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ARTICLE

Density-dependent interactions in an Arctic char – brown trout system: competition, predation, or both?

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Abstract: In the study of mechanisms structuring fish communities, mixed competition–predation interactions where large predators feed on prey fish versus those in which small predators compete with prey fish for a shared prey have been the focus of substantial research. We used a long-term data set from a system inhabited by brown trout (*Salmo trutta*) (predator) and Arctic char (*Salvelinus alpinus*) (prey) to evaluate whether mixed interspecific interactions were present in this system as suggested in other studies focusing on this species pair. We found no evidence for a negative interspecific density dependence in individual performance in either Arctic char or brown trout. In contrast, a negative intraspecific density dependence was present, especially in Arctic char. Furthermore, large brown trout condition showed a positive response to encounter rate with Arctic char (related to the density of small Arctic char). The most parsimonious interaction module to explain the Arctic char – brown trout interaction patterns in the studied system does therefore not need to include interspecific competition. We suggest that size-structured mixed competition–predation interactions in different systems are realized as being either mainly structured through interspecific predation or by competition depending on species life history characteristics and environmental conditions.

Résumé : Dans l'étude des mécanismes qui structurent les communautés de poissons, les interactions mixtes de concurrence–prédation au cours desquelles de grands prédateurs se nourrissent de poissons proies alors que des petits prédateurs se disputent avec ces derniers des proies communes ont fait l'objet de nombreuses études. Nous avons utilisé un ensemble de données de longue durée portant sur un système habité par la truite de mer (*Salmo trutta*) (prédateur) et l'omble chevalier (*Salvelinus alpinus*) (proie) afin d'évaluer si des interactions interspécifiques mixtes étaient présentes, comme le suggèrent d'autres études centrées sur cette paire d'espèces. Nous n'avons rien noté qui indiquerait la présence d'une dépendance interspécifique négative de la densité sur le plan de la performance individuelle tant de l'omble chevalier que de la truite de mer. En revanche, il y avait bel et bien une dépendance intraspécifique négative de la densité, en particulier chez l'omble chevalier. En outre, l'embonpoint des grandes truites de mer présentait une réaction positive par rapport à la fréquence des rencontres avec des ombles chevaliers (reliée à la densité des petits ombles chevaliers). Il n'est donc pas nécessaire que le mode d'interaction le plus parcimonieux pouvant expliquer les motifs d'interactions entre ombles chevaliers et truites de mer dans le système étudié inclue la concurrence interspécifique. Nous postulons que les interactions mixtes concurrence–prédation structurées par la taille dans différents systèmes sont principalement structurées par la prédation interspécifique ou par la concurrence, selon les caractéristiques des cycles biologiques des espèces et les conditions ambiantes. [Traduit par la Rédaction]

Introduction

The density-dependent factors that structure ecological communities are the subject of continuous discussion in ecology. Ecologists in general have been largely focused on studying the relative roles of competition and predation, particularly their interplay (Leibold 1996; Mylius et al. 2001; Borer et al. 2007). In many systems predation and competition are intertwined, in that a consumer species may both compete with and be preyed upon by a predator such as in intraguild predation (IGP) systems (Holt and Polis 1997; Diehl and Feissel 2000; Mylius et al. 2001). IGP systems have been suggested to be particularly prevalent in fish communities because individuals undergo major ontogenetic niche changes over their life cycle, leading to life history IGP (Werner and Gilliam 1984; Olson et al. 1995; Byström et al. 1998). The IGP system here consists of smaller individuals of the IG predator competing with IG prey, whereas larger individuals of the IG predator prey on the IG prey (also termed mixed life history competition–predation) (Werner and Gilliam 1984; Olson et al. 1995; Byström

et al. 1998). For size-structured IGP systems where individual growth of predator and prey depends on food levels, theory predicts that coexistence of IG predator and prey is fragile when IG predator and IG prey are of relatively similar size and the IG predator can mature on the shared resource alone (Van de Wolfshaar et al. 2006; Hin et al. 2011). This expectation has been supported by both field and laboratory experimental studies (Persson et al. 2007a; Schröder et al. 2009). In light of these theoretical and experimental results, the mechanisms promoting coexistence of predator and competing prey in size-structured fish communities and the question of whether predation and interspecific competition occur at the same time have therefore become important issues to analyze.

Here we investigate the long-term temporal dynamics in Lake Takvatn, Norway, inhabited by brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*). This species pair has historically been presented as a classic example of competition-induced interactive segregation (Nilsson 1978; Jansen et al. 2002; Ulvan et al. 2012).

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Furthermore, IGP involving both interspecific competition and predation has in many studies been suggested to characterize the Arctic char – brown trout system based on substantial evidence for the presence of interspecific piscivory, especially in brown trout (Langeland et al. 1991; L'Abée-Lund et al. 1992). In a previous paper, we provided evidence for the existence of alternative stable community states consisting of either a single population of Arctic char or coexisting populations of Arctic char and brown trout (Persson et al. 2007*b*). The simplest explanation for the occurrence of these alternative stable states is based on a combination of intraspecific competition in Arctic char and size-dependent interspecific predation by brown trout (De Roos and Persson 2002), without invoking any interspecific competition between the two species. In this scenario, strong intraspecific competition in Arctic char will lead to a stunted Arctic char population with low population fecundity. Interspecific predation from brown trout will reduce the strong intraspecific competition in Arctic char through thinning and, in turn, lead to increased population fecundity and eventually more small Arctic char prey suitable for predacious brown trout.

Because the above explanation does not incorporate the presence of interspecific competition between Arctic char and brown trout, it contrasts with all other studies on this species that have invoked either interspecific competition (Nilsson 1963, 1965; Ulvan et al. 2012) or a simultaneous mixture of interspecific competition and predation (e.g., Langeland et al. 1991) to explain community patterns in this species pair. The aim of the present study was to test whether the interaction between Arctic char and brown trout in Lake Takvatn also involves the simultaneous presence of interspecific competition in addition to interspecific predation by brown trout on Arctic char. Assessing the importance of interspecific competition as a structuring factor in fish communities not only has implications for the management of these communities, but is also important in a wider context, as theory (discussed above) suggests that simultaneous mixed competition–predation interactions reduce the persistence of consumers and predators.

For our analysis we took advantage of the large between-year variation in densities observed for Arctic char and brown trout in Takvatn, which allowed us to investigate the presence of different types of density dependence. We first tested whether the habitat use of Arctic char was dependent on brown trout density, since classic competition studies on brown trout and Arctic char have used brown trout induced habitat shifts in Arctic char as evidence for interspecific competition (Nilsson 1963, 1978). Second, we tested whether Arctic char growth rate was negatively related to brown trout density. Third, we tested whether brown trout performance (body condition) at different sizes was negatively affected by Arctic char density and whether large brown trout condition was positively related to encounter rate with Arctic char. In the presence of simultaneous mixed competition–predation, we expected small brown trout to be negatively affected by Arctic char via interspecific competition for shared resources, whereas large brown trout performance was expected to be positively related to Arctic char density through predation (see Persson and De Roos 2012).

Materials and methods

System studied

Lake Takvatn is a low-productivity lake with a surface area of 15 km² and a catchment area of 66 km² in northern Norway (Klemetsen et al. 1989). The lake is dimictic, and the ice-free season normally lasts from the end of May until November (Dahl-Hansen 1995). Birch (*Betula pubescens*) trees dominate the vegetation along the shores, and the lake is almost devoid of helophyte and floating leaf vegetation. The submerged vegetation is dominated by mats

Fig. 1. Catch per unit effort (CPUE; no. of fish per 100 m² gillnet area per night) of Arctic char in the littoral, profundal, and pelagic habitats and brown trout (littoral habitat) from 1980 to 2006.
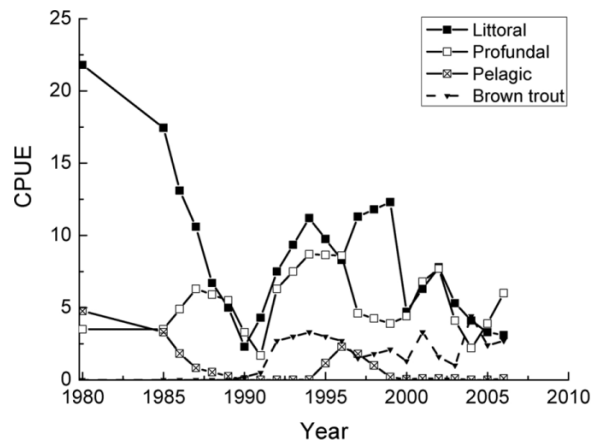
of *Nitella* in the 4–11 m zone. The maximum depth of the lake is 80 m.

Brown trout was the only species in the lake until the 1930s. Extensive fishing led to the decline of brown trout, and Arctic char was introduced in 1930 (Klemetsen et al. 1989). By 1980, the Arctic char population had increased to a high density and was totally dominated by small-sized char. Threespined sticklebacks (*Gasterosteus aculeatus*) were introduced to Lake Takvatn in 1950 and today form a dense population in the lake. Since long-term trends have not been documented for sticklebacks, as they have been for Arctic char and brown trout (Klemetsen et al. 2002), the focus of the analysis was restricted to the latter two species. Intensive fishing of Arctic char using funnel traps with a mesh size of 12 mm took place from 1984 to 1989, when a total of 666 000 Arctic char (31.3 t) were removed with baited funnel traps (Amundsen et al. 1993; Klemetsen et al. 2002). Another 25 000 char were removed in 1990 and 1991, after which the reduction was terminated. In 1989, the density of char had decreased to below 30% of the initial level as a result of intensive fishing (Fig. 1).

The long-term effects of the heavy thinning of Arctic char have been covered elsewhere (Klemetsen et al. 2002; Persson et al. 2007*b*) and are only shortly reported here as a background to the analyses of different possible mechanisms structuring the system. The removal of Arctic char in 1984–1989 resulted in an increase in the density of brown trout starting in 1990, and from 1992 until 2006, brown trout density remained more or less constant (Fig. 1). Strong evidence that the preremoval and postremoval periods represents two alternative stable states is provided by the fact that individual growth rates of Arctic char and brown trout population density have remained high over several generations (1992–2006) (see Persson et al. 2007*b*).

Sampling and measurements

Arctic char and brown trout were sampled using a standardized series of gillnets in the littoral (<15 m), profundal (25–40 m), and pelagic (offshore, 0–6 m) zones of the lake. Net series of single nets with mesh sizes from 10 to 52 mm (knot to knot) were used from 1983 to 1988 (Klemetsen et al. 1989; Amundsen et al. 1993). From 1989, we changed to 40 m long multimesh nets with eight panels ranging from 10 to 45 mm. In the littoral and profundal zones, 1.5 m deep benthic nets were used, whereas 6 m deep floating nets were used in the pelagic habitat. The nets were set overnight (~12 h) for 3–4 nights, and on each sampling occasion the catch effort was usually >25 gillnet nights in the littoral, 8–12 in the profundal, and 6–8 in the pelagic habitat. Owing to extensive gillnet area and sampling time and the integrated range of mesh sizes in each standardized gillnet, the fish catches were in general

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Fig. 2. Density of Arctic char in the pelagic (pel) and profundal (prof) habitats as a function of littoral Arctic char density (*a*) and brown trout density (*b*).
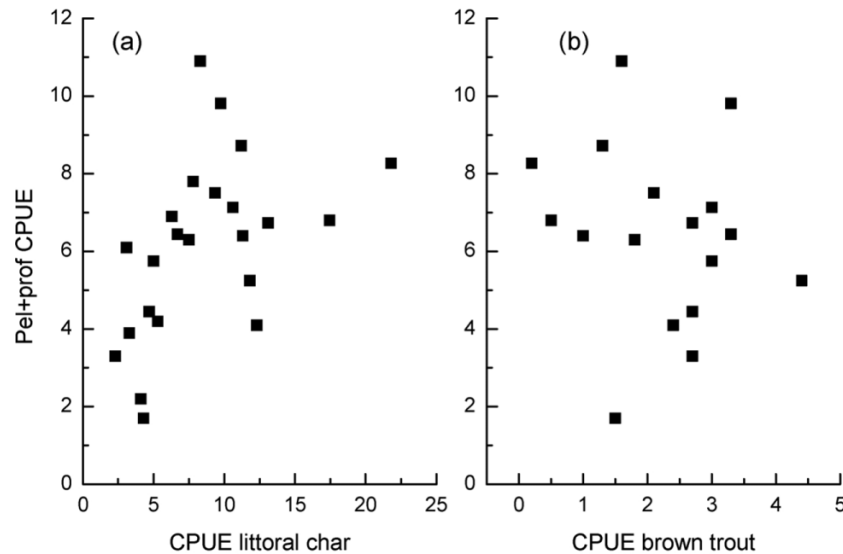
evenly distributed among the nets. Population densities were compared between years using estimates of catch per unit effort (CPUE). The CPUE was standardized as number of fish caught per 100 m² gillnet area per night during August sampling periods to avoid any effects of seasonal variability in activity levels and catchability (Amundsen et al. 2007).

Each fish was weighed and measured (fork length), and otoliths were taken for age determination from random subsamples of fish. Ageing of fish (Arctic char) was based on surface readings of otoliths submerged in glycerol (Klemetsen et al. 2002). Individual growth rates of Arctic char were estimated as specific growth rate (SGR, %):

$$SGR = (\ln W_{t-l} - \ln W_t) \times 100$$

where W_t and W_{t-1} are the wet masses of a year class of Arctic char in the year under consideration and in the previous year, respectively (see also Amundsen et al. 2007). The specific growth rates of Arctic char were related to fish density (CPUE). The study period of growth rates of char was 1980–2005, and years with missing or few data points (1981–1985, 1988, 1993, 1995, 1996, 1998, and 2002) were excluded from the analysis. For brown trout, data on size at age was not present for the whole study period. Instead, the size-dependent performance of brown trout in different years was measured as body condition estimated as the wet mass for four different lengths (100, 200, 300, 400 mm). Body masses of brown trout of different body lengths were estimated from mass–length regressions in different years (1998–2006). These regressions were based on sample sizes of 12–148 individuals, with years having samples sizes <10 individuals were excluded from the analyses (1988, 1991, 1998).

Relative encounter rates of brown trout of different sizes with different size classes of Arctic char in different years were calculated from a prey–predator function, determined by three linear relationships between prey and predator body length (*p*): a lower boundary with slope δ as a function of predator body length below which the predator cannot see the prey, an upper boundary with slope ε above which the predator cannot capture the prey because of prey evading and gape-width constraints, and an optimal prey–predator size ratio with slope ϕ. Between the lower and upper boundaries δ*p* and ε*p*, respectively, the attack rate on differently sized prey for a specific predator length (*p*) was assumed to increase linearly with victim size from zero at δ*p*, to an optimum at

ϕ*p*, to thereafter decrease and become zero when victim length reaches ε*p*. Parameter values of δ, ϕ, and ε for brown trout are 0.07, 0.2, and 0.4, respectively (L'Abée-Lund et al. 1992; Hyvärinen and Huusko 2006). Because we calculated encounter rates in different years relative to each other, the optimum attack rate occurring at ϕ*p* was set to 1 without loss of generality. Total encounter rates for two size classes of brown trout (300, 400 mm) with Arctic char in different years were calculated by summing encounter rates with different char sizes using CPUE data for arctic char partitioned into different char size classes (5 mm classes).

Statistical analyses of patterns were largely based on regressions (linear regressions based on log-transformed data). For model selection of Arctic char density dependence, we used the Akaike information criteria (AIC). For all regressions presented, tests for autocorrelations (ARIMA) at lag 1 were carried out, in all cases yielding $P > 0.1$.
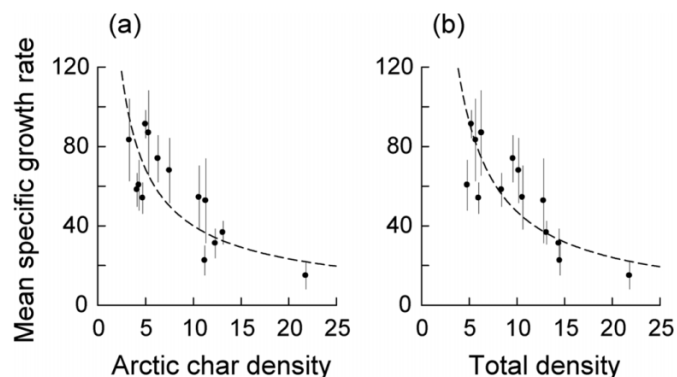
Results

Density-dependent habitat use and performance of Arctic char

The range of densities present over the study years (1980–2006) was 2.3–21.8 (10-fold difference) for Arctic char and 0.2–4.2 (20-fold difference) for brown trout. Catches of Arctic char in the pelagic habitat were overall low, whereas the density of Arctic char in the profundal habitat after the thinning was as high as in the littoral habitat (Fig. 1). Brown trout were predominantly captured in the littoral habitat (978 out of 994 total captured individuals during 1980–2006). In total, only 5 brown trout individuals were captured in the profundal habitat before, during, and after the experimental thinning of Arctic char, and 11 individuals were captured in the pelagic habitat in 2002–2004. The patterns in density-dependent habitat use of Arctic char suggest that this was largely intraspecifically driven, as Arctic char use of the pelagic and profundal habitats was strongly affected by Arctic char density ($n = 23$, $R^2 = 0.25$, $P = 0.02$), but not by brown trout density ($n = 17$, $R^2 = 0.003$, $P = 0.48$; Fig. 2).

A strong intraspecific density dependence in individual growth rate of Arctic char was present, as detected by regression of Arctic char mean SGR on CPUE ($R^2 = 0.66$, $P < 0.001$, AIC = 118.2; Fig. 3*a*). Adding trout density did not improve the regression model, as trout CPUE was not significantly associated with SGR ($P = 0.19$), and the AIC associated with the expanded model did not decrease ($R^2 = 0.70$, $P < 0.001$, AIC = 118.0; Fig. 3*b*). Hence a model only

Fig. 3. Mean annual specific growth rate (%; ± standard error) of littoral Arctic char as a function of (*a*) its own density and (*b*) total salmonid density (Arctic char plus brown trout) from 1980 to 2005. Power curves fitted to the data are as follows: (*a*) $Y = 0.240 \times 10^3 X^{-0.776}$; $R^2 = 0.66$, $P < 0.001$; (*b*) $Y = 0.447 \times 10^3 X^{-0.975}$; $R^2 = 0.68$, $P < 0.001$.

Table 1. Regressions of body condition (g) of different-sized brown trout on total density of Arctic char, density of Arctic char <15 cm (both catch per unit effort, CPUE), and encounter rate with Arctic char.

Brown trout size (mm)	Total density			Density <15 cm			Encounter rate		
	$F_{[1,16]}$	P	Slope	$F_{[1,16]}$	P	Slope	$F_{[1,14]}$	P	Slope
100	0.10	0.760	0.02	1.58	0.227	−0.07			
200	5.28	0.036	0.07	2.22	0.156	0.04			
300	3.17	0.095	0.10	6.20	0.025	0.10	6.68	0.023	0.10
400	2.14	0.164	0.12	6.35	0.024	0.15	11.0	0.006	0.20

Note: For brown trout sizes of 100 and 200 mm, no estimates of encounter rates are given because their small sizes resulted in either zero (100 mm) or very low encounter estimates (200 mm). Regressions were based on log-transformed data.

incorporating Arctic char density was the superior one. Furthermore, a model incorporating only brown trout density showed no relationship with char mean SGR ($R^2 = 0.01$, $P = 0.71$, AIC = 133.1).

Density dependence in brown trout performance

No negative effect of Arctic char density on brown trout performance was present that would provide evidence for an interspecific competitive effect of Arctic char on brown trout. Instead, very weak positive relationships (brown trout body condition versus total Arctic char density) or for larger size classes of brown trout even significant positive relationships with Arctic char density (brown trout body condition versus Arctic char <15 cm density) were present (Table 1; Fig. 4). The latter pattern can be related to the fact that small Arctic char represent prey for large-sized brown trout, where a higher density of small Arctic char implies a higher encounter rate for large-sized brown trout with prey. This interpretation was supported by a positive relationship between the condition of large-sized brown trout and estimates of encounter rate with Arctic char in different years (Table 1, Fig. 4). It should be noted that the significance of these relationships depended on the inclusion of the two data points with the lowest density of char <150 mm and the lowest encounter rate (Fig. 4). A significant negative intraspecific density dependence was present for brown trout of size classes 200 and 300 mm, whereas no significant intraspecific density dependence was present for the size classes 100 and 400 mm (Table 2).

Discussion

Evidence for interspecific competition in Lake Takvatn

The large between-year variation in densities observed for both Arctic char (10-fold) and brown trout (20-fold) in Takvatn allowed us to investigate the presence of different types of density dependence. We found that the performance of Arctic char was largely explained by intraspecific density dependence. In contrast, brown trout density neither explained the individual growth rate, nor the habitat use of Arctic char. Similarly, we found no evidence for a negative interspecific competitive effect of Arctic char on brown trout in the size range of 100–400 mm. If anything we found positive relationships between Arctic char density and brown trout condition. Except for the effect of encounter rate with Arctic char for large brown trout condition, these positive relationships were, however, not overly strong and would disappear if corrections for multiple tests would have been made (observe that the latter does not affect our major conclusion about the lack of negative effects of Arctic char on brown trout). Although data on individual growth rates rather than size-specific conditions for brown trout would have been preferable, the most parsimonious

explanation for the pattern in density dependence in Arctic char and brown trout does thus not need to include interspecific competition.

The lack of evidence for interspecific density dependence with respect to competition in the time series from Lake Takvatn is in conflict with existing views on the interactions between this species pair. In fact, the Arctic char and brown trout system has generally been interpreted as a classic example of a system driven by interspecific competition. This interpretation has mainly been based on evidence from seasonal shifts in diet and habitat use (Nilsson 1965; Hegge et al. 1989), comparisons of lakes with sympatric and allopatric populations (Nilsson 1963; Halvorsen et al. 1997; Hesthagen et al. 1997), and small-scale experiments (Jansen et al. 2002). In contrast, there is a lack of evidence for interspecific competition using the kind of long-term data present for Lake Takvatn. Still, in a comparative study covering 18 Norwegian lakes, Ulvan et al. (2012) showed a negative effect of Arctic char presence on the food consumption of brown trout, particularly in winter.

An explanation for this discrepancy in the results between studies may be that system characteristics determine whether interspecific competition between brown trout and Arctic char is present. There are two pieces of information suggesting that the major interactions present may actually vary between systems. First, the habitat use of Arctic char and brown trout in Takvatn appears to be much more similar than in some other studies (Nilsson 1963; Hegge et al. 1989; Langeland et al. 1991). This relates especially to the extended use of the littoral habitat and the limited use of the pelagic habitat by Arctic char in Takvatn. Second, the extent to which brown trout use tributaries and outflows as nursery habitats and habitats for growth among smaller brown trout may differ between systems, leading to differences in the extent to which interspecific competition is operating. The latter hypothesis could be tested by comparing Arctic char and brown trout populations as a function of the amount of running water relative to lake size or circumference.

Mixed interspecific competition–predation interactions

To more broadly address the question about the interactions between Arctic char and brown trout, especially the role of interspecific competition (i.e., Ulvan et al. 2012), we need to consider the Arctic char – brown trout system in the context of mixed competition–predation (IGP) theory given that interspecific piscivory has been documented based on diet analyses, especially for brown trout (L'Abée-Lund et al. 1992; Amundsen 1994). Unstructured IGP theory predicts that alternative stable states may occur at intermediate productivities between a state with predator, intermediate consumer, and shared resource coexisting and the other state with only predator and shared resource present owing to predator-induced extinction of the intermediate consumer (Holt and Polis 1997; Diehl and Feissel 2000; Mylius et al. 2001). The

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Fig. 4. Body condition (wet mass, g) of different-sized trout (100, 200, 300, 400 mm) as a function of (*a*) Arctic char <150 mm, (*b*) total Arctic char density, and (*c*) encounter rate with Arctic char of different sizes. For encounter rate, estimates are given only for brown trout of sizes 300 and 400 mm.
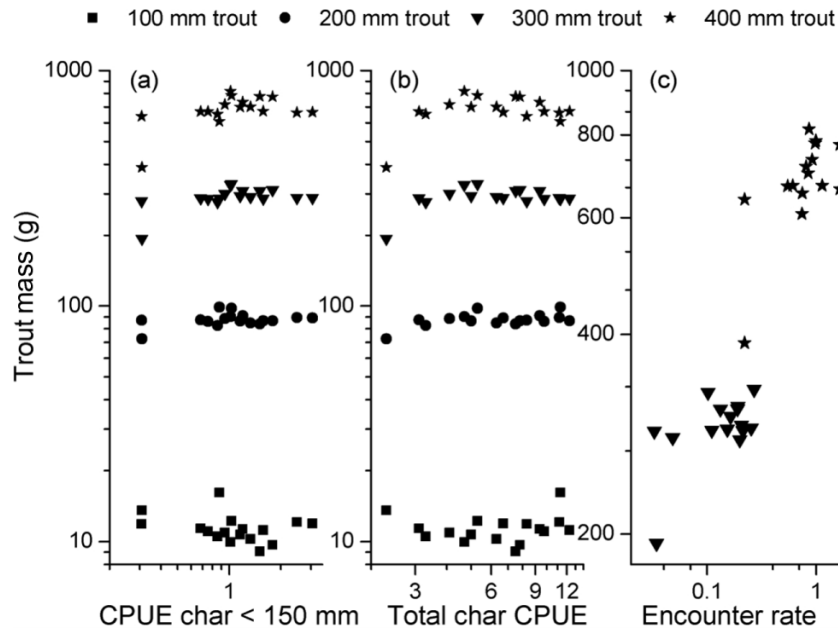

Table 2. Regressions of body condition (g) of different-sized brown trout on total density of brown trout (catch per unit effort, CPUE).

Brown trout size (mm)	$F_{[1,13]}$	P	Slope
100	0.47	0.470	−0.070
200	5.87	0.032	−0.072
300	4.98	0.046	−0.073
400	1.65	0.220	−0.074

Note: Data includes the years 1992–2006, with data lacking for 1998 owing to low captures of brown trout. Regressions were based on log-transformed data. Slopes shown above were untransformed after the analyses.

documented presence of alternative stable states in Lake Takvatn is, however, between either a state with predators (brown trout) and consumers (Arctic char) coexisting (present state) or a state with only consumers (Arctic char) (state before the Arctic char reduction) (Persson et al. 2007*b*).

In the case with size-structured IGP, where small individuals of the predator compete with the intermediate consumer whereas large individuals of the predator prey on the intermediate consumer (Walters and Kitchell 2001; Van de Wolfshaar et al. 2006; Persson and De Roos 2012), the theoretical predictions depend especially on the life history of the top predator (De Roos and Persson 2013). If the ontogenetic niche shift of the predator from feeding on the shared resource(s) to feeding on the intermediate consumer is more gradual and the predator can mature on the shared resource, the likelihood of coexistence between predator and intermediate consumer is restricted. Here, alternative stable states are expected to be present at intermediate productivities, but the different states are either a consumer–resource state or a predator–resource state (Van de Wolfshaar et al. 2006). (These predictions are — as predictions further down — insensitive to whether predator and intermediate consumer share more than one resource.) Correspondingly, experimental evidence for the lack of coexistence between predator and intermediate consumer is present both from laboratory and whole-lake field experiments on fish communities (Persson et al. 2007*a*;

Schröder et al. 2009). Schröder et al. (2009) also showed the presence of alternative stable states with either predator or intermediate consumer present.

In contrast, if the predator cannot mature on the shared resource but needs the consumer for maturation, theoretical studies show the possible existence of alternative stable states in IGP systems consisting of predator, intermediate consumer, and shared resource coexisting as one state and the other state consisting of intermediate consumer and resource (Hin et al. 2011; De Roos and Persson 2013). These two different alternative states are hence those that were observed for the brown trout – Arctic char system in Takvatn (Persson et al. 2007*b*). Still, we are hesitant to claim that competition from the intermediate consumer on juvenile predators is the mechanism behind these alternative stable states. This hesitation relates to the fact that brown trout, in contrast to model assumptions, can mature on the shared resource (zooplankton, macroinvertebrates), a fact reflected in the presence of many lakes with brown trout as the only fish species.

At the same time, the study of Hin et al. (2011) points to the interesting phenomenon that the IGP system in the coexistence state is largely structured by predation (competition is negligible) and the community dynamics resemble that of a linear food chain (i.e., Oksanen et al. 1981). An experimental parallel to this theoretical observation has been found for the IGP system consisting of Eurasian perch (*Perca fluviatilis*) (predator) and roach (*Rutulis rutilus*) (intermediate consumer). For this species pair, a long-term, whole-lake experimental study suggests that the dynamically important interaction between the two species is a predatory effect of Eurasian perch on roach (Persson and De Roos 2012). The resource productivity of this experimental system was dominated by benthic macroinvertebrate production. Persson and De Roos (2012) also hypothesized (without providing any empirical data) that in systems where resource productivity is dominated by pelagic zooplankton, the interaction between this species pair may in contrast be dominated by competition.

The data set on brown trout and Arctic char in Takvatn has demonstrated a positive effect of small char density on large trout (see also Persson et al. 2007*b*). The analysis we have carried out here does not provide any negative effects of either total char or

small char density on brown trout performance in the size range of brown trout ranging from 100 mm to 400 mm. Since brown trout <100 mm reside in tributary streams (Amundsen et al. 2013; P.-A. Amundsen, unpublished data) it is also unlikely that brown trout <100 mm are affected by interspecific competition from Arctic char. This leads us to suggest that the present interaction between Arctic char and brown trout in Takvatn is interspecifically largely structured through predation only, similar to what was found for the perch–roach system discussed above. We suggest that the fish community in Takvatn before the char reduction was mainly structured through interspecific competition from char on brown trout. No data are available, however, to test this suggestion. Furthermore, the circumstance that brown trout can obviously mature on alternative resources (i.e., zooplankton, macroinvertebrates) precludes any theoretical support for the idea that intraspecific competition (rather than low availability of small Arctic char) was the mechanism behind the alternative state of the fish community before the Arctic char reduction. This is so, as the alternative stable states in this case are expected to be either brown trout and resource or Arctic char and resource, and hence no coexistence state with both brown trout and Arctic char is expected (i.e., Van de Wolfshaar et al. 2006; see above).

In conclusion, size-structured IGP theory makes the general prediction that mixed interspecific predation–competition interactions are realized in the form of different states, where each state is interspecifically structured mainly through either predation or competition but not by both (Walters and Kitchell 2001; Van de Wolfshaar et al. 2006; Hin et al. 2011). Although differing in several respects, the patterns in the perch–roach system and the brown trout – Arctic char system in Lake Takvatn are both in line with such a view. This view, where either competition or predation structures the community, contrasts with the common view in fish ecology that the community is simultaneously structured by a mixture of interspecific predation and competition, where small predators are affected negatively (reduced individual growth) through competition from the intermediate consumer, whereas large predators are simultaneously affected positively (increased individual growth) through predation on the intermediate consumer (cf. Johannes and Larkin 1961; Lasenby et al. 1986; Olson et al. 1995). A problem with the majority of these studies is that they are generally rather short term (3–5 years) in contrast to the studies on Arctic char and brown trout in Takvatn and on perch and roach in two experimental lakes (Persson and De Roos 2012) (both >20 years). Hence the former studies may only represent transient dynamics. For example, Persson and De Roos (2012) observed a strong transient competitive effect of roach on perch on a time scale of 3–4 years (see also Byström et al. 1998), whereas the system was, as described above, regulated through interspecific predation only on the long term. A study that does not suffer from this problem is the study on the interactions between predatory largemouth bass (*Micropterus salmoides*) and its competing prey, bluegill (*Lepomis macrochirus*) (Olson et al. 1995). In this study, a comparison between individual growth of young-of-the-year bass and small bluegill density in different lakes showed a negative relationship, whereas the comparison between large largemouth bass individual growth and small bluegill density showed a positive relationship. This pattern is thus completely in line with the expectations of a mixed interspecific competition–predation scenario, although the patterns observed may potentially have been confounded by the fact that young-of-the-year bass individual growth was also negatively related to young-of-the-year density (i.e., intraspecific density dependence).

To summarize, although simultaneous mixed competition–predations interactions have been suggested to characterize interactions in fish communities, there are surprisingly few studies where this presumption has been critically tested (Olson et al. 1995; Persson and De Roos 2012). Although we do not have data on growth rate or body condition of brown trout <100 mm, the most parsimonious explanation for the patterns in density dependence in Arctic char and brown trout in Takvatn during the past 25 years can be based on interspecific predation and intraspecific density dependence in Arctic char and hence does not need to invoke interspecific competition. More studies are therefore needed, including both different species constellations as well as the same species constellation under different environmental conditions (e.g., variation in pelagic relative to benthic resource productivity, availability of competitive–predatory refuges such as stream tributaries), and over long time periods (several decades). Based on existing theory and empirical results, we advance the following testable hypotheses. First, size-structured IGP systems should manifest themselves empirically as systems mainly structured interspecifically through either predation or competition. Second, which structuring force dominates will depend on life history characteristics of the interacting species, environmental conditions (i.e., the ratio of littoral–pelagic habitat), and initial conditions (i.e., which species invaded the system first). Empirical studies to test these two hypotheses may first explain why different results have been obtained in different studies. Second, if our hypotheses yield further empirical support, this has major implications for management, as different interaction modules are expected to result in different risks for predator collapses to overexploitation (De Roos and Persson 2013).

Acknowledgements

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