

Niche segregation between Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): an experimental study of mechanisms

Peder A. Jansen, Henning Slettvoll, Anders G. Finstad, and Arnfinn Langeland

Abstract: Interactive competition has been suggested to be an important mechanism by which brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) segregate into benthic vs. pelagic niches. According to the interactive competition hypotheses, Arctic char and brown trout should have the same preference for prey. We tested this by studying foraging performance when char and trout were offered small pelagic *Daphnia longispina* and (or) large epibenthic *Gammarus lacustris* in 10-min foraging experiments with solitary fish and with fish competing pairwise. There were obvious behavioural differences between char and trout. Trout were profoundly more aggressive than char. In comparison, char chose small pelagic daphnids and were superior daphnid foragers. Trout chose large epibenthic gammarids and were superior gammarid foragers. When competing, char and trout segregated such that rate of feeding on the chosen prey type was similar to solitary foraging fish, whereas rate of feeding on the alternative prey type was close to zero. We suggest that the observed selective differences in foraging behaviour, choice of prey, and feeding rates play an important role in niche segregation between Arctic char and brown trout. Hence, our results conform more closely with selective processes, rather than interactive processes, as the founding mechanisms for such segregation.

Résumé : On croit que la compétition interactive est un mécanisme important qui amène la Truite brune (*Salmo trutta*) et l'Omble chevalier (*Salvelinus alpinus*) à s'isoler respectivement dans une niche benthique et une niche pélagique. D'après les hypothèses reliées à la compétition interactive, l'Omble chevalier et la Truite brune devraient avoir une préférence pour les mêmes proies. Nous avons évalué cette préférence en étudiant la performance de la quête de nourriture chez des ombles et des truites isolées et en compétition deux par deux; dans des expériences de quête de nourriture pendant 10 min, nous leur offrons de petites proies pélagiques, *Daphnia longispina*, et (ou) de grandes proies épi-benthiques, *Gammarus lacustris*. Il y avait des différences de comportement évidentes entre l'omble et la truite. Les truites étaient beaucoup plus agressives que les ombles. Par comparaison, les ombles choisissaient les petites daphnies pélagiques et étaient des consommateurs plus efficaces de daphnies. Les truites préféraient les gros gammars épibenthiques et étaient de meilleurs prédateurs de gammars. Dans les expériences de compétition, les ombles et les truites se séparaient de telle façon que les taux d'alimentation et le choix des proies étaient les mêmes que chez les poissons isolés; le taux d'alimentation sur les proies de rechange était à peu près nul. Nous croyons que les différences sélectives dans le comportement alimentaire, le choix des proies et les taux d'alimentation que nous avons observés jouent un rôle important dans la ségrégation des niches chez l'Omble chevalier et la Truite brune. En conséquence, nos résultats s'accordent mieux avec l'hypothèse basée sur les processus de sélection qu'avec celle reliée aux processus interactifs comme mécanisme explicatif d'une telle ségrégation.

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Introduction

Segregation by habitat is a common means by which ecologically similar species partition resources (Schoener 1974). Studies of closely related and ecologically similar species pairs of freshwater fishes have documented segregation into benthic vs. pelagic niches when living in sympatry; green sunfish (*Lepomis cyanellus*) and bluegill sunfish (*Lepomis*

macrochirus) (Werner and Hall 1976, 1977), cutthroat trout (*Oncorhynchus clarki*) and Dolly Varden char (*Salvelinus malma*) (Andrusak and Northcote 1971; Hindar et al. 1988), as well as brown trout (*Salmo trutta* L.) and Arctic char (*Salvelinus alpinus* (L.)) (Nilsson 1967; Svärdsön 1976; Langeland et al. 1991).

A pattern emerging from these studies is an asymmetric effect of one species on the other. Nilsson (1963, 1965) ar-

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P.A. Jansen,¹ H. Slettvoll, A.G. Finstad,² and A. Langeland.³ Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway.

¹Present address: Norwegian Ministry of Fisheries, P.O. Box 8118 Dep, N-0032 Oslo, Norway.

²Present address: Department of Natural History, Norwegian University of Science and Technology, N-7491 Trondheim, Norway.

³Corresponding author (e-mail: Arnfinn.Langeland@chembio.ntnu.no).

gued that resource utilization of brown trout and Arctic char is similar in allopatry, and that both species prefer relatively large epibenthic or surface insect prey found most abundantly in littoral areas. In sympatry, the more territorial and aggressive trout displace char from littoral areas to pelagic or deeper epibenthic habitats (Nilsson 1963, 1965). Hence, Nilsson emphasized interactive competition between the species causing niche segregation. In parallel, Hindar et al. (1988) and Andrew et al. (1992) noted that experimental populations of allopatric Dolly Varden char increased their use of shallow-dwelling zoobenthos, and expanded habitat distribution compared to that in sympatry. Allopatric cutthroat trout, however, showed little change in proportions of major prey types used and in habitat distribution. The authors argue that aggressive dominance of cutthroat trout is likely to explain the greater effect of competition on Dolly Varden char. Werner and Hall (1976, 1977) studied the effect of competition for preferred prey between the congeneric bluegill and green sunfishes. The authors showed a strong asymmetry in the competition function favouring the more aggressive green sunfish in the most prosperous vegetation habitat.

Arctic char and brown trout are well suited for studies of competitive interactions since they co-exist over extensive time in relatively simple communities and their morphologies are similar, as are their habitat and resource use in allopatric populations (Nilsson 1963, 1965). A remarkable diversity of dominance ratios and flexibility in population size structures exist among sympatric char and trout populations, and there is a long history of studies on competitive interactions between natural populations of these species in Scandinavia (see Svärdsön 1976). Such studies have mainly relied on comparisons of habitat and resource utilization between allopatric and sympatric populations (Nilsson 1967; Langeland et al. 1991). However, different resource levels between study sites may confound comparative studies of habitat and resource use (Werner 1986).

Against this background, we conducted experiments to study foraging performance in juvenile (1+ years old) Arctic char and brown trout preying on small pelagic *Daphnia longispina* O.F.M. and large benthic *Gammarus lacustris* G.O. Sars, and relate such performance to interactive vs. selective segregation. Specifically, we tested the prediction based on Nilsson (1963) that both char and trout should prefer the relatively large gammarids to small daphnids when feeding without interference from competitors. Furthermore, we compared rates of feeding on small daphnids and large gammarids between the species by offering each prey singly to solitary feeding char and trout. Finally, we studied the effect of interactive competition on feeding rates by letting pairs of char and trout compete for both prey types simultaneously, or for either prey singly. Agonistic behaviour of the fish during experiments was also recorded.

Materials and methods

Predators and prey

All fish used in the experiments were first-generation hatchery-reared offspring. The brown trout originated from the alpine Lake Femunden and the Arctic char from the alpine Korssjøen, both in Central Norway. Lake Femunden

holds a multispecies community of fish. Korssjøen holds a monomorph zooplankton-consuming Arctic char population along with sympatric brown trout. The fish had been fed only standard aquaculture fish feed prior to experiments. Fish were conditioned to experimental tanks and prey at least one week prior to experiments. During the conditioning and experimental periods, fish were fed only experimental prey. Prey were regularly collected from natural ponds and stored in the laboratory.

Experimental procedures and treatments

Experimental tanks were 120-L glass aquaria (80 cm × 40 cm × 40 cm) filled with 100 L of water. The aquaria were divided into two compartments (25 and 75 L) by a transparent gate. The bottom substrate consisted of pebble (1–5 cm in diameter, off-white to brown in colour). Water temperatures were kept at 11–13°C with continuous water flow through the aquaria (0.5 L·min⁻¹). Untreated water from Jonsvatnet, Trondheim, was used. Light intensity in daylight varied (underwater quantum sensor LI-192SA, LI-COR, inc., Lincoln, Nebr., U.S.A.) in the range 2.8–4.2 × 10¹⁷ photons·m⁻²·s⁻¹ (5.4–8.2 lx), in a 16 h day : 8 h night cycle.

All experimental aquaria were stocked with six fish; either three trout and three char (mixed species assemblage), or six trout or six char (conspecific assemblages). The fish were size differentiated for individual identification so that two were small (size range: 71–100 mm for trout; 74–107 mm for char), two were medium sized (84–121 mm for trout; 81–142 mm for char), and two were large (90–152 mm for trout; 109–161 mm for char). Prior to experiments, all fish were shut into the small aquarium compartment. One of three prey-type assemblages was added to the large compartment: (i) one-hundred *D. longispina* (counted using a pipette) of sizes 1.8 mm (±0.3 mm standard deviation (SD), *N* = 123), (ii) seven *G. lacustris* of sizes 7.4 mm (±0.88 SD, *N* = 30), or (iii) two prey types (100 daphnids + 7 gammarids). Daphnids were allowed to distribute and gammarids were allowed to settle on the bottom substrate for 3 min.

Experiment 1: solitary foraging fish

To test for difference in rate of feeding on the two prey types, solitary feeding fish were offered both prey types simultaneously, or either prey type singly. Solitary fish were shunted through the gate, or netted, to the large compartment containing prey. During the following 10 min the number of each prey type consumed was counted by eyesight. After experiments, fish were netted back to the small compartment. Excess prey were removed before subsequent experiments.

The experimental procedure was followed in a successive series for all six fish in experimental fish assemblages. In aquaria with conspecific fish assemblages, similar-sized pairs of fish were tested subsequently ensuring one test for all fish in a series of experiments. Otherwise, the sequence of fish tested was random. On rare occasions, when individual fish apparently did not actively seek prey, the results were discarded. Hence, we at least duplicated, and sometimes triplicated, every successive series of experiments. From this data we used the mean number of prey consumed during 10-min experiments for individual fish in later analyses. This procedure produced independent rates of feeding on the offered prey types for all fish in an assemblage (Table 1). Fish from

both mixed and conspecific fish assemblages were tested. Fish assemblages were only used for one prey-type assemblage.

Experiment 2: two fish competing

To test whether competition alters feeding rate compared to solitary foraging fish, pairs of trout and char were offered prey. The competition experiments were conducted upon conclusion of the solitary feeding experiments, with the same fish assemblages being offered the same prey assemblages. Competition experiments were only done in mixed-species fish assemblages. The number of gammarids consumed during 10-min experiments was counted for both fish simultaneously. The number of daphnids consumed in 30 s was counted for one randomly chosen fish and then the number was counted for the competitor fish the next 30 s, throughout experiments. After experiments, fish were netted back to the small compartment. Excess prey were removed before subsequent experiments.

In a series of competition experiments within a fish assemblage each trout competed pairwise against each char, producing nine experimental trials. The sequence of trials with individual fish was random. Feeding rate for individual fish was calculated from the mean number of prey consumed in three experimental trials (against each of the opponent species). No experiments were discarded. This procedure produced rates of feeding on the offered prey types for all six fish in each of the experimental fish assemblages (Table 1).

Prey and predator behaviour

To relate prey consumption to fish behaviour, we present descriptive observations on prey and predator behaviour. In the competition experiments, we recorded the number of attacks launched by one fish towards the other. An attack was recorded when one fish chased the other with accompanying threat display (Kalleberg 1958). We also noted when gammarids were caught on the substratum or swimming in the water column.

Data analyses

The rate of feeding on prey is presented as the mean number of prey consumed per fish over the 10-min experimental period. In the competition experiments we doubled the observed number of daphnids consumed as an estimate of the total number consumed, since daphnid consumption was only observed every half minute per fish. Furthermore, rate of feeding on prey and the number of launched attacks for individual fish is averaged over the three experimental trials, involving each fish from the opponent species group. All statistical tests used are Student's *t* tests (two tailed). The threshold level of significance was set at $p < 0.05$.

Results

Prey and predator behaviour

The gammarids distributed in a plane over the substrate where they could be hidden when inactive. When active, the gammarids crawled over the substratum, or swam, mostly over short distances and close to the substratum. The daphnids distributed over the volume of the tank.

Trout searching for gammarids normally positioned centrally in the aquarium, with the tail fin close to the substratum. When gammarids were encountered, quick, voracious attacks were launched, after which the fish returned to the fixed position. Trout caught 54% of gammarids on the substratum and 46% swimming in the water column ($n = 626$). Daphnid consumption by trout was characterized by an uneven start and stop movement.

Char typically cruised about the aquarium. Attacks on gammarids were slower and more hesitant than for trout. Char caught 11% of gammarids on the substratum and 89% in the water column ($n = 218$). Char normally picked consecutive daphnids while cruising at a constant speed, and were consistently positioned higher in the water column than trout.

Trout were markedly more aggressive than char (Figs. 1a–1c). Prey assemblage did not significantly affect the number of launched attacks for either char or trout. Analyses of relationships between the number of launched attacks and prey consumption did not give conclusive results.

Experiment 1: solitary foraging fish

There was no significant effect of mixed vs. conspecific fish assemblage on feeding rate in any of the three prey-type assemblages (Figs. 2a–2d), with the exception of trout feeding on gammarids in one prey-type experiment ($t_{13} = 2.25$, $p = 0.042$). Hence, results from mixed and conspecific assemblages are pooled in further statistical treatment.

Char and trout clearly chose different prey types. Char consumed nine times the number of daphnids consumed by trout, whereas trout consumed 3.2 times the number of gammarids consumed by char (Figs. 2a, 2c). No fish diverged from this choice of prey-type pattern since all char consumed more daphnids than any trout, and vice versa concerning gammarids.

Char and trout choice of prey type was related to differences in consumption rate. Char feeding rate was significantly higher than for trout when offered only daphnids ($t_{22} = 3.31$, $p = 0.003$; Fig. 2b). Conversely, trout feeding rate was significantly higher than for char when offered only gammarids ($t_{28} = 5.63$, $p < 0.001$; Fig. 2d).

Prey assemblage significantly influenced char and trout rate of feeding on the nonchosen prey, but not that of the chosen prey. Char more than doubled rate of feeding on gammarids when offered only such, compared with when two prey types were offered ($t_{43} = 6.27$, $p < 0.001$; Figs. 2c, 2d). Conversely, trout increased rate of feeding on daphnids nearly sevenfold when offered only such, compared with when two prey types were offered ($t_{40} = 9.15$, $p < 0.001$; Figs. 2a, 2b). Rate of feeding on daphnids for char was 66.9 and 65.8 (Figs. 2a, 2b), and rate of feeding on gammarids for trout was 4.93 and 4.90 (Figs. 2c, 2d), in experiments with one prey type and two prey types, respectively.

Experiment 2: two fish competing

When char and trout competed for two prey types, they segregated. Char rate of feeding on gammarids was only 0.3, whereas rate of feeding on daphnids was similar to solitary foraging char (Figs. 3a, 3c). Trout feeding rate on daphnids was less than 5, whereas rate of feeding on gammarids was similar to solitary foraging trout (Figs. 3a, 3c).

Table 1. Number of aquaria and fish used in the foraging experiments with different prey and fish assemblages.

Prey assemblage	Fish assemblage	No. aquaria	No. fish	
			Arctic char	Brown trout
Two choice	M	6	18	18
	C	4	12	12
Single-prey daphnids	M	2	6	6
	C	2	6	6
Single-prey gammarids	M	3	9	9
	C	2	6	6

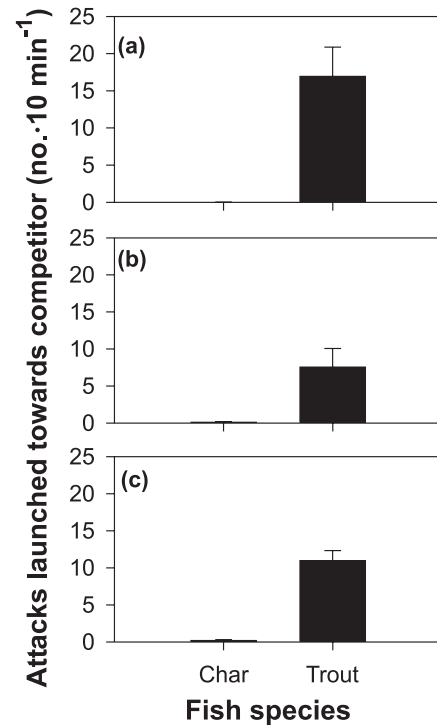
Note: C, conspecific; M, mixed species.

The effect of trout on rate of char feeding on the non-chosen prey was more severe than the effect of char on feeding rate of trout on the nonchosen prey. Trout rate of feeding on gammarids was about 15-fold that of char in trout–char competition for one prey type (Fig. 3d). Conversely, char rate of feeding on daphnids was about double that of trout (Fig. 3b).

Discussion

The present foraging experiments revealed marked differences between char and trout in behaviour, choice of prey type and rate of feeding on the two prey types. Trout aggression and territoriality agree fully with previous reports (Kalleberg 1958; Nilsson 1963). Char, on the contrary, showed little aggression, positioned high in the water column, and cruised constantly during foraging. Comparatively, char chose small pelagic *D. longispina*, whereas trout chose large epibenthic *G. lacustris*, when given the option to prey on both prey types. Feeding rate varied significantly between the species according to choice of prey type when only one prey type was offered. When offered both prey types, the presence of nonchosen prey did not affect rate of feeding on chosen prey. The fish used had only experienced standard aquaculture fish feed prior to experiments. Thus, prey choice and consumption rate reflected innate differences between experimental Arctic char and brown trout, and was not influenced by previous learning.

The differences in choice of prey type, feeding rate, and behavioural performance emphasize a selective foundation for niche segregation between Arctic char and brown trout. Our prediction, based on Nilsson (1963), that both species would prefer gammarid prey, was rejected. Nilsson's (1963) basis for suggesting similar prey preference in char and trout was partly founded on foraging experiments and partly founded on observing similar diets in stomach contents from allopatric char and trout. In the foraging experiments food pellets of different coloration were offered to char and trout, and either on the surface or on the bottom of aquaria. Although behavioural differences were emphasized, there was no apparent difference in the ranking of food categories between char and trout. Nilsson concluded that trout and char had the same preferences for the offered foods. This discrepancy compared to our results may relate to the different experimental foods. It is more likely that the natural prey offered in the present study more accurately reflects prey

Fig. 1. Mean (+ standard error) number of launched attacks over 10 min towards competitor in Arctic char and brown trout pairwise competition experiments with (a) single prey type daphnia, (b) single prey type gammarus, and (c) two prey types.

choice in nature. Furthermore, no pelagic prey was offered in Nilsson's (1963) experiments.

Nilsson (1963, 1965) reported striking similarities in resource utilization between natural populations of allopatric char and trout. Both species were reported to prefer *Gammarus*, *Lymnaea*, ephemeropterid nymphs, and terrestrial insects (Nilsson 1963). These are relatively large prey found abundantly in littoral and near-shore areas. However, there are at least two problems with Nilsson's conclusions. First, there is no mention of the size of char and trout that Nilsson studied other than size distributions being similar between species. Judging from the composition of mesh sizes in the gang of gillnets used to sample fish (Nilsson 1965), and more recent studies on gillnet selectivity (e.g., Finstad et al. 2000), it is probable that the sampled fish have been grossly biased towards the larger fish in the populations. Effects of size on trophic ecology (e.g., size-related foraging efficiency and energy demand reinforcing ontogenetic niche shifts in fish) have increasingly been emphasized (see Werner 1986; Ebenman and Persson 1988). Arctic char are commonly reported to shift from foraging small prey in the pelagic to larger benthic prey (Hindar and Jonsson 1982; Forseth et al. 1994). Thus, we suspect that pelagic zooplankton prey plays a more dominant role as a resource for allopatric char than was inferred from Nilsson's samples, as is supported by more recent studies (Langeland 1986; Langeland et al. 1991). Further contributing to this line of evidence is that zooplanktivorous char may do very well in terms of growth and food acquisition (Hegge et al. 1989; P.A. Jansen, personal observations). Second, niche comparisons between allopatric and sympatric populations are likely to be con-

Fig. 2. Mean (+ standard error) rate of feeding on (a, b) daphnids and (c, d) gammarids by solitary foraging fish offered both daphnids and gammarids (two prey types, upper panels), or either prey type singly (single prey type, lower panels), over 10-min experiments. Solid bars, conspecific experimental units; open bars, mixed species units.

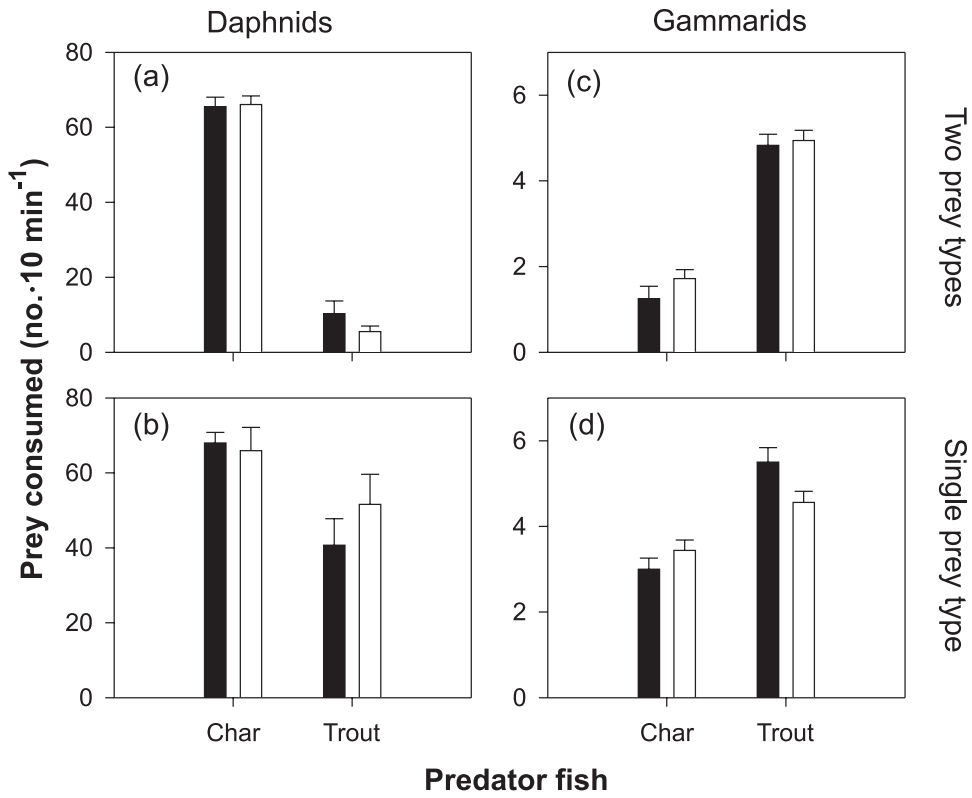
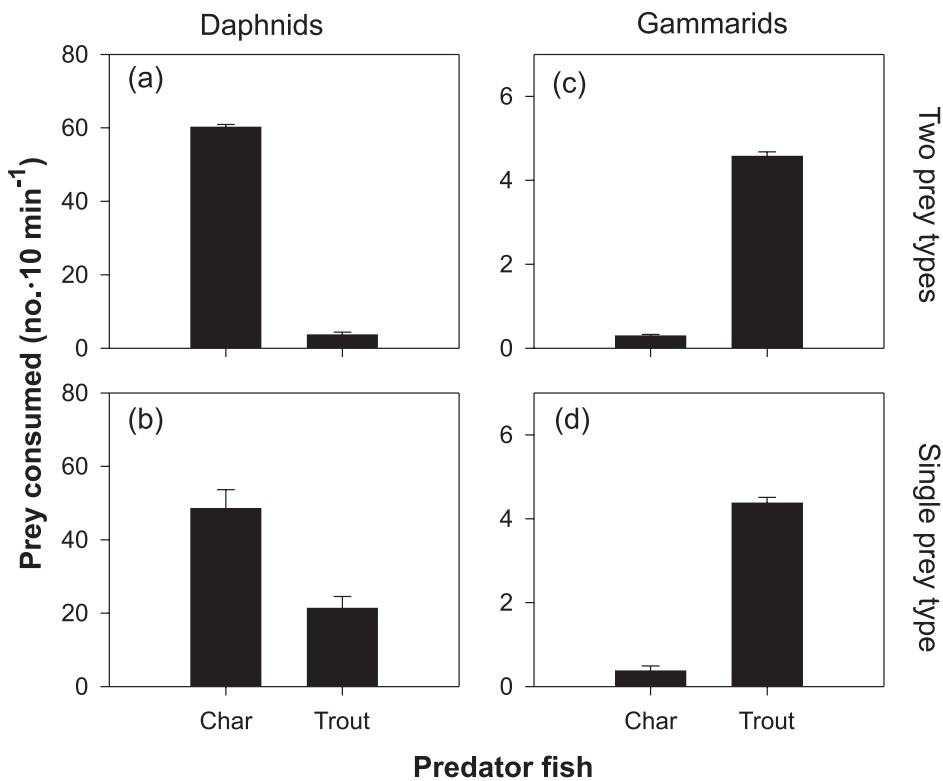


Fig. 3. Mean (+ standard error) rate of feeding on (a, b) daphnids and (c, d) gammarids by pairwise-competing Arctic char and brown trout offered both daphnids and gammarids (two prey types, upper panels), or either prey type singly (single prey type, lower panels), over 10-min experiments.



founded by differences in resource abundance or availability between study sites (Nilsson and Pejler 1973; Werner 1986).

In the competition experiments described here, char and trout segregated with respect to proportions of daphnids and gammarids consumed when offered both prey types. Consumption of the nonchosen prey was close to zero for both species. This was a trivial result since prey depletion during the experiments was in the order of 60–80% for both prey types, which implied that after having depleted the chosen prey type, also the alternative prey type would be depleted by the competitor fish. Nevertheless, the result is instructive in demonstrating that exploitation of resources can lead to interactive segregation (*sensu* Nilsson 1967).

Apart from trout being profoundly more aggressive than char, there were no simple relationships between aggressive behaviour and prey consumption. However, aggressive behaviour may be more beneficial in holding favourable foraging positions in the long run, as shown for stream salmonids (e.g., Nakano et al. 1999), than in the present experiments where prey abundance quickly diminished. Nevertheless, the profound aggression in trout illustrates a potential for interference processes playing a role in segregation between Arctic char and brown trout. Also, the present results agreed with the notion that trout had a larger competitive effect on char than vice versa (Nilsson 1967; Hindar et al. 1988; Langeland et al. 1991).

In conclusion, the present foraging experiments revealed selective differences between small Arctic char and brown trout in foraging behaviour, choice of prey, and rate of feeding on prey. In comparison of the species, Arctic char chose small pelagic daphnids and were superior daphnid foragers with respect to feeding rate. Brown trout chose large epibenthic gammarids and were superior gammarid foragers. We suggest that these selective differences in foraging performance play an important role in niche segregation between Arctic char and brown trout. Hence, our results conform more closely with selective processes, rather than interactive processes, as the founding mechanisms for such segregation. This conclusion was also reached by Schutz and Northcote (1972) in an experimental study of feeding behaviour and interaction of cutthroat trout and Dolly Varden char.

References

- Andrew, J.H., Jonsson, N., Jonsson, B., Hindar, K., and Northcote, T.G. 1992. Changes in use of lake habitat by experimentally segregated populations of cutthroat trout and Dolly Varden char. *Ecography*, **15**: 245–252.
- Andrusak, H., and Northcote, T.G. 1971. Segregation between adult cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. *J. Fish. Res. Board Can.* **28**: 1259–1268.
- Ebenman, B., and Persson, L. 1988. Dynamics of size-structured populations: an overview. *In* Size structured populations: ecology and evolution. *Edited by* B. Ebenman and L. Persson. Springer-Verlag, London. pp. 3–9.
- Finstad, A.G., Jansen, P.A., and Langeland, A. 2000. Gillnet selectivity and size and age structure of an alpine Arctic char (*Salvelinus alpinus*) population. *Can. J. Fish. Aquat. Sci.* **57**: 1718–1727.
- Forseth, T., Ugedal, O., and Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic char, *Salvelinus alpinus*. *J. Anim. Ecol.* **63**: 116–126.
- Hegge, O., Dervo, B.K., Skurdal, J., and Hessen, D.O. 1989. Habitat utilization by sympatric arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in Lake Atnsjø, south-east Norway. *Freshw. Biol.* **22**: 143–152.
- Hindar, K., and Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic char (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. *Can. J. Fish. Aquat. Sci.* **39**: 1030–1045.
- Hindar, K., Jonsson, B., Andrew, J.H., and Northcote, N. 1988. Resource utilisation of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia*, **74**: 481–491.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L., and *Salmo trutta* L.). *Rep. Inst. Freshw. Res. Drottningholm*, **39**: 55–98.
- Langeland, A. 1986. Heavy exploitation of a dense resident population of Arctic char in a mountain lake in Central Norway. *N. Am. J. Fish. Manag.* **6**: 519–525.
- Langeland, A., L'Abée-Lund, J.H., Jonsson, B., and Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *J. Anim. Ecol.* **60**: 895–912.
- Nakano, S., Fausch, K.D., and Kitano, S. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *J. Anim. Ecol.* **68**: 1079–1092.
- Nilsson, N-A. 1963. Interaction between trout and char in Scandinavia. *Trans. Am. Fish Soc.* **92**: 276–285.
- Nilsson, N-A. 1965. Food segregation between salmonid species in North Sweden. *Rep. Inst. Freshw. Res. Drottningholm*, **46**: 58–78.
- Nilsson N-A. 1967. Interactive segregation between fish species. *In* The biological basis for fresh water fish production. *Edited by* S.D. Gerking. Blackwell Scientific Publications, Oxford. pp 295–313.
- Nilsson, N.-A., and Pejler, B. 1973. On the relation between fish fauna and zooplankton in North Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm*, **53**: 51–77.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science*, **185**: 27–39.
- Schutz, D.C., and Northcote, T.G. 1972. An experimental study of feeding behaviour and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). *J. Fish. Res. Board Can.* **29**: 555–565.
- Svårdson, G. 1976. Inter-specific population dominance in fish communities of Scandinavian lakes. *Rep. Inst. Freshw. Res. Drottningholm*, **55**: 144–171.
- Werner, E.E. 1986. Species interactions in freshwater fish communities. *In* Community Ecology. *Edited by* J. Diamond and T.J. Case. Harper & Row, New York. pp. 344–358.
- Werner, E.E., and Hall, D.J. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science*, **191**: 404–406.
- Werner, E.E., and Hall, D.J. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology*, **58**: 869–876.