

WHO MAKES THE BEST OF IT?
**Alternative feeding strategies of European
perch (*Perca fluviatilis*) and their consequences**

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'Naturwissenschaftler sammeln zunächst nur Einzelheiten.
Wenn sie genug Einzelheiten haben, machen sie Tatsachen daraus.
Wenn sie genug Tatsachen haben, bringen sie sie in ein System.
Wenn sie genug Systeme haben,
lassen sie das Ganze sein und fangen wieder von vorne an'

Erwin Chargaff (Biochemiker, 1905-2002)

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INTRODUCTION

Individual specialisation has frequently been ignored mostly because it was considered to occur rarely or to have minor impact on ecological processes (Patterson 1983; Taper & Case 1985). Thus, niche theory was often used to describe the ecology of a whole species, rather than taking into account the fact that individuals of the same species might forage on different resources (e.g. Feinsinger et al. 1981; Linton et al. 1981). The optimal diet theory (Pulliam 1974; Werner & Hall 1974) explains why individuals do not use the whole range of profitable food resources even if these are available. To maximise fitness, individuals select a particular diet which is determined by the energy content of alternative prey, encounter rates, and how effective the forager is at detecting, capturing, handling and digesting the prey. Following this hypothesis it seems to be quite obvious that in conjunction with different phenotypes, individual specialisation frequently occurs (Svanbäck & Bolnick 2005). One of the first to refer to individual specialisation to explain the forces that create and maintain phenotypic variation within natural populations was Van Valen (1965) with his niche variation hypothesis. Van Valen stated that niche width broadens in the absence of interspecific competition. Expanded niche width can either be explained by all individuals using a broader food spectrum, or by increased specialisation. Then each individual has a narrow individual niche width, but the resource overlap between conspecifics remains small. Thus intraspecific competition is minimised.

Recently the latter explanation of broadened niche widths was confirmed for several species by Bolnick et al. (2007), who found that more generalised populations also tend to be more ecologically heterogeneous. Svanbäck and Bolnick (2007) showed that resource competition promotes niche variation within populations and presented experimental evidence confirming that competition drives ecological diversification within natural populations. Three-spined sticklebacks (*Gasterosteus aculeatus*) started to add alternative prey types to their diet when the population density in enclosures was increased and hence, the competition for available resources was high. Since phenotypically different individuals added different alternative prey, the specialisation of the population also increased. Resource competition can modify the degree of individual specialization in several ways, explained with a model of Svanbäck and Bolnick (2005). They assume that individuals have a first-choice prey, second-choice prey, etc. Depending on the phenotype (influencing for example handling times, attack rate) individuals start adding the next ranked resource at

different times. If all individuals have identically ranked preferences for all resources, the specialisation is high when the population density - and hence intraspecific competition - is low. With increasing densities the specialisation also increases, although all fish have the same lower-ranked resources. But due to the fact that some phenotypes switch later than others, the diet variability increases. If individuals share some of their top-ranked resources but have different rankings for less preferred resources, the same pattern of the specialisation development as in the first scenario is observed. First specialisation is low, but it then increases with increasing population density. However, at medium densities the specialisation is much higher than in scenario one. If individuals have different first-choice preferences and their lower ranked resources also differ, the specialisation is highest at low densities. With increasing densities the specialisation might decrease slightly, due to casual overlap of diet when some phenotypes have switched to the next ranked resource. True for all three scenarios is the fact that, at high population densities individuals become generalists and the specialisation is low or not existing.

One form of specialisation of perch (*Perca fluviatilis*) was shown to be early piscivory. Usually perch is known to perform two ontogenetic niche shifts during its development, first preying on zooplankton, later changing to macroinvertebrates and finally becoming piscivorous at a length of about 150 mm (Thorpe 1977; Persson & Greenberg 1990; Byström et al. 1998), a size which perch usually reach after 2 to 3 years. These niche shifts are accompanied by a habitat shift from the pelagic, where perch feed on zooplankton, to the littoral where perch become benthivorous (e.g. Persson 1993). However, several studies have shown that perch can also switch to piscivory during their first months of life (Borcherding et al. 2000; Beeck et al. 2002; Borcherding 2006). Brabrand (1995) even found early piscivory at a length of 10.5 mm. The consumption of the alternative high-energy food resource fish leads to increased growth rates of about 1.2 mm day^{-1} (Borcherding et al. 2000); hence piscivorous fish soon exceed their planktivorous siblings in length. Beeck et al. (2002) presented a study in which young-of-the-year (YOY) perch developed into a slow-growing and a fast-growing size-cohort. Stomach content analyses revealed that the small, slow-growing size-cohort fed predominantly on zooplankton, whereas the large, fast-growing cohort was piscivorous, preying on bream larvae during early summer (Beeck et al. 2002). Thus, the typical observed switch from zooplanktivory

to benthivory and then from benthivory to piscivory was displaced by an alternative diet shift from zooplanktivory directly to piscivory.

Based among other things on these findings, Borcharding et al. (in prep.) developed a model to answer the question of why only a part of the perch population is able to prey on bream larvae and to grow extremely fast. They showed that perch shift habitats with a certain length which was marginally variable over the years. With the switch to the littoral, specialisation increased as perch started - each in its own individual fashion - to add new prey items to its diet, including bream larvae. If perch hatched several days before bream, the whole age cohort of YOY perch was able to prey on bream and the size differences between individuals stayed small. Marginal differences of perch length were also observed if bream hatched much earlier than perch and no predation occurred, due to the fact that bream were already too large for gape-size limited perch. But in between the total match and the mismatch situation, only the largest perch were able to feed on bream when arriving in the littoral, leading to increased size differences and the development of a bimodal size distribution. Additionally the amount of bream available was a key factor. Small perch could only reach large sizes when the mean consumption exceeded about 3.5 bream per perch per day. Large perch mostly benefited from predation on bream at consumption rates of a maximum of one bream per perch per day and did not increase further in size with a further increase of the mean consumption rate. Hence, size differences between small-sized and large-sized perch are most distinct at a consumption rate of two bream per perch per day (Borcharding et al. in prep.). If via early piscivory size differences become large enough, intraguild cannibalism will soon occur (Urbatzka et al. 2008).

Intraguild cannibalism has been shown in a few studies on perch to contribute to the development of two size-cohorts (e.g. Brabrand 1995; Urbatzka et al. 2008). However most of the studies on cannibalism focused on interguild cannibalism (e.g. Claessen et al. 2000; Persson & De Roos 2006). Cannibals were often shown to share a resource with their victims, which means that not only predator-prey interactions, but also intraspecific competition (Claessen et al. 2000; 2002) may affect interactions with their prey. Cannibals derive direct energetic benefit from cannibalism by feeding on their conspecifics, while at the same time reducing competition for shared resources (Claessen et al. 2000; 2002; Byström 2006). Recent studies have focused on the combined effects of intraspecific competition and cannibalism, showing that

large individuals, so-called “giants”, can develop under certain conditions (Persson et al. 2000; 2004; Byström 2006). If animals start to feed on their YOY siblings early in the year, when these are still relatively small, these cannibals are able to control the number of their smaller siblings and thus diminish intraspecific competition for the shared resource. However, the lower energetic value of small fish means that the cannibals do not develop into giants. If they become cannibalistic later in the year, when their YOY siblings have reached larger sizes, they derive greater energetic benefit from their cannibalism. In this situation, however, cannibals are not able to control their siblings and reduce the intraspecific competition for the shared resource. Thus, they take the risk of being outcompeted by their smaller siblings, but are able to reach high growth rates due to the high energy uptake when feeding on large siblings. Hence, only a few individuals become giants (Claessen et al. 2000). Empirical evidence for these suggestions was found in Arctic char (*Salvelinus alpinus*) populations, where within a strong recruit cohort, some individuals avoided competition when they started to cannibalise. These individuals accelerated their growth and developed into giants (Byström 2006).

The development of so-called giants brings several advantages for the large fish. In studies on early piscivory of perch and the development of the bimodality within the YOY age cohort Beeck et al. (2002) documented that male perch of the larger size-cohort were already mature after the first winter. Thus they probably contribute considerably to the gene pool of the next perch generation. Other advantages for the larger perch compared to the small perch resulting from the establishment of a stable bimodality might be higher energy reserves in autumn and less winter mortality. Energy reserves of fishes are positively correlated to size (Brett & Groves 1979; Thompson et al. 1991; Schultz & Conover 1997; Sogard & Olla 2000; Huss et al., in press). Thus, the smaller the fish the sooner its energy reserves will become depleted, resulting in size-related mortality rates, which is also described in many other studies on winter mortality (Post & Evans 1989; Post et al. 1998; Lappalainen et al. 2000; Biro et al. 2004; Byström et al. 2006).

This study should bring insights into the mechanism, i.e. the specialisation on alternative food resources leading to intra-guild cannibalism and the establishment of a bimodal size distribution of the YOY perch population (Huston & DeAngelis 1987). With high levels of competition for the preferred food resource, some perch might specialise on alternative food resources to avoid competition. These

individuals might be favoured in terms of growth if they specialise on a higher-energy resource than their conspecifics. This growth acceleration might then enable cannibalism, producing a few large individuals (giants). To test these hypotheses, four experimental ponds were stocked with either adult perch or a combination of adult perch and bream (*Abramis brama*). The offspring and the abundance of food resources were monitored to examine the mechanisms behind the development of early piscivory and intra-guild cannibalism.

The establishment of a bimodal size distribution due to early piscivory and cannibalism might bring several advantages for the large size-cohort, especially with the first winter acting as a bottleneck for the recruitment success of YOY perch. Size-dependent relationships of energy storage and depletion may affect the survival of perch during winter, suggesting that lower depletion rates of the energy reserves in larger individuals lead to higher mortality rates and lower recruitment of smaller individuals to the adult population. This study focused on size-dependent mortality rates and on the effects of temperature on winter mortality in fish. Over two winters the energy reserves and mortality of two size classes of YOY perch were studied in pond experiments. The first experiments were performed in 2005/06, when the temperature was relatively low and comparable with the average winter temperature of the last few decades. The second set of field experiments were carried out during the winter of 2006/07, when the temperature exceeded average temperatures. To support the field data, additional laboratory experiments were conducted, in which YOY perch were starved or fed different amounts of food. Thus data on mortality rates, the usage of energy stores (glycogen, fat, protein) and the influence of food supply during winter could be obtained.

Furthermore this study should clarify whether the same mechanism that causes the development of two size-cohorts, via early specialisation of perch on bream larvae and cannibalism, also applies when other prey fish are available instead of bream. Therefore, in experimental ponds the growth and development of YOY perch was monitored in the presence and absence of bream and roach respectively. First suggestions about the influence of early piscivory and cannibalism on the population dynamics are given.

The specialisation on alternative food resources was shown on the one hand to be dependent on the phenotype of the fish, since the ability to catch and handle food items related to the phenotype of the predator causes fish to specialise on different

resources. On the other hand the use of different prey types might lead to morphological adaptations to the food resource preyed on. Hence, the two size-cohorts developing in cannibalistic systems might not only differ in size but also in morphological traits. Field data (Beeck et al. 2002) were analysed to get hints on distinct phenotypical differences between the two size-cohorts. However, although stomach content analyses revealed that the large cohort was at least temporarily piscivorous while the small cohort fed on zooplankton, it was not possible to rule out the possibility that other food resources were used as well (Beeck et al., 2002). Therefore in a second step, mesocosm experiments were performed in which YOY year perch were fed with either zooplankton or with fish for 40 days. This part of the study was designed to help reveal the extent of morphological variation due to the consumption of different food resources.

All field studies on the development of a population crucially depend on the success of catching representative fish samples to draw a reliable picture of the population. The capture success of each fishing method depends on factors such as activity of the fish, abundance or the habitat the method is used in. Especially in cases of bimodality with different behaviour of the two size-cohorts (feeding, activity, habitat use) extreme differences in the length-frequency distribution of perch sampled using different methods were expected. In the shallow experimental ponds in a parallel sampling design the capture success of electrofishing and gillnetting with multi-mesh gillnets was examined. To obtain additional information on the sampling of YOY perch in larger and deeper waters, three different gravel pit lakes were studied, employing both methods. For development of perch larvae in the pelagic zone after hatching, bongo-net fishing was used in spring as a third standard method. The methodological comparison should help to draw conclusions on how to improve fish stock assessment.

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CHAPTER I

Making the best of it: how the necessity to use alternative food resources induces cannibalism

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Abstract

Cannibalism in fish has various effects at population as well as at individual level. Cannibals derive direct energetic benefit from cannibalism by feeding on their smaller conspecifics, while at the same time reducing competition for the shared resource. Avoiding intra-cohort competition can force fish to use alternative feeding strategies and hence leads to greater specialisation within the population, which may subsequently stimulate cannibalism. The present study examined specialisation and intra-guild cannibalism by young-of-the-year (YOY) perch (*Perca fluviatilis*) after hatching in four experimental ponds. As zooplankton levels decreased, YOY perch started to specialise, suggesting that increased intraspecific competition forced fish to try alternative feeding strategies. Larger YOY perch then fed on energetically richer resources (bream larvae and tadpoles) and hence outgrew their smaller conspecifics, becoming large enough to enable cannibalism. Thus, the widening of initial size differences by feeding on bream and tadpoles served as a stepping stone towards cannibalism. This differentiation into two size classes and two different feeding strategies was shown to be a stable pattern within the YOY perch population, as indicated by stable isotope analyses.

Introduction

Cannibalism occurs in a wide range of animals (Polis 1981) and has also been shown to occur in many fish species, such as pikeperch (*Sander lucioperca*) (Lappalainen et al. 2006) and Arctic char (*Salvelinus alpinus*) (Byström 2006). Most of the studies focused on interguild cannibalism (Claessen et al. 2000; Persson & De Roos 2006), although intraguild cannibalism has been documented as well (Brabrand 1995; Urbatzka et al. 2008). Cannibalism has various effects at the population as well as individual levels. Cannibalistic populations might exist where a non-cannibalistic population would go extinct (see "life boat mechanism": Vandenbosch et al. 1988) and the existing population size distribution might be affected by cannibals (Claessen et al. 2000; 2002). Cannibals were often shown to share a resource with their victims, which means that not only predator-prey interactions, but also intraspecific competition (Claessen et al. 2000; 2002) may affect interactions with their prey. Cannibals derive direct energetic benefit from cannibalism by feeding on their conspecifics while at the same time reducing competition for shared resources (Claessen et al. 2000; 2002; Byström 2006). Recent studies have focused on the combined effects of intraspecific competition and cannibalism, showing that large individuals, so-called "giants", can develop under certain conditions (Persson et al. 2000; 2004; Byström 2006).

If animals start to feed on their young-of-the-year (YOY) siblings early in the year, when these are still relatively small, these cannibals are able to control the number of their smaller siblings and thus diminish intraspecific competition for the shared resource. However, the lower energetic value of small fish means that the cannibals do not develop into giants. If they become cannibalistic later in the year, when their YOY siblings have reached larger sizes, they derive greater energetic benefit from their cannibalism. In this situation, however, cannibals are not able to control their siblings and reduce the intraspecific competition for the shared resource. Thus, they take the risk of being outcompeted by their smaller siblings, but are able to reach high growth rates due to the high energy uptake when feeding on large siblings. Hence, only a few individuals become giants (Claessen et al. 2000). Empirical evidence for these suggestions was found in Arctic char populations, where within a strong recruit cohort, some individuals escaped competition when they started to

cannibalise. These individuals accelerated their growth and developed into giants (Byström 2006).

Intra-cohort competition might not only enhance cannibalism but might also lead to greater specialisation within the population (Bolnick 2001), since individual diet specialisation has been shown to reduce intraspecific competition (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007). Niche differentiation is related to a number of factors, such as ontogenetic niche shifts (Werner & Gilliam 1984), polymorphisms (Skúlason & Smith 1995) and individual-level variation (Bolnick et al. 2003).

In this study we focused on specialisation and intra-guild cannibalism by young-of-the-year (YOY) perch (*Perca fluviatilis*). If high competition for the preferred resource leads to individual diet specialisation, some individuals might be favoured in terms of growth due to the fact that they specialise on a more energetic resource. This growth acceleration might then enable cannibalism, producing a few large individuals (giants). To test these hypotheses, four experimental ponds were stocked with either adult perch or a combination of adult perch and bream (*Abramis brama*). The offspring and the abundance of food resources were monitored to examine the mechanisms behind the development of early piscivory and intra-guild cannibalism.

Materials & Methods

Experimental set-up

Field experiments were conducted in four ponds laid out in a single line, indicated in the paper as P1, P2, P3 and P4, and connected via overflows (0.4 – 0.7 ha) at a fish farm in Lohmar, Germany (50°49'34.00''N 7°12'59.42). To prevent fish from passing from one pond to the next, the overflows were blocked by nets. The ponds have a maximum depth of 2 m. The water is oligotrophic to mesotrophic with a submerged helophyte and nymphaeid macrophyte vegetation (Urbatzka et al. 2008). Since these ponds have a relatively flat and shallow bottom, no clear differentiation exists between a littoral and a pelagic zone. The ponds were fishless before they were stocked with adult perch and bream in April 2006. All ponds were stocked with 12 to 17 kg perch ha⁻¹ (25 to 36 individuals per pond). P3 and P4 were additionally stocked with adult bream (75 kg ha⁻¹ / 23 individuals in P3 and 82 kg ha⁻¹ / 32 individuals in P4). Before stocking, the length of each fish was documented. Total length (TL) of perch ranged from 19 to 33 cm and that of bream from 45 to 64 cm. In P1, a population of topmouth gudgeon (*Pseudorasbora parva*), an invasive exotic fish species, established, in addition to the perch, probably by introduction via a creek.

Sampling

Zooplankton and macroinvertebrates were sampled every two and four weeks, respectively. Within one hour during the daytime, six samples of zooplankton were taken at different representative spots in the pond, using a Schindler-Patallas trap (mesh size 100 µm) and preserved in ethanol 96%. Under the stereomicroscope, individuals were counted and identified to genus level. Ten randomly chosen individuals per sample were measured to the nearest 0.01 mm. Published length-mass equations (for further details see Heermann & Borchering 2006) were used to calculate the biomass (mg wet weight l⁻¹). Macroinvertebrates in the sediment were sampled with a Birge–Eckmann grab at three representative spots in the pond and sieved through a net of 1 mm mesh size. Macroinvertebrates living in the vegetation (submersed and emerged vegetation) were sampled with a dip net (mesh size 1 mm) at three spots distributed over the pond. To this end, the dip net was repeatedly moved along a 0.5 x 0.3 x 1 m section through representative parts of the vegetation near the shore (Heermann et al., unpublished data). Samples taken from the

vegetation and the pond sediment were preserved in ethanol 96%; numbers were counted and ten randomly chosen individuals per sample were measured to the nearest 0.1 mm. We determined the biomass from published length-mass equations as described above and expressed it as g wet weight m⁻² for the sediment samples and as catch per unit of effort (CPUE) [g section⁻¹] for the samples from the vegetation.

After the perch had hatched (at the beginning of May), the offspring was monitored first weekly, then biweekly from mid-June on using electro-fishing and gillnetting with multi-mesh-sized gillnets (for further details see Scharf et al., in press). In mid-October 2006, all fish were extracted from the ponds, all ponds being emptied completely to measure the total wet weight biomass of fish per pond. All fish were weighed before three to four subsamples (about 200 to 700 fish per sample) were taken to measure the fish (to the nearest 0.5 mm), in order to obtain a length-frequency distribution (LFD). Length-weight regressions of these data and the total wet weight biomass of fish per pond were used to calculate the number of individuals per pond.

During the season, fish were deep-frozen immediately after catching for stomach content analyses. Length (TL) (to the nearest 0.5 mm) and wet weight (to the nearest 0.01 g) were recorded and the stomach content of 8 to 40 perch was analysed. To this end, perch were dissected under a stereomicroscope and the stomach was weighed full and empty using a high-precision balance to the nearest 0.01 mg. Stomach contents were identified to genus level, and the food spectrum of each perch was expressed as the weight percentage composition of food items identified to genus level. The diet items were counted per genus, and ten individuals per genus were measured. Published length-mass equations were again used to calculate the wet weight of the content. To detect early length-dependent differences in the use of food resources by perch, their stomach content was analysed separately for small and large perch at each sampling date. Perch smaller than the calculated mid-value (mean of the smallest and the largest individual) were assigned to the small size-cohort, while the others were assigned to the large size-cohort. Finally, the index of stomach fullness (Hyslop 1980) for each fish was calculated to describe the wet weight of the prey as a percentage of the perch's wet weight. The LFD of the perch population in each pond was used to calculate the 5% and 95% percentiles of the perchs' size distribution at each sampling date.

Stable isotope analysis

Additional fish, macroinvertebrate and zooplankton samples were taken and immediately deep-frozen for stable isotope analyses. Perch were sampled on 6th June, 20th July and 17th October, while bream larvae were sampled only in pond 4 on 6th June. Topmouth gudgeon larvae in P1 were sampled on 6th June. Macroinvertebrates were sampled on 22nd June, 30th July and 13th September in all ponds. Zooplankton samples with sufficient material for stable isotope analysis were taken on 6th June and 28th June in P1, on 6th June and 20th July in P2, on 28th August in P3 and on 20th July in P4.

Plankton samples were cleared of algae and non-zooplanktic organisms before pooling the six zooplankton samples from one pond. The six macroinvertebrate samples from one pond were treated in the same manner. Fish smaller than 40 mm were used whole, while fish from 41 to 80 mm were decapitated and gutted and the fins were removed, and only the muscle tissue was used from fish larger than 81 mm. When fish were very small, 2 to 3 fish from one sampling date had to be pooled to obtain enough material. Prey fish, bream larvae and topmouth gudgeon larvae were separately pooled in the same way. After drying at 70°C for 48 h, the fish, zooplankton and macroinvertebrates were ground to a fine powder using a mortar and pestle and liquid nitrogen. The stable carbon and nitrogen isotopes composition was assessed with a Carlo Erba NA 1500 elemental analyser and a Thermo Finnigan DeltaPlus mass spectrometer. Carbon and nitrogen isotopic ratios are expressed in delta notations ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), defined as the parts per thousand (‰) deviation from a reference material:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

IEAE-N-2, ammonium sulphate and IAEA-CH-6, sucrose served as reference materials. The standard deviation of replicates of the reference material was 0.6‰ for $\delta^{15}\text{N}$ and 1.4‰ for $\delta^{13}\text{C}$.

The trophic position of each perch and of the food resources was estimated according to the method developed by Vander Zanden & Rasmussen (1999), which involves first calculating a general baseline curve for the primary consumers. This then allows the measured $\delta^{15}\text{N}$ to be corrected and the trophic position to be calculated. In this study we focused on the zooplankton data representing the primary consumers, since the zooplankton included no predatory species.

Data analysis

The degree of specialisation of the perch population was calculated with DietA1 (Guimarães et al. 2006), which is based on niche pairwise overlap between individuals (Schoener 1968). An index of 1 reflects no inter-individual overlap within the population, while an index of 0 indicates that all individuals use the same resource (for further details see Bolnick et al. 2002). The index of specialisation (E) was then regressed with the mean biomass of zooplankton, the mean index of stomach fullness (ISF) and the size difference (5% percentile-95% percentile). One-way ANOVA was used to test for significant distinctions in the size difference of perch (based on the 5% and 95% percentiles) for each pond. We also used one-way ANOVA to test for differences in the index of specialisation (E) between the perch populations in the ponds. All analyses were performed with SPSS 15.0 (SPSS Corp.).

Results

At the beginning of June, zooplankton biomass greatly decreased in all ponds, to an average level (\pm SD) of about 0.64 ± 0.33 mg wet weight l^{-1} , and remained at low levels from then on in nearly all cases (Fig.1). It was not until a few weeks later, in mid-July, that the biomass of macroinvertebrates living in the vegetation also decreased, to an average (\pm S.D.) of 0.03 ± 0.01 g wet weight section $^{-1}$ (Fig. 1), except for P3, where the biomass had been low ever since the beginning of the season. After this decrease in most ponds, the macroinvertebrate biomass remained at a low level. Macroinvertebrates in the sediment did not show a clear general pattern in their biomass changes over time (Fig.1).

Figure 2 shows the LFD of YOY perch, YOY bream and topmouth gudgeon in the fish extracted from the ponds in mid-October. YOY perch in P3 and P4 had developed a bimodal size distribution. In P3, 1.7 % of the YOY perch individuals (25% of the YOY perch biomass in the pond) formed the large size-cohort (> 100 mm TL), growing to sizes of up to 165 mm. In P4, 2.5 % of the YOY perch individuals (28% of the YOY perch biomass) reached sizes of up to 185 mm TL. In P2, few perch (0.2% of the YOY perch individuals, 5% of the YOY perch biomass) grew to larger sizes, up to 140 mm TL. In P1, the YOY perch population remained unimodal, with lengths of YOY perch ranging from 50 to 90 mm TL (Fig. 2).

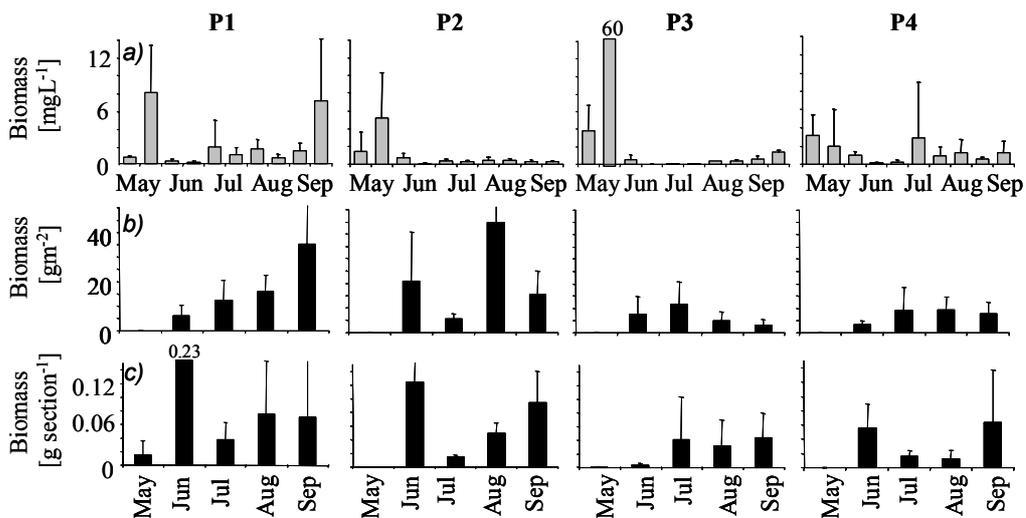


Figure 1: (a) Mean biomass of zooplankton [mg wet weight $l^{-1} \pm SD$] and macrozoobenthos (MZB) (b) sampled from the bottom [g wet weight $m^{-2} \pm SD$] and (c) caught in the vegetation [g wet weight section $^{-1} \pm SD$] at the beginning and in the middle of each month in all ponds.

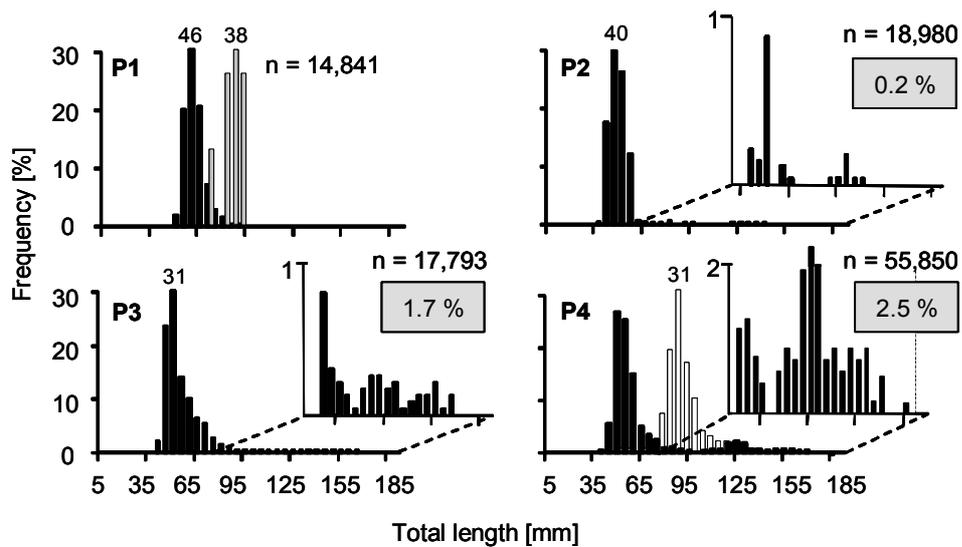


Figure 2: Length-frequency distribution of the fish extracted from all ponds in October 2006. black = YOY perch, grey = topmouth gudgeon, white = bream. Grey boxes show the percentage of large perch among the total number of individuals of perch per pond. In the right part of the graph, the x-axis is enlarged to illustrate more clearly the LFD of the large perch. n = total number of perch. Due to predation by YOY perch, there were no bream left in P3.

In P1, the size difference (Fig. 3) between the 5% and 95% percentiles remained small throughout the season, illustrating that the YOY perch population did not split up into two size-cohorts at any time. These results for YOY perch in P1 differed significantly from those in P3 and P4 (ANOVA: $F_{3,16}=6.058$, $p=0.006$, Bonferroni post hoc-test, $P1 < P3, P4$; $p < 0.05$), where the size difference increased steadily soon after the perch hatched and finally resulted in differences of up to 150 mm (between the smallest and largest individuals), creating a bimodal size distribution. The length distributions of YOY perch in P3 and P4 differed neither from each other nor from those in P2. In P2, the size difference in YOY perch became more distinct than in P1,

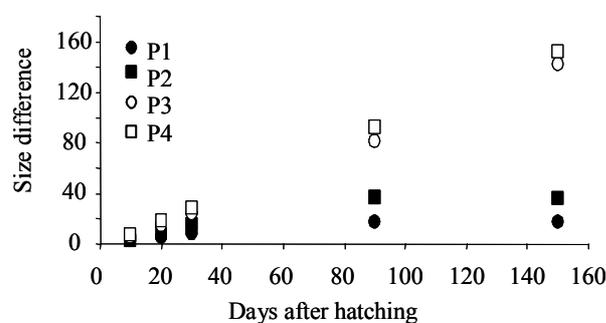


Figure 3: Size difference between the 5% and 95% percentiles of the length-frequency distribution of the YOY perch population.

but came nowhere near the size differences found for YOY perch in P3 and P4 (Fig. 3), which means that only a few YOY perch in P2 grew to larger sizes, although not as large as in P3 and P4 (Fig. 2).

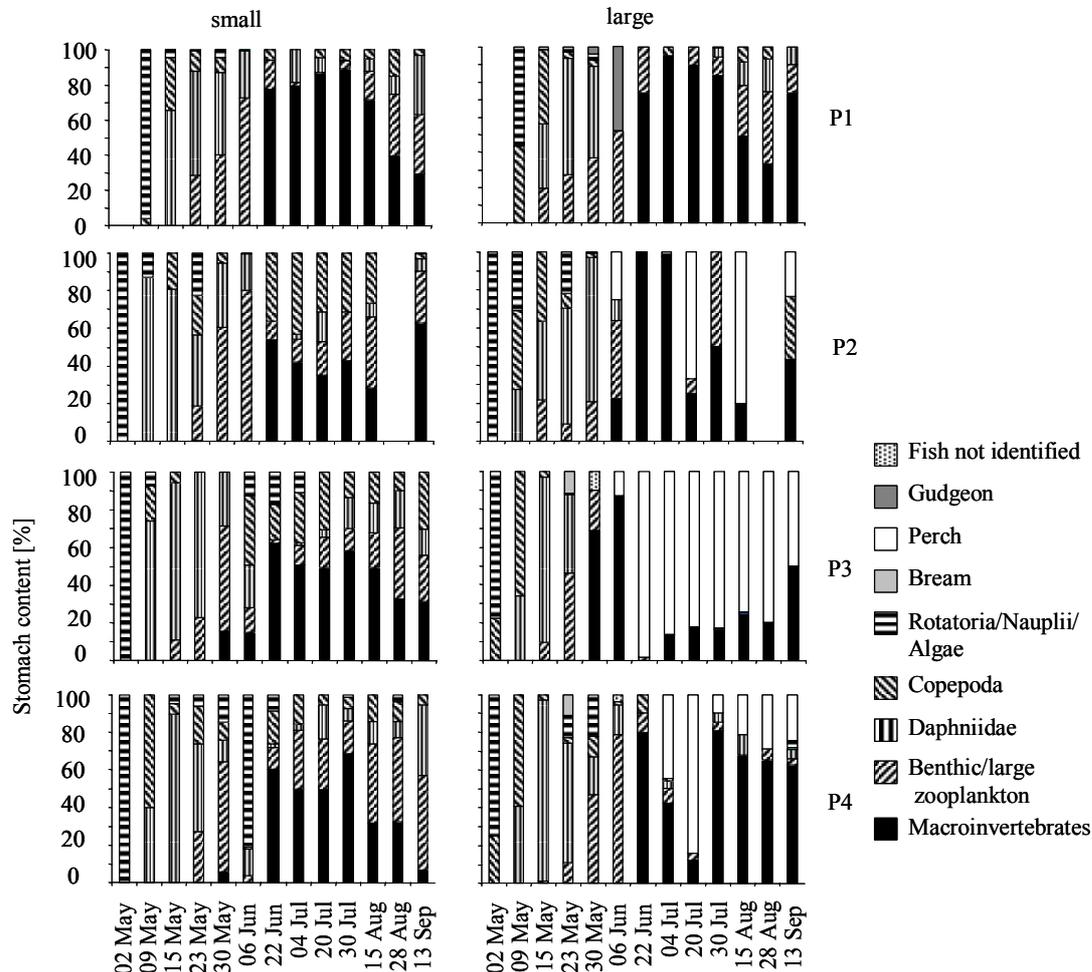


Figure 4: Stomach content [%] of two size classes of YOY perch throughout the season. Where data are missing not enough perch were available for analyses.

Stomach content analyses revealed that differences in the food resources used by small and larger YOY perch had developed in all ponds just a few weeks after hatching. Slightly larger (about 2 mm) YOY perch already fed on copepods, while the smaller ones (6-9 mm) still fed still on rotifers and nauplius larvae (Fig. 4). Afterwards, YOY perch in all ponds increasingly incorporated benthic zooplankton (e.g. *Chydorus*) in their diet. From 22nd June on, YOY perch used large amounts of macroinvertebrates as food, except in P3, where they already fed on zoobenthos on 30th May. YOY perch used almost all zoobenthic organisms present, except molluscs, but fed mainly on ephemeroptera, zygoptera and chironomids. In addition,

piscivory by YOY perch occurred in P3 and P4 on 23rd May, where larger YOY perch fed on bream larvae. From 4th July on, larger YOY perch then became cannibalistic, while also still consuming macroinvertebrates. In P1, piscivory by YOY perch was only detected at two early sampling dates (30th May and 6th June) with the larger YOY perch feeding on topmouth gudgeon larvae. In P2, without preying on bream larvae before larger YOY perch became cannibalistic, with macroinvertebrates and benthic zooplankton as additional food from 6th June on. The small YOY perch in all ponds regularly used copepods, daphniids and benthic plankton, sometimes even switching back to low-energy resources, such as rotifers and nauplius larvae (Fig. 4).

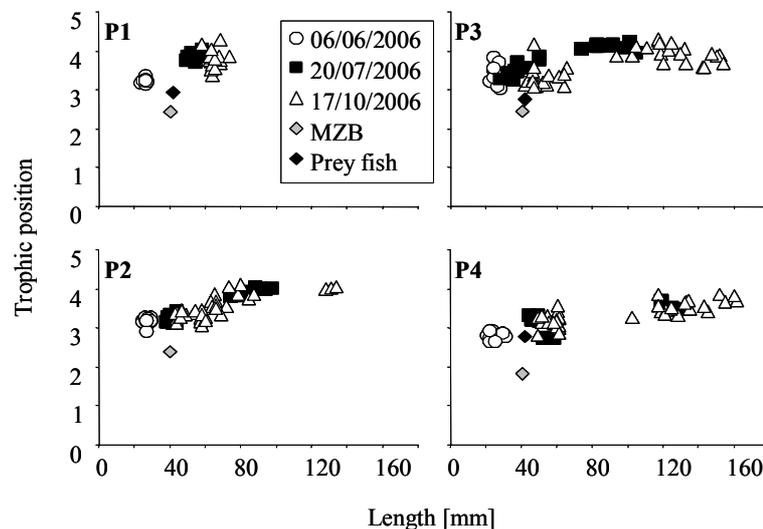


Figure 5: Trophic position of YOY perch in June, July and October 2006, and mean trophic position of macrozoobenthos (MZB). The trophic position of prey fish is based on topmouth gudgeon in P1 and YOY bream in P4.

The calculation of the trophic position (TP) based on the stable isotope analyses revealed that the TP of YOY perch increased with length (Fig. 5). In P1, the size range of YOY perch at each sampling date remained relatively narrow, so the data for the different dates did not overlap. YOY perch started in June at a TP of around 3.3, which was slightly higher than that of topmouth gudgeon. In mid-July, the TP of YOY perch was between 3.5 and 4, and remained at this level in October. In P2, the TP of YOY perch in June varied around 3. In mid-July, YOY perch in P2 clearly split up into two size-cohorts with the smaller YOY perch at a TP of 3 to 3.5, while the TP of larger YOY perch increased to around 4. In October, the differentiation

between these two cohorts was no longer clear, since a continuum of sizes and TPs was found, with the largest YOY perch at a TP of 4 and the smallest at a TP of around 3. The trophic development of the perch populations in P3 and P4 showed a similar pattern. In mid-July, YOY perch began to split up into two size-cohorts, which is clearly reflected by the TP values, with the small YOY perch having a TP of around 3 to 3.5 and the larger YOY perch one of around 4 (Fig. 5).

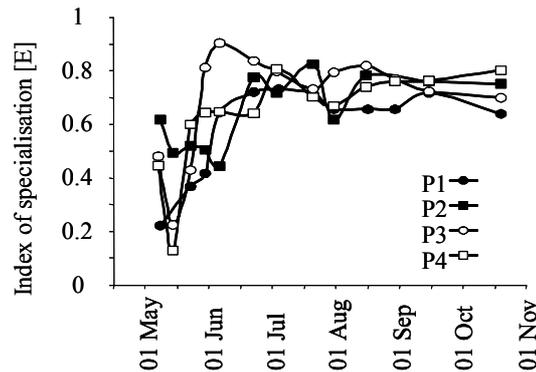


Figure 6: Index of specialisation [E] of the YOY perch population for all sampling dates.

The index of specialisation (E) of the YOY perch population increased a few weeks after hatching in all ponds and then remained at a high level (Fig. 6). Although there were no significant differences between the ponds in the trends towards specialisation of YOY perch (ANOVA: $F_{3,42}=0.652$, $p=0.586$), the specialisation trend in P1 was least distinct. The first clear increase in the level of specialisation of the YOY perch population was correlated to the use of bream larvae as a food resource in P3 and P4. In P1, topmouth gudgeon was preyed on, and in P2, YOY perch fed on large benthic animals, such as *Corixa* and tadpoles.

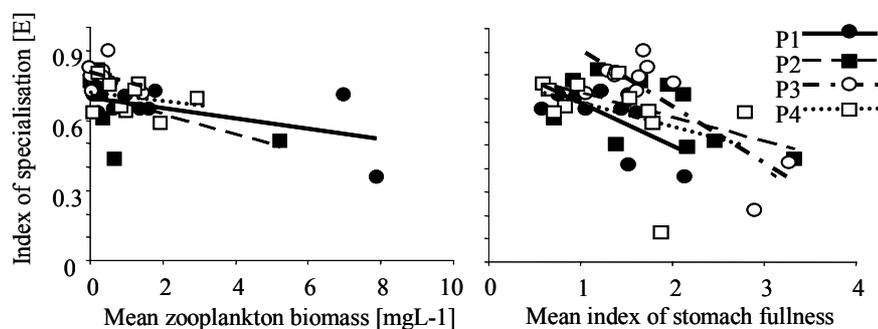


Figure 7: (A) Index of specialisation [E] plotted against the mean zooplankton biomass [mg wet weight l⁻¹] and (B) mean index of stomach fullness of YOY perch at all sampling dates.

In all ponds, the index of specialisation of YOY perch was negatively correlated to the mean zooplankton biomass (Pearson correlation: $n=34$, $p<0.001$). A similar picture was presented by the significant correlation between the index of specialisation and the mean index of stomach fullness in YOY perch (Pearson correlation: $n=42$, $p<0.001$, Fig. 7), with specialisation increasing with decreasing stomach fullness indices.

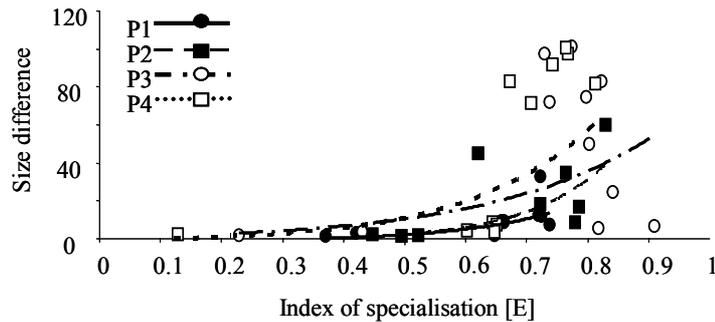


Figure 8: Size differences between the 5% and 95% percentiles of the length-frequency distribution of the YOY perch population plotted against the index of specialisation [E] for all sampling dates.

The index of specialisation was also significantly correlated to the size difference of YOY perch (5%-95% percentile) (Pearson correlation: $n= 41$, $p<0.001$, Fig. 8), showing that high specialisation levels are associated with a large difference in the size of YOY perch. However, the correlation was no longer clear at specialisation index values higher than 0.7, indicating that if the size difference increases above a certain value, the specialisation will not increase proportionally, if at all.

Discussion

Part of the YOY perch population in our study became piscivorous at an early age, preying on bream or topmouth gudgeon larvae. Where bream larvae were fed on, YOY perch soon switched to intra-guild cannibalism, which was also reflected in the stable isotope values. The negative correlations between the degree of specialisation of the YOY perch population and the amount of zooplankton and the index of stomach fullness provide the first evidence that the mechanism leading to cannibalism is related to early specialisation on high-energy resources.

Just a few days after hatching, there was a length-dependent variation in the preferred food resources of YOY perch, with slightly larger YOY perch consuming larger amounts of energy-rich food (copepods). At this time, the level of specialisation within the population did not increase. This is in agreement with the results of other studies, which showed that niche breadth was independent of larval size (Sassa et al. 2008). Thus, the different preference of YOY perch might not be caused by the larger ones specialising on copepods, but might reflect that larger YOY perch show greater swimming skills and are less gape-sized limited than their smaller siblings. The early size differences in YOY perch might be caused by several factors, such as a delay in the hatching of some perch (Brabrand 1995), different behaviour of perch larvae (see Johnson 2008) or variation in egg strand size, which has been shown to translate into variation in initial larval size (Huss et al. 2007). Since large fish are more effective foragers than small fish, due to their higher visual acuity (Walton 1996) and faster swimming (Beamish 1978), an initial size difference would quickly become more distinct.

Just a few weeks after the appearance of these early feeding patterns, zooplankton, which represented the YOY perch's preferred food resource at that time, decreased strongly, which was also reflected in decreasing indices of stomach fullness. With increased competition for a dwindling resource, fish are forced to switch to alternative food resources not used by conspecific competitors (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Svanbäck et al. 2008). This is illustrated on the one hand by our stomach content analyses of the YOY perch, which showed that in response to the lack of zooplankton all YOY perch started to incorporate macroinvertebrates into their diet. On the other hand, declining amounts of zooplankton and falling indices of stomach fullness were related to an increased

degree of specialisation within the population, suggesting that a lack of food stimulated YOY perch to establish new feeding strategies and therefore favoured specialisation and ecological diversification. This is in agreement with previous results, demonstrating that both individual diet specialisation and inter-individual niche variation might reduce intraspecific competition (Robinson & Wilson 1994). Threespined stickleback (*Gasterosteus aculeatus*) started to add alternative prey types to their diet when their population density increased and resource competition was therefore high. Phenotypically different individuals added different alternative prey, thus increasing diet variation among individuals (Svanbäck & Bolnick 2007). We suggest that a similar mechanism is behind the differentiating resource use of YOY perch in our ponds. At this time, YOY perch are probably not only different in size but also in morphology, as morphology has been shown to change in relation to the food resource within just a few weeks (Heermann et al. 2007; Borcharding & Magnhagen 2008). Although these studies were not performed on larvae but on juvenile fish, their findings suggest that three weeks after hatching, the YOY perch in our ponds differed morphologically from each other, producing one of the necessary conditions for increased diet breadth (Svanbäck & Bolnick 2007).

The first clearly noticeable increase in the index of specialisation correlated with larger YOY perch feeding on topmouth gudgeon in P1, bream in P3 and P4, and with feeding on large zoobenthos such as tadpoles in P2. Based on the optimal diet theory (Schoener 1971), Svanbäck and Bolnick (2005) developed a model to explain the increase in specialisation within a population, demonstrating that individual specialisation occurs when there are efficiency trade-offs in using alternative resources. Such a trade-off depends on densities of the forager in relation to its food resources, and individual specialisation tends to increase with increasing intraspecific competition (Svanbäck & Persson 2004). As intraspecific competition increases due to the fact that YOY perch need more and more food while growing, the critical limit in the trade-off between different food resources has been suggested to differ with size (Persson et al. 1998). YOY perch have been shown to first share their preferred resource with other conspecifics (in this case zooplankton). Later, as the resource decreases further, fish add another, somewhat less preferred resource to their diet. The resource chosen and the time when fish start to feed on it differ for each phenotype (Svanbäck & Bolnick 2005). In our case, larger YOY perch may start to feed earlier on alternative food resources (e.g. fish larvae) due to their morphological

abilities, while smaller YOY perch are forced to keep feeding on zooplankton until morphological constraints are sufficiently reduced to allow the use of new resources. Since fish is the energetically more profitable resource, piscivorous perch will grow faster than their siblings which do not prey on fish (Buijse & Houthuijzen 1992; Borcharding et al. 2007). In many piscivorous fish species, individuals that do well in the competition for the shared resource in an early life stage also perform better as a predator later on (Persson 1988). Thus, initial size differences between the small and large YOY perch became more distinct with the use of bream larvae and energetically equivalent resources such as tadpoles. Later, when these resources also decreased due to predation, the largest YOY perch in the ponds became cannibalistic. Thus, the alternative food resources like bream and tadpoles seem to have served as a stepping stone towards cannibalism. YOY perch morphology may change in relation to their piscivorous diet (Heermann et al. 2007) and therefore improve foraging performance on the prey type used (Parsons & Robinson 2006).

Cannibals often share a common resource with their victims (Persson et al. 2004), as was also the case in our study, viz. macroinvertebrates. Thus, the cannibal benefits from both feeding on the victims and from the reduced competition from victims for the shared resource (Polis 1988). Claessen et al. (2000) showed that perch that derive energetic profit from cannibalism do not control their victims in terms of abundance. Consequently, there is still a high competition for the shared resource and only a few individuals can grow to very large sizes. Our study seems to reveal a similar mechanism, since no more than 2.5 % of the individuals became “giants”. Given that cannibalistic YOY perch obtained most of their energy from feeding on their siblings, and only to a small extent from feeding on macroinvertebrates, large YOY perch were hardly affected by the depletion of macroinvertebrates in the vegetation in July. Conversely, the small YOY perch, which lacked zooplankton and macroinvertebrates, were now even forced to switch back to low-energy resources such as rotifers and nauplius larvae, so that they failed to grow and remained relatively small, with minimum sizes of 40 mm. In contrast to the fact that early piscivory led to cannibalism, perch in P1 did not switch to cannibalism after having fed on topmouth gudgeon larvae. In this pond, all YOY perch, regardless of size, fed mainly on macroinvertebrates and did not split up into a bimodal LFD, reaching moderate sizes of about 60 mm without intra-guild cannibalism.

It is commonly known that stomach content analyses give only a snapshot of the feeding situation (Urbatzka et al. 2008). Therefore, it is not possible to determine whether a perch, once it chooses a higher-energy resource, really remains at a higher trophic level for a longer period, in other words, will stick to its prey. Since stable isotopes provide information about the long-term feeding behaviour (Beaudoin et al. 1999), we used them to detect continuous feeding patterns of perch. In June, all YOY perch showed little variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. This is in agreement with findings by Nunn et al. (2007), who showed that young fish larvae had narrow diet spectra. But as early as mid-July, YOY perch in the ponds showing cannibalism (P2, P3 and P4) split up into two cohorts, in terms of both size and trophic position. Only the larger YOY perch were able to reach higher trophic levels, which remained consistent until October (see also Urbatzka et al. 2008). Since the turnover time in muscle tissue has been shown to be relatively long (MacAvoy et al. 2001), the picture arising from stable isotope analyses reflects at least the last month of the perch's diet. Changes to higher trophic levels therefore give evidence of a long-term use of higher-energy food resources, showing that YOY perch in the ponds, once they reached higher trophic levels by feeding on bream and being cannibalistic, did not change to other food resources again.

In summary, size-specific differences in the food spectra of YOY perch occurred shortly after hatching, and were followed by a period of specialisation, when larger YOY perch fed on fish or energetically equivalent resources. This process of individual specialisation was correlated with decreasing zooplankton biomass, suggesting that the increasing intraspecific competition forced YOY perch to use alternative resources. After using bream and tadpoles as a stepping stone, the larger YOY perch finally became cannibalistic. This differentiation into two size classes and two different feeding strategies was shown to be not merely temporary, but to represent a stable pattern within the YOY perch population. Regarding the positive correlation between the index of specialisation and the size difference of YOY perch in the ponds, one question remains to be answered: Did the size difference enable a higher degree of specialisation or did the specialisation lead to greater size differences? Since perch most probably differed not only in size but also in morphology, these initial differences are assumed to be the basis for the increase in individual specialisation (c.f. Robinson & Wilson 1994; Skúlason & Smith 1995).

This first period of individual specialisation then initiated a self-perpetuating process, in which larger YOY perch were able to increase their size advantage and finally became cannibals, while small YOY perch that (1) lacked food resources (zooplankton and macroinvertebrates) and (2) reduced their activity due to predation by their cannibalistic conspecifics (Scharf et al., in press) remained small, as in a stunted population. Hence, a stable bimodality established, leading to several advantages for the large size-cohort, such as higher lipid content and less winter mortality (Heermann et al., unpublished data).

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CHAPTER II

Temperature and size-dependent energy storage and winter mortality in fish

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Abstract

Size is a crucial factor for the survival of fish in their first winter. In laboratory only the smallest perch (*Perca fluviatilis*) suffered from high mortality rates, even if all were fed with low amounts of food. However, feeding the fish reduced the mortality rate. The pond experiments (cold winter 2005/06 and warmer winter 2006/07) showed that although small perch did not reduce their feeding activity, they suffered from high mortality during both winters. However, the ones who survived the winter rebuilt their energy stores. Large perch demonstrated low rates of mortality during the cold winter. During the warm winter, however, mortality was nine-fold higher than during the first winter. Besides the constitution of fish in autumn, temperature can change mortality rates in an indirect manner. The temperature itself did not influence the mortality of large perch (low mortality rates were observed in the laboratory although the temperature was comparable to the one of 2006/07); the loss of ice coverage which can function as a shelter probably increased the vulnerability of large perch to avian predators.

Introduction

In temperate areas, the seasonal availability of food affects the energy storage of many animals; cycles of accumulation and depletion of energy reserves are evident in invertebrates (Dratnal et al. 1993), fishes (Larson 1991), birds (Blem 1976) and mammals (Mrosovsky 1976). Larger individuals of any particular age class tend to have proportionately larger energy stores (Thompson et al. 1991; Huss et al. in press), which means that smaller individuals often have higher mortality rates (Post and Evans 1989; Griffiths and Kirkwood 1995). A greater body weight is also assumed to be an advantage (1) because depletion rates of energy stores can be expected to decrease in larger individuals with respect to the allometric scaling of metabolic rates (Calder 1996), (2) because it enhances the range of profitable food which cannot be captured by smaller individuals (e.g. Keast and Eadie 1985), and (3) because it lowers vulnerability to predation (e.g. Persson et al. 2004).

Consequently, winter mortality strongly depends on the size range of a species; too many smaller individuals can cause a bottleneck in the population (Smith 2007; Daunt et al. 2007; Toney and Coble 1979; Byström et al. 1998; Biro et al. 2004). For fish it was shown that in addition to size-dependent effects, the duration of the winter season, the period of ice coverage (Lappalainen et al. 2000) and the temperature (Byström et al. 2006) also influence winter mortality. During winter, fish mostly rely on their energy stores (Garvey et al. 2004), which are glycogen, fat and protein. After the depletion of glycogen, fat and then finally protein stores are metabolised (see also Collins and Anderson 1995). The amount of the major energy reserve lipid was shown to vary with body size, with smaller individuals regularly having a lower lipid content (Biro et al. 2004; Borcharding et al. 2007). Furthermore, the type of resource consumed during summer may influence accumulated energy contents in fish (Xu et al. 2001; Craig et al. 1999).

Temperature is an important factor for all physiological processes, not only directly and indirectly affecting energy storage and energy depletion (Schultz and Conover 1999; Van Dijk et al. 2005), but further influencing behaviour, growth and mortality. (Kieffer and Tufts 1998; Mehner and Wieser 1994*a,b*; Elliott and Hurley 2001; Johnson and Evans 1991). The temperature dependence of many physiological and ecological processes (e.g. mismatch-situations) has increasingly been the subject of research with respect to global climate change (Edwards and Richardson 2004;

Battisti et al. 2006; Rindorf and Lewy 2006; Petchey et al. 1999; Thomas et al. 2004).

In addition to size-dependent relationships of energy storage and depletion and its effects on survival, our study also aimed at examining the effects of temperature on winter mortality in fish. For this purpose, we studied the energy reserves and mortality of two size classes of young-of-the-year (YOY) perch (*Perca fluviatilis*) in pond experiments. The first experiments were performed in 2005/06, when the temperature was relatively low and comparable with the average winter temperature of the last few decades. The second set of field experiments were carried out during the winter of 2006/07, when the temperature exceeded average temperatures. To support the field data, we conducted additional laboratory experiments in which YOY perch were starved or fed different amounts of food. Thus we could obtain data on mortality rates, the usage of energy stores (glycogen, fat, protein) and the influence of food supply during winter. We hypothesized lower depletion rates of the energy reserves in larger individuals and consequently higher mortality rates and lower recruitment of smaller individuals to the adult population.

Material and Methods

We obtained temperature data from a weather station at Düsseldorf airport (51°16'47.52''N 6°45'53.98''E), Germany, which is about 50 km from the field study site. Water and air temperature are significantly correlated to each other and the mean values of water temperature in 2005/06 and 2006/07 could be calculated. The average temperature of 2005/06 equals that of 1961-1999. The ponds were at least partly covered with ice (mid-December to mid-March, see Fig. 1) in 2005/06 for a period of 91 days. The mean water temperature was about 3.3°C. The ponds were at no time covered with ice during the unusually warm winter in 2006/07, and the water temperature averaged 7.5°C.

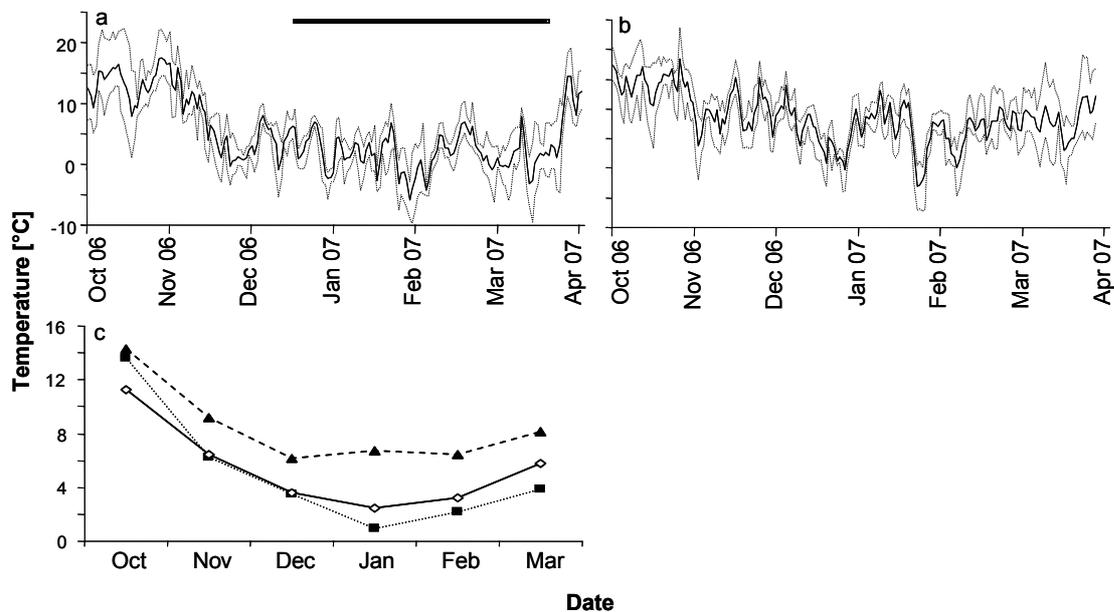


Figure 1: Mean daily air temperature [°C] (—) and minimal and maximal air temperature [°C] (.....) in Düsseldorf in winter (a) 2005/06 and (b) 2006/07, as well as periods of ice coverage (—) of ponds 1-4. (c) Mean monthly air temperature [°C] in winter 2005/06 (.....■.....) and 2006/07 (-▲-), as well as the average temperature [°C] per month (—◇—) from 1961 to 1999 in Germany.

Laboratory experiments

The laboratory experiments started a few days after the stocking of the ponds. Fish used for the experiments were taken from the same group of perch used to stock the ponds. They were given two days of acclimatisation in the laboratory and were then transferred to nine 60 l aquaria in a cooling room. The room was slowly cooled to 8°C, which corresponds to the mean water temperature of 7.5°C during winter

2006/07. We kept fish at a 11:13 day:night regime, which equals the mean day-light-ratio from October to March in Germany.

In 2005/06 we brought all size classes (mean sizes: small 53 mm, medium 85 mm, large 123 mm) used in the field to the laboratory. Three aquaria per size class were each stocked with either 20 fish (small perch) or five fish (medium-sized and large perch). Fish were starved for 140 days; the mortality was monitored every one to two days, and dead fish were removed and frozen.

In 2006/07 we used only the small size-cohort (mean size 48 mm) for laboratory experiments. Three aquaria per treatment were each stocked with 20 fish. The three treatments differed in the quantity of food offered: the fish were fed daily with frozen *Cyclops* spp. with biomasses of either 1.5%, 3% or 6% of the mean body weight of fish in each aquarium. As in the previous year, the experiments lasted for 140 days; we checked the mortality every one to two days, and dead fish were frozen. In both years we killed fish still living at the end of the experiments (with a blow to the head) and froze them. They were used for lipid, glycogen and protein analyses, as well as for weighing and measuring. The mortality rate and the condition factor were calculated. For the latter, the formula after Fulton (Bagenal and Tesch 1978) was used: $K = 10^5 * W / T_L^{-3}$, where W = wet weight [g] and T_L = total length [mm].

Pond experiments

We used four ponds (0.4 – 0.7 ha) at a fish farm in Lohmar, Germany (50°49'34.00''N 7°12'59.42''E) to conduct field experiments. The ponds are maximally two meters deep and oligo- to mesotrophic, the banks are partly covered with emergent vegetation (*Typha* spp., *Juncus* spp., *Carex* spp., *Acorus* spp.) and over-hanging trees and bushes. In addition, huge areas of submerged (*Potamogeton* spec., *Chara* spec.) or floating vegetation (*Nymphaea* spp.) can be found (Scharf et al. in press). The ponds are connected by overflows and are situated in a row. The inflowing stream water flows from pond one to the next, with the final outlet at pond 5, which was not used in this study.

In October 2005 we stocked the ponds with 0+ perch of different size-cohorts (Tab. 1). Pond one (P1) and two (P2) were stocked with only large (mean $T_L = 123$ mm) or small perch (mean $T_L = 53$ mm), respectively. In order to create a possible cannibalism situation, we stocked P3 with large and small perch (1 large : 9 small) and P4 with small and medium-sized (mean $T_L = 85$ mm) perch (1:9).

Field experiments were conducted in a similar manner in 2006/07: We stocked P1 and P2 with small perch (P1: mean $T_L = 59$ mm; P2: mean $T_L = 43$ mm), P3 and P4 were stocked with small (P3: mean $T_L = 51$ mm; P4: mean $T_L = 54$ mm) and large (P3: mean $T_L = 130$ mm; P4: mean $T_L = 131$ mm) perch with a ratio of about 1:60 for P3 and 1:6 for P4. In 2006/07 the density of fish per ha was, when comparable (not for P2 since here different size classes were stocked), up to twelve times higher than in 2005/06 (Tab. 1). In both years, we caught some perch with gill nets (6 to 20 mm mesh size) and by electro-fishing (two weeks after stocking) for analyses of stomach contents of perch in autumn, as well as for glycogen, fat and protein analyses.

In March 2006 and in February 2007 the experiments were terminated by extracting the fish from the ponds. All ponds were emptied completely, thus the total biomass of fish per pond could be obtained. We weighed fish before taking three to four subsamples (about 200 to 700 fish per sample) that were deep-frozen for further analyses. We measured the length of perch to the nearest 0.5 mm. Using length-weight regressions of these data and the total biomass of fish per pond we calculated individuals per ha per pond. The loss of fish during the season was calculated for each size class separately.

We performed stomach content analyses of 6 to 30 perch per size-cohort. The stomach was weighed full and empty, the contents were determined to genus level; we then could calculate the percentage composition. We also calculated the index of stomach fullness (Smyly 1952) as well as Fulton's condition factor for each fish. Another 15 to 40 perch per size class and pond were kept frozen for analyses of fat, glycogen and protein.

To get an indication of the quantity of food available during winter, we sampled zooplankton and macroinvertebrates twice each winter (Nov 05/Mar 06, Nov 06/Jan 07). Six parallel samples of zooplankton were taken with a Schindler-Patallas-trap (mesh size 100 μm) and preserved in 96% ethanol. We counted individuals under the stereomicroscope and determined them to genus level; ten randomly chosen individuals per sample were measured to the nearest 0.01 mm. The biomass (mg wet weight l^{-1}) could be calculated using published length-mass equations (Bottrell et al. 1976; Mehner et al. 1995). We sampled macroinvertebrates

Table 1: Individuals ha⁻¹, mean total length (T_L) and mean condition factor (K) of perch at stocking and fish extraction from ponds 1-4 in 2005/06 and 2006/07, as well as percent loss of individuals over winter and the significance of the condition factor's change (Student's t-test). Also shown is the mean condition factor of perch at the beginning and end of laboratory experiments in 2005/06 and 2006/07, and the significance of the condition factor's change. SD=standard deviation. * = significant difference (p>0.05)

| FIELD | | | Stocking | | | Extraction of fish | | | Loss [%] | Change of K |
|-------------------|----|------------|-----------------------|--------------------------|-------------|-----------------------|--------------------------|-------------|----------|-------------|
| | | | Iniv ha ⁻¹ | T _L [mm] ± SD | K ± SD | Iniv ha ⁻¹ | T _L [mm] ± SD | K ± SD | | |
| 2005/06 | P1 | small | 3250 | 53 ± 4 | 0.85 ± 0.05 | 1175 | 56 ± 4 | 0.94 ± 0.05 | 64 | * |
| | P2 | large | 463 | 123 ± 17 | 1.12 ± 0.10 | 420 | 121 ± 15 | 1.14 ± 0.07 | 9 | |
| | P3 | small | 2633 | 53 ± 4 | 0.85 ± 0.05 | 750 | 59 ± 5 | 0.90 ± 0.07 | 72 | |
| | | large | 288 | 123 ± 17 | 1.12 ± 0.10 | 252 | 124 ± 18 | 1.10 ± 0.06 | 13 | |
| | P4 | small | 14286 | 53 ± 4 | 0.85 ± 0.05 | 5483 | 57 ± 4 | 0.86 ± 0.06 | 62 | |
| | | medium | 1571 | 85 ± 8 | 1.03 ± 0.13 | 1474 | 85 ± 7 | 0.95 ± 0.13 | 6 | * |
| 2006/07 | P1 | small | 31266 | 59 ± 5 | 1.00 ± 0.05 | 13738 | 63 ± 5 | 0.87 ± 0.07 | 56 | * |
| | P2 | small | 37668 | 43 ± 5 | 0.90 ± 0.06 | 1580 | 60 ± 8 | 0.91 ± 0.05 | 96 | |
| | P3 | small | 12489 | 51 ± 8 | 0.96 ± 0.03 | 7684 | 53 ± 7 | 0.85 ± 0.22 | 38 | * |
| | | large | 531 | 130 ± 18 | 1.07 ± 0.06 | 111 | 130 ± 15 | 1.07 ± 0.09 | 79 | |
| | P4 | small | 33718 | 54 ± 7 | 0.87 ± 0.05 | 2726 | 60 ± 6 | 0.82 ± 0.12 | 92 | |
| | | large | 1489 | 131 ± 17 | 0.95 ± 0.10 | 672 | 134 ± 15 | 0.91 ± 0.07 | 55 | |
| LABORATORY | | | | | | | | | | |
| 2005/06 | | small 0% | | 53 ± 4 | 0.85 ± 0.05 | | | 0.50 ± 0.08 | | * |
| | | medium 0% | | 85 ± 8 | 1.03 ± 0.13 | | | 0.79 ± 0.07 | | * |
| | | large 0% | | 123 ± 17 | 1.12 ± 0.10 | | | 0.98 ± 0.08 | | * |
| | | | | ± | | | ± | | | |
| 2006/07 | | small 1.5% | | 48 ± 5 | 0.82 ± 0.07 | | | 0.51 ± 0.13 | | * |
| | | small 3% | | 48 ± 5 | 0.82 ± 0.07 | | | 0.48 ± 0.05 | | * |
| | | small 6% | | 48 ± 5 | 0.82 ± 0.07 | | | 0.50 ± 0.08 | | * |

in the sediment with a Birge–Eckmann-grab (three parallel samples) and sieved the sample through a net of 1 mm mesh size. Macroinvertebrates living in vegetation (submersed and emerged vegetation) were sampled with a dip net (mesh size 1 mm, three parallel samples) repeatedly moved through the vegetation along a section of 0.15 x 0.3 x 1 m. Samples taken in vegetation and from the ground were preserved with ethanol 96% and counted. Ten randomly chosen individuals per sample were measured to the nearest 0.1 mm. We determined the biomass with published length-mass equations (Mehner et al. 1995; Heerkloss 1996; Benke et al. 1999) and expressed it as g wet weight m⁻² for the sediment samples and CPUE [g section⁻¹] for the vegetation samples.

Analyses of body composition

To determine which energy stores in perch are important during winter and to what extent they had been depleted, we analysed fat, glycogen and protein. 14-20 fish per size class of the stocked fish each of 2005 and 2006, 15-40 fish per size class of the fish samples from the ponds each in 2006 and 2007, and the fish of the laboratory experiments (start: 14-20 per size class in 2005, 15-38 per size class in 2006; end of the experiments: 15-44 per treatment in 2006, 19-20 per treatment in 2007) were used for the analyses, which were conducted after the fish had been gutted and the head and fins removed. If necessary, 2-5 smaller fish were pooled to obtain the necessary amount of tissue. If they were too big to be used as a whole, sections of the front, middle and back of the fish were used as one sample. For measuring fat, glycogen and lipids, we used the mid-infrared transmission (MIT) spectroscopy technique (Elvingsson and Sjauna 1992) with equipment (Miris AB, Uppsala, Sweden) calibrated for fish tissue. For further details see Byström et al. (2006). Results were noted as g per fish.

All perch of the small size class died in winter 2005/06, while only four of the medium and one of the large perch died. We removed the latter two groups from further calculations. In 2006/07, almost all of the fish in one of the three aquaria fed with 1.5 % food died within the first few days because they did not accept frozen *Cyclops* spec. as food; none of the fish from this aquarium were used for any calculations. At the end of the experiment most perch had died (159 of 190). Only dead perch were considered for further calculations.

Statistics

To test the change of the condition factor over winter, we calculated the residuals based on the condition factor - size relationship for fish caught in autumn and spring and then tested the data with Student's t-tests for each size class and each pond. The same was done for the condition factors of fish from laboratory experiments. We tested the change of the index of stomach fullness over the season using Student's t-test for each pond and each size class. In the same way we used Student's t-tests to test for differences in the mean size of perch at the stocking and the fish sampling. Differences in the mortality of perch in the field were calculated with Chi-square tests and Student's t-tests. To see if the amount of food fed in the laboratory had any influence on the mortality rate in the laboratory, first the cumulative mortality of perch was graphed against time for each aquarium (three replicates per treatment for 0%, 3% and 6%, two for 1.5%). We fitted each graph using the equation after Boltzmann:

$$y = \left(\frac{A_1 - A_2}{1 + e^{\frac{x - x_0}{dx}}} \right) + A_2$$

The number of days when 25%, 50% and 75% of the fish had died was calculated using the corresponding fitted parameters. We then compared the calculated results with an ANOVA and Tukey-HSD (see Norf et al. 2007). To test for significant differences of fat, protein and glycogen contents the percentage of each was arc sine square root transformed. We tested each size class separately using an ANCOVA with the size as covariate; differences between the groups were tested with Bonferroni post-hoc test. Origin 7.5 (OriginLab, USA), SPSS 14.0 (SPSS Corp., USA) and Winstat (Microsoft, USA) were used for all analyses.

Results

Body composition

In the laboratory experiments, starved small perch had significantly lower values of fat and protein and higher values of glycogen compared to measurements before the start of experiments (Tab. 2, Fig. 2). The minimum values lay around 0.01 g fat, 0.03 g protein, and the maximum value for glycogen around 0.01 g. Fat and protein in starving large (mean fat: 0.39 g, mean protein: 3.95 g) and medium-sized (mean fat: 0.07 g, mean protein: 0.55 g) perch were significantly lower than before the start of experiments. Also, the increase in glycogen (large: to mean 0.05 g, medium: to mean 0.13 g) was significant, but was not as distinct in larger perch as in small and medium-sized perch (Tab. 2; Fig. 2). All small perch that had been fed had significantly decreased their protein content to around 0.05 g (ANCOVA: $F_{3,57}=47.327$, $p<0.0001$, Bonferroni post hoc-test: start>6%, 3%, 1.5%), while glycogen significantly increased when perch were fed 6% of their mean body weight to about 0.04 g; otherwise the glycogen content did not change. (ANCOVA: $F_{3,57}=6.302$, $p=0.001$, Bonferroni post hoc-test: only significant difference 6%>start). The fat content of all fed small perch significantly decreased to about 0.01 g (ANCOVA: $F_{3,57}=18.261$, $p<0.0001$, Bonferroni post hoc-test: start>1.5%, 3%, 6%; Tab. 2, Fig. 2).

Table 2: Statistical values of the difference between fat, glycogen and protein content before and after winter or at the start and end of the experiments in 2005/06, using ANCOVAs.

| FIELD | | | df | | Fat | | Glycogen | | Protein | |
|-------------------|----|-----------|----|----|-------|---------|----------|---------|---------|---------|
| | | | | | F | p | F | p | F | p |
| 2005/06 | P1 | small | 1 | 22 | 94.71 | <0.0001 | 13.47 | 0.001 | 20.01 | <0.0001 |
| | P2 | large | 1 | 26 | 0.01 | 0.921 | 0.41 | 0.526 | 0.46 | 0.502 |
| | P3 | small | 1 | 22 | 66.29 | <0.0001 | 23.98 | <0.0001 | 7.86 | 0.010 |
| | | large | 1 | 26 | 18.07 | <0.0001 | 6.16 | 0.020 | 3.80 | 0.062 |
| | P4 | small | 1 | 22 | 73.50 | <0.0001 | 13.61 | 0.001 | 1.58 | 0.222 |
| | | medium | 1 | 27 | 0.59 | 0.449 | 77.47 | <0.0001 | 3.39 | 0.077 |
| LABORATORY | | | | | | | | | | |
| 2005/06 | | small 0% | 1 | 27 | 4.29 | 0.048 | 71.97 | <0.0001 | 45.98 | <0.0001 |
| | | medium 0% | 1 | 27 | 25.51 | <0.0001 | 91.07 | <0.0001 | 126.41 | <0.0001 |
| | | large 0% | 1 | 26 | 23.30 | <0.0001 | 4.35 | 0.047 | 25.53 | <0.0001 |

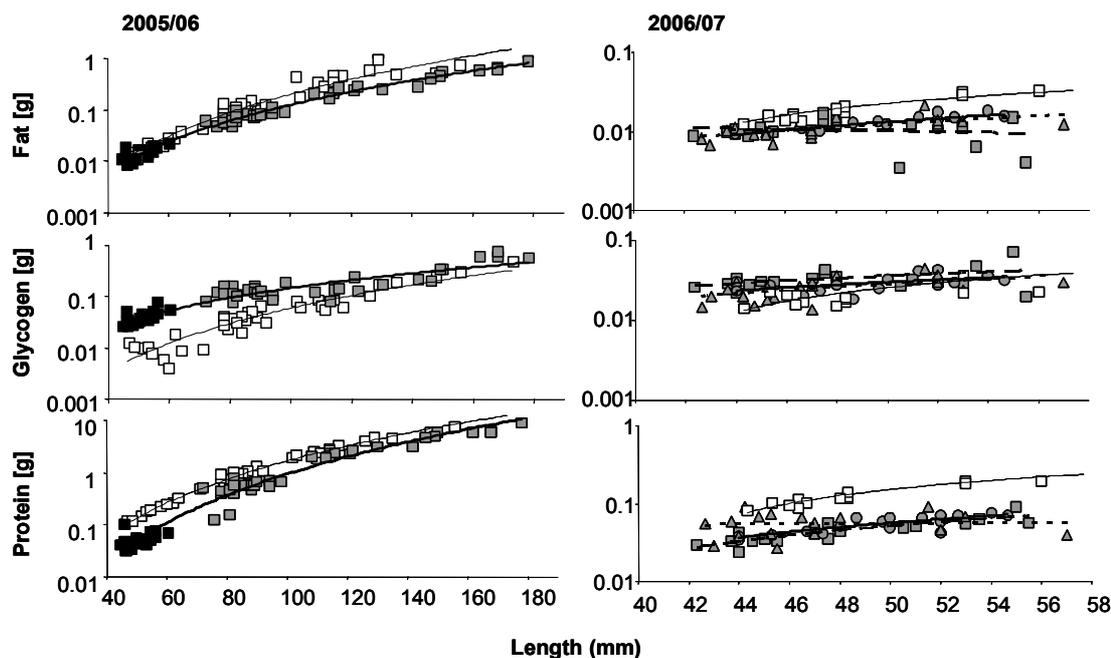


Figure 2: Fat, glycogen and protein [g] of perch of different body lengths before the experiment (—□—) and after having been fed with *Cyclops spp.* for several weeks; the daily food biomass equalled 6% (—□—), 3% (—○—), 1.5% (—△—) and 0% (—□—perch alive at the end of the experiment; —■— perch dead at the end of the experiment) of the perch's mean body mass.

In the pond experiments fat and protein were positively correlated to the size of the perch. Small perch that had survived the winter showed a significant higher proportion of fat, glycogen, and (except for small perch from P4 in which the protein content did not change) also protein compared to measurement of the levels before stocking (Tab. 2, Fig. 3). Fat increased from about 0.02 to 0.06 g, glycogen from about 0.01 to 0.02 g and protein from about 0.23 to 0.33 g. Medium-sized perch in P4 had increased glycogen (from mean 0.04 to 0.12 g) values while the fat and protein content did not change. Large perch in P3 lost fat (from mean 0.51 to 0.47 g), but gained glycogen (from mean 0.15 to 0.33 g); protein remained the same, while the values of large perch in P2 did not change over winter (Tab. 2, Fig. 3).

Mortality rates

In the laboratory experiments the mortality of perch was size-selective (small starving: $r^2=0.41$ $p<0.001$, small fed 1.5%, 3%, 6% included: $R^2=0.12$, $p<0.001$). After 136 days, 100% of the starving small perch had died, while at the end of the experiment (after 140 days) 85% of small perch fed with *Cyclops spp.* equalling 1.5% of the perch's body mass had died. 90% of the small perch that were fed with

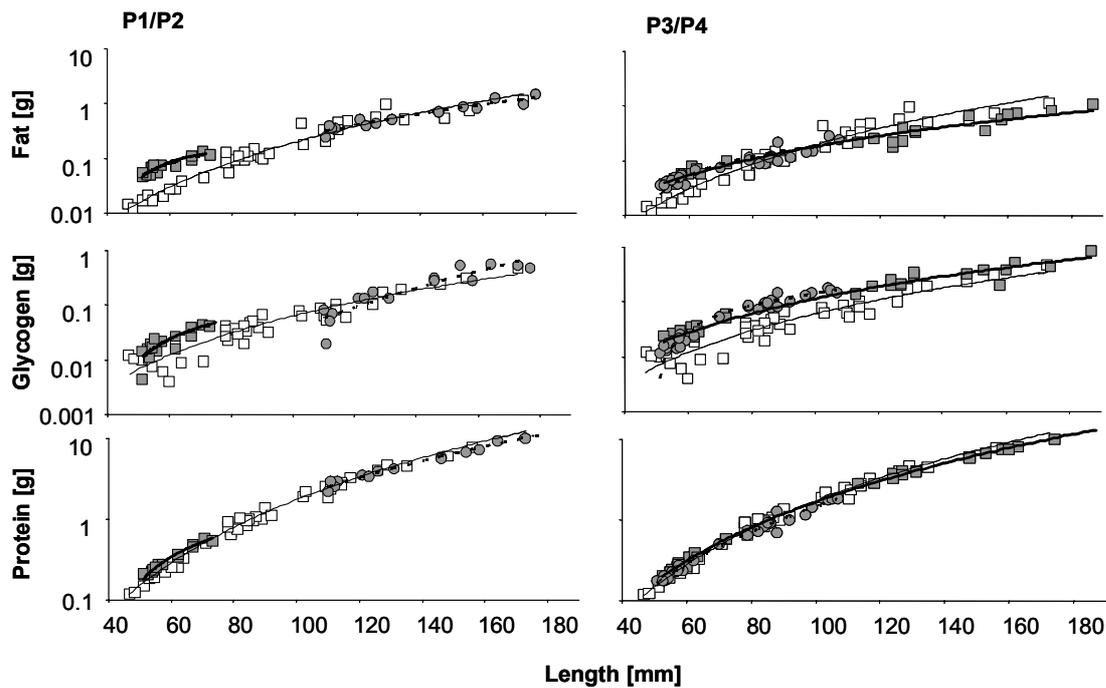


Figure 3: Fat, glycogen and protein [g] of perch of different body lengths in 2005/06, two weeks after stocking (\square) and at the fish extraction in pond 1 (\blacksquare) and 2 (\bullet) shown on the left side of the figure and pond 3 (\blacksquare) and 4 (\bullet) shown on the right side of the figure.

and 68% of the ones that were fed with 6% had died after 140 days (Fig. 4). Comparing the number of days until 50 % of the perch had died showed that the mortality of perch fed with 6% occurred significantly later than for the starving perch (ANOVA: $F_{3,7}=4.843$, $p=0.039$; Tukey-HSD-test: $6\%<0\%$). The same was found for the date by which 75% had died (ANOVA: $F_{3,7}=11.849$, $p=0.040$; Tukey-HSD-test: $6\%<0\%$), but not for 25%, for which no significant difference could be detected (ANOVA: $F_{3,7}=1.113$, $p=0.406$). Perch fed with 3% and 1.5% did not differ in mortality rate from either starving perch or perch fed with 6%. The number of dead medium-sized and large perch was significantly lower than that of small perch (Student's-t-test: $t_{6,11}=-9.856$, $p<0.0001$; Fig. 4).

During the cold winter 2005/06, 62% to 72% of the small perch died, and the mortality between ponds with possible cannibalism (P3 and P4) did not differ in the mortality of small perch compared to P1 (χ^2 -test P1/P3 $p=0.364$, P1/P4 $p=0.776$; Tab. 1). Mortality of the large perch was around 9% in P2 and about 13% in P3. Approximately 6% of the medium-sized perch died in P4. During the warm winter of 2006/07, the mortality of small perch was between 39% and 96% and was not

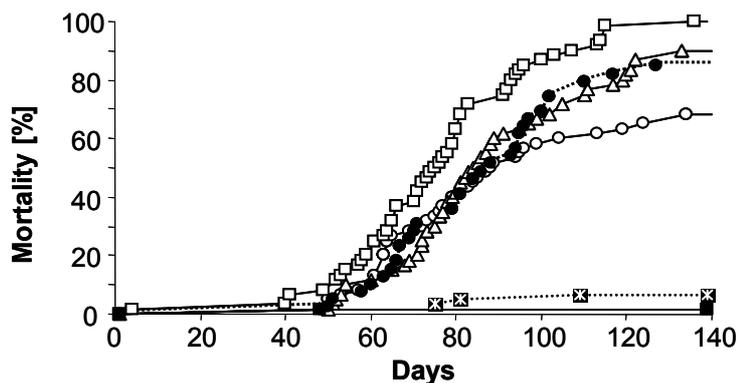


Figure 4: Mortality of small, medium-sized and large perch fed with *Cyclops* spp., the biomass of which equalled 6% (small —○—), 3% (small —△—), 1.5% (small —●—) and 0% (small —□—, medium-sized —×—, large —■—) of the perch's mean body mass.

significantly different from the mortality of small perch in 2005/06 (Student's t-test: $t_{3,4}=-0.275$, $p=0.795$). As in the previous year, mortality of small perch in the ponds where cannibalism was possible (P3 and P4) did not differ from that in the other ponds (Student's t-test: $t_{2,2}=-0.323$, $p=0.777$). In contrast, the mortality of large perch was significantly higher than the previous year in both ponds: 55% died in P4 and about 80% in P3 (Student's t-test: $t_{2,2}=-4.566$, $p=0.045$; Tab. 1).

Size, condition, stomach contents and food resources

Comparing the mean size of small perch in autumn (stocking) and spring (fish extraction) of both years reveals a significant increase in size, while the mean size of large and medium-size perch remained the same. In autumn 2005/06, the mean condition factor of perch was positively correlated to the length of the fish (small: 0.85, medium-sized: 1.03, large: 1.12); this correlation was not as distinct in 2006/07 (small: between 0.87 and 1.00, large: 0.95 for in P4 and 1.07 in P3). There were no overall tendencies of changes in condition during either winter (Tab. 1).

In autumn 2005 and 2006, analyses of stomach contents (Fig. 5) revealed that small perch fed mainly on plankton and benthos, large perch on fish (30% of the stomach content in 2005/06 and an average of 70% of the stomach content in 2006/07), benthos and plankton, while medium-sized perch fed mostly on benthic organisms. In spring 2006 and 2007, the small and medium-sized perch had not changed their diet, whereas large perch fed mainly on macrozoobenthos and only a little on fish (7% in 2006 and on average 8.7% in 2007).

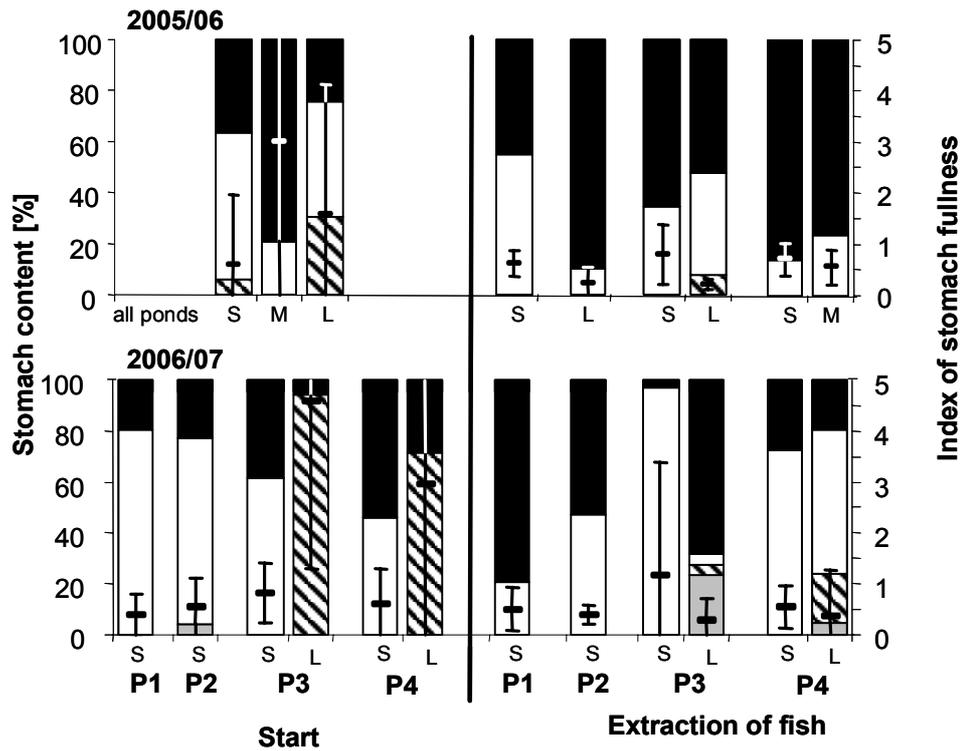


Figure 5: Stomach content analyses of perch two weeks after stocking and at the fish extraction from ponds 1-4 in 2005/06 and 2006/07 (bars), as well as the indices of stomach fullness (mean \pm S.D (—)). ■ macroinvertebrates, □ zooplankton, ▨ fish, ▩ rest.

Table 3: Statistical values of the difference between mean size and index of stomach fullness (ISF) before and after winter in 2005/06 and 2006/07, using Student's t-tests.

| | | | Mean size | | ISF | |
|---------|----|--------|-----------|---------|-----|---------|
| | | | df | p | df | p |
| 2005/06 | P1 | small | 1938 | <0.0001 | 42 | 0.929 |
| | P2 | large | 622 | 0.217 | 48 | 0.022 |
| | P3 | small | 1918 | <0.0001 | 41 | 0.540 |
| | | large | 605 | 0.653 | 43 | 0.036 |
| | P4 | small | 2076 | <0.0001 | 42 | 0.727 |
| | | medium | 1963 | 0.250 | 24 | 0.023 |
| 2006/07 | P1 | small | 1989 | <0.0001 | 36 | 0.423 |
| | P2 | small | 2045 | <0.0001 | 43 | 0.211 |
| | P3 | small | 2969 | <0.0001 | 34 | 0.489 |
| | | large | 69 | 0.901 | 34 | <0.0001 |
| | P4 | small | 759 | <0.0001 | 37 | 0.684 |
| | | large | 153 | 0.357 | 35 | 0.004 |

The indices of stomach fullness (Fig. 5) significantly decreased from autumn to spring for medium-sized (from mean 2.3 to 0.55) and large perch in both years (2005/06: from mean 1.59 to 0.21; 2006/07: from mean 3.83 to 0.34), while there were no changes in small perch (2005/06: around 0.8; 2006/07: around 0.6; Tab. 3).

Table 4: Mean biomass [fresh weight mgL^{-1}] of zooplankton and of zoobenthos [fresh weight gm^{-2}] sampled by Birge-Eckmann-grab, as well as Catch Per Unit Effort (CPUE) of zoobenthos caught with the dip net in the vegetation in ponds 1-4 in 2005/06 and 2006/07. n for all =3.

| PLANKTON | | 28-Nov-05 | 22-Mar-06 | 7-Nov-06 | 9-Jan-07 |
|----------|--|---|---|---|---|
| | | Biomass [mgL^{-1}] \pm SD |
| P1 | | 0.53 \pm 0.47 | 0.14 \pm 0.08 | 0.05 \pm 0.06 | 0.16 \pm 0.36 |
| P2 | | 4.29 \pm 2.73 | 0.29 \pm 0.20 | 0.11 \pm 0.09 | 0.25 \pm 0.12 |
| P3 | | 2.14 \pm 1.78 | 0.81 \pm 1.19 | 0.52 \pm 0.40 | 0.62 \pm 0.85 |
| P4 | | 2.75 \pm 2.50 | 0.27 \pm 0.08 | 0.53 \pm 0.63 | 2.67 \pm 3.74 |

| BENTHOS | | 28-Nov-05 | 22-Mar-06 | 7-Nov-06 | 9-Jan-07 |
|---------|--------|---|---|---|---|
| | | Biomass [gm^{-2}] \pm SD /CPUE \pm SD | Biomass [gm^{-2}] \pm SD /CPUE \pm SD | Biomass [gm^{-2}] \pm SD /CPUE \pm SD | Biomass [gm^{-2}] \pm SD /CPUE \pm SD |
| P1 | grab | 336.51 \pm 162.35 | 22.54 \pm 6.85 | 14.50 \pm 2.84 | 5.23 \pm 2.99 |
| | veget. | 32.55 \pm 25.30 | 45.95 \pm 14.38 | 1.79 \pm 0.95 | 3.11 \pm 2.59 |
| P2 | grab | 22.06 \pm 11.03 | 19.22 \pm 21.26 | 29.07 \pm 11.62 | 13.03 \pm 9.03 |
| | veget. | 38.93 \pm 14.41 | 28.78 \pm 10.82 | 7.33 \pm 5.32 | 1.14 \pm 1.09 |
| P3 | grab | 6.38 \pm 2.42 | 8.53 \pm 5.34 | 17.18 \pm 13.23 | 5.52 \pm 3.64 |
| | veget. | 10.82 \pm 7.87 | 4.59 \pm 2.11 | 9.54 \pm 3.73 | 3.27 \pm 2.43 |
| P4 | grab | 7.62 \pm 1.51 | 16.71 \pm 12.94 | 34.39 \pm 23.94 | 3.68 \pm 2.64 |
| | veget. | 5.36 \pm 1.54 | 5.16 \pm 1.64 | 5.39 \pm 2.37 | 5.59 \pm 7.17 |

The zooplankton density in the ponds (Tab. 4) was lower in 2006/07 than in 2005/06. In 2005/06 the amount decreased from autumn to spring (March) from between 0.53 and 4.29 mgL^{-1} to between 0.14 and 0.81, while it increased the second year from between 0.05 and 0.53 to between 0.16 and 0.62 mgL^{-1} . The amount of benthic organisms (Tab. 4) caught with the grab (mostly Oligocheata, *Sialis* spp., *Chironomus* spp.) was found to be the same during autumn of both years. Over winter it decreased in 2006/07 but stayed the same in 2005/06. The biomass of organisms caught with the dip net tended to be less in autumn 2005 than in 2006. No changes over winter could be detected.

Discussion

Laboratory experiments

In our laboratory experiments fish died when the fat content decreased to 0.01 g, which corresponds to about 2% of the fish's biomass. The lethal limit of protein was 0.03 g, corresponding to about 9% of the biomass. The glycogen content of the starved was distinctly higher at the end of the experiments, suggesting a mobilisation of energy in the body. Mortality in medium-sized and large perch was slight, whereas small perch suffered from high mortality rates even if they were fed with low amounts of food. Fish which were fed little amounts of food had a significantly lower mortality rate (noticeable after a time-lag of several days) than unfed fish. Because energy stores are related to size, a size-dependent mortality was also noticeable within the small size class.

Size is a crucial factor regarding the bottleneck of first winter-survival. Energy reserves of fishes are positively correlated to size (Brett and Groves 1979; Sogard and Olla 2000; Thompson et al. 1991; Schultz and Conover 1997; Huss et al. in press) and small fish use their energy stores at higher rates (Miranda and Hubbard 1994; Sutton and Ney 2001; Schultz and Conover 1999). Thus, the smaller the fish the sooner its energy reserves will be depleted, resulting in size-dependent death rates, which is also described in many other studies on winter mortality (Post et al. 1998; Lappalainen et al. 2000; Biro et al. 2004; Byström et al. 2006; Post and Evans 1989). Newsome and Leduc (1975) showed that perch will die when the fat content decreases to less than 2%. This result was also found in our laboratory experiments; the fat content for perch that had died lay around 2% (whether fed or starving), while the lowest level of protein content of dead perch was around 8% to 9%. In starving fish first glycogen, then the fat is consumed, and finally if these stores are used up muscle protein will be transferred into energy (Collins and Anderson 1995; Jobling 1980; Evans and Claiborne 2006). Thus, even if the fat has decreased to about 2% the fish will not die immediately but only after the protein stores are depleted as well. In the present laboratory experiments, protein and fat stores as well as the condition factor at the start of the experiment were positively related to the size of perch. Since the fat content of all perch was around or even below the critical 2% level, the lipid reserves of all size classes can be assumed to be depleted, meaning that two of the energy stores were already empty and the most important energy reserve left for the

perch was protein. Because larger perch still had higher reserves of protein, size-dependent mortality rates occurred. All of the small starving perch had died after 136 days, while only 27% of the medium-sized perch and 7% of the large perch had died by the end of the experiment. Small fish in both treatments (starved or fed with small amounts of food) died size-dependently, with the smallest fish dying earlier than the only slightly larger individuals. The condition factor illustrated the depletion of reserves and decreased for all size-classes of the starving perch and also for all fed perch. This agrees with results of Thompson et al. (1991) who demonstrated that the loss in energy stores was related to decreasing condition factors. In contrast, other studies showed that the decrease in energy stores is not necessarily illustrated by the condition factor (Pangle et al. 2004). With the loss of fat and protein, the water content in the tissue can increase (Sogard and Olla 2000; Méndez and Wieser 1993; Pastoureaud 1991), which is why the fish will not lose weight even when the energy stores are depleted. Thus, it might be suggested that only a large decrease in energy stores which is not compensated by water can be detected with the condition factor.

Mortality of fish has been shown to decrease when the fish are fed (Kirjasniemi and Valtonen 1997a; Pangle et al. 2004; Thompson et al. 1991) due to reduced rate of energy store depletion (see Byström et al. 2006). This is in accordance with results of the laboratory experiments in the present study which demonstrated that a certain amount of food (6% of the body weight) was needed before the mortality significantly decreased. In addition, the effect only became obvious after several days, in this case when 50% of the fish had died (for starving perch after 73 d, for perch fed with 6% after 100 d). Later on, the decrease in mortality with food intake became more distinct (for starving perch after 86 d, for perch fed with 6% after 128 d).

The changing levels of glycogen give additional information on the energetic status of perch. Glycogen is a form of carbohydrate usually present in the liver and in muscle tissue if the fish has been feeding well (Méndez and Wieser 1993; Hall et al. 2006) and is thus a good indicator of the state of nutrition. While studying starving golden perch (*Maquaria ambigua*), Collins et al. (1995) found an initial decrease of the glycogen level followed by an increase, even though the fish were still starving, indicating the mobilisation of other energy reserves. Similar results were also detected for rainbow trout (*Oncorhynchus mykiss*, Kiessling et al. 1991).

A comparable outcome also appeared in our laboratory experiments, in which the glycogen of small perch had increased to relatively high levels (for unfed perch to about 0.01 g), irrespective of food quantity (little or none). For fish which were starving but still alive, glycogen levels increased to 0.05 g for large and to 0.13 g for medium-sized perch. Here the increase in glycogen indicates a bad constitution of the fish.

Pond experiments

The pond experiments showed that although small perch did not reduce their feeding activity, they suffered from high, size-selective mortality during both the warm and the cold winter. However, the ones who survived the winter were able to rebuild their energy stores and to increase condition. Large perch decreased their feeding activity during winter and were hardly affected by mortality during the cold winter. During the warm winter, however, mortality was nine times higher than in the first year.

For fish, energy depletion increases with increasing water temperature (Schultz and Conover 1999), thus, a higher mortality rate of perch during the warm winter of 2006/07 would have been expected. In contrast, the small perch were found to have similar mortality rates for both winters. The condition of the small perch was not optimal for surviving the winter; their fat stores were already low in autumn (about 0.02 g / 1.5% in 2005, and max. 0.03 g / 2% in 2006); this autumn malnourishment explains the higher mortality rates of the small perch (up to 94%) compared to those of medium-sized (6%) and large perch (11%) during the colder, more normal winter (average temperature of 2005/06 equals that of 1961-1999).

The mean size of small perch in the ponds increased significantly over both winters, whereas it did not change for large and medium-sized perch. This could be due to growth (Karas 1990; Foy and Paul 1999) or to size-selective mortality. Since size-dependent mortality rates were detected in the laboratory and a winter-increase in length has been found to be related to size-dependent mortality in fishes (Toneys and Coble 1979), the mortality of small perch in the ponds is likely to be size-selective. The similar mortality rates of small perch for the two winters might be due to the fact that although small perch were not well nourished during autumn (relatively low levels of indices of stomach fullness: 0.8 in 05/06 and 0.6 in 06/07 compared either to medium-sized [2.3 in 2005/06] or large perch [1.59 in 05/06 and 4.69 in 06/07]), they were able to keep their level of feeding during winter. Laboratory results

revealed that feeding delays starvation, so that the mortality rates of small perch might have been even higher if they had consumed less.

While small perch held their feeding level to compensate low reserves, medium-sized and large perch ate significantly less during the cold winter, as has also been found for other fish species (Byström et al. 2006). Even though the content of fat and protein as well as the condition factor was positively correlated to the size of fish, the fat content of large perch was also low (slightly above 0.5 g / 2%). Thus, as for the small perch, fat reserves can be assumed to be more or less depleted already by late autumn, which would suggest that the feeding activity of larger perch does not decrease over winter. Obviously, their remaining energy stores were large enough to endure winter with only little feeding activity, which is not only attributable to their size; the quality of the food is also essential (Xu et al. 2001; Craig et al. 1999; Rennert et al. 2005; Borcharding et al. 2007). Stomach content analyses of perch from the pond showed that each size class fed on slightly different food resources in autumn: the small ones on plankton and benthos, medium-sized perch mainly on benthic organisms, while the larger perch additionally fed on fish. Autumnal piscivory, which has been shown to lead to large energy reserves (Borcharding et al. 2007; Niva 1999), thus enabled large perch to survive the winter without feeding.

Feeding perch have to invest energy when searching and hunting for prey (Bolnick and Ferry-Graham 2002). Thus, perch face a trade-off situation; spending energy to feed and reduce the probability of mortality due to depleted energy reserves or saving energy when resting and not feeding. In this study, feeding was probably the only possible option for small perch. Their energy reserves were too low to endure the whole winter without feeding; in addition, their total metabolic demand was lower than that of larger perch (Clarke and Johnston 1999), meaning that they would find enough food even if food resources were scarce.

Even when consuming 6% of their body mass, the smallest individuals of the perch in the laboratory experiments died and a significant decrease in mortality of this experimental group became obvious only after 70 days. This size-selective mortality and the decrease of mortality over time can be assumed to have also occurred for the smallest perch in the ponds during autumn and early winter. Feeding at a low level then would support only the largest individuals within the total group of small-sized perch. However, those slightly larger perch that had survived were able to rebuild their energy stores over winter, so that they are in better condition after winter than

they had been in autumn (for small perch in 2005/06 fat increased from about 1.5 / 0.02 g to 3.2 % / 0.06 g , and protein from about 0.23 g to 0.33 g), which is in accordance with the results of Kirjasniemi et al. (1997b), who detected increasing fat and protein levels in pikeperch (*Stizostedion lucioperca*) when fish were fed during winter. However, in contrast to the results from the laboratory experiments, this change in energy reserves was not strong enough to be detected with the condition factor. Except for large perch in P3 (with a slight decrease in fat), the levels of fat and protein of all perch either increased or remained the same. In addition, all size classes of perch in the ponds had slightly higher glycogen levels after the cold winter of 2005/06 than before it. While the increase in glycogen in the laboratory perch illustrated an insufficient condition, here the gain in glycogen (which was not as strong as in the laboratory and accompanied an increase in fat and protein) might be more attributable to an improvement in the perch's condition (see also Hall et al. 2006; Méndez and Wieser 1993).

The large perch had changed their food spectrum by spring. Only very little fish was found in their diet; they fed mainly on plankton and benthic organisms. Thus, the large perch had reduced their energy costs, since they had stopped preying on fish which requires longer hunting and handling times (Galarowicz and Wahl 2005; Breck 1993). The fact that large perch reduced the amount of fish in their diet and of feeding in general probably explains the lack of difference in mortality of small perch in ponds where cannibalism was possible and in the ones where it was not possible. Thus, small perch are not so much threatened by cannibalism during winter as by starving.

What caused the dramatically higher mortality of the large perch in the warm winter 2006/07 (ca. 80%) compared to the winter before (ca. 11%)? As in 2005/2006, large perch again showed decreased feeding activity (index of stomach fullness changed from 4.7 in autumn 2006 to about 0.3 in spring 2007); it thus could be suggested that the higher mortality rate is related to an increased energy demand caused by higher temperatures (Schultz and Conover 1999). However, the mortality was not dependent on size, which should have been the case if caused by the energy depletion (due to the size-dependence of energy stores). In addition, almost no mortality could be detected for large perch during the “warm” laboratory experiments (8°C). Lappalainen (2000) found that the size-dependent mortality of pikeperch (*Stizostedion lucioperca*) decreased with a longer duration of ice-cover. During the

warm winter 2006/07, there was no ice coverage which could have been functioned as shelter against birds such as heron (*Ardea cinerea*) and particularly cormorant (*Phalacrocorax carbo*) (compare Schlosser 1988); the latter have been shown to cause substantial mortality of fish (Warke and Day 1995), especially due to the fact that their numbers have been rapidly increasing recently (Keller 1995). More and more cormorants use the area around the study site as winter-habitat but also as a breeding site (LÖBF NRW 2005); here, the density of cormorants is about 60 individuals (Landesfischereiverband Westfalen und Lippe e.V., 2005. http://www.ruhrfischereigenossenschaft.de/images/pdf/karte_kormoranzahlen_nrw.pdf). During the warm winter 2006/07, cormorants were frequently observed on all ponds of the fish farm, including the four ponds used in our study (Andreas Pilgram, personal observation 2006). Perch are an important part of the cormorant's diet (Suter 1997). The daily intake of the cormorant increases during winter (Keller 1995), and the birds are known to prey selectively on the larger fish (Bokranz 1999; Veldkamp 1995). Hence, the impact of the birds on the large perch must be assumed to be much higher in 2006/07 than in 2005/06 when the ponds were covered by ice for several months (see also Mous 2000).

The global mean temperatures have risen at an increasing rate (the last 50 years double the rate of the last 100 years), and 11 of the 12 last years rank among the warmest since 1850. Cold extremes decreased as well, as the total number of frost days per season and the greatest warming happens during winter and spring in the northern hemisphere (IPCC 2007). More frequent warmer winters will probably not lead to a different feeding-behaviour of perch, at least on the short term. Perch are also not directly threatened by higher mortality due to the higher temperature. However, the higher temperature will bring a loss of ice coverage, which especially in shallow water bodies without any other structures will mean a loss of shelter. Hence, mainly the larger perch are threatened by mortality due to predatory birds, which strongly affects the recruitment success of larger perch. In studies on the bimodality within the YOY age cohort, it was found that the larger male perch already mature after the first winter (Beeck et al. 2002), so that they probably contribute considerably to the gene pool of the next perch generation. The smaller perch were not able to catch up in size, thus the bimodality within the year class can be followed over several years, with the larger perch being mainly cannibalistic (Beeck 2003). These advantages for the larger perch could be wiped out by warming

winters, so that changes in the size and age-structure of the population as well as of competitive relationships (ratio of small to large perch) could become irrevocable.

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CHAPTER III

Competition, predation, cannibalism: the development of young-of-the-year perch populations in ponds with bream or roach

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Abstract

Competition affects fish in various ways and several mechanisms to avoid competition have been developed. One strategy to escape from competition is specialisation on alternative food resources, such as fish larvae. Early specialisation on piscivory can induce cannibalism and support the development of a bimodal size-distribution of the population. Within two years the occurrence of early piscivory with predation of perch on bream (in 2006) and roach (in 2007) larvae resulting in cannibalism and the development of two size-cohorts of perch was studied in experimental ponds. Bream hatched 12 days after perch, while roach hatched simultaneously with perch. Roach then grew twice as fast as bream larvae. In ponds with bream larvae a section of the perch population became early piscivorous. Consequently the perch population was ultimately bimodally distributed with the large perch being cannibalistic. In ponds with roach no piscivory and cannibalism occurred and the perch population was unimodally distributed. Although the piscivorous/cannibalistic large size-cohort of perch in 2006 reached up to 180 mm TL after its first summer, the small size-cohort of perch in ponds with bream was significantly smaller than perch in ponds with roach in 2007. In cases of bimodality the large size-cohort experiences several size-related advantages, such as early maturation and less winter mortality. However, the large size-cohort represents a maximum of 2.5 % of the population, while the largest section of the population (the small size-cohort) can not benefit from early maturation and low winter mortality, but suffers from high mortality rates during winter. Perch in 2007, which did not prey on roach larvae and were unimodally distributed, reached larger sizes than the small cohort in 2006. Since these fish probably suffered less from winter mortality than small perch in 2006 (size-dependent energy storage), the total recruitment success might be higher for fish in 2007 than in 2006, which could be of advantage considering the whole population. However, whichever strategy is better - a few large perch and numerous very small perch, or all perch of the same size but not as little – is subject to speculation and requires further investigation.

Introduction

Competition may affect fish in various ways, causing changed food spectra and expanded feeding niche width (Syväranta & Jones 2008), influencing growth and size of fish (Bashey 2008), changing morphological variation within a population (Olsson et al. 2006) or the species composition of a fish community (Persson 1983). To avoid competition fish were shown to change the preferred habitat (Persson & Greenberg 1990a; Schulze et al. 2006), switching from the littoral to the pelagic or vice versa. Another possibility to adapt to competition is to modify the foraging behaviour. For example, ruffe (*Gymnocephalus cernuus*) feeds predominantly at night, thereby reducing competitive interference from perch (*Perca fluviatilis*) (Schleuter & Eckmann 2006). Not only do diel adaptations occur; there are also modifications in the choice of food resources. Suffering from competition with roach (*Rutilus rutilus*), perch switch from zooplanktivory to benthivory (e.g. Persson 1986; 1987). Resource competition might also be reflected in niche variation within populations and can drive ecological diversification within natural populations (Svanbäck & Bolnick 2007). Under the pressure of competition fish start to add alternative prey types to their diet. As such, phenotypically different individuals add different alternative prey, thus increasing diet variation and the degree of specialisation of the population (Svanbäck & Bolnick 2005).

Cannibalism was shown to derive from specialisation on bream larvae (Heermann et al. Chapter I; Borcharding et al. in prep.). Perch which are early piscivorous have increased growth rates compared to planktivorous conspecifics (Borcharding et al. 2000), and thus are soon able to feed on their smaller siblings (Beeck et al. 2002). Under certain conditions a few perch can develop into giants from being cannibalistic (Byström 2006; Borcharding et al. in prep.; see also Claessen et al. 2000; 2002). Giant perch benefit from their size, resulting in early maturation (Beeck et al. 2002) or reduced winter mortality. (Post & Evans 1989; Post et al. 1998; Lappalainen et al. 2000; Biro et al. 2004; Byström et al. 2006).

However the smaller conspecifics suffer from predation pressure by the cannibals. Predator avoidance has crucial effects on the prey, for example leading to morphological changes (Eklöv & Svanbäck 2006; Hoverman & Relyea 2008), causing shifts to more secure habitats (Hölker et al. 2007) and resulting in changes of diel activity patterns (König et al. 2006) and behaviour (Magnhagen & Borcharding

2008). Besides direct effects on the prey itself, predation pressure can also affect following generations of prey, influencing the offspring size (Bashey 2008) and was even shown to have influence on metapopulation level (White 2008) causing delayed maturation, reduced fecundity or mating effort (see Bolnick & Preisser 2005). Bolnick and Preisser (2005) demonstrated that the effects of predators on their prey depend on competition. When competition is weak, predators have negative effects on prey growth, maturation, and decrease of prey density. However, if competition increases or resources become more limiting, predation even has stronger negative effects on prey density, but a weaker effect on prey growth and development time. Peacor (2002) predicted that predation reduces prey growth at high resource levels. However at low resource levels predation increases prey growth rate. At low resource densities consumers exploit their resources beyond the maximum due to strong competition, which results in lower growth rates. Predation suppresses consumer foraging, thus resource density can decrease again, compensating suppressed consumer foraging and leading to higher consumer growth rates. In a cannibalistic system, where few giants develop, not only the contribution of these large individuals to the population dynamics seems to be important, but also the development (e.g. growth rates, winter mortality) of the small, much more numerous individuals must have effects on the population.

In this study we focused on the occurrence of early piscivory with predation of perch on bream and roach larvae resulting in cannibalism and the development of two size-cohorts of perch. Therefore, in experimental ponds the growth and development of young-of-the year (YOY) perch was monitored in the presence and absence of bream and roach, respectively. Furthermore first suggestions on the influence of early piscivory and cannibalism on population dynamics are given.

Materials and Methods

Study site and experimental set up

We used four ponds, indicated in the paper as P1, P2, P3 and P4 (0.4 – 0.7 ha) at a fish farm in Lohmar, Germany (50°49'34.00''N 7°12'59.42''E) to conduct our field experiments. The ponds are connected by overflows and are situated in a row. To prevent fish from passing from one pond to the next, the overflows were blocked by nets. The ponds are maximally two meters deep and oligo- to mesotrophic with submerged helophyte and nymphaeid macrophyte vegetation (Scharf et al. in press; Urbatzka et al. 2008). The mean zooplankton biomass in all ponds in 2006 (\pm SD) was 2.85 ± 9.51 (mg wet weight l^{-1}), in 2007 the mean biomass of all ponds was 3.01 ± 5.36 (mg wet weight l^{-1}). Mean macroinvertebrate biomass (\pm SD) sampled in the sediment and in the ground averaged out at 10.62 ± 11.61 g wet weight m^{-2} in the sediment and 0.05 ± 0.06 (CPUE) [$g\ section^{-1}$] in the vegetation. The macroinvertebrate and the zooplankton biomass were at no time significantly different between the years. For further details on the sampling procedure as well as on the results of the food resources refer to Heermann et al. (Chapter I, II).

The ponds were fishless before they were stocked with adult perch and bream in April 2006 and adult perch and roach or adult perch and bream in 2007. In 2006, all ponds were stocked with 12 to 17 kg perch ha^{-1} (25 to 36 individuals per pond); P3 and P4 were additionally stocked with adult bream (75 kg ha^{-1} / 23 individuals in P3 and 82 kg ha^{-1} / 32 individuals in P4). In 2007, all ponds were stocked with 12 to 21 kg perch ha^{-1} (23 to 39 individuals per pond); P1 and P2 were additionally stocked with adult bream (83 kg ha^{-1} / 25 individuals in P1 and 76 kg ha^{-1} / 26 individuals in P2), while P3 and P4 were additionally stocked with adult roach (77 kg ha^{-1} / 107 individuals in P3, 86 kg ha^{-1} / 51 individuals in P4).

Before stocking, the lengths of each fish were documented. Total length (TL) of perch ranged from 19 to 33 cm in 2006 and from 15 to 42 cm in 2007. The size of stocked bream ranged between 45 and 64 cm in 2006 and between 34 and 59 cm in 2007; the size of adult roach in 2007 ranged between 15 and 34 cm. In 2006, topmouth gudgeon (*Pseudorasbora parva*), an invasive fish species, established a stable population in P1, in addition to the perch, probably introduced via a creek.

Sampling

Fish were sampled after perch had hatched (end of April/beginning of May in 2006, mid-April in 2007). Until June sampling was performed weekly, afterwards biweekly using electro-fishing and gillnetting with multi-mesh-sized gillnets (for further details see Scharf et al. in press). At the end of the season (mid-October) all ponds were emptied completely, extracting the fish from the ponds to measure the total wet weight biomass of fish per pond. In order to obtain a length-frequency distribution (LFD) of perch per pond, three to four subsamples per pond (about 150 to 750 fish per sample) were taken to measure the fish (to the nearest 0.5 mm). Length-weight regressions of these data and the total wet weight biomass of fish per pond were used to calculate the number of individuals per pond.

For further analyses all fish were deep-frozen immediately after catching. In the laboratory length (TL) (to the nearest 0.5 mm) and wet weight (to the nearest 0.01 g) of all fish were recorded. Based on the length-frequency distribution of perch, fish could be assigned to either the small or the large size-cohort. For these cohorts the mean total length of perch was calculated for each sampling date. In addition the mean total length for all bream and roach, as well as the growth rates [mm day^{-1}] per sampling date were calculated. To compare the density of bream and roach the catch per unit effort (CPUE) was determined. CPUE for electrofishing (CPUE_E) was calculated as the mean number of perch caught per point (including zero samples). For gillnets (CPUE_N) the nominal catches were converted to standardised catches using the following equation:

$$\frac{\left(\frac{A_s}{A_n} \cdot C_n \right)}{t}$$

where A_s = area of standard net (219.3 m^2), A_n = area of the net used [m^2], C_n = nominal catch, and t = exposure time [h].

To express the ratio of bream:roach, the mean values of CPUE_E for bream and roach in P4 from day 9 to 48 after perch's hatching and the mean values of CPUE_N for bream and roach in P4 from days 100 to 150 after perch's hatching were calculated. For the ratio of bream:roach at the time of fish extraction the total number of bream and roach of P4 were compared.

Stomach content analyses of 7 to 40 perch were performed dissecting perch under a stereomicroscope and weighing the full and empty stomach (to the nearest 0.01 mg). Stomach contents were identified to genus level, and the food spectrum of each perch was expressed as the weight percentage composition of food items identified to genus level. The diet items were counted per genus, and ten individuals per genus were measured. Published length-mass equations were used to calculate the wet weight of the content (for details see Heermann & Borchering 2006; Scharf et al. in press). Based on the assignment of perch to either the small or the large size-cohort, stomach content analyses were graphed for each cohort separately. The index of stomach fullness (Hyslop 1980) for each fish was calculated to describe the wet weight of the prey as a percentage of the perch's wet weight.

Statistics

Since in 2007 perch hatched earlier than in 2006, perch in 2007 were older than perch in 2006 when extracting the fish from the ponds. Hence, the length of perch in October was corrected using the pond-specific growth rates for the whole season. Thus the calculated length of perch in 2007 and measured length of perch in 2006 correspond to the same age of perch. Using a one-way ANOVA, differences of these calculated lengths of small perch in 2007 and the measured lengths of small perch in 2006 were tested. If ten or more fish of both species were caught the mean length of perch and bream in 2006 and the mean length of perch and roach in 2007 were tested with Student's t-tests. All analyses were performed with SPSS 15.0 (SPSS Corp.).

Results

In 2006, perch hatched in all ponds between 25th April and 4th May, while hatching of perch in 2007 occurred about two weeks earlier between 14th and 15th April. In 2007, lower amounts of perch larvae developed than expected in P2 and P3 and no perch at all were found in P1. Bream in 2006 hatched about 12 days after perch, while roach in 2007 (only in P4) hatched simultaneously with perch (Fig. 1). Neither bream in P1 and P2 nor roach in P3 developed in 2007 as expected. Due to the establishment of topmouth gudgeon in P1 in 2006 and because no fish at all developed in 2007, P1 was excluded from further analyses. During weeks two and four of life, bream in 2006 grew by 0.13 mm per day while roach in 2007 exceeded bream in growth (growing by 0.26 mm per day) during the same period.

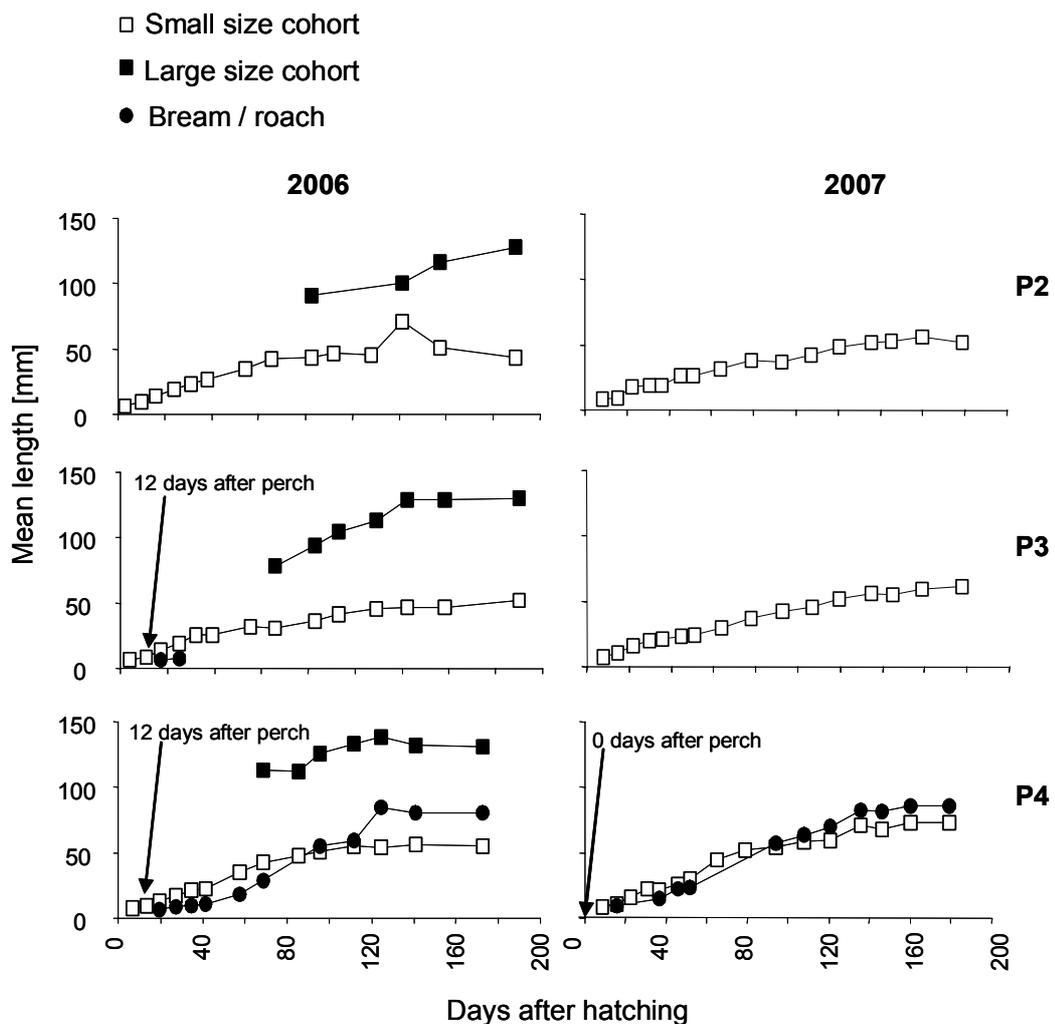


Figure 1: Mean length [mm] of perch (small and large size-cohort in 2006, one cohort in 2007), bream in 2006 and roach in 2007 in P2, P3 and P4. Arrows indicate hatching of bream and roach.

In 2006 the perch population of P2, P3 and P4 developed into two size-cohorts with the first clear two-peaked length-frequency distribution on 20th July in P2 and on 3rd July in P3 and P4 (Fig.1). Until October, the perch populations of P3 and P4 had developed a clear bimodal size distribution. 1.7 % of the total number of perch in P3 and 2.5 % in P4 belonged to the large size-cohort and reached a maximum size of 180 mm. (Fig.2) In P2 there were only some larger perch (0.2 % of the total number of perch) reaching a maximum size of 140 mm (Fig.2).

In 2007 the perch population was unimodally distributed in all cases, with a maximum perch size of 90 mm (Fig.2). In October 2006 at the time of the extraction

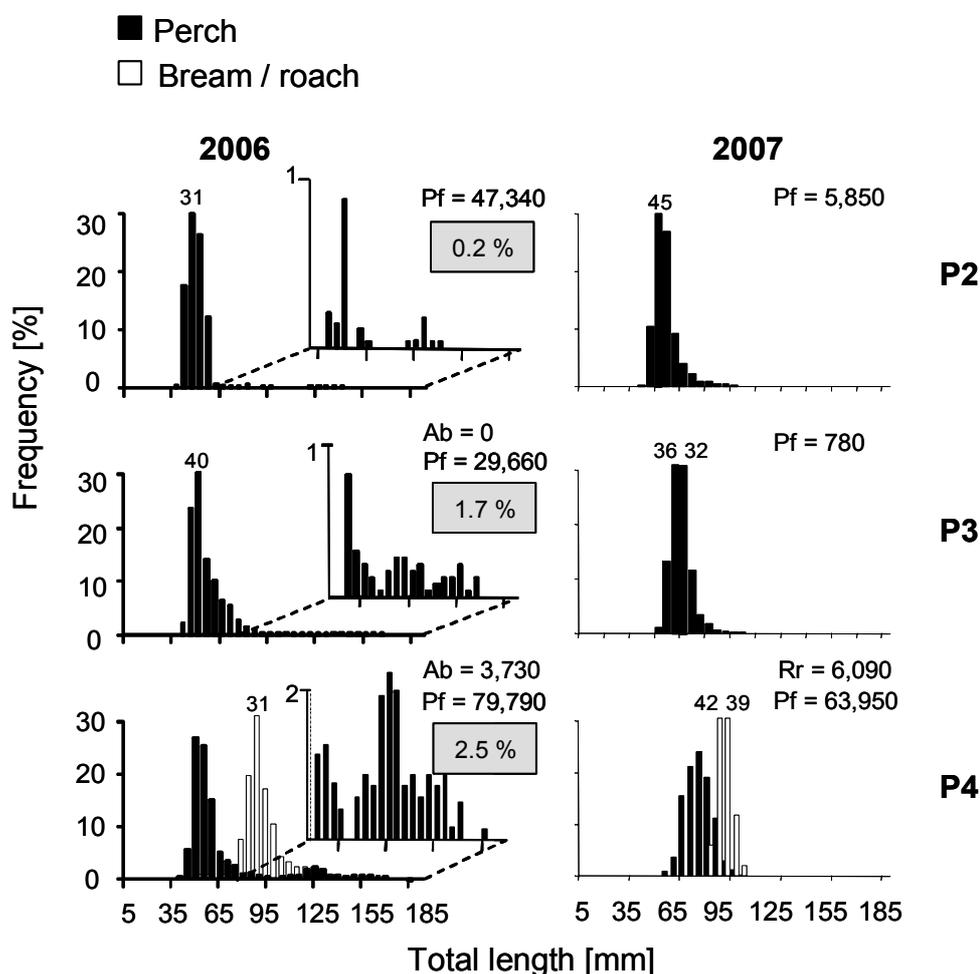


Figure2: Length-frequency distribution of the perch and bream extracted from P2, P3 and P4 in October 2006 and of perch and roach extracted from P2, P3 and P4 in October 2007. For 2006, grey boxes show the percentage of large perch among the total number of individuals of perch per pond. In the right part of the graph, the x-axis is enlarged to illustrate more clearly the LFD of the large perch. Numbers indicate individuals ha^{-1} in each pond. Pf = perch, Ab = bream, Rr = roach. Due to predation by YOY perch, in 2006 there were no bream left in P3.

of the fish from the ponds, the total number of perch in P2 was eight-fold higher than in 2007, and the ratio of perch in P3 was even 39:1. However, the total number of perch ha^{-1} in P4 was comparable in both years (2006: 79,800, 2007: 64,000) (Fig. 2). In 2006, bream larvae in P3 were totally eaten by perch within about 20 days after bream's hatching (Fig.1), while still 3,700 bream were extracted from P4 in October 2006 (Fig.1, 2). In October 2007, 6,100 roach were caught in P4 (Fig.1, 2). The ratio of bream:roach from day 9 to 58 after perch hatching calculated from the mean CPUE of electrofishing was bream:roach = 4:1. From day 100 to 150 the ratio calculated from the mean CPUE of gillnettings resulted in bream:roach = 1:5, while the ratio in October on fish extraction was bream:roach = 1:2.

In 2006, bream in P3 were significantly smaller than perch on both sampling dates when bream occurred (Fig.1) (Student's t-test: 15th May $t_{58,74}=49.475$, $p<0.0001$; 25th May $t_{35,460}=91.637$, $p<0.0001$). In P4, bream were significantly smaller than perch until July (Student's t-test: 15th May $t_{58,100}=36.829$, $p<0.0001$; 23rd May $t_{50,207}=47.582$, $p<0.0001$; 30th May $t_{33,101}=38.872$, $p<0.0001$; 06th June $t_{60,10}=10.714$, $p<0.0001$; 03rd July $t_{36,14}=6.592$, $p<0.0001$) but significantly exceeded perch of the small size-cohort in length in mid-October (Fig.1) (Student's t-test: $t_{542,194}=-33.848$, $p<0.0001$). The size of bream in P3 and P4 ranged between 40 to 54% of that of perch on all sampling dates until beginning of July. On 3rd July in P3 bream had already grown to 86 % of the size of perch's small cohort. On 5th June 2007, roach in P4 were significantly smaller than perch (Student's t-test: $t_{61,14}=-4.142$, $p<0.0001$), but had already reached 80% of the perch's size. From 17th July onwards roach were significantly larger than perch (Fig.1) (Student's t-test: 17th July $t_{83,23}=-3.702$, $p<0.0001$; 7th September $t_{31,11}=-4.988$, $p<0.0001$; 21st September $t_{21,11}=-5.065$, $p<0.0001$; 10th October $t_{1506,101}=-17.065$, $p<0.0001$). In 2006, perch from the small-sized cohort were significantly smaller than perch in 2007 when comparing by pond (mean [mm] \pm SD 2006 P2: 43 ± 5 , P3: 52 ± 10 , P4: 55 ± 9 ; mean [mm] \pm SD 2007 P2: 52 ± 7 , P3: 61 ± 7 , P4: 72 ± 8) (ANOVA: $F_{6,9841}=2186.304$, $p<0.0001$, Bonferroni post hoc-test, P2, P3, P4 in 2006 < P2, P3, P4 in 2007 $p<0.0001$).

In 2006 after a period of planktivory (until mid to end of May) in all ponds, early piscivory occurred (on 23rd May) in P3 and P4, with perch preying bream larvae. Instead of preying on fish, perch in P2 fed to a great extent on large macroinvertebrates, such as *Corixa* and tadpoles (see Heermann et al. Chapter I).

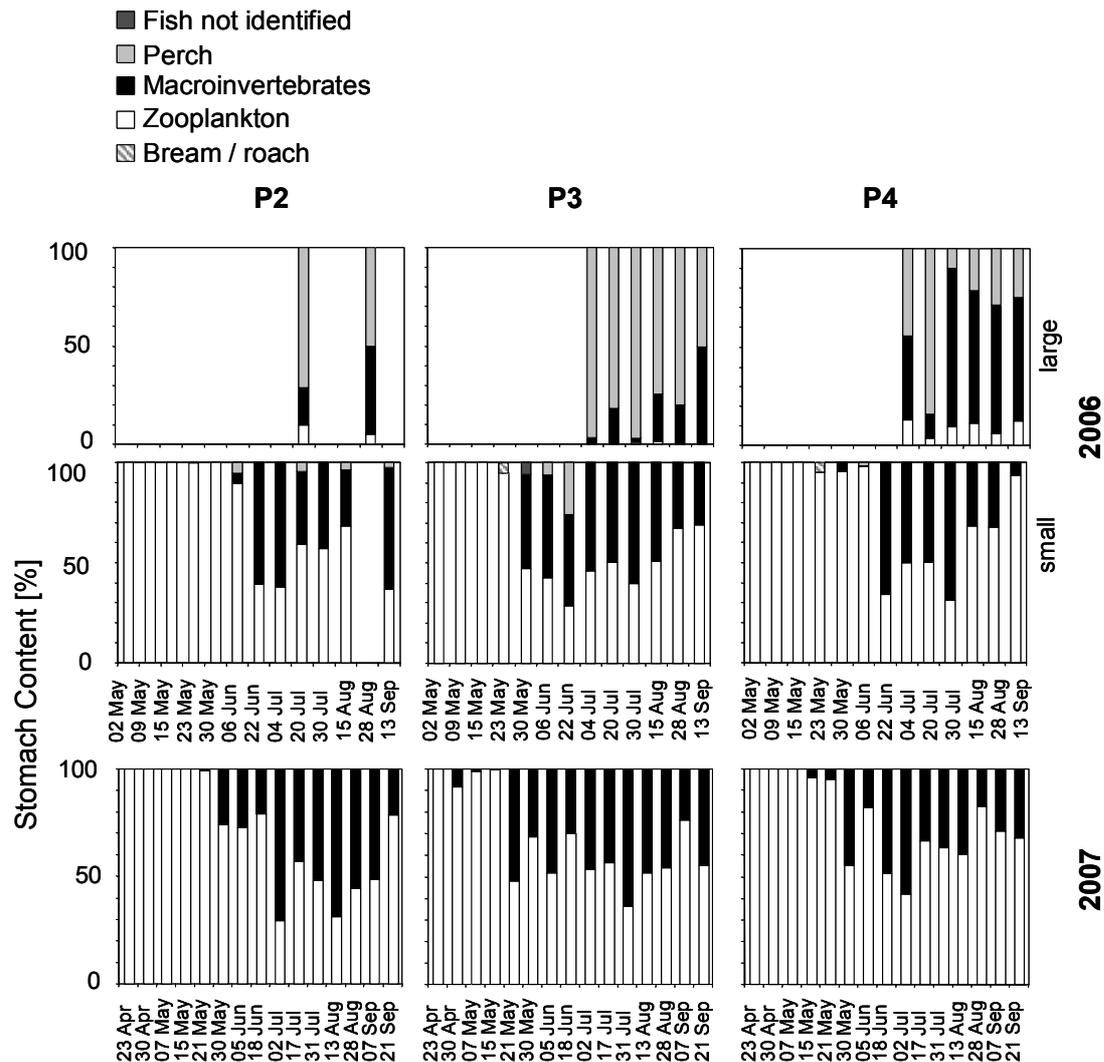


Figure 3: Stomach content [%] of perch in P2, P3 and P4 throughout the season in 2006 and 2007. Where data are missing for the small size-cohort in 2006, not enough perch were available for analyses.

From 4th July on, larger YOY perch in P2, P3 and P4 became cannibalistic, while also still consuming macroinvertebrates. The small YOY perch in all ponds regularly used copepods, daphniids and benthic plankton, sometimes even switching back to low-energy resources, such as rotifers and nauplius larvae. Moreover piscivory of the small size-cohort was rarely observed (Fig. 3) in P2 and P3.

In 2007 until mid May perch in all ponds fed on zooplankton, then beginning increasingly to incorporate macroinvertebrates into their diet. In P3 fish had already begun consuming macroinvertebrates by 30th April (Fig. 3).

Discussion

In this study bream hatched 12 days after perch, while roach hatched simultaneously with perch. Roach then grew twice as fast as bream larvae. In ponds with bream larvae, a section of the perch population became early piscivorous, thus the perch population was ultimately bimodally distributed with the large perch being cannibalistic. In ponds with roach, neither piscivory nor cannibalism occurred and the perch population was unimodally distributed. Despite the fact that the piscivorous/cannibalistic large size-cohort of perch in 2006 reached up to 180 mm TL after their first summer, the small size-cohort of perch in ponds with bream was significantly smaller than perch in ponds with roach.

Early piscivory was shown to be one form of individual specialisation of perch (Heermann et al. Chapter I, Borcharding et al. in prep.), which can occur already during the first months of perch life (Brabrand 1995; Borcharding et al. 2000; Beeck et al. 2002; Borcharding 2006). Increased growth rates are the consequence of the use of the high-energy resource fish (Borcharding et al. 2000, 2007), hence the section of the population which becomes early-piscivorous soon exceeds its planktivorous siblings in length. Thus already during the first growing season a stable bimodal size distribution can be established (Beeck et al. 2002), with the large size-cohort ultimately becoming cannibalistic (Urbatzka et al. 2008). This corresponds to results from the ponds with bream, where some perch specialised at an early stage on bream larvae (also refer Heermann et al. Chapter I). With the reduction of bream, perch soon switched to cannibalism, further enabling high growth rates and the development of maximum sizes of 180 mm. Hence large perch benefit in two ways, firstly by reducing competition for zooplankton with smaller siblings and bream by using an alternative food resource and secondly by diminishing the number of competitors (see also Claessen et al. 2000; 2002; Byström 2006).

The bream:roach ratio, which was 4:1 until two months after perch hatching had changed in favour of roach to 1:5, clearly illustrating that there was a high predation pressure by perch on bream but not on roach larvae. This was supported by stomach content analyses, showing that piscivory at no time occurred in ponds with roach larvae. This suggests that here perch were suffering both from interspecific competition with roach and intraspecific competition with their conspecifics. Roach

is the more efficient feeder especially at low zooplankton concentrations (Persson & Greenberg 1990b). Moreover roach is able to use blue-green algae and detritus as additional food resources (Byström & Garcia-Berthou 1999). One possibility for perch to escape from competition with roach is to use a different habitat than its competitor, (Persson & Greenberg 1990c; Kahl & Radke 2006). However, the ponds are shallow and no differentiation between pelagic and littoral occurs. For perch another possibility to avoid competition with roach is to switch from planktivory to benthivory, as was shown to occur in many other studies (Persson 1986, 1987; Byström et al. 1998) and probably also was the case in this instance, where perch started to feed on macroinvertebrates on 30th of April, at the earliest. However, irrespective of the presence or absence of roach, in all ponds perch, more or less simultaneously began to incorporate macroinvertebrates into their diet. This leads to the conclusion either that the intraspecific competition with conspecifics dominates interspecific competition with roach and forces all perch to expand their diet spectrum, or that due to the absence of a clear differentiation between littoral and pelagic, macroinvertebrates were available from immediately after hatching and are consumed as soon as the size of perch allows.

Why did early piscivory only occur in ponds with bream larvae?

In laboratory experiments Brabrand (2001) demonstrated successful predation on roach with perch ranging between 10 and 63 mm. Comparing these results with field data in Norway illustrated that also under natural conditions perch should be able to develop early piscivory preying on roach (Brabrand 2001). YOY perch need to be about 50% bigger than their prey for successful predation on roach (Brabrand 2001). In our study, however, roach hatched simultaneously with perch; hence gape-size limited perch could not reach the size advantage necessary for piscivory. Although roach were significantly smaller than perch on 5th June roach had about 80 % of the perch size, thus not even the largest perch would have been able to successfully prey on roach.

Compared to perch hatching, bream hatched later than roach (12 days later than perch in 2006), a fact already documented in the temperate European zone (Molls 1999). In addition, the growth rate of bream in P4 two to four weeks after hatching was only half the rate of roach. This could be due to several factors. Apparently bream partly spawns several times a season (Nunn et al. 2002), while roach is a single spawner (Rinchar & Kestemont 1996). Multiple spawning events would have

led to stagnant mean lengths of bream and to a broadened length-frequency distribution. Another reason could have been that the largest bream are selectively preyed upon. However, in our study the length differences of individual bream were small (max. 7 mm) and obviously there was a high predation pressure on bream, resulting in the total erasure of bream in 2006 in P3 only two weeks after early piscivory occurred for the first time, suggesting that all sizes of bream were preyed on. It seems more likely that predator avoidance behaviour caused low growth rates of bream due to a shift of the prey to less profitable microhabitats (Downes 2001).

Low growth rates were also observed for perch of the small size-cohort in 2006. These perch were significantly smaller than perch in 2007, although the biomass of zooplankton and macroinvertebrates were similar in both years. Fish are known to have growth rates negatively correlated to the population density (Parrish & Margraf 1993; Tonn et al. 1994; Schlosser 1998; Taylor et al. 2001). In P2 and P3 the density of fish was much lower in 2007 than in 2006, which could explain the size advantage of perch in 2007. However in P4 the density was only slightly higher, while the size difference in P4 between 2006 and 2007 was most distinct (mean of 18 mm), a fact not supporting the former explanation. Another reason for lower growth rates could be interspecific competition with bream. But roach in particular is known to be a strong competitor which distinctly affects perch (Persson 1983; 1986). Due to a relatively low attack rate but high growth rates and a high energy demand, perch is most vulnerable to density-dependent effects and competition (Byström & Garcia-Berthou 1999) and was shown to have reduced growth rates in the presence of roach (e.g. Persson & Greenberg 1990b; Byström et al. 1998). Indirectly, via resource limitation, roach even negatively affects the fecundity and gonad mass of perch (Persson 1990). Based on these findings reduced growth would have been expected also in P4 in 2007. Since the number of roach in P4 in 2007 at the fish extraction was about twice as high as the number of bream in P4 in 2006, even smaller sizes of perch in 2007 would have been likely.

Hence, most probably the reduction of perch's growth in 2006 is caused by perch suffering from predation by their larger conspecifics. Predator avoidance behaviour causes prey to shift to habitats with lower risk (Eklöv & Svanbäck 2006). Such habitats have often been proven to be structured or vegetated (Pettersson & Brönmark 1993; Snickars et al. 2004; Borcharding 2006; Magnhagen & Borcharding 2008). The new habitat might be more secure but can also be less profitable (Downes

2001). Fish were also shown to change their activity patterns (Alvarez & Nicieza 2003; König et al. 2006) or to strongly reduce activity (Vainikka et al. 2005; Hölker et al. 2007) and food intake (Mikheev et al. 2006). Reduced activity of the small size-cohort of perch was also found in the ponds in 2006 (refer to Scharf et al. in press), suggesting that perch were hiding in the vegetation from their larger cannibalistic conspecifics, thus probably forced to reduce food intake, which then led to minimised growth rates.

This contrasts with studies on competition and predation pressure, suggesting that the negative effect of predators on the growth of their prey weakens under highly competitive conditions (Bolnick & Preisser 2005) or even reverses into a positive effect, elevating growth rates of prey. Resource density should then increase due to suppressed feeding activity of the prey, which in turns leads to higher growth rates of the latter (Peacor 2002). In our study, however, perch in ponds with high competition (high densities) and predation pressure showed decreased growth rates.

Early specialisation of perch on bream larvae leads to cannibalism of some individuals and a bimodal size distribution of the perch population with the development of a few “giants”. These giants do have several advantages compared to the small perch, such as lower winter mortality due to higher energy reserves (Post & Evans 1989; Post et al. 1998; Lappalainen et al. 2000; Biro et al. 2004; Byström et al. 2006; Heermann et al. Chapter I) and early maturation already after the first winter (Beeck et al. 2002). However, in our study giants represent no more than 2.5 % of the population, while the bulk of the population (the small size-cohort) can not benefit from early maturation and low winter mortality, but in fact suffers from high mortality rates (up to 96 %) during winter (Heermann et al. Chapter II, see also Byström et al. 1998). Although perch in 2007 did not prey on roach larvae and could not develop into giants, they reached larger sizes than the small cohort in 2006. Since energy reserves of fishes are positively correlated to size (Brett & Groves 1979; Thompson et al. 1991; Schultz & Conover 1997; Sogard & Olla 2000; Huss et al. in press), these fish probably suffered less from winter mortality than small perch in 2006. Thus, the total recruitment success might be higher for fish in 2007 than in 2006, which could be of advantage for the population as a whole. However, whichever strategy is better - a few large perch and numerous very small perch, or all perch of the same size but not as little - would require further investigation.

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CHAPTER IV

Two size classes of 0+ year perch: is phenotypic plasticity based on food resources?

Two size classes of 0+ year perch: is phenotypic plasticity based on food resources?

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Perch *Perca fluviatilis* of age 0+ years were caught in a gravel pit lake in June (unimodal size distribution) and in July (bimodal size distribution) to analyse morphological differences between the two growth cohorts. Independent of size, 0+ year perch developed a deeper body and perch of the large size cohort had an even deeper body than perch of the small size cohort. This might have been adaptations to either piscivory or planktivory, but might also be a hint that 0+ year perch of the small size cohort were undernourished and that they developed on a different trajectory than individuals of the large size cohort. In a second step the study was extended with a mesocosm experiment. This part of the study was designed to provide preliminary evidence for the extent to which morphological variations may be due to the consumption of different food resources when other factors such as habitat use could be neglected. Two groups of 0+ year perch in four mesocosms were fed for 40 days with the same biomass of either plankton or cyprinids. Although the experimental groups at the end of the experiment did not differ in size, they differed in morphology. The mouth of the piscivorous 0+ year perch became larger, the pectoral fins and the centre of mass of the posterior abdomen were shifted backwards. These results provide further evidence that the type of food is important and might lead to further functional adaptations in morphology.

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Key words: 0+ year perch; early piscivory; food; morphometry; resource polymorphism.

INTRODUCTION

The ability of one genotype to produce alternative morphologies in response to different environmental conditions is called ‘phenotypic plasticity’ and leads to polymorphism within one population. Phenotypic plasticity has been demonstrated for various organisms (Skúlason & Smith, 1995; Smith & Skúlason, 1996; Agrawal, 2001; West-Eberhard, 2002). A plastic response to changing environmental conditions is hypothesized to increase the fitness of individuals (Price *et al.*, 2003). Consequently, phenotypic plasticity is not only designated as an important strategy for organisms to cope with environmental variation

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(Scheiner, 1993) but also may be a driving factor in evolutionary processes (Smith & Skúlason, 1996; Agrawal, 2001). Morphological variation in relation to habitat use and feeding on different food items associated to these habitats is regularly referred to as 'trophic polymorphism' (Skúlason & Smith, 1995; Smith & Skúlason, 1996).

Trophic polymorphism as well as ontogenetic diet and habitat shifts seem to be common especially in fishes (Smith & Skúlason, 1996). High divergence in morphology occurs in many fish species (Day *et al.*, 1994; Wimberger, 1994; Robinson & Wilson, 1996; Mittelbach *et al.*, 1999) and is often related to the use of different habitats (Skúlason & Smith, 1995; Smith & Skúlason, 1996) and an increase in fitness when shifting habitats (Ehlinger, 1990; Schluter, 1993; Svanbäck & Eklöv, 2004). In addition, adaptation to diet was shown to trigger the development of diverging morphologies (Mittelbach *et al.*, 1999; Andersson *et al.*, 2005; Olsson & Eklöv, 2005). Persson (1988) described two distinct ontogenetic diet niche shifts for perch *Perca fluviatilis* L.: perch feed on zooplankton as larvae and small juveniles, then shift to macroinvertebrates and finally become piscivorous when 2 or 3 years old. These diet shifts are regularly related to habitat shifts and are linked with ontogenetic shape changes (Hjelm *et al.*, 2000). Perch were found to develop a deeper body when feeding on macrozoobenthos in the littoral zone and a more slender body when feeding on zooplankton in the pelagic zone (Svanbäck & Eklöv, 2003). A deep body and long fins are hypothesized to be adaptations for high manoeuvrability while searching in the vegetated littoral habitat (Webb, 1984; Ehlinger & Wilson, 1988; Ehlinger, 1990). It is tempting to argue that a specific prey type or habitat is responsible for observed morphological variation, but organisms may also undergo ontogenetic changes independently from environmental conditions (Gilbert, 2000). Consequently, it is difficult to determine the proximate factor for the observed variation in morphology.

Olsson & Eklöv (2005) presented an experimental study in which both habitat structure and feeding mode play important roles in morphological divergence. Habitat structure actually contributed much more to the morphological variation than the feeding mode did (Olsson & Eklöv, 2005). Recently, Beeck *et al.* (2002) presented a study in which 0+ year perch developed into a slow-growing and a fast-growing size cohort and both cohorts used the same habitat with only minor structural diversity. Stomach content analyses revealed that the small, slow-growing size cohort fed predominantly on zooplankton, whereas the large, fast-growing cohort was piscivorous during early summer (Beeck *et al.*, 2002). Thus, the typical observed switch from zooplanktivory to benthivory and then from benthivory to piscivory was displaced by an alternative diet shift from zooplanktivory directly to piscivory. Consequently, the individuals of the study of Beeck *et al.* (2002) may allow further insights into how a diet shift may affect a distinct morphology, as perch are likely to experience an ontogenetic trade-off in optimal morphology (Olsson & Eklöv, 2005).

In a first step, the present study focused on the individuals of the bimodal 0+ year age group of perch presented by Beeck *et al.* (2002), *i.e.* on the morphology of individuals using the same habitat (a gravel pit lake) but feeding on different food resources. At the beginning of June, the size distribution was unimodal; a bimodality in the size distribution developed by the beginning of

July. Detailed analyses of diet, growth and interspecific interactions showed that small perch fed on zooplankton, whereas the prey biomass of the large perch was dominated by bream *Abramis brama* (L.) larvae (Beeck *et al.*, 2002). The flexible ontogenetic diet shifts as well as the morphological variation between different habitats suggest rapid adaptations to environmental conditions (Hjelm *et al.*, 2001). The bimodal size distribution of 0+ year perch that developed within <1 month may therefore reflect not only different growth rates due to different food intake but also related morphological variation. Although stomach content analyses revealed that the large cohort was at least temporarily piscivorous while the small cohort fed on zooplankton, it is not possible to rule out the possibility that other food resources were used as well (Beeck *et al.*, 2002). Therefore, in a second step the study was extended with a mesocosm experiment in which 0+ year perch were fed with either zooplankton or with fishes for 40 days. This part of the study was designed to help reveal the extent of morphological variation due to the consumption of different food resources; other factors such as habitat use could be neglected.

MATERIAL AND METHODS

FIELD SAMPLES

Fish were collected in Lake Speldrop (51°46'51" N; 6°22'42" E), a gravel pit lake at the Lower River Rhine, Germany, where mining stopped *c.* 40 years ago. The lake's area is 7 ha and its maximum depth 16 m. Most of the banks are steep (>60°) and consist mainly of sand and gravel. Submerged vegetation is almost absent. Lake Speldrop is highly eutrophic (chlorophyll *a* concentrations of 20–50 µg l⁻¹ during summer; G. Heinze, pers. comm.) and stratified during summer with a small epilimnion of *c.* 5 m depth between July and October (Beeck *et al.*, 2002).

Juvenile perch (age group 0+ years) were caught with a beach seine (mesh-size: 1 mm, length: 10 m) and gillnets (mesh-sizes 6, 8, 10, 12, 15 mm, length: 15–20 m) between June and July 1999 in the littoral zone of the lake. The nets were set 1 h before sunset and 1 h before sunrise the following morning for 4 h. All perch were measured [total length, L_T (mm)] and weighed [wet body mass, M (g)]. Fish were stored in 4% formaldehyde for morphometric analyses.

MESOCOSM EXPERIMENTS

Juvenile perch were caught by electrofishing in a floodplain lake (51°46'60" N; 6°19'60" E) of the Lower River Rhine, Germany, in June 2005. Because the perch here are not usually piscivorous during their first year the population does not develop a bimodal size distribution (A. Scharbert, pers. comm.). Four mesocosms (round fish tanks of 1.1–1.8 m³ without any internal structures) were stocked with 20 perch each (mean L_T 41 mm). Another 20 perch were deep-frozen in water as reference material for the morphological analysis. Since fish were frozen in water and defrosted with care any change of body morphology influencing the analysis can be excluded. After 2 days of acclimatization, perch of two mesocosms were fed with fish larvae [bream and white bream *Blicca bjoerkna* (L.)] (range of L_T of prey fishes at beginning of the experiment: 12–17 mm; at the end of the experiment: 20–33 mm) for 40 days; perch of the other two mesocosms were fed with zooplankton (mainly *Daphnia* spp. and copepods). The total biomass of the fish prey was calculated using L_T and M regressions (Molls, 1997), and approximately the same mass of zooplankton was given to the other two mesocosms.

Both groups were fed with a sufficient ration of prey to ensure good food conditions based on laboratory experiments (Borcherding *et al.*, in press).

MORPHOMETRIC ANALYSIS AND STATISTICS

Fish of field ($n = 93$) and mesocosm experiments ($n = 91$) were photographed together with a ruler using a digital camera. Before being photographed, all fish were placed on a piece of styrofoam with a cavity to avoid deformation. Fourteen landmarks as well as the ruler endpoints were digitized with the tpsDigit and tpsUtility software (available at: <http://life.bio.sunysb.edu/morph/>) and the x - y co-ordinates were recorded (Fig. 1). Fish samples of field experiments were grouped for the analysis according to the time of catch and the affiliation to a growth cohort; fish of laboratory experiments were grouped according to the food resource with which they were fed (Table I). The further analysis was done with the Integrated Morphometrics Package (IMP) (<http://www2.canisius.edu/~sheets/morphsoft.html>).

All photographs were re-scaled to the same magnification with the IMP software CoordGen6. Centroid size (the square root of the sum of squared distances of all landmarks from their centroid) was calculated for all specimens, and in the following analysis, ln-transformed centroid size (LCS) was used as size variable. In geometric morphometrics, size is defined as the information in the landmark configurations that is not altered by arbitrary translations, rotations and rescaling of all of the data points (Kendall, 1977). The generalized least squares Procrustes superimposition method fits all specimens in a data set to an estimated mean (reference) specimen by minimizing the sum of squared distances between landmarks of each specimen and the corresponding landmarks of a reference specimen (Rohlf & Slice, 1990). Procrustes superimposition was performed with all specimens with the IMP software programme CoordGen6. The shape change of groups (*e.g.* small and large growth cohort or piscivorous and planktivorous fish) was analysed with a canonical variates analysis (CVA) using the software CVA Gen6. CVA is a method for finding the set of axes that allows for the greatest possible discrimination between two or more groups. Partial warp scores were computed and a MANOVA followed by a CVA were conducted. The tests of significance of the canonical variate axes are all based on Wilk's λ value at a $P < 0.05$ level of significance. CVA Gen6 was also used to depict the deformation as vectors on landmarks for all samples.

Fish from the field survey differed in size and the two growth cohorts developed at different growth rates. Therefore, potential morphological differences were examined for allometric effects. To test for allometry in the data set, it was appropriate to compute non-uniform (partial warp scores) and uniform components of shape from a thin-plate spline decomposition (TPS; Bookstein, 1991), as these variables have the appropriate

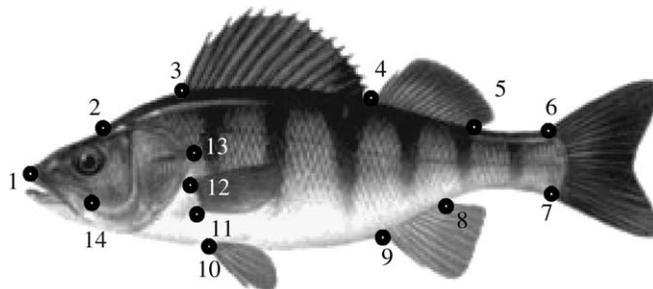


FIG. 1. Digitized landmarks (1–14) of juvenile perch used in the analysis of morphological variation in the bimodal size distribution.

TABLE I. Samples for morphometric analyses

| Date | Cohort/group | <i>n</i> | Mean \pm s.d. L_T (mm) | Mean \pm s.d. M (g) |
|-----------|--------------------|----------|----------------------------|-------------------------|
| June 1999 | Unimodal | 28 | 59 \pm 5 | — |
| July 1999 | Small | 30 | 74 \pm 1 | — |
| | Large | 35 | 94 \pm 7 | — |
| June 2005 | Starting point | 20 | 41 \pm 2 | — |
| July 2005 | Piscivorous fish | 33 | 69 \pm 5 | 4.0 \pm 1.0 |
| | Planktivorous fish | 38 | 67 \pm 5 | 3.6 \pm 0.9 |

n, number analysed; cohort/group, perch were pooled either according to the affiliation to a growth cohort or to the food resource used; L_T , total length; M , wet mass.

(2k–4) d.f. The uniform and non-uniform (partial warp scores) components were calculated using the IMP programme PCAGen6. The PCAGen6 software programme calculates a consensus specimen from all input data by a Procrustes superimposition and uses this consensus as a reference specimen in calculating the partial warp scores. Non-uniform (partial warp scores) and uniform components of shape were then used in a regression analysis of the shape change as a function of ln-centroid size (Bookstein, 1991, 1996; Zelditch & Fink, 1995; Kim *et al.*, 2002). The IMP software Regress6 was used for this purpose. The overall shape change was analysed with a MANCOVA by combining the partial warp scores and the uniform components with cohort as the grouping variable and LCS as the covariate (Zelditch *et al.*, 2000). A significant interaction term between the cohorts and the covariate was interpreted as indicating that the cohorts had different ontogenetic growth trajectories. When that interaction was significant, shapes were standardized by regressing each population on size separately and calculating residuals, which were then added to the predicted shape at some specified value of LCS, where the predicted value is taken from the regression model. With the standardization of the data to a specific value of LCS, the variance attributable to LCS can be removed, leaving the shape variation that is not attributable to size. The standardization procedure was performed with the IMP software Standard6. The means of the standardized shape variables of the two cohorts were then compared with a bootstrapped Goodall's *F*-test, and the morphometric distance between them was measured as a (partial) Procrustes distance between them; CI for that distance were obtained by bootstrapping; bootstrapped partial Procrustes distance between the cohorts was calculated with the IMP software TwoGroup6. Bootstrap tests were carried out to determine the probability that the observed differences between the groups could have arisen by chance.

As the individual fish in the mesocosm experiment cannot be used as replicates (pseudoreplication; Hurlbert, 1984) a different statistical approach was applied. For each mesocosm, the mean CVA scores of the separating axis were calculated and finally compared with a *t*-test using SPSS (ver.12.0 SPSS Corp.).

RESULTS

FIELD SAMPLES

The multivariate regression of partial warp scores plus uniform components on LCS did not reveal allometric growth within both growth cohorts. The canonical variate analysis of the two growth cohorts found one significant CVA axis ($\lambda = 0.141$, χ^2 , d.f. = 24, $P < 0.001$, eigenvalue = 6.104). The graphical presentation of the canonical variate scores of the two growth cohorts

along the first two canonical variate axes is given in [Fig. 2(b)]. Only one specimen of the small cohort could not be discriminated from the large cohort along the first canonical variate axis. Ontogenetic shape changes are depicted by changes in the location of shape co-ordinates [Fig. 2(a)]. The most striking differences in shape between the two growth cohorts at individual landmarks are at the posterior region of the head at the dorsal midline and the insertion and posterior end of the first dorsal fin (landmarks 2, 3 and 4) as well as at the tail (landmarks 5, 8 and 9). More subtle differences in shape are at the origin of the pectoral fins and at the end of the operculum (landmarks 11, 12 and 13). When observing all the differences between the growth cohorts over the whole configuration of landmarks [Fig. 2(a)], it becomes obvious that the large growth cohort has a deeper body in comparison to the small growth cohort.

To examine ontogenetic shape change not attributable to size, partial warp scores plus uniform components were standardized to LCS 4.43 (equals a length of *c.* 84 mm, which is the mean L_T of the pooled samples). The results of the comparison between the means of the two groups before and after the standardization procedure show that the means of the two growth cohorts were still significantly different after removing size-dependent variation from the data (before: $F_{24,1512}$, $P > 0.01$, distance = 0.030, 95% percentile range = 0.026–0.037; after: $F_{24,1512}$, $P > 0.01$, distance = 0.032, 95% percentile range = 0.029–0.037). The observed shape change between the two growth cohorts is not based on size-dependent variation and the morphological difference between them was not an effect of one having a larger mean size than the other, *i.e.* the large growth cohort was not an allometrically scaled-up replica of the smaller one.

After the inclusion of juvenile perch from June into the CVA, *i.e.* the inclusion of fish before the bimodal size distribution had occurred, two significant canonical variate axes were found (axis 1: $\lambda = 0.008$, χ^2 , d.f. = 48, $P < 0.001$, eigenvalue = 38.78; axis 2: $\lambda = 0.333$, χ^2 , d.f. = 23, $P < 0.001$, eigenvalue = 2.0). The first canonical variate axis discriminated the June sample from the later samples (July, small and large growth cohort) and explained most of the observed shape change [Fig. 2(d)]. Between June and July, the juvenile perch developed a smaller head (landmark 2), a deeper body (landmarks 3, 4 and 9) and a shorter tail (landmarks 5 and 8), independent of affiliation to a growth cohort [Fig. 2(c)]. The deepening of the body, however, was not as distinct as between the two growth cohorts [Fig. 2(a)]. The second canonical variate axis discriminated the small growth cohort from the June sample and from the large growth cohort [Fig. 2(f)]. In other words, the unimodal June sample and the large growth cohort were morphologically more similar to each other than to the small growth cohort. The shape change implied by the second canonical variate axis is displayed in [Fig. 2(e)]. The small growth cohort had a more slender body than the large growth cohort and the June sample (landmarks 2, 3 and 4). The tail was longer and more downwardly curved (landmarks 5, 8 and 9), and the pectoral fins as well as the end of the operculum were shifted ventrally (landmarks 11, 12 and 13).

There was a detectable shape change between the unimodal size distribution in June and later samples of July (independent of the affiliation to a growth cohort) after which the two growth cohorts diverged along two independent ontogenies. Furthermore, the CVA indicates that the shape of the small growth

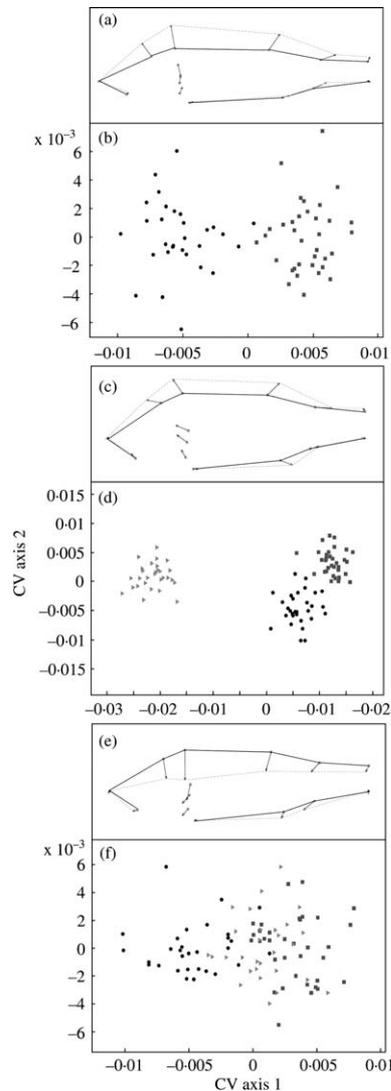


FIG. 2. Morphometric analyses of the field samples. (a) Shape change correlated with the first CVA axis between the two growth cohorts of 0+ year perch from Lake Speldrop 1999, obtained by regressing the shape on the CVA axis scores, depicted as growth vectors starting from the small cohort and (b) canonical variate scores of the small ● and the large ■ growth cohort, depicted along the first and the second canonical variate axis. (c) Shape change correlated with the first CVA axis between the June sample and the two growth cohorts of 0+ year perch from Lake Speldrop 1999, obtained by regressing the shape on the CVA axis scores, depicted as growth vectors starting from the June sample and (d) canonical variate scores of the June sample ►, the small ● and the large ■ growth cohort, depicted along the first and the second canonical variate axis. (e) Shape change correlated with the second CVA axis between the small growth cohort and the large growth cohort and the June sample of 0+ year perch from Lake Speldrop 1999, obtained by regressing the shape on the CVA axis scores, depicted as growth vectors starting from the large growth cohort and (f) canonical variate scores of the June sample ►, the small ● and the large ■ growth cohort, depicted along the second and third canonical variate axis.

cohort differed from the shape of the unimodal size distribution and the shape of the large growth cohort.

MESOCOSM EXPERIMENTS

During the experiment, 0.18 g prey fishes (3.81 individuals) per perch per day and 0.15 g zooplankton per perch per day were given in each of the two mesocosms. Piscivorous fish grew 0.70 mm day⁻¹ and planktivorous ones 0.66 mm day⁻¹, so that by the end of the experiment the two groups did not differ in size (mean L_T of piscivorous fish: 69.2 mm; mean L_T of planktivorous fish: 67.4 mm; *t*-test, d.f. = 69, $P > 0.05$) or mass (mean M of piscivorous fish: 3.96 g; mean M of planktivorous fish: 3.59 g; *t*-test, d.f. = 69, $P > 0.05$). Thus, differences in shape were not related to size differences, and it was not necessary to test the data set for allometry for the comparison of the two experimental groups.

The canonical variate analysis of the three groups ('starting point', piscivorous fish and planktivorous fish) resulted in two significant CVA axes (axis 1: $\lambda = 0.043$, χ^2 , d.f. = 48, $P < 0.001$, eigenvalue = 9.303; axis 2: $\lambda = 0.445$, χ^2 , d.f. = 23, $P < 0.001$, eigenvalue = 1.246). The first axis divided the 'starting point' group from the piscivorous and planktivorous fish [Fig. 3(d)]. The prey-independent change in shape during ontogeny is shown in [Fig. 3(c)]. Fish developed a deeper body (landmarks 3, 4, 9 and 10) as shown before with the field samples. In addition, the pectoral fins (landmarks 11 and 12) and the operculum (landmark 13) were shifted dorsally and backwards. The tail of the fish developed to a shorter and more slender form (landmarks 5 and 8), as also occurred in the fish of the field samples.

In a second step, the 'starting point' group was excluded to analyse whether there were differences in shape between piscivorous and planktivorous fish. Based on the mean CVA scores of the separating axis, the planktivorous and the piscivorous groups differed significantly [*t*-test, d.f. = 2, $P < 0.05$; Fig. 3(b)]. Although planktivorous and piscivorous fish had the same size, there were distinct differences in shape. Piscivorous 0+ year perch developed a larger mouth (landmark 14), while their pectoral fins (landmarks 11 and 12) and centre of mass of the posterior abdomen were shifted upwards and backwards [landmarks 4, 5, 8 and 9; Fig. 3(a)]; the fish tail was then curved downwards, as already shown for the large growth cohort of the field samples.

DISCUSSION

The present study showed that both size classes of the bimodal size distribution of 0+ year perch from Lake Speldrop differed significantly in shape. In most cases, bimodality was attributed to a difference in resource use: slow-growing individuals fed on zooplankton and fast-growing individuals on fishes (DeAngelis & Coutant, 1982; Beeck *et al.*, 2002). An increasing number of studies have shown that different resource uses can lead to distinct ecomorphotypes that are adapted to their specific prey (Skúlason & Smith, 1995; Smith & Skúlason, 1996; Mittelbach *et al.*, 1999; Svanbäck & Eklöv, 2003). Interestingly, none of the studies on the development of a bimodal size distribution in juvenile fishes have investigated the relationship between growth, resource use and variation in shape.

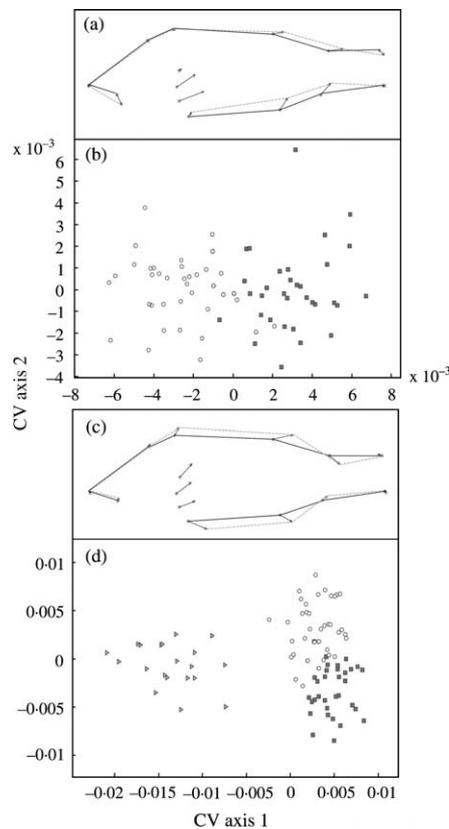


FIG. 3. Morphometric analysis of the mesocosm experiments. (a) Shape change correlated with the first CVA axis between the piscivorous and the planktivorous group of 0+ year perch in the mesocosm experiments, obtained by regressing the shape on the CVA axis scores, depicted as growth vectors starting from the planktivorous group and (b) canonical variate scores of the planktivorous ○ and the piscivorous ■ group, depicted along the first and the second canonical variate axis. (c) Shape change correlated with the first CVA axis between the 'starting point' group and the piscivorous and planktivorous group of 0+ year perch in the mesocosm experiments, obtained by regressing the shape on the CVA axis scores, depicted as growth vectors starting from the 'starting point' group and (d) canonical variate scores of the 'starting point' group ▶, the planktivorous ○ and the piscivorous ■ group, depicted along the first and the second canonical variate axis.

The juvenile perch for the present study were taken from a eutrophic gravel pit lake, where they regularly develop a bimodal size distribution. (Beeck *et al.*, 2002; Beeck, 2003). A fraction of the 0+ year perch year class shifted to a piscivorous diet and avoided interspecific competition with cyprinids for zooplankton by eating their potential competitors. They eliminated all juvenile bream in the lake between June and July in the years 1999, 2000 and 2001 and developed into a small and a large growth cohort with different resource uses (Beeck, 2003). Sub-samples from the fish of 1999 were taken for the analysis of shape change. A rapid ontogenetic shape change in body form within 1 month as well as a divergence between two morphs was documented. The large, mainly piscivorous growth cohort had a deeper body than the smaller

planktivorous growth cohort, independent of size. This could illustrate adaptations to diet, since a slender body form with a terminal mouth is generally a characteristic of planktivorous perch (Schluter, 1993) and of perch which feed in open habitats (Olsson & Eklöv, 2005). Streamlined bodies are better adapted to search for widely dispersed plankton because such morphology reduces drag during steady swimming (Webb, 1984; Webb & Weihs, 1986).

Svanbäck & Eklöv (2002) also found a positive correlation between the body depth of perch from the littoral zone and the proportion of fishes in their diet. They argued that high manoeuvrability may be of general importance for a piscivore, as predatory perch adjust their attack speed to the prey escape speed to facilitate manoeuvrability during attacks (Lundvall *et al.*, 1999). In several studies, a deeper body and a subterminal mouth have also been shown to be characteristic of benthivorous perch and of perch which feed in the littoral habitat (Hjelm *et al.*, 2001; Olsson & Eklöv, 2005). A deep body and long fins are hypothesized to be adaptations enabling a high manoeuvrability while searching in the vegetated littoral habitat (Webb, 1984; Ehlinger & Wilson, 1988; Ehlinger, 1990). Lake Speldrop, however, has very steep banks with virtually no submerged vegetation, *i.e.* a very small, simply structured littoral zone (Beeck *et al.*, 2002; Beeck, 2003) and macroinvertebrates never played an important role in the diet of juvenile perch in the present study. Therefore, adaptations to complex habitats and to a benthivorous feeding mode may not be the factors triggering the difference in morphology between the small and the large growth cohort.

Besides diet and habitat use as factors influencing morphology, the results from Lake Speldrop suggest also that the ontogenetic growth trajectory in juvenile perch, independent of the diet niche, may contribute to a large extent to the observed shape change. Between June and July 1999, both the small planktivorous and the large piscivorous growth cohort developed a shorter tail and a deeper body compared to the shape of the population at the beginning of June, when the size distribution was unimodal. It is tempting to argue that a specific prey type or habitat is responsible for observed morphological variation, but organisms undergo ontogenetic changes independently of environmental conditions (Gilbert, 2000). Thus, the development of a deeper body could be the species-specific ontogenetic growth trajectory in juvenile perch (Svanbäck & Eklöv, 2002) and not the result of different resource use.

The comparison between the morphological differences of the unimodal size distribution and the two growth cohorts further suggests that the growth trajectory of body morphology of the large, piscivorous and the small, planktivorous growth cohort lie on different growth trajectories. Again this could illustrate adaptations to diet. Due to the fact that the large growth cohort was morphologically more similar to the unimodal cohort of June, however, it might also be argued that the large, piscivorous cohort lies on the species-specific growth trajectory, while the growth trajectory of the smaller, planktivorous perch differs from the species-specific growth trajectory. Fish of the small size cohort might be undernourished and therefore are suggested not to be able to follow the species-specific trajectory and to develop a deeper body.

The maximum growth rate for perch feeding on zooplankton is *c.* 0.6 mm day⁻¹ (Byström & Garcia-Berthou, 1999), whereas it can reach up to 1.5 mm day⁻¹ for juvenile piscivorous perch (Beeck *et al.*, 2002). Furthermore, juvenile

perch feeding on fishes are able to store more energy in lipid reserves than planktivorous perch (Borcherding *et al.*, in press), revealing that fishes are a more profitable food source. For these reasons, a slender body morphology may not only be an adaptation to planktivorous feeding but could also indicate undernourishment. For example, the proportion of empty stomachs in the small growth cohort was twice as high as in the large growth cohort in September 1999 (Beeck *et al.*, 2002). Piscivorous and planktivorous fish did not differ in outer body shape in the mesocosm experiments and both grew at similar rates ending up at the same L_T and M . In these experiments, the influence of a different state of nutrition and of different growth rates can be excluded and, thus, the results support the theory that the differences in shape between the small and large growth cohort of Lake Speldrop were due to the small cohort being undernourished, while different habitat conditions did not play any role.

Although the piscivorous and planktivorous fish in the mesocosm experiments had similarly deep bodies, distinct morphological differences between them became obvious. Piscivorous fish in the experiment developed a more subterminal mouth than planktivorous fish, which is known to be an adaptation to piscivory (Norton, 1995) that helps the predator to capture relatively large prey and to reduce gape-size limitation and postcapture efforts (Hart & Hamrin, 1988; Christensen, 1996; Mittelbach & Persson, 1998). During ontogenetic development, both the piscivorous and the planktivorous group showed a shift of the pectoral fins upwards and backwards, towards the centre of the fish. This shape change was more distinct in piscivorous fish. The development of a larger mouth led to an expansion of the head and the lower jaws and secondarily might have led to the additional shift of the pectoral fins in such fish. As the pelvic fins were shown to be important for manoeuvrability (Svanbäck & Eklöv, 2002), the upwards and backwards shift of the pectoral fins might also lead to an improved manoeuvrability, especially when the fish is turning (J. Ohlberger, pers. comm.), and could be an adaptation to piscivorous feeding. It then seems to be of advantage for planktivorous fish to have their pectoral fins more ventrally situated to float in the water while searching for prey. Another difference in shape between planktivorous and piscivorous fish, which developed during the mesocosm experiments, regards the centre of mass of the tail. Piscivorous fish were more downwardly curved than planktivorous fish; the centre of mass was shifted upwards and backwards, confirming the results of the field study. Olsson & Eklöv (2005) argued that downward curving was correlated to high growth rates and upward curving to low growth rates. The mesocosm experiment, however, revealed no differences in growth rate; this question needs further investigation. Nevertheless, the shift of the centre of mass of the posterior abdomen could also increase the swimming speed necessary for catching fish prey (J. Ohlberger, pers. comm.).

In conclusion, the growth cohorts of the bimodal size distribution clearly differ in shape. The adaptive significance of such differentiations, however, needs further studies, especially concerning the relationship of certain morphological changes and their effect on the swimming ability and manoeuvrability of the fish. Nevertheless, resource polymorphism between the two cohorts is evident, as the development of different phenotypes was accompanied with different resource usage in the mesocosm experiments.

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CHAPTER V

Development of abundance and size structure of young-of-the-year perch populations using three methods

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Abstract

The reliable assessment of fish populations, which can vary in their spatial and demographic structure, assumes that the results are independent of the assessment method used. To test this assumption for the size structure of the young-of-the-year (YOY) age cohort of perch, three gravel pit lakes and four shallow ponds were monitored using three sampling methods from May to October. While bongo nets were used for early juveniles in the pelagic zone, electrofishing and multi-mesh gillnets were used later in the year when perch had moved to the littoral zone. Since bigger perch (post-larvae) switch from the pelagic to the littoral zone during ontogenesis, bongo net catches during June in the pelagic area of the lakes sampled only the smaller perch, while simultaneous electrofishing in the littoral zone caught bigger perch. Later in the season in the littoral zone, smaller perch were caught only by electrofishing and the bigger ones with gillnets. Monthly samples caught by electrofishing and gillnets in the experimental ponds from June to September showed even larger differences between the sizes of perch. Because the size distribution of the YOY perch cohort in the ponds had broadened considerably, there was sometimes no overlap in the length-frequency distributions between the two methods used, clearly demonstrating that using a single method is not sufficient for drawing a complete picture of the population size structure. This was verified by the removal of fish from the experimental ponds in October. Our results give clear evidence (and thus confirm previous studies) that using one method alone would result in an incomplete picture of the development of the size structure of the YOY perch population, due to the facts that (1) not all perch switch simultaneously between different habitats during ontogenesis and (2) that swimming performance, habitat-specific occurrence and activity change with size, thus affecting the method-specific catchability. Consequently, at least two appropriate methods must be used in an overlapping/parallel sampling design in order to draw a reliable picture of the development of the YOY perch population in any given body of water.

Introduction

Fish sampling programs and devices must provide accurate measurements of both changes in abundance and variations in the size structure of the population in order to obtain key parameters like density, growth or mortality rates. Furthermore, survey design must provide adequate spatial and temporal resolution (Pepin and Shears, 1997) to enable field samples to reveal habitat-related ecological processes. Proper understanding of the processes that influence population dynamics of fishes in temperate waters is based on extensive knowledge of recruitment from the juvenile to the adult stage (Persson and Greenberg, 1990; Post and McQueen, 1994). Differential food uptake in terms of quality and quantity affects not only the size of juvenile fishes (Byström and Garcia-Berthou, 1999; Borcharding et al., 2000; Beeck et al., 2002; Persson et al., 2004) but also their morphology (Svanbäck and Eklöv, 2002; Eklöv and Svanbäck, 2006; Olsson et al., 2006; Heermann et al., 2007), their behaviour in the trade-off between foraging and predation risk (Borcharding, 2006; Magnhagen and Borcharding, 2008; Borcharding and Magnhagen, 2008; Olsson et al., 2007) and the energy reserves that can be used up during periods of food shortage in winter (Griffiths and Kirkwood, 1995; Borcharding et al., 2007). Thus, knowledge of the ecological processes in juvenile fishes during the period from hatching in spring until the first winter is essential in order to understand recruitment into the adult stage.

Besides methodological constraints on the accurate sampling of larval and juvenile fish, the assessment of development may be further complicated when ontogenetic habitat shifts occur. After hatching, Eurasian perch (*Perca fluviatilis*) move to the pelagic zone and remain there for 1-2 months before they return to the littoral zone (Wang and Eckmann, 1994). This habitat shift may be associated with a size-related ontogenetic shift in their diet (Persson and Greenberg, 1990). Early piscivory in juvenile perch leads to a bimodal length-frequency distribution (LFD) after the first summer (cf. Beeck et al., 2002). To study this, Urbatzka et al. (2008) conducted experiments in shallow experimental ponds to quantify food uptake and related growth of young-of-the-year (YOY) perch. Because the ponds were not only shallow but also contained extended areas of submerged vegetation, the authors used electrofishing, which was expected to be the best method for that habitat (Cowx, 1989). During the sampling period from June until the end of August, only perch

smaller than 60 mm in total length (TL) were caught in the ponds, and the calculated growth rates were low in comparison to samples from gravel pit lakes of the same geographical region (cf. Borcharding et al., 2007; Urbatzka et al., 2008). However, after draining the ponds at the end of the experiment and extracting all the perch, the LFD revealed that about 10 % of the approximately 45,000 YOY perch ha⁻¹ were larger than 100 mm TL; the largest were 175 mm TL (Urbatzka et al., 2008). This example raises the question as to why all these larger perch were never caught in the experimental ponds during the summer season, although an appropriate and generally accepted method was used.

In our study we repeated the experiments of Urbatzka et al. (2008) in the ponds. In addition to electrofishing, however, we also applied multi-mesh gillnets (Appelberg, 2000) which were especially adapted to the small (0.4-0.7 ha) and shallow ponds and to the size of juvenile perch. We expected to find extreme differences in the LFD of perch sampled using the two methods in a parallel sampling design. To be able to give more general recommendations for the sampling of YOY perch in larger and deeper waters as well, we additionally investigated three different gravel pit lakes using both methods. With respect to the development of the perch larvae in the pelagic zone after hatching, we used bongo-net fishing in spring as a third standard method (Pepin and Shears, 1997; Wanzenböck et al., 1997; Tischler et al., 2000). In addition to the methodological comparison with overlapping electrofishing in the littoral zone, the results should help determine whether the offshore period of perch is time-restricted (Wang and Eckmann, 1994) or whether it depends on a critical size in relation to developmental stage (Urho, 1996).

Materials and Methods

Study sites

The YOY perch populations of three gravel pit lakes situated by the Lower River Rhine were sampled (Borcherding et al., 2007). The first lake, Lake Speldrop, is situated near Rees ($51^{\circ}46'50''\text{N}$, $6^{\circ}22'42''\text{E}$; Germany). Excavation here stopped in the 1960s without any following reconstruction of the biotope. This eutrophic lake has a surface area of about 7 ha and a maximum depth of about 16 m. The depth depends on the groundwater level, which in turn depends on the water level of the River Rhine. With the exception of some small littoral areas of moderate incline, the banks are steep (inclination of about $30 - 45^{\circ}$) and mainly covered with gravel, bricks and other construction debris. Sedimented sludge is completely absent and submerged macrophytes are not established. Phanerophytes grow along almost the entire shoreline, protecting the lake from wind so that there is usually a stable summer stagnation with an anoxic hypolimnion starting at a depth of about 5 to 6 m.

The second site, the mesotrophic Lake Reeser Meer, was partly reconstructed during the early 1990s. It is also situated near Rees ($51^{\circ} 45'\text{N}$, $6^{\circ} 28'\text{E}$, Germany). Its surface area is about 28.5 ha; the maximum depth is about 17 m, depending on the groundwater level. Due to reconstruction, the littoral zone is not as homogeneous as in Lake Speldrop. Some of the gentle slopes are covered with sedimented sludge, others are covered with gravel. Where aquatic plants are present, a submerged macrophyte (*Elodea* sp.) is prominent, covering the entire littoral zone in some areas. Due to the absence of phanerophytes, especially along the northwestern shore line, the lake is not as well protected from the wind as Lake Speldrop. Both waters lie outside the normal floodplain of the River Rhine, in contrast to the third investigated water, Lake Pfeiffer.

Lake Pfeiffer is located near Xanten ($51^{\circ}38'16''\text{N}$, $6^{\circ}29'02''\text{E}$; Germany) and is situated in the floodplain of the River Rhine. Consequently, during periods of high water it is temporarily connected with the Rhine via an oxbow. The lake is mesotrophic and more shallow than the other two lakes discussed above. Its maximum depth is about 5 m, depending on the water level of the River Rhine, and its surface area is about 7 ha. The shoreline is surrounded by phanerophytes, and the littoral zone is similar to that of Lake Speldrop; so most banks are steep, except one with a moderate inclination, and sedimented sludge is almost completely absent. The

littoral zone of Lake Pfeiffer is normally covered with *Elodea* sp. down to a depth of approximately 3 m, but in 2006 these macrophytes were found only in small, irregularly spread patches. In contrast to the other lakes, the presence of woody debris greatly increases the structural diversity of the littoral zone.

In addition to sampling the gravel pit lakes, YOY perch populations were monitored in four ponds with areas of 0.4 to 0.7 ha and maximum depths of 2 m (mean depths of about 1 m, Urbatzka et al., 2008). The ponds are situated near Lohmar (50°49'33''N, 7°12'59''E; Germany). These ponds are fed by a small stream, are situated in a line and are connected by overflows. They are oligo- to mesotrophic. The ponds were completely drained in late winter. Ponds 3 and 4 were later restocked with calculated ratios of mature perch and bream *Abramis brama* (not further considered in this study), and ponds 1 and 2 restocked solely with mature perch. When the parental fish had spawned, they were removed from the ponds by gillnetting to guarantee undisturbed development of the offspring. The ponds were partially to completely covered by submerged vegetation e.g. *Potamogeton* sp. or *Chara* sp., and therefore the structural diversity of these waters can be characterized as relatively complex.

Fish sampling

Bongo net sampling

Immediately after hatching, larval perch undertake a clear habitat shift into the pelagic zone where they stay until the early fingerling stages (Wang and Eckmann, 1994). Using bongo nets, we caught the perch from larval to early fingerling stages weekly in the pelagic zone of the lakes (cf. Pepin and Shears, 1997; Wanzenböck et al., 1997). Sampling was always performed after sunset (Wang and Eckmann, 1994; Guillard et al., 2006). In the experimental ponds, however, no bongo net trawling was possible because the ponds are too shallow and large areas are covered with submerged vegetation.

We used two parallel bongo nets fixed to an aluminum boat (4 m length) with a 3.7 kW outboard motor (Fig. 1). The mouth of each net was 0.5 m in diameter, stabilized by a stainless steel frame. The main cylinders of the net had dark entrances and were 1.8 m long, followed by 0.5 m long cones (Fig. 1). The mesh size was adapted to the developmental stage of the fish, with three different mesh sizes being used: 0.75 mm by 1.5 mm, to 1.5 mm square, and at least 3 mm square. The towing speed ranged

from 3.8 km h^{-1} for the smallest mesh size to 6.9 km h^{-1} for the net with biggest mesh size. The push net was fixed on a steel frame which could be lowered down to 1.5 m. The other net was a trawl which was connected by rope to a hoist. An iron weight of 32 kg was fixed on the distal side of the net frame. The weight held the bongo net vertical during towing. Additionally, the net was braced by two 0.5 mm diameter stainless steel wires fixed on the lower third of the net's frame. These wires were 0.5 m long and ran together to a small polyamide rope which was fixed to a frame on the front of the boat. The trawl net was used down to a depth of 4 m. At top speed, the net with the biggest mesh size was usable down to 2 m. The amount of filtered water was estimated with a flow meter (Hydrobios, Kiel, Germany). On every sampling date, four surveys were performed with both type of nets, resulting in a total of eight samples taken in different depths (3x 0.5-1m; 2x 1-1.5m, 1x 1.5-2m; 1x 2.5-3m; 1x 3.5-4m). To standardize the number of perch caught during the season, irrespective of the sampling depth (not considered in this study), the catch per unit effort for this method (CPUE_B) was calculated as follows: first the mean density was calculated for three depth classes (<1m, 1.5-3m, >3m, including zero samples) and then averaged as individuals per m^3 for one date and location. All caught fish were immediately fixed in 4% formaldehyde solution.

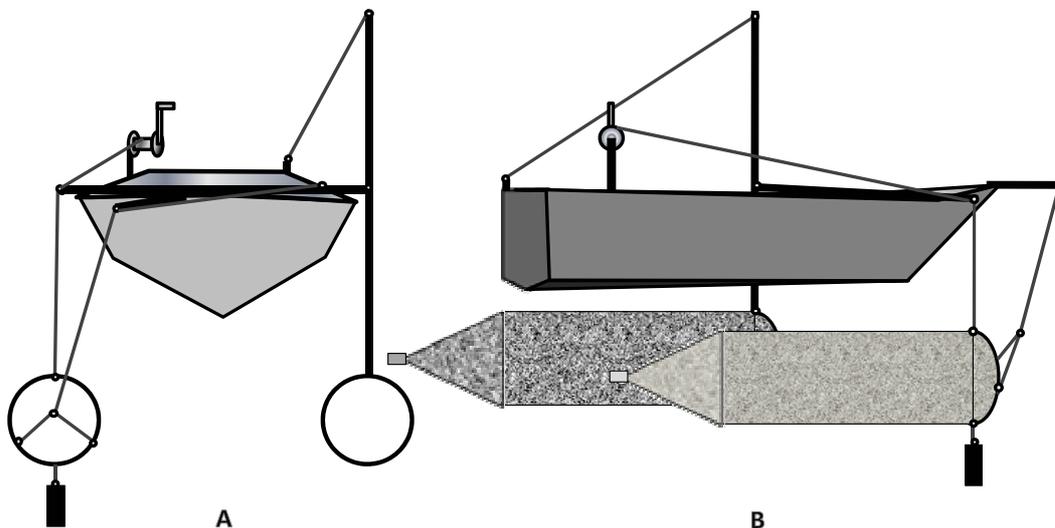


Figure 1: Schematic diagram of the boat and the bongo net construction; front view (A), right side view (B).

Electrofishing

The larval fish in the ponds were sampled monthly by electrofishing (EFGI 4000 J. Brettschneider, Germany), with point abundance sampling (PAS) by boat (modified after Persat and Copp, 1989; Beeck et al., 2002). A 10 cm diameter ring anode was used initially and this was changed later to a 12.5 cm diameter one (when the perch were larger). Fish were collected at fifty randomly chosen points per pond, covering all kind of habitats (littoral zones, but also in the middle of the pond). In the gravel pit lakes, perch return to the littoral zone after their pelagic phase. During that period we started to investigate the littoral zone by electrofishing with the aforementioned fishing gear and the 12.5 mm ring anode in the afternoon until evening hours. We approached the littoral zone from the pelagic zone as silently as possible and collected fish at an average of 85 randomly chosen points. Because of the steep gradient of the lake banks, the sampling area was always very close to the bank in order to observe shallow areas up to 1.5 m maximum depth of. Starting in late May, electrofishing in the lakes was performed weekly until mid-June, and afterwards every two weeks. All perch were immediately ice-cooled and later deep-frozen. The catch per unit effort of the PAS ($CPUE_E$) is the mean number of perch caught per point (including zero samples).

Gillnet fishing

We used two types of sinking polyamide monofilament multi-mesh gillnets (Appelberg, 2000). For the younger stages of perch the nets had mesh sizes 6, 8, 10, and 12 mm and for the older stages we used, in addition, multi-mesh gillnets with 15 and 20 mm mesh size. Six of the nets with smaller mesh sizes and at least two of those with larger mesh sizes were used on each sampling date. Each net was 6 m long and 1.5 m high. Each of the mesh panels of the smaller sizes were 2.25 m², whereas the bigger ones were 4.5 m² per panel. The nets were set in the evening for between 1.5 and 2.5 hours, depending on the expected density of perch. Applying this method provides some advantages over a gang of different single-mesh nets which are normally used: firstly, the multi-mesh panels are much smaller than commonly available single-mesh nets, reducing the number of captured fish drastically when applied at high perch densities as in our waters; secondly, using more nets with all the mesh sizes allows the coverage of all different habitats in the littoral zone with the complete set of mesh sizes, and thirdly, identical nets set in

parallel can be additionally used to calculate a mean CPUE and its variation, and this irrespective of the mesh-size selectivity (cf. Appelberg et al., 1995), which otherwise has to be taken into account.

In the gravel pit lakes, bi-weekly gillnet fishing started in mid-June when perch switched to the littoral zone. In the experimental ponds, gillnet fishing was always conducted simultaneously with electrofishing but at different places to avoid the possibility of electrofishing scaring fish into the nets. All perch were preserved in 4% formaldehyde solution. To allow the comparison of perch caught during the season, the catch per unit effort (CPUE_N) was formulated as follows:

$$\text{gillnet fishing:CPUE}_N = \frac{\left(\frac{A_s}{A_n} \cdot C_n \right)}{t}$$

with A_s = area of standard net (219.3 m²), A_n = area of the net used [m²], C_n = nominal catch, and t = exposure time [h].

Fish removal from the experimental ponds

All ponds were completely drained at the end of the pond experiments in mid-October. All fish were caught in a metal-sieve chamber at the outlet. The fish biomass per pond was weighed and four sub-samples with a total number of about 1060 to 2480 perch per pond were measured. Finally, the total number of individuals per pond was calculated.

Statistics

Although no direct comparison of the different CPUEs is possible, and thus no overall absolute abundance of perch can be given, the seasonal changes in the relative densities can be estimated with the sampling method-specific CPUEs. In addition, the overlap of the different methods is a first step in understanding the quantitative differences between them. Irrespective of these failures in the overall estimation of quantitative densities, the total length (TL) of all sampled fish was measured to the nearest 1 mm, and all length data were used to produce LFDs separately for each method, which were compared with ANOVAs using SPSS (Ver. 14.0.1, SPSS Inc.). In all cases the length data were used as the dependent variable, while date, method and lake were the independent variables.

Results

Hatching of perch in the gravel pit lakes started around the end of April. Perch fry in the shallowest Lake Pfeiffer were found one week earlier than in the other investigated lakes. After hatching, the perch fry in the lakes were caught by bongo net trawling. The density of the perch fry increased continuously during the first three weeks (Fig. 2). In the middle of May, perch fry density in Lake Speldrop peaked at 1.8 ind.m^{-3} , before stabilizing at a somewhat lower level by the end of May. In Lake Pfeiffer the variation in abundance was similar in sequence and range to that of Lake Speldrop, while in Lake Reeser Meer the steady increase lasted until the beginning of June (4.4 ind.m^{-3}). The results of bongo netting revealed that some perch hatched two to three weeks later than their siblings (Fig. 2).

We started the PAS surveys in the littoral zone of the gravel pit lakes in late May; early enough to rule out any larval perch abundance there. At the return of the post-larvae to the littoral zone, the individuals were between ca. 30 and 40 mm TL, whereas the smaller individuals (which stayed in pelagic zone) had TLs of between 14 and 22 mm (Fig. 2). The numbers of fish in the bongo net catches decreased rapidly from the beginning of June onwards; this fishing method was therefore stopped after the third week of June. For all parallel catches of bongo and electrofishing, the statistical analysis revealed significant size differences depending on the method, explaining about 4% of the total variance (Table 1). The perch caught by electrofishing in the littoral zone were always larger than those caught with the bongo nets in the pelagic areas (Fig. 3).

Table 1: Three-way ANOVA testing the effect of the three gravel pit lakes, sampling date and fishing method (bongo net versus electrofishing) on the mean TL of perch in the gravel pit lakes for all dates on which the two methods caught perch at the same time (see Fig. 2).

| | df, df_{err} | F | P |
|------------------|-----------------------|-------|---------|
| Lake | 2, 2335 | 368.3 | <0.0001 |
| Date | 2, 2335 | 89.9 | <0.0001 |
| Method | 1, 2335 | 137.2 | <0.0001 |
| Lake*Date | 0 | | |
| Lake*Method | 2, 2335 | 18.1 | <0.0001 |
| Date*Method | 2, 2335 | 0.54 | 0.586 |
| Lake*Date*Method | 0 | | |

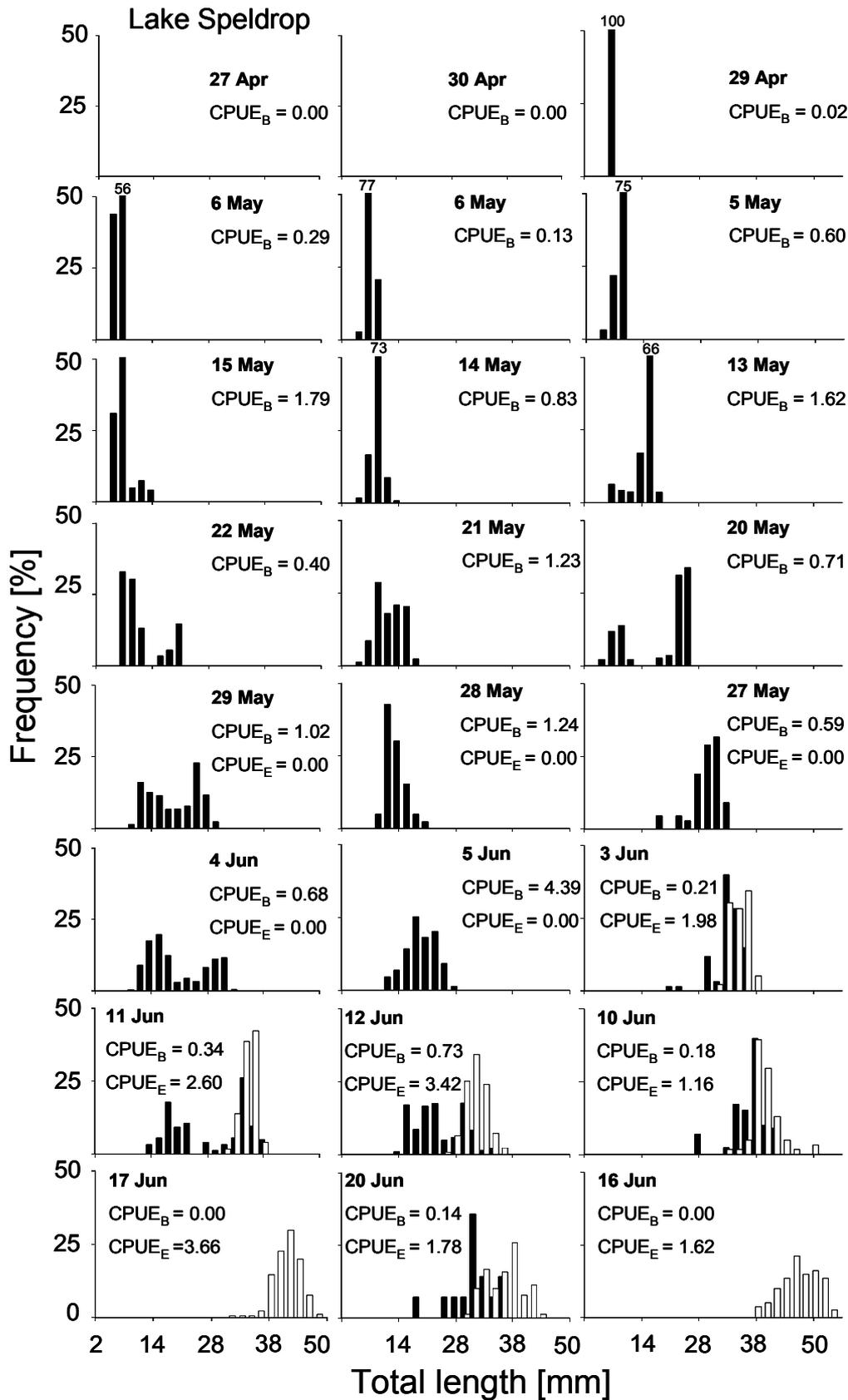


Figure 2: Length-frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in spring 2006 using bongo net fishing (black columns, CPUE_B) and electrofishing (white columns, CPUE_E).

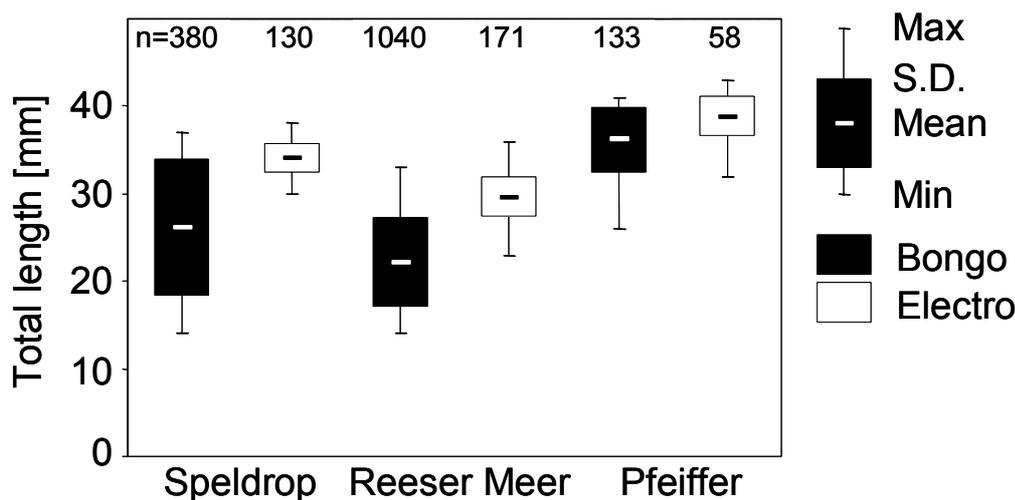


Figure 3: Box-plot of perch sizes from the three gravel pit lakes caught using bongo nets (black) and electrofishing (white) around June 11 2006. n = number of perch

From mid-June onwards we started gillnet fishing in the littoral zone; the three methods thus overlapped for each lake. First, perch were caught with the 6 mm mesh size from about 40 mm onwards (Fig. 4). With increasing size of the fish, first the CPUE_N revealed an increasing trend while, later on, catches oscillated more or less without recognizable trends in the three gravel pit lakes. For the first samples from mid-June onwards, the mean sizes of the perch caught with either electrofishing or gillnets did not differ considerably (Fig. 5). In the following period, however, the accordance of the LFDs of both methods decreased (significant interaction term Date x Method, ANOVA, df=6, 1558, F=36.4, p<0.0001), especially in Lake Speldrop where the biggest YOY perch were caught with gillnets only and the smallest ones (50 mm in October) only with PAS (Fig. 4).

In contrast to Lake Speldrop, in Lake Reeser Meer there was a relatively good accordance observable between these two methods, although, as also found in Lake Speldrop, the biggest individuals were caught by the gillnets and not by PAS. In Lake Pfeiffer, the CPUE_E showed a remarkable and early decrease by the beginning of July and persisted at a low level (Fig. 4). This corresponded with observations that YOY perch were no longer visible in the shallow areas of the lake's littoral zone. This was in clear contrast to both the other lakes. Overall the statistical analysis revealed significant differences in the sizes of the perch caught with electrofishing and gillnets. For each lake, around 7 % of the total variability of the sizes could be

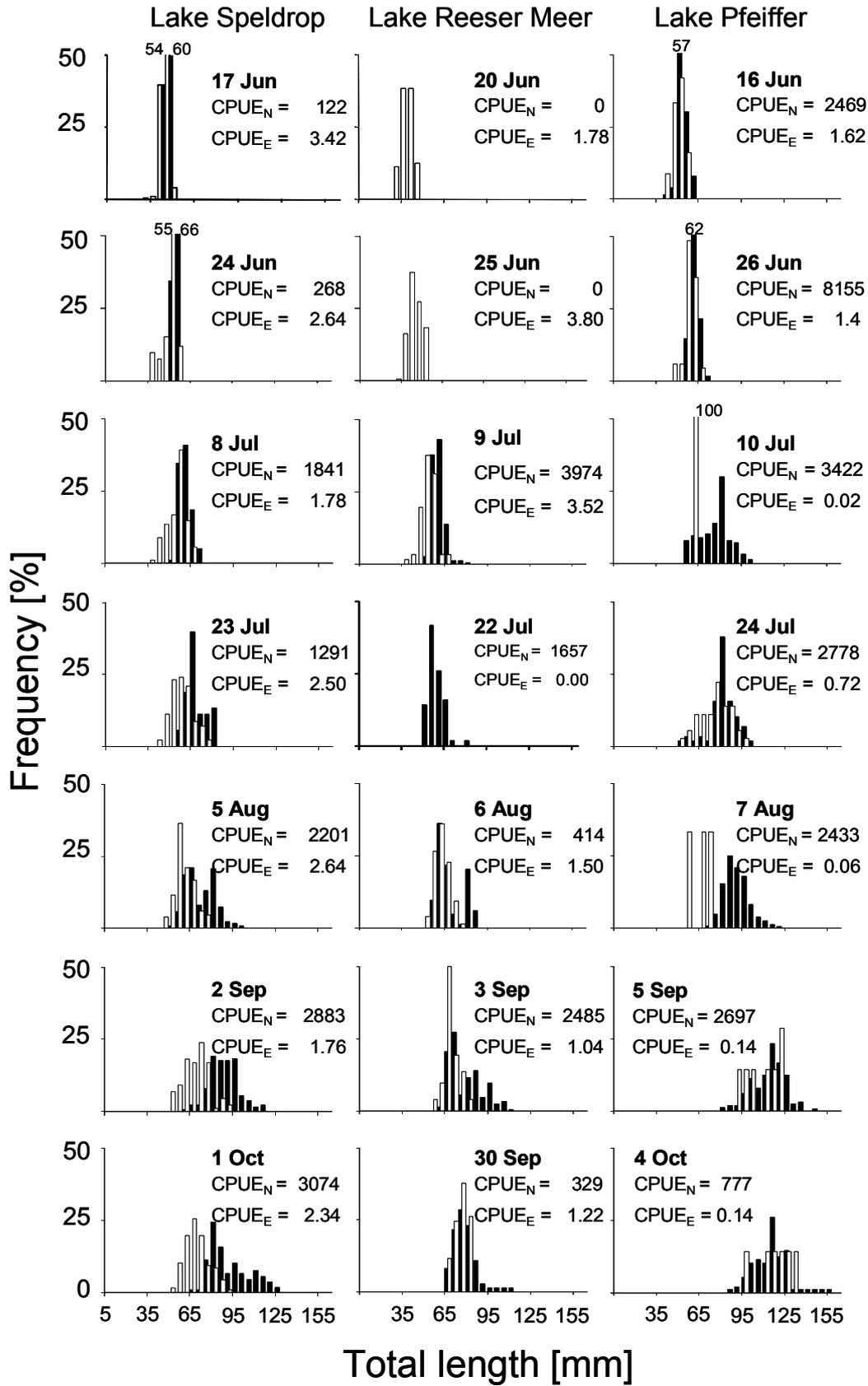


Figure 4: Length-frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in summer 2006 using electrofishing (white columns, CPUE_E) and gillnets (black columns, CPUE_N)

Table 2: Two-way ANOVAs testing the effect of sampling date and fishing method (electrofishing versus gillnets) on the mean TL of perch in the gravel pit lakes for all dates on which the two methods were used at the same time and the CPUE_E was >0.5 (cf. Fig. 4).

| Lake Speldrop ($r^2=0.744$) | df, df _{err} | <i>F</i> | <i>P</i> |
|----------------------------------|-----------------------|----------|----------|
| Date | 6, 1558 | 298.7 | <0.0001 |
| Method | 1, 1558 | 282.7 | <0.0001 |
| Date*Method | 6, 1558 | 36.4 | <0.0001 |
| Lake Reeser Meer ($r^2=0.603$) | | | |
| Date | 4, 1100 | 270.8 | <0.0001 |
| Method | 1, 1100 | 164.3 | <0.0001 |
| Date*Method | 3, 1100 | 5.79 | 0.001 |
| Lake Pfeiffer ($r^2=0.800$) | | | |
| Date | 2, 462 | 309.1 | <0.0001 |
| Method | 1, 462 | 82.2 | <0.0001 |
| Date*Method | 2, 462 | 7.66 | 0.001 |

Table 3: Two-way ANOVAs testing the effect of sampling date and fishing method (electrofishing versus gillnets) on the mean TL of perch in the experimental ponds for all dates on which the two methods were used at the same time and the CPUE_E was >0.5 (cf. Fig. 6).

| Pond 1 ($r^2=0.840$) | df, df _{err} | <i>F</i> | <i>P</i> |
|------------------------|-----------------------|----------|----------|
| Date | 2, 85 | 118.6 | <0.0001 |
| Method | 1, 85 | 8.00 | 0.006 |
| Date*Method | 2, 85 | 22.7 | <0.0001 |
| Pond 2 ($r^2=0.708$) | | | |
| Date | 3, 143 | 13.7 | <0.0001 |
| Method | 1, 143 | 91.6 | <0.0001 |
| Date*Method | 3, 143 | 11.0 | <0.0001 |
| Pond 3 ($r^2=0.874$) | | | |
| Date | 3, 158 | 68.3 | <0.0001 |
| Method | 1, 158 | 640.3 | <0.0001 |
| Date*Method | 3, 158 | 27.4 | <0.0001 |
| Pond 4 ($r^2=0.680$) | | | |
| Date | 1, 93 | 10.4 | 0.002 |
| Method | 1, 93 | 11.5 | 0.001 |
| Date*Method | 1, 93 | 3.49 | 0.065 |

explained by the methods used (all $p < 0.0001$; Table 2), and the perch caught with gillnets were always larger than those sampled with electrofishing (Fig. 5).

The hatching period of perch in the experimental ponds started in the beginning of May, similar to that in the gravel pit lakes, but in the ponds the period lasted only about one week, i.e. less time than in the lakes. After the hatching of perch we used only the PAS method in parallel with gillnets to study the development of the juvenile perch. In the last third of June, gillnets caught some bigger individuals of the YOY perch, which did not occur in the electrofishing samples (Fig. 6). The $CPUE_E$ results for the ponds had similar ranges to those for the gravel pit lakes. Gillnet catches were, however, about 20 times lower in the ponds. At this time, the resulting LFDs of both methods partly overlapped but still the biggest individuals were almost exclusively taken by gillnets whereas the smallest ones were only caught by the PAS (Fig. 6). Until the end of August, gillnet fishing in ponds 1 and 4 gave similar results for the smaller-sized perch compared with the catches by electrofishing; electrofishing was thus stopped at this time.

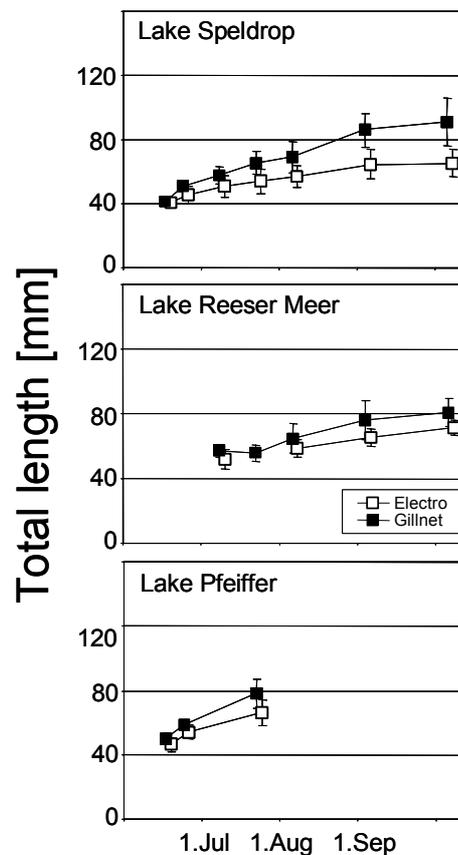


Figure 5: Mean TL \pm S.D. of perch caught in the gravel pit lakes using electrofishing (white) and gillnets (black) for all samples in 2006, when the $CPUE_E$ was >0.5 .

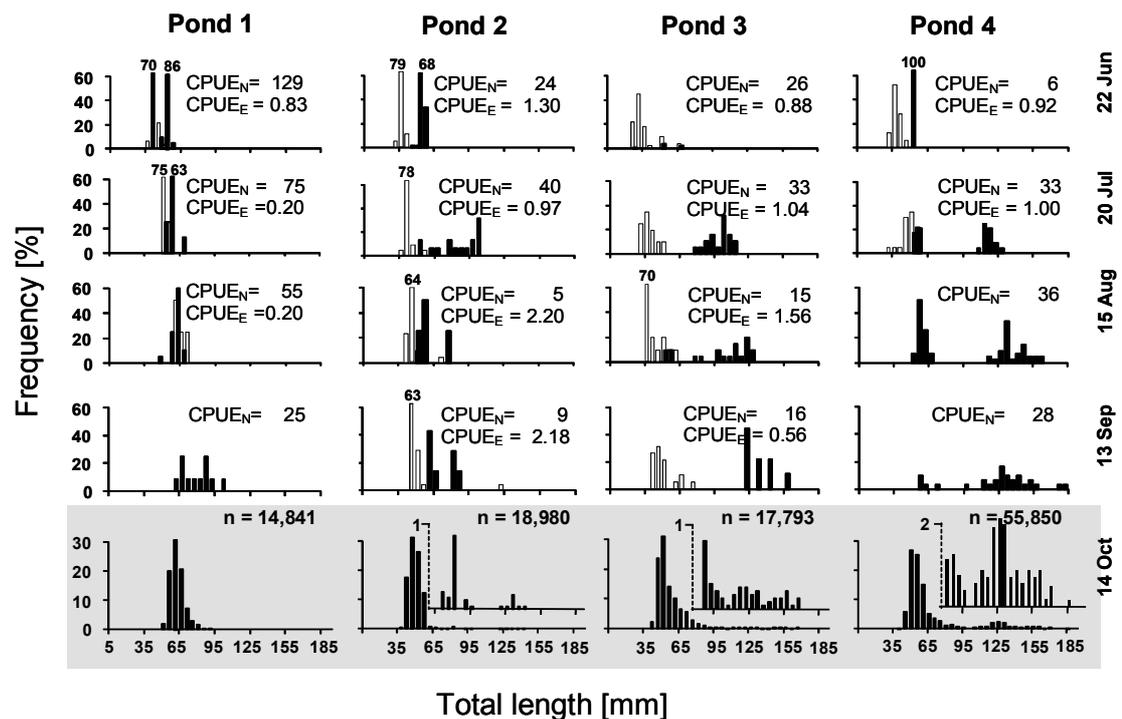


Figure 6: Length-frequency distribution and CPUE of YOY perch in the experimental ponds caught on different sampling dates in summer 2006 using electrofishing (white columns, $CPUE_E$) and gillnets (black columns, $CPUE_N$). In addition, the total number of perch and the LFD (grey shaded) of each pond from the fish extraction in mid-October are given. Here the frequency of the perch >85 mm TL is shown with higher resolution on the Y-axis.

In contrast, the smallest perch in ponds 2 and 3 were only caught by electrofishing and not by gillnets; both methods were thus used until the end of the sampling period. Again the statistical analysis revealed a significant effect of the fishing method, explaining lower percentages for ponds 1 (2%) and 4 (10%), but quite a high percentage for ponds 2 (30%) and even 59% for pond 3. As for the gravel pit lakes, the perch caught by gillnet were always larger than those caught by electrofishing (Fig. 7 and Tab. 3).

Table 4: Results of the fish removal from the experimental ponds in mid-October.

| Pond | All perch | Perch < 100 mm TL | Perch > 100 mm TL | | TL_{max} [mm] |
|------|--------------------------|-------------------|-------------------|-----------------|--------------------|
| | [Ind. ha ⁻¹] | Individuals [%] | n | Individuals [%] | |
| 1 | 37,100 | 100.0 | 0 | 0.0 | 90 |
| 2 | 47,500 | 99.8 | 38 | 0.2 | 137 |
| 3 | 29,700 | 98.3 | 302 | 1.7 | 165 |
| 4 | 79,800 | 97.4 | 1,452 | 2.6 | 182 |

To compare the results of our two fishing methods in the experimental ponds with the relative abundance of sizes within the LFDs, we emptied the ponds completely and sampled all fish. In accordance with the range of sizes caught on the last sampling date in September, the size ranges of perch at the time of removal were quite similar. However, the shape of the corresponding LFDs was completely different (Fig. 6); the abundance of the small perch was much higher than expected from the final catches in September (cf. Fig. 6 and Tab. 4).

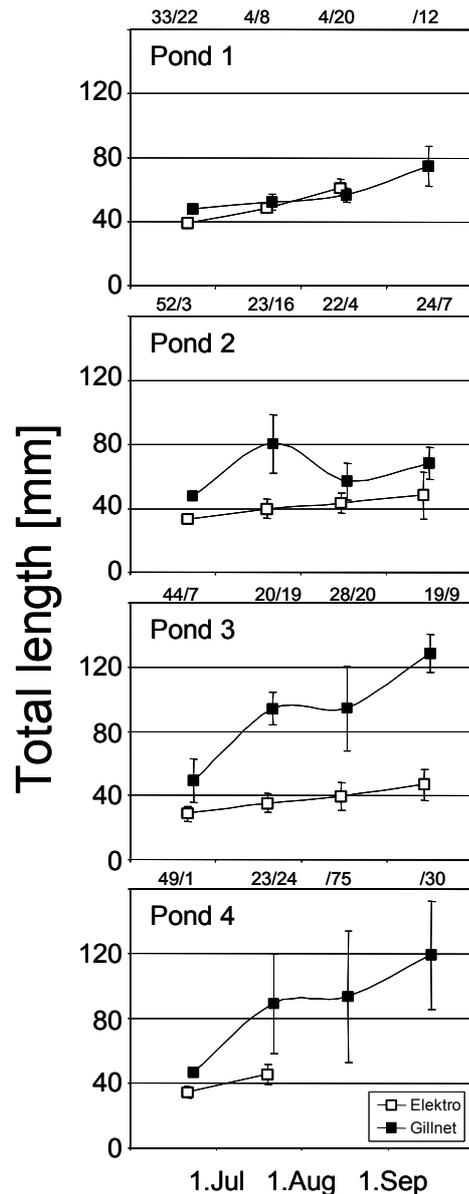


Figure 7: Mean TL \pm S.D. of perch caught in the experimental ponds using electrofishing (white) and gillnets (black) for all parallel samples in 2006. The number of perch is given above each panel (electrofishing/gillnets).

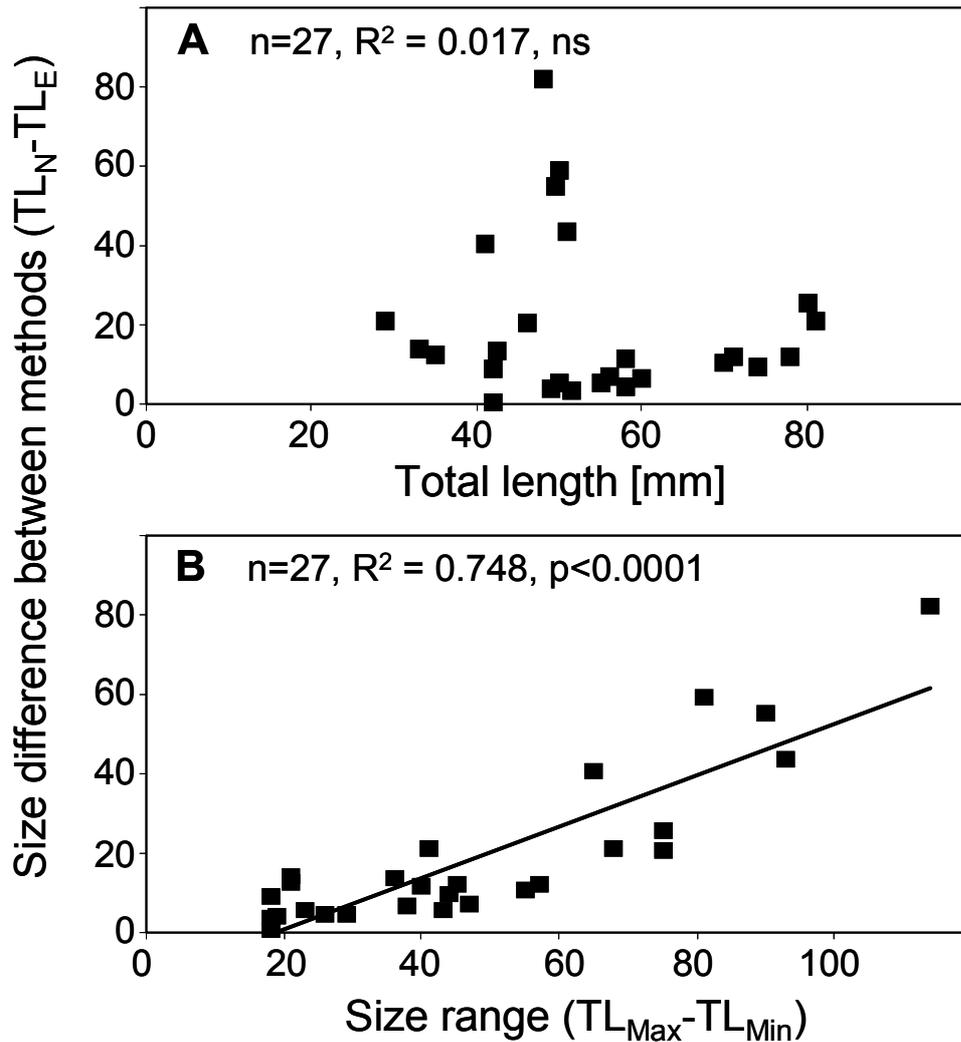


Figure 8: The absolute difference between the mean TL of all perch from the gillnet catches (TL_N) and the catches by electrofishing (TL_E) according to the median perch size of both sampling methods (A), and the absolute size range of all sampled perch (B) for all parallel catches in 2006.

In order to describe a more general trend for the observed difference between electrofishing and gillnets that includes the three different gravel pit lakes as well as the shallow experimental ponds, a regression of these differences on the independent variable ‘fish size’ was computed. This independent variable was chosen because increasing differences over the course of the season became obvious, especially for the gravel pit lakes (cf. Fig. 5). Because the number of perch caught usually varied greatly between the two methods, we had to use the median of the TL as the independent variable. Although there was a significant relationship between the median TL and the observed difference between samples from electrofishing and gillnets for the samples from the gravel pit lakes ($R^2=0.628, p<0.01, n=17$), there was no overall significant relationship for all values including the ponds (Fig. 8A).

However, using the absolute size range of all captured perch as an independent variable reveals a highly significant correlation with the observed difference between the samples from electrofishing and gillnets (Fig. 8B). Thus, the more the LFD of a perch population widened, the larger was the difference between the two sampling methods.

Discussion

Bongo net sampling and electrofishing

In the first part of the study, bongo net sampling was the only applicable method for catching larval perch in the lakes. Especially in waters with an extended pelagic area such as the gravel pit lakes, this is the most practical method for following the development of perch fry after hatching. When using push or trawl nets, several factors which influence catch efficiency must be taken into account. To reduce the forewarning of larval fish by the noise of the vessel itself or its propeller (Ona and Godo, 1990), we attached the fishing gear to the front third of the boat. Visibility, e.g. with respect to light intensity or transparency, can reduce catch efficiency, as fishes with visual perception are better able to avoid an approaching net (Glass and Wardle, 1989). Therefore, our bongo nets had a dark entrance and always the bongo net sampling was done after sunset (Wang and Eckmann, 1994; Guillard et al., 2006). Thus, we reduced the expected catch variability during the day that might depend on visibility and on ontogenetic-determined behaviour, such as diurnal horizontal or vertical migration of perch larvae (e.g. Cech et al., 2005; Scharf, unpublished results). Juza and Kubecka (2007) recommend a 3×3 m trawl for quantitative night sampling of the fry community. Nevertheless, net openings between 40 and 80 cm revealed no significant difference in the density of captured post-larval fish, whereas smaller nets were less efficient (Mooij, 1996). Although it can be assumed that bigger openings are more effective, both net size and mesh size strongly affect another important factor: the towing speed (Mous et al., 2002). When using mesh sizes of between 0.75 and 3 mm, the achieved speed of 3.8 - 6.9 km h⁻¹ was adequate to compensate for the escape speed of perch larvae larger than 40 mm TL (Pepin and Shears, 1997). Overall we can assume that the catch efficiency of the bongo net sampling was quite good for the ontogenetic stages of perch in the pelagic area of the gravel pit lakes, which is confirmed by our estimated densities of up to 100-fold more than other European waters (cf. Wanzenböck et al., 1997; Cech et al., 2005; Guillard et al., 2006; Cech et al., 2007; Juza and Kubecka, 2007).

The successive LFDs of our bongo net samples clearly show the addition of smaller perch larvae to the existing cohort. The addition of these smaller larvae on successive sampling dates can be considered as providing a reliable estimate of the length of the hatching period, which was in the range of two to three weeks in the gravel pit lakes.

Spawning and hatching of perch is temperature dependent, and the spawning period can last between one and more than nine weeks (Thorpe, 1977; Sandström et al., 1997; Gillet and Dubois, 2007). In particular, the length of the spawning period is important for the assessment of the YOY age cohort of perch (Huss et al., 2007) because related differences in size of early and late hatching larvae may be the basis for size-specific development within the YOY cohort, e.g. due to food abundance, competition for food, predation and other seasonal processes that are size dependent (e.g., Brabrand, 1995; Mehner et al., 1998a; 1998b; Byström and Garcia-Berthou, 1999; Beeck et al., 2002; Graeb et al., 2004).

There is an ongoing discussion as to whether the offshore period of perch is time-restricted (Wang and Eckmann, 1994) or whether it depends on a critical size in relation to developmental stage (Urho, 1996). Our results support the latter hypothesis, as there were no major size differences in the post-larval perch between the three lakes on arrival in the littoral zone, but the duration of the pelagic period was found to vary in consecutive years (Beeck, Borcharding, Scharf, unpublished results). In the littoral zone, where bongo net sampling is restricted, perch were caught first with electrofishing. Consequently, we assumed that the observed significant size difference between bongo netting and electrofishing was partly related to habitat-specific occurrence of the juvenile perch. However, it could also be that a part of the perch population stayed in the pelagic zone but was not caught because of the size-specific escape capability when fishing with bongo nets (cf. Post et al., 1997; Tischler et al., 2000; Cech et al., 2005; Juza and Kubecka, 2007). In such a case, other methods should be applied to test for larger perch in the pelagic zone, either using hydroacoustics in combination with pelagic gillnets (e.g. Imbrock et al., 1996; Schmidt et al., 2005) or by purse seining (Radke et al., 1997; Tischler et al., 2000).

Electrofishing and gillnet catches

While bongo net sampling or other trawling methods as well as hydroacoustics or purse seining are most efficient for the pelagic zone, electrofishing is more appropriate in the littoral zone (Cowx, 1989). Here, the depth limitation of electrofishing due to the restricted range of the electric field is of minor importance (Copp and Garner, 1995). For the efficiency of capture by electrofishing, two contrasting size-related processes are important: (1) the mobility of juvenile fish

increases as they develop and enhance their escape probability from the effective field, and (2) the susceptibility of fish to electricity increases with increasing body size (Copp and Garner, 1995). However, Copp and Garner (1995) indicated that size selectivity is of limited importance in the capture of YOY freshwater fish when using PAS with stealth in the littoral zone, as used in our studies.

Limits in the efficiency of gillnets are also size-specific, because the lowest mesh size of 6 mm allows no catches of fish smaller than about 40 mm TL (Appelberg, 2000). To use gillnets for sampling smaller sizes of fish as well, standardization attempts with respect to the Water Framework Directive of the European Union now recommend 5 mm as the minimum mesh size (Prchalova et al., this volume). Nevertheless, above a TL of 50 mm all sizes of perch can be caught with gillnets as used in this study. We started gillnet fishing when we expected perch larger than 40 mm TL at our study sites. In June, when using electrofishing and gillnets simultaneously in the gravel pit lakes, there were only small size differences in the fish between the samples from the two methods. Over the course of the sampling period, however, a significant difference became obvious, as gillnet catches always contained the largest YOY perch compared with those from the parallel electrofishing. This trend increased during the season throughout all the investigated lakes but showed the strongest effect in Lake Speldrop. Comparable trends were also found for the experimental ponds that contained no larger perch (pond 1) or only a very small number (pond 2), as revealed by the fish removal at the end of the experimental period. However, for the ponds 3 and 4, in which more than 1% of the YOY perch were larger than 100 mm TL in October, extreme differences in the mean size of fish in the samples from electrofishing or gillnets were found. The search for a more general trend in the size differences of fish between the two methods revealed, for the gravel pit lakes, a significant positive correlation with increasing size of the YOY perch populations. However, for both the gravel pit lakes and the experimental ponds, the absolute size range of all catches was clearly the better predictor of differences in the mean size of fish in electrofishing and gillnet catches. In the gravel pit lakes of our investigation, $CPUE_E$ values increased with the successive habitat shift of the juvenile perch to the littoral zone. While the efficiency of electrofishing is primarily less dependent on the activity of the individuals, gillnets can only catch fish that are active during the fishing period and at the fishing locality where the nets are set. Thus, missing sizes of a fish population in gillnet catches

cannot solely be seen in the light of efficiency of the nets, but must be interpreted more with respect to the activity patterns and habitat-specific occurrence of the target individuals.

In Lake Speldrop, the smallest perch were always caught by electrofishing in the shallow areas of the littoral zone (depth <50 cm), but not in the somewhat deeper parts of the littoral zone, where gillnets were set only a few metres away. Although the YOY perch were big enough (≥ 50 mm in October) to be trapped in the gillnets, they were never caught with this method. In Lake Pfeiffer, the $CPUE_E$ decreased sharply in the beginning of July. Here all juvenile perch (which were significantly larger than in Lake Speldrop) avoided the shallow areas, although the littoral zone has a similar morphology to that of Lake Speldrop and although there is a higher degree of structural diversity due to woody debris and submerged vegetation. These results for the gravel pit lakes give clear evidence that size-specific occurrence of the perch caused the observed size differences between electrofishing and gillnet catches. The reason for this differential occurrence in the different habitats may be related to size-specific patterns of foraging, competition or predation (Eklöv and Diehl, 1994; Beeck et al., 2002; Olsson and Eklöv, 2005; Borcharding, 2006; Eklöv and Svanbäck, 2006; König et al., 2006; Borcharding et al., 2007; Magnhagen and Borcharding, 2008; Olsson et al., 2007). In lakes with more shallow but unstructured littoral zones, beach seining is also a very effective method for estimating densities of fish up to sizes of about 100 mm TL (e.g., Staas, 1996; Jurajda et al., 1997). However, this method could not be used either in the gravel pit lakes with their steep banks or in the ponds with their dense submerged vegetation.

The only type of habitat in the experimental ponds is shallow water with large amounts of submerged vegetation and thus a high degree of structural complexity. Here the differences between the LFDs from electrofishing and gillnet sampling must be due to reasons other than those for the gravel pit lakes. In particular, the differences in the LFDs of the ponds 3 and 4 at the final sampling date in September (as compared with the actual populations in the ponds, as revealed by the fish removal in October) verify that the small-sized perch were clearly underrepresented in all samples. This is in accordance with the magnitude of variation in $CPUE_E$ values in the ponds that were of a similar range as seen in the lakes, whereas the $CPUE_N$ values were around 20-fold lower than in the lakes. In contrast to the habitat-specific occurrence patterns in the lakes, this gives clear evidence that the small

perch in the experimental ponds were obviously not active, thus being caught in lower numbers in the gillnets. In contrast to the gillnet samples, PAS is relatively independent of the swimming performance of the fish (not to be confused with the escape ability) and consequently this method is also suitable for resting or slow-swimming fish that are not trapped by gillnets. We know (1) from stomach analyses that large-sized YOY perch prey on their small-sized siblings in the ponds (Urbatzka et al., 2008, Heermann and Borcharding, unpublished results), and that (2) small-sized YOY perch are more timid than their larger siblings when foraging for food under the risk of predation (Borcharding, 2006; König et al., 2006). Consequently, we assume reduced swimming activity of the small-sized perch in the experimental ponds due to high predation pressure by their cannibalistic siblings, for which no risk from predatory fish exists.

Conclusions

In order to monitor the development of a YOY perch population over their first summer, e.g. to study size-related influences of food abundance, competition or predation (Persson et al., 2004), it is absolutely necessary to find and to follow all size classes on all sampling dates (cf. Beeck et al., 2002). Important aspects of the life-cycle may otherwise be missed or may lead to misinterpretations, as suggested by Urbatzka et al. (2008). Observed differences between the bongo net catches and electrofishing, and between electrofishing and gillnet samples in the gravel pit lakes, were assumed to depend partly on the different occurrence of different size classes of perch at the sampling locations, due either to time differences in the size-specific habitat shift or to small-scale differences where perch stay in the littoral zone. However, the observed differences between electrofishing and gillnet samples in the shallow experimental ponds presumably depend on differences in the activity level of small and large YOY perch, possibly forced by differential predation risk (Magnhagen, 2006; Heermann and Borcharding, unpublished results). While confirming preliminary studies (Wanzenböck et al., 1997; Tischler et al., 2000), our results offer additional evidence that at least two of the three methods used in this study should be applied in an overlapping and parallel sampling design, in order to be sure of obtaining all relevant data on the development of the size structure of the YOY perch population of interest. To extend knowledge of the habitat-specific

occurrence of perch after they arrive in the littoral zone, additional sampling of the pelagic zone should be carried out using more efficient methods such as purse seining or hydroacoustics. Furthermore, the sampling design must be extended when differences in the vertical distribution are expected (cf. Cech et al., 2005). Especially when unknown perch populations are studied, an extended and well-designed sampling programme is absolutely necessary to obtain reliable results on certain aspects of the life-cycle.

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ABSTRACT

Cannibalism in fish has various effects on the population as well as on individuals. Cannibals derive direct energetic benefit from cannibalism by feeding on their smaller conspecifics, while at the same time reducing competition for the shared resource. Avoiding intra-cohort competition can force fish to use alternative feeding strategies (e.g. becoming early piscivorous feeding on bream larvae) and hence leads to greater specialisation within the population, which may subsequently stimulate cannibalism. Early piscivory and cannibalism leads to the development of a stable bimodality which brings several advantages and adaptations especially for larger fish, such as morphological changes to piscivory, higher energy stores (lipid, protein) and reduced winter mortality. Defined pond and laboratory experiments were provided to gain insights into (1) the mechanism leading to cannibalism via specialisation on alternative food resources and the establishment of a bimodal size distribution, (2) the advantages for the large size-cohort especially considering the first winter as a bottleneck for the recruitment success of young-of-the-year (YOY) fish, (3) whether in the system of early piscivory and intraguild cannibalism, fish larvae can be substituted as prey by alternative food resources and (4) the morphological adaptations on the food resource used, irrespective of the habitat fish prefer.

As zooplankton levels decreased, YOY perch (*Perca fluviatilis*) started to specialise, suggesting that increased intraspecific competition forced fish to try alternative feeding strategies. Larger YOY perch then fed on resources richer on energy (bream larvae and tadpoles) and hence outgrew their smaller conspecifics, becoming large enough to enable cannibalism. This differentiation into two size classes and two different feeding strategies was shown to be a stable pattern within the YOY perch population, as indicated by stable isotope analyses.

If bream was substituted by roach, no piscivory occurred and perch were unimodally distributed. Relative to perch, roach hatched earlier than bream and also grew faster, preventing gape-limited perch to feed on roach. However, these perch were significantly larger than the small size-cohort in the cannibalistic system, suggesting that due to predation pressure of cannibals, small perch reduced their activity (which was documented by comparing the gill net catches of the two cohorts) and showed reduced growth rates.

The two size-cohorts that developed by cannibalism showed different potential for surviving the winter. In the laboratory only the smallest perch suffered from high

mortality rates, even when all were fed with low amounts of food. However, feeding the fish reduced the mortality rate. The pond experiments (cold winter 2005/06 and warmer winter 2006/07) showed that although small perch did not reduce their feeding activity, they suffered from high mortality during both winters. However, those who survived the winter rebuilt their energy stores. Large perch demonstrated low rates of mortality during the cold winter. During the warm winter, however, mortality was nine-fold higher than during the first winter. Low mortality rates were observed in the laboratory although the temperature was comparable to the one of 2006/07. Therefore one can conclude that the loss of ice coverage which can function as a shelter against avian predators might be more responsible for the high mortality rates of large perch than the temperature itself.

The food consumed not only changes the energy reserves of fish but also their morphology. Distinct morphological changes related to piscivory and planktivory were documented in field and mesocosm studies. The mouth of the piscivorous YOY year perch became larger, the pectoral fins and the centre of mass of the posterior abdomen were shifted backwards. These findings provide evidence that the type of food is important and might lead to further functional adaptations in morphology.

Furthermore fish may differ in habitat-specific occurrence and activity related to size, as was the case for the two size-cohorts in those ponds with cannibalism. As a consequence of this, and also as a result of the fact that the size distribution of YOY perch had broadened considerably, there was sometimes no overlap in the length-frequency distributions between gillnetting and electro-fishing, clearly demonstrating that using a single method is not sufficient to draw a complete picture of the population size structure.

Intraguild cannibalism and the related development of bimodal size distribution often might not be recognised, since only 1 to 10 % of the perch population choose this alternative feeding strategy. However, the resultant large size-cohort can have considerable repercussions for the perch population.

KURZZUSAMMENFASSUNG

Das Auftreten von Kannibalismus in einer Population beeinflusst nicht nur die betroffenen Individuen, sondern wirkt auch auf die ganze Population und deren Dynamik. So profitieren Kannibalen in zweierlei Weise von ihrer Ernährungsart, zum einen durch den Energiegewinn beim Fressen ihrer kleineren Artgenossen und zum anderen dadurch, dass sie den Konkurrenzdruck bezüglich der mit den kleineren Artgenossen geteilten Futterressource vermindern. Ein hoher Konkurrenzdruck kann auch dazu führen, dass sich einzelne Individuen auf alternative Futterressourcen konzentrieren und dabei beispielsweise früh piscivor werden. Durch diese Nutzung alternativer Futterressourcen steigt die Diversität der genutzten Nahrungsressourcen und somit der Spezialisierungsgrad der gesamten Population. Die frühe Piscivorie durch die Spezialisierung auf Fischlarven kann nachfolgend einer kannibalischen Ernährungsweise zugute kommen, was wiederum die Bildung einer stabilen zweigipfeligen Größenverteilung der Population nach sich zieht. Die große Kohorte erfährt dabei einige Vorteile und Anpassungen, wie zum Beispiel morphologische Adaptation an die piscivore Ernährungsweise, erhöhte Speicherung von Energiereserven (Lipide und Protein) und damit verbunden verminderte Wintermortalität.

Bezüglich des Phänomens der frühen Spezialisierung auf eine piscivore Ernährungsweise und die damit einhergehende Entwicklung des Kannibalismus sollten Teich- und Laborexperimente Details zu folgenden Punkten liefern: (1) zum Mechanismus, der via Spezialisierung auf alternative Futterressourcen zum Kannibalismus führt und dadurch eine zweigipfelige Größenverteilung ermöglicht, (2) zu den Vorteilen, die sich aus dem erhöhten Wachstum für die Fische ergeben, besonders bezüglich dem Flaschenhals Wintermortalität, der ein entscheidendes Kriterium für den Rekrutierungserfolg von 0+ Fischen darstellt, (3) zu der Frage, ob in dem System mit auftretender früher Piscivorie und Intra-Kohort-Kannibalismus, Fischlarven als Beute durch alternative Nahrungsressourcen ersetzt werden können und (4) darüber, ob morphologische Anpassungen an die genutzten Futterressourcen, unabhängig von dem präferierten Habitat der Barsche auftreten.

Ausgelöst durch eine Verminderung der Nahrungsressource Zooplankton trat ein erhöhter Spezialisierungsgrad innerhalb der Population der 0+ Barsche (*Perca fluviatilis*) auf, was vermuten lässt, dass der erhöhte intraspezifische Konkurrenzdruck die Fische dazu gezwungen hat, alternative Ernährungsstrategien zu nutzen. Die größeren Barsche haben sich im Zuge dessen auf energiereichere

Ressourcen (Brassenlarven und Kaulquappen) konzentriert und wuchsen dadurch schneller als ihre kleineren Artgenossen, bis sie schließlich groß genug waren um sich als Kannibalen zu ernähren. Diese Aufspaltung in zwei Größenkohorten, basierend auf unterschiedlichen Ernährungsstrategien kann, wie Stabile-Isotopen-Analysen zeigten, als konsistentes Muster innerhalb der Barschpopulation betrachtet werden.

Wurden die Brassenlarven durch die alternative Ressource Rotaugenlarven ersetzt, trat keine Piscivorie auf und die Größenverteilung der Barsche blieb eingipfelig. Relativ zu den Barschen schlüpften Rotaugen früher als Brassen und wuchsen außerdem innerhalb ihrer ersten Lebenswochen doppelt so schnell, was verhinderte dass die maulspaltenlimitierten Barsche die Rotaugen fressen konnten. Trotzdem waren eben diese Barsche am Ende der Wachstumsperiode signifikant größer als die kleine Kohorte im kannibalischen System, was darauf hinweist, dass die kleinen Barsche auf den Prädationsdrucks durch die Kannibalen mit verminderter Aktivität (dieses wurde auch anhand der Stellnetzfänge der beiden Kohorten dokumentiert) und reduziertem Wachstum reagierten.

Die zwei Größenklassen, die sich durch den Kannibalismus entwickelten, unterschieden sich entscheidend in ihren Voraussetzungen den Winter zu überdauern. Unter Laborbedingungen wurden nur bei den kleinsten Fischen hohe Mortalitätsraten dokumentiert, die sich allerdings durch Futterzugabe etwas verminderten. In den Teichen hingegen (im kalten Winter 2005/06 und im warmen Winter 2006/07) litten die kleinen Barsche in beiden Wintern unter hoher Sterblichkeit, obwohl sie ihre Futteraktivität nicht reduzierten. Erstaunlicherweise konnten jedoch diejenigen Barsche, die den Winter überlebten, ihre Energiereserven über den Winter hinweg aufbauen. Bei den großen Barschen wurden nur geringe Verluste während des kalten Winters verzeichnet, wohingegen die Mortalität im warmen Winter jedoch auf das bis zu neunfache anstieg. Der Grund hierfür ist weniger in der Temperatur (es wurden niedrige Mortalitätsraten im Labor dokumentiert, obwohl die Temperatur hier vergleichbar zu der von 2006/07 im Freiland war), als eher im Verlust der Eisbedeckung zu sehen, die Schutz vor piscivoren Vögeln geboten haben könnte.

Dass im Vorfeld Futterressourcen nicht nur Einfluss auf die akkumulierten Energiereserven und somit auf die Wintermortalität haben können, zeigten Versuche zur Morphologie bei piscivoren und planktivoren Barschen. Diese ergaben deutliche

morphologische Unterschiede zwischen den beiden Ernährungstypen, in der Art dass sich das Maul der piscivoren 0+ Barsche vergrößerte und die Brustflossen und der Schwerpunkt der Schwanzregion nach hinten verlagert wurden. Diese Ergebnisse lassen darauf schließen, dass die Ernährungsweise funktionale morphologische Anpassungen hervorrufen kann.

Fische unterscheiden sich weiterhin durch habitatspezifisches Auftreten und größenabhängige Aktivität, ein Fakt der ebenfalls für die beiden Größenkohorten in den Teichen mit Kannibalismus gezeigt werden konnte. Aufgrund dessen und weil sich die Größenverteilung der Barsche im Laufe der Wachstumsperiode stark verbreitert hatte, gab es zeitweilig keinerlei Überlappung der Längenhäufigkeitsverteilungen der mit Elektrofischen gefangenen Barsche, und derer, die mit Stellnetzen gefangen wurden, Dies belegt eindeutig, dass eine Fangmethode nicht genügt, um ein verlässliches Bild der Größenstruktur einer Population zu erhalten.

Das Phänomen des Kannibalismus innerhalb einer Altersklasse und die damit verbundene zweigipfelige Größenverteilung werden aufgrund der Tatsache, dass nur etwa 1 bis 10 % der Barsche den alternativen Ernährungsweg der frühen Piscivorie und des Kannibalismus wählen, wahrscheinlich häufig übersehen. Tatsächlich konnte jedoch gezeigt werden, dass die große Kohorte nicht zu missachtenden Einfluss auf die ganze Population haben kann.

TEILPUBLIKATIONEN

- Heermann, L., Beeck, P., and Borcharding, J. 2007 Two size classes of 0+ year perch: is phenotypic plasticity based on food resources? *Journal of Fish Biology* **70**, 1365–1377.
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Submitted papers:

- Heermann, L., Scharf, W., van der Velde, G., and Borcharding, J. Making the best of it: how the necessity to use alternative food resources induces cannibalism.
- Heermann, L., Eriksson, L.-O., Magnhagen, C., and Borcharding, J. Temperature and size-dependent energy storage and winter mortality in fish.

ERKLÄRUNG

Köln, den 15.09.2008

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Abbildungen und Tabellen - die anderen Werken im Wortlaut oder dem Sinn nach entnommen habe, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von den auf der folgenden Seite angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, dass ich solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde.

Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von PD Dr. habil Jost Borcharding betreut worden.

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