

Asymmetric competition drives lake use of coexisting salmonids

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Abstract To what degree are population differences in resource use caused by competition and the occupation of adjacent positions along environmental gradients evidence of competition? Habitat use may be the result of a competitive lottery, or restricted by competition. We tested to what extent population differences in habitat use of two salmonids, cutthroat trout (*Oncorhynchus clarki*) and Dolly Varden charr (*Salvelinus malma*) were influenced by interspecific competition. We hypothesized that the depth distribution of Dolly Varden charr would be affected by competition from the more littoral and surface-oriented cutthroat trout, and that the depth distribution of cutthroat trout would be little affected by competition from Dolly Varden charr. Sympatric populations of cutthroat trout and Dolly

Varden charr were created by reciprocal transfers of previously allopatric populations in two experimental lakes. We found evidence of asymmetric competition, as Dolly Varden charr were displaced from littoral habitats when sympatric with cutthroat trout, whereas cutthroat trout remained unaffected by the presence of Dolly Varden charr. Evolved differences between the species, and differences between experimental lakes, also contributed to population differences in habitat use, but asymmetric competition remained as the main driver of different depth distributions in sympatry.

Keywords Habitat shift · Interactive segregation · *Oncorhynchus clarki* · Reciprocal transfer experiment · *Salvelinus malma*

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Introduction

There has been considerable debate to what degree population differences in resource use are caused by competition, and whether occupation of adjacent positions along environmental gradients is evidence of competition (Taniguchi and Nakano 2000; Connolly and Moko 2003). Is it a competitive lottery (Munday 2004) or coexistence where one or both species are restricted in the presence of the other (Bøhn and Amundsen 2001)? Studying two species of coral-dwelling goby [*Gobiodon histrio* (Valenciennes) and *Gobiodon erythrospilus* Bleeker] with similar patterns of habitat use, Munday (2004) demonstrated that there was a priority effect where the first species to occupy a vacant coral patch excluded an interspecific intruder of similar body size. On the other hand, a whitefish [*Coregonus lavaretus* (L.)] population invaded by vendace [*Coregonus albula* (L.)] changed its habitat from pelagic to littoral areas (Bøhn and Amundsen 2001). The habitat segregation

observed was asymmetric, with vendace as the superior entrant. Such invasions appear to be competition constrained and newly established species tend to be competitively dominant over previously established ones, as shown for fruit flies by Duyck et al. (2006).

In asymmetric competition the loss in fitness of some participants is much greater than that of the others, as when large plants suppress the growth of smaller neighbours (Schwinning and Weiner 1998; Rajaniemi and Reynolds 2004). In canopy tree competition most pairwise interactions appear strongly asymmetric, making a clear competitive hierarchy among shade-tolerant species (Canham et al. 2006). In anuran larvae such as *Bufo bufo* (L.) and *Bufo calamita* (Laurenti) asymmetric competition was manifested by reduced survival and growth rates of *B. calamita* when interacting with the other, but not vice versa (Bardsley and Beebe 2001). Likewise, competition between island spotted skunk *Spilogale gracilis* Merriam and island fox *Urocyon littoralis* Blaird affected skunks more than foxes (Crooks and Vanvuren 1995). Furthermore, culling of Eurasian badgers [*Meles meles* (L.)] was associated with increases in sympatric red fox [*Vulpes vulpes* (L.)] in England (Trewby et al. 2007). Thus, asymmetric competition has been documented over a large range of species from plants to mammals.

Salmonid fish are an important group used in studies of species interactions because of their similar morphology and ecology. Many of these studies have been performed with trout and charr in Scandinavia (e.g. Nilsson 1963; Langeland et al. 1991), and on the west coast of North America (Andrusak and Northcote 1971; Northcote 1995). Allopatric populations of lake-dwelling trout and charr have similar niches with the preferred food items being insect larvae, amphipods and molluscs in the littoral zone, and adult arthropods on the lake surface. In sympatry, trout still use the preferred littoral and near-surface resources, whereas charr usually feed in deeper, offshore habitats (Hindar and Jonsson 1982; Andrew et al. 1992).

To test if differences in habitat use in allopatric and sympatric situations were caused by asymmetric competition (Weiner 1990; Robertson 1996), evolved differences (Langeland et al. 1991; Forseth et al. 2003), or prior residence (Munday 2004), a 30-year removal, reciprocal transfer experiment was initiated with cutthroat trout [*Oncorhynchus clarki* (Richardson)] (hereafter trout) and Dolly Varden charr [*Salvelinus malma* (Walbaum)] (hereafter charr) in three lakes of the University of British Columbia Research Forest (Northcote 1995). Such whole-lake experiments are important because of the ecological realism of the results (Biro et al. 2007), and the reciprocal transplant is a strong experimental technique for analysing factors that limit species distributions (e.g. Krebs 1985; Martin and Martin 2001). In our case, the trout is an aggressive, territorial species exhibiting behaviours suitable when

feeding on littoral zoobenthos and surface prey. It dominates Dolly Varden charr in competition for food items introduced to pairs of similar-sized cutthroat and Dolly Varden charr at the surface and at the bottom in aquarium experiments (Schutz and Northcote 1972). Charr, on the other hand, have better visual capacity under low light intensity than trout, and thus are able to find food in deeper and darker waters (Henderson and Northcote 1985). Thus, evolved differences between the two species may explain why charr use the deep epibenthic habitat, but not why their resource uses are more restricted in the presence of trout.

We tested whether the depth distribution of trout and charr differed between sympatry and allopatry, and between the natural sympatric situation in Loon Lake and the experimental situations in Eunice and Katherine lakes. In 1974, charr and trout were transferred from a sympatric situation in Loon Lake to allopatry in two fishless lakes; charr to Katherine Lake and trout to Eunice Lake, respectively (Hume and Northcote 1985). Eight years after the transfers, allopatric trout exploited near surface waters as in sympatry, and the vertical habitat overlap between allopatric and sympatric trout during summer was approximately 80% (Hindar et al. 1988). Allopatric charr, on the other hand, had widened their habitat use to include the shallow littoral zone in addition to deeper parts of the lake as in sympatry with trout. The average vertical overlap in distributions between allopatric and sympatric charr was less than 40% (Northcote 1995). Thus, this whole-lake experiment suggested that the change in habitat use of charr was due to competitive release from sympatry in the donor lake to allopatry in the new experimental lake. We could not, however, rule out lake differences as an alternative explanation for widened habitat use of charr (Hindar et al. 1988). To resolve this dilemma and provide unequivocal evidence for asymmetric competition, new sympatric stocks were formed through reciprocal transfers between Katherine and Eunice Lakes in 1994 (Northcote 1995). In the case of asymmetric competition, charr should be displaced from near-surface waters and use the deep areas of both experimental lakes, whereas the superior competitor, trout, should remain unaffected by the transfer. The results of the reciprocal transfer experiments are reported here, and thereby complete a long-term series of whole-lake and laboratory experiments studying mechanisms and effects of interspecific competition between cutthroat trout and Dolly Varden charr.

Materials and methods

Study sites

The present study was carried out in three lakes in the University of British Columbia Research Forest (49°19'N,

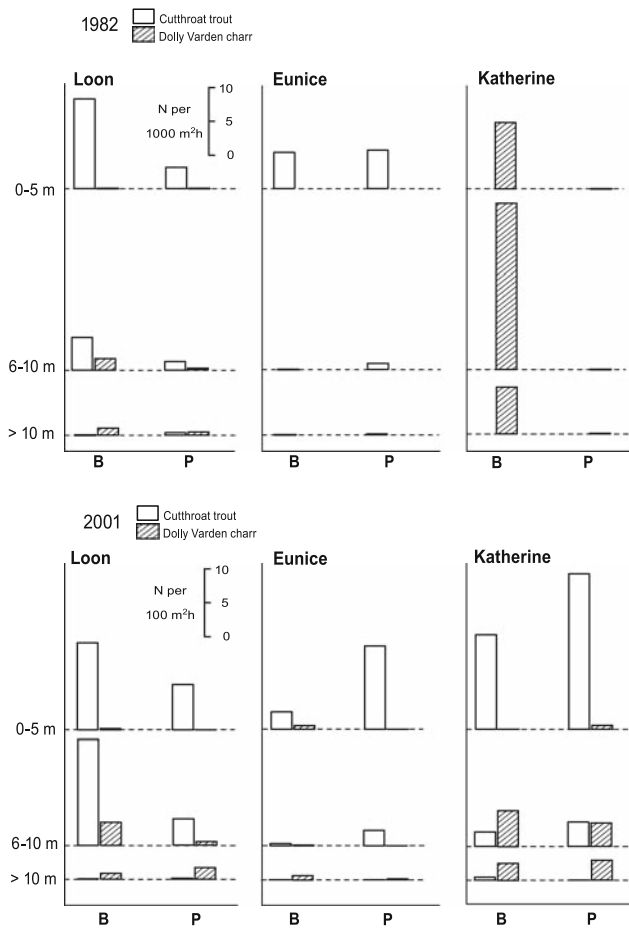


Fig. 1 Catch per unit effort [= (number of fish)/(net area × hours fished)] of cutthroat trout and Dolly Varden charr in Loon, Eunice and Katherine Lakes during summer 2001. Epibenthic (B) and pelagic (P) catches are shown for three depth categories within lakes. CPUE from 1982, before the reciprocal transfers (i.e. when Eunice and Katherine Lakes held one species only), is shown for comparison. Note the difference in scale between years

122°34'W) about 50 km east of Vancouver, British Columbia (see Fig. 1 in Northcote and Clarotto 1975) in late July 2001. The lakes are situated in the coastal mountain uplands at elevations between 340 and 505 m. Specific characteristics of the lakes are presented by Northcote and Clarotto (1975). Loon Lake (surface area 48.6 ha, maximum depth 62 m) supports cohabiting native populations of trout and charr, but no other fish species. Schnabel population estimates of subadult and adult trout and charr in the lake were respectively 7,300 and 3,100 (Hume and Northcote 1985). Eunice Lake (surface area 18.2 ha, maximum depth 42 m) and Katherine Lake (surface area 20.7 ha, maximum depth 29 m) were both fishless until 1974.

Between October 1974 and June 1976 a total of 1,571 trout and 881 charr were transferred from Loon Lake to Eunice and Katherine Lakes, respectively (Hume and Northcote 1985). The sample sizes are sufficient to assume genetical homogeneity between the donor and transplanted

stocks (Frankham et al. 2002). The transplanted fish of both species were between 5 and 25 cm in fork length. The larger individuals probably spawned within a year after release. When studied in 1982, the transplanted populations were self-sustaining (Jonsson et al. 1984; Hindar et al. 1988; Andrew et al. 1992).

Between late April and early May 1994, fifty-five charr from Katherine Lake were transferred to Eunice Lake and 41 trout from Eunice Lake were transferred to Katherine Lake. These sample sizes are much smaller than the original transfers but still sufficient to capture most of the heterozygosity and most of the common alleles in the source populations (Frankham et al. 2002, p. 426). All fish were in good condition when released. The trout from Eunice Lake ranged in length from 10 to 25 cm, whereas the charr from Katherine Lake ranged in length from 15 to 27 cm. We investigated the spatial distributions 7 years later when the released fish had reproduced several times and were well established in the lakes.

Sampling and treatment of the materials

In July 2001 a total of 284 trout and 145 charr were caught in Loon Lake, 123 and 54 in Eunice Lake, and 242 and 166 in Katherine Lake. Bottom and pelagic gill nets were set from the surface to the bottom and emptied during dawn and dusk. Each depth contour was represented by one night set and one day set during the sampling period. The bottom nets were 2 m and the pelagic nets 6 m in vertical dimension. The bottom nets were placed in gangs with mixed mesh sizes, from 10 to 45 mm, from the shoreline to the greatest depth. The pelagic net gangs were set over the deepest area of each lake (Andrew et al. 1992). We recorded the depth where each net was set by use of a Furuno 50 kHz paper recording echo sounder. The depth where each fish was caught was determined from its position in the net. Fork length was measured to a precision of 0.1 cm, with sex and degree of sexual maturity categorized into sexually immature and mature individuals. The fish were separated into sexually immature and mature individuals. Ages were determined from scales in trout and from otoliths in charr (sensu Jonsson et al. 1984).

Statistical analyses

Catch per unit effort (CPUE) was calculated for both pelagic and epibenthic nets. Depth categories were defined as in previous reports (Hindar et al. 1988; Andrew et al. 1992): 0–5, 5–10, 10–15, 15–20 and 20–40 m. The depth distributions of trout (X_i) and charr (Y_i) catches across depth categories $i = 1, \dots, 5$ were compared with a numerical simulation test (see Appendix). Conditioning on $\sum X_i = N_{\text{trout}}$ and $\sum Y_i = N_{\text{charr}}$, we tested the hypothesis that the

distribution of X_i and Y_i is the same provided that the efforts (λ_i and ω_i , respectively) were the same. As test statistic, we used the standard χ^2 statistic, which was simulated under the null hypothesis $H_0: \alpha_i = c\beta_i$, where α_i and β_i are unknown (density) and c is a scaling factor for different total abundance of the two species (Appendix). The P -value of the test was determined as the fraction of the simulated test statistics that were larger than the one observed.

The test structure applied was as follows:

1. The depth distribution does not differ between trout and charr.
2. The depth distribution of sympatric populations does not change over time (1982 versus 2001 data in Loon Lake).
3. The depth distribution does not differ between natural sympatry and experimental allopatry (1982 data—competitive release).
4. The depth distribution does not differ between experimental allopatry (1982) and experimental sympatry (2001 data—competitive displacement).

This approach was chosen over more standard ways of testing catch and effort data (e.g. Maunders and Punt 2004) because rejecting specific hypotheses about interactions is more informative than rejecting an overall hypothesis of catch variation. Bonferroni correction was applied to multiple tests of the same hypothesis.

Epibenthic and pelagic catches were treated separately. Comparisons were done between the August sampling of 1982 and the 2001 sampling. The first day and night of sampling in the 1982 catches were used in the tests, as CPUE tended to decrease during subsequent catches.

Results

Sympatric populations

Trout and charr had significantly different depth distributions in Loon, Eunice and Katherine Lakes in summer 2001 (all observed $\chi^2 > 49$, 2–4 *df*, all $P < 0.001$). This was evident in both pelagic and epibenthic netting (Fig. 1). In all three lakes, trout were more pelagic and stayed closer to the surface than charr. CPUE of trout was low deeper than 10 m, whereas the catch of charr was high deeper than 10 m in all lakes (Fig. 1). These results were similar to the findings for the 1982 sampling of sympatric populations in Loon Lake. The catch of cutthroat trout has increased especially in Loon Lake since 1982. This quantitative difference has not changed the qualitative difference in spatial distribution between trout and charr. Thus, such density differences appear not to influence the qualitative outcome of the

interspecific competition between these species, with trout being closer to the surface than charr.

Sympatry versus experimental allopatry

In our previous study (during summer 1982), we found that trout did not expand their depth distribution in experimental allopatry, whereas charr moved into the littoral (shallow epibenthic) zone when in allopatry. Using the simulation test statistic, we found no significant difference between the depth distributions of allopatric trout (Eunice Lake) and sympatric trout (Loon Lake) in the pelagic zone (observed $\chi^2 = 4.21$, 2 *df*, $P = 0.11$). In the epibenthic zone, we found a significantly different depth distribution between allopatric and sympatric trout (observed $\chi^2 = 7.41$, 1 *df*, $P = 0.006$), the difference being that allopatric trout were more constrained and occurred only in the littoral (0–5 m) depth category. Experimentally allopatric charr in Katherine Lake exhibited a significantly different epibenthic depth distribution than sympatric charr in Loon Lake (observed $\chi^2 = 12.95$, 2 *df*, $P = 0.003$). Pelagic netting caught only a single charr in Katherine Lake, and no difference was evident from pelagic charr in Loon Lake (observed $\chi^2 = 0.65$, 1 *df*, $P = 0.55$). An earlier summer 1982 sample from Katherine Lake (Andrew et al. 1992) gave eight charr in pelagic netting; their depth distribution was also non-significantly different from sympatric charr in Loon Lake (observed $\chi^2 = 1.17$, 2 *df*, $P = 0.68$).

Experimental allopatry versus experimental sympatry

In Eunice Lake, the previously allopatric trout population seemed little affected by the presence of charr in July 2001 (Fig. 1). No significant change in depth distribution from 1982 was found, either in the pelagic zone (observed $\chi^2 = 1.99$, 2 *df*, $P = 0.41$) or in the littoral and epibenthic zones (observed $\chi^2 = 3.08$, 2 *df*, $P = 0.19$).

In Katherine Lake, the previously allopatric charr changed their habitat distribution in the presence of trout in the epibenthic zone, but not in the pelagic zone (Fig. 1). No charr was found in the littoral zone, and its epibenthic depth distribution was significantly different from that of trout (observed $\chi^2 = 77.20$, 2 *df*, $P < 0.0001$). In the pelagic zone, only one charr was caught in the August 1982 sampling near the bottom, and the pelagic depth distribution did not differ between 1982 and 2001 (observed $\chi^2 = 1.45$, 2 *df*, $P = 0.40$). Testing against an earlier summer 1982 sample from Katherine Lake also gave a non-significant result for the depth distribution of pelagic Dolly Varden from allopatry to sympatry (observed $\chi^2 = 3.53$, 2 *df*, $P = 0.18$).

The depth distribution of trout in Eunice Lake was not different from that of trout in Katherine Lake, either in the epibenthic (observed $\chi^2 = 1.99$, 3 *df*, $P = 0.57$) or the

pelagic habitat (observed $\chi^2 = 0.205$, 1 *df*, $P = 0.65$). However, the depth distribution of charr in Eunice Lake was significantly different from charr in Katherine Lake in the epibenthic zone (observed $\chi^2 = 17.47$, 3 *df*, $P = 0.0004$); Eunice charr being more littoral than Katherine charr, whereas no difference was found in the pelagic zone (observed $\chi^2 = 1.21$, 2 *df*, $P = 0.45$). There was no age- or size-related difference in habitat use between the species in relation to sympatry and allopatry.

Discussion

Our long-term removal and reciprocal transfer experiments provide strong evidence of competitive displacement of charr by trout from littoral habitats in sympatry. The sympatric distribution of the experimental charr populations is significantly different from that of charr before the introduction of trout in Katherine Lake (Hindar et al. 1988; Andrew et al. 1992). It resembles the distribution of this species in its original sympatric location in Loon Lake, as well as in many lakes where they coexist with trout (Andrusak and Northcote 1971). This shows that the changed habitat use of charr in sympatry with trout results from interspecific competition with the introduced trout displacing charr from the littoral zone. It is not a result of prior residence as found for some fishes feeding inside coral reefs where space is limited (Munday 2004), or in larval anurans of the species *Hyla crucifer* Wied-Neuwied and *Bufo woodhousii* Girard (Lawler and Morin 1993). In the latter case, earlier arrival increased the competitive impact of *Bufo* on *Hyla*, but failed to generate a competitive effect of *Hyla* on *Bufo*.

Habitat displacement by introduced species has been observed also in other species pairs. Introduced red shiner (*Cyprinella lutrensis* Baird and Girard) displaced the threatened cyprinid spikedace (*Meda fulgida* Girard) into swifter current, probably causing a dramatic decline of this species (Douglas et al. 1994). Experimental manipulations of two larval anurans, *Pelodytes punctatus* Daudin and *B. bufo*, showed that *Bufo* individuals increased their use of the water column in the presence of the other, while *Pelodytes* did not change their space use (Richter-Boix et al. 2004). Furthermore, the darter *Etheostoma zonale* (Cope) excluded *Etheostoma olmstedi* Storer from riffle and run habitats (Grey et al. 2005), and exotic brown trout (*Salmo trutta* L.) displaced cutthroat trout from low-flow areas in streams (McHugh and Budy 2005). Such effects of competition may be best observed when new species are introduced, as revealed in our transfer experiment.

The difference in depth distribution between the original sympatric distribution of charr in Loon Lake, and their experimentally allopatric distribution in Katherine Lake, can now only be explained as a competitive release. Even

though this shift to more littoral habitats in allopatry was also interpreted as being a probable result of competitive release in previous papers (Hindar et al. 1988; Andrew et al. 1992), that finding alone could not exclude lake differences as an alternative explanation. This alternative no longer seems valid.

Similar competitive releases have been found for the neotropical ants *Solenopsis geminate* Fabricius and *Pheidole radoszkowskii* (Mayr), where the foraging activity of *Solenopsis geminate* increased when it was released from competition from *Pheidole radoszkowskii*, but not the other way round (Perfecto 1994). Likewise, two spiny pocket mice, *Heteromys australis* Thomas and *Heteromys anomalus* (Thompson), in northwestern South America use different habitats in sympatry, whereas *Heteromys anomalus* inhabits areas ecologically suitable for both species in an isolated area where *Heteromys australis* is absent likely for historical reasons (Anderson et al. 2002). This, and other examples for rodents (Fasola and Canova 2000) and gulls (Kildaw 1999), also indicate that both present and past competition influence habitat use of populations.

In our study, the competitive effect is asymmetrical in that charr but not trout altered its habitat use in presence of the other. Effects of asymmetric competition has been demonstrated for a number of species pairs from plants (e.g. Wedin and Tilman 1993; Weiner and Damgaard 2006) to invertebrates (Pereira and Do Prado 2005; Yasuda et al. 2004; Fowler-Finn and Hebets 2006) and vertebrates such as amphibians (Morin and Johnson 1988; Parris and Semlitsch 1998; Smith et al. 2004) and fish (Bøhn and Amundsen 2001; Berec et al. 2006). Bøhn and Amundsen (2001) claimed that vendace, as a specialized zooplanktivore, reduced zooplankton availability and made this resource unprofitable for whitefish. In other salmonids, such as brown trout and Atlantic salmon (*Salmo salar* L.), habitat use by juvenile salmon appears restricted through interactive segregation, brown trout being more aggressive and a better defender of deep pool areas in rivers than salmon (Heggenes et al. 1999), whereas juvenile coho salmon (*Oncorhynchus kisutch*) defend deep, low-velocity pools and displace steelhead trout (*Oncorhynchus mykiss*) into shallow, high-velocity riffles (Young 2004). Likewise, interference competition gives the Australia swamp rat (*Rattus lutreolus*) priority over the bush rat (*Rattus fuscipes*) to the preferred moist habitats containing important food and shelter resources (Maitz and Dickman 2001).

In our study, the movement of charr to pelagic and profundal habitats appeared to result from evolved differences between the species investigated, making profundal areas relatively more profitable for charr in the presence of trout. A similar difference is exhibited by Arctic charr [*Salvelinus alpinus* (L.)] and brown trout in Scandinavia (Nilsson 1963; Langeland et al. 1991; Jansen et al. 2002), where

Arctic charr feed more in pelagic and deep, epibenthic habitats in sympatry with brown trout than in allopatric situations. Such sympatric habitat differences may partly reflect evolved differences in resource use of the species, also indicated by morphological character displacement being due to interspecific competition (Forseth et al. 2003; Pfennig et al. 2006). Evolved differences in habitat preference are also observed in large catfishes in Lake Texoma, Texas-Oklahoma (Edds et al. 2002), and in an assemblage of subtidal cottids in the San Juan Islands, Washington (Norton 1991), where present interspecific competition appears to be of little importance.

Laboratory experiments have shown solitary Dolly Varden charr to be more efficient than solitary cutthroat trout when feeding on both exposed and buried benthic prey (Schutz and Northcote 1972). During interactive feeding by similar-sized pairs of the two species, however, trout was the dominant individual and outcompeted charr even when only benthic prey was present. The dominant behaviour of trout functions well when feeding on surface insects and littoral zoobenthos, decreasing the profitability of this zone for charr. The relative profitability of the alternative deep, epibenthic habitats may be higher for sympatric charr as trout chiefly stay in littoral and epilimnic waters. Charr have better visual capacity under low light intensity than trout, and thus are able to find food in deeper and darker waters than the other species (Henderson and Northcote 1985). The minimum quantity of irradiance that maximizes reaction distance to prey was 2 orders of magnitudes lower in Dolly Varden charr than cutthroat trout. The continuously moving, unaggressive behaviour of charr may also make zooplankton feeding in pelagic water more profitable than for trout. Thus, the interspecific dominance and feeding activity of trout may render the profundal and pelagic habitats relatively more profitable than the littoral zone for charr. In this way, their segregation in sympatry is interactive, as charr change their habitat in the presence of the other. Thus, coexistence is probably maintained by the fact that the subordinate species has the ability to endure in the less favourable habitats, similar to earlier findings from, for instance, desert ants *Cataglyphis bicolor* Fabricius and *Cataglyphis savignyi* (Dufour), where the former forces the other into inferior habitats (Dietrich and Wehner 2003).

We found some differences between the depth distributions of the two species in the different experimental lakes, but these differences did not mask the biological significance of interspecific competition. The more littoral distribution of charr in Eunice Lake is similar to the observation of a more shallow/near-surface distribution of trout after transfer to this lake in 1982 (Hindar et al. 1988; Andrew et al. 1992), indicating that profundal waters are less profitable in Eunice Lake than in the other lakes. Thus, lake differences contribute to distributional differences between

populations, but do not mask the effects of interspecific competition acting more strongly on charr than on trout.

We conclude that habitat uses of trout and charr are affected by asymmetric competition as well as other factors such as evolved differences in resource use and lake differences. Our study strongly suggests that asymmetric competition is the main driver causing charr to be displaced from littoral habitats when sympatric with trout, while trout remain unaffected by the presence of charr. This accords with our prediction based on the results of earlier field and laboratory experiments testing the mechanisms of interspecific competition between these two salmonid species.

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Appendix

“Comparing distributions when observations are weighted”.

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