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Feeding ecology of piscivorous brown trout (*Salmo trutta* L.) in a subarctic watercourse

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Feeding ecology of piscivorous brown trout was studied in the Pasvik watercourse, Norway and Russia. The watercourse is heavily regulated for hydroelectric purposes, and 5000 brown trout > 25 cm are stocked annually to compensate the negative impacts of the impoundments. Stocked and wild trout had almost identical diets consisting mainly of vendace *Coregonus albula* and partly of whitefish *Coregonus lavaretus*. Vendace has recently invaded the watercourse, and totally dominated the brown trout diet in the upstream part, where it has become the dominant species in the pelagic habitat. In the downstream part, where vendace were less prevalent, whitefish contributed to a larger extent to the trout diet. No correlation between predator (brown trout) and prey (vendace) lengths was found in the upstream part, and only a weak positive correlation was found in the downstream part. The length of whitefish eaten by brown trout, in contrast, showed a positive correlation with predator length in both the upstream and downstream part. The prey selection of brown trout was, to a large extent, explained by the differences in density and size-structure of coregonids in the two sampling areas.

Introduction

Brown trout, *Salmo trutta* L., exhibit large variation in feeding ecology, and have the capability to include a wide range of prey in the diet, ranging from small zooplankton to relatively large fish (Jonsson 1989). Predators are often selective in their feeding, and species composition, density, size-structure, habitat choice and behaviour of the prey are important factors that influence the diet of the predator (Popova 1978, Wootton 1990, Sandlund & Næsje 1992). Further, as predators grow they tend to broaden their diet to include larger prey (Ivlev 1961, Wilson 1975, Shine 1991, Mittelbach & Persson 1998), a transition generally attributed to ontogenetic increases in predator mouth gape and swimming speed (Ivlev 1961, Keast 1985, Persson *et al.* 1996). Larger prey has larger energy contents, but require on the other hand a higher energy expenditure for searching, pursuiting and handling (Townsend & Winfield 1985, Crawley &

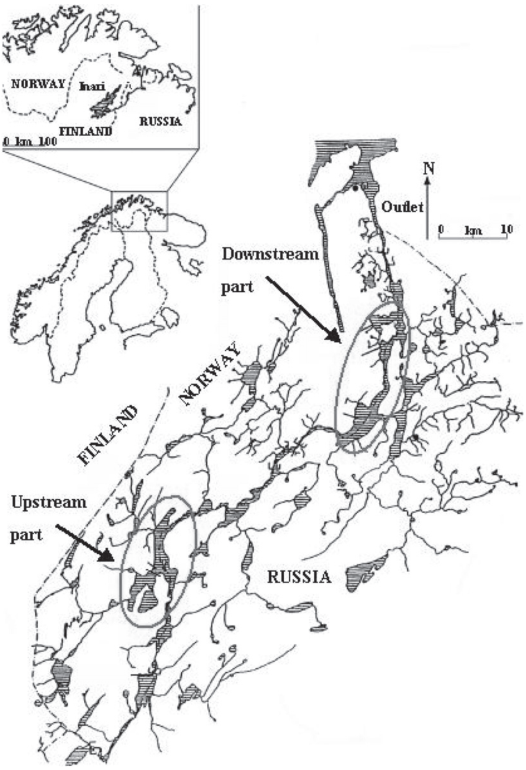

Fig. 1. Map of the Pasvik watercourse. Circles show the upstream and downstream sampling areas.

Krebs 1992). A vast amount of studies support the hypothesis of a positive relationship between length of predator and their prey (Crowder & Cooper 1982, Sandlund & Næsje 1992, Jackson 1997, Lima 1998, Niva & Julkunen 1998, Næsje *et al.* 1998, Kahilainen & Lehtonen 2001), whereas some other studies have reached contrasting conclusions (reviewed in Juanes 1994). Brown trout usually become piscivorous at a size of 20–25 cm (Campell 1979, L'Abée-Lund *et al.* 1992, Damsgård 1995), and the ontogenetic changes in diet represent both a higher energy intake and higher growth efficiency (Garman & Nielsen 1982, Næsje *et al.* 1998, Jonsson *et al.* 1999). Especially in lakes with whitefish *C. lavaretus* and vendace *C. albula*, large and fast growing brown trout may become an effective piscivorous predator in the pelagic habitat (Lind 1978, Mutenia & Salonen 1991, Sandlund & Næsje 1992, Vehanen 1998).

The subartic Pasvik watercourse (70°N) is the single most diverse fish community in northern Norway with 15 species recorded (Amundsen *et al.* 1999). The watercourse consists of a chain of consecutive lakes, and lake dwelling species like whitefish and perch *Perca fluviatilis* dominate the fish communities. The lacustrine characteristic of the watercourse has been further enhanced by the construction of several dams (1953–1978) for hydroelectric purposes, and 5000 brown trout > 25 cm are stocked annually to compensate negative effects of the impoundments on spawning and nursery areas for the trout.

Recently vendace has invaded the Pasvik watercourse. It was introduced into Lake Inari, northern Finland around 1960 (Mutenia & Salonen 1994), and reached a high population density during the 1980s (Mutenia & Ahonen 1990). During this period the vendace migrated downstream into the Pasvik watercourse, where it was recorded for the first time in 1989 (Amundsen *et al.* 1999). As vendace invaded the upstream part of the watercourse, it has competitively replaced whitefish as the dominant fish species in the pelagic zone (Bøhn & Amundsen 1998, 2001, Amundsen *et al.* 1999). The gradual downstream expansion of vendace in the Pasvik watercourse has facilitated a study of selective feeding both on species and size of prey in piscivorous brown trout. Different impacts of the invader upstream and downstream, resulting in a high proportion of vendace (relative to whitefish) available as prey in the upstream part and a low proportion of vendace available downstream, imply different available feeding resources for the brown trout. Accordingly, the main objective of the study was to compare the feeding habits of stocked and wild piscivorous brown trout in the upstream versus the downstream part of the watercourse, representing two different communities with respect to species and size composition of fish prey.

Study area

The subarctic Pasvik watercourse originates from Lake Inari (1102 km^2) in northern Finland, runs into Russia and then defines the border between Norway and Russia for a length of approximately 120 km (Fig. 1). The Norwegian–Russian part of the river system has a total area of 142 km^2, a catchment area of 18 404 km^2, and a mean annual water flow of 175 m^3 s^{-1}. There are altogether seven water impoundments (hydroelectric reservoirs) in the watercourse. Most rapids and waterfalls have disappeared, and today lakes and reservoirs linked together by short and slowly flowing river sections dominate the river system. The average annual amplitude in the water fluctuations are relatively small, usually less than 80 cm. The ice-free season in the lakes and reservoirs lasts from May/June to October/November. Mean water temperature during summer time is around 12 °C with a maximum approaching 17–18 °C. The lakes and reservoirs are oligotrophic with some humic impacts, neutral pH (6.11–7.07), and a Secchi-depth ranging from 2 to 6 m.

Altogether 15 fish species have been recorded in the Pasvik watercourse. The most commonly occurring species in the lakes in addition to brown trout are vendace *Coregonus albula*, whitefish *Coregonus lavaretus* (L.) *sensu lato*, perch *Perca fluviatilis*, pike *Esox lucius* and burbot *Lota lota*. The whitefish occur as two different morphs; the sparsely gill-rakered whitefish (mean gill number 23.3, hereafter denoted s.r. whitefish), and the densely rakered form (mean number 33.7, hereafter denoted d.r. whitefish) (Amundsen *et al*. 1999, 2004). The two whitefish morphs are easily separated and identified from differences in gill morphology (Amundsen *et al*. 2004).

Material and methods

A total of 479 brown trout (Table 1) were sampled throughout the ice-free season in 1998–1999 by local fisherman using gill nets (primary 39–52 mm bar mesh size) and several rod-fishing equipments. The length and weight of each fish were measured, and time and place of catch were recorded. The stomachs were removed and deep-frozen. Wild and stocked brown trout were discriminated and identified by the degree of fin damage, defining individuals with fin damage as stocked fish, after the same method described for farmed Atlantic salmon (Lund *et al*. 1989). In addition, all stocked fish released in 1999 (5341 individuals, mean size 28.4 cm, range 21–38.5 cm) were marked by removing the adipose fin. The brown trout length ranged from 23–70 cm in the total catch-sample with a mean length of 37.7 and 38.8 cm for wild and stocked trout respectively (Fig. 2). Vendace and d.r. whitefish were sampled in the upstream and downstream parts during June, August and September 1998–1999, using pelagic gill nets with bar mesh sizes (knot to knot) of 8, 10, 12.5, 15, 18.5, 22, 26 and 35 mm. The pelagic nets were set at the water surface and consisted of two different types: 40-m long and 4-m deep, and 16-m long and 12-m deep, respectively. A total of 709 vendace and 490 whitefish were sampled. All fish were measured in mm (fork length) and weighed in grams.

In the laboratory, brown trout stomach samples were analysed and the contents categorized into 6 different prey groups. Fish prey items were identified to species and whitefish to morph by gillraker examination if possible. Other prey items like aquatic insects (e.g. *Ephemeroptera*, *Trichoptera*, *Plecoptera, Odonata*), beetles (*Coleoptera*) and chironomids (*Chironomidae*) were pooled into one group called invertebrates. The length of undigested fish prey was measured, and the linear correlation between prey fish length and the predator length was calculated. Prey abundance (A_i, %), i.e. the proportion of each diet category in the stomachs (sum of all categories = 100%), was calculated as follows:

$$A_i = 100\Sigma S_i/\Sigma S_{tot}, \quad (1)$$

Table 1. Catches of wild and stocked brown trout from the two sampling areas in 1998 and 1999.

	Upstream part		Downstream part		
	Wild brown trout	Stocked brown trout	Wild brown trout	Stocked brown trout	Total
1998	10	106	3	40	159
1999	38	114	10	158	320
Total	48	220	13	198	479

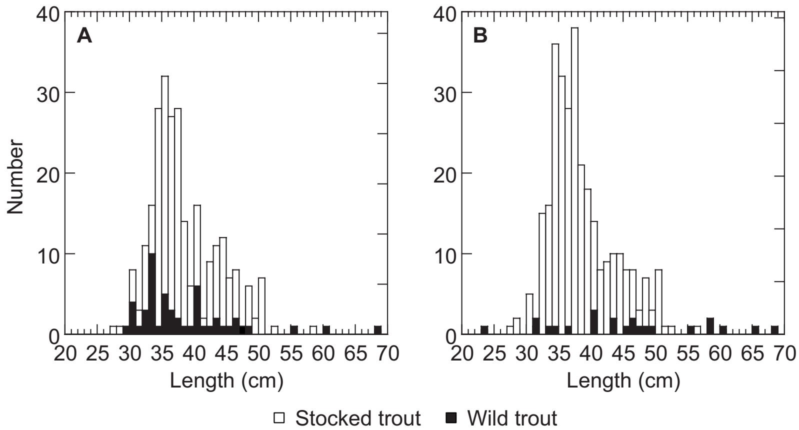

Fig. 2. Length distribution of native and stocked brown trout in the (**A**) upstream and (**B**) downstream part of the Pasvik watercourse.

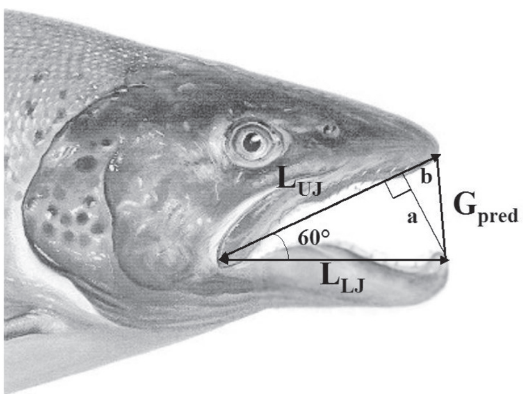

Fig. 3. Measurements of lower jaw (L_{LJ}) and upper jaw (L_{UJ}) for the estimation of gape size (G_{pred}) of brown trout (*see* text for details). Note that the angle in the figure is smaller than 60°.

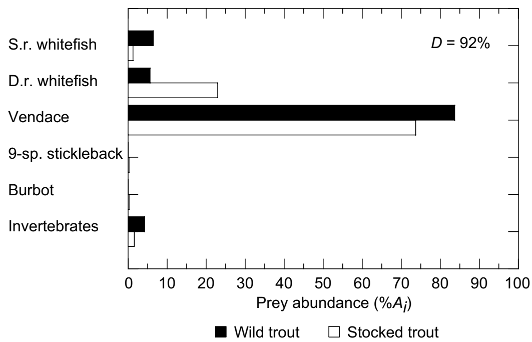

Fig. 4. Prey species composition and the diet overlap value (D) of wild and stocked brown trout.

where S_i is fullness for diet category i and S_{tot} is the total stomach fullness (Amundsen *et al.* 1996).

Diet similarities between wild and stocked trout, and between trout from the upstream and downstream parts were calculated with the percentage overlap index, D (Schoener 1970, Krebs 1999):

$$D = \Sigma\min(A_{ij},A_{ik}), \quad (2)$$

where D is the diet overlap, and A_{ij} and A_{ik} are the prey abundance of prey i for predator j and k, respectively. $D > 60\%$ expresses a significant overlap according to Wallace (1981).

According to Wankowski (1979), maximum mouth opening during food uptake in salmonids is 60°. The lower jaw (L_{LJ}) and the upper jaw (L_{UJ}) lengths in mm were recorded from each brown trout, and the gape size was calculated using trigonometry (Fig. 3). Distances a and b in Fig. 3 were calculated as: $a = L_{LJ} \sin 60$, and $b = L_{UJ} - L_{LJ} \cos 60$. G_{pred} could then be calculated as $G_{pred} = (a^2 + b^2)^{0.5}$, giving the formula:

$$G_{pred} = [(L_{LJ} \sin 60)^2 + (L_{UJ} - L_{LJ} \cos 60)^2]^{0.5} \quad (3)$$

Results

Vendace was the dominant prey species of both wild and stocked brown trout (Fig. 4). Wild and stocked trout had highly similar diets with a dietary overlap of 92%, therefore in the further analyses, wild and stocked trout are pooled.

In the upstream part of the watercourse, brown trout fed almost exclusively on vendace,

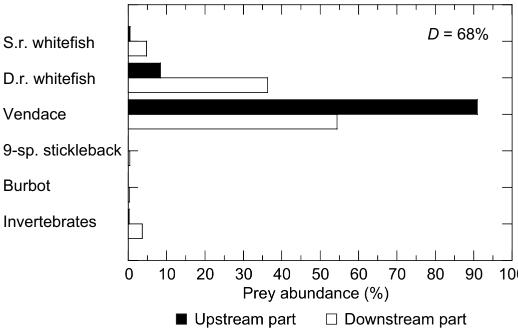

Fig. 5. Prey species composition and the diet overlap-value (*D*) of brown trout in the upstream and downstream parts.

which formed about 90% of the diet, whereas d.r. whitefish contributed 8% (Fig. 5). In the downstream part, vendace also dominated as prey species (60%), but d.r. whitefish contributed a larger proportion to the brown trout diet (38%). Overall, the diet similarity between trout from the upstream and downstream parts was relatively high ($D = 68\%$).

Different patterns emerged when comparing the diet of different size groups of brown trout. In the upstream part, all length groups of brown trout were feeding on vendace (Fig. 6). In the downstream part, small sized brown trout were feeding mainly on vendace, but the relative proportion of d.r. whitefish and s.r whitefish increased with the length of the brown trout. The largest size group of brown trout in the downstream part fed almost exclusively on the two whitefish morphs.

The mean lengths of vendace and d.r. whitefish eaten by brown trout were 8.3 cm (SD = 1.7, range 5.5–13 cm) and 7.8 cm (SD = 2, range 4.5–13.5 cm), respectively (Fig. 7). Both prey species consumed were significantly larger in the upstream part as compared with the downstream part (Mann-Whitney test: $p < 0.05$). Within both sampling areas, vendace and d.r. whitefish eaten by brown trout were smaller than the observed lengths for the two species in the pelagic gill-net catches (Fig. 7) (Mann-Whitney test: $p < 0.05$).

No correlation was found between the lengths of brown trout and vendace (predator and prey) in the upstream part, and only a weak positive correlation in the downstream part (Fig. 8A and Table 2). A positive correlation between the lengths of brown trout and d.r. whitefish was found in both areas (Fig. 8B and Table 2). The relative minimum and maximum prey-to-predator lengths varied between 10%–36.2% (mean 21%) and 9.5%–32.9% (mean 19.7%) for vendace and whitefish, respectively. Both prey species eaten by brown trout were much smaller than the calculated maximum gape size of the predator (Fig. 8).

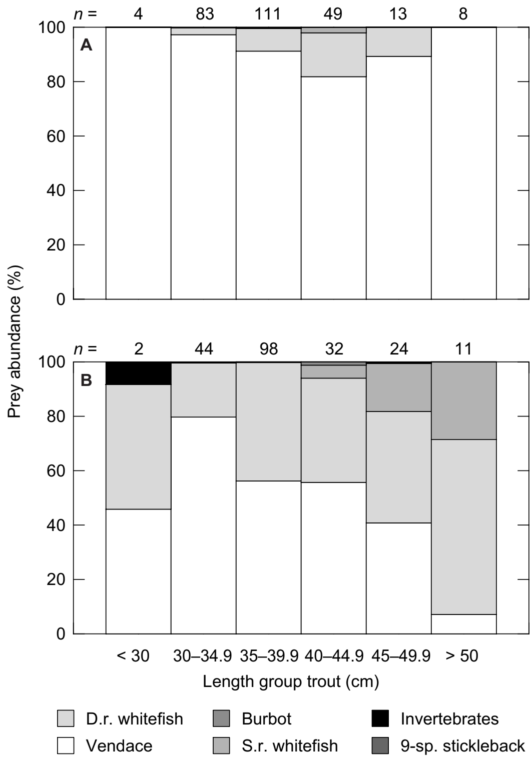

Fig. 6. Prey species composition of different length groups of brown trout in (**A**) the upstream and (**B**) downstream parts.

Discussion

A high proportion of fish in the diet of brown trout is common in lakes where small sized coregonid species reach high densities (Lind 1978, Mutenia & Salonen 1991, Sandlund & Næsje 1992, Vehanen 1998). In the present study, the diet of both wild and stocked brown trout was similarly dominated by vendace. The slightly higher proportion of vendace in the diet of wild trout may

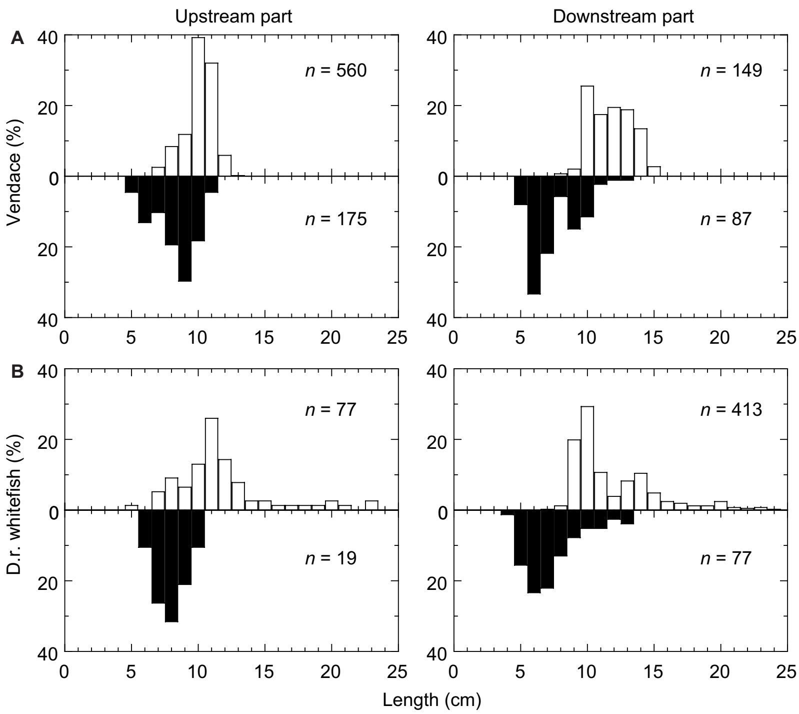

Fig. 7. Length distribution of (**A**) vendace, and (**B**) d.r. whitefish caught by gillnets in the pelagic zone (upper, open bars) and from brown trout stomachs (lower, solid bars).

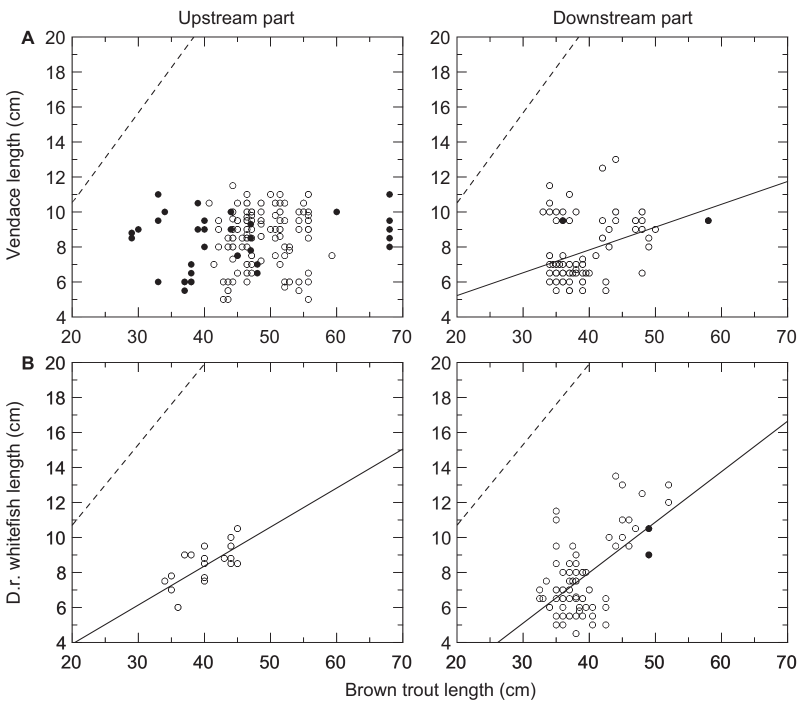

Fig. 8. Relationship between brown trout length and (**A**) vendace length and (**B**) d.r. whitefish length from the upstream and downstream parts. Solid circles represent wild trout, open circles stocked trout. Dotted line shows the calculated gape-size limitation for brown trout.

have resulted from proportionally larger wild trout samples taken in the upstream part of the watercourse, where vendace was the dominant species in the pelagic zone. It is shown that brown trout are able to start feeding on invertebrates a few hours after stocking (O'Grady 1983, Jonsson 1989), but also that feeding on fish may require more time and experience (Hesthagen & Johnsen 1992). The food uptake of predators depends on experience in catching movable prey (Vinyard *et al*. 1982, Dill 1983, Paszkowski & Olla 1983), and capture success increases quickly in experiments with various food items (Stradmeyer & Thorpe 1987). On the other hand, it is shown in cannibalistic arctic charr that previous experience with fish prey did not result in a significant increase in numbers of prey captured (Amundsen *et al*. 1995). In this study, a similar piscivorous diet of wild and stocked brown trout indicates that the stocked trout quickly adopt the feeding behaviour and habitat use of the wild fish. This also corresponds with the similar and high growth rates of 7–8 cm year^{-1} observed for both wild and stocked trout in the watercourse (H. Jensen unpubl. data).

Some biologically significant differences in the brown trout diet were observed between the upstream and downstream part of the Pasvik watercourse (Fig. 5). In the upstream part, vendace and d.r. whitefish had approximately a 90/10 contribution to the diet, closely corresponding to the proportion of the two prey species in the gillnet catches. In the downstream part, the proportion of vendace and d.r. whitefish was approximately 60/40 in the stomachs, but 30/70 in the gillnet catches. Thus, the brown trout seem to prefer vendace over whitefish. However, the mean sizes of vendace and whitefish found in the stomachs were in the lower size-range of the gill net catches, possibly giving a bias in the comparison, e.g. due to a larger age-0 group of vendace. The observed prey size selection in the present study indicates a positive capture success on small prey fish for the piscivorous brown trout. Fast-start performance increases sharply with increasing fish length (Webb 1978, 1984), suggesting that larger coregonid prey have a greater ability to avoid attacks than smaller. Larger prey are also more difficult to handle than small prey.

Vendace was the dominant prey species for all length groups of brown trout in the upstream part (Fig. 6). According to optimal foraging theory, predators should feed on the prey that give the highest net energy yield (MacArthur & Pianka 1966, Pyke *et al*. 1977, Townsend & Winfield 1985). In the upstream part, a suggested high capture success and very high density of small vendace in the pelagic zone might overrule a higher gross energy content of larger whitefish, thus explaining the positive selection of the vendace as prey for the brown trout. In the littoral zone of the watercourse, potential prey species for piscivorous fish are nine-spined stickleback, d.r. whitefish, s.r. whitefish and burbot, but the contribution of these prey species to the diet of brown trout was very low. These littoral prey species are eaten mainly by pike, burbot and large perch (Amundsen *et al*. 2003). The brown trout seem to avoid competition from the other species in the littoral piscivorous guild, preferring coregonid prey in the pelagic habitat (Bøhn *et al*. 2002). Small-sized pelagic vendace is also the preferred prey of brown trout in many Finnish lakes (Vehanen & Aspi 1996, Niva & Julkunen 1998).

Ontogenetic niche shifts are common for several fish species to increase foraging efficiency and to reduce predation risk during the life span (Werner & William 1984, Juanes 1994). In the downstream part, vendace was the dominant prey species of brown trout up to 40–45 cm, but the proportion of d.r. and s.r whitefish in the diet increased with the predator length, suggesting a change in feeding behaviour of larger brown

Table 2. Linear regression of prey length (vendace, L_{ven} and d.r. whitefish, L_{whi}) versus predator length (brown trout, L_p) from the upstream and downstream part of the watercourse. df is the degrees of freedom. Significant *p* values are shown in boldface.

Parameter	Site	Regression	r^2	*F* ratio	df	*p* value
Vendace *vs*. brown trout	Upstream	$L_{ven} = 8.117 + 0.001L_p$	0.007	1.173	173	0.28
	Downstream	$L_{ven} = 2.613 + 0.130L_p$	0.135	13.26	85	< **0.01**
D.r. whitefish *vs*. brown trout	Upstream	$L_{whi} = -0.550 + 0.223L_p$	0.475	20.03	17	< **0.001**
	Downstream	$L_{whi} = -3.553 + 0.288L_p$	0.361	50.02	75	< **0.001**

trout (Fig. 6). The increased proportion of especially d.r. whitefish eaten by brown trout in the downstream lake, shows that large trout have the ability to include larger prey in their diet.

No correlation was found between the lengths of brown trout (predator) and vendace (prey) in the upstream part, and only a weak positive correlation was observed in the downstream part (Fig. 8A). The main reason for this seems to be the limited maximum fish size in the vendace population, reaching a growth asymptote at a size smaller than 15 cm in the watercourse (Amundsen *et al.* 1999, Bøhn & Amundsen 2001, Bøhn *et al.* 2002). Within this narrow size-range, the whole vendace population is suitable as food for brown trout larger than 25–30 cm. D.r. whitefish, in contrast, grows out of the predation size-range of the trout within 3–4 years (Bøhn *et al.* 2002); positive correlations were found between the length of the trout and the length of the d.r. whitefish prey in both sampling areas. Plots of predator-to-prey length often show large variation in the range of prey sizes, and larger predators often include both small and large prey items (Popova 1978, Juanes 1994, Juanes & Conover 1995, Scharf *et al.* 2000). In the present study, the length of each individual prey was plotted against predator length instead of the mean size of prey for each individual predator. By using mean size of prey better correlations may be reached, but this also masks interesting individual variation (Juanes 1994). The increased proportion of whitefish with increasing brown trout length in the downstream part reflects a higher preference for relatively large sized coregonid prey. Strong correlations in length between piscivorous predators and their prey fish are well documented in other systems (Crowder & Cooper 1982, Sandlund & Næsje 1992, Jackson 1997, Lima 1998, Niva & Julkunen 1998, Næsje *et al.* 1998, Kahilainen & Lehtonen 2001). The food choice of brown trout in the Pasvik watercourse was apparently not gape limited, as also found elsewhere (L'Abée-Lund *et al.* 1992, Damsgård 1995). The present method of measuring the length of upper and lower jaws to calculate the maximum gape size has previously not been decribed, but proved to be a fast and convenient method. The regression equation for the gape size limitation resembles results from other studies (Damsgård 1993), and the method may successfully be applied to other fish species as well.

This study shows that brown trout larger than 25 cm are piscivorous predators in the subarctic and coregonid dominated Pasvik watercourse. Vendace was the most important prey, followed by whitefish. No significant differences in the diet were observed between wild and stocked trout. Vendace was the dominant prey species for all size-classes of brown trout in the upstream part of the watercourse, whereas whitefish proportion in the diet increased downstream, especially for the larger sized brown trout. The prey selection of brown trout thus seems, to a large extent, explained by the differences in abundance and size-structure of the coregonids in the upper and lower part of the watercourse.

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