

Trophic ecology of brown trout (*Salmo trutta* L.) in subarctic lakes

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Abstract

In subarctic lake systems, fish species like brown trout are often important predators, and their niche performance is a key characteristic for understanding trophic interactions and food web functioning at upper trophic levels. Here, we studied summer habitat use and stomach contents of brown trout under both allopatric and sympatric conditions in six subarctic lakes to reveal its trophic role, and population- and individual-level niche plasticity. In allopatry, brown trout mainly used the littoral habitat, but less commonly also the pelagic zone. In sympatry with stickleback, there was always a considerable habitat overlap between the two species. In contrast, sympatric populations of brown trout and Arctic charr generally revealed a distinct habitat segregation. In the sympatric systems, there was in general a distinct resource partitioning between the trout and charr, whereas the observed diet overlap between trout and stickleback was much larger. Trout modified their individual dietary specialization between the littoral and pelagic zone, always being lower in the littoral. Piscivorous behaviour of trout was only found in sympatric systems, possibly contributing to a competitive advantage of trout over charr and stickleback. Hence, the trophic level of trout was strongly related to the fish community composition, with a higher trophic level in sympatric systems where piscivorous behaviour was frequent. These changes in the trophic level of trout linked with the observed food resource partitioning might be an important mechanism in the ecosystem functioning of subarctic lakes in order to allow coexistence among sympatric-living fish species.

Keywords: Coexistence, piscivory, resource partitioning, allopatry, sympatry

Running headline: Trophic ecology of lacustrine trout

Introduction

Mechanisms that may allow competitive coexistence of lake-dwelling fish species have received large attention over the last decades. Some authors have stated that asymmetric competition could be considered as the main driver of observed differences in habitat use in sympatry (Bøhn & Amundsen 2001; Berec et al. 2006; Jonsson et al. 2008), whereas others have hypothesised the importance of various other mechanisms to explain competitive coexistence among species (see for example, Genner et al. 1999; Amarasekare 2003; Gabler & Amundsen 2010). The possible role of a third, intermediate fish species for stable coexistence among competing species has also been emphasised (Amundsen et al. 2010; Eloranta et al. 2011). It is important to note that in lakes, the littoral zone is in general more productive and is inhabited by large-bodied zoobenthos, while the pelagic zone usually offers relatively scarce and small-bodied zooplankton as prey for the fish (Schindler & Scheuerell 2002). In fact, pelagic fish often are highly specialised to feed on small-bodied zooplankton, whereas littoral fish commonly are less specialised, showing a more plastic foraging behaviour (Eloranta et al. 2013), although may also include individuals with specialised benthivorous, planktivorous or piscivorous diets (Bolnick et al. 2003; Araújo et al. 2011; Eloranta et al. 2013). In this respect, the majority of studies about niche segregation among fish species in lake ecosystems are focused on the point of view that niche segregation is related to the pelagic-littoral axis, when in reality it may be more complex (Brodersen et al. 2012). An expanded perspective is also to consider the pelagic-profundal axis in order to explain niche segregation and resource partitioning between species and to reveal the importance of generalist fish species as couplers of benthic and pelagic food-web compartments in lakes (Eloranta et al. 2013). Indeed, in spite that lakes at high latitudes are simpler than systems at southern latitudes, the role that generalist fish species are able to develop in subarctic lakes can be very important (Christoffersen et al. 2008). However, few studies have combined the study of population niche plasticity and individual dietary specialisations with the study of the habitat and diet overlap to explain resource partitioning among generalist fish species in these types of systems.

Brown trout *Salmo trutta* L. (hereafter trout) is indigenous to Europe, North Africa and western Asia, but has been introduced into at least 24 countries outside Europe and has now a world-wide distribution inhabiting both running waters and lentic systems (Klemetsen et al. 2003; Budy et al. 2013). In some subarctic lakes brown trout is the only fish species present,

but frequently it is found to coexist with other fish species like Arctic charr *Salvelinus alpinus* (L.) (hereafter charr) and/or three-spined stickleback *Gasterosteus aculeatus* L. (hereafter stickleback) (e.g. Amundsen 1994; Hesthagen et al. 1997; Eloranta et al. 2013). In sympatry in northern lake systems, trout is usually considered competitively superior to charr and stickleback in the littoral habitat (Hegge et al. 1989; Hesthagen et al. 1997; Forseth et al. 2003; Klemetsen et al. 2003), but there are also several examples where introduced charr has become the dominant fish species and the native brown trout population is more or less excluded from the lake system (Nilsson 1963; Svårdson 1976; Amundsen et al. 1993). The trophic ecology is important for pattern and processes within such fish communities (e.g. Hegge et al. 1989; Forseth et al. 2003; Brodersen et al. 2012; Eloranta et al. 2013), and here we explore the resource niche utilization and interactions of brown trout in subarctic lakes by comparing allopatric trout populations with trout populations living in sympatry with charr and/or stickleback.

Salmonids are in general considered as generalists and opportunistic foragers, and their diets often reflect the relative abundance of prey in the environment (e.g. Hynes 1970; Hunt & Jones 1972; de Sostoa & Lobon-Cervia 1989; Klemetsen et al. 2003). Trout feed mainly on invertebrates captured close to the surface and near the shoreline, but some individuals may also move far offshore to feed (Hesthagen et al. 1997; Klemetsen et al. 2003; Eloranta et al. 2013). Piscivory also commonly occur in brown trout (L'Abée-Lund et al. 2002; Jensen et al. 2004; 2008). Charr has generally a high niche plasticity, being able to feed on a wide variety of invertebrate prey including zooplankton, surface insects and certain littoral prey types as well as on small prey fish including cannibalism (Amundsen 1994; Amundsen et al. 2010; Eloranta et al. 2013). Stickleback is a bottom-feeder that mainly eats macroinvertebrates and small semi-benthic cladocerans, but can also consume zooplankton, terrestrial prey at the water surface, and small fish fry and eggs (FitzGerald & van Havre 1987; Willacker et al. 2010; Sánchez-Hernández et al. 2012).

In allopatric populations in lakes and reservoirs, trout mainly uses the littoral and near-surface waters but may also feed on zooplankton in the pelagic zone (Klemetsen 1967; Schei & Jonsson 1989; Borgström et al. 1992; Brodersen et al. 2012). Opposite, in trout-charr sympatric systems, although both species are able to utilise both the pelagic and littoral zone, trout in general occupies the littoral whereas charr more commonly exploit all habitat types, but especially the pelagic and profundal zone (Hegge et al. 1989; Langeland et al. 1991;

Cavalli et al. 1998; Saksgård & Hesthagen 2004; Eloranta et al. 2013). On the other hand, a recent study demonstrated that trout, in sympatry sticklebacks, preferred to leave the littoral zone to use the pelagic habitat for feeding (Brodersen et al. 2012). In the same study it was also found that the abundance of pelagic prey items in the trout's diet was higher in sticklebacks-trout systems than in allopatric trout populations or trout-charr systems (Brodersen et al. 2012).

In the present study, through the exploration of habitat and diet utilization of trout, charr and stickleback, we have addressed the trophic niche plasticity at both the individual and population level of trout living in allopatry or in coexistence with the other two fish species (including sympatric trout-stickleback, trout-charr and trout-charr-stickleback systems) in six subarctic lakes in northern Norway. We hypothesized that (i) the coexistence of sympatric living species is related to extensive niche segregation and predicted a distinct resource partitioning pattern with trout predominantly residing in the littoral habitat feeding on macrobenthos and surface insects, charr dominating and feeding in both the pelagic and profundal habitats, and stickleback predominantly utilizing the littoral zone feeding on small-sized prey. We further hypothesised that (ii) trout both at the individual and population level would have a narrower trophic niche in sympatry than in allopatry, and that (iii) piscivorous behaviour is an important interaction for brown trout living in sympatry with the other fish species.

Material and methods

Study area

The six study lakes, Storvatn (67°56'N, 16°00'E), Forsanvatn (67°54'N, 15°42'), Fjerdevatn (67°46'N, 15°58'E), Rekvatn (67°56'N, 16°04'E), Makkvatn (67°50'N, 15°49'E) and Skilvatn (68°04'N, 15°53'E), are all oligotrophic, dimictic and relatively deep lakes situated within a approx. 20 x 30 km large area in the Hamarøy region in subarctic northern Norway (Fig. 1). The lakes are located in separate small watercourses. They are ice-covered for 6–7 months from November/December to May/June. The lakes are surrounded by mountains, and birch (*Betula pubescens* Ehrh.) and scattered pine (*Pinus sylvestris* L.) forests. Rekvatn and Forsanvatn are regulated for hydroelectric purposes. Skilvatn has slightly more turbid water than the other five study lakes as also reflected by the Secchi depth (see Table 1). The six lakes included two allopatric trout populations (lakes Storvatn and Forsanvatn) and four lakes with sympatric fish populations. Among the latter, three different systems were included: 1)

trout in sympatry with stickleback (lake Fjerdevatn), 2) trout in sympatry with charr (lake Rekvatn) and 3) trout, charr and stickleback in sympatry (lakes Makkvatn and Skilvatn).

Fish sampling

The study was carried out in midsummer 2013 between July 30 and August 8. Using previously described methods (e.g. Amundsen & Knudsen 2009; Eloranta et al. 2013), fishes were sampled in the littoral, profundal and pelagic habitats of the lakes using 40 m long multi-mesh survey gillnets, set overnight for 11–13 hours for 1–3 nights in each lake. In order to obtain a good size representation of all fish populations, we used multi-mesh gillnets with eight randomly distributed 5-m gillnet panels of different mesh sizes (10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm knot-to-knot). In the littoral and profundal, we used 1.5 m deep bottom nets on the bed of both zones. The survey in the pelagic zone was made with 6 m deep floating nets, set from the surface above 20 m depth. Some additional trout and charr were also sampled using 30 m long and 1.5 m high single mesh-sized (26, 29, 30, 36, and 45 mm) benthic gill nets. Additionally, 6 and 8 mm mesh-sized gillnets were used to catch three-spined sticklebacks. Catch per unit effort (*CPUE*), i.e. the number of fish caught per 100 m² gillnet and night, was estimated for each fish species from the littoral, pelagic and profundal habitats using data only from the multimesh gillnet samples.

In the field, each fish was identified, and their size (fork length, mm) and weight (g) was determined. The fish were dissected, and the stomachs were removed and preserved in 96% ethanol for later diet analysis. In the laboratory, a visual evaluation of total fullness was made ranging from empty (0%) to full (100%). Prey items were identified to the lowest taxonomic level possible, and their contributions to the total stomach contents were estimated according to Amundsen et al. (1996). The prey taxa were grouped in ten categories according to Eloranta et al. (2013): (I) cladoceran zooplankton (*Bosmina* sp., *Daphnia* sp. and *Holopedium* sp.), (II) predatory cladoceran zooplankton (*Bythotrephes* sp.), (III) copepod zooplankton, (IV) molluscs (mostly *Lymnaea* sp., Valvatidae snails and *Pisidium* sp. mussels), (V) Amphipoda (*Gammarus lacustris* Sars 1863), (VI) Chironomidae larvae, (VII) Trichoptera larvae (both house-living and free-living larvae), (VIII) other benthos (mostly Ephemeroptera, Megaloptera, Tipulidae, Plecoptera and the semi-benthic *Eurycercus* sp. chydorid), (IX) pleuston (mainly chironomid pupae and exogenous prey items such as terrestrial insects, but also some pupae and aerial imagoes of aquatic insects) and (X) fish. In some stomachs, only the parasites of prey fish (mainly the stickleback parasite

Schistocephalus solidus) and no host remains were found, and in these cases their presence was used as a marker of the inclusion of fish prey in the diet.

In order to explore habitat and diet overlap among the species, the Schoener's overlap index was calculated using the following equation: $\alpha = 1 - 0.5(\sum |P_{xi} - P_{yi}|) \times 100$ (Schoener 1970), where P_{xi} is the proportion of habitat/prey group i used by species x and P_{yi} is the proportion of habitat or prey group i used by species y . The overlap index has a minimum of 0 (no prey overlap), and a maximum of 100% (all items in equal proportions), and the overlap is usually considered significant when the value of the index exceeds 60% (Wallace 1981). Niche breadth (B) was calculated using Levin's index: $B = 1/\sum P_i^2$ (Levins 1968), where P_i is the proportion of each prey type i in the diet expressed as fraction rather than percentage (Amundsen et al. 2010). Additionally, in order to study the individual dietary specialisation, the proportional similarity (PS_i) index was calculated as: $PS_i = 1 - 0.5\sum |P_{ij} - Q_j| = \sum \min(P_{ij}, Q_j)$ (Bolnick et al. 2002), where the variable P_{ij} is the proportion of resource category j in the diet of individual i , and Q_j the proportion of resource category j in the diet of the whole population. This index compares each individual's diet with the diet at the population level, with values ranging between 0 and 1. For individuals specializing on a single or few prey items, the PS_i values tend to be low, whereas for individuals that consume resources in a similar proportion as the entire population, the PS_i values approach 1 (Bolnick et al. 2002). Finally, the overall prevalence of individual specialisation was calculated as the inverse of the average individual PS_i values (Quevedo et al. 2009).

Statistical analyses

A principal component analysis (*PCA*) was used to study differences in the feeding among species according to the specific prey types consumed by each of them. Also, diet data matrices were analysed using between-class analysis (*BCA*) in order to explore the affinity of the species in the *PCA*. *BCA* is a method used to explore similarities between grouped classes (see e.g. Bornette et al. 1994 or Chessel et al. 2004 for details). In the present study, data analysis proceeded in four steps: 1) the *dudi.pca* function was employed to perform a principal component analysis of a data frame, 2) the *scatter* function was used for plotting the prey-categories axes, the position of species and the eigenvalues of the *PCA*, 3) *s.label* function was used for estimating the gravity centers of each fish species and 4) the *s.class* function was used to test differences in the projection of the feeding with ellipses and gravity

centers grouped by species and habitat. For each analysis, the method and the class indicator are specified in the legends of the figures. In order to explore the statistical significance of the between-group analysis, a permutation test (Monte-Carlo test) was used (see Thioulouse et al. 2012 for further details). Graphical outputs and permutation analyses were computed with the ADE4 library implemented in R freeware (Ihaka & Gentleman 1996). The ADE4 library (see Thioulouse et al. 1997) can be freely obtained at <http://cran.es.r-projet.org/>.

Prior to statistical analysis, all data were tested for normality of distribution using the Shapiro–Wilk ($n < 50$) and Kolmogorov–Smirnov ($n > 50$) tests (Zar 1999). The homogeneity of variances among the different groups was tested using Levene’s test. The non-parametric Mann–Whitney U-test for non-normal data was used to test within-lake differences in fork length, as well as for PS_i among species and between the littoral and pelagic zone. The outputs of the statistical comparisons are given in Tables S1, S2 and S3 in supporting information. The Spearman rank correlation was used to examine the correlation between predator and fish prey size in piscivorous individuals. A significance level of $P = 0.05$ was used in all analyses. Statistical analyses were performed using IBM SPSS Statistics 20 software (IBM Corporation, Armonk, NY, USA).

Results

A total of 558 trout, 330 charr and 40 sticklebacks were caught, of which 450 trout, 287 charr and 40 sticklebacks were randomly chosen for *SCA*. The fork length of trout, charr and stickleback used for the *SCA* ranged between 85–447 mm, 91–328 mm and 20–59 mm, respectively. In the sympatric systems, the trout was significantly larger than charr in Rekvatn and significantly smaller in Makkvatn, whereas no significant differences were found in Skilvatn (Tables 1 and S1). Littoral-caught trout were significantly larger than littoral-caught charr only in Rekvatn, whereas pelagic-caught charr were significantly larger than pelagic-caught trout in Makkvatn (Table S1). The frequency of empty stomachs was highly variable within and between species, varying in trout from 2.5% in Forsanvatn to 14.3% in Rekvatn. Except for Skilvatn, the frequency of empty trout stomachs was higher in the littoral (range: 2.9–14.3%) than in offshore waters where no empty stomach was found. In Skilvatn, in contrast, the percentage of empty stomachs in trout was higher in the pelagic (33.3%) than in the littoral zone (6.8%). The percentage of empty stomach in charr ranged from 0% in Makkvatn to 17.1% in Skilvatn, whereas for stickleback no empty stomachs were

found. More details of gill net catches, sample sizes and empty stomachs are given in Table S4.

Habitat use

In all study lakes, trout were predominantly caught in the littoral zone, but were also present in the pelagic zone in some lakes (Fig. 2). Sticklebacks were only found in the littoral zone, whereas charr were caught in all habitat types. The trout density was relatively low in Fjerdevatn, Rekvatn and Skilvatn (*CPUE* ranging from 3.6 to 8.5 fish 100 m⁻² night⁻¹) compared to Storvatn, Forsanvatn and Makkvatn (*CPUE* from 17.6 to 32.8 fish 100 m⁻² night⁻¹). In spite of these differences, trout was the most abundant fish species in Fjerdevatn and Makkvatn as well as in the littoral zone of Rekvatn. Based on Wallace's (1981) similarity index threshold of 60%, the fish species showed substantial habitat segregation, except between trout and stickleback where the overlap was always high (>93%; Fig. 3).

In allopatry, trout predominantly used the littoral zone, but was also found in the pelagic zone in Forsanvatn. In sympatric conditions, the most noteworthy finding was that in the trout-charr system (Rekvatn), trout was only present in the littoral zone, whereas in the trout-charr-stickleback (Skilvatn and Makkvatn) and trout-stickleback (Fjerdevatn) systems trout was also caught in the pelagic zone (Fig. 2). The proportion of pelagic-caught trout in allopatric systems (12% in Forsanvatn) was higher than in sympatric systems (ranging between 5 and 6%).

Feeding

According to the estimated diet overlap, the three fish species showed clear dietary segregation in all sympatric situations (Fig. 3; see Table S5 in supporting information for detailed *SCA* data), except for trout and stickleback in Makkvatn (in the littoral zone), where they both fed substantially on pleuston and Trichoptera larvae (79% diet overlap).

No major differences were found between the study systems in respect to the principal diet composition of trout, which in all cases was dominated by pleuston (chironomid pupae and terrestrial insects). However, some important differences were found among systems in the contribution of prey items other than pleuston (Fig. 4). For instance, the proportion of cladoceran zooplankton was considerable in the diet of the allopatric trout population in Forsanvatn. Similarly, in sympatry only with sticklebacks (Fjerdevatn), the trout's diet was in

addition to the dominance of pleuston also characterised by a significant presence of fish prey and large cladocerans, which together contributed approx. 40% of the diet. In Rekvatn (trout-charr system), trout in contrast supplemented their pleuston-dominated diet with benthic invertebrates. Also in the trout-charr-stickleback systems trout predominantly completed their diet with benthic invertebrates, in particular Trichoptera larvae, as well as fish prey. Finally, in the pelagic zone of lakes without charr competitors (i.e. the allopatric and trout-stickleback systems), the trout combined pleuston with zooplankton prey, whereas in the presence of charr, the trout feed almost exclusively on pleuston (96% and 88% in Skilvatn and Makkvatn, respectively).

Piscivorous behaviour was only observed in sympatric systems (Table 2), and the proportion of piscivorous fish varied among these lakes (between 3% in Rekvatn and 36% in Skilvatn). When it was possible to identify the fish remains, prey fish were always stickleback except in Rekvatn (trout-charr lake) where remains of salmonid fish prey were observed. The maximum number of prey fish engulfed by an individual trout was 43 (all 0+ sticklebacks with sizes between 7 mm and 12 mm); these were found in the stomach of a trout with a fork length of 145 mm in Skilvatn. Moreover, using pooled data, a weak size-dependent prey selection was revealed for piscivore trout ($R = 0.520$; $P = 0.032$, linear regression equation: prey-fish size (mm) = $0.016 \times$ trout size (mm) – 1.543).

The first two axes of the *PCA* accounted for 42.2% of the total variance, with axes 1 and 2 explaining 23.2% and 19% of the total variance, respectively. The interpretation of the axes in the *PCA*, i.e. position of species, position of prey categories and eigenvalues, are shown in Fig. 5a and Fig. 5b. From the species distribution in the *PCA* according to littoral- and pelagic-caught fish (figure 5c), the permutation test confirmed that the difference between the six species/habitat groups was significant ($P = 0.004$). In general, the trout populations were distributed towards the lower part of the graph due to their preference of pleuston. The charr populations in contrast grouped in the upper part due to their preference of cladoceran zooplankton, whereas the stickleback populations were located towards both the lower and left parts of the graph due to their inclusion of some prey types that quite rarely were utilized by trout and charr, such as Chironomidae larvae and copepods. However, there was some dietary overlap between individuals caught in different habitats, like e.g. between littoral- and pelagic-caught trout (Fig. 5c). Although the differences among groups in Fig. 5d was not significant (permutations test; $P = 0.055$), some important differences were seen among them.

In particular, the *PCA* revealed a clear dietary segregation between trout and charr. Interestingly, there was also a distinct segregation in the diet use of allopatric and sympatric trout, with the diet ellipse of allopatric trout being situated in-between the ellipses of sympatric trout and charr.

The trophic niche width measured as Levins index ranged from 1.5 (trout in Storvatn) to 4.7 (stickleback in Skilvatn). The niche width of trout was considerable lower in Storvatn than in the other populations (Table 3). In general some differences in this index were found between systems; in the trout-stickleback system the Levins index was higher in trout than in stickleback, whereas in the trout-charr system this index was higher in charr than in trout. In the case of systems with all three species, the highest trophic niche width was always found in sticklebacks. Regarding the proportional similarity index, trout caught in the littoral zone generally had lower PS_i -value (i.e. higher degree of individual specialisation) than charr but higher than stickleback (Fig. 6), but the only statically significant difference was found between charr *versus* stickleback in Skilvatn (Table S1). Opposite, in the pelagic zone and in sympatry (Makkvatn and Skilvatn) trout revealed statically higher PS_i -values than charr (Table S1 and Fig. 6). Both trout and charr showed more ample PS_i -values in the pelagic zone in comparison with the littoral zone, except in Skilvatn where no differences were found for charr (Table S2). There were also distinct differences in individual specialisation of trout between lakes (Table S3), with higher PS_i -values in allopatry than in sympatry in the littoral zone (Fig. 6). In the pelagic zone, in contrast, significant differences in PS_i -values were chiefly absent (Table S3). Prevalence values for individual specialization (i.e. the inverse of the average individual PS_i values) are shown in Table 3.

Discussion

In systems in which brown trout is the only salmonid species present, trout is able to forage in both the littoral and pelagic zone, whereas in sympatric systems where other species like charr is present, trout and the coexisting species may adopt different strategies to overcome potential interspecific competition and facilitate coexistence through e.g. resource partitioning (e.g. Nilsson 1963; 1967; Eloranta et al. 2013). In the present study, we observed a clear food resource partitioning between trout and charr into population specialisations using the littoral *versus* the pelagic habitat and food resources as indicated by low overlap in both habitat and diet use. The resource use overlap between trout and stickleback was in

contrast considerable, but the interactions between these two species are particularly complex since the trout also to a large extent utilized the stickleback as prey.

In allopatric populations, the trout may use both the littoral and pelagic habitats, but the abundance was higher in the littoral than in the pelagic zone, as also have been demonstrated by previous studies (e.g. Schei & Jonsson 1989; Borgström et al. 1992; Brodersen et al. 2012). In the sympatric systems, in contrast, the habitat distribution appeared to be strongly related to competitive interactions between the fish species, especially between trout and charr. Hence, our findings illustrate a classic interactive segregation that frequently has been demonstrated for sympatric salmonid populations (e.g. Nilsson 1965; 1967; Jonsson et al. 2008). The role of trout may be particularly important in this respect as this species usually is considered to be competitively superior relative to charr in the littoral habitat (Hegge et al. 1989; Hesthagen et al. 1997; Forseth et al. 2003; Klemetsen et al. 2003). The habitat use of trout varied among the present study systems, but in general the two salmonid fish species showed substantial habitat segregation with trout dominating in the littoral habitat and charr in the pelagic and profundal habitats. A similar pattern has been documented in many other studies addressing the habitat use of trout and charr (e.g. Langeland et al. 1991; Cavalli et al. 1998; Saksgård & Hesthagen 2004). In fact, when only trout and charr were present in the lake (Rekvatn), the trout distribution was restricted to the littoral zone. However, in the lakes where additionally also stickleback was present (Skilvatn and Makkvatn), as well as in the trout-stickleback lake (Fjerdevatn), the trout occurred both in the littoral and pelagic habitats. These findings are congruent with Brodersen et al. (2012), who found that in the presence of sticklebacks, the proportion of trout inhabiting the pelagic habitat was higher relative to trout living in allopatry or in sympatry with charr. Hence, when stickleback is present in the ecosystem, trout may appear partly to be displaced towards the pelagic zone to reduce any competitive interactions with stickleback, although this may result in increasing competition with charr.

The present study shows that pleuston, i.e. chironomid pupae, trichoptera pupae and adult stages of various aquatic and terrestrial insects, accounted for a high abundance of the diet of the three studied species. Pleuston was especially important for trout, in which it was always the most abundant prey type, but it was also important in charr and stickleback (Fig. 4). In this respect, and considering the phenology of the pleuston, these taxa are especially abundant during the summer. For example in subarctic lakes, the abundance of Chironomidae

larvae in the profundal has normally been shown to be highest in June, followed by a peak emergence period of pupae and adults during July and August (e.g. Aagaard 1978a; 1978b; Mousavi & Amundsen 2008). Hence, pleuston may be an important energy input during summer for the acquisition of energy storage to overcome the later winter. In fact, the feeding intensity in fishes is strongly linked with the acquisition of energetic reserves (e.g. Rikardsen et al. 2006), and although salmonids in lakes are able to feed continuously during the ice-covered period, their feeding intensity is much lower than during the summer (Amundsen & Knudsen 2009). Therefore, the summer acquisition of energy reserves may be particularly important in northern lakes where the ice-covered period is long (Biro et al. 2005; Huss et al. 2008). For the present subarctic lakes, a combination of aquatic and terrestrial based pleuston may appear to provide an important energy source for brown trout and other fish species.

The habitat segregation found between the current fish species is a major driver of the observed niche segregation in food resources. In fact, although the diet similarity between fish species varied strongly among lakes, the dietary overlap was in general low and in accordance to Wallace (1981) only biologically significant (i.e. >60%) for trout *versus* stickleback in Makkvatn. Many studies have highlighted the differences in diet composition between trout and charr (e.g. Hegge et al. 1989; Langeland et al. 1991; Hesthagen et al. 1997; Björnsson 2001a;b; Saksgård & Hesthagen 2004), whereas fewer studies have addressed resource partitioning between trout and stickleback (but see e.g. Bolger et al. 1990; Brodersen et al. 2012). Also the multivariate *PCA* approach demonstrates a distinct resource partitioning between the species. The high diet similarity between trout and stickleback in Makkvatn constitutes a distinct exception in this respect, but fish species may also adopt other mechanisms to overcome potential resource competition such as differences in diel activity patterns or in prey size as previously demonstrated from running waters (Sánchez-Hernández et al. 2011). Furthermore, the piscivorous behaviour of trout observed in the sympatric systems might help alleviate any effects of competition with other co-occurring species via predation (Sánchez-Hernández et al. 2011). Piscivorous fishes can have an important role as top predators in aquatic system, as for example in respect to trophic cascades (see Ellis et al. 2011 and references therein) or mediation of coexistence (Byström et al. 2013). In our case, the percentage of piscivore trout varied considerably among the sympatric populations, but was generally higher than observed in previous studies (e.g. L'Abée-Lund et al. 1992 and Saksgård & Hesthagen 2004, which both found an average frequency of piscivorous trout around 5%). Suggestively, the high degree of piscivore behaviour in trout found in the

sympatric systems may contribute to a competitive advantage in highly interactive communities. The high degree of piscivory may also be related to the similar preferences in habitat use observed for trout and stickleback, facilitating high predator-prey encounter rates that make the sticklebacks more vulnerable to predation by trout. Moreover, the presence of the stickleback parasite *Schistocephalus solidus* in several trout stomachs likely reflects that infected sticklebacks might be easier to hunt and consume as previously have been demonstrated by a number of studies (see e.g. Barber & Huntingford 1995 and references therein), and which further demonstrates the high complexity of interactions in these systems.

Trout in allopatry did not exhibit a wider trophic niche width than in sympatry. In the case of the systems with all three species present, the highest trophic niche width was always found in sticklebacks. This finding is in agreement with the results from the *PCA*, which showed that the stickleback populations had the widest *PCA* distribution due to the inclusion of some prey types that were quite rarely utilized by trout and charr. Noteworthy in the present trout-charr systems, the trophic niche width was higher in charr than in trout as previously also have been found in other studies from subarctic lakes (Eloranta et al. 2013). However, these findings are opposite to the observations from the experimental studies carried out by Forseth et al. (2003), who found that the Levins index for trout (2.9) was more than double of the value for charr (1.16). Also, the degree of individual dietary specialisation varied among species and systems in the present study (i.e. allopatric *versus* sympatric), but interestingly trout always showed a higher degree of individual specialisation in the littoral than in the pelagic. In particular, all individual trout were specialised on pleuston in the littoral, whereas in the pelagic zone, we found that specimens fed mainly on a wider prey spectrum, including Cladocera and predatory Cladocera as well as pleuston, thus reducing their degree of individual specialisation. In addition, our findings revealed that littoral caught brown trout had a higher degree of individual specialization in sympatry with charr and sticklebacks than in allopatry, suggesting that interspecific competition for food and habitat may result in behaviourally-mediated foraging specializations in trout.

In conclusion, the interactions and resource partitioning patterns documented here among fish species in subarctic lakes are similar to observations from localities further south, suggesting that these mechanisms are robust across regions with no or minor geographical or climatic impact. Our study furthermore revealed that the trophic level of trout was related to the fish community composition; in sympatric systems trout showed a higher trophic level due to

frequent piscivorous behaviour, whereas no piscivory was observed in allopatric systems. These changes in the trophic level of trout linked with the observed food resource partitioning is likely an important mechanism in the ecosystem functioning of these subarctic lakes in order to allow coexistence among the sympatric-living fish species.

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References

- Aagaard, K. 1978a. The chironomids of Lake Målsjøen. A phenological, diversity, and production study. *Norwegian Journal of Entomology* 25: 21–37.
- Aagaard, K. 1978b. The Chironomidae of the exposed zone of Øvre Heimdalsvatn. *Ecography* 1: 261–265.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6: 1109–1122.
- Amundsen, P.-A. 1994. Piscivory and cannibalism in Arctic charr. *Journal of Fish Biology* 45: 181–189.
- Amundsen, P.-A. & Knudsen, R. 2009. Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake, Norway. *Aquatic Ecology* 43: 765–775.
- Amundsen, P.-A., Gabler, H.-M. & Staldvik, F.J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology* 48: 607–614.
- Amundsen, P.-A., Klemetsen, A. & Grotnes, P. 1993. Rehabilitation of a stunted population of Arctic charr by intensive fishing. *North American Journal of Fisheries Management* 13: 483–491.
- Amundsen, P.-A., Knudsen, R. & Bryhni, H. 2010. Niche use and resource partitioning of Arctic charr, European whitefish and grayling in a subarctic lake. *Hydrobiologia* 650: 3–14.

- Araújo, M.S., Bolnick, D.I. & Layman, C.A. 2011. The ecological causes of individual specialization. *Ecology Letters* 14: 948–958.
- Barber, I. & Huntingford, F.A. 1995. The effect of *Schistocephalus solidus* (Cestoda: Pseudophyllidea) on the foraging and shoaling behaviour of three-spined sticklebacks, *Gasterosteus aculeatus*. *Behaviour* 132: 1223–1240.
- Berec, M., Krivan, V. & Berec, L. 2006. Asymmetric competition, body size, and foraging tactics: testing the ideal free distribution in two competing fish species. *Evolutionary Ecology Research* 8: 929–942.
- Biro, P.A., Post, J.R. & Abrahams, M.V. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. *Proceedings of the Royal Society of London Series B* 272: 1443–1448.
- Björnsson, B. 2001a. The trophic ecology of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Ellidavatn, a small lake in southwest Iceland. *Limnologica* 31: 199–207.
- Björnsson, B. 2001b. Diel changes in the feeding behaviour of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Ellidavatn, a small lake in southwest Iceland. *Limnologica* 31: 281–288.
- Bøhn, T. & Amundsen, P.-A. 2001. The competitive edge of an invading specialist. *Ecology* 82: 2150–2163.
- Bolger, T., Bracken, J.J. & Dauod, H.A. 1990. The feeding relationships of brown trout, minnow and three-spined stickleback in an upland reservoir system. *Hydrobiologia* 208: 169–186.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28.
- Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanbäck R. 2002. Measuring individual-level resource specialization. *Ecology*, 83, 2936–2941.
- Borgström, R., Brabrand, Å. & Solheim, J.T. 1992. Effects of siltation on resource utilization and dynamics of allopatric brown trout, *Salmo trutta*, in a reservoir. *Environmental Biology of Fishes* 34: 247–255.
- Bornette, G., Amoros, C., Castella, C. & Befly, J.L. 1994. Succession and fluctuation in the aquatic vegetation of two former Rhône River channels. *Vegetatio* 110: 171–84.

- Brodersen, J., Landkildehus, F., Lauridsen, T.L., Malmquist, H.J., Amsinck, S.L., Bjerring, R., Søndergaard, M., Johansson, L.S. & Jeppesen, E. 2012. Short- and long term niche segregation and individual specialization of brown trout (*Salmo trutta*) in species poor Faroese lakes. *Environmental Biology of Fishes* 93: 305–318.
- Budy, P., Thiede, G.P., Lobón-Cerviá, J., Fernandez, G.G., McHugh, P., McIntosh, A., Vollestad, L.A., Becares, E. & Jellyman, P. 2013. Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. *Ecology* 94: 356–367.
- Byström, P., Ask, P., Andersson, J. & Persson, L. 2013. Preference for cannibalism and ontogenetic constraints in competitive ability of piscivorous top predators. *PLoS ONE* 8: e70404.
- Cavalli, L., Chappaz, R. & Gilles, A. 1998. Diet of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in sympatry in two high altitude alpine lakes. *Hydrobiologia* 386: 9–17.
- Chessel, D., Dufour, A.B. & Thioulouse, J. 2004. The ade4 package - I: One-table methods. *R News* 4: 5–10.
- Christoffersen, K.S., Jeppesen, E., Moorhead, D.L. & Tranvik, L.J. 2008. Food-web relationships and community structures in high-latitude lakes. In: Vincent, W.F. & Laybourn-Parry, J. ed. *Polar Lakes and Rivers: Limnology of Arctic and Antarctic Aquatic Ecosystems*. New York: Oxford University Press, pp. 269–289.
- de Sostoa, A. & Lobon-Cervia, J. 1989. Observations on feeding relationships between fish predators and fish assemblages in a Mediterranean stream. *Regulated Rivers: Research & Management* 4: 157–163.
- Ellis, B.K., Stanford, J.A., Goodman, D., Stafford, C.P., Gustafson, D.L., Beauchamp, D.A., Chess, D.W., Craft, J.A., Deleray, M.A. & Hansen, B.S. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 108: 1070–1075.
- Eloranta, A.P., Knudsen, R. & Amundsen, P.-A. 2013. Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology* 58: 207–221.
- Eloranta, A.P., Siwertsson, A., Knudsen, R. & Amundsen, P.-A. 2011. Dietary plasticity of Arctic charr (*Salvelinus alpinus*) facilitates coexistence with competitively superior European whitefish (*Coregonus lavaretus*). *Ecology of Freshwater Fish* 20: 558–568.

- FitzGerald, G.J. & van Havre, N. 1987. The adaptive significance of cannibalism in sticklebacks (Gasterosteidae: Pisces). *Behavioral Ecology and Sociobiology* 20: 125–128.
- Forseth, T., Ugedal, O., Jonsson, B. & Fleming, I.A. 2003. Selection on Arctic charr generated by competition from brown trout. *Oikos* 101: 467–478.
- Gabler, H.-M. & Amundsen, P.-A. 2010. Feeding strategies, resource utilisation and potential mechanisms for competitive coexistence of Atlantic salmon and alpine bullhead in a sub-Arctic river. *Aquatic Ecology* 44: 325–336.
- Genner, M.J., Turner, G.F. & Hawkins, S.J. 1999. Foraging of rocky habitat cichlid fishes in Lake Malawi: coexistence through niche partitioning? *Oecologia* 121: 283–292.
- Hegge, O., Dervo, B.K., Skurdal, J. & 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. *Freshwater Biology* 22: 143–152.
- Hesthagen, T., Jonsson, B., Ugedal, O. & Forseth, T. 1997. Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. *Hydrobiologia* 348: 113–126.
- Hunt, P.C. & Jones, J.W. 1972. The food of brown trout in Ilyn Alaw, Anglesey, North Wales. *Journal Fish Biology* 4: 333–352.
- Huss, M., Byström, P., Strand, Å., Eriksson, L.-O. & Persson, L. 2008. Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 2149–2156.
- Hynes, H.B.N. 1970. *The ecology of running waters*. Liverpool: Liverpool University Press.
- Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5: 299–314.
- Jensen, H., Bøhn, T., Amundsen, P.-A. & Aspholm, P.E. 2004. Feeding ecology of piscivorous brown trout (*Salmo trutta* L.) in a subarctic watercourse. *Annales Zoologici Fennici* 41: 319–328.
- Jensen, H., Kahilainen, K.K., Amundsen, P.-A., Gjelland, K.Ø., Tuomaala, A., Malinen, T. & Bøhn, T. 2008. Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1831–1841.
- Jonsson, B., Jonsson, N., Hindar, K., Northcote, T. & Engen, S. 2008. Asymmetric competition drives lake use of coexisting salmonids. *Oecologia* 157: 553–560.

- Klemetsen, A. 1967. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jølstervann, west Norway. *Nytt Magasin for Zoologi* 15: 50–67.
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon, *Salmo salar* L., brown trout, *Salmo trutta* L., and Arctic charr, *Salvelinus alpinus* L.: A review of aspects of their life histories. *Ecology of Freshwater Fish* 12: 1–59.
- L'Abée-Lund, J.H., Aass, P. & Sægrov, H. 2002. Long-term variation in piscivory in a brown trout population: effect of changes in available prey organisms. *Ecology of Freshwater Fish* 11: 260–269.
- L'Abée-Lund, J.H., Langeland, A. & Sægrov, H. 1992. Piscivory by brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish Biology* 41: 91–101.
- Langeland, A., L'Abée-Lund, J.H., Jonsson, B. & Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal Animal Ecology* 60: 895–912.
- Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. New Jersey: Princeton University Press.
- Mousavi, S.K. & Amundsen, P.-A. 2008. Seasonal variations in the profundal chironomidae (Diptera) assemblage of a subarctic lake. *Boreal Environment Research* 17: 102–112.
- Nilsson, N.-A. 1963. Interactions between trout and char in Scandinavia. *Transactions of the American Fisheries Society* 92: 276–285.
- Nilsson, N.-A. 1965. Food segregation between salmonid species in north Sweden. *Reports of the Institute of Freshwater Research Drottningholm* 46: 58–78.
- Nilsson, N.-A. 1967. Interactive segregation between fish species. In: Gerking, S.D. ed. *The biological basis of freshwater fish production*. Oxford: Blackwell, pp. 295–313.
- Quevedo, M., Svanbäck, R. & Eklöv, P. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology* 90: 2263–2274.
- Rikardsen, A.H., Amundsen, P.-A., Knudsen, R. & Sandring, S. 2006. Seasonal marine feeding and body condition of sea trout *Salmo trutta* (L.) at its northern distribution area. *ICES Journal of Marine Science* 63: 466–475.
- Saksgård, R. & Hesthagen, T. 2004. A 14-year study of habitat use and diet of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in Lake Atnsjoen, a subalpine Norwegian lake. *Hydrobiologia* 521: 187–199.

- Sánchez-Hernández, J., Servia, M.J., Vieira-Lanero, R. & Cobo, F. 2012. Application of the analysis of prey ecological characteristics (traits) for the study of the feeding behaviour of bottom-feeder fishes: the example of the stickleback (*Gasterosteus gymnurus* Cuvier, 1829). *Limnetica* 31: 59–76 (in Spanish with English summary).
- Sánchez-Hernández, J., Vieira-Lanero, R., Servia, M.J. & Cobo, F. 2011. Feeding habits of four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using prey traits. *Hydrobiologia* 667: 119-132.
- Schei, T.A. & Jonsson, B. 1989. Habitat utilization of lake-feeding, allopatric brown trout. In: Brannon, E.L. & Jonsson, B. ed. *Proceedings of the salmonid migration and distribution symposium*. Seattle: University of Washington, pp. 156–168.
- Schindler, D.E. & Scheuerell, M.D. 2002. Habitat coupling in lake ecosystems. *Oikos* 98: 177–189.
- Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51: 408–418.
- Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. *Reports of the Institute of Freshwater Research Drottningholm* 55: 144–171.
- Thioulouse, J., Chessel, D., Dolédec, S. & Olivier, J.-M. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7: 75–83.
- Thioulouse, J., Prin, Y. & Duponnois, R. 2012. Multivariate analyses in soil microbial ecology: a new paradigm. *Environmental and Ecological Statistics* 19: 490–499.
- Wallace, R.K. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110: 72–76.
- Willacker, J.J., von Hippel, F.A., Wilton, P.R. & Walton, K.M. 2010. Classification of threespine stickleback along the benthic–limnetic axis. *Biological Journal of the Linnean Society* 101: 595–608.
- Zar, J.H. 1999. *Biostatistical Analysis*. New Jersey: Prentice Hall.

Table 1. Physical characteristics of the study lakes and the mean (range in parentheses) fork length of all charr, trout and stickleback from the six study lakes in summer 2013. *Missing data.

	Storvatn	Forsanvatn	Fjerdevatn	Rekvatn	Makkvatn	Skilvatn
Altitude (m a.s.l.)	157	257	79	297	123	35
Secchi depth (m)	5	26	*	10	5.5	3.5
Temperature (°C)						
Surface	17	12	*	14	16.2	17.4
5m	13.7	*	*	14	14.2	14
10m	8.2	*	*	13.9	10.6	6.9
15m	6.9	*	*	11.2	8.6	5.4
20m	6.7	*	*	8.1	7	*
Fork length (mm)						
Brown trout	173.7 (85–365)	226.5 (110–373)	245.4 (134–447)	158.7 (85–310)	202.9 (103–310)	192.6 (123–303)
Arctic charr	-	-	-	147.5 (89–270)	216.3 (93–268)	188.5 (91–328)
Stickleback	-	-	45.9 (38–59)	-	40.5 (20–53)	50.5 (37–59)

Table 2. Piscivorous behaviour of trout and charr. *Fish remains, impossible to measure the size.

	Storvatn	Forsanvatn	Fjerdevatn	Rekvatn	Makkvatn	Skilvatn
<u>Trout</u>						
Piscivorous behaviour (%)	0	0	31.3	3.2	14	36.2
Size of prey fish (mm)	-	-	43 (25–72)	87	*	11 (7–39)
Number of prey fish engulfed by trout	-	-	1.9 (1–4)	1 (1–1)	3.2 (1–11)	10 (1–48)
<u>Charr</u>						
Piscivorous behaviour (%)	-	-	-	1.1	1.4	6.2
Size of prey fish (mm)	-	-	-	*	*	38 (27–49)
Number of prey fish engulfed by charr	-	-	-	1 (1–1)	1 (1–1)	5.1 (1–20)

Table 3. Summary of trophic niche metrics based on individual variation in stomach contents (B = Levins index and $1 - IS$ = prevalence of individual specialization, where $IS = \text{mean} \pm \text{SD}$). Samples sizes (n) are shown.

	n	B	$1 - IS$
<u>Storvatn</u>			
Trout	88	1.5	0.31 ± 0.24
Littoral trout	88	1.5	0.31 ± 0.24
Pelagic trout	0	-	-
<u>Forsanvatn</u>			
Trout	115	2.5	0.41 ± 0.18
Littoral trout	101	2.6	0.44 ± 0.17
Pelagic trout	14	1.8	0.21 ± 0.16
<u>Fjerdevatn</u>			
Trout	44	2.8	0.54 ± 0.18
Littoral trout	42	2.8	0.56 ± 0.17
Pelagic trout	2	2	0.23 ± 0.04
Stickleback (littoral)	2	2	0.50 ± 0.05
<u>Rekvatn</u>			
Trout	54	2.5	0.49 ± 0.17
Littoral trout	54	2.5	0.49 ± 0.17
Pelagic trout	0	-	-
Charr	85	3.6	0.42 ± 0.19
Littoral charr	26	3.1	0.47 ± 0.21
Pelagic charr	3	1.4	0.14 ± 0.03
Profundal charr	56	3.1	0.41 ± 0.17
<u>Makkvatn</u>			
Trout	75	2.6	0.48 ± 0.20
Littoral trout	61	3.1	0.55 ± 0.12
Pelagic trout	14	1.3	0.23 ± 0.24
Charr	71	1.9	0.64 ± 0.24
Littoral charr	9	1.9	0.52 ± 0.25
Pelagic charr	53	1.7	0.64 ± 0.25
Profundal charr	9	2.8	0.80 ± 0.01
Stickleback (littoral)	12	3.2	0.57 ± 0.18
<u>Skilvatn</u>			
Trout	43	2.6	0.52 ± 0.24
Littoral trout	41	2.7	0.54 ± 0.11
Pelagic trout	2	1.1	0.20 ± 0.26
Charr	107	2.7	0.47 ± 0.16
Littoral charr	65	2.8	0.49 ± 0.16
Pelagic charr	41	2.4	0.45 ± 0.14
Profundal charr	1	1	0
Stickleback (littoral)	26	4.7	0.63 ± 0.15

Figures

Fig.1. Location of the sampling sites in the Hamarøy region, northern Norway.

Fig. 2. Catch per unit effort (*CPUE*) of trout, charr and stickleback caught using multimesh gill nets from the littoral, profundal and pelagic habitats in the six study lakes.

Fig. 3. Between-species overlaps (percent overlap index) in (a) habitat use, (b) littoral diet and (c) pelagic diet, and between-lake similarity comparisons of (d) habitat use, (e) littoral diet and (f) pelagic diet of trout, charr and stickleback from Storvatn, Forsanvatn, Fjerdevatn, Rekvatn, Makkvatn and Skilvatn. The overlap/similarity is considered high when the index value exceeds 60% (dashed line). The dietary overlaps/similarities are based on the 10 prey categories shown in Fig. 4.

Fig. 4. Proportion of different prey groups in the stomach contents of trout, charr and stickleback. Data are presented for each lake and habitat (littoral and pelagic).

Fig. 5. Principal component analysis (*PCA*) plot based on 10 prey categories. This is a composed plot made of: A- the gravity centers of each fish species (upper left), B- a plot of prey-categories axes, position of species and eigenvalues projected into *PCA* (upper right), C- the projection of the species with ellipses and gravity center grouped by species and habitat (bottom left) and D- the projection of the species with ellipses and gravity center (bottom right). Abbreviations include trout (T), charr (C), stickleback (S), littoral (L), pelagic (P), profundal (Pr), Storvatn (Sto), Forsanvatn (For), Fjerdevatn (Fje), Rekvatn (Rek), Makkvatn (Mak), Skilvatn (Ski), sympatric (Syp) and allopatric (Allo).

Fig. 6. Estimated means for individual diet specialisation quantified as the proportional similarity (PS_i) of the diet utilisation in the littoral and pelagic zone of each fish species. Error bars represent 95% confidence intervals. Low PS_i -values indicate high level of individual specialisation. Trout (black bars), charr (open bars) and stickleback (grey bars).

Figure 1

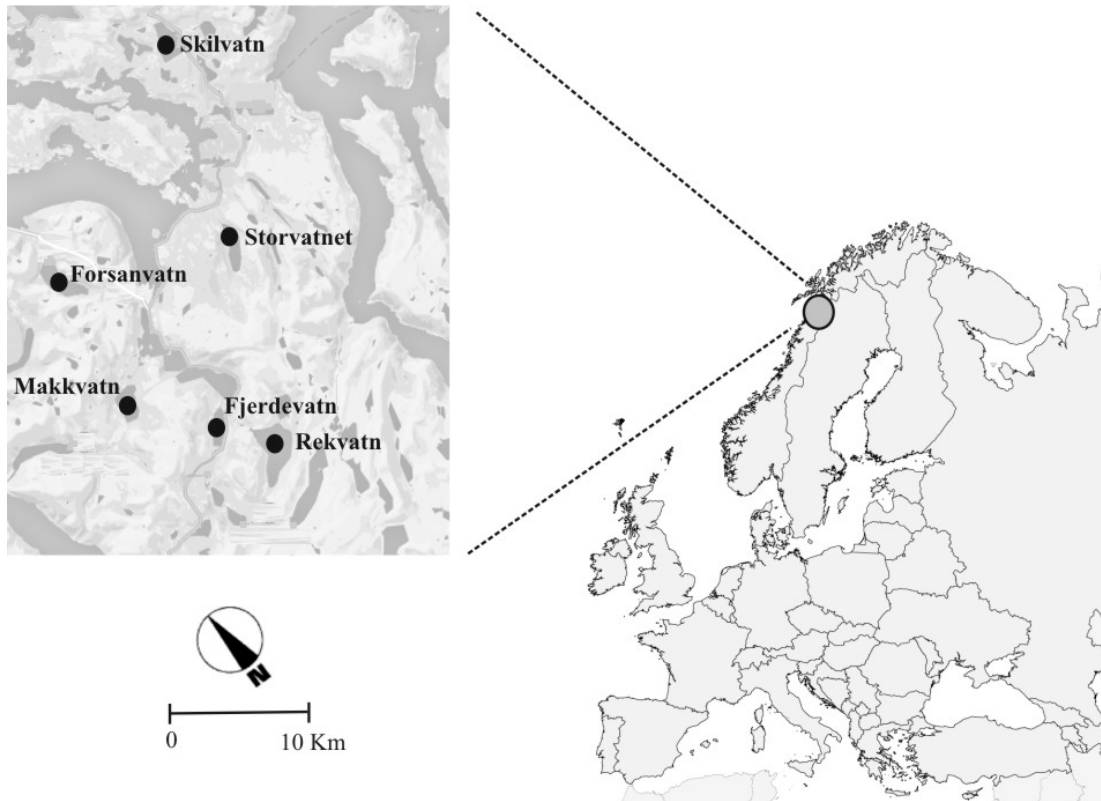


Figure 2

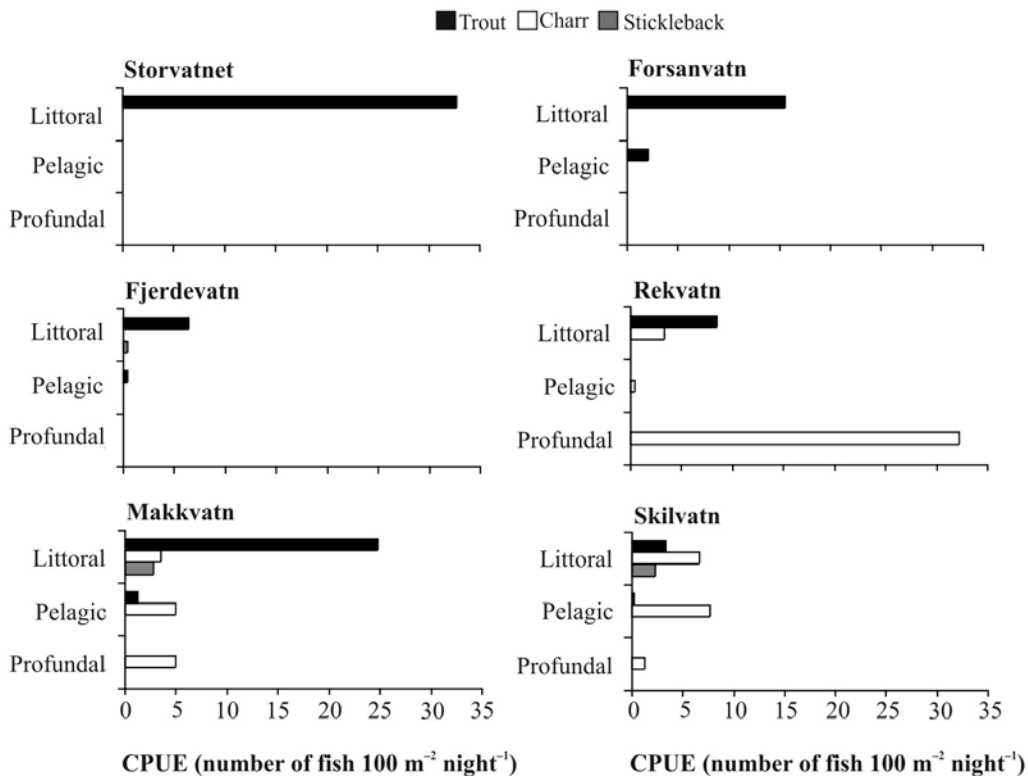


Figure 3

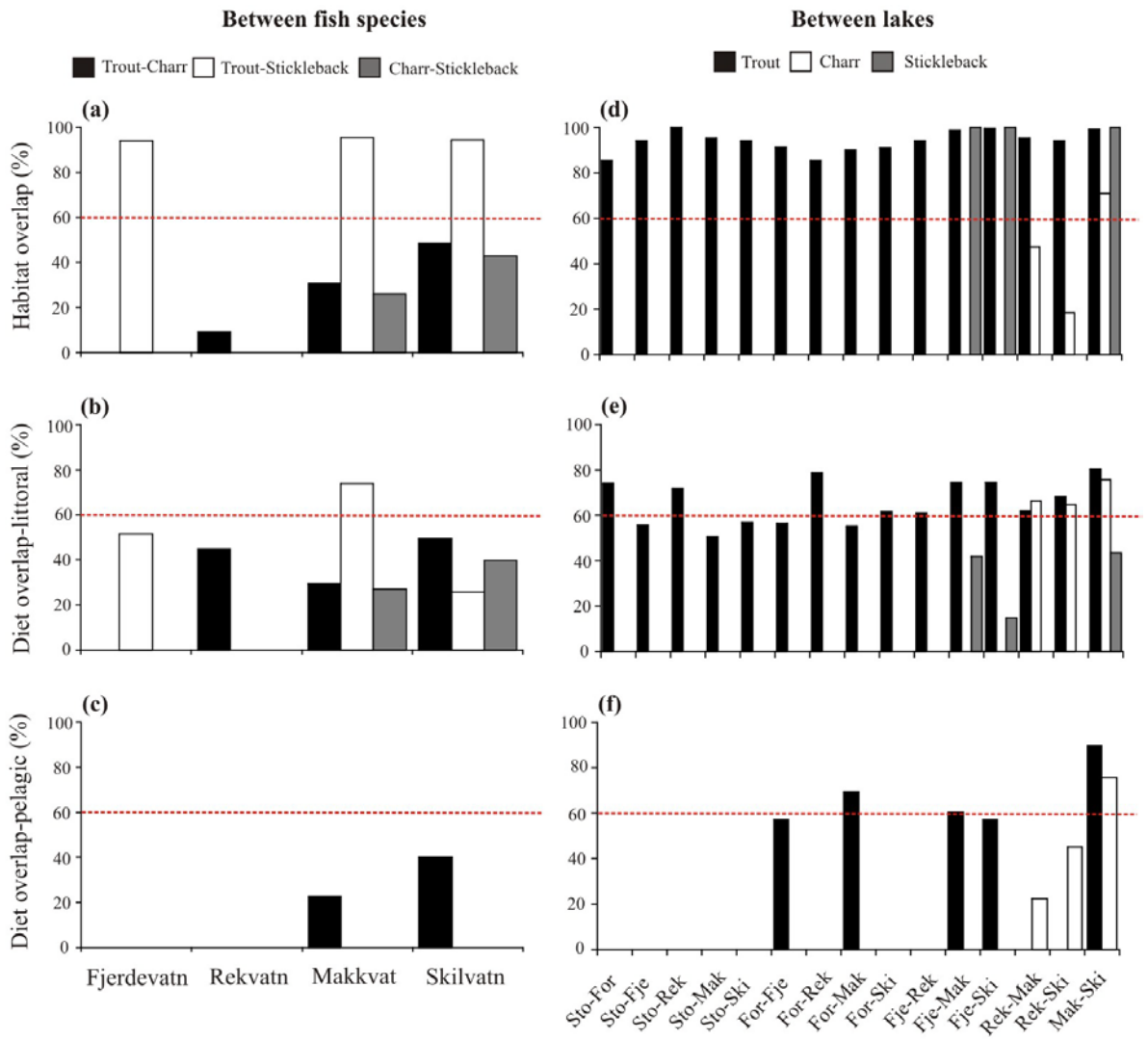


Figure 4

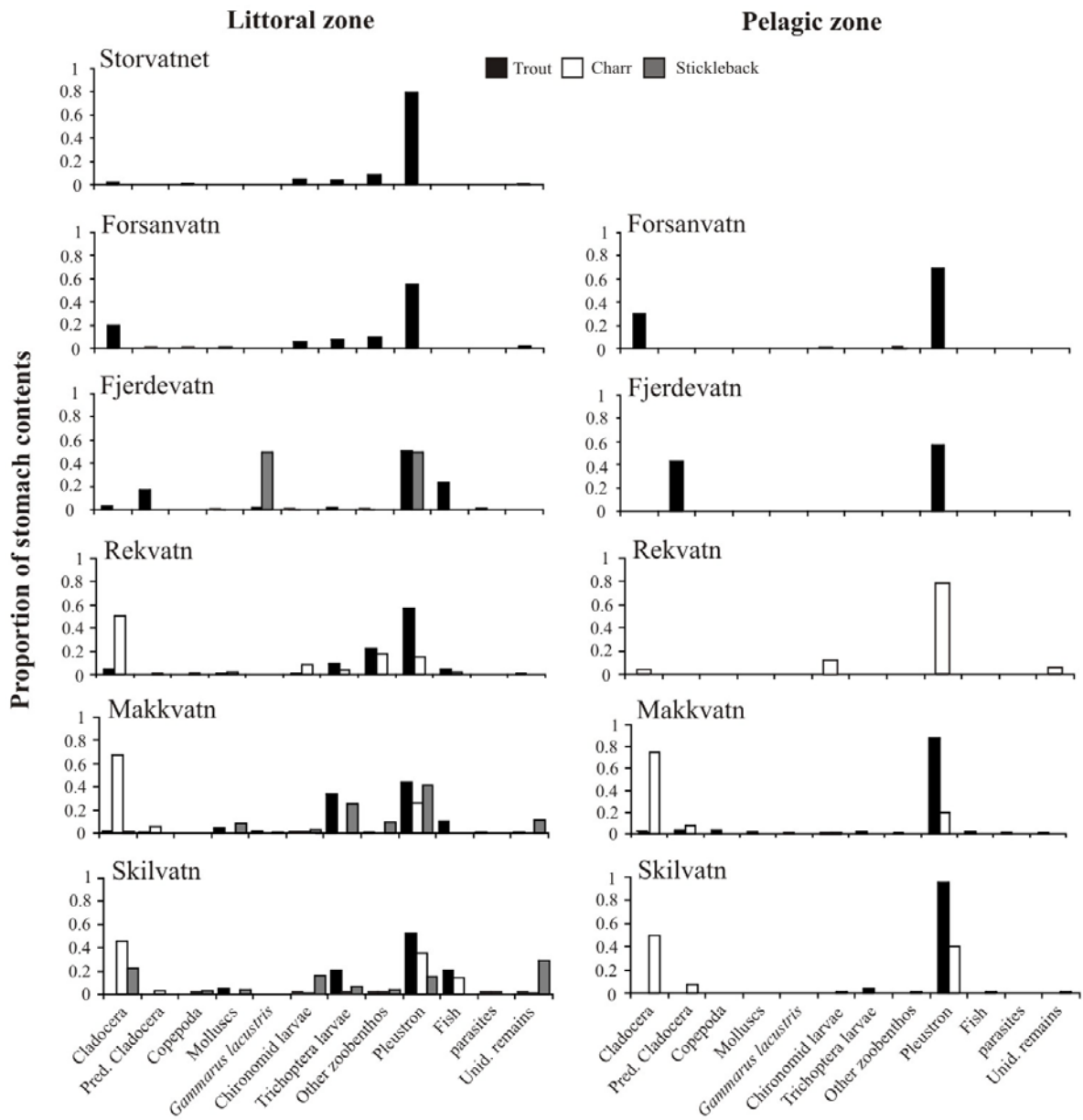


Figure 5

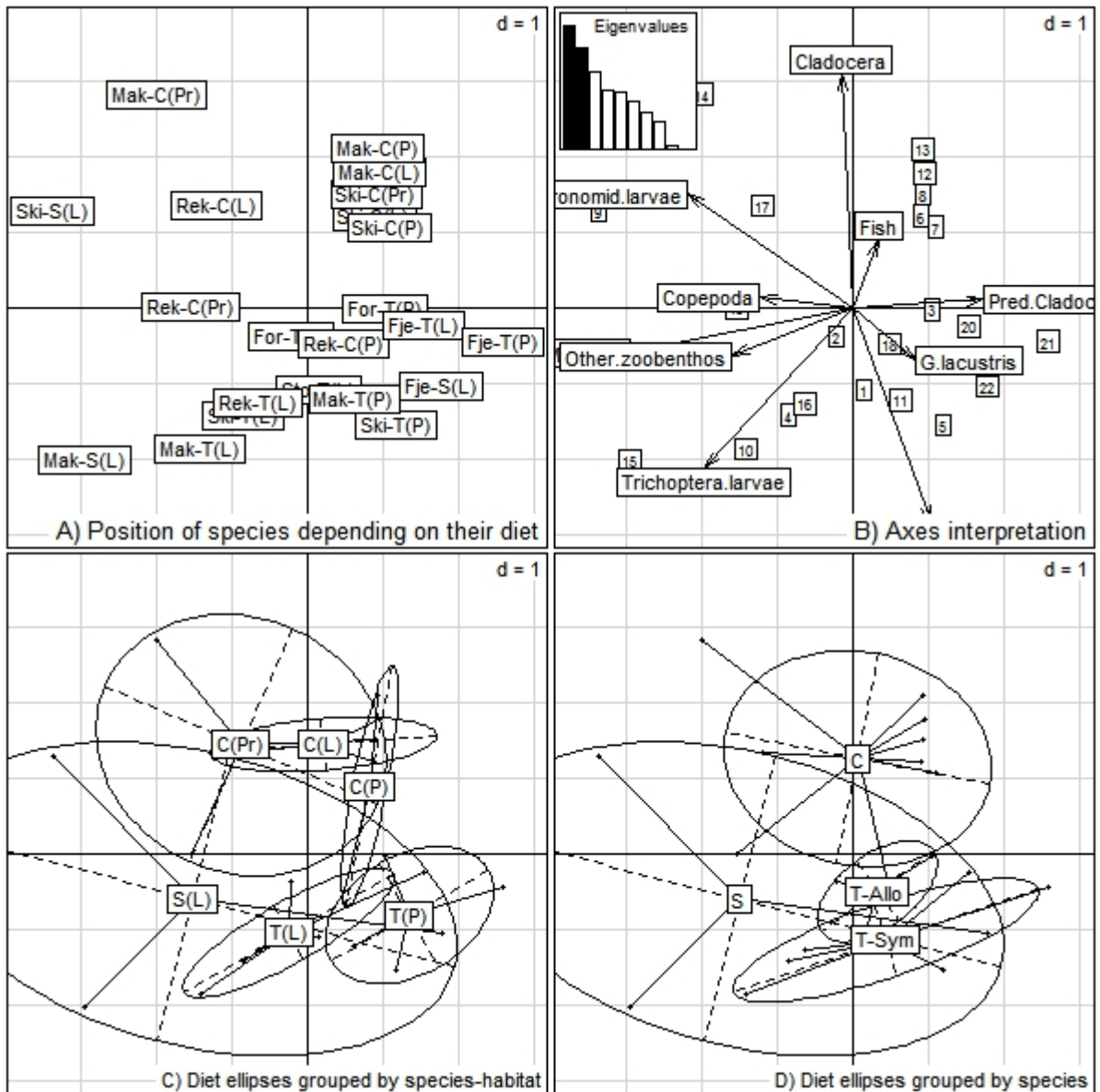
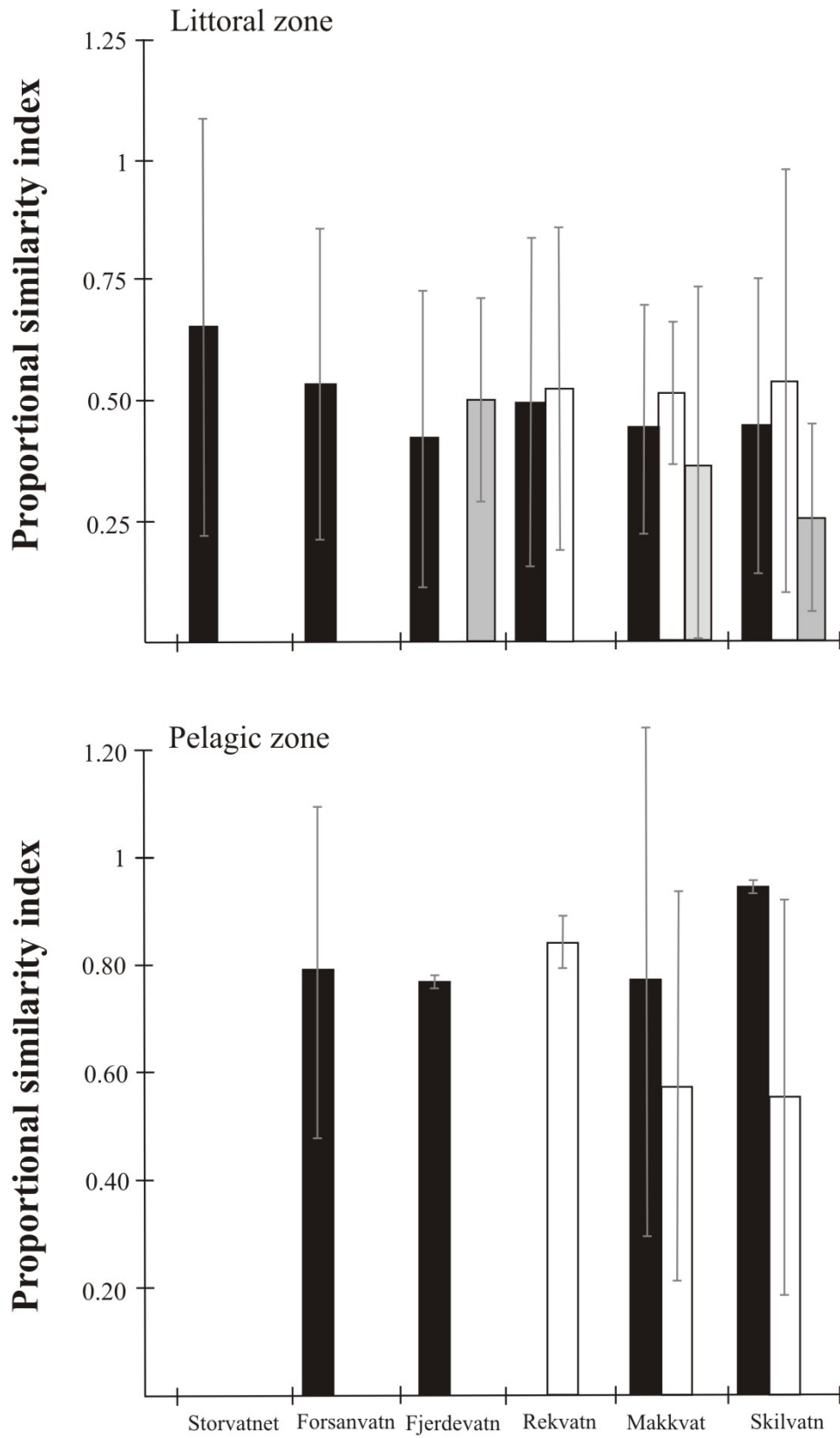


Figure 6



Supporting information:

Table S1. Statistical comparisons of fork lengths and proportional similarity (PS_i) among species (trout, charr and stickleback) and habitats (pelagic-caught and littoral-caught). Profundal-caught fish are not included as only charr was captured in this habitat. *No trout was found in the pelagic habitat. **Sticklebacks were only caught in the littoral habitat. Statistically significant differences ($P < 0.05$) are shown in bold.

Table S2. Statistical comparisons of fork lengths and proportional similarity (PS_i) between fish of each species caught in the littoral and pelagic zone, respectively. Statistically significant differences ($P < 0.05$) are shown in bold. Analyses for trout in the Storvatn and Rekvatn lakes as well as for all stickleback populations are not showed because comparisons were impossible (i.e., no pelagic individuals were caught).

Table S3. Statistical comparisons of the proportional similarity (PS_i) index of trout between lakes. Statistically significant differences ($P < 0.05$) are shown in bold. No pelagic trout were caught in Storvatn and Rekvatn.

Table S4. Numbers of trout, charr and stickleback obtained from all gill nets and from multi-mesh gill nets, and the number of analysed stomachs, empty stomachs and catch per unit effort ($CPUE$). Data are presented by habitat (littoral, pelagic and profundal). No trout were caught in the profundal, and stickleback was always caught in the littoral habitat.

Table S5. Mean \pm SD (range in parentheses) proportion of different prey taxa in the stomach contents of the three fish species sampled from the six study lakes in summer 2013. No trout were caught in the profundal and stickleback was always caught in the littoral habitat.