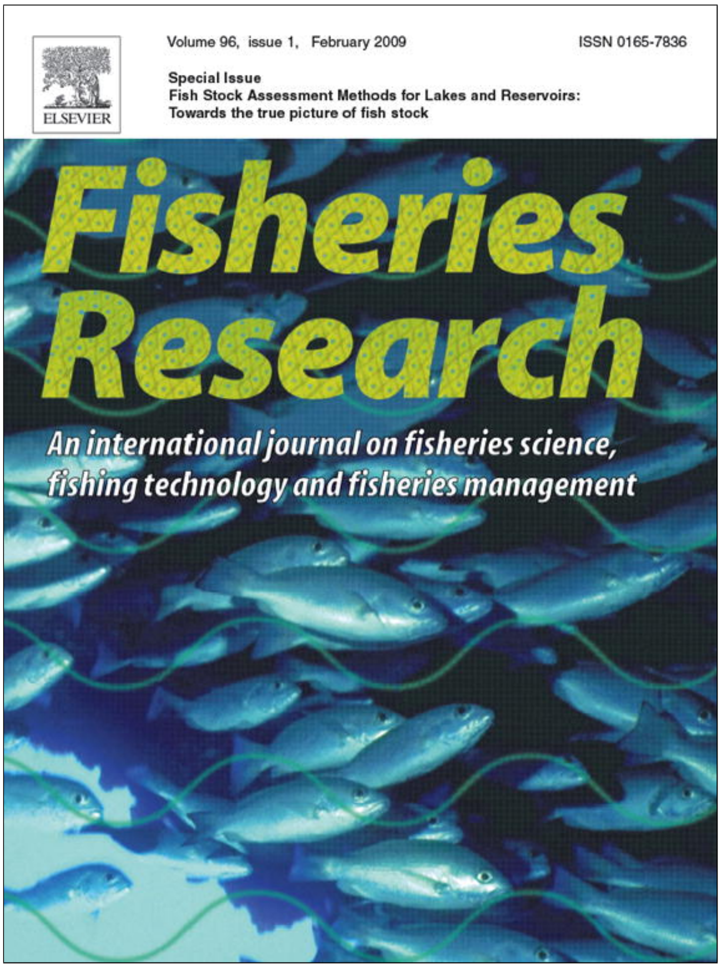
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Development of abundance and size structure of young-of-the-year perch populations using three methods

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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.

1. 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; Borcherding 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 (Borcherding, 2006; Olsson et al., 2007; Borcherding and Magnhagen, 2008; Magnhagen and Borcherding, 2008) and the energy reserves that can be used up during periods of food shortage in winter (Griffiths and Kirkwood, 1995; Borcherding 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

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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. Borcherding 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).

2. Materials and methods

2.1. 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°46′50″N, 6°22′42″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°) 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 5–6 m.

The second site, the mesotrophic Lake Reeser Meer, was partly reconstructed during the early 1990s. It is also situated near Rees (51°45′N, 6°28′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°38′16″N, 6°29′02″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 0.4–0.7 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.

2.2. Fish sampling

2.2.1. 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

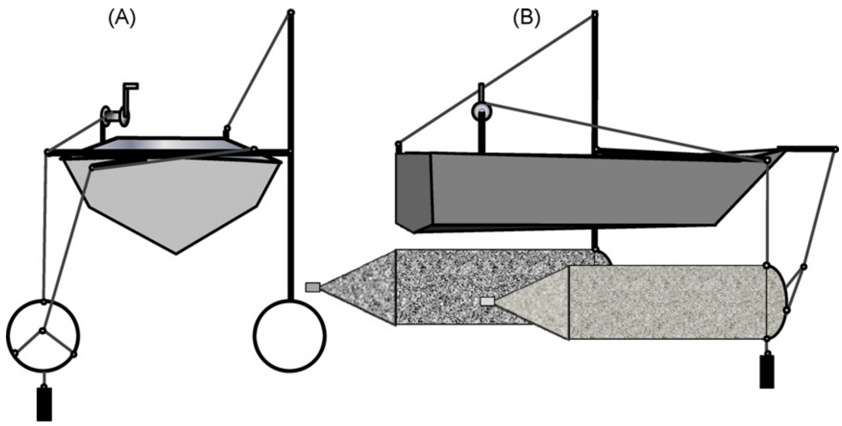

Fig. 1. Schematic diagram of the boat and the bongo net construction: front view (A) and right side view (B).

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 (3× 0.5–1 m, 2× 1–1.5 m, 1× 1.5–2 m, 1× 2.5–3 m, and 1× 3.5–4 m). 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 (<1, 1.5–3, and >3 m, 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.

2.2.2. *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 50 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 2 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).

2.2.3. *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 m^2, whereas the bigger ones were 4.5 m^2 per panel. The nets were set in the evening for between 1.5 and 2.5 h, 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:

$$\text{gillnet fishing}: CPUE_N = \frac{(A_s/A_n)C_n}{t}$$

with 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).

2.2.4. *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 1060–2480 perch per pond were measured. Finally, the total number of individuals per pond was calculated.

2.2.5. *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

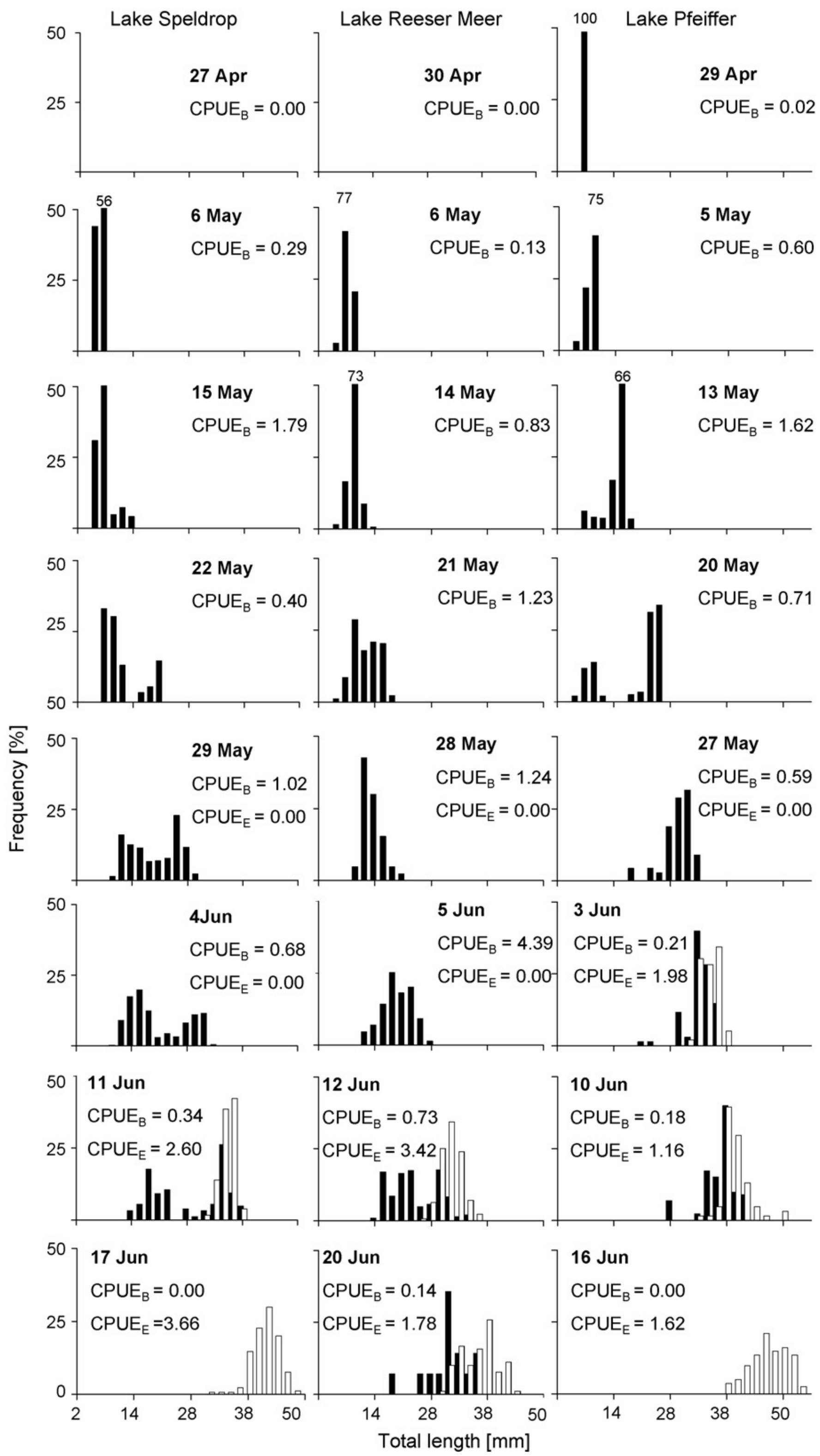

Fig. 2. Length–frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in spring 2006 using bongo net fishing (black columns, CPUE$_B$) and electrofishing (white columns, CPUE$_E$).

quantitative differences between them. Irrespective of these failures in the overall estimation of quantitative densities, the total length 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.

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		

3. Results

Hatching of perch in the gravel pit lakes started around the end of April. Perch fry in the shallowest Lake Pfeiffer were found 1 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 3 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 2–3 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).

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

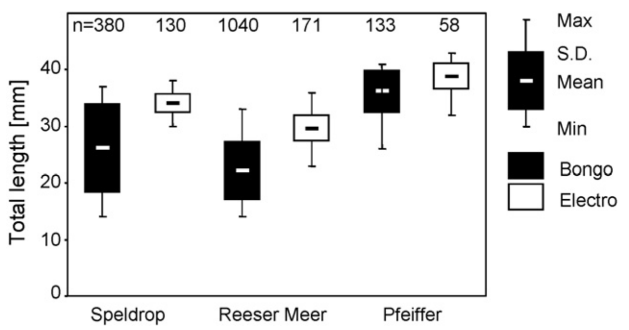

Fig. 3. Box-plot of perch sizes from the three gravel pit lakes caught using bongo nets (black) and electrofishing (white) around 11 June 2006, n = number of perch.

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}	F	P
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

the LFDs of both methods decreased (significant interaction term Date × 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 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 1 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. 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 Table 3).

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

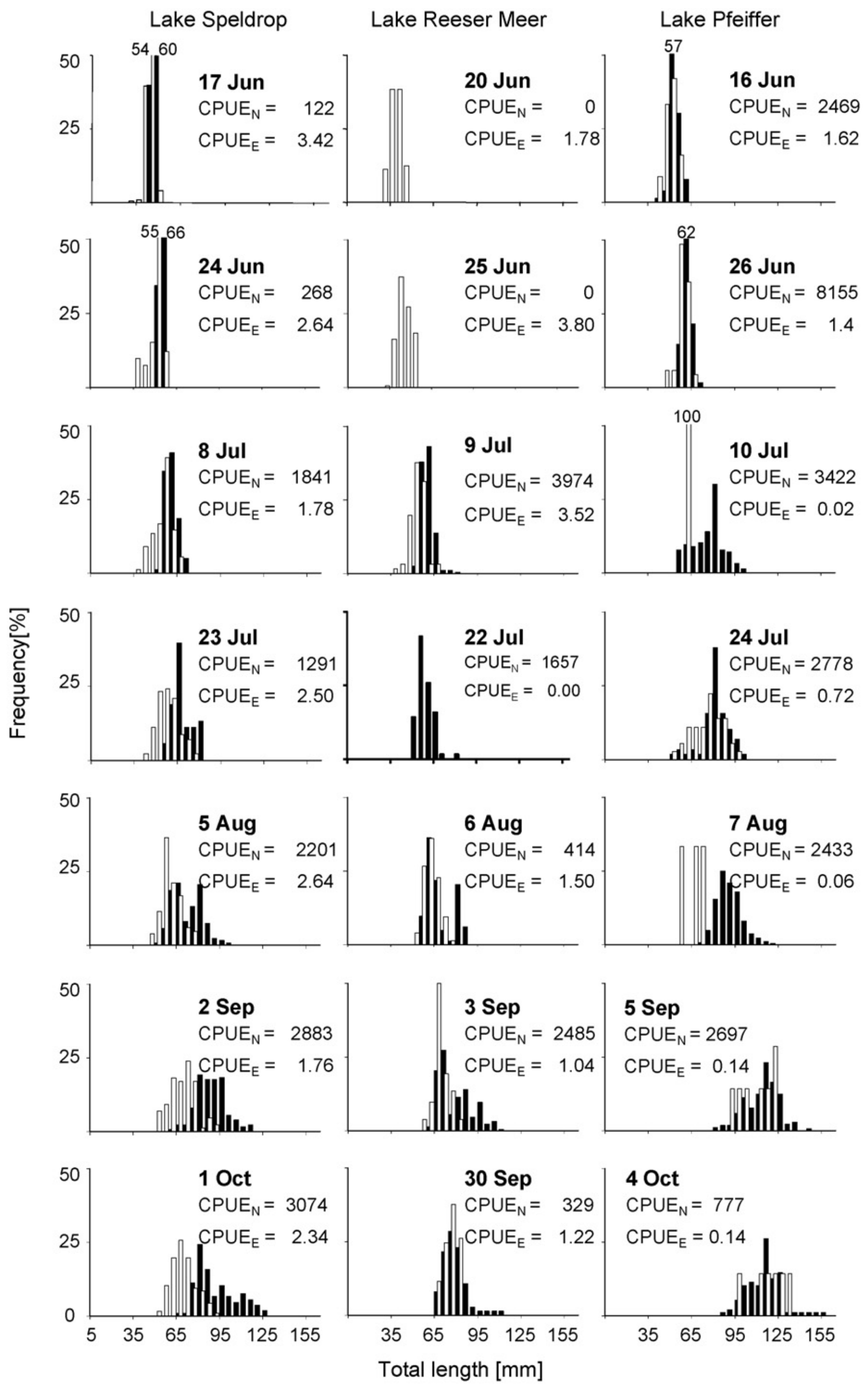

Fig. 4. Length–frequency distribution and CPUE of YOY perch in the gravel pit lakes caught on different sampling dates in summer 2006 using electrofishing (white columns, $CPUE_E$) and gillnets (black columns, $CPUE_N$).

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 Table 4).

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

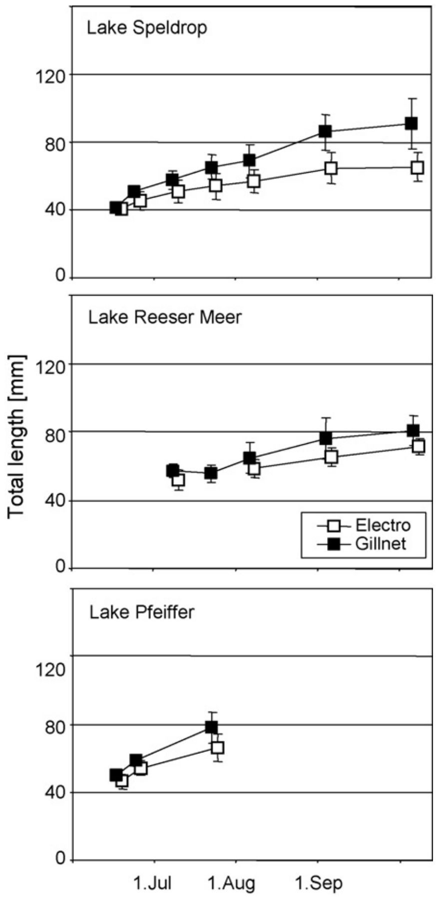

Fig. 5. Mean TL ± S.D. of perch caught in the gravel pit lakes using electrofishing (white) and gillnets (black) for all samples in 2006, when the $CPUE_E$ was >0.5.

(Fig. 8B). Thus, the more the LFD of a perch population widened, the larger was the difference between the two sampling methods.

4. Discussion

4.1. 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 m × 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

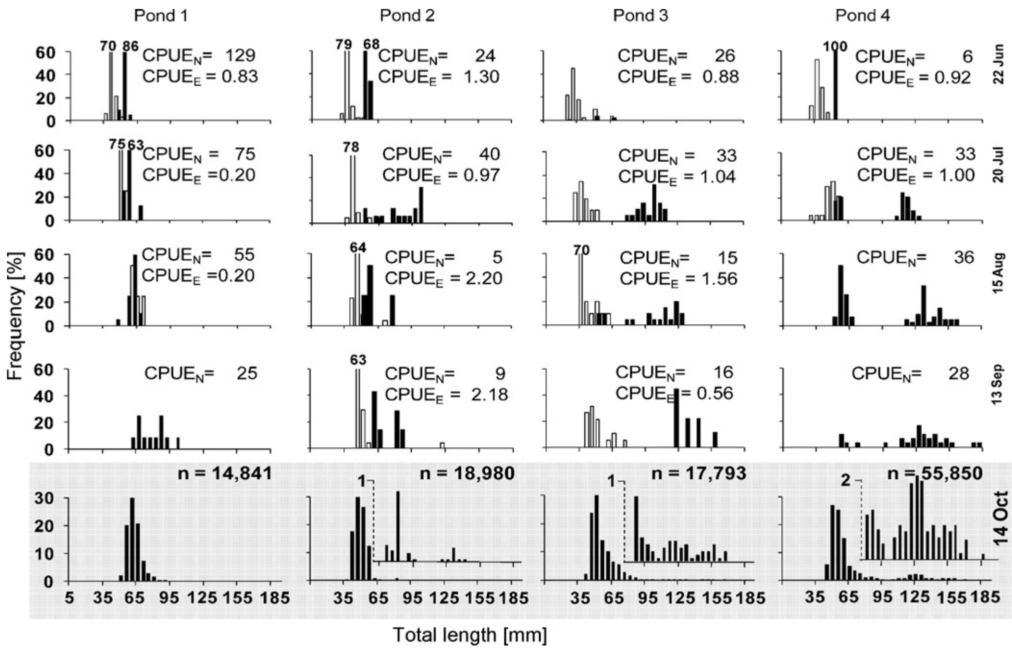

Fig. 6. Length–frequency distribution and CPUE of YOY perch in the experimental ponds caught on different sampling dates in summer 2006 using electrofishing (white columns, $CPUE_E$) and gillnets (black columns, $CPUE_N$). In addition, the total number of perch and the LFD (grey shaded) of each pond 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.

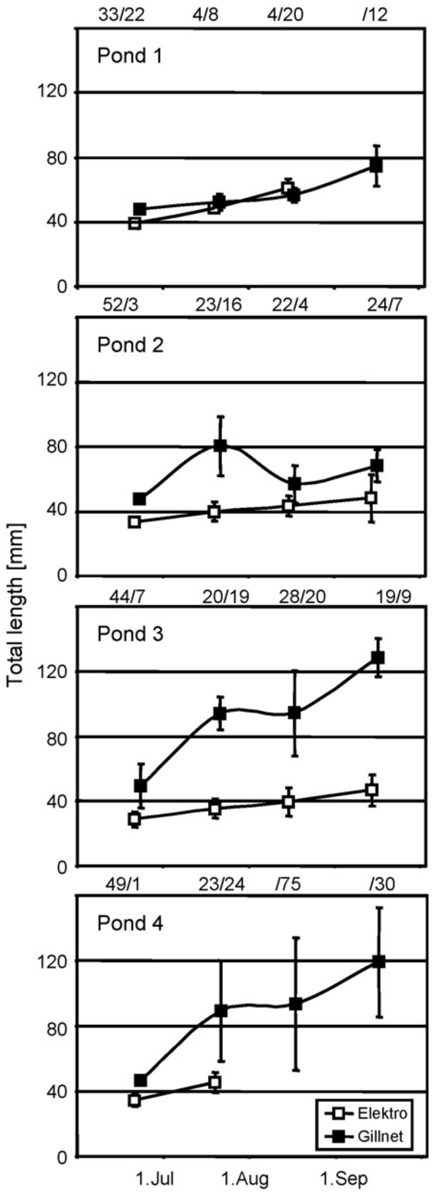

Fig. 7. Mean TL ± S.D. of perch caught in the experimental ponds using electrofishing (white) and gillnets (black) for all parallel samples in 2006. The number of perch is given above each panel (electrofishing/gillnets).

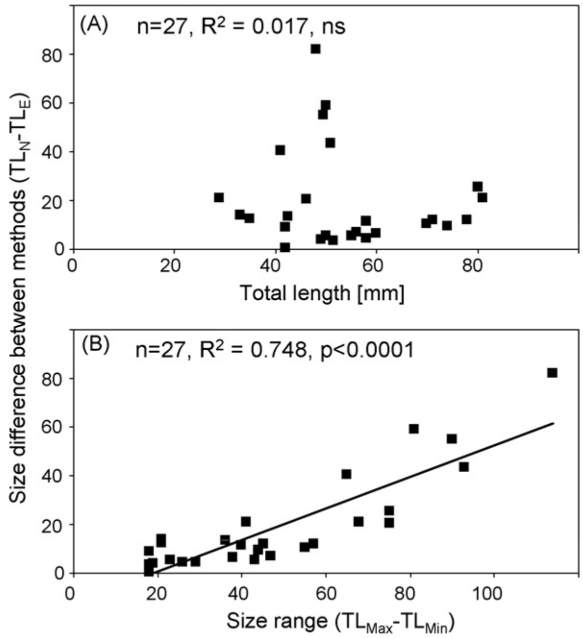

Fig. 8. The absolute difference between the mean TL of all perch from the gillnet catches (TL_N) and the catches by electrofishing (TL_E) according to the median perch size of both sampling methods (A), and the absolute size range of all sampled perch (B) for all parallel catches in 2006.

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, 2007; Guillard et al., 2006; 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 2–3 weeks in the gravel pit lakes. Spawning and hatching of perch is temperature dependent, and the spawning period can last between 1 and more than 9 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,b; 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, Borcherding, 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

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}	F	P
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

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

Pond	All perch (ind. ha^{-1})	Perch < 100 mm TL	Perch > 100 mm TL		TL_{max} (mm)
		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	1452	2.6	182

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).

4.2. 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., 2009). 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; Borcherding, 2006; Eklöv and Svanbäck, 2006; Koenig et al., 2006; Borcherding et al., 2007; Olsson et al., 2007; Magnhagen and Borcherding, 2008). 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 Borcherding, 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 (Borcherding, 2006; Koenig 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.

5. 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 Borcherding, 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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