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Two different feeding tactics of young-of-the-year perch, *Perca fluviatilis* L., inhabiting the littoral zone of the lowland Sulejow Reservoir (Central Poland)

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Abstract

The feeding pattern of young-of-the-year (YOY) fish was investigated in a field experiment in the sparsely vegetated littoral zone of the Sulejow Reservoir in June 2007. Perch received special emphasis in this study. During the study period, the part of the reservoir selected to conduct the research was densely inhabited by YOY fish (up to 20 individuals per square metre). The dominant YOY species were perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). Analyses of stomach/gut contents showed that large zooplankters and benthic prey contributed significantly to the diet of YOY fish. For perch, two distinct feeding tactics were observed. Fish collected by trapping in unvegetated gaps among beds of macrophytes preyed almost exclusively on daphnids and copepods, whereas individuals seined in shallow water among macrophytes ate mostly the larvae of benthic insects. The observed division of YOY perch into two feeding groups may indicate an attempt to decrease the level of both intra-specific competition among the cohort's members and inter-specific competition between perch and roach.

Key words: juvenile fish, littoral, feeding behaviour, zooplankton.

1. Introduction

The foraging behaviour of YOY perch has been the topic of numerous laboratory and field studies (e.g., Persson, Greenberg 1990a; 1990b; Diehl, Eklow 1995; Mehner *et al.* 1998; Hjelm *et al.* 2000; Horppila *et al.* 2000; Wanzenböck *et al.* 2006; Borcherding, Magnhagen 2008). The ontogenetic shift by juveniles from zooplankton to benthic prey is a well-recognised phenomenon. This shift usually serves to optimise the growth rate of YOY fish (Persson, Greenberg 1990b; Byström *et al.* 1998; Hjelm *et al.* 2000). The time of the shift depends not only on the size of the fish but also on the abundance of alternative prey, the strength of inter- and intraspecific competition, and the presence of predators (Persson 1986; Bergman 1990; Diehl 1993; Diehl, Eklow 1995; Sharma, Bystrøm 2008). It has generally been found that YOY perch inhabiting open water eat zooplankton, whereas conspecifics living in the littoral zone feed on benthic prey (Diehl 1992; Hjelm *et al.* 2001; Svanbäck, Eklöv 2008; Kratochvil *et al.* 2008). The division of the YOY perch into two groups differing in feeding pattern even results in changes in the morphological traits of the perch (Hjelm *et al.* 2001; Svanbäck, Eklöv 2002; Borcherding, Magnhagen 2008).

However, investigations of the stomach contents of YOY perch collected from the littoral zone have frequently shown that some individuals do not forage only on benthic prey. Rather, some individuals forage exclusively on zooplankton, and others have mixed diets (Horppila *et al.* 2000; Okun, Mehner 2005). Possibly, these zooplanktivorous specimens represent a particular fraction of littoral-dwelling fish that are likely to penetrate the water column more actively, forage among macrophytes and specialise in feeding on zooplankton. In contrast, another fraction of the population would consist of benthivorous fish that are less active and spend much more time closer to the bottom. If this hypothesis is true, one would expect that the amount of zooplankton in the stomachs of fish collected by trapping in the water column would be much greater than the amount of zooplankton in the stomachs of fish collected by beach seining. Alternatively, if all YOY perch in the littoral zone exhibit similar activity and frequently change their foraging habitats, the probability of catching fish which stomachs contained zooplankton or benthic prey should be the same no matter where the fish were actually caught.

The aim of the field research presented in this paper was to determine whether food niche diversification actually occurs among YOY perch at a small spatial scale within the littoral zone.

1.1. Study site

The Sulejow Reservoir is a shallow, lowland reservoir situated in central Poland along the middle course of the Pilica River. The maximum length of the reservoir is 15.5 km, and the maximum width is 2.1 km. At maximum capacity (75×10^6 m^3), the reservoir covers 22 km^2, with a mean depth of 3.3 m and a maximum depth of 11 m. The shoreline is approximately 54 km in length. The mean water retention time of the reservoir is 30 days. The Sulejow Reservoir is an eutrophic ecosystem. The mean total phosphorus concentration during the last ten years was approximately 137 µg dm^{-3}, ranging from 13 to 1053 µg dm^{-3} (Wagner *et al.* 2009). The dominant species of bloom-forming cyanobacteria is *Microcystis aeruginosa* Kutzing. These microorganisms produce microcystin-LR, -YR and -RR (Tarczyńska *et al.* 2001; Jurczak *et al.* 2005). The mean chlorophyll concentration during growth seasons is approximately 30 mg m^{-3}, but it can exceed 100 mg m^{-3} during phytoplankton blooms (Wagner *et al.* 2009). The mean summer biomass of zooplankton sampled in the pelagic zone has ranged during last 10 years between 4 mg and 11 mg l^{-1} and consists primarily of cladocerans: *Daphnia cucullata* (Sars), *D. longispina* (O.F.Müller), *Leptodora kindtii* (Focke) and *Bosmina coregoni* (Baird) (Wojtal-Frankiewicz, unpublished data). The adult fish stock is composed mostly of roach (*Rutilus rutilus* L.), common bream (*Abramis brama* L.), white bream (*Blicca bjoerkna* L.), pikeperch (*Stizostedion lucioperca* L.), perch (*Perca fluviatilis* L.), bleak (*Alburnus alburnus* L.) and asp (*Aspius aspius* L.). Perch and roach dominate the YOY fish community in the littoral zone (Frankiewicz, unpublished data).

Investigations were conducted in a vegetated lacustrine part of the reservoir (Tresta Bay) where the following macrophytes were present: *Potamogeton lucens* L., *Polygonum amphibium* L., *Elodea Canadensis* Michx., *Galium palustre* L., *Carex acuta* L., *Equisetum fluviatile* L., *Eleocharis palustris* (L.) Roem. & Schult., *Gliceria fluitans* (L.) R.Br. and *Iris pseudoacorus* L. The coverage of all species at sample sites was about 50%.

2. Materials and methods

YOY fish were collected on 23-24 June 2007 in the littoral zone using two methods: beach seine netting (to sample all fish from the shallow, vegetated part of the littoral) and plastic traps fixed in the water column (to catch fish active in unvegetated gaps among beds of submerged macrophytes). Five sets of double bottles (of 1.5 dm^3 volume) were placed in water approximately 1 m deep, 30 cm above the bottom. The distance from the shore and between traps was about 10 m and 3 m, respectively. The opening of one bottle was directed towards the bank to trap fish moving away from shore. The opening of the other bottle was directed towards the pelagic zone to trap fish moving inshore (Fig. 1). The bottles were set out at 6 p.m. and then emptied twice, at 11 p.m. and 6 a.m. This time schedule was chosen based on the finding from earlier research in Sulejow Reservoir that intense foraging activity of YOY perch occurred mostly at dusk and dawn (Zalewski *et al.* 1990). The beach seining was conducted after dusk using 10 m long net with a mesh size of 1 mm.

Fish were anaesthetised and preserved in 10% formalin. Each fish was measured to the nearest 0.5 mm (LT) and weighed to the nearest 0.01 g. The stomach contents of perch were weighed to the nearest 0.1 mg. The prey were counted under a microscope and identified to the lowest practical taxon. The numerical contribution (Hyslop 1980) of a given prey category to the content of each stomach was calculated. The Mann-Whitney U-test was used to compare differences in the number of fish collected in the traps with regard to time (dusk, dawn) and movement direction (inshore, outshore). To test for the habitat effect (traps vs. beach seining) on the fish length, weight, fullness index and the numerical contribution of the main prey categories to the stomach contents, *t*-test was applied. To test for time and traps orientation effects on the parameters analysed, we performed two-way ANOVA test with the time and traps orientation as categorical factors and individual fish length, weight, fullness index and the numerical contribution of the main prey categories to the stomach contents as dependent variables. Data on prey numbers in perch stomachs were $\log_{10}(x + 1)$ transformed to achieve normality and homoscedasticity.

3. Results

The numbers of YOY perch collected in traps were 73 at dusk (41 and 32 in inshore- and outshore-oriented traps, respectively) and 43 at dawn (24 and 19 in inshore- and outshore-oriented traps, respectively). Number of fish in each set of five bottles was highly variable and comparison of trapped fish distribution with regard to both time and movement direction did not reveal significant differences (Mann-Whitney U-test, $p = 0.17$ and $p = 1$, respectively). Perch collected by using a beach net had significantly higher length, weight and fullness index than trapped fish (*t* test: $t = 4.03$, $df = 147$, $p < 0.001$; $t = 3.59$, $df = 147$, $p < 0.001$; $t = 3.38$, $df = 87$, $p < 0.01$, respectively) (Fig. 2). Perch trapped in the morning had significantly lower body weight and stomach fullness than fish trapped at night (two-way ANOVA: $F_{1,112} = 4.33$, $p < 0.05$; $F_{1,70} = 4.26$, $p < 0.05$, respectively). Differences in perch length between morning and night samples were not significant (two-way ANOVA: $F_{1,112} = 2.42$, $p = 0.12$). Perch length, weight and fullness index did not differ significantly between inshore- and outshore-oriented traps (two-way ANOVA: $F_{1,112} = 1.95$, $p = 0.17$; $F_{1,112} = 0.76$, $p = 0.39$; $F_{1,70} = 0.03$, $p = 0.86$, respectively). Time/traps orientation interactions were not significant (two-way ANOVA: $F_{1,112} = 1.95$, $p = 0.17$; $F_{1,112} = 0.76$, $p = 0.39$; $F_{1,70} = 0.03$, $p = 0.86$, for perch length, weight and fullness index, respectively).

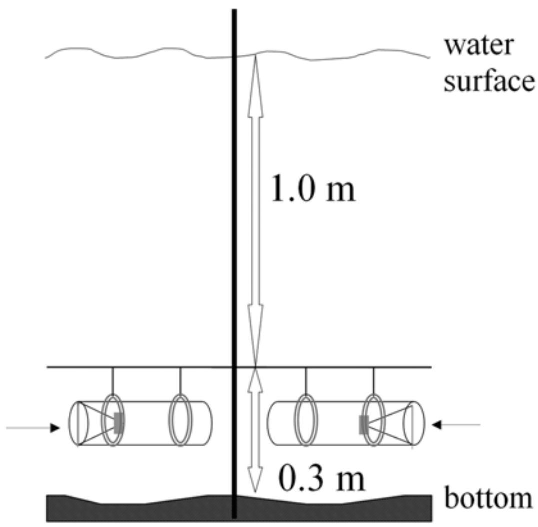

Fig. 1. Diagram of traps used for collecting YOY perch.

The numerical contribution of the main prey categories to the stomach content of YOY perch differed strongly between trapped fish and fish collected by using a beach net (Fig. 3). Daphnids and predatory cladocerans, *Leptodora kindtii*, were not present in the stomachs of seined perch. The numbers of copepods found in perch stomachs obtained from trap samples were significantly higher than those found in the seine sample (*t* test: $t = 2.87$, $df = 81$, $p < 0.01$) (Fig. 3). Unlike trapped perch, seined fish preyed mainly upon benthic insects, mostly chironomid larvae (Fig. 3). These differences were highly significant (*t* test: $t = 8.56$, $df = 81$, $p < 0.001$).

L. kindtii were significantly more numerous in the stomachs of perch trapped at night than in the stomachs of fish trapped in the morning (two-way ANOVA: $F_{1,67} = 82.15$; $p < 0.001$) (Fig. 3). Significant differences were also found for *Daphnia* sp. These filtering zooplankters were much more numerous in the food of perch entering traps from the open water than in the food of perch entering traps from the bank (two-way ANOVA: $F_{1,67} = 10.44$; $p < 0.01$) (Fig. 3). Copepods were the other noteworthy group of zooplankton whose contribution to the food of the perch varied significantly. They were more numerous in the stomachs of perch trapped at night than in the stomachs of fish trapped in the morning (two-way ANOVA: $F_{1,67} = 19.01$; $p < 0.001$) (Fig. 3). Time/traps orientation interactions were not significant for any prey categories. Differences in the contribution of benthic organisms to the food of trapped perch were not analyzed due to the low number of these prey.

4. Discussion

The feeding ecology of YOY perch has already been well characterised in different freshwater ecosystems (e.g. Persson, Greenberg 1990a; 1990b; Diehl, Eklow 1995; Mehner *et al.* 1998; Hjelm *et al.* 2000; Horppila *et al.* 2000; Vašek *et al.* 2006; Borcherding, Magnhagen 2008). The most characteristic life-history phenomena described for these fish are the presence of horizontal migration from the littoral to the pelagic zone and back during the first months of life (Wang, Eckman 1994; Urho 1996) and the presence of ontogenetic shifts in the utilisation of food resources, from zooplankton to benthos and finally to fish (Thorpe 1977; Persson 1990; Hjelm *et al.* 2000). The occurrence and timing of this ontogenetic shift are highly variable and

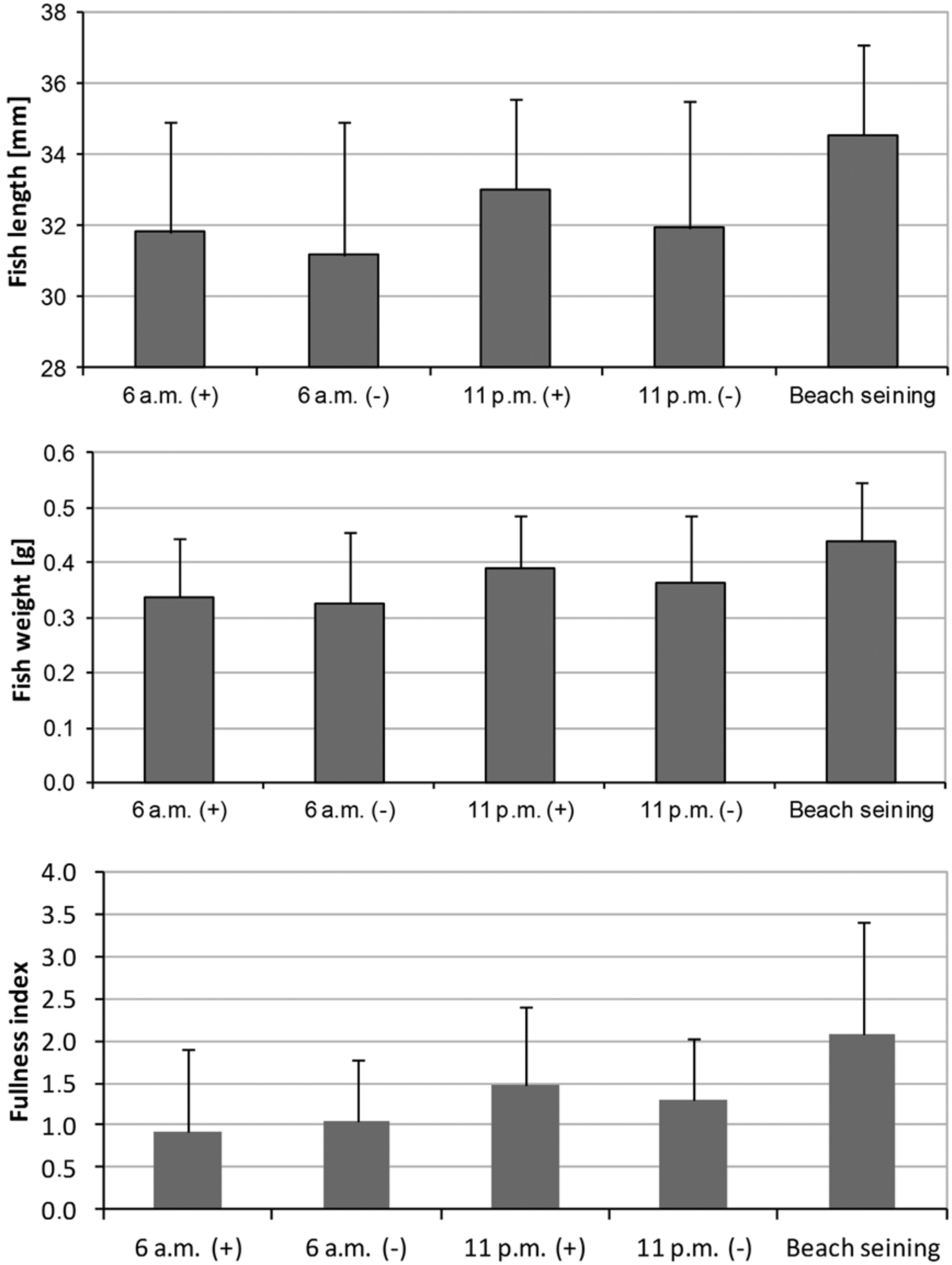

Fig. 2. Comparison of length, weight and fullness index of YOY perch from traps and from beach seining (boxes indicate means values, whiskers indicate standard deviations).

(+) – traps directed towards the bank; (-) – traps directed towards the open water.

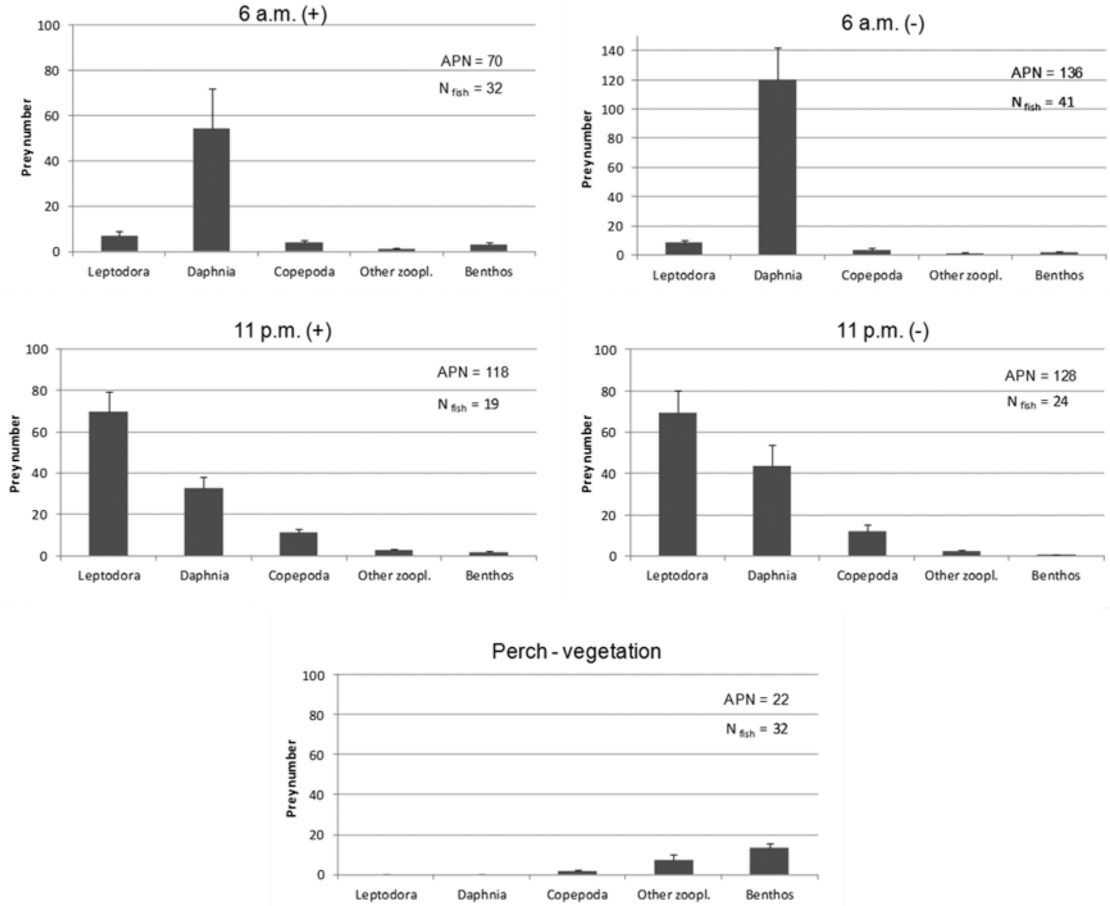

Fig. 3. Contribution (by number) of the main food categories of YOY perch from traps and from beach seining (boxes indicate means values, whiskers indicate standard errors).

APN – average prey number by fish; N_{fish} – number of fish used for food analyses. (+) – traps directed towards the bank; (-) – traps directed towards the open water.

depend mostly on prey availability (Persson 1986; Byström *et al.* 1998), on the intensity of inter- and intraspecific competition (Bergman 1990; Persson, Greenberg 1990a,1990b; Diehl 1993), and on the threat of predation (Persson 1991; Diehl, Eklow 1995; Sharma, Bystrøm 2008). The need to adjust to a complex pressure of environmental stressors results in the highly diverse feeding pattern of YOY perch reported in numerous studies (Zalewski *et al.* 1990; 2006; Kahl, Radke 2006; Quevedo, Olsson 2006; Olsson *et al.* 2007; Huss *et al.* 2008; Urbatzka *et al.* 2008). However, some general patterns may be described. The main food of YOY perch foraging in the pelagic zone consists of zooplankton and is dominated by daphnids (Svanbäck, Eklow 2002; Vašek *et al.* 2006). Benthic macroinvertebrates are usually predominant in the stomach contents of perch foraging in the littoral zone (Zalewski *et al.* 1990; Okun, Mehner 2005). In the littoral zone, the relative contribution of benthic prey to the diet of YOY perch should increase with the size of the fish (Guma'a 1978; Treasurer 1990). However, in the presence of competitors (e.g. YOY roach) they may be forced to use benthic prey at a fairly small size (Persson, Greenberg 1990a, 1990b). The time of the known shift to benthivory also depends on the relative abundance of benthic macroinvertebrates and zooplankton (Persson, Greenberg 1990b) as well as on the presence of superior competitors for benthic prey, like ruffe and/or older conspecifics (Bergman, Greenberg 1994). Generally, the growth rate of juvenile perch is higher if large cladocerans are available (e.g., Mehner *et al.* 1995; Romare 2000). Thus, an early shift towards benthic food may reflect unfavourable conditions for perch (Persson 1986; Byström *et al.* 1998). The finding that YOY perch released from competition with roach continued to feed on zooplankton through the autumn may support this hypothesis (Persson 1986). However, our observation that YOY perch of a size typical for the zooplanktivorous stage and feeding on zooplankton were smaller than those eating benthic prey demonstrates the unpredictability of foraging behaviour. Actual foraging patterns seem to depend on subtle differences in prey availability and in the overall biotic background.

This research and our previous studies (Wojtal *et al.* 2003) have demonstrated that different fractions of the YOY perch specialise on different food resources on a small spatial scale. This finding is in agreement with the conclusions of Quevedo, Olsson (2006) that large variations in the isotope composition of perch individuals caught in the littoral zone of a mesotrophic lake must result from enduring utilisation of different prey categories at the microhabitat scale.

It should be emphasized that our conclusions about differences between the stomach contents of trapped and seined perch are rather conservative. It is not unlikely that some YOY perch from the "zooplanktivorous fraction" were also caught during beach seining.

Perch foraging in littoral areas face competition with two species of superior competitors. Juvenile roach are superior competitors for zooplankton (e.g. Persson 1987), and ruffe are superior competitors for benthic prey (Bergman, Greenberg 1994; Schleuter, Eckmann 2006). In years of high juvenile perch density, intraspecific competition may also have strong influence on the feeding behaviour of the perch (Persson, Greenberg 1990a; Svanbäck, Persson 2004). Such circumstances may lead to many possible responses that can serve to diminish inter- and intraspecific competition. One such response is the spatial segregation of juvenile perch between littoral and pelagic zone, a phenomenon that has been frequently reported (e.g. Post *et al.* 1997; Hjelm *et al.* 2001).

Another possible response to such competition is the performance of diurnal migrations between these two zones (e.g. Gliwicz, Jachner 1992). Because the numbers of fish entering traps from the open water and from the bank did not differ, it is unlikely that the differences in stomach contents observed in our studies resulted from the diurnal migration of YOY perch. Moreover, assuming that zooplanktivorous perch were feeding in the pelagic zone during the day and stayed in the littoral during the night, they should not be trapped with recently eaten (undigested) zooplankton in the morning in the littoral zone. By analogy, if these fish stayed in the pelagic zone during the night, fed there at dusk and dawn and hid in the littoral during the day, they would not be caught at night with their stomachs full of zooplankton. Therefore, trapped fish more likely represented the fraction of perch permanently foraging on zooplankton above the bottom and entering traps by chance.

Overall, our data show that individual-based perch foraging decisions do in fact result in food niche diversification at a low spatial scale inside the littoral zone, at least at high YOY densities.

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