Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild

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Abstract

The feeding ecology of three piscivorous fish species; perch (*Perca fluviatilis*), pike (*Esox lucius*) and burbot (*Lota lota*), was studied in the subarctic Pasvik watercourse (69 ºN), northern Norway and Russia. All three species primarily occupied the benthic habitats in the watercourse. Perch and burbot exhibited distinct ontogenetic niche shifts in food resource use; perch changing from a dominance of zooplankton to zoobenthos to fish, and burbot from zoobenthos to fish. Fish prey dominated the diet of all the investigated size-classes of pike, but small-sized pike (<20 cm) were not represented in the sample. Fish prey size was positively related to predator size in all three species. Whitefish (*Coregonus lavaretus*) was the dominant prey of pike and large-sized burbot and perch. Nine-spined sticklebacks (*Pungitius pungitius*) was also an important prey and appeared to be a dietary stepping-stone enhancing the transition from invertebrate feeding to consumption of large-sized whitefish prey for all three predators. A cluster analysis separated the different size groups of the three predator species into five functional feeding groups, most of them containing two or all three species. Within these feeding groups, and especially among the piscivorous size-classes, there was a strong and significant interspecific overlap in prey selection, and the dietary similarities between the species were in general much larger than the intraspecific similarities between ontogenetic stages. All three piscivorous species are important top predators in the aquatic food web of the watercourse, and their ontogenetic diet shifts and resource partitioning patterns generate a substantial food web complexity in this subarctic ecosystem.

Introduction

Studies of ecological interactions and food webs have to clarify the functional groups within a given community. In animal taxa where juveniles quickly adopt the niche of the adults, e.g. in birds and mammals, the functional group becomes the species. In fish, which have plastic life histories and ontogenetic niche shifts, other and more complex functional groups than the species may be identified. Understanding of niche shifts and resource partitioning may therefore refine and complicate simple food webs based on the species level as entity, replacing this entity with potentially numerous functional groups where the ontogeny may add additional characteristics within each species.

Piscivory may be an important structuring factor in fish communities of lake ecosystems (e.g. Fortunatova & Popova, 1973, Popova 1978; Robinson & Tonn, 1989; He & Kitchell, 1990; Hambright et al., 1991; Chapleau et al., 1997). Typically, piscivorous fish undergo ontogenetic diet shifts, feeding on invertebrates before they become large enough to consume fish (Werner & Gilliam, 1984; Mittelbach & Persson, 1998). Different adaptations and strategies exist, and Keast (1985) described three types of piscivorous fish: specialists that become piscivorous at the age of few weeks, 'secondary' piscivores that are fish-eaters only later in life, and thirdly, species in which piscivory is limited to occasional consumption of fish larvae. Northern pike (*Esox lucius*), Eurasian perch (*Perca fluviatilis*) and burbot (*Lota lota*) are important piscivorous fish in the benthic habitats of many European freshwater communities (e.g. Frost, 1954; Kipling & Frost, 1970; Vøllestad et al., 1986; Vøllestad, 1992; van Densen, 1994). Perch is a secondary or facultative piscivore, generally switching to a fish diet at a size of about 12-15 cm (Persson, 1983; van Densen, 1994; Mittelbach & Persson, 1998). Pike is a specialist fish predator with several typical

piscivorous adaptations including a large-sized, fusiform body with a large mouth, large teeth and heavy jaws (e.g. Keast & Webb, 1966; Keast 1985; Wootton, 1998), and may switch to a piscivorous diet at sizes less than 5 cm (Frost, 1954). Perch is often an important prey for pike (Frost, 1954; Lawler, 1965; Diana, 1979; Soupir et al., 2000), but pike is an opportunistic predator that may include many other fish species in their diet (Diana, 1979; Mann, 1982; Keast, 1985; Vøllestad et al., 1986; Sammons et al., 1994). Burbot has also been shown to be an important fish predator (Bailey, 1972; Vøllestad, 1992; Rudstam et al., 1995), but has received less attention than the other two species. Habitat preferences of these piscivorous predators are assumed to be quite different. Pike are generally found in the littoral zone in vegetation areas close to the shore (Diana et al., 1977; Chapman & Mackay, 1989; Persson et al., 1991), but may also use the pelagic zone in turbid water (Vøllestad et al., 1986). Burbot increased in density with increasing depth from 10 - 80 m in lake Mjøsa, Norway (Sandlund et al., 1985), and is usually regarded as a typical profundal dwelling species. Perch are found in most lake habitats (e.g. Persson, 1983), but in lakes where pike and perch co-occur, perch have been found to be most prevalent in the pelagic zone (Persson et al., 1991).

Whereas vast information exists on piscivorous predators in temperate populations, especially with respect to perch and pike (e.g. Frost, 1954; Popova & Sytina, 1977; Popova, 1978; Keast, 1985; Persson et al., 1991; Treasurer et al., 1992; Mittelbach & Persson, 1998), little is known about piscivory in arctic and subarctic lake systems. In the subarctic Pasvik watercourse, northern Norway and Russia, pike, perch and burbot coexist in a lacustrine piscivore fish guild, which also includes a sparse population of brown trout (*Salmo trutta*). High-latitude ecosystems are usually assumed to have low species diversity (e.g. Rohde, 1992; Rosenzweig, 1995; Ricklefs, 1996), but in the Pasvik watercourse a total of 15 fish

species have been recorded, of which 11 occur in the lakes. Whitefish (*Coregonus lavaretus*) is the dominant species in the watercourse, but perch, pike and burbot are numerous, and nearly 50 % of the total commercial yield during 1991 to 1993 was piscivorous species. The objective of the present study was to examine the feeding ecology within this subarctic piscivorous fish guild, with special emphasis on ontogenetic niche shifts and resource partitioning, and to compare the level of differentiation between ontogenetic stages, both within and between species, with the level of differentiation between species.

Material and methods

Study area

The Pasvik watercourse (69 ºN, 30 ºE) runs along the national border between Norway and Russia, originating from Lake Inari in Finland. The Norwegian-Russian part of the watercourse is 120 km long, has a total area of 142 km^2, a catchment area of 18,404 km^2, and a mean waterflow of about 175 m^3/s. There are altogether seven water impoundments in the watercourse. Rapids and waterfalls have disappeared, and the river system is now dominated by a number of consecutive lakes and reservoirs. The water level fluctuations are small, and usually less than 80 cm. The ice-free season in the lakes and reservoirs last from May/June to October/November. The maximum water temperature in summer may approach 17-18 ºC, but during most of the ice-free period the temperature is below 10 ºC. The lakes are oligotrophic with some humic impacts, and with Secchi-depths from 2-5 m. The geology in the region is dominated by bedrock, mainly containing gneiss. The watercourse is surrounded by a birch- and pinewood landscape with stretches of boggy land. The annual mean air temperature is low (-3 ºC), and the minimum and

maximum monthly mean temperatures are -13.5 ºC and +14.0 ºC, respectively. The precipitation in the area is low, with an annual mean of 358 mm.

Whitefish (*C. lavaretus sensu lato*) is the dominant species in the watercourse, but perch (*P. fluviatilis*), pike (*E. lucius*), burbot (*L. lota*) and nine-spined sticklebacks (*Pungitius pungitius*) also commonly occur. Vendace (*Coregonus albula*) has recently invaded the watercourse after being introduced to Finnish headwaters in the 1960's (Amundsen et al., 1999).

Fish sampling and analyses

Sampling of perch, pike, burbot and brown trout was carried out from June to September 1991-1993 in four lake localities in the watercourse. Only minor variation was found in the piscivore diet between localities, years and seasons, and samples from the different lakes and sampling occasions have therefore been pooled in the analyses. Fish were sampled in the littoral (<8m), profundal (>12m) and pelagic zones using gill nets (bar mesh size 10-74 mm). Each fish was measured (fork length) and weighed. The stomach content was identified and the relative volumetric importance of the different prey species in each stomach was estimated and expressed as percent abundance (Amundsen et al., 1996). The fork length of prey fish in the stomachs was measured when possible.

A cluster analysis was carried out to generate a dendrogram classifying the diet relationships between different size-classes of fish. Eucladian distance and the unweighted pair-group method (UPGMA) were used in the analysis (Krebs, 1999). Dietary overlap was further calculated as percentage overlap (Krebs, 1999):

$$P_{jk} = \left[\sum_{1}^{n} (\text{minimum } p_{ij}, p_{ik}) \right] * 100 \qquad (1)$$

where P_{jk} is the percentage overlap between species j and species k, p_{ij} and p_{ik} the proportions of fish prey i used by species j and k, and n the total number of diet categories. Wallace (1981) considered the overlap to be biologically significant when the index value exceeds 60 %.

Results

Habitat distribution

Perch predominated in the piscivore fish community of the Pasvik watercourse, constituting 67.8% of the total sample (n=1,007). Pike also occurred commonly and made up 22.1% of the catches of piscivorous fish, whereas burbot and brown trout made up a minor part of the piscivorous fish, constituting 7.9% and 2.2% of the total sample, respectively. The major proportion of the piscivorous predators was caught in the benthic habitats, and especially in the littoral zone, constituting 82.7% of the total sample, whereas the profundal and pelagic zone contributed 15.8 and 1.5%, respectively. Perch dominated the catches both in the littoral and profundal zone (Fig. 1), and only two out of 683 perch were caught in the pelagic. Most pike were caught in the littoral zone, but some were caught in the profundal and a few also in the pelagic zone. Burbot were exclusively caught in the benthic habitats, and made up 20 % of the profundal catches. Brown trout had its largest relative contribution in the pelagic catches, but the fish material comprised only a few trout (n=22). Neither of the species exhibited any significant differences in size distribution between the three habitats (Kruskal-Wallis test, $p > 0.05$).

Diet

The size-distribution of perch in the catches ranged from 7.0 to 32.0 cm. The smallest piscivorous perch was 7.3 cm, and fish were found to be the dominant food item in stomachs of perch larger than 17.5 cm (Fig. 2a). Nine-spined sticklebacks were the dominant fish prey for perch up to 22.5 cm length. Perch in the size range 22.5-30 cm had consumed comparable amounts of nine-spined sticklebacks and whitefish, whereas whitefish was the dominant prey for perch larger than 30 cm. Only on one occasion, a perch individual was found with more than one species of fish prey in their stomach (whitefish and nine-spined sticklebacks), although several prey fish frequently were found in each predator. Zooplankton dominated the diet of perch smaller than 10 cm, and zoobenthos was an important group of food items in all length groups. Only one cannibalistic perch was found; an 18.7 cm large individual that had eaten a 3.6 cm conspecific fry.

The size-distribution of pike in the samples ranged from 17.1 to 73.0 cm, and the smallest pike found with fish in the stomach was 20.5 cm. Fish was the main prey in all size groups, and pike larger than 50 cm had exclusively consumed whitefish (Fig. 2b). Nine-spined sticklebacks were together with whitefish the most important prey for the size group from 20 to 40 cm. Perch and burbot were also occasionally found as prey fish for pike in the intermediate size group (40-50 cm). Several prey fish were frequently found in the same pike, but only five fish had more than one species of prey fish in their stomachs. No cannibalistic pike were found.

The length of burbot in the catches varied from 13.8 cm to 61.5 cm. The smallest piscivore burbot was 17.8 cm, and fish was the main food item for burbot larger than 20 cm

(Fig. 2c). In the smallest size group (10-20 cm), zoobenthos was the predominant food component, whereas zooplankton never was found in the stomachs. Nine-spined sticklebacks and whitefish were important prey fish for most size groups of burbot. Cannibalism was observed on two occasions in large burbot (>50 cm). Lamprey larvae (*Lampetra* sp.) were found in one burbot stomach together with whitefish.

Brown trout were caught in the size range from 21.0 cm to 54.8 cm. Whitefish was the dominant prey (prey abundance 54.2%), followed by surface insects (27.8 %) and 9-spined sticklebacks (7.7 %). As the samples included only a few brown trout (n=22, of which 16 had food remains in their stomachs), these are not included in the further analyses.

Feeding groups and dietary overlap

A cluster analysis of the dietary data distributed the different size-classes of the predator species into two main clusters; one consisting of fish feeding mainly on invertebrates and partly also fish (Fig. 3; *A*), and the other group being almost exclusive piscivorous (*B*). The invertebrate feeding group further split into two groups; one feeding mostly on zooplankton (perch 5-10cm; *C*), and another feeding on zoobenthos and nine-spined sticklebacks (*D*). The latter again consisted of one group with a predominance of zoobenthos (including perch in the size range 10-17.5 cm and burbot 10-20 cm; *E*), and another with a mixture of zoobenthos, sticklebacks and whitefish prey (including perch 17.5-30 cm and burbot 20-30 cm; *F*). The cluster consisting of piscivorous fish also split into two groups; one with a mixture of whitefish and other prey fish species (including perch >30cm, pike 20-40 cm, and burbot 30-40 and 50-60 cm; *G*), and the other with a total dominance of whitefish prey (including burbot 40-50 cm and pike >40 cm; *H*). Thus, a total of five functional feeding groups could be identified, their diet predominantly consisting of 1)

zooplankton (*C*), 2) zoobenthos (*E*), 3) a combination of zoobenthos and fish (*F*), 4) a combination of nine-spined sticklebacks and whitefish (*G*), and 5) whitefish (*H*).

According on the cluster analysis, the different size-classes of perch, pike and burbot were distributed into respectively four, two and three functional feeding groups, and the diet overlap between these groups was explored using the percent overlap index. A large dietary overlap often occurred between the three fish species (Table 1). Especially among the large-sized, piscivorous feeding groups (i.e. perch and burbot >30 cm and pike >20cm) the overlap between the three species was high, ranging from 71.0 to 82.3 % and averaging 77.6 %. Within-species overlaps between different ontogenetic stages were in contrast much smaller and usually less than 60%. For perch, the intraspecific dietary overlap ranged from 25.4 to 61.5 % (Table 1), with an average of 44.0 %. For burbot the intraspecific dietary overlap ranged from 19.0 to 62.3 %, averaging 36.7 %, whereas the two size groups of pike had an overlap of 68.2 %.

Size distributions of prey fish

For all three predator species, the length distribution of prey fish sampled from the fish stomachs were bimodal with a marked peak between 3-5 cm composed of nine-spine sticklebacks, and a second wider and flatter mode to the right consisting mainly of whitefish (Fig. 4). Perch ate fish prey in the size range from 1.8 to 13 cm, whereas burbot and pike ate fish prey in the range from 1.7 to 22 cm and 1.8 to 25 cm, respectively. For burbot and especially perch, small-sized prey fish dominated the diet as a result of heavy predation on nine-spined sticklebacks. Pike selected prey fish of a wider size range, and did not exhibit a similar strong dominance of the smallest size groups consisting of nine-spined sticklebacks.

The length of whitefish eaten by pike was significantly larger than whitefish eaten by perch (mean length 12.2 cm and 8.9 cm, respectively; Mann-Whitney U-test, $p < 0.001$). Whitefish eaten by burbot (mean 11.8 cm) were also significantly larger than whitefish eaten by perch ($p < 0.001$), whereas there were no significant difference between pike and burbot ($p = 0.81$). The mean length of nine-spined sticklebacks eaten by burbot (4.4 cm) was larger than sticklebacks eaten by perch (3.6 cm; Mann-Whitney U-test, $p < 0.001$) and pike (3.9 cm; $p < 0.05$), whereas there were no significant difference between perch and pike ($p = 0.188$).

Predator-prey length relationships

For perch, pike and burbot the mean length of fish prey increased significantly with increasing predator size (Fig. 5). The predator-prey length relationships were described by linear regression using the following equations:

Perch: $Py = 0.203\ Pr + 0.380$ (n=251, r^2=0.217, $p < 0.001$) (2)

Pike: $Py = 0.288\ Pr - 2.951$ (n=117, r^2=0.215, $p < 0.001$) (3)

Burbot: $Py = 0.161\ Pr + 0.851$ (n=84, r^2=0.239, $p < 0.001$) (4)

where *Py* is fish prey length and *Pr* predator length (both in cm). The increase in prey size with increasing predator size was mainly a result of larger whitefish being consumed by the larger predators, whereas the size of nine-spined sticklebacks did not increase with increasing predator size (regression analyses, $p > 0.05$). These small-sized prey fish were mostly consumed by the smaller predators. On average, the ratio of fish prey length (all prey taxa combined) relative to predator length was similar for the three predator species (perch = 22.3 %, pike = 21.3 %, and

burbot = 18.7 %). However, differences in prey to predator ratios were more apparent with respect to whitefish prey alone, particularly for perch. Whitefish prey were on average 37.6 % of the perch size (n=31). The percentage declined with increasing size of perch, the length of whitefish prey being c. 40 % of the predator length at a perch length of 20 cm and c. 30 % at a length of 30 cm. The average whitefish prey of pike was 28.0 % of the predator length (n=67), decreasing from c. 40 % at a pike length of 20 cm to 25 % at a length of 50 cm. For burbot, the average whitefish prey was 26.2 % of the predator length (n=22).

Discussion

Only minor differences in habitat selection were found between pike, perch and burbot. All three species had their main distribution in the littoral and profundal, suggesting that these three species represent a piscivorous guild in the benthic habitats of this subarctic ecosystem. Pike is described as a typical solitary hunter that usually hides in vegetated areas of the littoral zone (Diana et al., 1977; Chapman & Mackay, 1989; Persson et al., 1991; Greenberg et al., 1995), and appeared to prefer this habitat in the Pasvik watercourse. Perch often become pelagic in sympatry with pike (Person et al., 1991), but this was not found in the present study. Perch dominated the samples both in the littoral and profundal, but were almost absent in the pelagic zone. Burbot is regarded as a typical profundal dwelling species (Sandlund et al., 1985), and in the Pasvik watercourse, the highest relative contribution of burbot occurred in the profundal samples. Burbot were, however, most frequently caught in the littoral, even though Svärdson (1976) proposed pike to be a superior competitor in this habitat. Brown trout had its highest relative contribution in the pelagic samples, but only a few specimens were caught. In lakes, brown trout

feeding on fish are most commonly found in the pelagic zone (Vehanen, 1995; Næsje et al., 1998).

Perch exhibited several ontogenetic niche shifts in their food resource use. In the smallest size groups, zooplankton was the dominant food category, whereas the intermediate size groups had most frequently been feeding on zoobenthos. The diet of the larger perch was dominated by fish; firstly nine-spined sticklebacks and thereafter whitefish in the largest perch. Similar ontogenetic niche shifts have frequently been shown in perch (e.g. Boisclair & Leggett, 1989; Hayes & Taylor, 1990; Hjelm et al., 2000), demonstrating gape-limited feeding and an increased size-span of potential prey with increasing size of the predator. Nine-spined sticklebacks were particularly important prey. Even at a size as small as 7 cm the perch were able to consume the small-sized sticklebacks, and they were present in all size groups of perch. The inclusion of fish prey in the diet is of large importance for the somatic growth of perch (Persson, 1983; LeCren, 1992; Heath & Roff, 1996). Nine-spined sticklebacks appeared to be an important dietary stepping-stone for the initiation of piscivory in perch and also for the predatory fish to rapidly reach a size where they also are able to consume whitefish. A similar role of nine-spined sticklebacks was also seen in the diet ontogeny of burbot and pike, suggesting that sticklebacks play a key role for the commonness of piscivory in the fish community of the watercourse.

Pike had almost exclusively eaten fish prey. Similar results have also been found in several other studies (Mann, 1982; Keast, 1985; Vøllestad et al., 1986; Sammons et al., 1994; Soupir et al., 2000), confirming the great ability and adaptation for fish predation in pike. But also pike is a gape-limited predator, and the size-span of fish prey increased with increasing predator size (Fig. 5). As perch, pike is highly flexible with respect to which prey size and taxa they consume (Mann, 1976, 1982; Chapman et al., 1989). In Pasvik, the dominant prey fish of pike was whitefish, which are numerous in the watercourse (Amundsen et al., 1997, 1999; Bøhn et al.,

2002). Also Vøllestad et al. (1986) found whitefish to be the main prey of pike when present, whereas other studies have found whitefish to have a low contribution to the diet of pike even though being a common species in the fish community (Lawler, 1965; Diana, 1979). In many studies, perch has been found to be the main prey species of piscivorous pike (Allen, 1939; Frost, 1954; Le Cren et al., 1977; Diana, 1979; Kipling, 1983; Soupir et al., 2000). In the Pasvik watercourse, however, perch were only on two occasions found in the stomachs of pike. This was probably not a result of scarce opportunities to catch perch, as this species was indeed common in the watercourse. Experimental studies have shown that piscivorous fish prefer soft-rayed over spiny-rayed prey fish (Beyerle & Williams, 1968; Mauck & Coble, 1971; Eklöv & Hamrin, 1989), and the gillcover and mid body spines of perch may reduce their predation hazard (Eklöv & Hamrin, 1989). Whitefish is further more shallow-bodied than perch, and pike have been shown to prefer shallow-bodied over deeper-bodied fish due to a longer handling time of the latter (Nilsson & Brönmark, 2000). Thus, the fish predation of pike in the Pasvik watercourse was highly selective as both perch and whitefish were numerously present as potential prey, but only whitefish were consumed in large amounts.

The burbot in the Pasvik watercourse were highly piscivorous and fish was the main component in the diet of most examined size groups, supporting the findings of many other studies (Petkevich & Nikonov, 1969; Bailey, 1972; Sorokin, 1976; Nilsson, 1979; Popova & Reshetnikov, 1982; Sandlund et al., 1985; Vøllestad, 1992; Rudstam et al., 1995; Fratt et al., 1997; Tolonen et al., 1999). Van Densen (1994), however, classified burbot as a less piscivorous species than perch, but this is not consistent with our observations. Fish made up a larger part of the diet in burbot than in perch, and burbot also utilized a larger diversity of prey species and sizes. Hence, burbot appears to be an effective fish predator throughout most of its life span. Both in burbot, pike and perch, only one single species of fish prey was usually found in each predator,

even though several individuals usually had been eaten. Fish prey are probably difficult to catch and handle due to their large size and ability to escape. Different species may also have contrasting strategies to avoid predation. Experience can promote capture success of prey types that are difficult to handle (Bence, 1986), and individual specialisation towards specific prey species may represent an optimal behaviour of piscivore fish (Amundsen et al., 1995, 1997).

There was a high overlap in resource use within the benthic piscivorous fish guild in the Pasvik watercourse. Mainly two prey species, nine-spined sticklebacks and whitefish, were consumed, and both were important prey for all three piscivorous species. Some differences in resource use could be observed along the prey size axis, pike consuming the largest whitefish prey and perch the smallest. This was partly due to the larger size-range of pike, but probably also reflects a stronger piscivore adaptation in pike. Still this seemed to have only minor importance for the overall resource partitioning, and the three predator species exhibited a high diet similarity. Thus, the fish community in the watercourse includes three important top predators with limited resource partitioning, contributing to a complex food web in this subarctic aquatic ecosystem. The food web complexity was further enhanced by the several ontogenetic niche shifts undertaken by the three predator species. Five functional feeding groups were identified from the cluster analysis of diets. Three of the groups included all three predator species, whereas the zooplankton feeding group was represented by small-sized perch only, and the zoobenthos feeding group by intermediate-sized perch and burbot. However, both pike and burbot are likely to undergo both planktivore and benthivore life stages during their ontogeny, but some of these stages were probably not detected due to an under-representation of small-sized fish in our data set. In burbot a relatively high infection of the parasite *Triaenophorus nodulosus* demonstrated that some zooplankton consumption occurred at least in early life stages, as this cestode is transmitted to burbot through the ingestion of planktonic copepods.

Zooplankton feeding by juveniles and a subsequent shift to zoobenthos has been demonstrated in dietary studies of small-sized burbot (e.g. Ryder & Pesendorfer, 1992). Similar ontogenetic diet shifts may also occur in pike (Frost, 1954). Thus, all three piscivorous species undergo a parallel set of ontogenetic niche shifts, but the duration of the different stages apparently exhibits large interspecific differences. These ontogenetic shifts may generate a high intricacy of inter- and intraspecific interactions in the fish community, including exploitative and interference competition and competitive bottlenecks. Juvenile competitive bottlenecks are common in piscivorous fish (e.g. Werner, 1986, Persson & Greenberg, 1990, Byström et al., 1998), especially since piscivore adaptations usually involve trade-offs and constraints for the predator with respect to invertebrate feeding (Werner, 1977, 1986, Werner & Gilliam, 1984, Eklöv & Persson, 1995). Piscivorous fish are therefore during their early ontogeny assumed to be competitive inferior to their prospective fish prey (Werner, 1977, Persson, 1988, Byström et al., 1998). In Pasvik the dense stock of whitefish, feeding both on zooplankton and zoobenthos, represents a strong potential competitor for the juveniles of all three piscivores. However, the presence of nine-spined stickleback prey seems to play a key role in maintaining a high biomass of piscivorous fish in the watercourse, alleviating the effects of juvenile competitive bottlenecks by a rapid transition of the piscivorous predators through their invertebrate feeding stages.

In conclusion, pike, perch and burbot are important top predators in the aquatic food web of the Pasvik watercourse. Whitefish is the principal prey of large-sized fish, but nine-spined sticklebacks serve an important role as a dietary stepping-stone for initiation of piscivorous feeding. The three predators exhibited a high interspecific dietary overlap, and the major component of differentiation in the piscivore fish guild was along the axis of ontogeny within each species. The multitude of ontogenetic niche shifts generates other functional groups than the species, leading to an increased food web complexity in this subarctic ecosystem.

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References

Allen, K. R., 1939. A note on the food of pike (*Esox lucius* L) in Windermere. J. Anim. Ecol. 8: 72-75.

Amundsen, P.-A., B. Damsgård, A. M. Arnesen, M. Jobling & E. H. Jørgensen, 1995. Cannibalism and prey specialisation in Arctic charr, *Salvelinus alpinus* (L.). Env. Biol. Fishes 43: 285-293.

Amundsen, P.-A., H.-M. Gabler & F. J. Staldvik, 1996. A new method for graphical analysis of feeding strategy from stomach contents data. J. Fish Biol. 48: 607-614.

Amundsen, P.-A., S. Siikavuopio & G. Christensen 1997. Significance and temporal persistence of individual specialization in cannibalistic Arctic charr, *Salvelinus alpinus*. Nordic J. Freshw. Res. 73: 28-34.

Amundsen, P.-A., F. J. Staldvik, A. A. Lukin, N. A. Kashulin, O.A. Popova & Y.S. Reshetnikov, 1997. Heavy metal contamination in freshwater fish from the border region between Norway and Russia. Sci. Total Env. 201: 211-224.

Amundsen, P.-A., F. J. Staldvik, Y. S. Reshetnikov, N. Kashulin, A. Lukin, T. Bøhn, O. T. Sandlund & O. A. Popova, 1999. Invasion of vendace (*Coregonus albula*) in a subarctic watercourse. Biol. Conserv. 88: 405-413.

Bailey, M. M., 1972. Age, growth, reproduction, and food of the burbot, *Lota lota* (Linnaeus), in southwestern Lake Superior. Trans. Am. Fish. Soc. 101: 667-674.

Bence, J. R., 1986. Feeding rate and attack specialization: the roles of predator experience and energetic tradeoffs. Env. Biol. Fish. 16: 113-121.

Beyerle, G. B. & J. E. Williams, 1968. Some observations of food selectivity by northern pike in aquaria. Trans. Am. Fish. Soc. 97: 28-31.

Boisclair, D. & W. C. Leggett, 1989. Among-population variability of fish growth. 2. Influence of prey type. Can. J. Fish. Aquat. Sci. 46: 468-482.

Byström, P., L. Persson & E. Wahlström, 1998. Competing predators and prey: juvenile bottlenecks in whole-lake experiments. Ecology 79: 2153-2167.

Bøhn, T., P.-A. Amundsen, O. A. Popova, Y. S. Reshetnikov, & F. J. Staldvik, 2002. Predator avoidance of coregonids: habitat choice explained by size-related prey vulnerability? Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 57: 183-197.

Chapleau, F., C. S. Findlay & E. Szenasy, 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. EcoScience 4: 259-268.

Chapman, L. J. & W. C. Mackay, 1989. Ecological correlates of feeding flexibility in northern pike (*Esox lucius*). J. Freshw. Ecol. 5: 313-322.

Chapman, L. J., W. C. Mackay & C. W. Wilkinson, 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. 46: 666-669.

Diana, J. S., 1979. Feeding patterns and daily ration of a top carnivore, the northern pike (*Esox lucius*). Can. J. Zool. 57: 2121-2127.

Diana, J. S., W. C. Mackay & M. Ehrman, 1977. Movements and habitat preference of northern pike (*Esox lucius*) in Lac. Ste. Anne, Alberta. Trans. Am. Fish Soc. 106: 560-565.

Eklöv, P. & S. F. Hamrin, 1989. Predatory efficiency and prey selection: interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinus erythrophthalmus*. Oikos 56: 149-156.

Eklöv, P. & L. Persson, 1995. Species-specific anti-predator capacities and prey refuges: interactions between piscivorous perch (*Perca fluviatilis*) and juvenile perch and roach (*Rutilus rutilus*). Behav. Ecol. Sociobiol. 37: 169-178.

Fortunatova, K .R. & O. A. Popova, 1973. Food and Feeding Relationships of Predatory Fish in the Volga River Delta. Nauka Press, Moscow. 299 pp. (In Russian)

Fratt, T. W., D. W. Coble, F. Copes & R. E. Bruesewitz, 1997. Diet of burbot in green Bay and western Lake Michigan with comparison to other waters. J. Great Lakes Res. 23: 1-10.

Frost, W. E., 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. 23: 339-360.

Greenberg, L. A., C. A. Paszkowski & W. M. Tonn, 1995. Effects of prey species composition and habitat on foraging by two functionally distinct piscivores. Oikos 74: 522-532.

Hambright, K. D., R. W. Drenner, S. R. McComas & N.G. Hairston, Jr, 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. Arch. Hydrobiol. 121: 389-404.

Hayes, D. B. & W. W. Taylor, 1990. Reproductive strategy in yellow perch (*Perca flavescens*) – effects of diet ontogeny, mortality and survival costs. Can. J. Fish. Aquat. Sci. 47: 921-927.

He, X. & J. F. Kitchell, 1990. Direct and indirect effects of predation on a fish community: a whole lake experiment. Trans. Am. Fish. Soc. 119: 825-835.

Heath, D. D & D. A. Roff, 1996. The role of trophic bottlenecks in stunting: a field test of an allocation model of growth and reproduction in yellow perch, *Perca flavescens*. Env. Biol. Fish. 45: 53-63.

Hjelm, J., L. Persson & B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122: 190-199.

Keast, A., 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Env. Biol. Fish. 12: 119-129.

Keast, A. & D. Webb, 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845-1874.

Kipling, C., 1983. Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. J. Anim. Ecol. 52: 989-999.

Kipling, C. & W. E. Frost, 1970. A study of the mortality, population numbers, year-class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. J. Anim. Ecol. 39: 115-157.

Krebs, C. J., 1989. Ecological Methodology. Harper & Row, New York. 654 pp.

Lawler, G. H., 1965. The food of the pike, *Esox lucius*, in Heming Lake, Manitoba. J. Fish. Res. Bd. Can. 22: 1357-1377.

LeCren, E. D., C. Kipling & J. C. McCormack, 1977. A study of the numbers, biomass and year-class strength of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. J. Anim. Ecol. 46: 281-307.

LeCren, E. D., 1992. Exceptionally big individual perch (*Perca fluviatilis* L.) and their growth. J. Fish Biol. 40: 599-625.

Mann, R. H. K., 1976. Observations on the age, growth, reproduction and food of the pike *Esox lucius* L. in two rivers in southern England. J. Fish Biol. 8: 179-197.

Mann, R. H. K., 1982. The annual food consumption and prey preferences of pike (*Esox lucius*) in the River Frome, Dorset. J. Anim. Ecol. 51: 81-95.

Mauck, W. L. & D. W. Coble, 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. J. Fish. Res. Bd. Can. 28: 957-969.

Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. 55: 1454-1465.

Nilsson, N.-A., 1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. Rep. Inst. Freshw. Res. Drottningholm 58: 126-129.

Nilsson, P. A. & C. Brönmark. 2000. Prey vulnerability to a gape-limited predator: behavioural and morphological impacts of northern pike piscivory. Oikos 88: 539-546.

Næsje, T. F., O. T. Sandlund & R. Saksgård, 1998. Selective predation of piscivorous brown trout (*Salmo trutta* L.) on polymorphic whitefish (*Coregonus lavaretus* L.). Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 50: 283-294.

Persson, L., 1983. Food consumption and competition between age classes in a perch Perca fluviatilis population in a shallow eutrophic lake. Oikos 40: 197-207.

Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations. In Ebenman, B. & L. Persson (eds.), Size-Structured Populations: Ecology and Evolution. Springer-Verlag, Berlin: 203-218.

Persson, L. & L. A. Greenberg, 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) - roach (*Rutilus rutilus*) interaction. Ecology 71: 44-56.

Persson, L., S. Diehl, L. Johansson, G. Andersson & S. F. Hamrin, 1991. Shifts in fish communities along the productivity gradient of temperate lakes – patterns and the importancy of size-structured interactions. J. Fish Biol. 38: 281-293.

Petkevich, A. N. & G. I. Nikonov, 1969. Burbot and Its Significance in the Fishery of Ob-Irtysh River Basin. Tumen. 31 pp. (In Russian)

Popova, O. A., 1978. The role of predaceous fish in ecosystems. In Gerking, S. D. (ed.), Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford: 215-249.

Popova, O. A. & Y. S. Reshetnikov, 1982. Changes in the Structure of Fish Communities during Eutrophication. Nauka Press, Moscow. 248 pp. (In Russian)

Popova, O. A. and L. A. Sytina, 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish. Res. Bd. Can. 34: 1559-1570.

Rhode, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65: 514-527.

Ricklefs, R. E., 1996. The Economy of Nature. 4th edition. W.H. Freeman and Company, New York, 678 pp.

Robinson, C. L. K. & W. M. Tonn, 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Can. J. Fish. Aquat. Sci. 46: 81-89.

Rosenzweig, M. L., 1995. Species diversity in space and time. Cambridge University Press. 436 pp.

Rudstam, L. G., P. E. Peppard, T. W. Fratt, R. E. Bruesewitz, D. W. Coble, F. A. Copes & J. F. Kitchell, 1995. Prey consumption by the burbot (*Lota lota*) population in Green Bay, Lake Michigan, based on a bioenergetic model. Can. J. Fish. Aquat. Sci. 52: 1074-1082.

Ryder, R. A. & J. Pesendorfer, 1992. Food, growth, habitat, and community interactions of young-of-the-year burbot, *Lota lota* L., in a Precambrian Shield lake. Hydrobiologia 243: 211-227.

Sammons, S. M., C. G. Scalet & R. M. Neumann, 1994. Seasonal and size-related changes in the diet of northern pike from a shallow prairie lake. J. Freshw. Ecol. 9: 321-329.

Sandlund, O. T., L. Klyve, & T. F. Næsje, 1985. Growth, habitat, and food of burbot *Lota lota* in lake Mjøsa. Fauna 38: 37-43 (in Norwegian with an English summary).

Schoener, T. W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 410-418.

Sorokin, V. N., 1976. Burbot of Lake Baikal. Nauka Press, Novosibirsk. 143 pp. (In Russian)

Soupir, C.A., M.L. Brown & L.W. Kallemeyn. 2000. Trophic ecology of largemouth bass and northern pike in allopatric and sympatric assemblages in northern boreal lakes. Can. J. Zool. 78: 1759-1766.

Svärdson, G., 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshw. Res. Drottningholm 55: 144-171.

Treasurer, J. W, R. Owen & E. Bowers 1992. The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. Env. Biol. Fish. 34: 65-78.

Tolonen, A., J. Kjellman & J. Lappalainen, 1999. Diet overlap between burbot (*Lota lota* (L.)) and whitefish (*Coregonus lavaretus* (L.)) in a subarctic lake. Ann. Zool. Fenn. 36: 205-214.

van Densen, W. L. T., 1994. Predator enhancement in freshwater fish communities. pp. 102-119. *In*: I.G. Cowx (ed.) Rehabilitation of Freshwater fisheries. Fishing News Books, Blackwell, Oxford.

Vehanen T., 1995. Factors influencing the yield of brown trout, *Salmo trutta* m. *lacustris* L., in northern Finnish lakes. Fish. Managem. Ecol. 2: 121–134.

Vøllestad, L. A., 1992. Age, growth and food of the Burbot *Lota lota* in two eutrophic lakes in southeast Norway. Fauna norv. Ser. A 13: 13-18.

Vøllestad, L. A., J. Skurdal & T. Qvenild, 1986. Habitat use, growth, and feeing of pike (*Esox lucius* L.) in four Norwegian lakes. Arch. Hydrobiol. 108: 107-117.

Wallace, R. K., 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110: 72-76.

Werner, E. E., 1977. Species packing and niche complementary in three sunfishes. Am. Nat. 111: 553-578.

Werner, E. E., 1986. Species interactions in freshwater communities. pp. 344-358. In: J. Diamond & T. Case (eds.) Community Ecology. Harper & Row, New York.

Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

Wootton, R. J., 1998. Ecology of Teleost Fish. Second edition. Chapman & Hall, London. 386 pp.

Table 1. Diet overlap (Percentage overlap; Krebs, 1989) between different size groups and species of fish. Large overlaps (>60%) are indicated in bold.

	Perch 7.5-10cm	**Perch** 10-17.5cm	**Perch** 17.5-30cm	**Perch** >30cm	**Pike** 20-40cm	**Pike** >40cm	**Burbot** 10-20cm	**Burbot** 20-30cm
Perch 10-17.5cm	47,6							
Perch 17.5-30cm	32,9	56,6						
Perch >30cm	25,4	39,8	**61,5**					
Pike 20-40cm	4,0	27,7	**64,2**	**75,5**				
Pike >40cm	4,4	11,1	33,0	**71,0**	**68,2**			
Burbot 10-20cm	31,7	**79,6**	59,0	35,4	31,7	6,4		
Burbot 20-30cm	31,7	58,3	**82,0**	45,3	48,0	46,8	**62,3**	
Burbot >30cm	7,6	23,4	45,1	**82,2**	**76,9**	**82,3**	19,0	28,9

Legends to figures:

Figure 1. Relative species composition of piscivore fish in samples from the littoral, profundal and pelagic zones in the Pasvik watercourse. n = number of observations.

Figure 2. Dietary composition of different size-classes of a) perch, b) pike, and c) burbot from the Pasvik watercourse. n = number of observations within each size-class (empty stomachs excluded).

Figure 3. Cluster analysis (UPMGA; distance = Euclidian distance) of the diet composition of different size groups of perch, pike and burbot. Letters indicate different feeding groups as referred to in the text.

Figure 4. Size distribution of prey fish consumed by a) perch, b) pike, and c) burbot. (Open bars = nine-spined sticklebacks, filled bars = whitefish, hatched bars = others).

Figure 5. Length relationships between predator and prey. a) Perch, b) Pike, and c) Burbot. (Triangles = nine-spined sticklebacks, circles = whitefish, squares = others.)

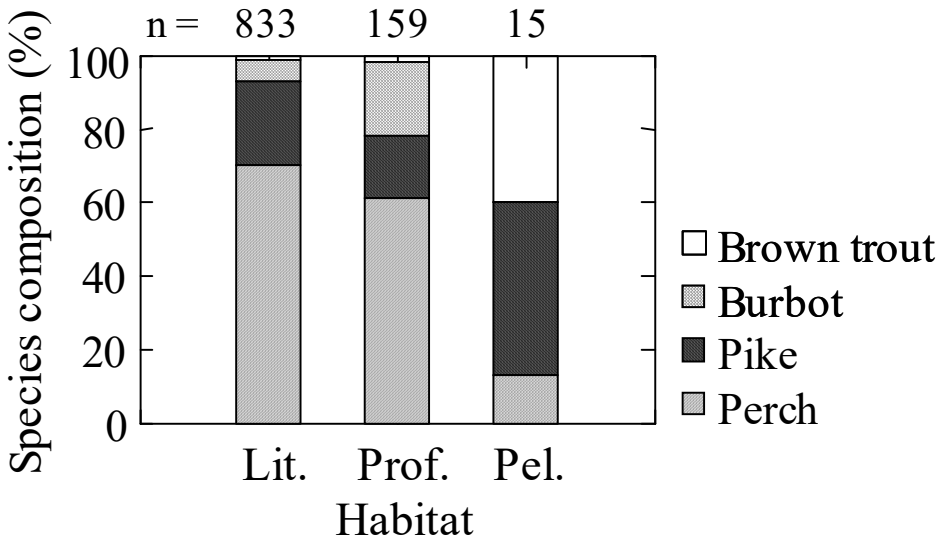
n = 833 159 15
Species composition (%)
100
80
60
40
20
0
Lit.
Prof.
Pel.
Habitat
Brown trout
Burbot
Pike
Perch

Figure 1

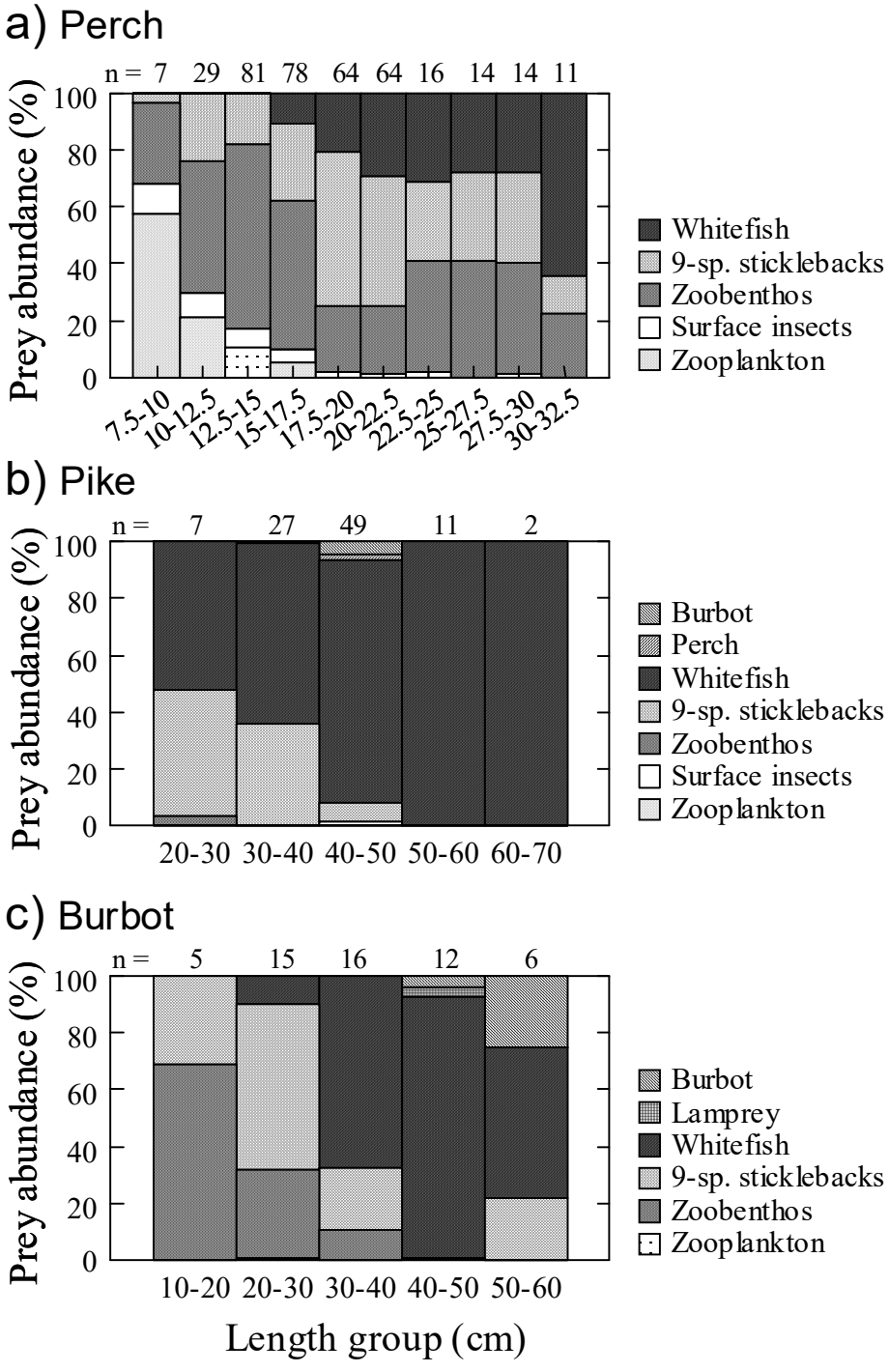
a) Perch
n = 7 29 81 78 64 64 16 14 14 11
Prey abundance (%)
100
80
60
40
20
0
7.5-10
10-12.5
12.5-15
15-17.5
17.5-20
20-22.5
22.5-25
25-27.5
27.5-30
30-32.5
Whitefish
9-sp. sticklebacks
Zoobenthos
Surface insects
Zooplankton
b) Pike
n = 7 27 49 11 2
Prey abundance (%)
20-30
30-40
40-50
50-60
60-70
Burbot
Perch
Whitefish
9-sp. sticklebacks
Zoobenthos
Surface insects
Zooplankton
c) Burbot
n = 5 15 16 12 6
Prey abundance (%)
10-20
20-30
30-40
40-50
50-60
Burbot
Lamprey
Whitefish
9-sp. sticklebacks
Zoobenthos
Zooplankton
Length group (cm)

Figure 2

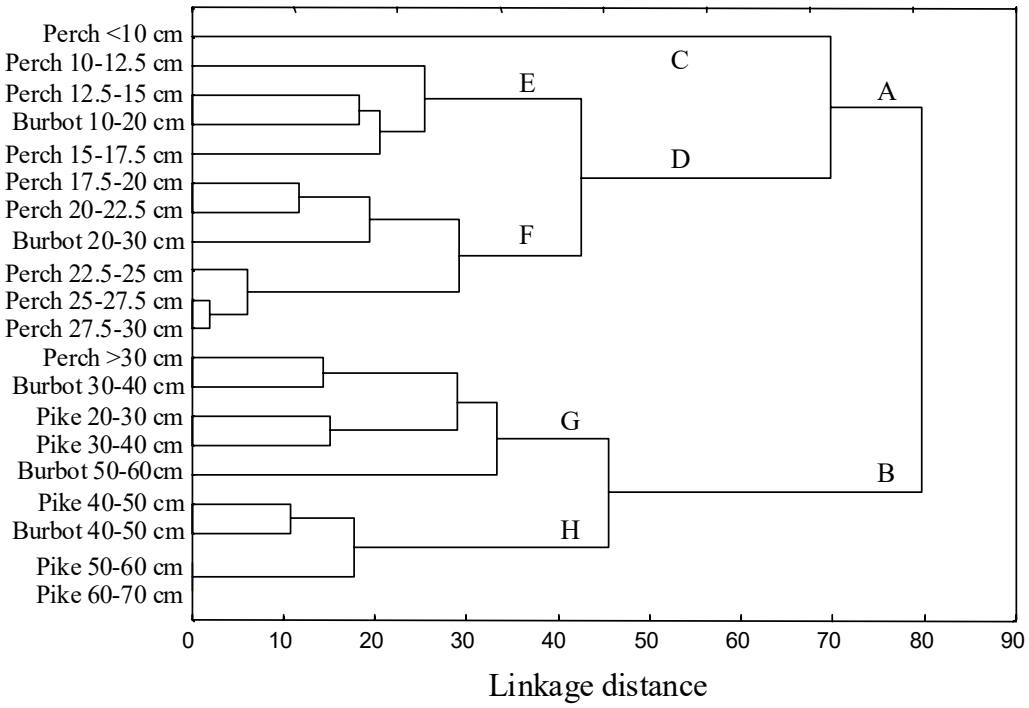
Perch <10 cm
Perch 10-12.5 cm
Perch 12.5-15 cm
Burbot 10-20 cm
Perch 15-17.5 cm
Perch 17.5-20 cm
Perch 20-22.5 cm
Burbot 20-30 cm
Perch 22.5-25 cm
Perch 25-27.5 cm
Perch 27.5-30 cm
Perch >30 cm
Burbot 30-40 cm
Pike 20-30 cm
Pike 30-40 cm
Burbot 50-60cm
Pike 40-50 cm
Burbot 40-50 cm
Pike 50-60 cm
Pike 60-70 cm
A
B
C
D
E
F
G
H
0
10
20
30
40
50
60
70
80
90
Linkage distance

Figure 3

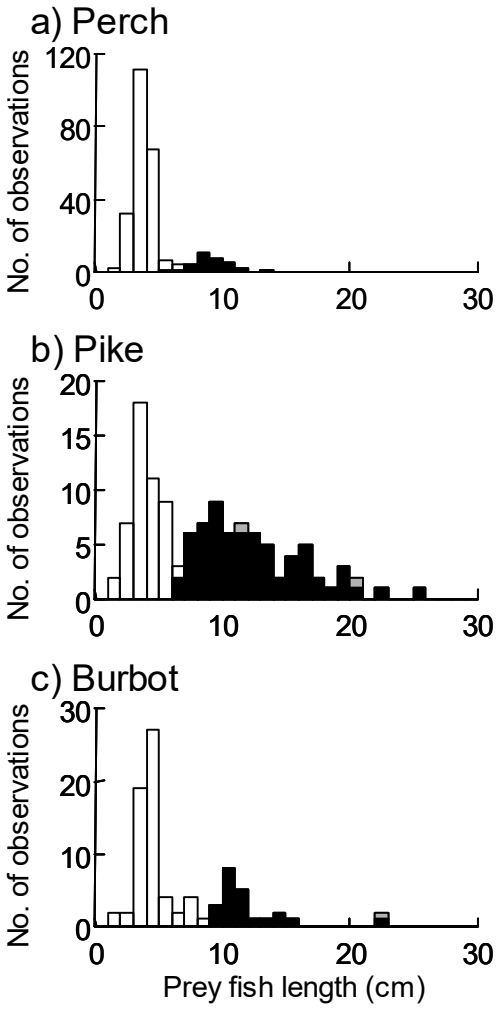
a) Perch
No. of observations
120
80
40
0
0
10
20
30
b) Pike
No. of observations
20
15
10
5
0
0
10
20
30
c) Burbot
No. of observations
30
20
10
0
0
10
20
30
Prey fish length (cm)

Figure 4

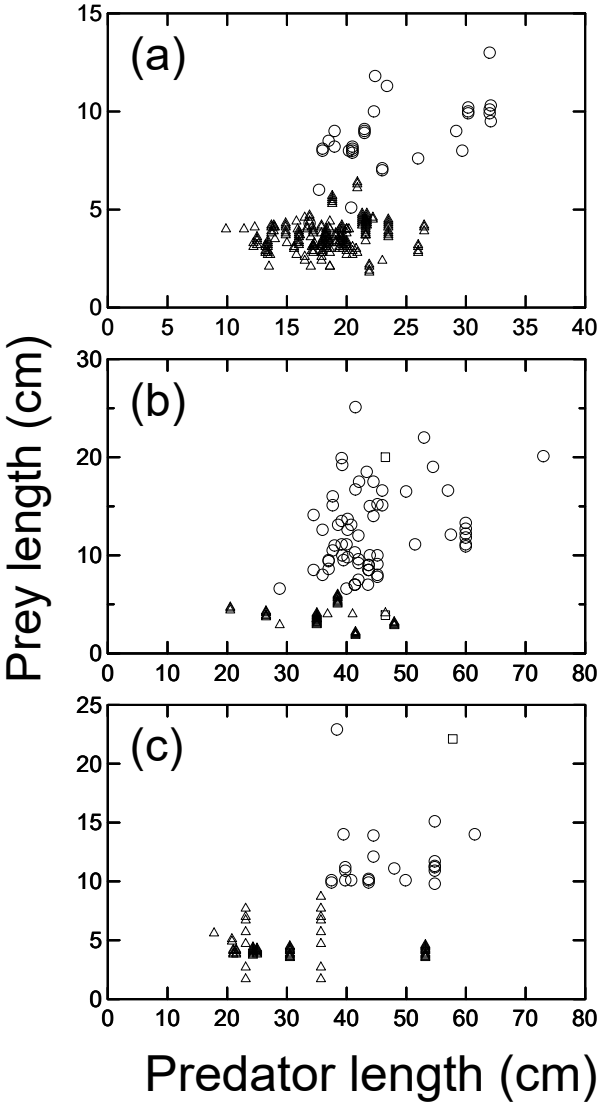

Figure 5