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Intraguild predation and cannibalism in age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*): Interactions with zooplankton succession, prey fish availability and temperature

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The preconditions for the ontogenetic diet shift from planktivory to piscivory in age-0 perch and age-0 zander were examined in the long-term biomanipulated Bautzen reservoir (Germany). Early piscivory already was observed in age-0 zander of approximately 20 mm total length, but occurred only in the largest (> 40 mm *TL*) perch specimens during early summer. The onset of piscivory was triggered by high water temperatures in late spring which enhanced the growth rates of the predators relative to their prey, and by the drastic decline in zooplankton abundances during that time. Due to the lack of other prey fish, cannibalism and mutual intraguild predation dominated in piscivorous zander and perch. Early piscivory in both species was additionally favoured by the biomanipulation experiment in Bautzen reservoir due to (1) an abundant *Daphnia* population in spring which increased the growth rates of the predators, and (2) the coexistence of perch and zander in high densities which is uncommon in naturally-structured waters.

1. Introduction

Ontogenetic diet shifts are widespread in size-structured populations (Werner & Gilliam 1984). In many piscivorous fishes, there is a succession from zooplanktivory as larvae and small juveniles, to benthivory as juveniles, and finally to piscivory as yearlings and adults (Willemsen 1977, Werner 1986, Fox 1989, Persson & Greenberg 1990). Zooplanktivory in adult fish may influence significantly the dynamics of their prey (Gliwicz & Pijanowska 1989), and this predation pressure may cascade down the whole aquatic foodweb (Carpenter *et al.* 1987, Mills *et al.* 1987, Benndorf 1995). But planktivorous age-0 fish also can drive the zooplankton succession in years of high recruitment (Cryer *et al.* 1986, Qin & Culver 1995). Thus the age-0 group may be the trophic link between piscivorous fish and zooplankton (Mills *et al.* 1987, Mehner *et al.* 1996a). However, the switch from planktivory to piscivory in age-0 fish also may be important, since then the trophic cascade is regulated from the top. A diet shift to piscivory early in life could be advantageous for a single individual, since a piscivorous fish can directly reduce the density of potential intraspecific (cannibalism) and interspecific competitors (intraguild predation, Polis *et al.* 1989).

In Central Europe, piscivory in zander (*Stizostedion lucioperca*) has been documented during the first year of life by Nagięć (1977), Van Densen (1985a) and Buijse and Houthuijzen (1992). Similar observations were made in the closely-related age-0 walleye (*Stizostedion vitreum vitreum*) in North America (Forney 1966, Kempinger & Carline 1977, Johnson *et al.* 1992). It was assumed that either the decline in zooplankton densities (Nagięć 1977) or the availability of suitable prey fish (Van Densen 1985a) were the main forces which induced the early switch in age-0 zander. The zander often coexists with another piscivorous percid species, the perch (*Perca fluviatilis* and *P. flavescens*, respectively; Van Densen 1985b, Johnson *et al.* 1992). However, the uptake of fish prey was found only occasionally in young-of-the-year perch (Spanovskaya & Grigorash 1977, Van Densen 1985b, Thiel 1989).

We hypothesized that the onset of piscivory in age-0 perch may be influenced by the relative availability of zooplankton and fish prey. Declining densities of large zooplankton species are a very common phenomenon in lakes in Europe during the summer (Sommer *et al.* 1986). However, the vulnerability of prey fish for age-0 perch may be rather limited in many waters, since the mouth gape of perch is smaller than that of the zander, thus resulting in a higher predator:prey size ratio than for zander (Collette *et al.* 1977). This difference also holds true for perch and zander larvae and juveniles (M. Plewa, unpubl. results). The diet switch to piscivory in age-0 perch additionally could be positively stimulated by a high water transparency, since, in contrast to the zander, the visual system of the perch is insufficiently adapted to low light intensities (Ali *et al.* 1977, Wahl *et al.* 1993).

In the long-term biomanipulated Bautzen reservoir (see below), (1) perch and zander are very abundant, (2) age-0 fish density is extraordinarily high, and (3) the population abundance of daphnids regularly declines in early summer. Consequently, the aim of our study was to examine whether both zander and perch become piscivorous during the first year of life, and determine the potential consequences of these early diet shifts on the development of the age-0 fish and zooplankton communities.

2. Material and methods

2.1. Study site

Bautzen reservoir is a hypertrophic, polymictic, man-made lake 70 km northeast of Dresden (Saxony, Germany). The surface area of the lake is 533 ha, mean depth about 7.4 m, and maximum depth about 12 m. A long-term biomanipulation experiment started in 1981 has strongly influenced structure and food pathways within the fish community (Schultz *et al.* 1992, Benndorf 1995). Due to continuous stocking and catch restrictions to anglers since 1981, the stocks of adult piscivorous fish (mainly zander, perch, and pike, *Esox lucius*) increased to about 40–50% of total fish biomass in 1993 and 1994 (Schultz *et al.* 1992; and unpubl. results). Considering the hypertrophic state of Bautzen reservoir, the fish community should be dominated by cyprinids (Persson *et al.* 1991, Kubecka 1993). But, as a consequence of direct and indirect predation effects of the high number of piscivores, the stocks of roach, *Rutilus rutilus*, and bream, *Abramis brama*, have drastically been depressed during the last five years (Schultz 1996). Therefore, the fish community of Bautzen reservoir represents a transient, enjuvenated stage of ichthyocoenosis succession with a fast-growing piscivorous perch stock and high densities of zander and ruffe (*Gymnocephalus cernuus*) (Kubecka 1993). Due to the declining stocks of cyprinids, the main zooplanktivorous fish are now the age-0 groups of the percids (Mehner *et al.* 1996a). Piscivorous 0+ groups occur in extraordinarily high densities (> 20 000 ind. ha^{-1} in September, Schultz *et al.* 1992, and unpubl. results). In addition, population density of the dominant cladoceran species *Daphnia galeata* has peaked in spring and autumn and declined in summer, during all years of investigation except for the period 1985–1987 (Köthe & Benndorf 1994, Mehner *et al.* 1995, Köthe *et al.* 1996).

2.2. Age-0 fish

Fish larvae and age-0 juveniles were sampled between June and the middle of September in 1993 and 1994. In 1993, mainly gill nets with mesh sizes of 6, 7, 10 and 13 mm were used (Table 1). Fleets of nets were set in several regions of the reservoir in different water depths (2 to 10 m). Fish larvae were additionally caught in littoral regions with a lift net (1 m^2, mesh size 1 mm). In 1994, a conical plankton tow net (0.35-m diameter, 2.5-m length, mesh size 780 µm) was used to sample the larvae. Later, age-0 fish were caught close to the shore by using a small seine net (15 m long, 4-mm mesh size; Table 1), and in deeper (> 2 m) regions by using fleets of gill nets as in 1993 (Table 1). Since catch-per-unit-effort data were not directly comparable between the different gears, the abundance of fish was estimated in relative terms only (Table 1).

All fish larvae were fixed in 3% formaldehyde solution immediately after capture. Larger fish were frozen (–18°C). In the laboratory, species were identified. The total length (mm, *TL*) of all specimens was measured and the mean length of each species was computed from the complete catch on one date. Where available, the stomach content of at least 10 specimens of both age-0 perch and zander was inspected (Table 1). The frequency of fish prey in the stomachs was determined, and the numerical composition of the prey fish species was calculated.

2.3. Zooplankton

Zooplankton was sampled in vertical series (2.5-m depth interval, 2-l Ruttner-sampler) from the deep-

Table 1. Overview of the gear used to sample age-0 fish in Bautzen reservoir in 1993 and 1994. The abundance of fish is indicated in relative terms (xxx = dominant, xx = present, x = rare, 0 = not present). The number of stomachs examined in age-0 perch and age-0 zander is given in brackets.

Date	Gear	Relative abundance of fish species					
		Perch		Zander		Ruffe	Roach
1993							
2 June	Lift net	xxx	(10)	0		0	0
10 June	Lift net, gill nets	xxx	(19)	x	(8)	0	0
18 June	Gill nets	xxx	(20)	xx	(10)	x	x
23 June	Gill nets	xxx	(23)	xx	(48)	x	x
29 June	Gill nets	xxx	(10)	xx	(3)	xx	0
9 July	Gill nets	xx	(26)	xx	(7)	xxx	0
15 July	Gill nets	xxx	(45)	xx	(14)	xx	x
27 July	Gill nets	xxx	(20)	0		xx	x
24 August	Gill nets	xxx	(43)	x	(3)	xx	x
2 September	Gill nets	xxx	(57)	xx	(25)	xx	x
7 September	Gill nets	xxx	(10)	xx	(20)	xx	x
9 September	Gill nets	xxx	(32)	x	(1)	xx	x
14 September	Gill nets	xxx	(25)	x	(5)	xx	0
1994							
9 June	Conical net	xxx	(43)	xx	(47)	x	xx
16 June	Seine net	xxx	(25)	xx	(24)	x	xx
28 June	Gill nets, seine	xxx	(31)	0		x	x
12 July	Gill nets, seine	xx	(100)	x	(6)	xxx	x
27 July	Gill nets, seine	xx	(83)	x	(1)	xx	xxx
9 August	Gill nets, seine	xxx	(151)	0		xx	xx
1 September	Gill nets, seine	xxx	(118)	0		xx	xx
13 September	Gill nets, seine	xxx	(121)	0		xx	xx
Total:			(1 012)		(222)		

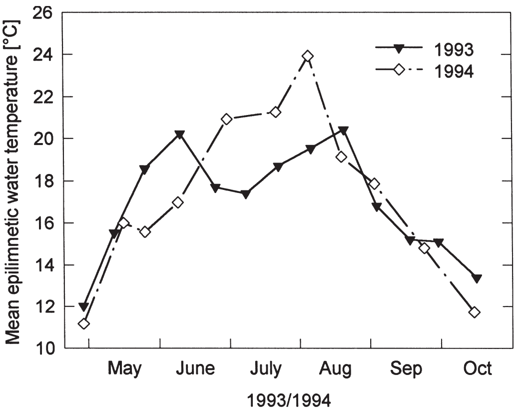

Fig. 1. Mean epilimnetic (0–5-m water depth) water temperatures (°C) in Bautzen reservoir from May until October, 1993 and 1994.

est part of the lake approximately twice a month between the middle of May and the middle of October. Secchi depth and mean epilimnetic water temperature were determined at 1-m intervals on the same dates. All zooplankton subsamples were concentrated through a 55-µm net. Large zooplankton (daphnids > 1.1 mm, *Leptodora kindtii*, *Chaoborus flavicans*) were collected by vertical hauls with two different plankton nets (500 and 750 µm, opening diameter 25 cm, flowmeter inside). The samples were immediately preserved in 3% formaldehyde solution containing 30 g saccharose l^{-1} (Haney & Hall 1973). Counts from all depth intervals were separately performed using a Kolkwitz chamber by numbering at least 50 specimens of each important species. These subsamples were averaged and expanded to obtain total zooplankton densities. Individual zooplankters were measured and grouped into 50-µm size classes by projecting them onto a screen which was connected with the microscope. Biomasses were calculated using length–weight regressions (Bottrell *et al.* 1976, Mehner *et al.* 1995).

3. Results

There were differences in the patterns of mean epilimnetic water temperatures in spring and summer 1993 and 1994 (Fig. 1). In 1993, water temperatures were significantly higher at the end of May and during the first weeks of June (about 19–21°C) than in 1994 (about 15–17°C; Fig. 1).

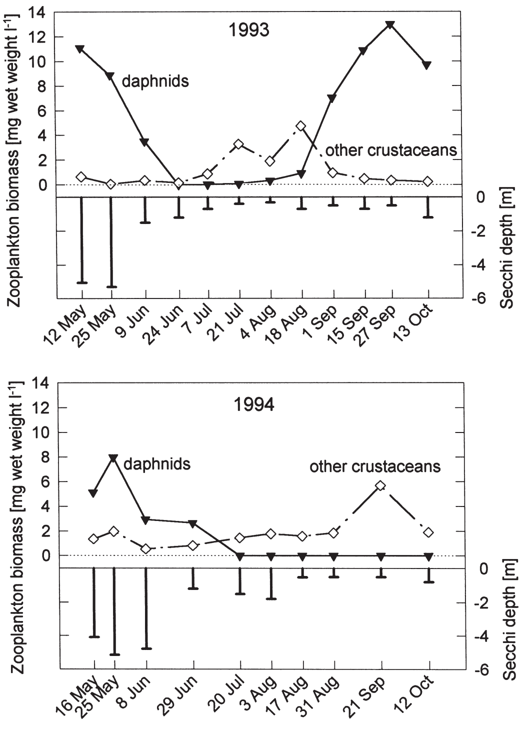

Fig. 2. Zooplankton biomass (mg wet weight l^{-1}) and water transparency (Secchi depth in m) in Bautzen reservoir from May until October 1993 (upper graph) and 1994 (lower graph). "Daphnids" are nearly exclusively *Daphnia galeata*, "other crustaceans" include *Bosmina longirostris, Chydorus sphaericus*, calanoid and cyclopoid copepods, *Leptodora kindtii* and *Chaoborus flavicans.*

In contrast, higher water temperatures were observed during summer 1994, than in the preceding summer (21°C vs. 17°C, Fig. 1).

The development of the zooplankton community showed a similar pattern in spring of both years (Fig. 2). High biomasses of *Daphnia galeata* (8–11 mg wet weight l^{-1}) in May were followed by a drastic decline of the population densities in June. In July and August, small cladocerans (*Bosmina longirostris, Chydorus sphaericus*) dominated instead, but their biomass never exceeded 4 mg wet weight l^{-1}. In 1993, a second population peak of *Daphnia galeata* was observed in autumn, whereas the population density of this large cladoceran species remained near zero in September and October 1994 (Fig. 2). The density of calanoid and cylopoid copepods, and of carnivorous cladocerans always was lower than 0.3 mg w.w. l^{-1}. The highest Secchi depths (> 5 m) were

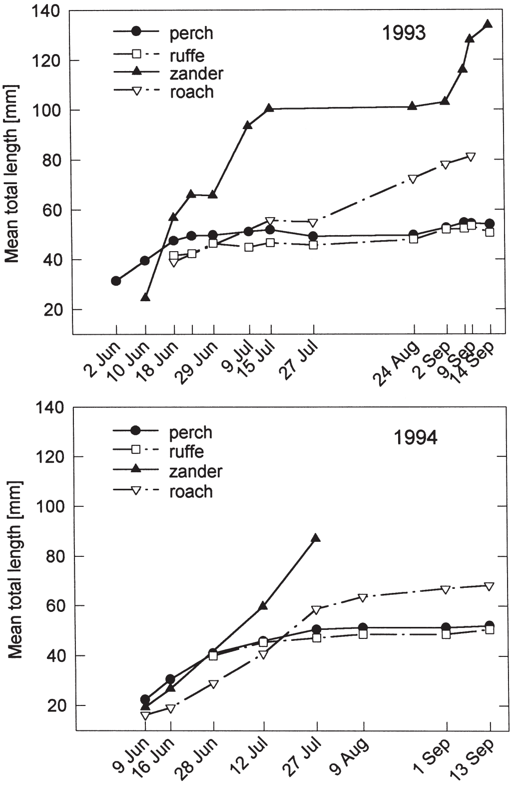

Fig. 3. Mean total lengths (*TL*, in mm) of age-0 fish in Bautzen reservoir between June and September 1993 (upper graph) and 1994 (lower graph).

measured during the spring peaks of *D. galeata* in both years (Fig. 2). In summer and autumn, water transparency was always < 1.5 m owing to strong blooms of algae (Benndorf 1995).

Age-0 perch dominated the catch at nearly all sampling dates in both years (Table 1). Ruffe also were present, but in lower abundances than the perch. Age-0 zander frequently were caught in 1993, but occurred in lower numbers in June and July 1994. In August and September 1994, no zander were sampled with either seine net or gill nets (Table 1). Age-0 roach regularly were caught in 1993, but in extremely low numbers. However, this species was very abundant in 1994 (Table 1).

The mean *TL* of perch increased from about 25–30 mm in June to about 55 mm in September in both years (Fig. 3). Growth was substantially higher in June than during summer. A similar growth pattern was observed in ruffe, although the length increase was slightly higher than in the perch during the summer 1993. Length of roach was lower than that of the perch in June in both years, but the roach reached higher final *TL*s than did the perch at the end of the season (about 80 mm in 1993, and 70 mm in 1994; Fig. 3). The most rapid growth was observed in age-0 zander. Within 6 weeks, the mean *TL* increased from about 20 mm to 90–100 mm in the middle of July (Fig. 3). From mid-July to August, zander lengths remained constant, but again strongly increased in September 1993.

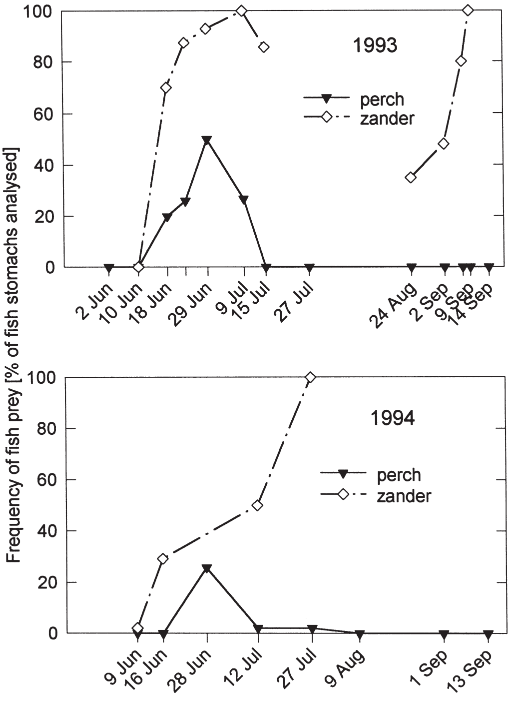

Fig. 4. Frequency of occurrence of fish prey (in % of fish analyzed) in the stomachs of age-0 zander and age-0 perch from Bautzen reservoir in 1993 (upper graph) and 1994 (lower graph).

Age-0 perch were piscivorous only for a limited period in both years. Maximum frequencies of fish consumed by perch (20–50% of the fish analyzed) were observed during the drastic decline of daphnids at the end of June in both years (Fig. 4), corresponding to a fish size of about 40 mm *TL*. From the middle of July onwards, perch did not consume fish. In contrast, frequencies of fish prey consumed by age-0 zander increased steadily from zero in June to 100% in July in both years (about 90–100 mm *TL*). From the end of July until the end of August 1993, zander piscivory was drastically depressed, but increased again in

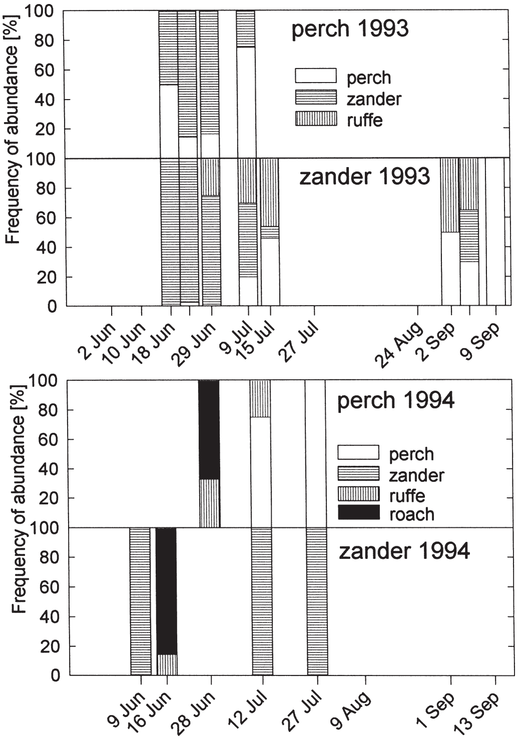

Fig. 5. Species composition (in % of abundance) of fish prey in the stomachs of piscivorous age-0 perch and age-0 zander from Bautzen reservoir in 1993 (upper two graphs) and in 1994 (lower two graphs).

September 1993. Values were not available for the same period in 1994. The main prey species for piscivorous age-0 perch were its own smaller conspecifics (cannibalism) and smaller zander in 1993 (Fig. 5). The degree of cannibalism in age-0 perch was higher in July than in June. In contrast, zander were almost exclusively cannibalistic in June, but preyed additionally on perch and ruffe later in the season in 1993 (Fig. 5). In June 1994, juvenile roach were eaten by both piscivorous age-0 percids (Fig. 5). In July of this year, however, the degree of cannibalism was close to 100% in both species.

4. Discussion

In this study, we have analyzed the interactions between piscivory in age-0 perch and age-0 zander, and the seasonal succession of the zooplankton community in Bautzen reservoir during two years. We have found that the summer decline of large daphnids coincided with the onset of piscivory in both percid species. However, the high availability of prey fish of suitable length appears to be the second prerequisite for these ontogenetic diet shifts. High water temperatures in spring stimulated piscivory in perch due to large size differences between predator and prey. In addition, the growth rate was higher during the piscivorous phase than during the predominantly zooplanktivorous phase of both zander and perch.

In both years, we observed a rapid decline in *D. galeata* biomass at the end of June. Since daphnids are the main prey items of small age-0 perch and zander (Spanovskaya & Grigorash 1977, Van Densen 1985ab, Hartmann 1986, Fox 1989), this decrease forced the fish to shift to another food source. In age-0 zander, the early onset of piscivory is a very common phenomenon. Van Densen (1985a) found that the zander predated on fish (mainly smelt, *Osmerus eperlanus*) already at *TL* = 20 mm in Lake Tjeukemeer (The Netherlands). Buijse and Houthuijzen (1992) observed the diet switch to piscivory in 60 and 70 mm *TL* classes of zander in Lake Ijssel (The Netherlands). In Oneida Lake (USA), age-0 walleyes started feeding on age-0 perch when walleyes had reached a length of 60–80 mm *TL* (Mills *et al.* 1987). In Bautzen reservoir, the sole prey fish of suitable length for age-0 zander were its own smaller conspecifics in late spring 1993 (Fig. 3). Consequently, the degree of cannibalism was nearly 100% (Fig. 5). Later in the year, the mean size of the zander was more than twice the length of the other age-0 percid species (Fig. 3), and, as a consequence, we found mainly ruffe and perch in the stomachs of zander in September 1993 (Fig. 5). According to Van Densen (1985a), 0+ zander can ingest prey fish which are even larger than 50% of the predator size. In 1994, small roach juveniles of that size were available to zander as prey fish for a short period (June 16, Fig. 3). But, due to the fast growth of roach and the large size of ruffe and perch relative to zander lengths in late June and July, the zander was forced to become cannibalistic (Fig. 5). This behaviour may have contributed to the strong decline in abundance of age-0 zander, which was reflected by the lack of these fish in the gill-net catches from August 1994 onwards (Table 1), although cannibalism by adult zander additionally may be important for this reduction (Mills *et al.* 1987, Mehner *et al.* 1996a).

The relative availability of zooplankton and fish prey also strongly influenced the degree of piscivory in age-0 perch. In contrast to zander, age-0 perch often switch to benthic food as a consequence of reduced zooplankton densities (Persson & Greenberg 1990, Wu & Culver 1992). The occasional uptake of fish prey by age-0 perch has been described only in a few studies from Europe (Spanovskaya & Grigorash 1977, Van Densen 1985b, Thiel 1989). In late June and July of both years, the majority of age-0 perch did feed on chironomids and small cladocerans (Mehner *et al.* 1995, 1996b). But, the largest specimens of the population became piscivorous. This diet shift obviously was not triggered by high water transparencies, because the *Daphnia* decline occurred simultaneously with a drastic reduction in Secchi depths (Fig. 2). The piscivorous age-0 perch preyed predominantly on juvenile zander (Figs. 4 and 5, and Mehner *et al.* 1995). However, the rapid growth of the zander led consequently to decreasing piscivory and increasing cannibalism in perch (Fig. 3), since no other prey fish of suitable lengths were available during the rest of the season. In June 1994, the length differences between all species were minor due to lower spring water temperatures (Fig. 1). Therefore, in 1994 the degree of piscivory in age-0 perch was negligible in comparison to 1993 (Fig. 4), and age-0 zander were absent from the middle of summer 1994 onwards (Fig. 1). It can be assumed that, in addition to predation by adult piscivores, the year-class strength of age-0 fish was markedly influenced by this decline in the level of (intraguild) predation and cannibalism in the age-0 groups. According to preliminary estimates, consumption by age-0 zander and perch was responsible for at least 30% of the total predation mortality of age-0 perch in Bautzen reservoir (Mehner *et al.* 1996a). Consequently, mean catch per unit of effort in the gill nets was nearly 8 times higher for age-0 perch in September 1994, compared with the preceding year, although the mean catch per unit effort for adult zander and perch did not differ significantly between both years (Mehner *et al.* 1996ab, and unpubl. results). In turn, the higher density of planktivorous age-0 fish may have prevented the recovery of the *D. galeata* population in late summer 1994 (Fig. 2). A similar key position of age-0 perch in the trophic cascade was found in Oneida Lake (Mills *et al.* 1987). Both the growth of walleyes (age-0 perch as prey) and the population abundance of daphnids (age-0 perch as predator) were directly connected with the annual age-0 perch density. In Bautzen reservoir, however, early piscivory in age-0 perch itself contributed to the regulation of the age-0 fish density, and therefore the trophic cascade was additionally stabilized.

The consumption of fish by zander and perch was also reflected in their growth rates. Growth rate was lower in periods when the degree of piscivory decreased. This was especially apparent in the nearly constant length of zander during July and August 1993 (Fig. 3). This cessation in growth coincided with the reduced amount of fish in the zander stomachs (Fig. 4), but also with declining water temperatures (Fig. 1). During that period, main prey items of zander were *Leptodora kindtii* and even daphnids (Mehner *et al.* 1996a). An increase in the growth of age-0 perch and zander after the switch to piscivory also was documented by Nagięć (1977), Thorpe (1977) and Van Densen (1985a). In Oneida Lake, the smallest age-0 walleyes (80 to 120 mm *TL*) ate predominantly planktonic prey during late August and September, while larger walleyes (*TL* > 120 mm) were predominantly piscivorous (Forney 1966). It is possible that the length data obtained directly from gill net catches may insufficiently reflect the real length composition of fish populations. This is attributed to the strong size selectivity of the gill nets (Hamley 1975). Nevertheless, due to the use of several mesh sizes and the inclusion of plankton net and seine net catches in 1994, the length relations between the fish species should have been adequately reflected.

Our study indicated that the early ontogenetic diet shift from planktivory to piscivory can regularly occur both in age-0 zander and age-0 perch. The switch was coupled with declining *Daphnia* densities, and the availability of prey fish of vulnerable size. Favorable predator length:prey length ratios for age-0 zander or walleye were observed in lakes inhabited by roach and bream (Nagięć 1977), smelt (Van Densen 1985a), or perch (Forney 1966, Johnson *et al.* 1992, this study). High temperatures during spring (Forney 1966) and summer (Buijse & Houthuijzen 1992) additionally can favour the onset of piscivory due to fast growth of the zander. For age-0 perch, prey fish of vulnerable size are obviously seldom available. However, the size difference between perch and their prey may reach sufficient values if (1) the growth rate of the perch immediately after hatch is outstanding due to high zooplankton densities and high water temperatures (as in Bautzen reservoir in spring 1993, Figs. 1 and 2), and (2) if another fish species, which hatches at least one month later and at small lengths, is present in high numbers (as the European zander). The combination of both conditions may be uncommon in most naturally-structured lakes. However, extraordinarily high *Daphnia* biomasses and high densities of artificially stocked and naturally-reproduced zander or walleye have often been observed in strongly top-down manipulated systems (Benndorf 1990, Carpenter & Kitchell 1992). Consequently, long-term biomanipulation should favour early piscivory in age-0 perch and zander, which in turn will increase the top-down predation pressure on the whole trophic foodweb.

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