al riesgo de predación, ajustando el tamaño al cual migran hacia la zona pelágica para alimentarse de zooplankton.

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