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Diet overlap between burbot (*Lota lota* (L.)) and whitefish (*Coregonus lavaretus* (L.)) in a subarctic lake

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The growth of burbot in ultraoligotrophic Kilpisjärvi, a lake in northern Finland, is slow. The mean lengths of age-5 and age-9 burbot were 198 mm and 217 mm, respectively. Stomach contents of 45 burbot (144–274 mm) and 331 whitefish (117–345 mm) were analysed to determine any possible diet overlap between the studied species. According to logistic regressions, the main diet of burbot longer than 257 mm was fish, whereas the smallest burbot (< 165 mm) ingested mainly insect larvae. The length-dependent probabilities of burbot ingesting certain food items did not differ between the ice-covered and open-water periods. During the ice-covered period burbot preferentially preyed on molluscs, insect larvae and benthic crustaceans, while most whitefish smaller than 274 mm ingested zooplankton. During the open-water period, more than 50% of whitefish smaller than 191 mm ingested zooplankton, while those in the length interval 127–244 mm preferred benthic crustaceans. The largest whitefish (> 294 mm) ingested insect larvae during the ice-covered period and insect pupae during the open-water period. Independently of season, most large whitefish (> 274 mm) ingested molluscs. The diet overlap between burbot and whitefish was thus highest during the ice-covered period.

1. Introduction

The growth of burbot *Lota lota* (L.) and whitefish *Coregonus lavaretus* (L.) is slow in the subarctic Kilpisjärvi, a lake in Finland (Tolonen 1997, Tolonen & Lappalainen 1999). The growth of burbot is known to decrease towards the northern latitudes (Lehtonen 1998) and to be site- and time-specific (Kjellman *et al*. 1993, Kjellman & Hudd 1996), but the specimens in Kilpisjärvi were still considerably smaller than what would have been expected compared with other studies in Finnish

Lapland (Eloranta 1982a, Lehtonen 1998). Even in Tshahkaljärvi, a lake located only 1 km east of Kilpisjärvi, large burbot are rather common.

The reason for the slow growth of burbot in Kilpisjärvi is not known, but Tolonen and Lappalainen (1999) noted a similarity between food items ingested by burbot and benthic whitefish. Both species commonly occur in northern Finland (Tammi *et al*. 1997) and additionally whitefish have been stocked at great densities in several lakes (e.g. Salojärvi 1992, Tammi *et al*. 1997).

Our objectives here were to determine the diets of burbot and benthic whitefish and to evaluate the possible diet overlap between these two species in Kilpisjärvi. Diet overlap between burbot and benthic whitefish was suggested by Scott and Crossman (1973) and Lehtonen (1998). Firstly, we studied the diets of both species during the open-water and ice-covered periods. Thereafter, diet overlap was evaluated with the Schoener index (Schoener 1970), as suggested by Wallace (1981).

2. Material and methods

2.1. Study area

Kilpisjärvi (33.7 km^2) is located in northwestern Lapland (69°03´N, 20°49´E, altitude 463 m) and drains via the Tornionjoki into the Gulf of Bothnia. It is an ultraoligotrophic clearwater lake, located in the subarctic birch-forest zone. The estimated integral primary production during the ice-free season is 2 g C m^{-2} (Tolonen 1999a). The lake is ice-free for about 140 days. The median date for ice break-up is 16 June and for lake freeze-over 25 November (Finnish National Board of Waters 1983). The maximum depth of the lake is 48 m, and the maximum water level amplitude 61 cm (Järnefelt 1956). The shorelines and near-shore sediment down to 5 m are dominated by rock and large stones.

In addition to burbot and whitefish, the fish fauna in Kilpisjärvi includes alpine bullhead *Cottus poecilopus* Heckel, minnow *Phoxinus phoxinus* (L.), Arctic charr *Salvelinus alpinus* (L.) and grayling *Thymallus thymallus* (L.). In addition, brown trout *Salmo trutta* L., pike *Esox lucius* L. and perch *Perca fluviatilis* (L.) occur in the lake.

2.2. Sampling of burbot and whitefish

The stomach contents of 45 burbot were analysed. Of these burbot, 15 were caught with benthic gill nets, which were set from the littoral to the semipelagic zone during the open-water period (August–September) in 1983 and 1992. The remaining 30 burbot were caught with rods during an ice-fishing competition in May 1998. Two of the burbots caught during the open-water period and three of those caught during the ice-covered period had empty stomachs.

The mean length of the burbot was 203 mm (min.–max. 144–274) and the mean mass 49 g (min.–max. 14–114). The age of the burbot was determined from otoliths (Eloranta 1975), which were roasted to a coffee-brown colour and broken into 2 parts through the nucleus. The annual rings were counted from otolith's broken surface.

Whitefish were captured between February and November in 1992 and 1993 with benthic gill nets with mesh sizes of 10, 12, 15, 20, 25, 30 and 35 mm (bar length). The nets were set at night from the littoral to the semipelagic zone at 3 sampling sites. The captured fish were removed at 12-h intervals during the summer and at 24-h intervals during the winter.

The stomach contents of 331 whitefish were analysed. One hundred and forty-five of these whitefish were caught during the open-water period (July–November), and 186 during the ice covered period (December–June) in 1992–1993.

Total lengths (mm) and wet weights (w.w.; g) of 109 whitefish caught during the open-water period and 180 caught during the ice-covered period were also measured. The mean length of the whitefish was 215 mm (min.–max. 117–345) and the mean mass 80 g (min.–max. 9–335).

2.3. Food analyses

After capture length and weight were measured, and the fish were frozen to preserve their stomach contents. When thawed, the fish were opened, and the stomach contents from the oesophagus to the pyloric curve were analysed under a stereoscopic microscope. Fish with empty stomachs were excluded from the diet overlap analyses.

Prey items were identified at least to order (when applicable) and counted. The wet weight (w.w.) for each food category was determined by weighing undigested food items from the stomachs (*see* Appendix). When analysing larger food items such as molluscs and insect larvae, calculations were based on reconstructed wet weight by counting partly digested food items as intact specimens (Hindar & Jonsson 1982). The food items were dried for 2 minutes on paper and weighed to the nearest 0.1 mg. The mean weight percentage of each food item in each stomach was calculated, and the figures obtained summed and divided by the number of stomachs analysed.

2.4. Statistical analysis

The proportion of fish utilizing a certain food category was analysed using logistic regressions (SAS 1989):

$$y = \exp(\alpha + \beta L)[1 + \exp(\alpha + \beta L)]^{-1} \quad (1)$$

or:

$$y = \exp(\alpha + \beta L + \gamma L^2)[1 + \exp(\alpha + \beta L + \gamma L^2)]^{-1} \quad (2)$$

where y is the occurrence of a food category in a single fish recorded as 0 or 1, L (mm) is fish length, and α, β and γ are constants to be estimated.

If a diet category made up less than 5% (w.w.) of the stomach content we recorded 0 for occurrence. Eq. 1 was used if, relying on preliminary graphic analysis, we expected an increasing or decreasing consumption with length. Eq. 2 was used if we expected a maximum consumption in a limited length interval. The difference between Eqs. 1 and 2 could be compared with the difference between first and second order regular regressions. Regular regressions are used to estimate the relationship of one continous variable with another, whereas logistic regressions are used to investigate the relation between a proportional and a continuous variable.

Diet overlap was analysed with the Schoener index (Schoener 1970):

$$\alpha_{\mathrm{Sch}} = 1 - 0.5\left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right) \quad (3)$$

where p_{xi} is a proportion of food category i in the diet of species x, p_{yi} is a proportion of food category i in the diet of species y, and n is the number of food categories.

The diet of both burbot and whitefish varies both seasonally and according to the length of the fish (e.g. Guthruf *et al.* 1990, Tolonen 1997). It could, therefore, be misleading to analyse the potential diet overlap between the two species if the length of the fish and the season were not taken into account. Our samples were too small to be divided into seasons or to distinctly separate length groups. To overcome this, we pooled the seasons, and analysed the diet overlap over floating length groups. We fixed the starting point at 345 mm for whitefish and at 140 mm for burbot. Then we gradually included smaller whitefish, and larger burbot into the diet overlap analyses. In these analyses we excluded detritus from food categories (e.g. Muth & Smith 1974, Persson 1983), as we assumed that neither fish species would gain any significant amount of energy from it. Diet overlap assessments based on less than 10 burbot or whitefish were excluded.

3. Results

3.1. Length-at-age of burbot

No significant differences were found between the lengths of burbot sampled during the open-water period with gill nets and burbot sampled with rods during the ice-covered period (t-test, $p > 0.10$).

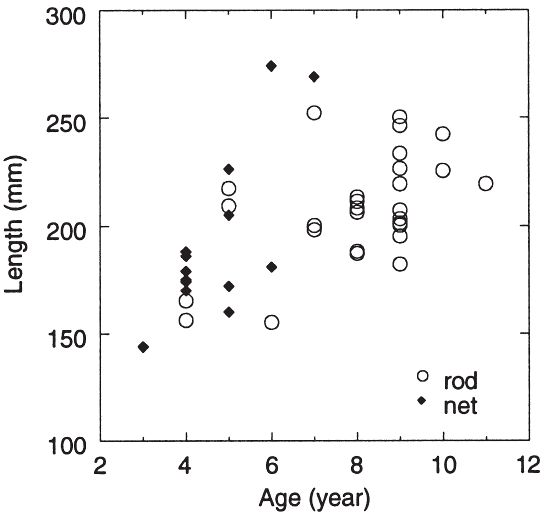

Fig. 1. Length-at-age of burbot in Kilpisjärvi. Samples taken with bottom gill nets and rods.

Since the length-mass relationships did not differ, either (GLM, $p > 0.10$), we pooled all burbot in the growth analyses. The length-mass relationship obtained was: $L = -24.9 + 60.1(\ln W)$ (W is fish weight (g); $R^2 = 0.85$, $p < 0.01$). This function tended to overestimate the mass of the largest burbot, however. Growth was fairly steady until age 5 (mean length = 198 mm, $n = 6$), but 20 cm decreased thereafter. Age-9 burbot had a mean length of only 217 mm ($n = 11$; Fig. 1).

3.2. Diet of burbot

The diet of burbot varied both seasonally and with the length of the fish. More burbot ingested detritus during the open-water period than during the ice-covered period (Fisher exact test, $p < 0.01$, Table 1). When the lake was ice covered more burbot ingested molluscs, insect larvae and benthic crustaceans (Fisher exact test, $p < 0.01$). When the diet was measured as %w.w., however, we could find no significant differences between the ice-covered and open-water periods for either insect larvae or benthic crustaceans (Mann-Whitney U-test, $p > 0.10$; Fig. 2). The seasons were therefore pooled for logistic analysis of insect larvae, benthic crustaceans and fish in the diet of different-sized burbot.

The probability of burbot ingesting fish in-

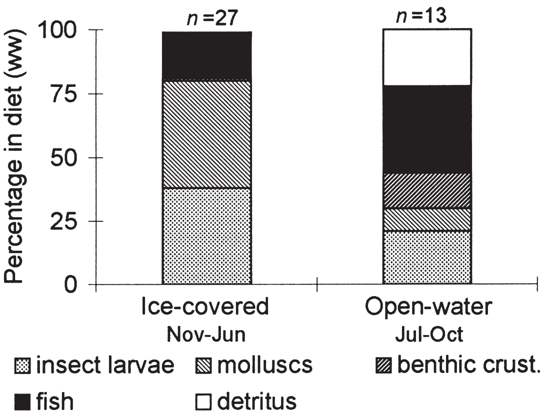

Fig. 2. Diet of burbot in Kilpisjärvi. The number of investigated fish is shown at the top of each column.

creased with length (Eq. 1, $p < 0.10$) (Fig. 3). A burbot 253 mm long had a 50% ($-\alpha\beta^{-1}$) probability of ingesting fish, and the proportion (%w.w.) of fish ingested also increased with length of burbot (Eq. 1, $p < 0.05$, 50% = 257 mm). The probability of ingesting insect larvae decreased with length, however (Eq. 1, $p < 0.05$, 50% = 233 mm), as did the proportion of insect larvae in the diet (Eq. 1, $p < 0.10$, 50% = 165 mm; Fig. 3). Only two burbot had eaten both fish and insect larvae, while five burbot had eaten neither fish nor insect larvae.

Neither the ingestion of benthic crustaceans nor that of molluscs varied significantly (Eq. 1, $p > 0.10$) with the length of burbot. In general, the 50% probabilities of ingesting certain food items could not be used to divide the burbot into distinct groups, as the values generally were close to either the minimum or the maximum length of burbot.

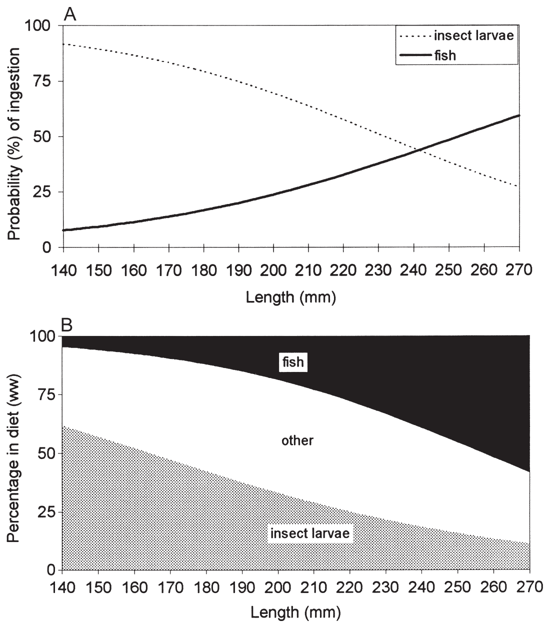

Fig. 3. Probability of burbot ingesting insect larvae and fish (A) and their proportions (%w.w.) in the diet as a function of length (B), estimated with logistic regressions.

3.3. Diet of whitefish

The diet of whitefish varied both with the season and with the length of the fish. During the open-water period more whitefish ingested benthic crustaceans (Fisher exact test, $p < 0.01$) and insect pupae (Fisher exact test, $p < 0.05$) than during the ice-covered period. During the ice-covered period more whitefish ingested plankton and insect larvae (Fisher exact test, $p < 0.01$). The same differ-

Table 1. Number of burbot that ingested different food items in Kilpisjärvi during the ice-covered and open-water periods.

	Ingested	Ice-covered	Open-water	Σn
Insect larvae	Yes	20	5	25
	No	7	8	15
Molluscs	Yes	22	3	25
	No	5	10	15
Benthic crustaceans	Yes	1	5	6
	No	26	8	34
Fish	Yes	6	5	11
	No	21	8	39
Detritus	Yes	0	4	4
	No	27	9	36

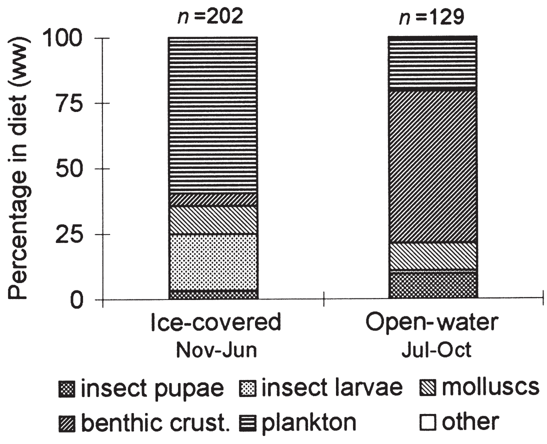

Fig. 4. Diet of whitefish in Kilpisjärvi. The number of investigated fish is shown at the top of each column.

ences were observed when measured as %w.w. of the diet (Fig. 4). The observed dietary differences were not due to differences in length, as we could find no significant differences in length of whitefish between the open-water and ice-covered periods (*t*-test, $p > 0.10$).

The probability of whitefish ingesting zooplankton decreased with the length of the fish during both studied periods (Eq. 1, $p < 0.01$; Fig. 5). The 50% ($-\alpha\beta^{-1}$) probability that a whitefish would ingest plankton occurred at 274 mm in length during the ice-covered period and at 191 mm during the open-water period. On the other hand, ingestion of insects increased with length (Eq. 1, $p < 0.01$). During the ice-covered period whitefish 294 mm long had a 50% probability of ingesting insect larvae and during the ice-free period whitefish of 330 mm length had a 50% probability of ingesting insect pupae. Only 5 whitefish had eaten both insect larvae and pupae. The proportion of molluscs ingested was independent of season, but increased with length (Eq. 1, $p < 0.01$). In most cases (> 50%) whitefish longer than 274 mm ate molluscs (Eq. 1, $p < 0.01$). The relationship with length was quadratic during the open-water period (Eq. 2, $p < 0.01$), when more than 50% of the whitefish within the length interval 127–244 mm ingested benthic crustaceans.

According to the above results, the whitefish were grouped into five length-intervals (Fig. 5). During the ice-covered period, zooplankton was the most important food category for small whitefish (length-group 117–260 mm; Fig. 6). For large

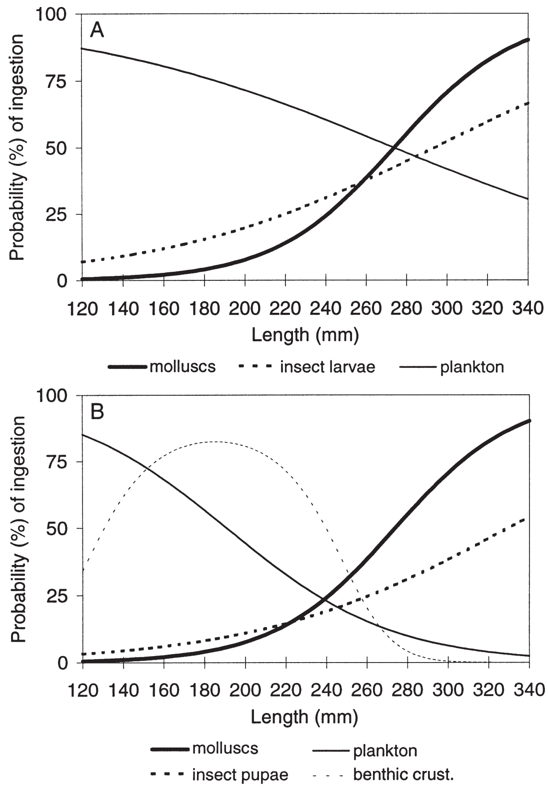

Fig. 5. Probability of whitefish ingesting different food categories as a function of length during the periods studied (A = Ice-covered, B = Open-water period), estimated with logistic regressions.

whitefish (> 260 mm), insect larvae was the most important food category during this period, although molluscs were also common in the diet. During the open-water period the most important food items for small whitefish (≤ 260 mm) were benthic crustaceans. During the same period the largest whitefish preyed mainly on molluscs and insect pupae.

3.4. Diet overlap between burbot and whitefish

A possible diet overlap between the studied species was first evaluated separately for the ice-covered and open-water periods. The burbot were divided into two length-groups by the length corresponding to a 50% probability for ingesting insect larvae (233 mm). Whitefish were grouped as above into two length-groups (≤ 260 and > 260 mm).

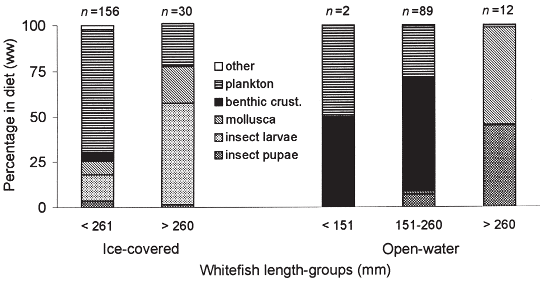

Fig. 6. Diet (%w.w.) of whitefish in different length-groups in Kilpisjärvi.

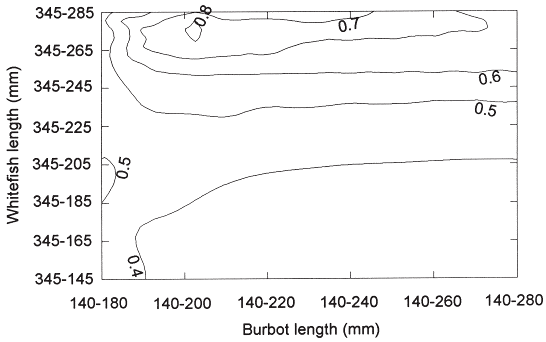

Fig. 7. Diet overlap (α_{Sch}) between burbot and whitefish. The overlap values are expressed as isopleths for whitefish and burbot of increasing length ranges. For burbot the minimum length is always 140 mm and for whitefish the maximum length is always 345 mm. In the upper left corner only a few specimens (≥ 10) are included; in the lower right corner the entire sample.

For the above groups, the diet overlap was most pronounced during the ice-covered period, especially between large whitefish (> 260 mm) and small burbot (< 230 mm; Table 2). At this time of year, both species ingested molluscs and insect larvae (Figs. 2 and 6).

There were problems with this grouping burbot by length. All the 50%-length-probabilities for ingesting a certain food item divided the burbot into very unequal groups. To overcome this, the open-water and ice-covered periods were pooled, the starting point was set at 345 mm for whitefish (maximum length) and at 140 mm for burbot (minimum length), and the diet overlaps were analysed over floating length-groups. The diet overlap was highest (α_{Sch} = 0.82) for burbot 140–202 mm long (n = 21), and whitefish 345–265 mm long (n = 24; Fig. 7). It (α_{Sch} > 0.80) was only detected within a small range of lengths. However, when only large whitefish were included, a considerable overlap (α_{Sch} > 0.70) was detected almost throughout the entire range of the burbot lengths.

4. Discussion

The results indicate that the diet overlap between burbot and whitefish exists in Kilpisjärvi. The overlap was most obvious between large whitefish and burbot in all size-groups. Since smaller whitefish utilised more planktonic food (Fig. 5; Tolonen 1997), the diet overlap between small whitefish and burbot is less extensive. The overlap was generally smaller during the open-water period than during the ice-covered period.

The diets observed in Kilpisjärvi appear to be typical for the respective species. Most studies have confirmed that burbot are omnivores, although adult burbot are primarily piscivores (Gottberg 1910, Baily 1972, Guthruf *et al.* 1990, Pulliainen *et al.* 1992, Rudstam *et al.* 1995). The larvae feed on plankton, and the juveniles on insects

Table 2. Diet overlap (α_{Sch}) between whitefish and burbot. Due to the small sample size for larger burbot during open water period, diet overlaps could not be estimated. Numbers of whitefish/burbot shown in parenthesis.

Period	Whitefish	Burbot	
		≤ 230 mm	> 230 mm
Ice-covered	≤ 260 mm	0.23 (150/22)	– (150/5)
	> 260 mm	0.64 (29/22)	– (29/5)
Open-water	≤ 260 mm	0.30 (96/11)	– (96/2)
	> 260 mm	0.22 (13/11)	– (13/2)

and crustaceans (Lehtonen 1973, Eloranta 1982a, Ryder & Psedendorfer 1992). The diet varies not only with the size of the fish but also seasonally, in order to give burbot a chance to feed on abundant food items (Guthruf *et al.* 1990).

The number of gill rakers reflects the feeding habits of whitefish. Densely rakered forms are more specialised zooplankton-feeders than sparsely rakered forms (Svärdson, 1952, Holmberg 1975, Bergstrand 1982), but small whitefish ingest zooplankton regardless of their gill raker count (Lindström 1962). According to Tolonen (1997), in Kilpisjärvi planktonic crustaceans, especially cladocerans, were the most common food of small whitefish during the open-water season. Mid-sized whitefish (150–220 mm) preyed mostly on the larvae and pupae of chironomids, while the largest fish fed on molluscs and chironomid larvae. The use of zoobenthos increased and that of insect pupae decreased towards the autumn in all size-groups of whitefish.

Typically, the mean number of gill rakers in whitefish declines northwards in the Baltic Sea and upstream in the Tornionjoki-Muonionjoki river system from 30.3 in the river mouth to 25.3 in the Könkämäeno near Kilpisjärvi (Himberg 1970). In 1983, the number of gill rakers of the Kilpisjärvi whitefish varied between 14 and 27 with a median number of 20 (Tolonen 1992). This suggests that a greater proportion of whitefish are benthic feeders towards the north, and an increasing diet overlap can thus be expected between burbot and whitefish in northern areas.

The diet overlap was the highest during the ice-covered period, which is also the time of year when adult burbot are growing (Eloranta 1982b). Thus, even if burbot and whitefish have different diets or habitats during the open-water period, it is possible that the diet overlap during the ice-covered period in Kilpisjärvi affects the growth of burbot. However, it should be noted that our sampling methods for whitefish (gill nets) and burbot (ice-fishing rods) differed during the ice-covered period. The diet overlap between the two species does not necessarily lead to food competition, but there seems to be a shortage of food in Kilpisjärvi. We have no consumption estimates for burbot, but in Kilpisjärvi whitefish are not feeding at even half of their physiological maximum (Tolonen 1999b).

According to McPhail (1997, and references therein) the diet overlap between burbot and other piscivorous fish exists, which suggests implicitly that competitive interaction may also exist. Burbot have been found to be more abundant and to show better growth in waters with declining numbers of lake trout (McPhail 1997). In Finland, it has been suggested that competition from pike may suppress the growth of burbot (Mutenia & Korhonen 1998). There, the structure of the burbot population was only known to a limited extent, however, and the slow growth might also have been due to the large size of the burbot population (Mutenia & Korhonen 1998). The opinions about the importance of interactions between burbot and other species are divided, however, since Carl (1992) found no apparent relationship between the abundance or growth of burbot and the abundance of lake trout. Instead, he suggested that a planktivore could suppress the burbot population through competition with burbot larvae for plankton or predation on larval burbot.

In Kilpisjärvi the growth of burbot older than 5 years and 200 mm or more in length is slow. Increase in length nearly ceases after five years of age (Tolonen & Lappalainen 1999). Most burbot thus have difficulty attaining lengths at which they could prey on other adult fish (Fig. 3). The observed diet overlap between large whitefish and burbot too small to prey on fish could form a bottleneck for growth (*see* Fig. 7). Competition may also not be limited only to the size-classes sampled. Ryder and Pesendorfer (1992) found that burbot ≤ 30 mm in length mainly ingest copepods. Significant diet overlap between larval burbot and small whitefish may therefore exist, which would fit the suggestion that a planktivore could suppress the burbot population both through competition with burbot larvae for planktonic food and/or through predation on larval burbot (Carl 1992).

The extensive whitefish stockings in Kilpisjärvi (more than 400 000 migratory whitefish fry were stocked between 1959 and 1964) may have increased the diet overlap between juvenile burbot and whitefish. As a result of the stockings, the catches of whitefish in Kilpisjärvi decreased drastically during the 1970s, and a decline in both the growth and the condition of the fish was obvious. The management of whitefish stocks is also problematic elsewhere in Lapland due to overpopulation and stunting of fish (Amundsen 1988).

Burbot fisheries are not important in northern Finland. Vehanen and Aspi (1996) estimated the mean burbot and whitefish yields to be 0.4 and 1.5 kg ha^{-1}, respectively. For Kilpisjärvi, we have no exact estimates of the yields, but according to local fishermen about 80% of the total catches are whitefish, while Arctic char accounts for about 20%, and the proportion of other fish species is minimal. Our sampling procedure with gill nets also yielded a minimal catch of burbot compared with that of whitefish. Likewise, burbot catches in an ice-fishing competition held annually in Kilpisjärvi since the early 1980s have been low (Tolonen & Lappalainen 1999): in the 1998 competition the total catch of burbot was only 2.4 kg and comprised 30 burbot. This was after 1 500 participants had fished for 2 h during two days. Thus, it appears evident that the burbot population in Kilpisjärvi is small.

At least three different approaches have been used to estimate food competition between species: direct observations of the diet overlap, comparison of differences in feeding between allopatric and sympatric populations, and controlled feeding experiments (Connell 1983, Schoener 1983). Habitat segregation has usually been found to be the most effective way of avoiding competition in aquatic environments (Werner 1979). We have, unfortunately, no estimates of habitats used by the species studied and therefore possible habitat segregation can not be evaluated. Furthermore, Kilpisjärvi is an ultraoligotrophic lake, and therefore slow growth of burbot is to be expected (cf. Kjellman & Hudd 1996, Tolonen 1997). However, the growth of burbot observed here is exceptionally slow when compared with that in other northern lakes (Lehtonen 1998).

In summary, the ingestion of many food items for both burbot and whitefish was length-dependent, and seasonal shifts were obvious. Furthermore, a considerable diet overlap was present between whitefish and burbot during the ice-covered period. However, it is premature to conclude that this diet overlap has reduced the growth of burbot. This is due to the small size of the burbot samples, which prevented us from comparing the seasonal diet and habitat overlaps between the studied species in detail.

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Appendix. Occurrence of various dietary taxa in Kilpisjärvi whitefish and burbot.

Food category	Taxon	Whitefish			Burbot
		age-class 2–3	age-class 4–5	age-class 6–10	
Molluscs	*Lymnaea peregra*		x	x	x
	Gyraulus acronicus	x	x	x	x
	Pisidium conventus	x	x	x	x
Insects	Chironomidae (larvae)	x	x	x	x
	Chironomidae (pupae)	x	x	x	
	Trichoptera, larvae		x	x	
	Tabanidae, larvae	x	x	x	
	Dicranota sp. larvae			x	
	Simulium sp.pupae/adult	x	x	x	
	Ceratopogonidae, larvae	x	x	x	
	Plecoptera, larvae		x	x	x
	Dytiscidae, larvae			x	x
	other Coleoptera,adult		x	x	
	Lepidoptera, adult		x	x	
Zooplankton	*Bosmina longispina*	x	x	x	
	Holopedium gibberum	x	x		
	Cyclops scutifer	x	x	x	
	Eudiaptomus graciloides	x	x	x	
Benthic crustaceans	*Eurycercus lamellatus*	x	x	x	x
	Alonopsis elongata	x	x	x	
	Cyclocypris ovum	x	x	x	
	Candona lapponica	x	x	x	
	Megacyclops sp.	x	x	x	x
	Gammarus lacustris				x
Fish	*Cottus poecilopus*			x	x
	Phoxinus phoxinus				x
	Coregonus lavaretus				x
Fish eggs	unidentified	x	x	x	x
Porifera		x	x		
Plants and detritus		x	x	x	x