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The diet and diel feeding activity of perch, *Perca fluviatilis* L., in a small lake in southern Finland

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Seasonal variations in the diet and diel feeding activity of perch were studied in a highly humic, small forest lake. Over the summer there was no clear change in the diet of perch of < 11 cm, whereas 11—13 cm fish fed on *Asellus aquaticus* and aquatic insect larvae in early summer but later concentrated on zooplankton. Perch of > 13 cm had a similar diet to fish of 11—13 cm during May—June, but later turned to corixids, water spiders and leeches. It appears that the intensity of predation by perch, the life histories of the prey species and decreasing oxygen conditions contributed to diet segregation and that a decreased availability of benthic food resulted in intraspecific competition.

A shift occurred from distinct morning and evening activity peaks in May and June towards a midday peak in July and August. Temporal segregation in feeding activity was not observed among perch of different sizes.

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1. Introduction

The perch, *Perca fluviatilis* L., is considered an opportunistic feeder with a diet largely determined by the availability of different types of food (MacLean & Magnuson 1977, Knight et al. 1984). In waters with rich invertebrate and fish faunas, perch generally switch during the course of a lifetime from planktonic to benthic food and later to fish (Allen 1935, McCormack 1970, Craig 1978, Goldspink & Goodwin 1979). However, the occurrence of such size-dependent diet segregation varies widely among perch populations. Along the coasts of the northern Baltic, perch of < 10 cm may be piscivorous, whereas in Lake Gjökvatn, Norway, 20 cm perch are still predominately planktivores (Klemetsen 1973).

In addition, perch in heterogeneous habitats may segregate spatially. The smallest fish inhabit the dense vegetation of the upper littoral, whereas the largest are most abundant outside the zone of macrophytic vegetation. Spatial segregation may compensate for a high diet overlap and the unavailability of large prey in the diet of perch (Sandheinrich & Hubert 1984).

This paper examines seasonal changes in the diet and diel feeding activity of perch in a small forest lake where the chance of either food or habitat segregation is limited. Specifically, it considers how perch of different sizes utilize the food resources of a lake that lacks other fish species (predators as well as prey) and has a narrow oxygenated littoral zone, resulting in limited access to benthic food. The occurrence of intraspecific competition for food among perch in these extreme conditions is also discussed (cf. MacLean & Magnuson 1977, Mittelbach 1981, Persson 1983).

2. Material and methods

2.1. The lake

Lake Horkkajärvi is a small, extremely humic forest lake in the Evo region of southern Finland. The lake is 0.011 km^2 in area with a maximum depth of 13 m. Table 1 summarizes its physicochemical properties. Lake Horkkajärvi is meromictic (Salonen et al. 1984), with a steep thermal and oxygen stratification (Fig. 1). The oxygenated littoral zone is small because of the steep shores. During 1979 this area decreased from 3000 m^2 in May to 600 m^2 in August, and returned to 3000 m^2 in September with incomplete autumnal circulation.

Initially, perch were the only fish present in the lake, although 200 individuals of young-of-the-year whitefish, *Coregonus peled* Gmelin, were introduced in autumn 1978. In spring 1979 the density of perch of > 2 years old was 1750 individuals per hectare and the perch biomass was 22.7 kg/ha (ww). The population exhibited a stunted growth rate (Table 2).

Table 1. Some physicochemical properties of the water in Lake Horkkajärvi during May–October in 1979 and 1980. Sampling depth = 1 m.

	1979		1980	
	Mean	Range	Mean	Range
pH	5.4	4.6–6.3	5.6	5.4–5.7
Alkalinity (meq/l)	0.03	−0.02–0.04	0.06	0.04–0.09
Colour (mg/l Pt)	310	210–410	260	230–310
Conductivity (μS/cm +20°C)	36	32–41	35	33–40
Total P (μg/l)	40	20–95	30	20–40
Total N (μg/l)	720	440–1080	630	530–710
Na (mg/l)	1.6	1.4–2.3	1.5	1.4–1.5
Mg (mg/l)	1.0	0.8–1.2	1.1	1.0–1.1
Ca (mg/l)	3.8	3.6–4.1	3.4	3.1–3.6

Table 2. Mean total lengths (mm) of perch at various ages in some small Finnish lakes, in a larger lake, Pääjärvi (13.6 km^2) and in a brackish water area, Tvärminne, in the western Gulf of Finland.

Lake/ watershed	Age (years)										Reference
	1	2	3	4	5	6	7	8	9	10	
Horkkajärvi	63	90	102	111	117	126	133	142	–	–	Rask 1983
Nimetön	57	98	125	152	167	178	–	–	–	–	Rask 1983
Karhujärvi	64	97	116	128	133	137	141	–	–	–	Rask 1984
Haukilampi	54	76	95	110	120	132	137	–	–	–	Tikka & Paasivirta 1979
32 small lakes	56	95	124	143	–	–	–	–	–	–	Sumari 1971
Pääjärvi	62	103	137	169	193	210	231	247	265	272	Viljanen 1975
Tvärminne	67	95	120	150	176	194	215	231	248	270	Koli et al. 1985

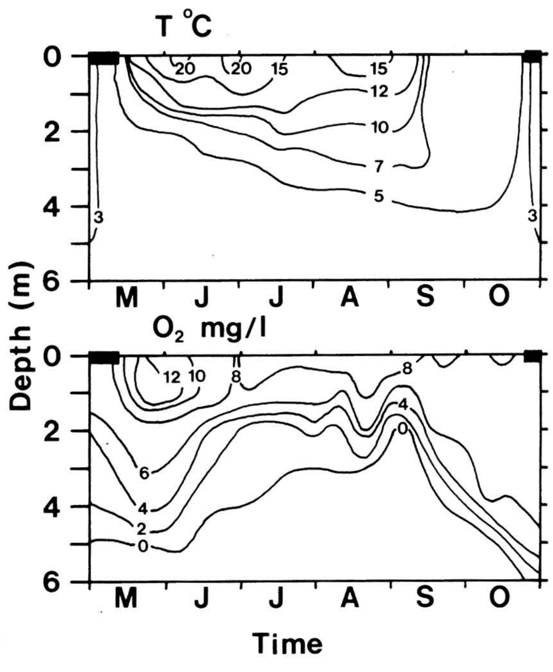

Fig. 1. The stratification of temperature and dissolved oxygen in Lake Horkkajärvi (0–6 m) during the summer, 1979.

2.2. Sampling

Samples of perch (10–20 individuals per sample, 300 in total) were taken every two weeks to determine diets. Traps (4–6 units, 1 cm square mesh) were kept in the lake overnight at depths of 0.5–1.5 m and emptied in the morning. These traps take perch of >8.5 cm total length. In addition, perch 1+ in age (n=50) were captured with a gill net (mesh size 9 mm).

To determine the diel activity and feeding patterns of perch, 24-h sampling programmes were performed on 24.–25.7.1979, 28.–29.8.1979, 10.–11.6.1980 and 27.–28.5.1981. Samples for food analyses (10 individuals per sample when possible, 340 in total) were taken every 2 h using the traps described above. Activity was determined in terms of the total number of fish caught in a 2-h period. The total solar radiation during three diel samplings was measured at Lammi Biological Station, 20 km south of the study area, with Kipp & Zonen solarimeter, see also Arvola (1984a).

Lengths (total length, mm) and weights (ww, g) of all fish were recorded and their ages determined from opercular bones (LeCren 1947).

Benthic samples were taken with a Kajak-Hakala core sampler (15.1 cm^2); 10 cores were taken from six sampling sites along the shoreline once or twice per month in 1979 and 1980. The benthos biomass was estimated as mg organic carbon/m^2 (Salonen 1979).

In both years zooplankton samples were collected weekly with a Sormunen-type tube sampler from one station in the middle of the lake and filtered through a net (mesh size 50 μm. The mean monthly densities of crustacean zooplankton were calculated.

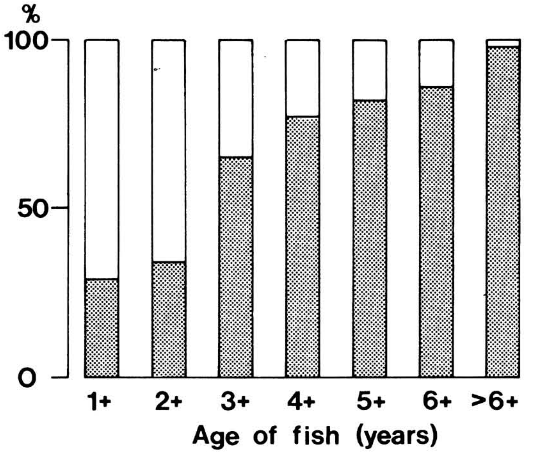

Fig. 2. The proportions of zooplankton (white) and benthos (shaded) in the diet of perch of different ages. The values are percentages of the total amount of fullness points per age group.

2.3. Stomach analyses

Stomach fullness was estimated using a volumetric points method (Windell 1971) with a scale of 0–24 points. Differences in diet composition within a length group at different times during the summer were compared with χ^2-tests (Windell & Bowen 1978).

The diet overlap between different length groups was calculated using an index of overlap given by Schoener (1970) and recommended by Wallace & Ramsey (1983):

$$\alpha_{xy} = 1-0.5\,(\Sigma \mid P_{xi}-P_{yi} \mid)$$

where α_{xy} is the overlap index, P_{xi} is the proportion of food category i in the diet of length group x and P_{yi} is the proportion of food category i in the length group y. The number of food categories (n) was 6.

The mean lengths of benthic food items eaten by perch of different sizes were compared using Students's t-test. Comparisons were made monthly between perch length groups and between months within length groups.

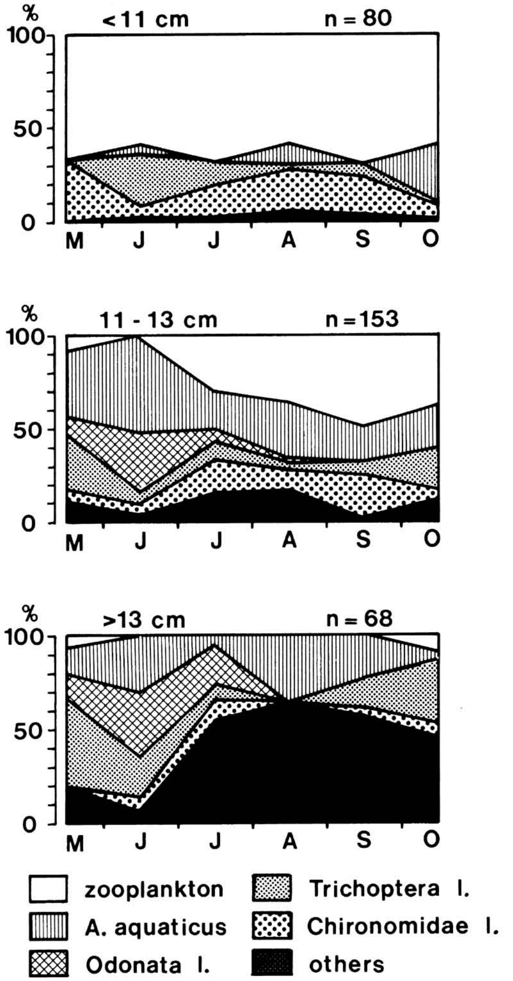

Fig. 3. The mean diet of perch in the three length groups in Lake Horkkajärvi during the summers 1979 and 1980. The values are percentages of the monthly total amount of fullness points.

3. Results

Because perch switch from benthic to plankton food during their life span (Fig. 2), the fish were divided into three length groups: small, of < 11 cm (< 4 years old), which fed mainly on zooplankton, medium, of 11–13 cm (4–5 years old), which fed on both zooplankton and benthos, and large, of > 13 cm (> 6 years old), which fed mostly on benthos. These length groups were comparable to the three smallest used by Allen (1935) and McCormack (1970) for Windermere perch. For analyses, the material from 1979 and 1980 was combined because the diet composition was similar in these years.

The diet of the smallest perch was similar throughout the summer (Fig. 3), 60–70 % of it being composed of crustacean zooplankton. The cladocerans, *Ceriodaphnia quadrangula* Müller and *Bosmina longispina* Leydig, were eaten most frequently, contributing 61 % of the total plankton eaten by perch. These two species made up a comparable proportion (65 %) of the plankton in lake samples. Owing to the low amount of littoral zooplankton species in the diet of perch (18 %, mainly *Poly-*

phemus pediculus L.), it was assumed that plankton samples, although taken in the middle of the lake, were representative of the zooplankton food resource available to perch (Fig. 4).

The diet of medium-sized perch differed significantly in June and September (χ^2-test, $P < 0.001$). At the beginning of the summer it was dominated by benthic animals, but later zooplankton became more important, contributing up to 50 % of the stomach contents (Fig. 3). The diet of large perch (>13 cm) was dominated by benthos throughout the summer (Fig. 3). As in the 11–13 cm length group, *Asellus aquaticus* L. and larvae of Odonata, Trichoptera and Chironomidae formed the main constituents of the diet in early summer. In July and August other invertebrates (Corixidae, Notonectidae, *Argyroneta aquatica* L., Hirudinea) became dominant and the diet was significantly different (χ^2-test, $P < 0.001$) from that in June.

Due to seasonal changes in the diet of perch of different sizes dietary overlap between the length groups varied during the summer. Between the groups <11 cm and 11–13 cm the overlap was 0.2 at the beginning of the growing season, but increased to 0.8 by September. Between the groups 11–13 cm and >13 cm the overlap was high (0.7) in May and June, but decreased to 0.3–0.4 in August–September.

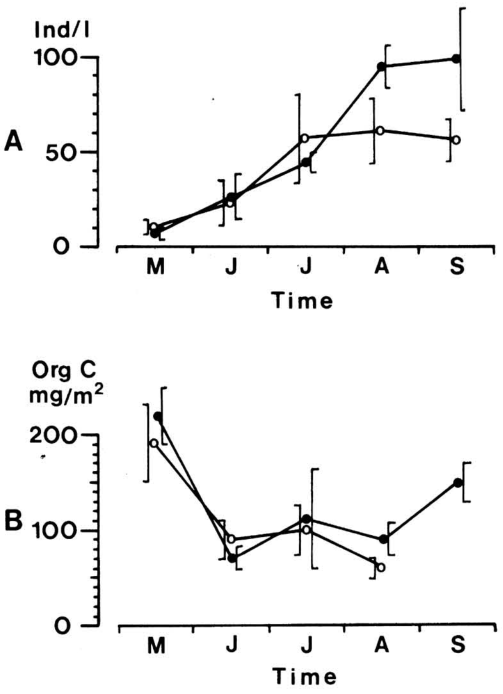

Fig. 4. (A) The density of crustacean zooplankton and (B) the biomass of benthic fauna in Lake Horkkajärvi during the summer 1979 (open circles) and 1980 (closed circles). Error bars = *SD*.

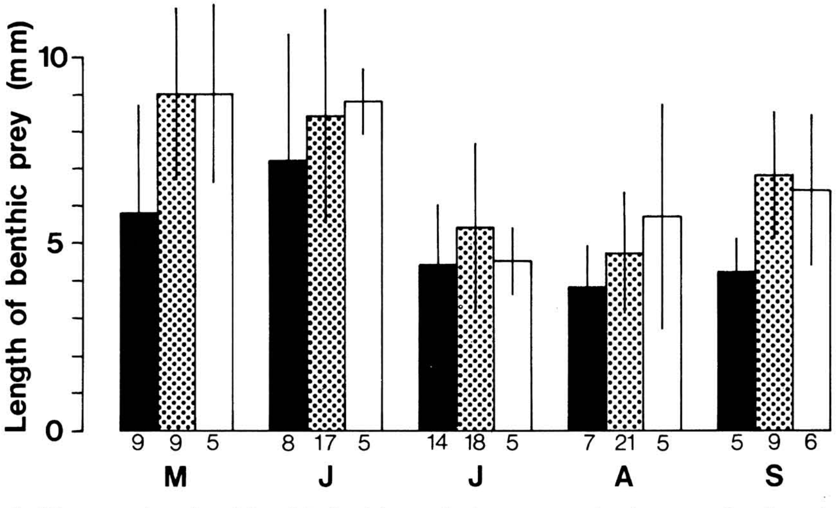

Fig. 5. The mean lengths of benthic food items during summer in the stomachs of perch of < 11 cm (black columns), 11–13 cm (pointed columns) and >13 cm (white columns). The numbers below the columns refer to the number of fish with benthic animals in their stomachs. Error bars are *SD*.

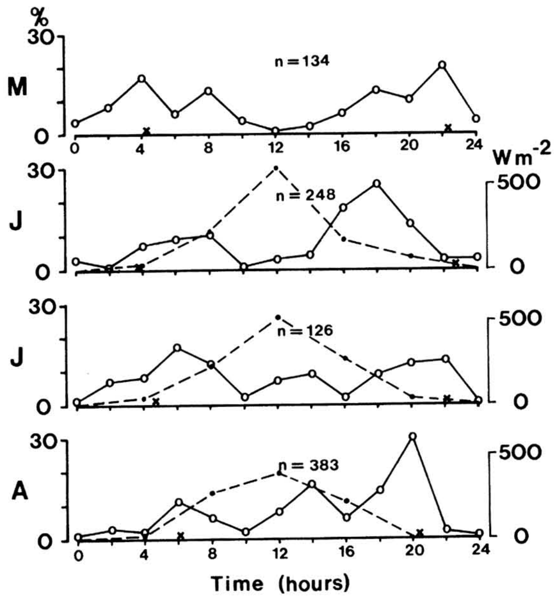

Fig. 6. The diel activity of perch in Lake Horkkajärvi based on catches in traps (% caught at 2 h intervals of total catch in 24 h). The total solar radiation (W m^{-2}, broken line) is also given. The points are mean values per hour during consecutive 4-hour periods. The crosses on the *x*-axis refer to the time of sunrise and sunset.

The mean lengths of the most important benthic animals eaten by perch (*Asellus aquaticus*, larvae of Odonata, Trichoptera and Chironomidae) varied during the course of the summer but did not vary so sharply between the fish length groups (Fig. 5). The only significant differences between fish length groups were observed in May and September ($<$11 cm and 11 − 13 cm, *t*-test, $P<0.05$). The length of prey decreased from June to July in all three length groups of fish (*t*-test, $P<0.001$ for $<$11 cm, $P<0.01$ for 11 − 13 cm and $>$13 cm).

The introduced whitefish did not appear to affect the availability of benthic food to perch because they foraged mainly on zooplankton. Whitefish also fed on *Hydracarina* and *Pisidium* mussels, which were not used by perch.

Perch changed from distinct morning and evening activity peaks in early summer to a midday peak in later summer (Fig. 6). The feeding rhythm corresponded to that of activity. For perch of $<$11 cm this pattern was clearest when they were feeding on zooplankton (Fig. 7), which formed the largest component of the diet in this length group (Fig. 3). In the 11 − 13 cm length group the transition from dawn and dusk activity to midday activity was clearest in conjunction with feeding on zooplankton, *Asellus aquaticus* and Trichoptera larvae (Fig. 8). The diel activity in both length groups peaked simultaneously; no apparent temporal segregation in feeding occurred.

4. Discussion

The main reason for observed changes in the diet of perch during the summer appeared to be an increase in zooplankton density, which reached its maximum in August − September, and a decrease in benthic biomass from May to June. The latter was probably due to increased predation pressure by perch after the water warmed up in May (cf. Post & Cucin 1984). For example, perch consumed 0.1 − 1.8 % of the *Asellus aquaticus* population per day (Rask & Hiisivuori 1985). The life cycles of some important food items also contributed to a decrease in the benthic biomass in the lake. The replacement of generations of *A. aquaticus* and the emergence of Odonata and Trichoptera were reflected in decreases in the mean lengths of benthic prey taken by perch from June to July.

Another potential reason for seasonal differences in the diet was deteriorating oxygen conditions in the lake during summer. The reduced area of the oxygenated littoral zone limited the development of the benthic community or the ability of perch to utilize it. In addition, the relatively low pH of the lake excluded pH-sensitive benthic animals (cf. Økland & Økland 1980) and might have contributed, at least temporarily, to reduced benthic food for perch. Thus, perch had to turn to another diet; medium-sized perch turned to zooplankton and large perch to non-benthic macroinvertebrates which were not closely dependent on an oxygenated bottom, e.g. corixids and water spiders.

This food segregation between the two size-groups of perch (11 − 13 cm and $>$13 cm) would seem to be the only possible reaction to the decreasing availability of benthic food in Lake Horkkajärvi since the lake basin with its steep shores, scanty macrophytic vegetation and shallow oxygenated epilimnion does not offer any opportunities for habitat segregation. These results do not agree with the general conclusions of Sandheinrich & Hubert

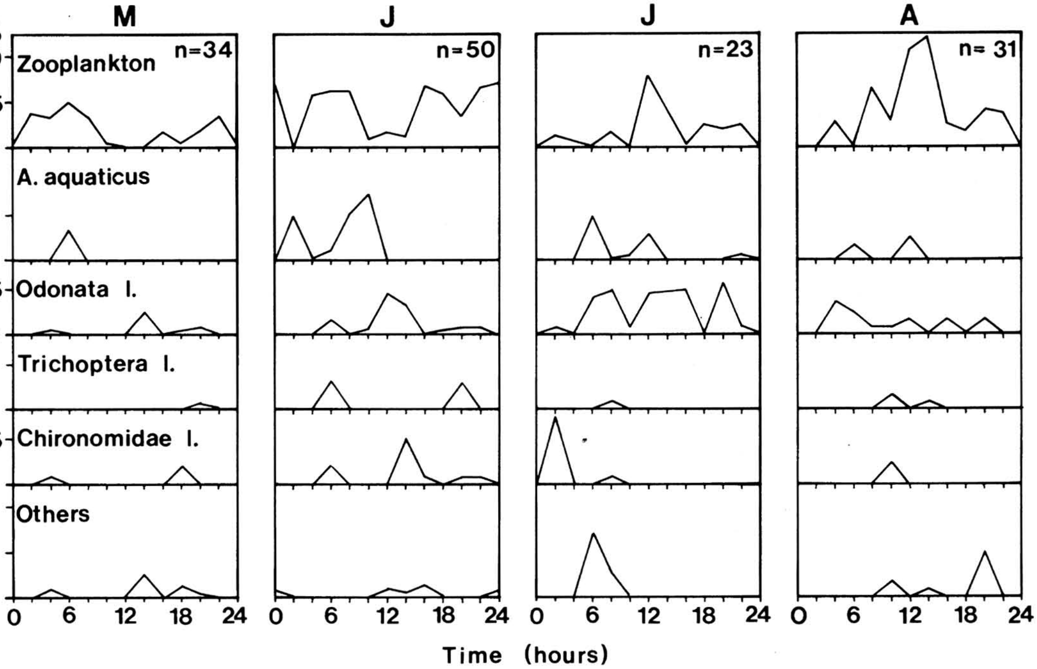

Fig. 7. The mean stomach fullness of perch of < 11 cm in Lake Horkkajärvi during the 24 h samplings. The values are percentages of the stomach volume.

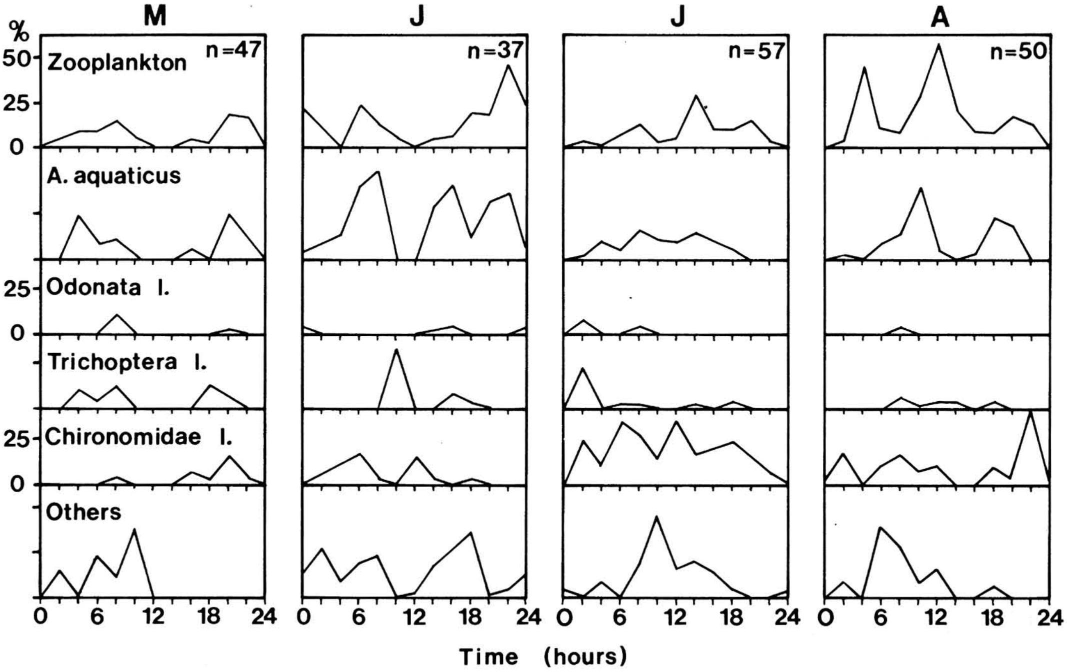

Fig. 8. The mean stomach fullness of perch of length group 11 – 13 cm in Lake Horkkajärvi during the 24 h samplings. The values are percentages of the stomach volume.

(1984), who stressed the importance of habitat segregation over food segregation in perch populations. It seems rather that resource partitioning in perch populations is determined by the opportunities offered by the environment and takes the form of food or habitat segregation, or both.

In lakes such as Horkkajärvi, intraspecific competition for food may occur, especially as there are no piscivorous fish to control the population density of perch. According to Nilsson (1960) a maximum intensity of intraspecific competition occurs when there is a minimum supply of common food available. In Lake Horkkajärvi this means that competition for benthic food was high from June onwards and resulted in food segregation during July—August. According to Hanson & Leggett (1985) an indisputable demonstration of competition requires that the changes in diet or diet overlap are accompanied by a reduction in fitness (decreased growth, fecundity or survival). Thus, the stunted growth of perch (Rask 1983), which is considered a phenotypic response to intraspecific competition (MacLean & Magnuson 1977), supports the assumption that perch in Lake Horkkajärvi compete for food.

In spite of increasing predation by perch during the summer, the density of crustacean zooplankton increased until August—September. This would indicate that there was no competition for plankton food between fish of <11 cm and 11—13 cm. This hypothesis is supported by the growth rate of Lake Horkkajärvi perch during their first two years, which is similar to that in other waters (cf. Table 2).

The changes in the diurnal feeding activity patterns of perch were similar to those observed by Craig (1977) and Persson (1983); see also Alabaster & Stott (1978), Müller (1978) and Eriksson (1978). Craig (1977) suggested that a certain amount of visual irradiance favours the activity of perch at dawn and dusk. Thus, the inactive period at noon would be a consequence of an excess of light. This is probably not the case in Lake Horkkajärvi, where the water was so stained that only 1 % of the total radiation penetrated to a depth of 1 m (Arvola 1984b). Craig (1977) further suggested that daytime feeding activity in perch later in the summer was a result of an increase in algal biomass, which reduced the irradiance below the activity limiting threshold. However, a similar pattern in the activity of perch was observed in Lake Horkkajärvi under relatively constant light conditions in the water. Therefore, the midday feeding peak later in the summer may be physiologically determined, allowing perch to attain a maximum energy intake for gonadal growth and an increase in energy reserves for the winter. Thus, this period could be comparable to spawning time when perch are also active independently of the dawn and dusk rhythm.

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