Alternative use of food resources causesintra-cohort variation in the size distribution ofyoung-of-the-year perch (Perca fluviatilis)

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Alternative use of food resources causes intra-cohort variation in the size distribution of young-of-the-year perch (*Perca fluviatilis*)

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Abstract – Body sizes of young-of-the-year (YOY) perch (*Perca fluviatilis*) at the end of their first summer are extremely variable and range in different studies between 4 and 15 cm. To analyse whether size divergences in YOY perch may be attributed to alternative use of food resources, adult perch were stocked into two previously fishless ponds and growth, size distribution and food intake of the YOY perch were recorded. In addition to perch, adult bream (*Abramis brama*) were introduced to produce juvenile bream that could serve as a food resource for YOY perch. The body sizes of YOY perch at the end of the experiment ranged from 32 to 168 mm with a bimodal size distribution. The combination of stomach content analyses and stable isotope signatures revealed that the small size cohort were planctivorous/benthivorous while the large size cohort was piscivorous/cannibalistic. Results implicated that different feeding behaviour contributed to the size divergences in YOY perch and that the extreme growth of the large size cohort was induced by piscivory.

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Key words: *Perca fluviatilis;* bimodal length-frequency-distribution; growth; early piscivory; stable isotope analysis

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Introduction

Individual growth is an important factor in the early life of fish determining their actual body size and therewith the potential to use certain food resources, the vulnerability to predators and the storage of energy in lipid reserves (Persson et al. 2004). Obtaining a size advantage may occur through a number of routes, and competition (Staffan et al. 2005), density-dependent growth (Byström & Garcia-Berthou 1999) or ontogenetic diet shifts (Persson & Greenberg 1990; Olson 1996) influence growth rates of individual fish, leading to the occurrence of size divergence within age cohorts. In many freshwater fishes, variation in body sizes within the young-of-the-year (YOY) cohort is typically driven by ontogenetic diet shifts (Persson & Brönmark 2002; Galarowicz & Wahl 2005). For a variety of reasons, the largest members of a cohort are often able to shift diets seasonally from invertebrates to fish whereas smaller individuals cannot make this shift (Van Densen et al. 1996; Mittelbach & Persson 1998; Frankiewicz et al. 1999). Because fish are an energetically profitable prey item, the larger individuals may enjoy increased growth rates over smaller individuals (Buijse & Houthuijzen 1992; Borcherding et al. 2000, 2007).

Perch (*Perca fluviatilis*) is a food generalist which undergoes ontogenetic diet shifts. They first feed on zooplankton, and switch to macrozoobenthos (Hartmann 1983; Berezina & Strel'nikova 2001) and/or fish prey (Thorpe 1977; Hjelm et al. 2000; Beeck et al. 2002) thereafter. These functional niches developing during ontogeny set constraints on the morphology and size-specific growth of perch (Hjelm et al. 2000; Olsson et al. 2006; Heermann et al. 2007). Body sizes of YOY perch at the end of their first summer are extremely variable and range between 4 and 15 cm (Thorpe 1977; Houthuijzen et al. 1993; Beeck et al. 2002; Borcherding et al. 2007). Differences in YOY body size are attributed to different productivity of lake systems, prey availability or the occasional onset of piscivory feeding in YOY perch. However, as in other freshwater piscivores, surprisingly little information is available on size-specific diets and growth rates during early life history (Mittelbach & Persson 1998).

In the present study, the growth of YOY perch and the development of size variation within the YOY cohort were experimentally examined in relation to their consumed food resources in their first year of life. Adult perch and bream (*Abramis brama*) were stocked into fishless ponds in spring to produce YOY fish of both species, and recovered at the end of the growing season. Bream was chosen as potential prey fish for perch mimicking the situation in lakes from the area of lower Rhine in Germany (Beeck et al. 2002). The growth, size distribution and food intake of the YOY perch were recorded in order to gain more information on body size variation among YOY fish in relation to their use of food resources. Stomach content analyses indicated the short-term feeding behaviour while stable isotope signatures reflected the long-term feeding behaviour of the juvenile fish.

Materials and methods

Experimental design

The study was conducted in two experimental ponds (Pilgram fish farm, Lohmar) that were previously empty of fish, lay dry during wintertime and were filled in spring. On 20 March 2001, adult perch and bream were stocked into these ponds in similar weight considering differences in the area of the ponds (pond A: 0.4 ha, 11.8 kg·ha^{-1} perch, 12 n; 79.0 kg·ha^{-1} bream, 31 n; pond B: 0.6 ha, 10.3 kg·ha^{-1} perch, 30 n; 75.3 kg·ha^{-1} bream, 40 n). The stocked fish remained in the ponds until the end of the experiment. About 50% of adult perch and about 85% of adult bream were recovered by the fish extraction at the end of the experiment. The total length (TL) of adult perch was 25.5 ± 4.5 cm at stocking and 30.9 ± 2.7 cm at the fish extraction while bream were 45.2 ± 3.5 cm and 48.2 ± 2.5 cm, respectively. The aim of the stocking scheme was to achieve a ratio of 1:10 of YOY perch to YOY bream after 14 days, which should mimic the natural competitive relationship in lakes from that area. This ratio depended on the number of eggs produced per kilogram of female fish and the survival rate of the hatched larvae in their first 14 days (for perch: Thorpe 1977; for bream: Kucharczyk et al. 1997). About 35,000 perch larvae and 350,000 bream larvae per hectare were expected in each of the ponds. No differences in water chemistry or food availability of zooplankton and macrozoobenthos were observed between the two ponds during the sampling season (for details: see Supporting data Tables S1 and S2).

Fish sampling

From the beginning of May until the beginning of July, the fish larvae and juveniles were caught once a week and from then on every 4 weeks until the end of the experiments in September. Five different standard methods were applied: (1) larvae nets of different sizes (34 or 40 cm^2 diameter, 1 mm mesh size), (2) a bongo net (42 cm diameter, 500 μm mesh size, 1.7 m length), (3) point abundance sampling by electrofishing carried out with portable electrofishing equipment (DEKA 3000 Lord) using a small ring anode (10 cm diameter), (4) a beach seine (1 mm mesh size, 10 m length) and (5) a pop-up net (2 mm mesh size, area 50 × 100 cm). The methods 1 and 2 were used for the earlier sample occasions while the others were used from then on. All sampled YOY fish were preserved in 4% formaldehyde solution. At the end of the experiments, the ponds were drained between September 25th and 28th 2001 by attaching a box (4 mm mesh size) to the drainage pipe. This allowed us to catch all fish and to measure subsamples to determine the length-frequency distribution (total length, [mm]). Individuals of YOY perch from the small and large size class were preserved in 4% formaldehyde for analysis of the stomach content or were frozen for stable isotopes analysis. Growth rates (mm day^{-1}) for the small and large sized YOY perch were calculated as the difference of means in TL at their first appearance and at the end of the experiment.

Stomach content analysis

Stomach contents of 10 randomly selected YOY perch were analysed biweekly if available. The gut content was identified to species or genus level and at least 10 randomly selected individuals of each prey were measured. Biomasses were calculated as wet weight using length-weight regressions (Bottrell et al. 1976; Mehner et al. 1995).

Stable isotope analysis

At the end of the experiments, individuals of the small and large-sized YOY perch from both ponds were taken for stable isotope analysis. 20 samples of muscle tissue of frozen perch were prepared from each size class, dried over night at 60 °C, freeze-dried with fluid nitrogen and homogenised with a mortar. These samples were analysed for stable nitrogen ratios using an Elemental Analyzer (Carlo Erba NA 1500) with an interface (Conflo III) connected to a mass spectrometer (DeltaPlus Thermo Finnigan). Stable isotope data are presented as the difference between ratios of the samples to a standard ($\delta = {}^{15}N/{}^{14}N$), expressed as units per mil (‰). As a standard for $\delta^{15}N$, ammonium sulphate IAEA-N-2 ($\delta = 20.3$) was used.

Results

Perch and bream larvae first appeared in mid-May. However, the total amount of fish caught before the drainage of the ponds in September was small, despite the use of a variety of sampling methods. 281 perch and 19 bream were caught in pond A at 10 sampling occasions during the season while 1100 perch and 45 bream were caught in pond B (for details: see Supporting data Table S3). The size distribution of YOY perch was unimodal during the sampling season in both ponds and YOY perch grew from about 15 mm in May to about 30 mm at the end of July. At the end of the experiments, the fish extraction revealed a high abundance of YOY perch with 17,000 perch in pond A and 30,000 perch in pond B, which is about 51% and 69% of the calculated numbers 14 days after hatching, respectively. The size distribution of the YOY perch was exceptionally wide, with sizes ranging from 32 mm up to 168 mm TL (Fig. 1). Two size classes of YOY perch were defined: small (< 100 mm TL), and large (>100 mm TL). The share of individuals of the large size class was 11% for pond A and 10% for pond B. In terms of biomass, however, the large-sized YOY perch contributed from 86% (pond A) to 62% (pond B). The mean growth rate during the experimental period for the YOY perch from the small size class was 0.35 mm·day^{-1}, while it was 0.85 mm·day^{-1} for the large size class. Only a few YOY bream were caught in ponds A and B (56 bream in pond A, 71 bream in pond B); their size distributions were unimodal with a mean of 109 mm TL (SD ± 5 mm) for pond A and 121 mm TL (SD ± 4 mm) for pond B.

Stomach content analysis

The diet composition of perch caught from May to September was investigated for 165 perch (pond A: $n = 75$; pond B: $n = 90$, Fig. 2). Zooplankton was the dominant prey category in May and the beginning of June, including especially *Daphnia* cf. *galeata* and copepods. Afterwards, zooplankton was found less abundantly in the stomachs of YOY perch, whereas the intake of macrozoobenthos steadily increased. The two size classes of YOY perch at the end of the experiments differed in their feeding behaviour. While the large sized YOY perch were cannibalistic, the small-sized YOY perch were planktivorous and benthivorous (Fig. 2).

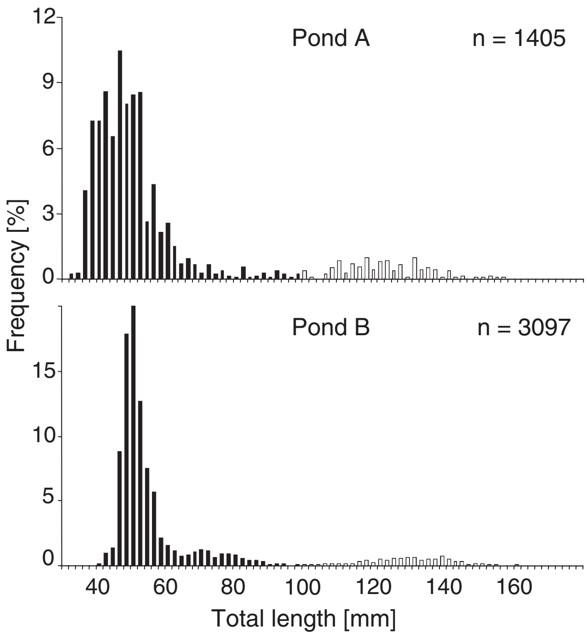

Fig. 1. Length-frequency distribution of YOY perch in ponds A and B at the end of the experiments (fish extraction, September 25th to 28th); n is the number of measured YOY perch. The black columns represent individuals of the small size class and the white columns individuals of the large size class.

Stable isotope analysis

Individuals of the small- and large-sized YOY perch from pond A and B at the end of the experiments differed in terms of their $\delta^{15}N$ signatures (Fig. 3). The large-sized YOY perch had significantly higher $\delta^{15}N$-values than the small-sized (*t*-test, $P < 0.001$) and the difference between the $\delta^{15}N$ values of the small and large size class was about 2‰.

Discussion

A bimodal size distribution of YOY perch was observed in both ponds at the end of the experiment (Fig. 1). About 10% of the YOY perch belonged to the large size class and contributed to at least 62% of the biomass, while the majority of YOY perch belonged to the small size class. In previous studies, TLs of 4–

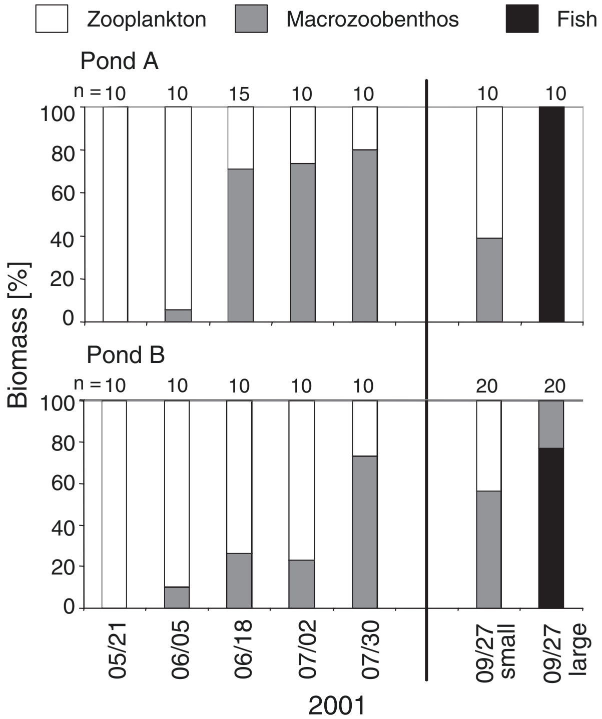

Fig. 2. Stomach content analysis of YOY perch from pond A and B from May to the end of the experiments in September 2001; n is the number of examined stomachs.

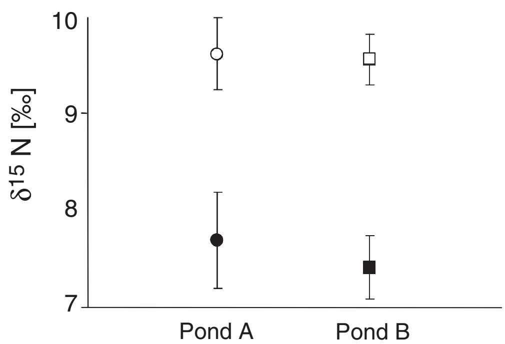

Fig. 3. Stable isotope analysis (mean δ^{15}N signatures ± SD from 20 individuals per size class) of the small and large sized YOY perch from pond A and B at the end of the experiments (fish extraction, September 25th to 28th). Black symbols represent the small size class, white symbols the large size class.

8 cm were regularly found for YOY perch at the end of their first year of life (Thorpe 1977; Radke & Eckmann 1999; Persson et al. 2000). Only few studies observed extreme growth of YOY perch up to 15 cm, e.g., a study of YOY perch feeding on *Neomysis integer* (Houthuijzen et al. 1993; Van Densen et al. 1996), feeding on bream larvae (Beeck et al. 2002), or feeding on a diet mixture of fish larvae and mysids (Borcherding et al. 2007). Although no age estimation of the YOY perch was conducted in the present study, it was evident that they were in their first summer since experimental ponds were fishless before the study and YOY perch were significantly lower in size compared to the stocked adult perch.

From other fish species (e.g., pikeperch, *Sander lucioperca*) it is well known that a bimodal size distribution can be induced by the onset of piscivory in some individuals of YOY that resulted in different growth rates (Van Densen et al. 1996; Frankiewicz et al. 1999). For analysing whether size divergences in the YOY perch were caused by an alternative use of food resources, stomach contents and stable isotopes signatures were investigated. While stomach content analyses reveal information about the short-term feeding behaviour of organisms, naturally occurring stable isotopes provide information about the long-term feeding behaviour (Beaudoin et al. 1999) and, thus, reveal features of the food web that otherwise would not be detectable. δ^{15}N is accumulated while ascending the food web, revealing the trophic position of an organism in the food web from phytoplankton to piscivorous fish (Pinnegar & Polunin 2000). In the present study, the size classes of YOY perch differed significantly in their δ^{15}N signatures with a difference of about 2‰. Differences of 3.4‰ are normally seen between two trophic levels (Vander Zanden et al. 1997; Gaye-Siessegger et al. 2004) and reflect the different position in the food web. Therefore, stable isotope data suggested that large-sized individuals of YOY perch had used food resources of a higher trophic level than individuals of the small-sized YOY perch.

The analyses of stomach contents at the end of the experiment showed a different short-term feeding behaviour of the two size classes. At this time, the large-sized YOY perch were mainly cannibalistic while the small-sized YOY perch were planktivorous or benthivorous. Cannibalism in percids occurs frequently (Claessen et al. 2000; Persson et al. 2000, 2006;) and can start at a size of 10.5 mm TL (Brabrand 1995). Cannibalism may serve as an additional food resource for the large size class of YOY perch and may have contributed to their extreme growth, a phenomenon also described for YOY pikeperch (Frankiewicz et al. 1999). The catches during the experimental period were restricted solely to the small size class of YOY perch and therefore for this period no data were available for the large size class. The stomach content analyses of individuals of the small-sized YOY perch demonstrated a switch from zooplanktivorous to zoobenthivorous feeding during the season. Combining the results of the stomach content analyses and of stable isotope signatures, however, data provide good evidence that size differences in YOY perch might be induced by the use of different food resources. Samples taken during the experimental season did not indicate a piscivorous feeding of YOY perch on

YOY bream, which is attributed to the fact that only the small size class was caught during the experimental season. From our studies in gravel pit lakes (Beeck et al. 2002) as well as recent studies in the same fish ponds (Heermann & Borcherding, unpublished data) we know quite well that YOY perch begin to prey on bream larvae from a size of about 28 mm TL onwards, and that large numbers of bream are then eaten within a few weeks only. Therefore, we assume a potential predation of YOY perch on YOY bream also in the present study.

In addition to an alternative use of food resources, other factors might have initiated the occurrence of size differences in YOY perch. (1) A different timing of hatching could enable cannibalism by perch larvae on their smaller siblings, resulting in a bimodal size distribution (Brabrand 1995). (2) Individual variations in the growth rates of juvenile fish: the differences in growth rates are increased by intense competition for food resources, resulting in growth retardation among the weaker competitors, while the fitter individuals are only slightly influenced by their competitors (Staffan et al. 2005). (3) Patchy prey distribution: this may have caused random effects that enabled some juveniles to forage on better prey from a bioenergetic point of view. Individual foraging behaviour and specialisation could have the same effect (Bolnick et al. 2003). Moreover, adult perch remained in the ponds until the end of the experiments and could potentially affect the size distribution of YOY perch by size-dependent predation. Maybe the foraging success was higher on a certain size class of the YOY perch (Lundvall et al. 1999), affecting individual boldness and by that competition for food (Westerberg et al. 2004; Magnhagen & Borcherding 2007).

In summary, the stocking of adult perch and bream in previous fishless ponds resulted in intra-cohort variation in the growth of YOY perch with a broad size distribution ranging from 32 to 168 mm. The combination of stomach content analyses and stable isotopes signatures provide evidence that size divergence in the YOY perch were caused by the alternative use of food resources. It is assumed that these flexible diet shifts in early ontogeny together with fast growth and the development of a bimodal size distribution represent a more general characteristic, which may be valid also for other aquatic ecosystems. Results further implicate that age determination of YOY perch might be a necessary analysis in field studies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Chemical characteristics of Pond A and Pond B. Data are presented as [mean (min/max)] between May and September 2001.

Table S2. Biomass of macrozoobenthos [g wet weight m^{-2}] and zooplankton (μg wet weight L^{-1}), mean values between May and September 2001. Zooplankton has been analysed biweekly, macrozoobenthos once a month.

Table S3. Sampling success for YOY perch and YOY bream from May to September 2001. The number of perch and bream [n] and their mean TL [mm] is given.

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