

Diurnal and seasonal resource partitioning in young brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*) and Alpine bullhead (*Cottus poecilopus*) in a subalpine lake in southeastern Norway

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Diurnal habitat and food segregation in young Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and Alpine bullhead (*Cottus poecilopus*) were studied in Atnsjø, a lake in southeastern Norway. The mean lengths \pm SD of the three species were 118 ± 20 mm ($n = 872$), 112 ± 14 mm ($n = 109$), and 66 ± 8 mm ($n = 70$), respectively. Epibenthic gillnet catches of all three species were much higher at night (21.00–05.00 GMT) than during the day (09.00–17.00 GMT). In general, there was segregation by depth zone between these three species, which were caught at night at mean depths of 17.3 ± 6.2 m, 7.9 ± 3.3 m, 13.6 ± 5.0 m, respectively. During the hours of darkness in spring and late summer, Alpine bullhead were more likely to be associated with the bottom than Arctic charr and brown trout. Arctic charr fed almost exclusively on zooplankton, while brown trout and Alpine bullhead fed largely on insect larvae and *Eurycercus lamellatus*. Although selective differences are partly responsible for resource partitioning between the two salmonid species and Alpine bullhead, interactive segregation may also occur.

Introduction

Resource use has a major influence on population and community interactions, on the dynamics of resource availability and on the fate of resources in ecosystems (Ross 1986). In fish communities with common demand for space and food, resources may be partitioned (Gerking 1994). Different species of fish partition their resources mainly along three axes; habitat, food and time (Ross 1986). Habitat segregation

and utilisation of different food items may be explained by exploitative and interference competition and selective differences (Nilsson 1967, Krohne 1998). In fish, the more important line of evidence for interspecific competition derives from patterns of resource use and partitioning by sympatric species (Wootton 1990).

Competition is most obvious among related species, while species of different families may coexist with minimal competition (Connell 1980). Salmonids and freshwater sculpins

Cottus spp. are taxonomically distinct and morphologically dissimilar species that often coexist in cool and well-oxygenated streams and lakes of the temperate subpolar northern hemisphere (Kottelat and Freyhof 2007). In Nordic lakes, the dominant species among these two taxonomically groups are brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*) and Alpine bullhead (*Cottus poecilopus*) (Rask *et al.* 2000).

It has been found that smaller brown trout commonly prefer shallow benthic habitats with a stony bottom that provides shelter (Nilsson 1963, Thorpe 1974, Svärdsön 1976, Savino and Stein 1982, Ehlinger 1990, Hegge *et al.* 1993). Lake-living sculpins also seem to prefer bottom areas with a stony substrate (Northon 1991). This is also the case in running water, as has been shown for Alpine bullhead in both field and experimental studies (Hesthagen and Heggenes 2003, Hesthagen *et al.* 2004).

Brown trout and Arctic charr exhibit major differences in behaviour, choice of prey type and rate of feeding. Brown trout is more aggressive, forming territories and dominance hierarchies, whereas Arctic charr is prone to shoal and are less likely to be involved in inter- and intraspecific aggressive interactions (Jansen *et al.* 2002). In sympatry, brown trout displace Arctic charr of similar size from more rewarding areas in shallow waters in the littoral zone to deeper waters during summer (Hegge *et al.* 1989, Langeland *et al.* 1991, Jansen *et al.* 2002). However, habitat segregation seems to be suspended between late autumn and spring, due to selective differences such as foraging on different food items and optimal growth temperatures (Langeland *et al.* 1991). Brown trout feed mainly on benthic prey and surface insects, as opposed to different zooplankton species for Arctic charr (Svärdsön 1976, Hegge *et al.* 1989, Dervo *et al.* 1991, Langeland *et al.* 1991, Saksgård and Hesthagen 2004). Although both species are visual feeders (cf. Henderson and Northcote 1985), Arctic charr are more capable than brown trout of foraging at low light intensities (Janssen 1980).

Less is known about sculpins and their interactions with salmonids in lakes. However, they seem to need certain amount of light for optimum foraging, as has been found for juvenile Bear Lake sculpin (*Cottus extensus*) (Never-

man and Wurtsbaugh 1992). This may indicate a preference for relatively shallow waters, e.g. similar to that of brown trout. However, evidence for competition between sculpins and salmonids is still weak (Holmen *et al.* 2003), and both experimental and field studies in running waters indicate that Alpine bullhead are potential habitat competitors of young brown trout (Olsen and Vøllestad, Hesthagen and Heggenes 2003, Holmen *et al.* 2003, Hesthagen *et al.* 2004).

In this study, we assessed diurnal and seasonal resource utilisation in Alpine bullhead in comparison with young brown trout and Arctic charr in a subalpine Norwegian lake. Our principal objective was to investigate possible interspecies competition for space and food between these two salmonid species and Alpine bullhead.

Studies on the resource utilisation of the two salmonid species in the lake were carried out also previously, but involved mainly larger and older specimens (Hegge *et al.* 1989, Dervo *et al.* 1991, Saksgård and Hesthagen 2004).

Study area

The study was carried out in Atnsjø (61°51'N, 10°13'E), which is a lake located in the unregulated Atna catchment in southeastern Norway (Fig. 1). Atnsjø is a slightly acid and oligotrophic subalpine lake (Blakar *et al.* 1997) that covers an area of 5.0 km² and is relatively deep, with mean and maximum depths of 35 and 80 m, respectively (Hegge *et al.* 1989). The lake lies 701 m above sea level, and is generally ice-free from late May until mid-November. The surface water temperature usually range between 10–13 °C in July and August, with the thermocline at a depth of 10–15 m (Hesthagen *et al.* 2004, Halvorsen and Papinska 2004). During the study period in 1995, the temperature in August ranged between 9.5 and 12.0 °C at depths of 1–35 m, as opposed to 4.0–7.0 °C in June and September (Table 1). In 1995, the water level was unusually high in spring due to a combination of intense snow-melt and heavy rain (Tvede 2004). Such a high flood is expected to occur at intervals of between 100–200 years (Erichsen 1995). The flood resulted in highly turbid water, with a Secchi depth of only 3.5 m, as compared

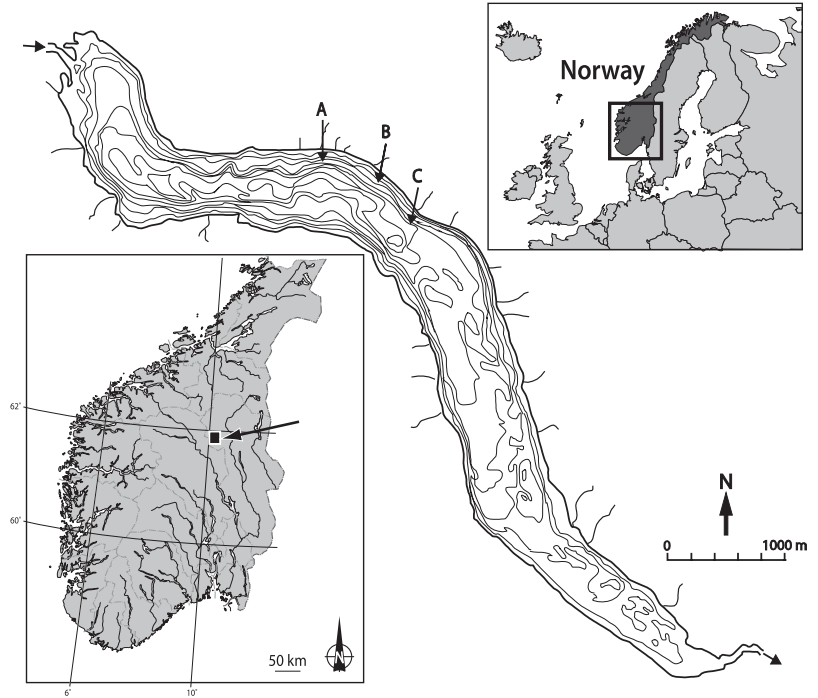


Fig. 1. Location of Atnsjø, outline of the lake with 10-m depth contours and positions of the three sampling stations for gill-nets: A, B and C.

with 6.0–9.5 m in subsequent months. The littoral zone of Atnsjø is steep, with depths of 4–5, 10–11 and 17–25 m at about 5, 10 and 15 m from the shoreline, respectively. Arctic charr, brown trout and Alpine bullhead are regarded as being native species to Atnsjø (Hesthagen and Sandlund 2004). The lake also contains a very sparse population of European minnows (*Phoxinus phoxinus*) that was introduced in the early 1960s.

Methods

Fish were sampled with benthic (25 m long × 1.5 m deep) and floating gillnets (25 m long × 3.0 m deep) of 8.0, 10.0 and 12.5 mm (knot to knot) mesh during four periods throughout the ice-free season in 1995: 14–19 June (spring), 7–11 August (late summer), 28–30 September (autumn) and 6–8 November (late autumn). The nets were set on a 200 m stretch in the north-eastern part of the lake (Fig. 1). The substrate was assessed by a diver and three stations were chosen on the basis of similarity in substrate and depth gradient; A, B and C. The substrate was divided into three categories: (i) a stony zone with stones of 30–80 cm in diameter at depths of

0 to 5 m, (ii) a vegetation zone of *Isoetes* spp. at about 4–5 to 9–12 m, and (iii) bottom covered with mud in deeper areas.

Three benthic gillnets with mesh sizes of 12.5, 10.0 and 8.0 mm were laid perpendicular to the shoreline in a continuous chain at stations A, B and C, respectively, i.e. each chain having a total length of 75 m. These three chains covered depths of 0–21, 0–28 and 0–41 m, respectively. Hence, only gillnets of 8.0 mm in mesh size were laid deeper than 28 m. The abundance of Alpine bullhead may be underrepresented in the gillnet catches as their morphology, with a large flattened head, results in lower catchability than

Table 1. Water temperature (°C) at different depths in Atnsjø in 1995.

Depth (m)	June	Aug.	Sep.	Nov.
1	7.0	12.0	6.0	2.5
3	7.0	12.0	6.0	2.5
5	6.5	11.1	6.0	2.5
9	6.0	10.5	6.0	2.5
15	5.5	10.2	6.0	2.5
20	5.0	10.0	6.0	2.5
25	5.0	10.0	6.0	2.5
35	4.0	9.5	6.0	2.5

salmonids. The three floating nets had the same mesh sizes as the benthic nets, and they were placed at depths of 0–3 m.

Both types of gillnets were laid at 8-hour intervals during the day (09:00–17:00 GMT) and at night (21:00–05:00 GMT). The capture site of each individual fish in the benthic nets was used to determine the distribution by depth zone (to the nearest metre) and vertical position in terms of distance from the bottom. We obtained total length (mm), weight (g), otoliths and stomach content of each fish. The catch per unit effort (CPUE) is presented as the number of fish caught per 100 m² gillnet area for 8 h fishing at different depths with 5-m intervals. Otoliths from all three fish species were later analysed for age. The stomach content was later identified in the laboratory, and all prey items were counted and the body length and width of intact individuals were measured under a stereomicroscope. Stomach contents were assessed as dry weight, using regression equations between body length/width and weight (Breistein and Nøst 1997). The diet is presented as percentage weight ($W_{\%}$) of each food category. Schoener's index (1968) was used to calculate diet overlap between different fish species.

Results

Fish length and age

No significant differences between the mean body lengths of any of the species were found during the study period with regard to season or intervals during the day, with mean values \pm SD for brown trout, Arctic charr and Alpine bullhead of 112 ± 14 ($n = 109$), 118 ± 20 ($n = 872$) and 66 ± 8 mm ($n = 70$), respectively (Kruskal-Wallis test: all p 's > 0.05). The dominant age groups of brown trout and Arctic charr were 1+ and 2+, as opposed to 4+, 5+ and 6+ for Alpine bullhead.

Distribution by depth zone during the day and at night

No fish were caught in floating gillnets. In the epibenthic zone, more fish of all species were

caught at night than during the day; especially brown trout ($n = 102$ vs. 7), but also Arctic charr ($n = 632$ vs. 240) and Alpine bullhead ($n = 45$ vs. 25). Generally, a significant depth segregation was observed for all the species both during the day and at night from spring to late autumn (Fig. 2). Brown trout stayed in relatively shallow waters during both periods; i.e. at mean depths of 10.0 ± 9.1 m and 7.3 ± 1.6 m, respectively. However, this species did not exhibit any significant seasonal difference in depth distribution (Mann-Whitney U -test: $p > 0.05$). Arctic charr remained significantly deeper during the day than at night, at mean depths of 20.1 ± 6.8 m and 17.3 ± 6.2 m, respectively ($p < 0.001$). They also remained in more shallow waters in spring (15.9 ± 6.0 m) and late summer (16.5 ± 4.7 m) than in autumn (21.3 ± 6.3 m) and late autumn (18.9 ± 5.5 m). Alpine bullhead were caught at a rather wide range of depths, with mean depths of 12.2 ± 4.6 and 13.6 ± 5.0 m during the day and at night, respectively. They did not exhibit any seasonal or diurnal variation in their depth distribution ($p > 0.05$).

Vertical distribution in the water column

All three species were caught at a mean distance from the bottom of 20–57 cm during the day and 16–68 cm at night. Arctic charr remained significantly higher in the water column than Alpine bullhead during the day in June (Mann-Whitney U -test: $p < 0.01$), and brown trout higher than Arctic charr in August ($p < 0.001$). Brown trout kept higher off the bottom than Alpine bullhead at night in both June ($p < 0.05$) and August ($p < 0.01$), while Arctic charr were higher than Alpine bullhead in August ($p < 0.05$). Brown trout did not exhibit any significant seasonal variation in vertical distribution ($p > 0.05$), although they tended to stay closer to the bottom in spring (33 ± 32 cm) than in late autumn (68 ± 51 cm). Arctic charr did not exhibit any seasonal variation in vertical distribution either at night or day ($p > 0.05$). However, in June, they were caught significantly closer to the bottom at night than during the day, 30 ± 27 cm vs. 40 ± 25 cm ($p < 0.05$), while the opposite was the case in August, with 38 ± 31 cm vs. 22 ± 13 cm ($p < 0.05$). Alpine

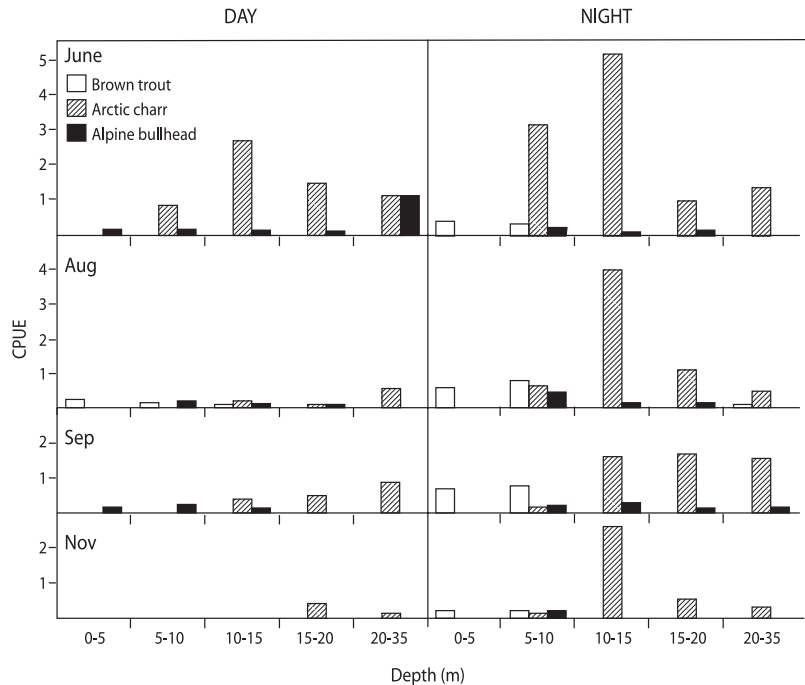


Fig. 2. Catches per unit of effort (CPUE) in numbers (CPUE = catch per 100 m² gillnet area and 8 h fishing) of Arctic charr, brown trout and Alpine bullhead in different depths zones in the epibenthic habitat of Atnsjø during day and night in June, August, September and November 1995.

bullhead stayed closest to the bottom at night in spring and late summer, but no significant diurnal or seasonal differences were found ($p > 0.05$). There was no significant relationship between body length and vertical distribution for either species studied (Kruskal-Wallis test: $p > 0.05$).

Diet and diet overlap

From spring to fall, Arctic charr fed almost exclusively on *Bosmina longispina*, which made up between 83_{w%} and 90_{w%} of their diet, while *Daphnia longispina* was their second most important food item (Fig. 3). In November, however, Arctic charr preyed most heavily on *D. longispina* (65_{w%}) and *Eurycercus lamellatus* (22_{w%}). They also ate the same food items both during the day and at night, except that *D. longispina* was only consumed during the day in September and *E. lamellatus* during the day in November. For brown trout the dominant food items during the hours of darkness were Trichoptera larvae in June (96_{w%}), surface insects (40_{w%}) and Trichoptera (25_{w%}) in August, and *E. lamellatus* and Trichoptera larvae in September (70_{w%} vs. 47_{w%}) and November (30_{w%} vs.

42_{w%}). In brown trout caught during the day in August, surface insects dominated the diet. In Alpine bullhead, chironomid larvae made up the main daytime diet (65_{w%}) and Trichoptera larvae (84_{w%}) were consumed at night in June. In August, *E. lamellatus* was their principal diet during the day (71_{w%}) and *B. longispina* at night (83_{w%}), as opposed to *E. lamellatus* both during the day (95_{w%}) and at night in September (75_{w%}). Trichoptera larvae were the only nighttime food item in November. In this period, no Alpine bullhead were caught during the day.

In general, small overlaps in diet between the three species were found, as expressed by Schoener's index. Exceptions were found for brown trout and Alpine bullhead at night in June (86%) and September (91%) (Table 2). Arctic charr and brown trout had small diet overlap, except during the day in August (55%), when both species preyed heavily on *D. longispina*.

Discussion

Young brown trout and Arctic charr in Atnsjø exhibited significant habitat segregation from spring to late autumn, being caught at night at

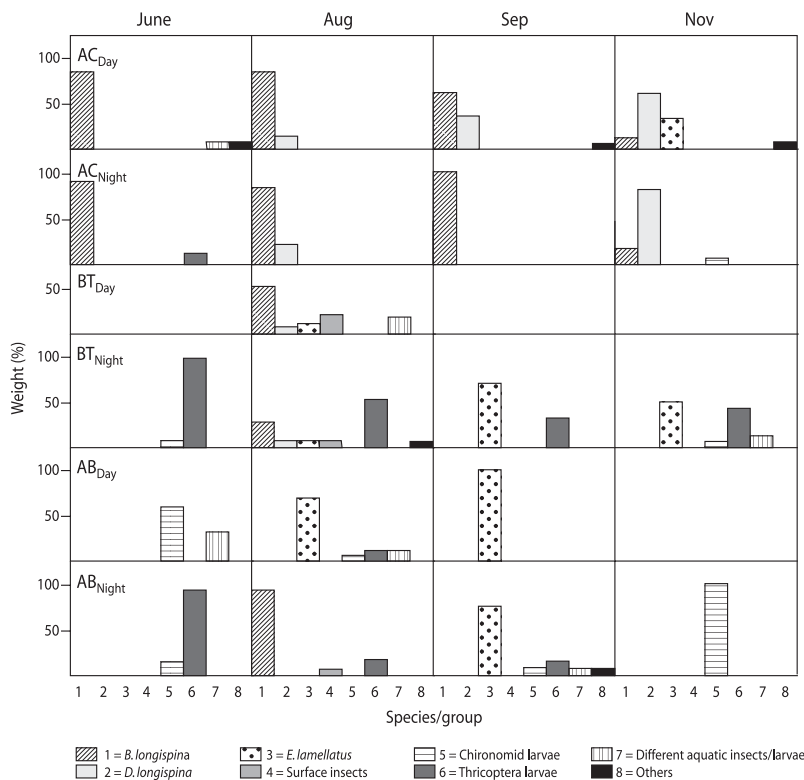


Fig. 3. Major food items (dry weight, W%) of Arctic charr (AC), brown trout (BT) and Alpine bullhead (AB) caught in the epibenthic habitat of Atnsjø at day and night in June, August, September and November 1995.

mean depths of about 8 and 17 m, respectively. Arctic charr fed mainly on various zooplankton species such as *B. longispina* and *D. longispina*, while brown trout preyed heavily on aquatic insects, surface insects and *E. lamellatus*. Brown trout caught during the day in August had also largely consumed *B. longispina* probably due to a peak in the abundance of this species (Halvorsen and Papinska 2004). Zooplankton has

also been shown to be an important food item for brown trout during the day elsewhere (Klemetsen 1967, Jonsson and Gravem 1985). The fact that brown trout consumed zooplankton during the day is probably because they are able to detect such small food items only at high light intensities (Schutz and Northcote 1972, Henderson and Northcote 1985). The difference in the food bases of brown trout and Arctic charr is probably related to interspecific competition, selective differences and asymmetric competition (Nilsson 1963, Langeland et al. 1991). Such differences in the use of space and food between brown trout and Arctic charr in Atnsjø have also been found among larger conspecifics in the study lake (Hegge et al. 1989, Dervo et al. 1991, Saksgård and Hesthagen 2004). As the most aggressive species, brown trout occupy the littoral zone, which is the most rewarding habitat. The littoral zone in Atnsjø has the highest density of aquatic insects (Aagaard et al. 1997). Furthermore, this zone has a stony bottom which provides shelter for smaller brown trout, enabling them to avoid or reduce aggression

Table 2. Diet overlap (%) between brown trout, Arctic charr and Alpine bullhead caught in epibenthic habitat of Atnsjø in June, August, September and November 1995, as shown by the Schoener's index.

Month	Trout versus charr		Trout versus bullhead		Charr versus bullhead	
	Day	Night	Day	Night	Day	Night
June		7	86		7	7
Aug.	55	32	19	41	0	82
Sep.		0		91	2	0
Nov.		3		3		4

and predation on the part of larger conspecifics (Savino and Stein 1982, Ehlinger 1990, Hegge *et al.* 1993).

However, there may also be some selective differences between species with respect to their use of space and food. Although Arctic charr are restricted to deeper areas, which may be less rewarding, they are capable of identifying and catching small zooplankton species at low densities and low light intensities (Nilsson and Pejler 1973, Jørgensen and Jobling 1990). The use of deeper water by young Arctic charr may also reflect an attempt to avoid predation, which is reduced in areas of low light intensity (Gliwicz 1986). It has been shown that the presence of large piscivorous fish affects the spatial distribution of young conspecifics, which move to habitats with less risk of predation (Fraser and Emmons 1984, Harvey 1991). Langeland *et al.* (1991) found a complete breakdown in habitat use and diet segregation in the autumn among larger brown trout and Arctic charr in several sympatric populations. This was not observed among smaller individuals of these two species in Atnsjø from spring to late fall.

Arctic charr were caught in shallower waters in spring than in autumn. This may be related to poorer water transparency in the spring in 1995 as a result of high inflow, which reduced the Secchi depth to only 3.5 m. Visual isolation reduces contact between young salmonids, as has been shown in Atlantic salmon (*Salmo salar*) and brown trout (cf. Kalleberg 1958). Much higher catches of Arctic charr during the day in June than in subsequent months in Atnsjø also indicate a more intense pattern of activity during the hours of daylight in the spring. They probably also moved to shallower waters in spring 1995 in order to feed on aquatic insects because low transparency and cold water this year yielded low densities of *B. longispina* (cf. Halvorsen and Papinska 2004). However, in late autumn, Arctic charr kept to shallower water than in late summer or autumn, probably because they switch from feeding on *B. longispina* to *D. longispina*. Arctic charr remained in deeper waters and closer to the bottom during the hours of daylight than at night. This use of space could be a response to the vertical distribution of zooplankton, which occurs at its highest density

in shallower water at night and deeper water at day (Halvorsen and Papinska 2004). Furthermore, during the day, fish are better protected against predation in deeper waters and closer to the bottom. Thus, the diurnal variation in use of space by Arctic charr seems to be a trade-off between the availability of food and the risk of predation (cf. Werner *et al.* 1983).

Alpine bullhead were caught at a rather wide range in depth, however, mainly at depths where the bottom consists to a large extent of fine material. It has previously been shown that lakewelling sculpins occupy bottom areas with a stony substrate (Northon 1991). This may indicate that Alpine bullhead in Atnsjø are displaced by brown trout to less attractive habitats of fine material. Large trout may also prey heavily on small sculpins (Smyly 1957, Newman and Waters 1984, Hanson *et al.* 1992). This is probably more severe in habitats with less structure with low access to shelter (Savino and Stein 1982). The littoral zone of Atnsjø has a relatively dense population of older brown trout (Hegge *et al.* 1989, Saksgård and Hesthagen 2004). The habitat use among salmonids and Alpine bullhead in Atnsjø may be analogous to that of juvenile brook trout (*Salvelinus fontinalis*) and slimy sculpin (*Cottus cognatus*) in Lake Ontario, where the latter species is displaced to the profundal zone (Owens and Bergstedt 1994). In Atnsjø, brown trout and Alpine bullhead largely utilized the same food resources, which suggests interference competition. This was especially the case at night in June and September, when their diets overlapped by 86% and 91%, respectively. Alpine bullhead preyed heavily on *B. longispina* at night in late summer, probably reflecting a peak in the abundance of this zooplankton species (Halvorsen and Papinska 2004). We suggest that shallow waters are the most rewarding foraging habitat for Alpine bullhead in Atnsjø, which offers best access to shelter in terms of stony substrate and food in terms of invertebrates. In a laboratory study, juvenile Bear Lake sculpin (*Cottus extensus*) fed much faster at optimal light intensity during the day than at night, indicating heavy dependence upon vision to feed (Neverman and Wurtsbaugh 1992). Similarly, as slimy sculpin in Lake Ontario shift from a shallow habitat and nocturnal feeding to continuous

activity in deeper water as they grow older, their nocturnal feeding in shallow water may reflect an attempt to avoid predators during the day (Brandt 1986).

Possible differences in temperature preferences, thermal limits of tolerance and maximum food consumption should be considered when discussing competition, interactions and habitat partitioning in different species of fish. The bullhead *Cottus gobio*, a species related to Alpine bullhead, had much wider thermal tolerance limits than Atlantic salmon and brown trout, with critical thermal limits at -4.2 and $+27.7$ °C, whilst cessation of feeding occurs at about $5-27$ °C (Elliott and Elliott 1995). The performance of young Arctic charr and brown trout during the prevailing temperature conditions found in Atnsjø should not be significantly different (Larsson et al. 2005, Fortseth et al. 2009). Thermal tolerance limits are thus not believed to explain any of the observed differences in resource utilization by the three fish species studied here.

In conclusion, selective differences are partly responsible for resource partitioning between young individuals of Arctic charr and brown trout, and Alpine bullhead in Atnsjø. However, Alpine bullhead might suffer from competition with brown trout in the littoral zone, where this salmonid species is relatively dense.

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