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Habitat segregation by sympatric juvenile Arctic charr and brown trout in shallow lake areas: a consequence of interspecific differences in predator avoidance?

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Abstract

In sympatry, juvenile brown trout (*Salmo trutta*) usually occupy the shallow and most productive areas (littoral zone) of lakes, while juveniles of Arctic charr (*Salvelinus alpinus*) are found in deeper, less productive parts. In contrast, when Arctic charr juveniles occur in allopatry, they often occupy shallow littoral areas as well. Habitat segregation has traditionally been interpreted as a trade-off between predation risk and energy gain, while the segregation of these two species has been explained by brown trout being more aggressive and competitively superior to Arctic charr. We hypothesize, however, that the marked habitat segregation between the two species may also be due to differences in predator avoidance. Accordingly, we conducted several laboratory tests, using Arctic charr and brown trout as potential predators. Live fish of the same species were offered as prey, either as small charr only, small trout only, or both small charr and small trout together. Artificial shelters were then introduced to examine the avoidance ability of prey fish against predatory fish. Our results showed that under these circumstances, access to shelters strongly decreased mortality in juvenile brown trout, but had no effect on juvenile Arctic charr mortality. Thus, the habitat segregation shown by sympatric juvenile Arctic charr and brown trout in lakes may be a consequence of interspecific differences in predator avoidance.

Keywords Juvenile salmonids · Habitat use · Competition · Shelter · Predator avoidance

Introduction

Segregation by habitat is one of the most important means by which ecologically similar species partition resources (Schoener 1974) and the differences between their patterns of resource use in sympatry and allopatry has been interpreted as evidence of competition, either through selective or interactive competition (Wootton 1998). Changes in fish abundance of species in response to invasion by new species (Bøhn et al. 2008) and experimental studies (Hasegawa et al. 2004) have given further evidence for competition. The intensity of interspecific competition may, however, be modified by predation; thus, the effects of competition may be difficult to disentangle from the effects of predation (Wotton 1998).

The two salmonid species, brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*), are two of the most widespread freshwater fish species in Northern Scandinavia and are found frequently in both allopatric and sympatric populations (Nilsson 1965; Klemetsen et al. 2003). In allopatry, small fish of both species seem to mainly exploit the littoral zone of lentic habitats (Nilsson 1963, 1967). In sympatry, however, juvenile brown trout often occupy the shallowest and the most productive lake areas, while juvenile Arctic charr are found at greater depths (Langeland et al. 1991; Klemetsen et al. 2003). Hegge et al. (2006) fished from June to October for several years in Lake Atnsjø, Norway, and found that although small individuals of both brown trout and Arctic charr occurred in the littoral zone, they were spatially segregated with brown trout dominating the

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most productive areas at depths of 0–5 m and Arctic charr at depths of 5–15 m.

Nilsson (1963, 1965) who studied Arctic charr and brown trout under natural conditions, and Fabricius (1953) and Fabricius and Gustavson (1954), who compared the same species in aquaria, claimed that the habitat segregation observed between the two species was due to brown trout being more territorial and aggressive in comparison with Arctic charr. Nilsson (1965) emphasized that the degree of aggressiveness seemed to be inversely proportional to the supply of food. Jansen et al. (2002) also found brown trout to be profoundly more aggressive than Arctic charr. Thus, differences in aggressiveness may result in Arctic charr being displaced from the littoral zone through interference competition by the more dominant trout, a conclusion also drawn in several other studies of ecologically similar fish species (see Wootton 1998 and Jonsson and Jonsson 2011 and references therein). However, differences between species in their ability to avoid predators in different situations have also been suggested to reinforce segregation in sympatric prey species (Lindström 1962).

Habitat use in fish is in general understood to be a trade-off between predation risk and feeding opportunities (L'Abée-Lund et al. 1993; Hammar 2014) and change in habitat use in the presence of a predator is, therefore, a well-known anti-predator behavior (Werner et al. 1983; Sih et al. 1988). Alternatively, fish may use physical shelters to hide and lower perceived risk from predators (Larranaga and Steingrimsson 2015), competitors (Spitzer et al. 2022), and to avoid predators (Kotler 1984; Godin 1997; Valdimarsson and Metcalfe 1998; Steele 1999). A corresponding decrease in piscivorous response has been demonstrated using artificial shelters (see Lundvall et al. 1999 and references therein). Interspecific interactions, however, may also influence the use of shelters, as described in field experiments with juveniles of two tropical damselfishes, *Dascyllus flavicaudus* and *Dascyllus trimaculatus*, which both shelter in branching corals and anemones. Increased mortality in the less aggressive species was induced by the two species occurring in sympatry due to displacement of less aggressive individuals to riskier locations (Holbrook and Schmitt 2002). In lakes with brown trout and Arctic charr, the shallow part of the littoral zone is typically stony, offering hiding places for small fish. In sympatry, competition for shelter between the two species may therefore be a challenge, in addition to food and interference competition. We hypothesize that the marked habitat segregation between juveniles of brown trout and Arctic charr in the shallowest lake areas is not an effect of interspecific competition alone, but may also be a consequence of species-specific differences in the ability to avoid predation. Accordingly, we conducted several laboratory experiments where brown trout and Arctic charr were used both as predators and prey in parallel trials with and without artificial shelters, and with either single prey species or both prey species together.

Materials and methods

Experimental design. Arctic charr (n = 60, 41–63 cm fork length, mean 52.2 cm, age = 3^+) of the hatchery-reared Lake Vårfluesjøen strain (Svalbard strain) and brown trout (n = 60, 37–48 cm fork length, mean = 41.4 cm, age = 3^+) of the hatchery-reared Lake Storvannet trout (Talvik strain) were used as predatory fish (Fig. 1). The mean weight of the Arctic charr and brown trout was 1,698 (619–3,598) g and 866 (502–1,356) g, respectively. Juvenile Arctic charr (Møkkeland strain) and brown trout (Talvik strain) were used as prey fish, with, respectively, mean length 10.2 (9.5–10.5) cm and 10.0 (9.5–10.5) cm (Fig. 1), and mean weight 10.1 g and 10.0 g. Juvenile groups had the same background, i.e., consisted of hatchery-reared fish. Both predatory and prey fish were fed only with dry pellets. Large Arctic charr and brown trout were fed during the two-week periods between trials, but before each trial, they were deprived of food for 72 h. Prey fish were not deprived of food before trials and predator fish were never trained to feed on prey fish. Predatory fish were held in '500-l tanks' (100 × 100 × 60 cm, water depth 60 cm) at a water temperature of 5–6 °C. The large fish were adapted to tank conditions for five weeks before the first

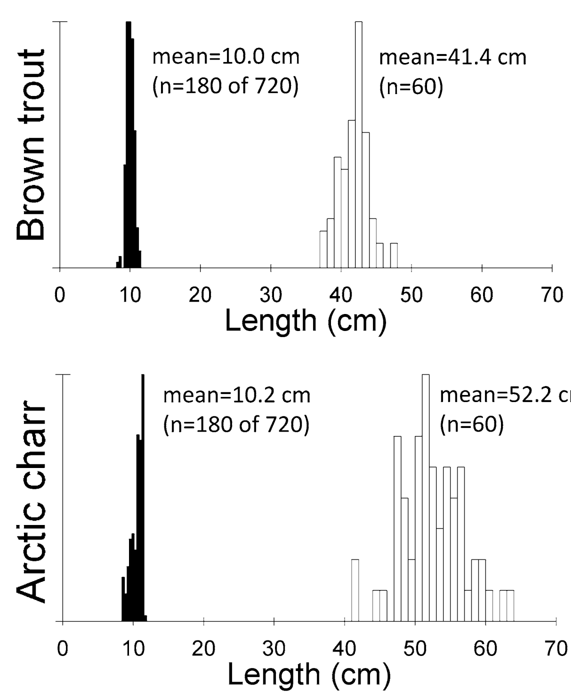

Fig. 1 Length distribution of brown trout and Arctic charr both as prey and predators used in the laboratory studies

trials and kept in the same tanks until the experiments were completed. All experiments were conducted under a daily light regime.

In each trial, 60 large Arctic charr or 60 large brown trout were divided into six tanks with ten fish per tank. Species of large fish were not mixed in the tanks, i.e., the tanks held only large Arctic charr or only large brown trout. In each trial and for each predatory species, a total of 360 prey fish were offered, i.e., 60 prey fish were offered in each tank for 24 h to simulate sympatric and allopatric occurrence of prey, with either 60 Arctic charr prey, 60 brown trout prey, or 30 Arctic charr prey plus 30 brown trout prey together, giving two replicates of each of these three treatments in each trial (Fig. 2). Initially, one trial was run with predatory Arctic charr in all six tanks, and one trial was run with predatory brown trout in all six tanks. To examine potential species-specific differences in the hiding ability of the prey fish against predatory fish, these trials were then repeated after introducing 30 artificial shelters in each tank. The shelters were made of black plastic boxes measuring 4.5 × 4.5 × 17 cm, allowing at least one prey fish to hide inside each box (Fig. 2). We observed that several small brown trout swam into boxes immediately after release into the tanks and trout were also observed inside many of the boxes at the end of the trials. We did not have access to video surveillance to register the behavior of fish during the trials. While predatory fish were reused, the same prey fish were never used in more than one trial. A total of 720 Arctic charr and 720 brown trout were offered as prey during the experiments, and the number of prey fish consumed was registered according to predator species, prey species, whether prey species occurrence was sympatric or allopatric, and whether shelter was available or not (see Figs. 2, 3). The study was approved by the Norwegian veterinary authorities with the predatory Arctic charr (Svalbard strain) studies carried out at the Tromsø Aquaculture Research Station, and the experiments with predatory brown trout (Talvik strain) at Talvik Research Station.

Statistical analyses. We used a logistic regression model where the fraction of available prey that was eaten was modeled assuming a binomial distribution for the observed number of prey eaten given all prey available of the same species at the onset of the experiment. The predictor variables were predator species (charr or trout predator), prey species (charr or trout prey), shelter availability (with or without shelter), and sympatry (mixed prey population of trout and char) or allopatry (only one prey species available). The most complex model evaluated included the interaction term between all four predictor variables. Tests for the null hypothesis of no variation in the proportion of prey eaten between the levels of the predictor terms were done using analysis of deviance (ANODEV) assuming a χ^2 distribution for the deviance explained by the term. Initial analyses showed that predator species differ in their response to shelter ($\chi^2 = 7.8$, 1 *d.f.*, $p = 0.005$). To make interpretations simpler, we therefore analyzed the experiments with predatory Arctic charr and brown trout separately.

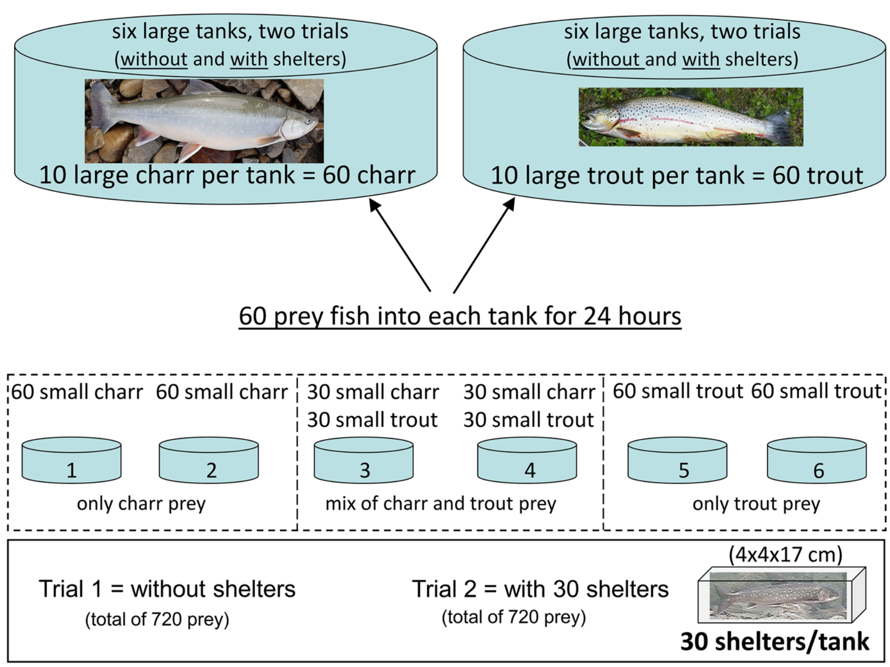

Fig. 2 Experimental design of the study, where the ability of juvenile Arctic charr and brown trout to seek shelter from predatory fish was examined. Two trials were run with predatory Arctic charr and two trials with predatory brown trout. Species of predators were not mixed, i.e., the tanks held only large Arctic charr or only large brown trout. For each predator species, the first trial was run without shelter, and the second trial with shelter. In each trial, a total of 360 prey fish were released, i.e., 60 prey fish in each tank. In tanks one and two, only charr prey was released; in tanks three and four, a mix of charr and trout prey was released; and in tanks five and six, only trout prey were released

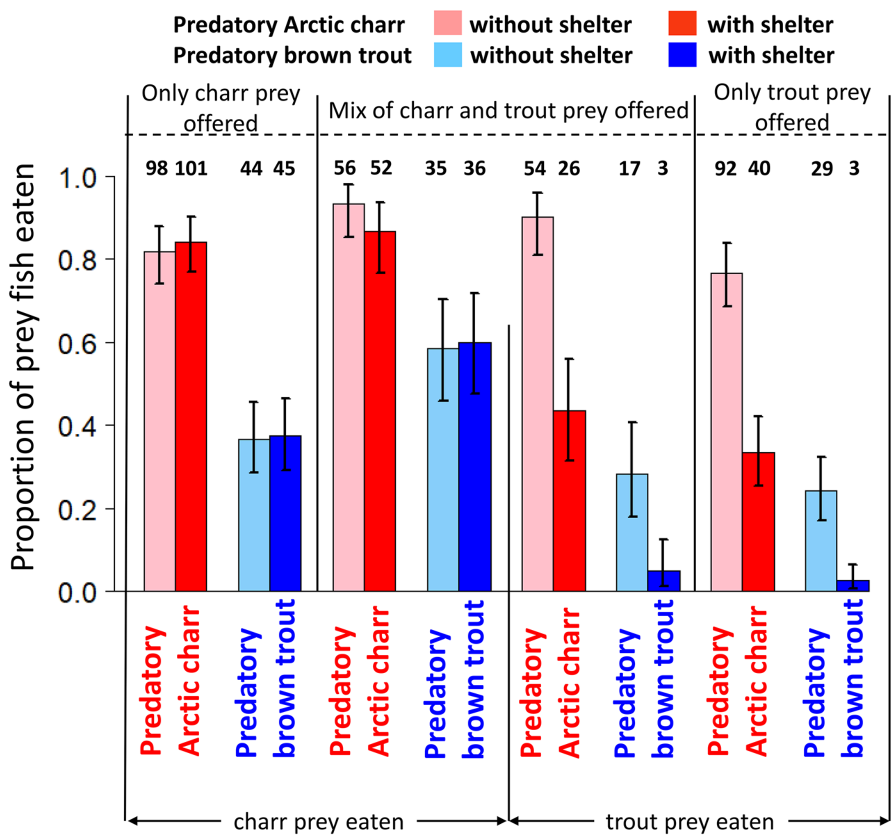

Fig. 3 The proportion of juvenile Arctic charr and brown trout eaten by predatory Arctic charr or brown trout in the experimental trials with no shelter or shelter present, and when the prey species occurred sympatric (offered as both charr and trout prey together) or allopatric (offered as only one prey species). Error bars show the 95% confidence intervals. The total number of prey eaten in each category in each trial is included above the bars

Results

Arctic charr as predator. In total, predatory Arctic charr consumed 307 charr prey and 212 trout prey, i.e., more than 70% of the total number of prey fish eaten during the four trials (Table 1), reflecting that predatory Arctic charr had a higher predation rate on both species of prey than predatory brown trout (Fig. 3). When there was no shelter available, the proportion of trout prey eaten was similar to the proportion of charr eaten, while a reduced proportion of trout prey was eaten when shelter was present. There was no evidence for a difference in the proportion of charr prey eaten by predatory charr with or without shelter (Fig. 3), but predation rates were higher for both species when they occurred as prey in sympatry compared to when only one prey species was available to predatory Arctic charr.

The statistical analyses showed a significant interaction between prey species and shelter (Table 2) due to the reduced proportion of trout prey eaten when shelter was present. However, Arctic charr still ate 66 of the 72 trout prey (91.7%) consumed in the experimental setups with shelters present, i.e., predatory Arctic charr exhibited a higher predatory efficiency than predatory brown trout in the presence of shelter. In addition, there was an additive effect of sympatry (Table 2, estimated coefficient on logit scale $\beta = 0.62$, SE $= 0.21$) suggesting that both species suffered higher predation rates when they occurred as prey in sympatry, compared to when only one prey species was available to predatory

Table 1 The number of charr prey and trout prey eaten by predatory Arctic charr and predatory brown trout in the trials with and without shelter. Numbers in brackets show the number of prey offered

	Charr prey No shelter	Charr prey With shelter	Trout prey No shelter	Trout prey With shelter	Charr prey In total	Trout prey In total	All prey In total
Predatory Arctic charr	154 (180)	153 (180)	146 (180)	66 (180)	307 (360)	212 (360)	519 (720)
Predatory Arctic trout	79 (180)	81 (180)	46 (180)	6 (180)	160 (360)	52 (360)	212 (720)
Total	233 (360)	234 (360)	192 (360)	72 (360)	467 (720)	264 (720)	731 (1,440)

Table 2 ANODEV (analyses of deviance) for the model describing the proportion of available prey individuals eaten by predatory Arctic charr and brown trout, using prey species (charr or trout), shelter (no shelter or shelter), sympatry (sympatric or allopatric prey species), and the prey species by shelter interaction as predictor variables

Source of variation	*d.f.*	Predatory Arctic charr		Predatory brown trout	
		Deviance	*P*	Deviance	*P*
Prey species	1	64.2	<0.0001	80.8	<0.0001
Shelter	1	50.9	<0.0001	10.9	0.001
Sympatry	1	8.5	0.004	14	0.0002
Prey species × shelter	1	26.3	<0.0001	29.6	<0.0001
Residual	11	8.6		5.1	

Arctic charr. There was no evidence for a 3-way or 2-way interaction between sympatry and prey species and/or shelter ($p > 0.10$).

Brown trout as predator. Overall, predatory brown trout consumed 160 charr prey and 52 trout prey (Table 1), reflecting that charr prey was, in general, more frequently eaten than trout prey by predatory brown trout (Fig. 3). A reduced proportion of trout prey was eaten when shelter was present, and predation rates were somewhat higher for both species when they occurred as prey in sympatry compared to when only one prey species was available to predatory brown trout.

The statistical analyses showed a significant interaction between prey species and shelter (Table 2) due to a reduced proportion of trout prey eaten when shelter was present (Fig. 3), and no evidence for a difference in the proportion of charr prey eaten by predatory trout with or without shelter (Fig. 3). In addition, there was an additive effect of sympatry (Table 2, estimated coefficient on logit scale $\beta = 0.70$, SE $= 0.19$), suggesting that both species' predation rates were somewhat higher when they occurred as prey in sympatry. There was no evidence for a 3-way or 2-way interaction between sympatry and prey species and/or shelter ($p > 0.30$).

Discussion

In the laboratory experiments, we found a marked difference in the predation rate of Arctic charr and brown trout prey, both by predatory Arctic charr and brown trout, probably reflecting differences in predator avoidance between the two species. Juveniles of both species were offered the same artificial shelters, but the juvenile Arctic charr did not take advantage of the provided shelters, resulting in the same level of mortality irrespective of whether shelters were available or not. In strong contrast, juvenile brown trout were able to take advantage of the shelters, resulting in substantially lower mortality when shelters were available.

In the presence of piscivores, potential fish prey typically change their habitat use and seek shelter to avoid predation, i.e., exhibit anti-predator behavior (Werner et al. 1983; Werner and Gilliam 1984; Sih 1987; Damsgård and Ugedal 1997). That shelter can reduce predation has also been demonstrated experimentally using artificial vegetation (Savino and Stein 1989; East and Magnan 1991) and rocks (Savino and Miller 1991) as shelter. Predation has also been shown to increase substantially in the absence of shelters (Belanger and Corcum 2003). Steele (1999) who experimentally tested for the effects of shelter and predators on the recruitment and survival of two temperate reef fishes, the Bluebanded goby (*Lythrypnus dalli*) and the blackeye goby (*Coryphopterus nicholsii*), found that predation caused greater mortality in areas with little shelter versus areas with abundant shelter.

In our trials without shelter, predator Arctic charr did not seem to prefer one prey species over the other, and/or the two prey species exhibited a similar (low) ability to avoid predation. Predatory trout, however, seemed to prefer to consume charr rather than trout prey, and/or trout prey exhibited a higher ability to avoid predation. The addition of artificial shelters in our tanks was supposed to simulate a natural situation where prey fish potentially could avoid predation, and the total mortality of trout prey was reduced by more than 60% after introducing shelters, while the mortality of charr prey was unchanged. The experimental design does not allow a detailed description of how the trout prey took advantage of the artificial boxes (shelters). Without video surveillance, we could not document the detailed behavior of the prey or the predators. We did observe, however, that many trout prey immediately swam into the boxes when released into the tanks and also were observed inside shelters at the end of the trials. This corroborates the hypothesis that the reduced mortality of trout prey was due to their more active use of shelters. The reduced mortality of trout prey in the presence of shelter occurred irrespective of predator species, and also whether prey was offered as a single (charr or trout prey) or mixed (charr and trout together) prey species. In contrast, charr prey did not take advantage of the shelter.

The experimental setup with as many as ten large piscivores in each tank may not reflect a natural situation and could potentially introduce interference among piscivores as well as increased prey mortality due to group foraging effects (Lundvall et al. 1999). In an earlier and similar experiment with predatory Arctic charr and charr prey, Svenning and Borgstrøm (2005) found that during four subsequent trials performed at 4-week intervals, nine of the 60 predators never ate any of the prey fish offered, while the 14 predators that ate prey fish in all four trials consumed more than 300 fish during the experimental period. Variation in individual food consumption and growth due to social interactions are well documented in salmonids such as Arctic charr (Jobling 1985; Jobling and Reinsnes 1986), Atlantic salmon

Salmo salar L. (Huntingford et al. 1990), and rainbow trout *Oncorhynchus mykiss* (Walbaum) (McCarthy et al. 1992). In Svenning and Borgstrøm (2005), the non-cannibalistic individuals may have been restricted in encountering prey due to social interactions. Similar interactions may have influenced our experiments causing heterogenous predation rates. However, the advantage of shelter for trout prey was still consistent across trials and predatory species.

In total, predatory charr ate more than 70% of the prey fish consumed in our trials. Amundsen et al. (1999) who ran similar experimental studies with four different predatory Arctic charr strains, offering only Arctic charr juveniles as prey, revealed that the Svalbard charr strain exhibited a significantly higher cannibalistic response than the three strains from mainland Norway, which in contrast showed mutual differences. Only one Svalbard strain was included in Amundsen et al. (1999) and they suggested that charr from High-Arctic populations may have stronger cannibalistic or predatory tendencies. This may also partly explain the high predation rate observed in predatory Arctic charr when compared to predatory brown trout in our experiments. In addition, the predatory Arctic charr used in the experiments were in general larger than the predatory brown trout, i.e., the mean weight of predatory charr was about twice the mean weight of the trout. As the consumption capacity scales with body weight, the predatory trout were expected to be substantially more constrained by digestion capacity than charr. Further, the experiments were conducted at relatively low water temperatures (5–6 °C), which might also have favored the cold water-adapted Arctic charr rather than the brown trout. Larsson (2005) found that the preferred temperature for Arctic charr is 5–6 °C lower than for brown trout. He also reported that the preferred temperature for Arctic charr was 4.5 °C lower than the reported optimal temperature for growth, contradicting the typically good match between the optimal temperature for growth and the preferred temperature for most fish, such as brown trout. Larsson (2005) concluded that Arctic charr and brown trout differ in thermoregulatory behavior under excess feeding, which may also in part explain the much higher consumption of prey by predatory Arctic charr in our experiments.

The difference in predation rates between the two species observed in our tank experiments is also reflected in the diet of both brown trout and Arctic charr under natural conditions. The low frequency of cannibalism found in lacustrine brown trout in lakes (Nilsson 1963, 1965; Frost and Brown 1967; Svärdson 1976; Aass 1990; L'Abée-Lund et al. 1992) may be partly due to the effective hiding ability of the juvenile trout in the coarse littoral substrate. Conversely, Arctic charr in both allopatric and sympatric populations is a common prey of large Arctic charr or brown troutl (Aass 1990; Svenning and Borgstrøm 1995; Klemetsen et al. 2002), and the results from our study indicate that this may be in part due to the inability of juvenile charr to hide. When living in sympatry with brown trout, juveniles of Arctic charr may be expelled from the littoral zone by aggressive juvenile trout which tend toward territorial behavior even in still water (Kalleberg 1958; Nilsson 1963; Jansen et al. 2002). In addition, juvenile Arctic charr may be exposed to high and persistent predation pressure in the littoral zone and find refuge in deeper areas of the littoral habitat (see Hegge et al. 2006) or move further down into the profundal zone (Damsgård 1993; Klemetsen et al. 2002) where predation pressure can be depressed due to lower temperature and less light.

The marked difference in mortality between small Arctic charr and brown trout in the presence of shelter observed in our experiments clearly indicates differences between the two species in the use of shelter, and thereby differences in predator avoidance behavior. In the relatively small experimental tanks used in the trials, however, the predatory fish and their prey were in constant visual contact, leading to potentially high encounter rates, and the only efficient way for the prey to avoid predation was likely to seek shelter. The experimental trials clearly showed that under these circumstances, small trout demonstrated a much more successful predator avoidance behavior than small charr.

The need for experimental studies of both competition and predation is recognized (see Fausch 1988) and can be insightful, given careful consideration of the uncertainties of extrapolation to natural conditions. Our results challenge the common suggestion that the observed segregation in habitat use between the two species in shallow lake areas is due to brown trout being more territorial and aggressive in comparison to Arctic charr, and give support to the role of interspecific differences in predator avoidance in forming these habitat preferences.

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Declarations

Conflicts of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethics approval The authors declare that all applicable international, national, and/or institutional guidelines for sampling, care and experimental use of fishes for the study were followed, and all necessary approvals were obtained.

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