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Size-specific food selection and growth in benthic whitefish, *Coregonus lavaretus* (L.), in a subarctic lake

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The summer diet of benthic whitefish (*Coregonus lavaretus* (L.)) was studied in an oligotrophic subarctic lake. The fish were caught with bottom gill net series during two open-water seasons in 1982–1983. Planktonic crustaceans, especially cladocerans, were the most common food of small (< 150 mm) whitefish. The mid-sized fish (150–220 mm) preyed mostly on the larvae and pupae of chironomids, which were also the most frequent prey of larger whitefish during July. Zoobenthos such as molluscs and chironomid larvae were the food most utilized by the largest fish (> 220 mm). The use of zoobenthos increased and that of insect pupae decreased towards the autumn in every size group of fish. Differences were significant within large fish ($p < 0.001$). Stomach fullness and the frequency of empty stomachs varied markedly from year to year; fluctuations were more pronounced in the larger fish. Between the smallest fish (< 150 mm) and the other size-groups a clear difference was present in the percentage of plankton food ($p < 0.001$), suggesting the presence of only minimal food competition. Improved growth of fish longer than 150 mm indicated a favorable effect of the diet shift. After the length of 200 mm was attained the diet similarity between size-groups was pronounced. Slow growth was probably caused by intraspecific food competition. After the fish attained the length of 240 mm rapid improvement in growth was observed.

Introduction

During the 1970s catches of the originally well conditioned whitefish in Lake Kilpisjärvi decreased drastically, and decline in growth as well as in condition of the fish was obvious (Tolonen 1992). Management of many whitefish stocks is problematic also elsewhere in Lapland, due to the overpopulation and stunting of fish (Amundsen 1988).

Fish have been shown to prefer habitats where feeding is energetically most advantageous (Werner and Mittelbach 1981), but interactions such as intraspecific competition (Haraldstad and Jonsson

1983, Persson 1983) and interspecific competition (Werner and Hall 1977) may also influence the foraging behavior and selection of feeding habitat by fish of various sizes.

The number of gill rakers reflect feeding habits of fish. Densely rakered gills are characteritic for more specialized zooplankton feeders than sparsely rakered ones (Bergstrand 1982). Many observations have shown that, when coexisting, various whitefish forms differ in selection of food and habitat (Bodaly 1979, Bergstrand 1982). Few observations have been made on size-specific food partitioning of monomorphic whitefish populations (Hessen *et al.* 1986).

Feeding habits of whitefish in northern Europe were studied e.g. by Jacobsen (1974), Palomäki (1981), Bergstrand (1982), Heikinheimo-Schmid (1982), Hessen *et al.* (1986), Huusko (1987) and Sandlund *et al.* (1987). The purpose of the present study was to investigate the size-specific food preferences and growth in benthic whitefish of subarctic Lake Kilpisjärvi. I also wanted to find out if the whitefish had seasonal and inter-annual variations in diet and feeding intensity.

Study area and fish community

Lake Kilpisjärvi (ỏami name: Cilbbesjavri) is located in northwestern Finnish Lapland (69°03´N, 20°49´E, alt. 463 m) and drains via the Tornionjoki River into the Bothnian Bay (Fig. 1). The study lake is a part of the subarctic birch-forest zone. The thermal growth season in the study area lasts 110 days, and the open-water period about 160 days. Average maximum surface water temperature of 13.9 °C was measured in August. The median date for lake freeze-over is 25 November and for ice break-up 16 June (Anon. 1983). The 35.3 km^2 lake consists of 2 basins and its catchment area covers 290 km^2. Maximum depth of the upper and lower basins is 48 m and 57 m, respectively, and the amplitude of the water level changes is 61 cm (Järnefelt 1956). The shores are mainly stony, and the stony bottom usually extends 5 meters down to the sediment layer.

Lake Kilpisjärvi is an oligotrophic, clear-water lake. Yearly values for phytoplankton primary production were estimated at about 3.3 g C m^{-2} (Tolonen 1992), which is comparable to the respective parameter estimated for the Canadian Arctic (Schindler 1972). The main factors limiting phytoplankton primary production are the low water temperature, short open-water season, and low availability of mineral phosphorus. The total zooplankton biomass during the open-water season of 1977 ranged between 1 g m^{-2} (early July) and 10 g m^{-2} (September). The first biomass peak in late July consisted of 70% copepods, mainly *Eudiaptomus graciloides,* and the second peak also of *Cyclops scutifer* (9%). The biomass of *Bosmina longispina* ranged between 55–88 mg m^{-2} until mid-August and peaked at the end of the month at 787 mg m^{-2}. In September the cladoceran biomass was 21.8% of the total zooplankton biomass, mainly due to the presence of *Holopedium gibberum* (17.7%; Tolonen 1992).

Only one whitefish form occurs in Lake Kilpisjärvi, and the distribution of gill-raker numbers is monomodal. The original whitefish of the lake, which had a gill raker count of 17–33 (mean = 22) no longer exist (Svärdson 1979). Lake Kilpisjärvi had also been stocked between 1959 and 1964 with 440 000 migratory whitefish fry (27–31 gillrakers) and the whitefish occupying the lake is obviously a hybrid of the original and stocked forms.

Other fish species in Lake Kilpisjärvi include the Arctic charr *Salvelinus alpinus* (L.), grayling *Thymallus thymallus* (L.), burbot *Lota lota* (L.), alpine bullhead *Cottus poecilopus* Heckel, minnow *Phoxinus phoxinus* (L.). Also few brown trout *Salmo trutta* L. and pike *Esox lucius* L. occur.

Material and methods

Material was collected from early July to late September 1982 and from early July to mid-October 1983. Whitefish samples were taken, using a series of 9 gill nets (1.8 × 30 m) with mesh sizes 12, 15, 20, 25, 30, 35, 45, 60, and 75 mm measured from knot to knot. The net series caught whitefish of ≥ 12 cm (total length), thus totally excluding the smallest fish. Experimental fishing was performed weekly from July to October 1982 and 1983 simultaneously at 6 sites (Fig. 1). The benthic gill nets were set in random order at a depth range of 2–20 m, and were kept in the lake overnight (12–18 h). Data on total length, weight, sex, date and location were all recorded for each

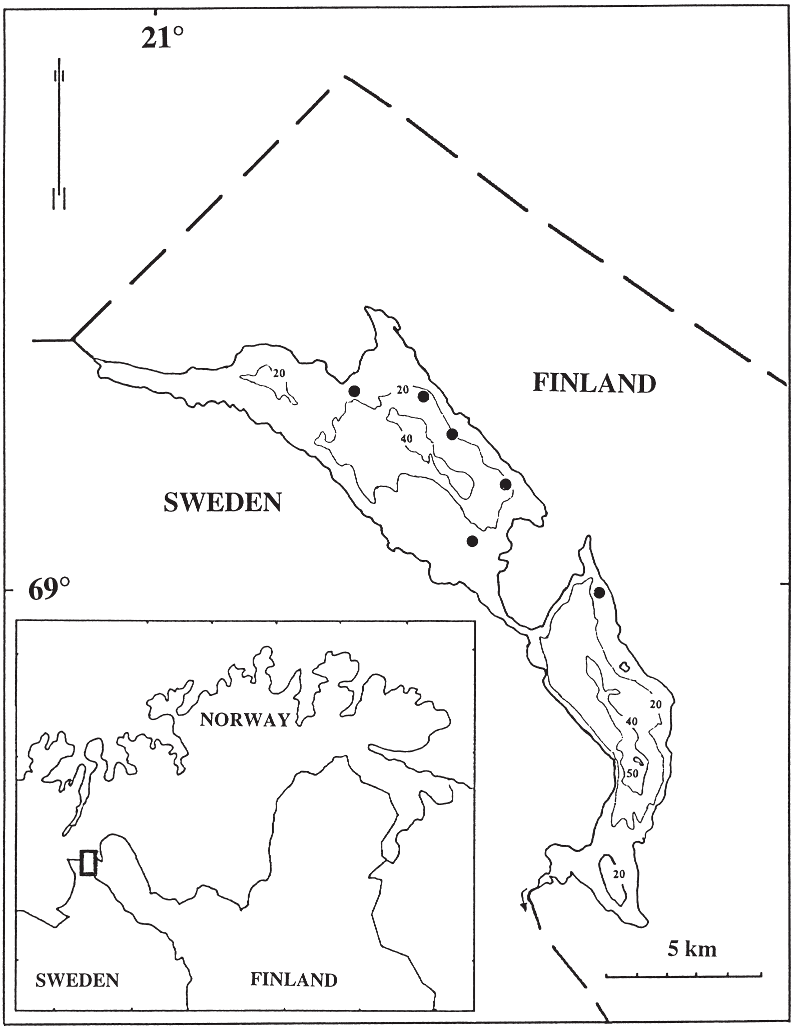

Fig. 1. Lake Kilpisjärvi with depth contours. Experimental fishing sites marked with dots.

specimen. Gill rakers from the first outer gill arch including all rudimentary gill rakers in both limbs were counted under a binocular microscope. The scales for age determination were taken from the ventral side of the fish between the origins of the pelvic fins (Eloranta 1975). The age of the fish was determined with a microfiche reader, using pressed plastic slide copies of the scales.

Random samples of fish were taken for stomach analyses from each fishing area. A certain long-term periodicity occurs in the growth of whitefish in the lake; thus it appeared reasonable to classify the study material in phase with the length-at-age curve (Fig. 2). The specimens were analyzed in 3 size categories: < 150 mm, 150–220 mm and > 220 mm. In average, the fish in the first group were 1–3 years, in the mid group 4–6 years and in the last group 7–12 years of age.

Stomachs used for diet analyses were stored frozen if not analyzed immediately. Frequency of occurrence and weight of the food items were used as the main criteria for characterization of the diets. The number of stomachs in which each food item occurred was recorded, and the frequency of occurrence was expressed as percentages of the total number of stomachs examined (Windell 1971). This method reveals the organisms that were fed upon, but gives no information on the proportions of various prey taxa; therefore, the diet of whitefish was also described in terms of wet weight proportions of various prey. Only the stomach contents from the oesophagus to the pylorus were analyzed. The fullness coefficient of the stomach was first scored on a scale of 0–3,

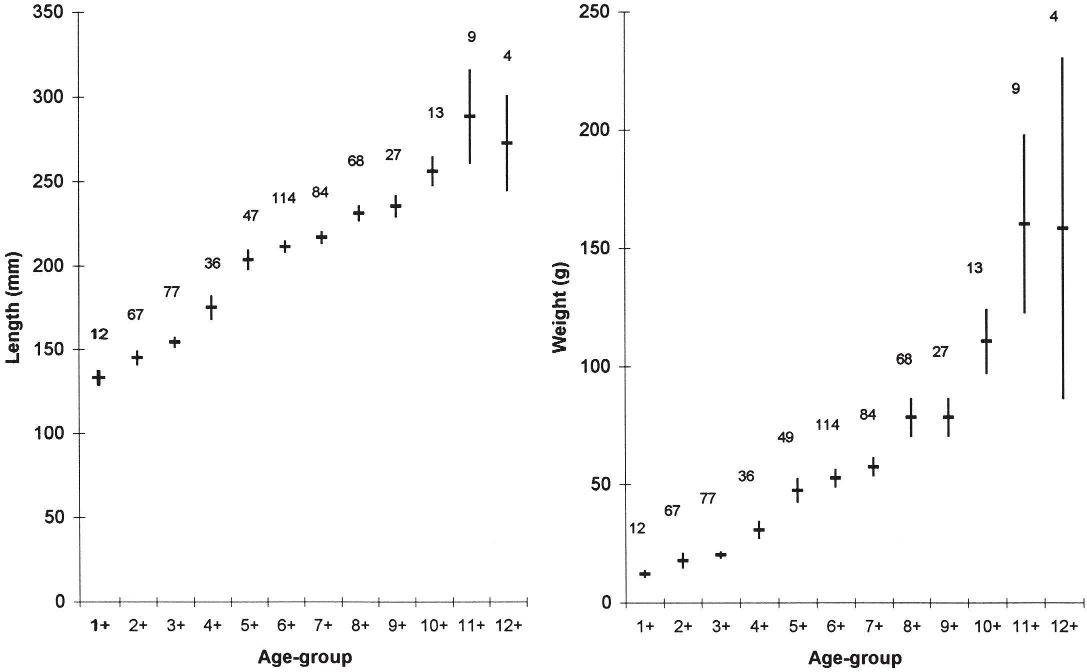

Fig. 2. Length- and weight-at-ages (with std error) of whitefish in Lake Kilpisjärvi in the pooled autumn sample of 1992–1983. Figures indicate numbers of specimens.

and the stomach contents were then weighed to the nearest mg. Within zooplankton food the comparison among species was based on counting 200 zooplankton specimens from each stomach. Larger prey items such as molluscs and insects were picked out separately and identified under a dissecting microscope. The entire study material for food analyses totaled 696 whitefish specimens: 287 in 1982 and 409 in 1983.

Results

Growth

The growth rate of the whitefish was studied by mesuring the mean length and weight at age in autumn samples. The whitefish population exhibited a bimodal age distribution. Individuals in the age-groups 6+ and 7+ occurred most frequently in the catch, and age-group 3+ was the third largest age-group. The age distribution was almost identical in both study years; thus the most probable reason for the poor catch of 4- and 5-year-old fish was selectivity in the experimental gill netting (Tolonen 1992).

Whitefish in Lake Kilpisjärvi grew slowly; a total length of 15.5 cm and weight of 19.5 g were achieved at 3 years of age (Fig. 2). Growth improved considerably thereafter; thus the mean length in age-group 5 is 20.3 cm and weight 46.1 g. After the fifth year growth decreases, and the mean length of 8-year-old fish was only 22.7 cm and weight 68.9 g. After the fish attained 9 years of age growth improved again, and the increase in weight was especially considerable (Fig. 2).

According to annual ring formation, growth of the smallest fish (< 150 mm) commenced in Lake Kilpisjärvi during the first half of July and that of the large fish about one week later. Of the small fish 100% showed new growth in the scales by the end of the month, while the corresponding percentage for the large fish was 80% (Fig. 3).

Seasonal variations in the diet

Clear changes both in the occurrence and proportions of various food items were observed in the course of the open-water seasons (App. 1, Fig. 4).

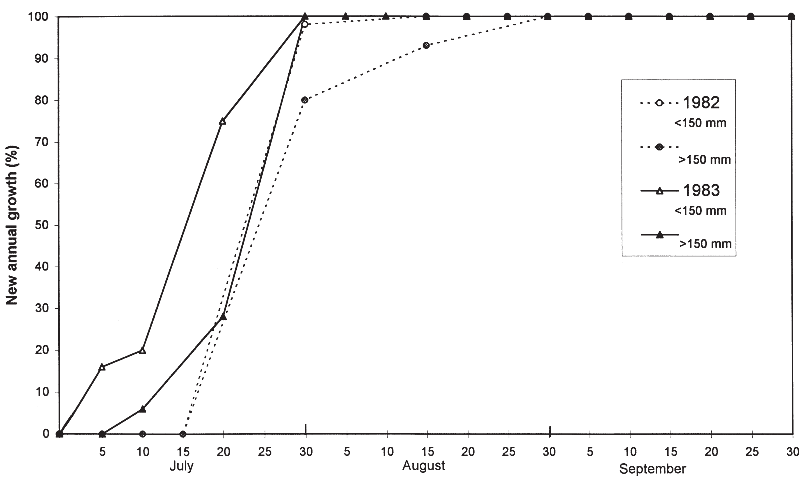

Fig. 3. Occurrence (%) of new annual growth detected in the scales of various-sized whitefish of Lake Kilpisjärvi during the summers of 1982 and 1983.

Whitefish fed mainly on benthic invertebrates; the frequency of occurrence of aquatic insect (mainly chironomids pupae decreased and that of larvae increased during summer in each size class of fish. The change in larvae was highly significant ($p < 0.001$), except in the smallest fish (Table 1). The highest monthly proportion (30–80%) of the total amount of food consumed was observed for chironomids such as *Abiscomyia virgo*, *Corynocera ambigua*, *Paratanytarsus hyperboreus* and *Micropsectra* sp., in July–August. Larvae and pupae of trichopterans were also of some importance in the diet (Fig. 4), while other insect larvae played minor roles as food sources of the whitefish. Hydracarina (6.6%), were also found regularly in the stomachs of large fish. The molluscs, *Lymnea peregra*, *Gyraulus acronicus* and *Pisidium conventus* formed the major component (20–63%) of the diet for the largest whitefish throughout the season, but their proportion increased towards the autumn in every fish size-class. Utilization of small molluscs (*Pisidium*) began during the 3rd summer in September.

Benthic cladocerans (mainly *Eurycercus lamellatus*) began to dominate significantly ($p < 0.001$) in frequency and volume towards the autumn in each size-class (Fig. 4, Table 1). The increase in ostracod food was also significant ($p < 0.001$) during the summer in all size-classes (Table 1), although due to their small volume, ostracods were an alternative food resource for the smallest fish only.

The proportions of zooplankton, especially the planktonic cladocerans *Bosmina longispina* and

Table 1. Monthly differences in frequency occurrences of some prey taxa in the stomachs of various sized whitefish (χ^2-test; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$).

Foraging habitat/Taxon	< 150 mm		150–220 mm		> 220 mm	
	July→Aug	Aug→Sep	July→Aug	Aug→Sep	July→Aug	Aug→Sep
SURFACE						
Chironomids, pupae	3.36 NS	5.11*	0.61 NS	3.28 NS	0.57 NS	0.45 NS
PLANKTON						
Bosmina	2.25	2.29 NS	0.59 NS	3.30 NS	0.44 NS	0.16
Copepoda	5.12*	1.48 NS	7.67**	32.59***	9.23**	15.00***
BENTHOS						
Chironomids, larvae	0.47 NS	0.37 NS	23.34***	13.59***	7.77**	13.05***
Lymnea	$n < 5$	$n < 5$	$n < 5$	$n < 5$	$n < 5$	$n < 5$
Pisidium	$n < 5$	$n < 5$	19.02***	10.15**	$n < 5$	$n < 5$
Cyclocypris	10.30***	15.20**	14.08***	80.22***	12.43***	$n < 5$
Eyrycercus	8.39**	14.06**	37.52***	37.55***	14.94***	20.59***

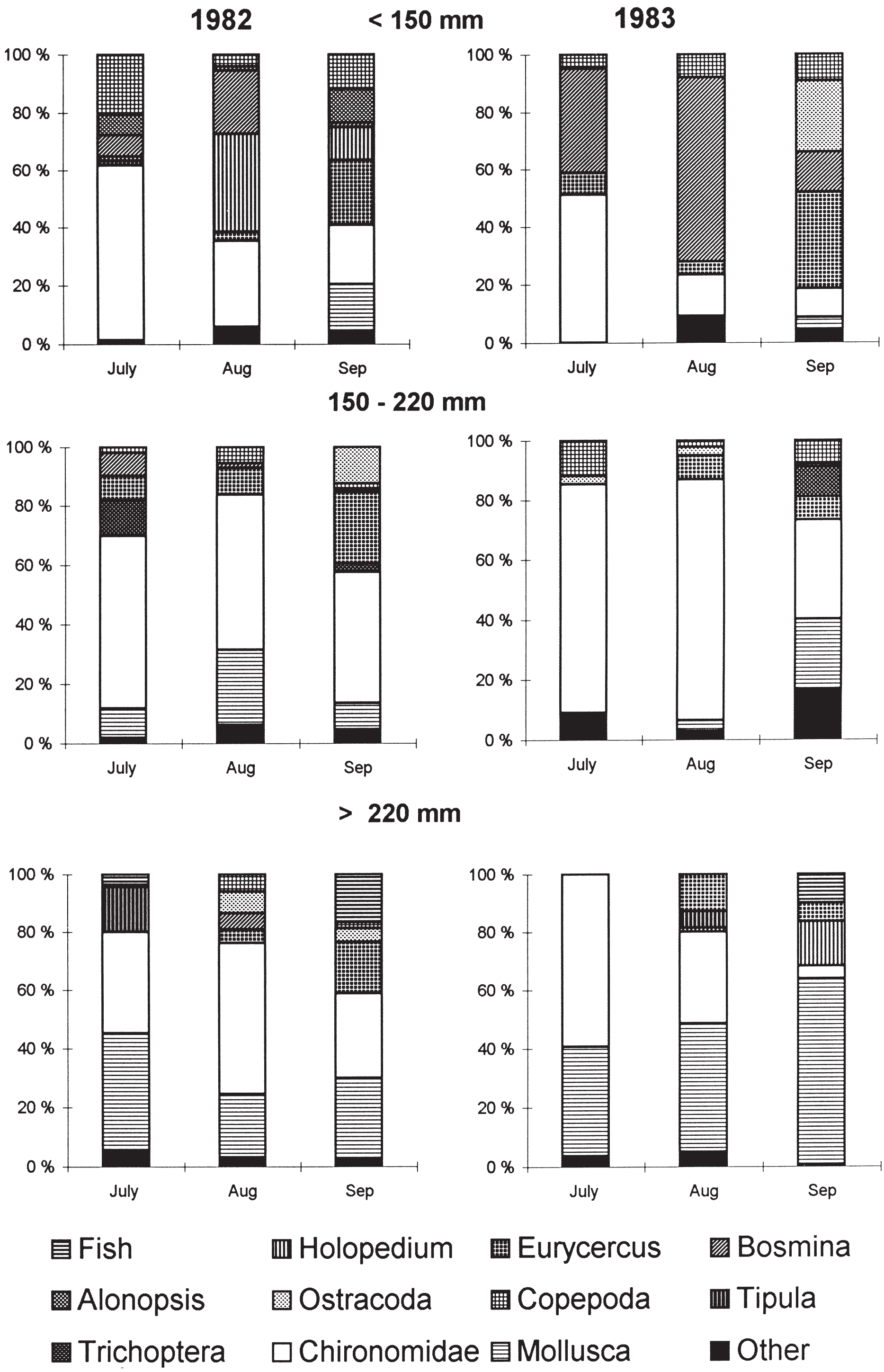

Fig. 4. Proportions (wet weight) of various prey taxa in the stomachs of benthic whitefish of Lake Kilpisjärvi during 1982–1983 according to the length group of the fish during the summers of 1982 and 1983.

Holopedium gibberum, increased in late July. In August these species dominated both in frequency and in volume in the diet of the small fish, although the monthly differences in frequency were not statistically significant. Other cladocerans, *Alonopsis elongata*, *Acroperus harpae*, *Chydorus sphaericus* and *Ophryoxus gracilis*, were of minor importance in the diet. The ostracods *Cyclocypris ovum* and *Candona lapponica*, occurred in the diet in late August.

Copepods consumed by the whitefish were most often *Cyclops scutifer*, but also large-sized *Megacyclops* species were found. The absence of *Eudiaptomus graciloides* was characteristic for the diet during most of the study period. When compared with *Eudiaptomus*, the preference for *Bosmina* was clear. The proportion of copepods was highest (20%) in the smallest fish in July 1983 (Fig. 4).

Of fish prey alpine bullheads comprised a maximum of 18% of the stomach contents of the largest whitefish. No cannibalism was observed during the study periods. The poriferan *Ephydatia müllleri* occurred mostly during autumn when the diversity of the diet was high and coarse material was common in the stomachs.

Ontogenetic changes in the diet

The composition of the diet among various size-groups reflected changes in food availability during the growth season. Emerging pupae of chironomids, which were assumed to be eaten from the surface, in addition to some terrestrial insects, were found most often in the stomach of mid-sized fish, and the difference was significant ($p < 0.01$) when compared with the smallest size-groups (Table 2). Planktonic crustaceans (*Bosmina*, *Holopedium*, *Cyclops*) peaked in August but only in the diet of the smallest fish (Fig. 5). The proportion of planktonic crustaceans was 60% in the diet of small fish and only 10% in that of large fish (Table 2). The change was highly significant ($p < 0.001$) between the 2 smallest size-groups. The proportion of chironomids peaked in the mid-sized fish up to 60% of the total amount of food, while the largest fish fed intensively on molluscs (40%). The increase among size-classes was significant within *Lymnea* ($p < 0.01$) and *Pisidium* ($p < 0.001$).

Inter-year variations in diet and stomach fullness

The variation in composition of the diet and the fullness of the stomachs varied considerably interannually reflecting changes in prey availability. During the early summer of 1983 the stomach contents were comprised much more of chironomid pupae than in 1982, and zooplankton prey were displaced by insect larvae and pupae. The proportions of planktonic cladocerans varied interannually in the diet; *B. longispina* was dominant in 1982, while *H. gibberum* in 1993. Proportions among 3 species of molluscs varied from year to year, but their total percentage of food analysed remained similar during both years.

The stomach fullness of any size-class of fish reflected mostly the proportion of the main prey taxa in the diet. In early July 1982 almost 40% of the small whitefish had empty stomachs (Fig. 6), when chironomids were still the major food in the diet. In late July, when *B. longispina* was the main prey species, food consumption was steady and no empty stomachs appeared. During the rest of the summer of 1982, the stomach fullness of the small fish (< 150 mm) was high due to the presence of benthic prey such as *Eurycercus*. During the 2nd summer in July, when the propor-

Table 2. Differences in frequency occurrence of some prey taxa between size-groups of whitefish (χ^2-test; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$).

Foraging habitat/Taxon	< 150 mm →150–220mm χ^2	150–220 mm →> 220 mm χ^2
SURFACE		
Chironomids, pupae	9.58**	2.92
adults	3.68	3.76
PLANKTON		
Bosmina	19.97***	8.10**
Holopedium	14.20***	5.28*
Cyclops	0.55	0.17
BENTHOS		
Chironomids, larvae	2.97	11.60***
Lymnea	4.85*	7.23**
Pisidium	5.07*	11.13***
Cyclocypris	7.20**	5.13*
Eurycercus	11.28***	7.55**

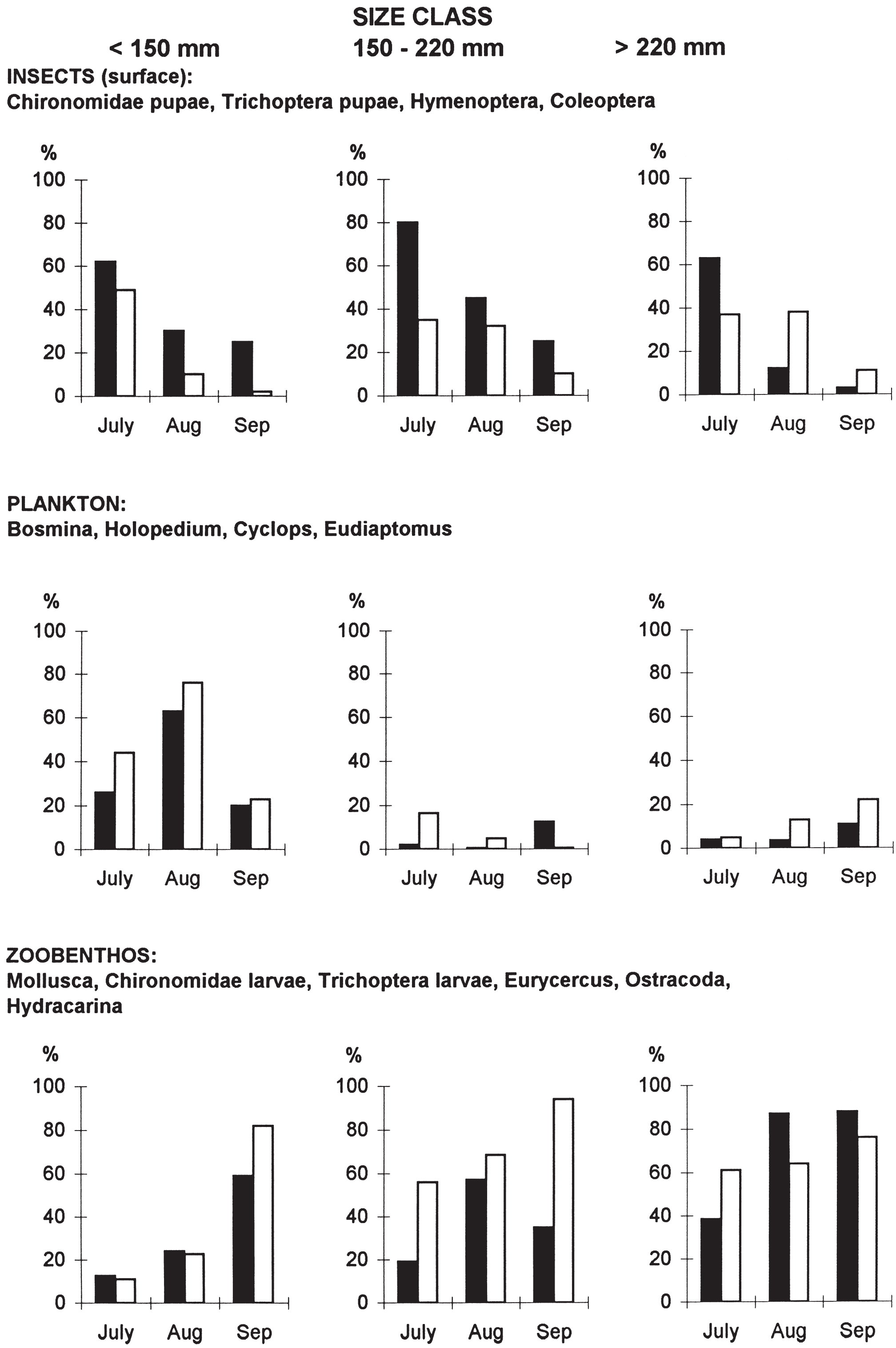

Fig. 5. Proportions of prey from various habitats (surface prey, zooplankton, zoobenthos) by whitefish of different length groups during the summers of 1982 (black bars) and 1983 (empty bars).

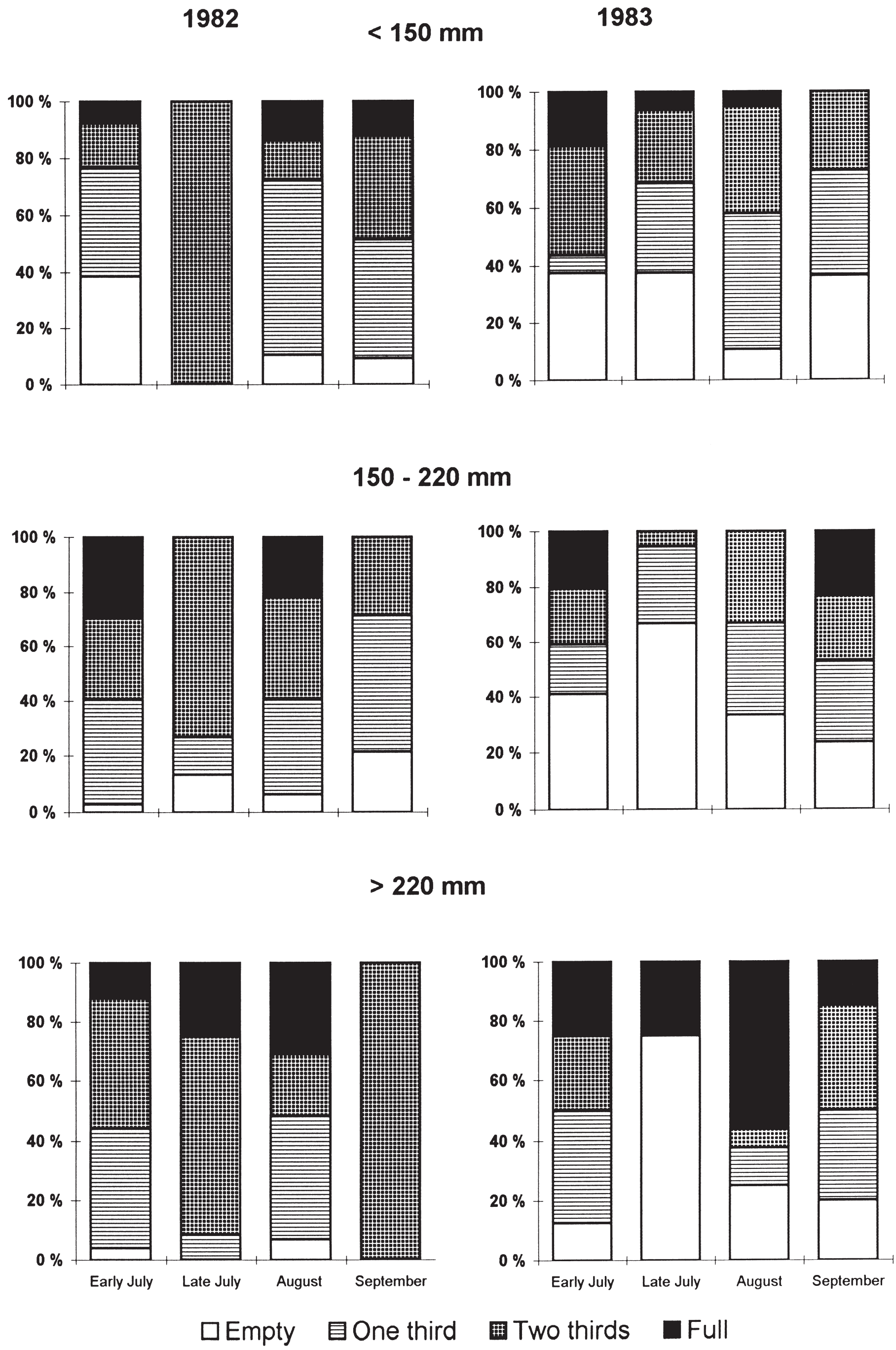

Fig. 6. Distribution of whitefish according to stomach fullness in 3 length groups during the summers of 1982 and 1983 in Lake Kilpisjärvi.

tion of chironomids was higher and fewer cladocerans (mainly *H. gibberum*) were consumed, almost 40% of the small fish had empty stomachs. Stomach fullness increased in late August due to the increased consumption of *Bosmina* and *Holopedium*, but in September almost 40 % of the stomachs were again empty.

Correspondingly, the amount of stomach content of large fish was clearly dependent on the availability of emerging chironomid pupae. The fullness was high throughout the summer 1982 when insect pupae were dominant in the diet, while in late July 1983 nearly 70% of the stomachs were empty when zoobenthos formed the bulk of the diet.

Discussion

Prey utilization

Cladocerans in the genus *Bosmina* are known as a preferred prey taxon of planktivorous whitefish (Huusko 1987, Sandlund *et al.* 1987, Koli 1991). In subarctic lakes in northern Sweden (Nilsson and Pejler 1973) and in northern Finland (Palomäki 1981), *B. coregoni* was found to be the most frequently consumed zooplankton taxon. Here, *B. longispina* and *H. gibberum* were the most prominent planktonic prey of benthic whitefish.

Under natural conditions, the spatial and temporal aspects of the habitats and prey availability may ultimately determine the choice of prey of fish (Hersey 1985, Palomäki *et al.* 1992). On the other hand, fish usually prefer to feed in the most energetically advantageous habitat available and change habitat when the profitability of one drops below that of another (Werner and Mittelbach 1981). In Lake Kilpisjärvi the proportion of large littoral cladocerans such as *Eurycercus* increased significantly in the diet of whitefish towards the autumn in every size category, which also corroborates the results of Palomäki (1981) from Lake Inarinjärvi. From the foraging point of view *Eurycercus,* as a slow and relatively large littoral cladoceran, is presumably an easy and energetically more advantageous prey to bottom-feeding whitefish than the planktonic *Bosmina,* while the smaller *A. elongata* occurred regularly only in the diet of small fish. Constantly moving slow cladocerans are assumed to be more vulnerable than the more rapidly swimming copepods (Hutchinson 1971, Drenner *et al.* 1978, Nilsson 1978, van Densen 1985).

Copepods dominated the plankton in the pelagial zone of the lake during the autumn of 1977, and accounted for 75% of the zooplankton biomass (Tolonen 1992). The foraging of smaller fish on copepods began earlier and more intensively, whereas that of larger fish was delayed. Hanazato *et al.* (1990) observed the same phenomenon in eutrophic lakes. *Cyclops* appeared to be consumed according to its availability; according to Grimås (1961), *Cyclops* accounted for 3.2–3.7% of the total zoobenthos in some lakes in northern Sweden. The percentage is comparable to the proportion of that genus in the whitefish diet in the present study, whereas the genus *Eudiaptomus* occurred rarely in the diet, although it dominated the pelagic zooplankton biomass toward the autumn. Reasons for the scarcity of this taxon in the whitefish diet may include to its particular swimming pattern and weak swarm affinity (Nauwerck and Ritterbusch-Nauwerck 1993). Berg (1970) in Italy and Heikinheimo-Schmid (1982) in Finland also found that planktivorous whitefish prefered cyclopids instead of the more abundant calanoids. Food analyses during 1992–1993 in Lake Kilpisjärvi, however, revealed that the winter food was comprised mainly of *Eudiaptomus*, probably due to the increased vulnerability of the hibernating copepodits aggregated on the bottom. The theories of optimal diets suggest that at low prey densities predators feed intensively on the most numerous prey species and at high prey densities on the species having the highest energy value (Pulliam 1974, Palomäki *et al.* 1992).

Stomach fullness and the frequency of empty stomachs varied markedly from year to year; the fluctuations were more pronounced in the larger size categories. Similar strong and irregular fluctuation in the stomach fullness of whitefish was observed by Heikinheimo-Schmid (1982) in Finland and by Jacobsen (1974) in Norway. The fullness of the stomach can also be considered as indicative of prey availability. Chironomids occurred as a main food taxon, when the majority of the stomachs were empty. Other factors affecting fullness are the digestibility of the food and the water temperature. As a whole the availability of food was obviously more constant during the summer of 1982 than the colder summer of 1983; thus empty stomachs appeared less frequently.

Intraspecific food competition and growth

In Lake Kilpisjärvi, benthic whitefish attained a mean total length of 21 cm at the age of maturation while the corresponding size in Lake Kemijärvi was 25 cm (Heikinheimo-Schmid and Huusko 1988). The difference in mean weight was more pronounced;

the weight of 8-year-old whitefish in Lake Kilpisjärvi was 70 g and in Lake Kemijärvi nearly 400 g. The growth rate in Lake Kilpisjärvi was low even when compared with other lakes in northwestern Finland (Tolonen 1992). Amundsen (1988) also reported a slow growth rate of benthic whitefish of Lake Stuorajavri, not far from the present study area. At both lakes the length-at-age curve levered after the 5th year of age. At 5 years of age whitefish first spawn in Lake Kilpisjärvi, probably causing stress and therefore a decrease in growth rate. A similar phenomenon also occurs in whitefish of Lake Stuorajavri where growth almost ceases when maturity is attained (Amundsen 1988).

In general, growth rates in whitefish populations have been shown to be density-dependent (Mills and Chalanchuk 1988, Sarjamo *et al.* 1989, Salojärvi 1992). According to Salojärvi (1992) it is possible to divide the growth process of whitefish into two phases; in younger age-groups growth is dependent on the cohort size and in the older age-groups on population size. The other factors affecting growth include both abiotic (e.g. water temperature) and biotic (e.g. species interactions). The growth season of whitefish in subarctic lakes is considerably shorter than in southern latitudes. In Lake Kilpisjärvi the onset of yearly growth was detected in the scales about one month later when compared with that in the Gulf of Bothnia, Baltic Sea, where growth begins in June (Lehtonen 1981). New annual growth was detected about first week after the fish had begun to prey upon B. *longispina;* thus it was important for yearly growth (Tolonen 1992).

Ontogenetic changes in niche utilization by size-classes of whitefish in Lake Kilpisjärvi were obvious. Specialization toward benthic food began when the total length of the fish was about 15 cm. Younger fish fed mainly on zooplankton during the most favorable growth season, while insect pupae were the most common prey of the mid-sized whitefish during the emergence of chironomid pupae in July and August. Palomäki *et al.* (1992) considered chironomids as some of the key species determining the timing of the diet shifts of whitefish. The diet overlap between juvenile and adult fish was minimal, while the length-at-age curve also showed a phase of accelerated growth after the third year, indicating a favorable effect of the diet shift. The importance of functional morphology in causing food segregation is widely known in other fish species (Werner 1977, Mittelbach 1984), but also in whitefish (Hessen *et al.* 1986). The small whitefish is incapable of swallowing large prey such as molluscs and other large-sized zoobenthos. The partial food segregation observed in the present study could also be the result of exploitative competition (Hessen *et al.* 1986), interference and predation by Arctic charr, which have been found to prey on young whitefish.

In Lake Kilpisjärvi the diet overlap between the largest size-classes of whitefish was pronounced; thus the intraspecific food competition may be the most probable explanation for the decreased growth. Intraspecific food competition inhibits growth and tends to prevent the shift to the next size category of prey, resulting in a situation in which several successive year-classes remain stunted (Salojärvi 1992). High parasite burdens also contribute to limiting the commercial exploitation of these populations. Encysted cestode plerocercoids, which may also affect growth rate, should especially be investigated in future.

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Appendix 1. Frequency of occurrence (%) of prey of benthic whitefish within 3 size groups (total length: I = < 150 mm, II = 150–220 mm, III = > 220 mm) in the upper basin of Lake Kilpisjärvi during July–October in 1982–1983.

	Year 1982									Year 1983											
	July			August			September			July			August			September			October		
Taxon	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
(*n*)	9	54	37	27	54	42	35	18	11	15	54	13	18	31	19	24	18	14	54	103	46
Mollusca																					
Lymnea	-	10	25	-	22	18	-	7	-	-	-	-	-	-	-	-	13	-	-	-	45
Gyraulus	-	16	19	-	3	18	3	-	-	-	-	-	-	-	-	-	14	3	-	44	29
Pisidium	14	19	19	5	39	36	14	14	-	-	2	-	-	8	-	-	6	14	11	43	100
Chironomidae																					
larvae	14	32	31	27	67	45	34	29	50	13	9	23	13	42	-	11	44	43	26	29	73
pupae	29	58	63	32	39	45	3	-	-	67	59	38	50	71	31	33	63	36	21	-	-
adults	14	3	3	-	3	-	3	7	-	-	7	23	-	-	-	-	25	7	11	-	18
Trichoptera																					
larvae	-	13	9	-	-	18	3	7	-	-	-	-	6	-	-	-	6	-	5	14	-
pupae	-	16	25	-	3	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tipula sp.	-	-	6	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other diptera	34	74	81	55	81	73	31	79	-	-	-	-	-	-	-	-	-	-	-	-	-
Insecta (terrestr.)	-	13	6	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladocera																					
Eurycercus	29	35	13	14	56	27	55	29	-	7	2	-	6	21	-	22	68	71	74	100	99
Bosmina	43	19	13	100	19	36	3	-	-	7	4	-	43	17	-	33	-	-	37	14	-
Alonopsis	-	-	-	5	3	-	21	-	-	-	-	-	13	-	-	11	6	-	32	-	-
Holopedium	-	-	-	-	3	-	-	-	-	-	-	-	13	-	-	67	6	-	32	43	-
Ophryoxus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	37	14	-
Copepoda																					
Cyclops	14	6	9	18	6	36	48	14	-	-	-	-	19	25	-	33	93	57	5	14	18
copepodids	-	-	-	5	3	-	21	29	-	27	17	15	-	13	8	11	6	-	26	43	-
nauplii	-	-	-	-	-	-	-	-	-	-	2	8	19	8	-	-	1	-	26	-	-
Eudiaptomus	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	6	-	5	14	-
Ostracoda																					
Cyclocypris	-	3	3	5	8	9	-	-	-	-	-	-	-	-	-	8	14	-	22	44	36
Candona	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	14	-
Hydracarina	-	-	6	-	3	9	-	-	-	-	-	-	-	-	-	-	6	7	-	-	18
Fish	-	-	3	-	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18
Porifera	-	-	3	-	-	-	-	7	-	-	-	-	-	-	-	-	-	18	-	29	36
Plants	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	12	7	-	-	-