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Food selection and vertical distribution of pelagic whitefish *Coregonus lavaretus* (L.) in Lake Tyrifjorden, Norway

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Zooplankton, almost exclusively cladocerans, was the main food of pelagic whitefish *Coregonus lavaretus* (L.) in Lake Tyrifjorden, southern Norway. Vertical distribution of whitefish and their zooplankton prey coincided during summer, as both were located close to the surface. In the autumn, however, the whitefish gradually became distributed at deeper layers close to the thermocline, in spite of high surface densities of preferred prey like *Daphnia*. The downwards migration coincided with an increased number of whitefish with empty stomachs. We suggest that the autumnal downwards migration is a pre-spawning behaviour that advances and synchronizes gonadal development in mature whitefish.

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INTRODUCTION

Since the early works of Hrbácek et al. (1961), several authors have stated that most species of planktivorous fish including coregonids prefer cladocerans, especially larger daphniids (Brooks and Dodson 1965, Brooks 1968, Zaret 1972, Werner and Hall 1974, O'Brien et al. 1976). Zooplankton prey preferred by whitefish include both *Daphnia* spp. and the smaller *Bosmina* spp. (Nilsson and Pejler 1973).

The distribution of food and the temperature regime in temperate lakes are subjected to seasonal variations. In spite of this the interactive seasonal migration pattern of zooplankton and fish has been offered little interest. However, surveys of pelagic fish indicate a preference for deeper layers in autumn (Eggers 1978, Hindar and Jonsson 1982).

In 1980, we studied the seasonal vertical distribution of both the whitefish *Coregonus lavaretus* (L.) and its zooplankton prey in Lake Tyrifjorden, southeastern Norway. Here we give data on food-selection of the whitefish, and further, we compare the distribution of the predator and its prey to see whether food abundance or other parameters are the regulating factors in the seasonal vertical distribution of the whitefish.

MATERIAL AND METHODS

The oligotrophic/mesotrophic Lake Tyrifjorden is situated in SE Norway (59°53'—60°08'N, 10°—10°21'E), 64 m above sea level. The lake has a surface area of 121 km^2, a maximum depth of 295 m, and a mean depth of 114 m. The limnology of the lake has been well documented (Strøm 1932, Langeland 1974, Berge 1983).

During surveys of the fish community 12 species of fish have been recorded (Skurdal and Qvenild 1982). Whitefish was the most abundant species, accounting for 60% of the total catch in number and almost 70% in weight. In Scandinavian lakes two or more morphs of whitefish often coexist (Svärdson 1979). In Lake Tyrifjorden, however, the whitefish were monomorphic with a mean of 32 gill rakers (Qvenild and Skurdal 1981).

We collected whitefish monthly during May—September 1980 with floating nets (6 m x 25 m, mesh size: 21—39 mm) set for 24 hrs at depths of 2—8 m, 10—16 m and 20—26 m. The nets caught whitefish in the length interval 23—33 cm with an efficiency of 75% or more (Qvenild and Skurdal 1981). From a total of 710 whitefish we analysed 393 stomachs in the field

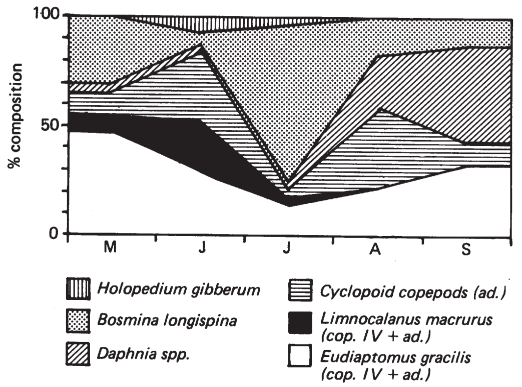

Fig. 1. Frequency composition of the main zooplankton species and groups in the 0—20 m layers of Lake Tyrifjorden during May—Sept. 1980.

and an additional 56 stomachs in the laboratory. Stomach fullness was subjectively evaluated on a scale from 0—5, where 0 represents empty stomach and 5 extended stomach. The zooplankton was surveyed quantitatively during daytime in the central part of the lake using a Clarke-Bumpus sampler (Clarke and Bumpus 1950). Samples were taken at 14 day intervals from early May through November from the layers 0—10 m, 10—20 m and 20—35 m. The net used had a mesh size of 95µm. For quantitative calibration of the sampling method, see Langeland and Rognerud (1974). The collected material was analysed to species except for nauplii and the smaller copepodites (cop. I—III). These are, however, not considered available prey because of their small size. The counts of zooplankton were converted to dry weight by conversion factors given in an earlier investigation from Lake Tyrifjorden (Langeland 1974) and other literature data (Bottrell et al. 1976, Larsson 1978).

Ivlev's (1961) electivity index was calculated according to the formula:

$$E = \frac{Fi - Pi}{Fi + Pi}$$

where F_i = proportion of prey in the stomachs, and P_i = proportion of prey in the zooplankton community. Based on the assumption that depth of capture corresponds to depth of feeding (cf. Horak and Tanner 1964, Houde 1967), we calculated Ivlev's index for the depth interval 0—20 m.

Table 1. Frequency (in %) of various prey categories in stomachs of whitefish *Coregonus lavaretus* in Lake Tyrifjorden.

Month No. of fish	May 100	June 106	July 87	Aug. 44	Sept. 56
Surface insects	20.0	8.2	2.9	—	—
Flowdrift	—	2.7	1.4	—	—
Aquatic insects	25.0	21.9	5.7	13.3	8.8
Plankton	90.0	100.0	97.1	100.0	100.0
Molluscs	—	—	—	—	8.8

RESULTS

There were marked seasonal variations in the composition of the zooplankton community during May—September (Fig. 1), including shifts in dominance between copepods and cladocerans. In May, June and August there was a copepod dominance, while cladocerans dominated in July and September. The cladocerans were dominated by *Bosmina longispina* (Sars, 1862), *Daphnia galeata* (Sars, 1862), *D. cristata* (Sars, 1862), and *Holopedium gibberum* (Zaddach, 1855). *Eudiaptomus gracilis* (Sars, 1862) and *Limnocalanus macrurus* (Sars, 1862) were the most abundant calanoid copepods, while cyclopoid copepods were dominated by small species such as *Mesocyclops leuckarti* (Claus, 1857), *Thermocyclops oithonoides* (Sars, 1863) and, to a smaller extent, *Cyclops scutifer* (Sars, 1862).

Whitefish showed almost obligate planktivory during late summer (Table 1). In spring and early summer, insects were frequently recorded in stomachs, although always together with plankton. In late autumn molluscs were found in a few stomachs, again co-occurring with plankton. Cladocerans were preferred prey throughout the season with a complete dominance of *Bosmina, Daphnia* and *Holopedium* which also were positively selected through most of the summer (Fig. 2). *Daphnia* were negatively selected in May and September (see discussion), whereas *Holopedium* were negatively selected in June. The larger *Leptodora kindtii* (Focke, 1844) and *Bythotrephes longimanus* (Leydig, 1860) were also recorded in the stomachs. Cyclopoid copepods were completely avoided, presumably because of their small size and escape abilities. Even the large calanoid *Limnocalanus macrurus* was only occasionally consumed, as was *Eudiaptomus gracilis*.

The seasonal vertical distribution of whitefish and of the main cladoceran species are given in Table 2 and Figure 3, respectively. In May, when no thermocline was established and zooplankton densities were low, the whitefish showed no specific depth preference. The feeding intensity was low (Fig. 4) and 81 % of the whitefish had empty stomachs. During early summer

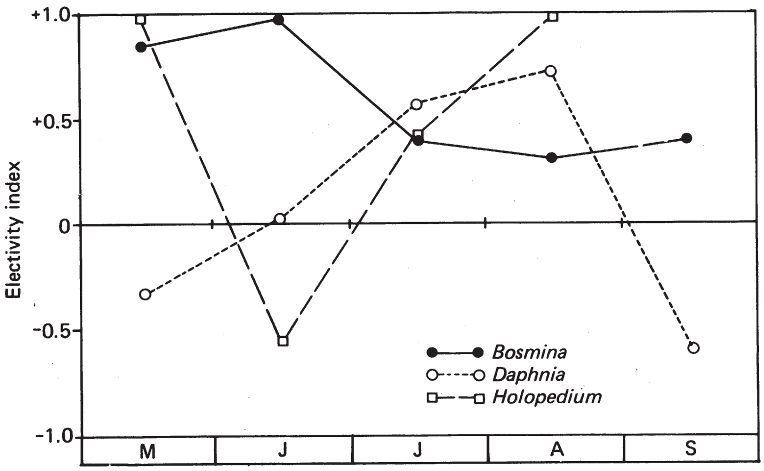

Fig. 2. Food selection of whitefish in Lake Tyrifjorden, based on the Ivlev (1961) index. Calculations are based on fish-catches and zooplankton samples in the 0—20 m layer. Copepods are not included, because of their deeper distribution (> 20 m) and low selectivity index (—0.75 — —1.0 throughout the summer).

Table 2. Catch per unit effort (number of fish/24 hrs/100 m^2) of whitefish *Coregonus lavaretus* in floating nets in Lake Tyrifjorden. Depth of the thermocline is also given.

Depth (m)	M	J	J	A	S
2— 8	3.6	10.6	19.0	0.3	4.1
10—16	1.2	1.1	3.6	11.7	4.8
20—26	6.3	0.1	0.3	1.1	11.2
Thermocline (m)	—	2-4	12-16	12-16	30

a thermocline was established and the abundance of zooplankton (prey) increased. Whitefish were concentrated in the food-rich surface layers (Table 2) and fed intensively. Compared to spring the frequency of whitefish with empty stomachs was low (Fig. 4) and the relative stomach fullness high. During autumn the whitefish were found in deeper layers, in spite of the high surface densities of *Bosmina* and *Daphnia. Daphnia,* especially, built up a large and dense population in the surface layers during autumn (Fig. 3). The downwards migration of whitefish coincided with an increase of whitefish with empty stomachs and a decrease in their relative stomach fullness. Further, the downwards migration followed the thermal gradient, locating the whitefish in the layers close to the thermocline (cf. Table 2).

During the summer it is not possible to distinguish with certainty between mature and immature whitefish. However, in August mature

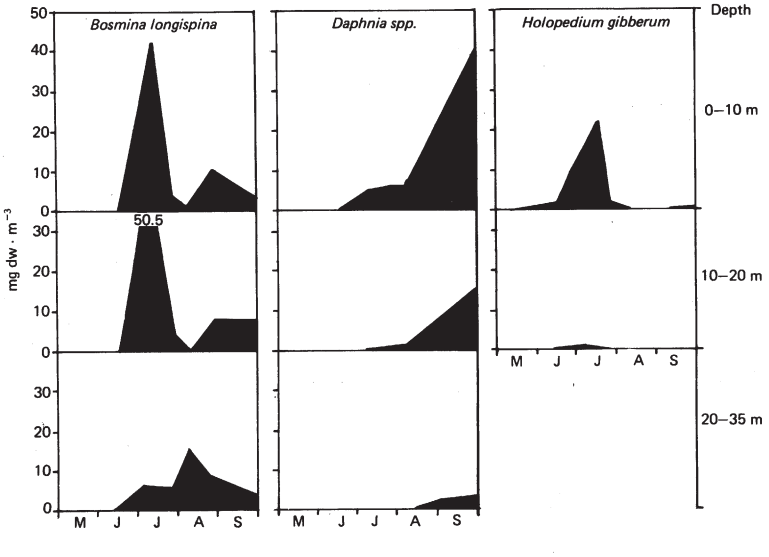

Fig. 3. Seasonal vertical distribution of the main cladoceran species in Lake Tyrifjorden.

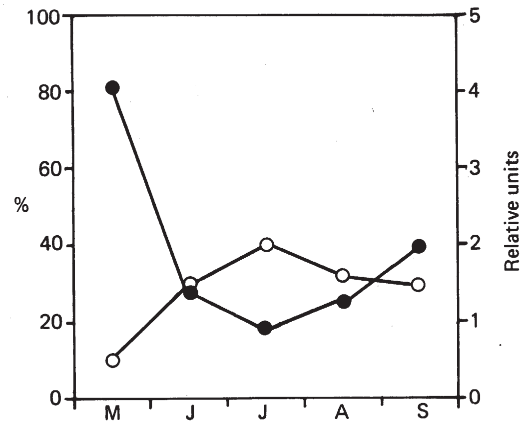

Fig. 4. Frequency of whitefish *Coregonus lavaretus* with empty stomachs (●) and relative stomach fullness (○).

and immature females are easily separated and in September one can separate between mature and immature individuals of both sexes. There were no significant differences in vertical distribution of mature and immature females in August ($\chi^2 = 2.52$, $p > 0.05$) or in mature and immature individuals of both sexes in September ($\chi^2 = 2.29$, $p > 0.05$). Thus, the observed downwards migration during autumn comprises both mature and immature whitefish.

DISCUSSION

The cladocerans *Bosmina, Daphnia* and *Holopedium* were the main prey species for the pelagic whitefish in Lake Tyrifjorden, whereas copepods were almost completely avoided as prey. Even the calanoid copepods *Limnocalanus macrurus* and *Eudiaptomus gracilis,* which constituted more than 70% of the zooplankton biomass in May and June, were only occasionally consumed. Earlier investigations on preferences among planktivorous whitefish also found the same preference for cladocerans (Nilsson and Pejler 1973, Sandlund et al. 1981, Bergstrand 1982). Bergstrand (1982) also observed a large fraction of copepods in the diet, but only in the most densily rakered morph.

Daphnia were negatively selected in May and September, and this is partly explained from the respective vertical distribution of whitefish and *Daphnia*. In September the whitefish were distributed to the 10—20 m layers, whereas the density of *Daphnia* was especially high in the surface layers. Such a vertical separation between prey and predator will cause obvious errors in the interpretation of the Ivlev index at these periods (cf. O'Brien and Vinyard 1974).

The nets were set 24 hrs at each depth interval, whereas zooplankton sampling was performed during daytime. As the sampling depths were divided in at least 10 m layers (0—10, 10—20 and 20—35 m), we expect the errors due to diurnal vertical migration to be negligible, because migrations among cladocerans are unlikely to exceed 5—10 m (Pennak 1944). The larger copepods may perform extensive migrations (McLaren 1963), but these are of little interest here as they make up only a minor fraction of the whitefish diet.

The crucial point is that during summer and early autumn, the whitefish was well-fed, and the distribution of whitefish corresponded to that of its main food items, *Daphnia* spp., *Holopedium* and *Bosmina*. Conversely, in late autumn whitefish occurred at depths below 20 m, in spite of high surface densities of *Daphnia* (cf. Table 2 and Fig. 4). This downwards migration coincided with an increased number of whitefish with empty stomachs and a decrease in relative stomach fullness. Thus, in spring and summer, the distribution of the whitefish is regulated mainly by prey abundance, which itself is probably regulated by the thermal stratification. During autumn, on the other hand, food abundance has little influence on the vertical distribution of whitefish compared to temperature.

During hydroacoustic surveys, diel migration through a strong thermocline was observed in the Lake Tyrifjorden whitefish, and these migrations exceeded 10 m during summer and early autumn (Lindem 1980, Skurdal unpubl.). The advantages of spending feeding time in the epilimnion and non-feeding time in the colder hypolimnion should be obvious in view of the reduced respiration costs in colder water (McLaren 1963, Brett 1971, O'Brien and Wright 1983). However, in September, thermal stratification was weak and food densities low below 20 m. Energy gain alone therefore can not explain why the whitefish gradually became concentrated in deeper layers during autumn.

The whitefish in Lake Tyrifjorden spawn either in the lake or in the rivers. The mature whitefish caught in the pelagic zone in autumn are mainly lake spawners, as the river spawning stocks commence their spawning migration in early September and ascend the inlet rivers in September—October (Skurdal 1982). Spawning in the lake occurs in November—January at depths below 20 m.

In general, physical stimuli serve as proximate factors and ensure that the fish are ready to spawn at the most favourable time for the production and survival of eggs and fry (Liley 1969). Timing of spawning in teleosts is largely determined by environmental factors, and spawning has been advanced experimentally by manipulation of photoperiod and temperature (Crim 1982, Lam 1983, Bromage et al. 1984). Compared to surface layers both temperature and photoperiod are reduced in the layers below 20 meters. We suggest, therefore, that the autumnal downward migration by mature whitefish and the cessation of feeding may be interpreted as pre-spawning behaviour, resulting in advancement and synchronization of gonadal development. Arctic char *(Salvelinus alpinus)* are also observed to cease feeding and migrate into deeper layers in early autumn prior to the spawning period (Hindar and Jonsson 1982). In salmonids the behaviour prior to spawning probably is governed by processes connected to gonadal development and spawning site selection. Anadromous salmonids may cease feeding nearly a year before they spawn. Specific prespawning behaviour may therefore explain observations of apparently unprofitable distribution of fish in relation to their food resources prior to the spawning season. This only applies, however, to mature fish, and does not explain the concurrent downward migration of immature whitefish in Lake Tyrifjorden.

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