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Size-dependent predator–prey relationships between pikeperch and their prey fish

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Abstract – Predator–prey interactions in aquatic food webs depend on the sizes of both predator and prey. In the present study, size-dependent interactions between >70 mm total length pikeperch *Sander lucioperca* (L.) and four different prey species in the biomanipulated Bautzen Reservoir were investigated. Gape widths of 597 pikeperch were measured, and the stomach contents of 806 specimens were analysed. Additionally, total lengths (TL) and body depths of 1448 prey fish were determined. The highest prey length to predator length ratio (PPR) was 0.63. Total lengths of piscivorous pikeperch and total lengths of prey fish [pikeperch, ruffe *Gymnocephalus cernuus* (L.) and roach *Rutilus rutilus* (L.)] were positively and linearly related. This was not the case for prey perch (*Perca fluviatilis* L.) as all size groups of pikeperch fed strongly on age-0 perch. This study coupled with results of previous studies suggests that predation by pikeperch can have a major impact on the population dynamics of especially perch.

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Key words: *Sander lucioperca*; predator–prey interactions; piscivory; predator to prey ratio

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Introduction

Piscivorous fish are the top predators in many aquatic systems and knowledge of the sizes of prey included in their diets is, therefore, essential to identify their potential impact in structuring populations at lower trophic levels (Juanes et al. 2002). Together with Eurasian perch, pike (*Esox lucius* L.), and occasionally eel (*Anguilla anguilla* L.), pikeperch constitute the piscivorous fish community in many European temperate lakes, and is generally considered to be important as a predator in lakes with low water transparency. Pikeperch can be very important in controlling the juvenile fish community both by predation (Dörner et al. 1999; Wysujack et al. 2002) and by inducing nonlethal trait changes such as behavioural adaptations (Brabrand & Faafeng 1993; Schulze et al. 2006). Pikeperch has been described as a piscivorous ambush-pursuit predator patrolling the pelagic zones of lakes (Popova & Sytina 1977; Maitland & Campbell 1992) and, in contrast to perch and pike, pikeperch is highly active during twilight and at night (Popova & Sytina 1977; Jepsen et al. 2000; Schulze et al. 2006).

Predator–prey interactions within aquatic food webs are often strongly dependent on both predator size and prey size (Paine 1976; Olson 1996). The maximum realised prey size a predator can take may be explained by mechanisms, such as morphological constraints (Werner 1974; Nilsson & Brönmark 2000) or differences in behavioural capabilities (Christensen 1996). A prey item can be captured and eaten if the prey length/predator length ratio is within a specific range, which was referred to as the 'predation window' by Claessen et al. (2002), who studied the population-dynamic consequences of size-dependent predation using a model of a size-structured, cannibalistic perch population (Claessen et al. 2000, 2002). These authors suggested that the lower limit of the predation window has a major impact on population dynamics, whereas the upper limit mainly affects the population structure and individual life history.

The present study focuses on predator–prey relationships between pikeperch and four prey fish species, namely perch, pikeperch, roach and ruffe. Special attention is given to the relationships between predator lengths and prey lengths and the relationship between predator gape widths and prey body depths as well as to prey size/predator size ratios. As the four prey fish species are known to differ in morphology and habitat use, predation windows of pikeperch for the four prey fish species should also differ. Based on the results the impact of pikeperch on prey populations is discussed.

Study site

Bautzen Reservoir (51°13′N; 14°27′E) is a man-made lake (first impoundment 1974) situated about 70 km northeast of Dresden (Germany). The surface area of the reservoir is 533 ha, its mean depth of 7.4 m, and its maximum depth is 12 m. Only a small area of the littoral zone is sparsely vegetated with submerged macrophytes and, because of high exposure to wind, thermal stratification normally develops only for short periods. The phosphorus level of the reservoir is very high (mean summer TP: 140 $\mu g \cdot l^{-1}$ in 1997) and intensive recreational use is at least seasonally restricted due to extensive algal blooms and low water transparency. Biomanipulation of the reservoir started in 1977 (Benndorf et al. 1988). The enhancement of the piscivorous fish stock by stocking with pikeperch, pike, eel and European catfish (*Silurus glanis* L.) in combination with catch restrictions, led to a top-down control of the food web. Consequently, the proportion of piscivores in the total adult fish biomass increased: the biomass being dominated by percids rather than cyprinids (Dörner 2002) and age-0 perch is the dominating planktivore (Mehner et al. 1996a; Wagner et al. 2004; Table 1).

Table 1. Juvenile fish community in Bautzen Reservoir within the three investigated years. Numbers represent the proportions of the total fish stock (abundance) as based on average CPUE (individuals (100 m^2 net)$^{-1} \cdot h^{-1}$). Specimens of other species were only occasionally caught. Data are combined from Kahl et al. (2001); Dörner (2002) and Dörner & Wagner (2003).

Prey fish group	1995	1997	1998
Age-0 perch	0.4	29.1	66.9
Age-0 pikeperch	0.6	15.8	1.5
Age-0 ruffe	1.3	6.5	2.9
Age-0 roach	1.3	1.1	12.8
>age-0 ruffe	0.5	1.5	1.5
Age-1 roach	Strong year-class	Moderate year-class	Weak year-class
Age-1 perch	Strong year-class	Weak year-class	Strong year-class

Material and methods

Sampling methods and samples

Fish were sampled at monthly intervals using gill-nets from April to November in 1995. Two fleets of gill-nets were used with a bar mesh size of 6, 7, 10, 13, 18, 22, 25, 32, 40, 50, 60, 70 and 100 mm each (total net area of single fleet about $2000 \cdot m^{-2}$). The fleets were set at the bottom for 2–4 h during daytime and from dusk till dawn, generally close to the deepest areas, and in a water depth of 2–4 m. In 1997 and 1998, fish were sampled with a number of gill-nets of various mesh sizes (6–100 mm bar mesh size) from April to November. From the end May to the beginning of September in 1997 and from the middle of May to the middle of August in 1998 fish were sampled with a trawl from the littoral and pelagic zones (10-mm mesh size in the cod end; three samplings per area, average sampling speed 1.2 $m \cdot s^{-1}$). In both years, fishing was carried out at weekly intervals from May to July starting immediately after twilight. After the middle of July, sampling occurred every 2 weeks. The specific study presented here was not the main reason for the intensive sampling effort. Subsamples of pikeperch were taken from sampling schemes on detailed investigations on spatial and temporal fish habitat use, stock assessments, stock developments, and predator–prey interactions. No mass removal of planktivorous fish took place during the trawl fishing as most of the fish caught were released after length measurements.

Pikeperch were killed and placed on ice immediately after capture. All pikeperch were measured to the nearest 1 mm total length (TL). The largest internal dimensions of the predator mouth (hereafter referred to as gape width) were measured (nearest mm) using a calliper rule. The calliper rule was inserted into the fish mouth in horizontal (gape width) direction until a marked resistance was reached. In this position, gape width could be read directly from the calliper rule.

Pikeperch stomach contents were analysed by counting and measuring prey organisms under a binocular and a compound microscope. If prey fish were partly digested, total lengths were back calculated, based on measurements of five abdominal vertebrae (Mehner 1990). Corresponding maximum body depths (BD) of the age-0 prey fish total lengths (perch, pikeperch and roach) were calculated based on equations taken from Dörner & Wagner (2003). Maximum BD of ruffe and older than age-0 perch, pikeperch and roach were measured (nearest mm) using a calliper rule. This was performed at the position of the anterior edge of the dorsal fin. Based on these measurements, BD was calculated using TL-BD equations (Table 2), and BD values were plotted with the data of predator gape widths.

Table 2. Equations for the relationships between the prey fish total lengths (TL, in mm) and body depths (BD, in mm) for pikeperch prey fish in the Bautzen Reservoir (CI, confidence interval).

Prey species	Size range	Equation (95% CI)	N	R^2	P-value
Perch	75–205 mm TL	BD = 0.18*TL$^{1.05}$ (0.16–0.20; 1.03–1.07)	552	0.94	<0.001
Pikeperch	70–220 mm TL	BD = 0.11 *TL$^{1.06}$ (0.64–0.16; 0.98–1.14)	147	0.88	<0.001
Roach	72–220 mm TL	BD = 0.07 *TL$^{1.23}$ (0.06–0.08; 1.20–1.26)	201	0.98	<0.001
Ruffe	71–155 mm TL	BD = 0.08 *TL$^{1.21}$ (0.05–0.12; 1.11–1.30)	31	0.98	<0.001

Statistics

Maximum and minimum prey sizes eaten were determined as maximum and minimum values within 5 cm length classes of pikeperch. Prey size use patterns with ontogeny were examined using regression analysis. Prey size log (TL; BD) versus predator size (TL) scatter diagrams were plotted and least-squares regressions were fitted to estimate the relationship between prey size and predator size. Analysis of covariance (ANCOVA) was used to test for differences in slopes and intercepts for the different prey species. All analyses were performed using the program R (http://cran.r-project.org/).

Table 3. Relative fish prey composition by number (%) of pikeperch in the Bautzen Reservoir in 1995, 1997 and 1998.

Prey fish group	1995	1997	1998
Age-0 perch	9.4	56.9	70.6
Age-0 pikeperch	7.1	22.1	8.0
Age-0 roach	1.4	0.0	0.2
>age-0 perch	8.0	0.2	0.5
>age-0 pikeperch	4.2	0.3	0.0
>age-0 roach	30.2	6.4	8.0
Ruffe	39.6	14.2	12.8
N prey fish	212	602	564
N pikeperch analysed	230	302	274
Size range of pikeperch (TL, mm)	184–678	84–776	70–752

Results

A total of 806 pikeperch stomachs were analysed during the investigation (1995: 230, 1997: 302, 1998: 274). The size range of pikeperch analysed extended from 70 to 776 mm TL (Fig. 1). Pikeperch total length (TL) and gape width (GW) were strongly related (GW = 0.10 *TL + 0.56; 95% CI: 0.10–0.11, −0.55 to 1.68; $n = 597$; $R^2 = 0.95$; $P < 0.001$; Fig. 1).

The diet composition of pikeperch differed quite markedly in the 3 years investigated (Table 3). In 1997 and 1998, when age-0 perch and age-0 pikeperch were highly abundant (Table 1), they were the most important pikeperch food (Table 3). In contrast, ruffe and age-1 roach were the most important in 1995, a year with very low reproduction of all four prey fish species (Table 1). Ruffe contributed >10% to the fish prey by number in each year investigated (Table 3). TL of prey fish ranged from 18 to 202 mm for perch, from 24 to 220 mm for pikeperch, from 12 to 165 mm for ruffe, and from 31 to 215 mm for roach. Maximum prey lengths of perch ($n = 12$, $P < 0.01$), pikeperch ($n = 11$, $P < 0.001$), ruffe ($n = 11$, $P < 0.001$) and roach ($n = 11$, $P < 0.001$) and mean prey lengths of pikeperch, ruffe and roach (Fig. 2b–d) consumed by pikeperch increased significantly during the development of an individual. There was no significant increase in minimum prey lengths of the different prey fish species consumed during ontogeny (perch: $n = 12$, pikeperch: $n = 11$, ruffe: $n = 11$, and roach: $n = 11$; $P > 0.1$ in each case), i.e., the range of prey sizes eaten increase in larger predators (Fig. 2). Predator gape width and prey body depths (BD) were positively and linearly related (Fig. 3b–d). Maximum TL and BD for perch as prey were the highest for pikeperch >400 mm TL but no correlations between pikeperch TL and mean TL or BD of consumed perch were found (predator TL vs. prey TL: Fig. 2a, $n = 805$, $P = 0.34$; predator gape width versus prey BD: Fig. 3a, $n = 805$, $P = 0.25$). Similar-sized pikeperch (>200 mm TL) fed on larger roach than ruffe and pikeperch, and on larger pikeperch than perch. This was indicated by higher regression slopes and intercepts, respectively (pikeperch TL vs. prey TL: ANCOVA, roach-pikeperch: slope: F (386) = 18.00, $P < 0.001$; roach-ruffe: slope: F (417) = 28.03,

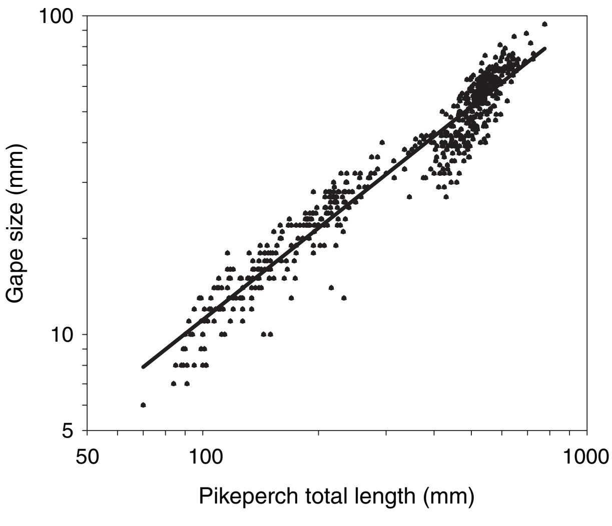

Fig. 1. Relation of log-log transformed data between total length and gape width for pikeperch from the Bautzen Reservoir ($y = -1.78 + 0.90350$*PTL $n = 110$, $R^2 = 0.54$, $P = <0.001$).

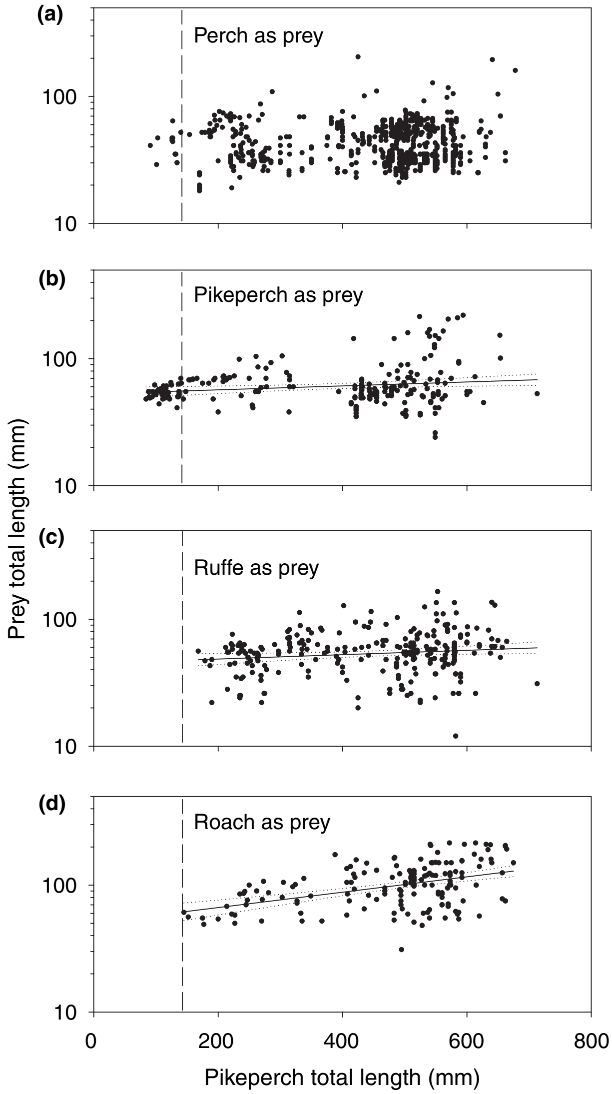

Fig. 2. Predator total length and prey total length for pikeperch as predators in the Bautzen reservoir. Medium dashed lines indicate the size (145 mm TL) when pikeperch started to feed on roach. For this measure, the stomach contents of 806 pikeperch were analysed. Linear regressions for the relationships between pikeperch total lengths (PTL) and log transformed prey total lengths for (b) pikeperch as prey ($y = 3.97 + 0.00036$ *PTL, $n = 225$, $R^2 = 0.03$, $P = 0.012$), (c) ruffe as prey ($y = 3.80 + 0.00040$ *PTL, $n = 256$, $R^2 = 0.02$, $P = 0.029$), and (d) roach as prey ($y = 3.92 + 0.00139$*PTL, $n = 162$, $R^2 = 0.19$, $P = <0.001$). Dotted lines represent the 95% confidence interval.

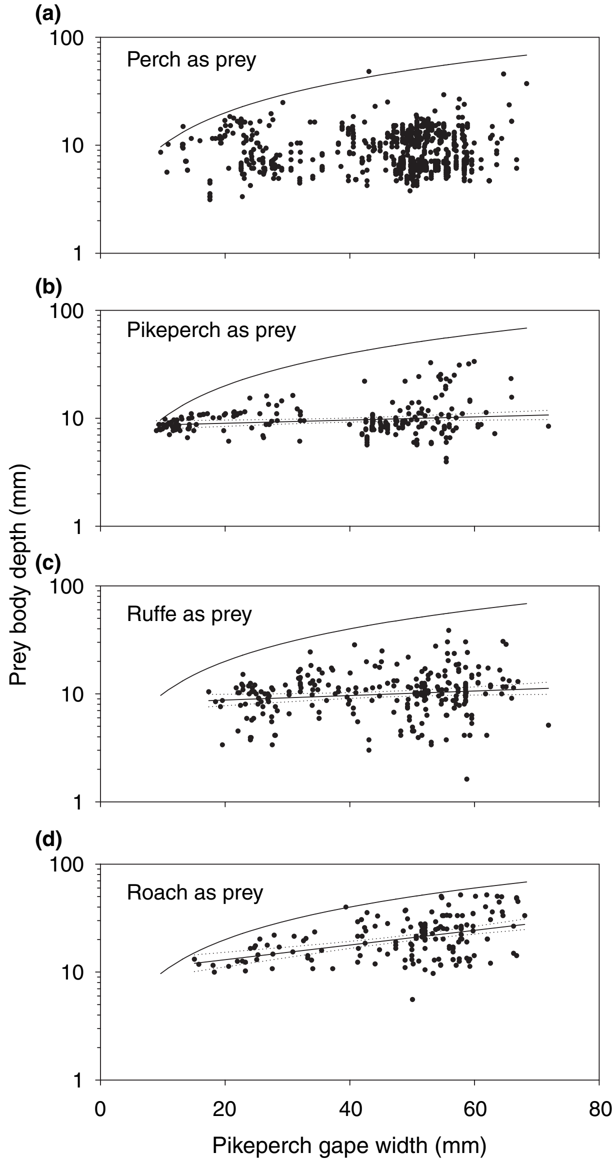

Fig. 3. Linear regressions and 95% CI (dotted lines) between gape width and prey body depth for pikeperch as predators in the Bautzen Reservoir. The 1:1-line indicates where the prey-body-depth-axis corresponds to the pikeperch-gape-width-axis. For this measure, the stomach contents of 806 pikeperch were analysed. Linear regressions for the relationships between pikeperch total lengths (PTL) and log transformed prey total body depth for (b) pikeperch as prey ($y = 2.14 + 0.00310$*PTL, $n = 225$, $R^2 = 0.02$, $P = 0.022$), (c) ruffe as prey ($y = 2.07 + 0.0050$*PTL, $n = 256$, $R^2 = 0.02$, $P = 0.023$), and (d) roach as prey ($y = 2.26 + 0.00157$*PTL, $n = 162$, $R^2 = 0.20$, $P = <0.001$). Dotted lines represent the 95% confidence interval.

$P < 0.001$; pikeperch-ruffe: intercept: F $(480) = 16.33$, $P < 0.001$; pikeperch gape width versus prey BD: ANCOVA, roach-pikeperch: slope: F $(386) = 35.04$, $P < 0.001$; roach-ruffe: slope: F $(417) = 28.21$, $P < 0.001$). BD of pikeperch and ruffe as prey was not different (pikeperch gape width versus prey BD: ANCOVA, pikeperch-ruffe: intercept: F $(480) = 0.55$, $P = 0.46$). As prey BD is derived directly from prey TL and gape width is linear related to fish length, F-values are identical for both relationships. Generally, prey BD were smaller than gape widths of predators, as indicated by the 1:1 line. In rare cases, prey BD were close to predator gape widths (Fig. 3a–d). There was no case of a larger prey BD than the corresponding predator gape width, which indicates that the method chosen was valid.

Prey TL/predator TL ratios (PPR according to Turesson et al. 2002) decreased with increasing predator size for all four prey species (Fig. 4a–d). The maximum prey size ratio for perch as prey was 0.50 (minimum ratio: 0.04, mean ratio: 0.11 ± 0.07 SD). Maximum prey size ratio for pikeperch as prey was 0.63 when a pikeperch of 98 mm TL consumed a conspecific of 62 mm (minimum ratio: 0.04, mean ratio: 0.23 ± 0.16 SD). The maximum prey size ratios

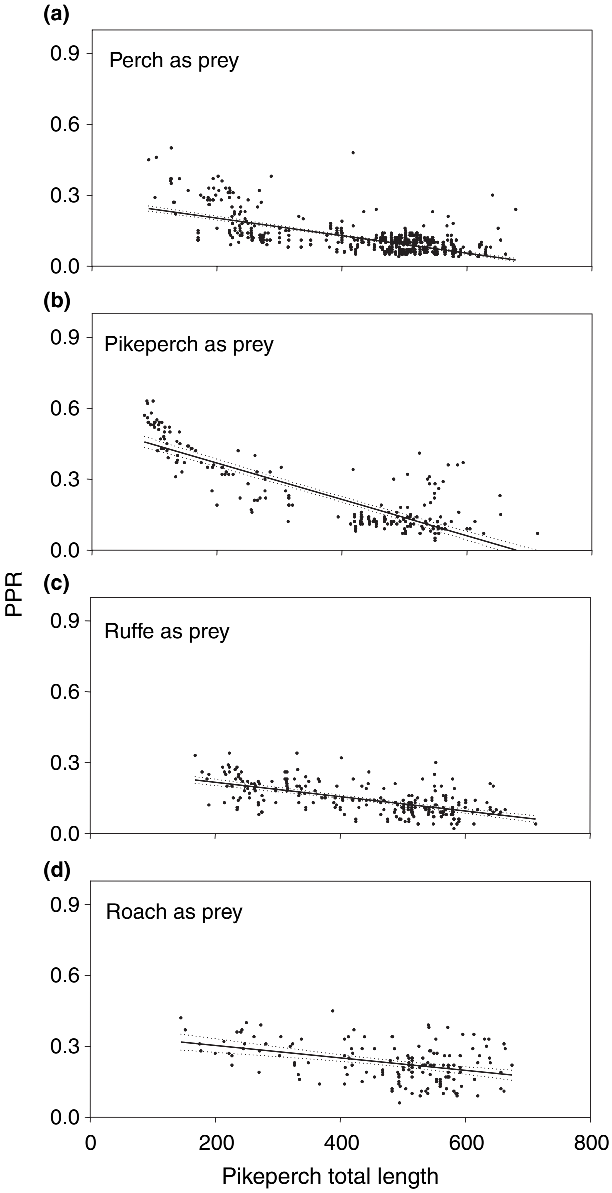

Fig. 4. PPR plotted against pikeperch total length. Solid lines indicate mean size ratios. For this measure, the stomach contents of 806 pikeperch were analysed. Linear regressions for the relationships between pikeperch total lengths and the prey length/predator length ratio for (a) perch as prey (P/P ratio = −0.0004*PTL + 0.28, n = 805, R^2 = 0.46, P = <0.001), (b) pikeperch as prey (P/P ratio = −0.0008 *PTL + 0.52, n = 225, R^2 = 0.70, P = <0.001), (c) ruffe as prey (P/P ratio = −0.003 *PTL + 0.28, n = 256, R^2 = 0.38, P = <0.001), and (d) roach as prey (P/P ratio = −0.0003 *PTL + 0.36, n = 162, R^2 = 0.16, P = <0.001). Dotted lines represent the 95% confidence interval.

for ruffe and roach as prey were 0.34 and 0.45, respectively (ruffe: minimum ratio: 0.02, mean ratio: 0.14 ± 0.07 SD; roach: minimum ratio: 0.06, mean ratio: 0.23 ± 0.08 SD).

Discussion

In the present study, size-dependent relationships between >70 mm TL pikeperch and their prey fish species in Bautzen Reservoir have been observed. The PPRs for all four prey species decreased with increasing predator size. The mean prey lengths and body depths of the three prey species ruffe, pikeperch, and roach increased with increasing predator size, whereas no such pattern could be detected for perch as prey. This was probably due to the fact that all size classes of pikeperch fed to a high extent on age-0 perch, which were the most abundant prey in the reservoir except in 1995 when age-0 perch were scarce and ruffe dominated the diet of pikeperch. Sizes of consumed perch and the increases in average size of consumed pikeperch were less than would be expected by an increase in predator size alone. This may be due to several factors such as food supply (e.g., the densities, size distribution, habitat selection and activity patterns of different prey species), differences in prey fish morphology, and size-selective feeding of pikeperch. Also variability in habitat selection and activity patterns between predatory pikeperch and its prey species and their different cohorts are likely to have influenced the patterns of size-related predator–prey interactions observed.

The general patterns of prey size use by predators in this study correspond well with previous studies of predation by fish (Juanes et al. 2002). The size of prey consumed increases with predator size. The range of prey sizes eaten also increases in larger predators as maximum prey size often increases rapidly while minimum prey size changes only slightly over a broad range of predator size (c.f. Hölker & Hammer 1994; Dörner & Wagner 2003 for other percids; Mittelbach & Persson 1998 for freshwater piscivores and Scharf et al. 2000 for marine piscivores). In addition, PPR decreased in relation to pikeperch in this study as shown for several marine piscivores (Scharf et al. 2000) and for pikeperch in freshwater systems (Keskinen & Marjomäki 2004; Lappalainen et al. 2006). The decline in PPR in pikeperch may be explained by size-selective predation on age-0 fish (Dörner et al. 1999; Turesson et al. 2002). In contrast, Hansson et al. (1997) detected a constant PPR in the Baltic Sea, which may indicate a continuous size spectrum and suitable good feeding conditions for pikeperch.

In common with other piscivores such as pike (Nilsson & Brönmark 2000), pikeperch are gape-limited and frequently swallow prey fish tail first in contrast to other predatory species such as brown trout (*Salmo trutta*) (Vehanen et al. 1998). Therefore, both prey size and prey body depth should be correlated with gape size of the pikeperch, because prey is swallowed whole. Consequently, comparisons of the relationships between pikeperch and their prey fish species with respect to the sizes of predator and prey should provide valuable information about the interactions in the food web. In a review about the ontogeny of piscivory and its ecological consequences, Mittelbach & Persson (1998) stated that piscivores with relatively large mouth gapes switch to piscivory at smaller sizes and were larger at age-1. The results of our study did not corroborate this statement. Pikeperch have smaller mouth gapes at the same sizes when compared to perch (mean gape width at 200 mm TL: pikeperch = 20 mm, perch = 25 mm; Dörner & Wagner 2003; this investigation), and both species become at least partly piscivorous within their first year in the Bautzen Reservoir (Mehner et al. 1996b; Dörner et al. 1999). Surprisingly, pikeperch fed on larger and therefore deeper prey fish than similar-sized perch, although the pikeperch had smaller mouth gapes. This unexpected variation in size-specific diet patterns between the two predators is probably not attributed to the spatial distribution of available prey because the larger part of the pikeperch and perch populations in the Bautzen Reservoir use similar habitats (Dörner et al. 1999). Instead, other factors, such as significant differences in feeding capacity associated with differences in gape morphology (Craig 1987), foraging behaviour and capture success (Turesson & Brönmark 2004), should also be taken into account.

Similar-sized pikeperch fed on larger roach than ruffe and pikeperch, and on larger pikeperch than perch. For ruffe as prey this pattern is not surprising and reflects their natural size distribution with ruffe reaching a lower maximum size than, e.g., roach. The dominance of small perch in the diet of pikeperch indicates the importance of age-0 perch as prey for pikeperch which has also been shown in other studies (e.g., Peltonen et al. 1996). In line with this, the impact of size-dependent predation on population dynamics and individual life history of Eurasian perch was intensely studied by Claessen et al. (2002). They identified different types of perch population dynamics which were, at least partly, determined by the lower limit of the predation window. With a low threshold in the predation window, cannibalism should regulate recruitment, resulting in coexistence of many year classes (Claessen et al. 2002). It should be taken into account that the analyses by Claessen et al. (2002) apply only to single species populations and depend on competition on shared resources and cannibalistic interactions between small and large individuals of the same species. In multispecies systems, such as the present one, alternative prey fish for adults are present making the population dynamics less likely to be strongly affected by recruitment *per se*. The observed minimum size of perch (18 mm TL) and pikeperch (26 mm TL) captured by pikeperch >70 mm TL are higher than those observed for perch as predator (perch: 12 mm TL, pikeperch 23 mm TL; Dörner & Wagner 2003) in the Bautzen Reservoir, but average prey size is low if compared to similar sized predators investigated in other studies (Mittelbach & Persson 1998). The relatively low size limit in combination with a low average prey size indicates that pikeperch has the capacity to affect recruitment success strongly and thus year class strength of both perch and pikeperch. This is further supported by findings in previous studies on pikeperch and perch in the Bautzen Reservoir, which have shown that: (i) several year classes coexist (Dörner 2002); (ii) both species become piscivorous very early in their life (Mehner et al. 1996a,b); (iii) pikeperch and perch feed size- and species-selective on age-0 perch and age-0 pikeperch (Dörner et al. 1999, 2003) and; (iv) that age-0 percid abundance was controlled by piscivorous perch and pikeperch (Dörner et al. 1999).

The minimum size of roach captured by pikeperch was at 27 TL mm rather high, and, in contrast to perch and pikeperch (as prey), pikeperch is probably not an important predator on age-0 roach. This is illustrated by the fact that the strong age-0 roach cohort in 1998 (Table 1) was not reflected in an increased consumption of age-0 roach by the pikeperch. This could be due to spatial separation of the age-0 cohorts of roach and predatory percids. Age-0 roach predominantly use the littoral zones of lakes (Persson et al. 2000), and are therefore probably not available for the more pelagically orientated pikeperch. In line with this, age-1 perch have been described as the most important predators of age-0 roach in the Bautzen Reservoir (Dörner 2002), whereas pikeperch becomes an important predator of roach later when roach get to age-1 and start to occupy the more the pelagic areas of the reservoir.

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