



Dietary niche partitioning in a piscivorous fish guild in response to stocking of an additional competitor – The role of diet specialisation

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ABSTRACT

Species belonging to the same ecological guild can coexist only if there are differences in their responses to limiting resources. Thus, competitor introductions may modify the niches of the resident competitors, but empirical studies are rare. The extent of niche modification might further depend on the species' trophic specialisation along the specialists-to-generalists axis. In this study, we performed a semi-natural experiment by introducing a trophically specialised piscivorous fish (pikeperch) to the resident predator guild of a trophic generalist (perch) and a trophic specialist (pike) in a temperate freshwater lake. Individual diet data were used to calculate total niche hypervolume and inter- and intraspecific dietary niche overlap to evaluate strength of competitive interactions before and after pikeperch introduction. In both pike and perch, there was a moderate niche compression in response to pikeperch stocking. Furthermore, whereas perch diet hypervolume did not overlap at all with that of pikeperch, the intersection of niche space between the two trophic specialists was highly asymmetrical in favour of pike due to its less specialised diet composition in comparison with pikeperch. The intraspecific dietary niche overlap between perch size classes reflected an enhanced partitioning, whereas that of pike size classes was found almost unchanged in response to pikeperch stocking. These empirical results corroborate that competitive interactions and the degree of specialisation may strongly shape the success of introductions of top-predators in freshwater ecosystems. The most specialised species may persist only if the competitors belong rather to the generalists along the specialisation continuum.

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Introduction

Ecological theory predicts that species belonging to the same ecological guild can coexist only if there are differences in their responses to limiting resources (MacArthur and Levins 1967). Accordingly, coexistence requires species to be different in the way they affect, and are affected by, resources and predators (Leibold 1995). The species-specific differences that allow coexistence can be considered as species' niche. A useful definition of a species' niche space is that it consists of four major axes: resources, predators, space and time (Chesson 2000). Coexistence thus requires niche partitioning between species that increases the strength of intraspecific competition relative to that of interspecific competi-

tion along at least one of those four niche axes (Amarasekare 2003). However, the flexibility to niche partitioning depends on the type of specialisation.

Species are often faced with an evolutionary trade-off between being specialist or generalists which is thought to represent a central mechanisms in the co-existence of species (Wilson and Yoshimura 1994). Results from a model suggest that generalist should show activity switches more often than specialists such that a higher flexibility to niche partitioning is expected in generalists.

Assessing the niche width in relation to invader success is reported to be a useful tool to predict the impact of invasions on different scales (Olsson et al. 2009). Whereas competition theory has advanced the understanding under which set of conditions coexistence is possible, empirical studies testing the theoretical predictions at ecologically realistic temporal and spatial scales are still surprisingly rare (Forrester et al. 2006; Weber and Fausch 2003) since those are highly expensive and time consuming. A valuable opportunity to test the theoretical predictions in semi-natural experiments is the introduction of predatory piscivorous fish species into isolated small lakes (Eby et al. 2006). Stocking top-predator fish species into freshwater systems is a long-term and widespread fishery management practice all over the world

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with consequences for ecosystem structure and function (see review in Eby et al. 2006). The effects provoked in the concerned ecosystem can be the desired ones as in the case of biomanipulation (Mehner et al. 2002), but also devastating effects of introduced predators have occurred leading to abundance declines of native species and even species extinctions (Cowx 1997; Craig 1992). Among others, interspecific competition of resident with introduced species has been one of the main factors evoking the abundance decline of the residents in aquatic and terrestrial ecosystems (Bohn and Amundsen 2001; Petren and Case 1996; Post and Rudstam 1992).

In the present empirical study, we provide an experimental whole-lake test of the prediction that coexistence between resident and introduced competitors at limiting resources requires modifications of the dietary niches within the predatory guild in response to predator fish stocking (see also Schulze et al. 2006a). Here, we compare in detail inter- and intraspecific dietary niche partitioning in the piscivorous top-predators perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in response to experimental pikeperch (*Sander lucioperca* (L.)) introduction. Pikeperch was locally absent in the lake for at least the last 100 years (pers. com. of lake owner). These three species commonly occur in lakes of the temperate zone of Central Europe (Mehner et al. 2005). However, in a subset of 67 north-German lakes, all three predators co-occurred with abundant populations in only two lakes (see Diekmann et al. 2005; Mehner et al. 2005) such that the experimental pikeperch introduction allowed to test for the effects of an artificially intensified competition among the three native predators. Perch can be classified as an ontogenetic trophic generalist switching frequently between piscivorous, zooplanktivorous and benthivorous feeding styles even as adult fish (Dörner et al. 2001; Matena 1998; Persson and Greenberg 1990). In contrast, pike and pikeperch are piscivorous specialists. Although larval and small juvenile pike and pikeperch also feed on zooplankton and other invertebrates (Bregazzi and Kennedy 1980; Haertel et al. 2002; Matena 1998), these species become piscivorous usually during the first year of life and at substantially smaller lengths than perch (Mittelbach and Persson 1998), and only occasionally feed on other prey types than fish as adults.

The realised trophic niche, the total community niche space, and the niche overlap were calculated according to (Litvak and Hansell 1990a), based on diet inspections before and within the first two years after pikeperch introduction. The trophic niche dimensions were calculated both between the species (interspecific overlap) and between the size classes of the predators (intraspecific overlap). We expected that the generalist perch being the weaker competitor for fish as prey than both the specialists pike and pikeperch. Therefore, we hypothesise that perch will display a higher flexibility to alter its diet composition than pike and pikeperch. Thus, interspecific competition will become a major structuring component after the introduction of pikeperch. Further, niche partitioning between the residential piscivores should increase at the costs of higher intraspecific overlap due to enhanced competition for fish. Our study focuses on the short-term (ecological) modifications in intra- and interspecific niche overlap, whereas long-term (evolutionary) adaptations in life histories within the guild (e.g. Bonsall et al. 2004), fostering the potential establishment of the introduced competitor, were not empirically investigated.

Material and methods

Study site

Lake Großer Vätersee (12 ha, maximum depth 11.5 m, mean depth 5.2 m) is situated about 70 km north-east of Berlin, Germany (60 m a.s.l.; $\varphi = 53.004695$, $\lambda = 13.552787$). The mesotrophic lake

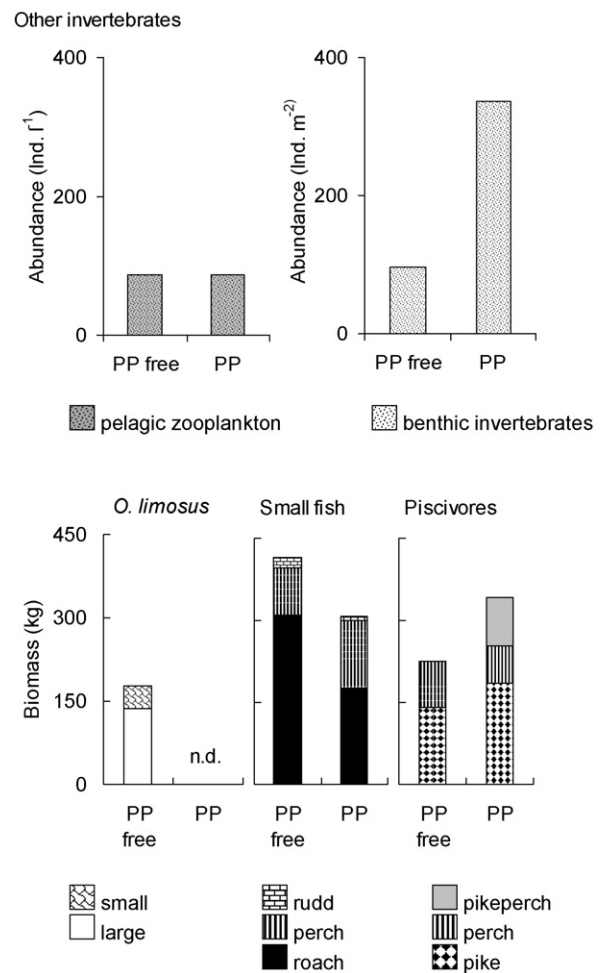


Fig. 1. Abundance of invertebrates (benthic invertebrates [Ind. m⁻²] and pelagic zooplankton [Ind. l⁻¹]), and lake wide standing stock of *O. limosus* (small: <6 cm, large: ≥6 cm body length), small fish (L_T < 16 cm; roach, perch, rudd), and piscivores (pike, perch [≥20 cm L_T], pikeperch) in Lake Großer Vätersee in the pikeperch-free (PP free) and pikeperch period (PP). Data from Haertel et al. (2002), Höfker et al. (2007), Haertel-Borer et al. (2005) and Schulze et al. (2006a). n.d. = no data. In case of invertebrates and piscivores the mean of two years (1997 and 1998 in PP free; 2001 and 2002 in PP) are given. Standing stocks of small roach, perch and rudd were estimated only in 1998 and 2002.

has no in- or outflow and the catchment is mostly covered by forest (see Kasprzak et al. 2000 for further details). Most of the lake's shore and the adjacent littoral zones are covered by reed (*Phragmites australis*) and *Chara* spp. The study was conducted as a whole-lake experiment whereby the effects of a controlled introduction of an additional predator were examined by fish sampling before (1997 and 1998) and after the pikeperch stocking (2001 and 2002). There are no commercial fisheries at the lake, and angling was forbidden for the duration of the experiment.

The piscivorous fish guild consisted of pike and large perch (>20 cm total length, L_T ; perch < 20 cm feed to a high proportion on invertebrates) in the years prior to the experiment (Fig. 1). As a competing top-predator, pikeperch was experimentally introduced by stocking specimens in the length range of 17.0–43.5 cm L_T in spring 2001 and 2002. The non-piscivorous fish guild in Lake Großer Vätersee was dominated by roach (*Rutilus rutilus* (L.)) and small perch (<16 cm L_T). Rudd (*Scardinius erythrophthalmus* (L.)) and bleak (*Alburnus alburnus* (L.)) were also frequent, but occurred in substantially lower numbers than perch and roach (Höfker et al. 2007). Other species in low numbers were besides others eel (*Anguilla anguilla*, L.), ruffe (*Gymnocephalus cernuus*, (L.)) and bream (*Abramis*

Table 1
Biomass of piscivorous species and abundance of prey fishes in Lake Großer Vätersee. Data were taken from Haertel et al. (2002), Schulze et al. (2006a) and Hölker et al. (2007).

		Unit	1997	1998	2001	2002
Piscivores	Perch (>20 cm L_T)	kg	70	96	88	48
	Pike	kg	156	127	134	236
	Pikeperch	kg	–	–	98	82
	Sum		226	223	320	366
Prey fish	Juvenile perch	Individuals		15,650		21,300
	Juvenile roach	Individuals		42,790		25,930
	Juvenile rudd	Individuals		2390		410
	Sum			60,830		47,640

brama (L.)). Lake-wide abundance of piscivores and prey fish before and after the stocking of pikeperch are shown in Table 1.

Invertebrate resources consisted of zooplankton (*Daphnia*, other cladocerans, copepods) in the pelagic zone and benthic invertebrates (insect larvae) in the littoral zone (Haertel et al. 2002; Hölker et al. 2007, Fig. 1). Furthermore, before pikeperch stocking, the spiny-cheek crayfish (*Orconectes limosus* Rafinesque) biomass was about 178 kg for the whole lake (Haertel-Borer et al. 2005, Fig. 1) whereas no data are available for the pikeperch period.

To minimise the impact of fishing on the predator populations, only non-lethal sampling methods were used, and fish were released into the lake after processing. Fishing was done once or twice per month from April to November in 1997 and 2001, and from March to November in 1998 and 2002. Electric fishing (all sampling years) from a boat and catch by gill nets (2001 and 2002) were conducted at both littoral and pelagic sites during day-time and night-time. Two rows of four gillnets, each with 25, 32, 40 and 50 mm mesh-size were set at the bottom of the lake simultaneously in the littoral area (c. 5–10 m from the reed stands at 3 m depth) and in the pelagic zone (c. 40–50 m from the reed stands at 6 m depth) approximately twice a month between June and October. Nets were set during the day (after sunrise and until sunset) and night (after sunset and until sunrise). The introduced pikeperch mainly occurred in pelagic gill nets, and was caught during day-time, twilight and night periods. In contrast, almost all large perch were caught with gill nets in the pelagic zone during day during the pikeperch-free period (Schulze et al. 2006a), but reduced the pelagic occurrence at both daytime and twilight periods, and became inactive during the night after pikeperch introduction (Schulze et al. 2006a). A large beach seine was used to remove the major part of the pikeperch population from the lake at the end of the experimental period in November 2002. For more details of the sampling procedures and habitat use, see Schulze et al. (2006a,b). All fish were measured to the nearest 0.5 cm L_T . Fishes caught by gill nets, electric fishing and the beach seine were used for diet analyses. Gill nets were set for short time intervals only, i.e. 2 h in winter and 1 h in summer, to prevent fish from dying and to reduce bias from continued digestion or regurgitation. Stomach contents (not total gut content) were obtained from anaesthetised fish (MS 222) by flushing with a compression sprayer, which enabled entire removal of the content. This was checked on dead and dissected fish at the end of the experiment. Stomach contents were preserved in 70% alcohol (1997/98) or deep frozen (–18 °C; 2001/02) until further processing in the laboratory. Stomach contents were examined under a stereoscopic microscope. Prey fish were determined to species level and in case of advanced digestion, identified from remaining hard structures (compared with Lake Großer Vätersee fish bone samples). Prey fish were counted, their length measured and mass was then back-calculated from length-mass relationships or hard part-length-mass relationships obtained from Lake Großer Vätersee fish and spiny-cheek crayfish samples.

The composite diet index of relative importance (IRI, George and Hadley 1979) was calculated from the proportions of biomass,

numbers and frequency of occurrence of prey organisms from filled stomachs to compensate for dimensional differences in biomass and numbers between fish and invertebrate prey types (see Cortes 1997). To facilitate sufficiently large group sizes in diet comparisons, diet data were seasonally summarised into spring (March, April, May), summer (June, July, August) and autumn (September, October, November) samples. Eight diet categories were chosen, namely perch, other percids (ruffe, *G. cernuus* (L.)), and unidentified young of the year (YOY) percids, roach, other cyprinids (rudd, bream, bleak, and unidentified YOY cyprinids), pike, unidentified fish, spiny-cheek crayfish and other invertebrates (*Chaoborus* sp., benthic insect larvae, gastropods and *Asellus* spp.).

Statistical analysis

For interspecific comparisons of trophic niches, season-specific diet compositions were obtained for pike, perch and pikeperch. To facilitate intraspecific comparisons, the diet composition of each species was further separated according to predator size classes (perch: I, 15–20 cm T_L ; II, 20–25 cm T_L ; III, 25–30 cm T_L ; IV > 30 cm T_L ; pike: I, 15–25 cm T_L ; II, 25–40 cm T_L ; III > 40 cm T_L ; pikeperch: I < 35 cm T_L ; II, 35–40 cm T_L ; III > 40 cm T_L). Accordingly, season-specific (spring, summer, autumn) diet composition data were theoretically available for 51 fish groups (3 seasons \times 7 fish size classes before stocking, 3 seasons \times 10 fish size classes after stocking). On three combinations (one in each perch, pike and pikeperch) less than two diet inspections could be included to form a group (see Fig. 2).

These cases were excluded from statistical analyses. All values were arcsin-squareroot transformed to stabilize the variances. Testing for outliers, the group pikeperch-III in spring (2 individuals, Fig. 2) had a strongly deviating diet composition (similarity based on Euclidean distances 3.47 SD distant to the grand mean similarity) and thus was also excluded (see McCune and Grace 2002). Accordingly, the final diet matrix consisted of 47 fish groups \times 8 diet categories, expressed as IRI values.

The calculation of the diet niche hypervolume followed the mathematical approach suggested by Litvak and Hansell (1990a). A principal component analysis (PCA) of the diet matrix was computed using PC-ORD (McCune and Mefford 1999), where the eigenvectors of the principal components were considered the resource axes. Food niche hypervolume for each species was computed by generating a product of size class-specific (analysis I, intraspecific competition) and species-specific (analysis II, interspecific competition) niche widths along those principal components, whose eigenvalues were >1. Niche width was defined by the dispersion of the projections of PCA scores along each component axis. The range (minimum to maximum value) was used to measure the dispersion and the hypervolume calculated from the axes then represents the diet niche of each species. The intraspecific total niche hypervolume (TNH) for each species, which represented the total resource space utilised by the size classes before and after pikeperch introduction, was calculated using the

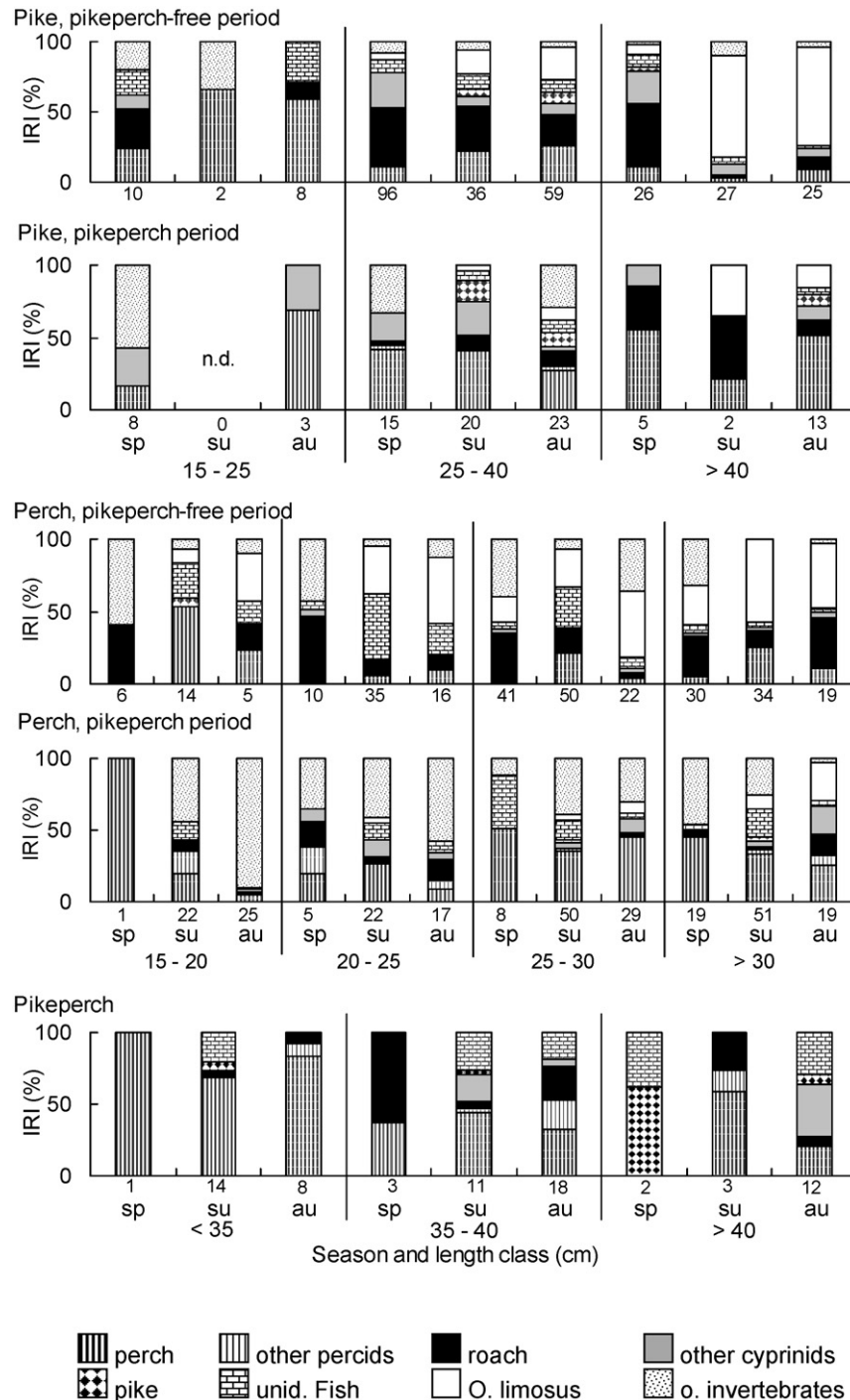


Fig. 2. Percent index of relative importance (IRI) of prey organisms for different length classes of perch, pike and pikeperch in spring (sp), summer (su) and autumn (au) in the periods before (pikeperch-free) and after (pikeperch) the stocking of pikeperch. Figures below columns indicate the numbers of filled stomachs analysed. unid. fish = unidentified fish; o. invertebrates = other invertebrates. n.d. = no data.

hypervolume per size class (analysis I). The TNH of the piscivorous guild was calculated the same way calculating the union of each species' hypervolume (analysis II). The TNH was divided into three or four categories (Litvak and Hansell 1990a). First, the hypervolume utilised by a single size class (analysis I) or single species (analysis II); second, the primary level of intersection (PLI), represented by the niche hypervolume shared by ≥ 2 species or size classes; third and fourth: the secondary (3 species or size classes) and tertiary level (4 size classes) of intersections (SLI and TLI, respectively).

Results

Diet composition

A total of 892 pike (5–101 cm L_T), 951 perch (15–40 cm L_T) and 245 pikeperch (28–55 cm L_T) were caught (including recaptures of previously marked fish). In perch, individuals were caught up to nine times during the whole experiment summing up to 264 recaptures. 39.9 and 42.6% of stomachs were empty before pikeperch stocking in perch and pike, respectively, 36.8, 57.6 and

Table 2

Correlation coefficients (Pearson's r) of axes scores of the principal component analysis (PCA) with the eight diet groups of piscivorous predators in Lake Großer Vätersee.

Diet category	Axis 1	Axis 2	Axis 3
Perch	−0.6367	−0.2186	−0.2417
Other percids	−0.0643	−0.126	0.0749
Roach	0.0751	0.2462	0.8004
Other cyprinids	−0.0506	−0.036	0.1161
Pike	−0.1011	0.0459	−0.0686
Unidentified Fish	−0.039	0.1293	−0.3342
<i>O. limosus</i>	0.2732	0.7644	−0.3674
Other invertebrates	0.7043	−0.5208	−0.1745

57.5% of stomachs were empty after pikeperch stocking in perch, pike and pikeperch, respectively. The diet composition was highly variable in all predators over the sampled seasons and size classes (Fig. 2), however, some general patterns could be found. In perch, all size classes consumed high proportions of spiny-cheek crayfish and benthic invertebrates with slightly higher proportions of smaller invertebrates in smaller size classes, indicating an ontogenetic diet shift to larger prey. In pike, invertebrates other than spiny-cheek crayfish were less often consumed. In both residential predators perch and pike, the proportion of spiny-cheek crayfish was high in the period before pikeperch introduction, but decreased after pikeperch stocking. Also the proportion of roach decreased in both species, whereas small perch was consumed in higher proportions by all piscivorous species after pikeperch introduction. In contrast to the residential piscivores, pikeperch did not consume any invertebrates during the experiment, but fed on perch, roach and other small unidentified fish (Fig. 2). Maximum size of consumed perch was 117 mm, 249 mm and 149 mm L_T in perch, pike and pikeperch, respectively. Maximum size of consumed roach was 138 mm, 200 mm and 106 mm L_T in perch, pike and pikeperch, respectively.

Resilience of analyses and diet niche construction

Diet niches for $n \geq 5$ full stomachs were calculated to test the resilience of the analysis (unpublished results). The results obtained for perch demonstrate that the main pattern remained quite stable. However, it is no longer possible to calculate a hypervolume, one of the main strengths of this analytical tool, for several of the pikeperch and pike size classes if $n \geq 5$ is applied. Consequently, analyses with samples of $n \geq 2$ were performed as this allows for integration of a larger data set which is necessary to realize the analyses for all size classes of perch, pike and pikeperch investigated.

Eigenvalues > 1 were found for the first three PCA axes, which in total extracted 75% of the total variance (32, 28 and 15%, respectively) of the diet matrix. The diet category perch had the highest negative and other invertebrates the highest positive correlation to the first axis (Table 2). Spiny-cheek crayfish was positively and other invertebrates negatively correlated to axis 2. Roach was positively and spiny-cheek crayfish negatively correlated to axis 3 (Table 2).

Intraspecific niches in pike and perch (analysis I)

In pike, the TNH moderately decreased from 0.068 to 0.041 (60% of the pikeperch-free value) after the introduction of pikeperch. Before the pikeperch stocking, the main part of the TNH was shared by pike-I and -III (50% and 48%, respectively, Table 3) and only a small proportion was occupied by pike-II (3%). After the introduction of pikeperch, the largest proportion of the TNH was occupied by the largest size class (74%) followed by pike-II (26%) and pike-I (4%). The diet space occupied by only a single size class was very high

Table 3

Percent of total niche hypervolume of size classes of pike and their intersections, and intersections for the pike population in the pikeperch-free and pikeperch period. Roman figures represent three size classes of pike: I = 15–25 cm, II = 25–40 cm, III = >40 cm L_T . 'Single size class': hypervolume shared by only one size class; PLI: primary level of intersection; SLI: secondary level of intersection.

	Pikeperch-free	Pikeperch
Pike I	49.5	4.1
Pike II	3.4	26.4
Pike III	48.0	73.5
Pike I \times II	No overlap	No overlap
Pike I \times III	No overlap	No overlap
Pike II \times III	0.9	4.0
Pike I \times II \times III	No overlap	No overlap
Single size class	99.1	96.0
PLI	0.9	4.0
SLI	No overlap	No overlap

in both the pikeperch-free (99%) and the pikeperch (96%) periods. Since pike-I did not overlap with either of the other size classes due to differences in the consumption of spiny-cheek crayfish (Table 1 and axis 2 in Fig. 3) SLI was zero in both periods. Accordingly, pike responded to pikeperch stocking with a moderate niche compression (less spiny-cheek crayfish in all size classes, axis 2; less roach in pike-I and -II, axis 3; Fig. 3).

In perch, the TNH drastically declined from 0.169 before to 0.019 (11% of the pikeperch-free value) after the introduction of pikeperch. This was due to condensed sections on nearly all three resource axes of all size classes of perch (Fig. 3): perch-I condensed on axis 1 (less perch, more invertebrates), whereas perch-III and -IV condensed on axis 1 due to the consumption of more perch. Perch-I and -II condensed on axis 2 (consumption of less spiny-cheek crayfish), and perch-I and -III condensed on axis 3 (less roach). Whereas in the pikeperch-free period, the niche space was dominated by the smallest size class perch-I occupying 90% of TNH, in the pikeperch period the largest size class perch-IV occupied the highest proportion of diet space (56% of TNH) followed by perch-II (26% of TNH; Table 4). The niche space occupied by only a single size class increased from 62 to 98%. In contrast, all two- and higher-level overlaps decreased substantially after pikeperch stocking. In many cases, total niche overlap became even zero attributable to the fact that perch-I fed strongly on invertebrates, but did not

Table 4

Percent of total niche hypervolume of size classes of perch and their intersections, and intersections for the perch population in the pikeperch-free and pikeperch periods. Roman figures represent four size classes of perch: I = 15–20 cm, II = 20–25 cm, III = 25–30 cm, IV = >30 cm L_T . 'Single size class': hypervolume shared by only a single size class; PLI: primary level of intersection; SLI: secondary level of intersection; TLI: tertiary level of intersection.

	Pikeperch-free	Pikeperch
Perch I	89.7	10.7
Perch II	27.8	26.2
Perch III	8.4	9.7
Perch IV	12.1	55.5
Perch I \times II	21.5	<0.1
Perch I \times III	8.4	No overlap
Perch II \times III	5.4	No overlap
Perch IV \times I	3.5	No overlap
Perch IV \times II	4.0	No overlap
Perch IV \times III	2.6	2.0
Perch I \times II \times III	5.4	No overlap
Perch I \times II \times IV	2.0	No overlap
Perch I \times III \times IV	2.6	No overlap
Perch II \times III \times IV	1.8	No overlap
Perch I \times II \times III \times IV	4.3	No overlap
Single size class	88.7	98.0
PLI	11.3	2.0
SLI	5.1	No overlap
TLI	4.3	No overlap

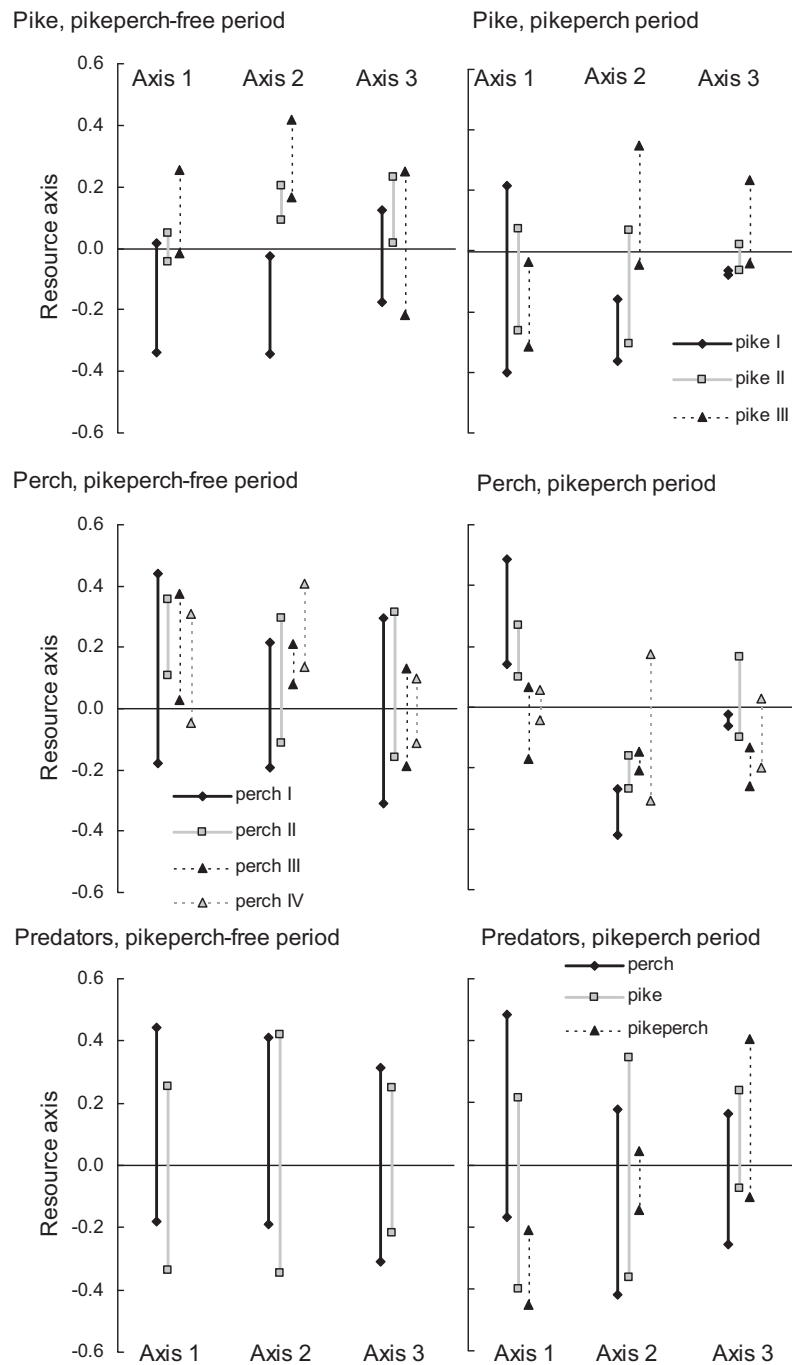


Fig. 3. Ranges on resource axes (dimensionless) occupied by perch size classes (I = 15–20 cm, II = 20–25 cm, III = 25–30 cm, IV = >30 cm L_T), pike size classes (I = 15–25 cm, II = 25–40 cm, III = >40 cm L_T) and all piscivores (perch, pike, and pikeperch) in the pikeperch-free and pikeperch periods.

consume spiny-cheek crayfish, whereas spiny-cheek crayfish was fed by bigger perch in expense of very low proportions of macroinvertebrates. Thus, the intraspecific overlap on axes 1 and 3 (Fig. 3) was zero. Consequently, the intraspecific segregation in perch size groups was substantially intensified after pikeperch introduction.

Interspecific niches (analysis II)

In the pikeperch-free period, the TNH was 0.302 of which perch occupied 72% and pike 66% (Table 5). 38% of the TNH were overlapped by both species. After the introduction of pikeperch, the TNH decreased to 0.264 (83% of the pikeperch-free value) and the proportion of TNH occupied by perch decreased to 63% and that of pike to 52%, whereas the introduced pikeperch occupied 9% of the

TNH. The overlap between perch and pike decreased to 19% of the TNH. Pikeperch overlapped with pike (4.3%), but not with perch. Thus, no space was overlapped by all three species. This was due to a non-overlap between perch and pikeperch on axis 1 (Fig. 3) which mainly differentiates fish consumers from invertebrate consumers (pikeperch consumed fish only, Fig. 2). The percentage of the TNH occupied by only one species was high in both periods and increased from 62 to 77% whereas the PLI decreased from 38 to 23% of the TNH after the introduction of pikeperch. Accordingly, the diet partitioning between the resident predators increased in response to stocking of the additional competitor. Further analysis of the food niche hypervolume showed that the niche overlap between perch and pike was nearly symmetric with similar percentages of

Table 5

Percent of total niche hypervolume of species and their intersections, and intersections for the total piscivorous guild in the pikeperch-free and pikeperch periods. Single species: hypervolume shared by only a single species; PLI: primary level of intersection; SLI: secondary level of intersection.

	Pikeperch-free	Pikeperch
Perch	71.9	62.6
Pike	66.3	51.9
Pikeperch	–	8.8
Perch × pike	38.2	19.0
Perch × pikeperch	–	No overlap
Pike × pikeperch	–	4.3
Pike × pikeperch × perch	–	No overlap
Single species	61.8	76.7
PLI	38.2	23.3
SLI	–	No overlap

species' space occupied by the other species in the pikeperch-free period (Table 6). These values decreased after the introduction of pikeperch, but were still symmetric in pike and perch. In contrast, there was an asymmetric niche overlap of the introduced pikeperch with pike, and pikeperch shared the highest proportions of diet space with another species (PLI = 49.1%), whereas the SLI was zero (Table 6).

Discussion

Ecological theory suggests that competition is an important species interaction when the resource is scarce (Begon et al. 1996). In Lake Großer Vätersee, the overall piscivorous fish biomass increased by 42% (2001) or 64% (2002) after pikeperch introduction, whereas the total abundance of the main prey fish declined by 22% (Haertel et al. 2002; Hölker et al. 2007, Fig. 1; Schulze et al. 2006a). Accordingly, pikeperch introduction likely resulted in an increased competition between the piscivorous species for prey fish in this lake leading to changes in energy flows and trophic relationships between resources and predators. As a consequence, the trophic interactions within the uppermost food web level were strongly impacted by the introduction of a specialist predator. The response of the piscivorous guild to the introduction included three main patterns, namely (1) a diet-niche compression accompanied by a reduced diet overlap between the two residential species perch and pike, (2) a strongly increased intraspecific diet segregation between the size classes of the trophic generalist perch, and (3) a highly asymmetrical diet overlap between the two trophic specialists pike and pikeperch in favour of pike. However, it has to be noted that the abundances of invertebrate prey and small prey fish such as roach and perch differed between the two periods. Whereas perch and invertebrate densities increased, abundances of small roach declined (Haertel et al. 2002; Hölker et al. 2007, Fig. 1; Schulze et al. 2006a,b). Accordingly, the observed changes in the diet composition of the piscivores may have been influenced also by a change in relative availabilities of certain prey types. However, our results support that intensified competition was a main cause of the modifications of diet niches in all predators.

The diet composition of pike in Lake Großer Vätersee with an overall low proportion of invertebrates and increasing proportion of fish prey in larger pike was comparable with reports from other lakes (Bregazzi and Kennedy 1980; Kangur and Kangur 1998; Lorenzoni et al. 2002), and reflects an early ontogenetic niche shift to piscivorous feeding (Mittelbach and Persson 1998). Accordingly, pike can be treated as a specialist piscivore (Kahilainen and Lehtonen 2003). Also in perch, the primary diet composition found in Lake Großer Vätersee was not different from several other European waters (Bergman and Greenberg 1994; Dörner et al. 2003; Jacobsen et al. 2002). According to the high number of prey groups used, perch is characterised as a generalist with a highly adaptive feeding strategy (Bergman and Greenberg 1994; Matena 1998). In perch, the TNH dramatically decreased after the introduction of pikeperch indicating that the food spectrum of perch became more homogeneous, attributable to the dominant use of small perch and invertebrates as prey and a strongly reduced proportion of spiny-cheek crayfish in the diet during the pikeperch period. This niche compression was somewhat surprising since it was expected that the generalist perch would rather expand its niche in response to increased competition by including prey organisms other than fish in its diet (Hanson and Leggett 1986). This expansion in diet composition was not found in Lake Großer Vätersee since perch already fed on invertebrates and spiny-cheek crayfish before pikeperch introduction. Thus, their diet niche was already highly diversified before competition became even more pronounced due to pikeperch stocking.

The percentage of TNH occupied exclusively by either perch or pike (single species) was 62% of TNH in the pikeperch-free period suggesting that the trophic niches of the residential piscivorous predators were already well separated in Lake Großer Vätersee. Nevertheless, the segregation became even more pronounced after pikeperch introduction, indicated by a further increase in the percentage occupied exclusively by a single species to 77%, and a reciprocal decrease of the PLI. Similarly, Litvak and Hansell (1990b) found that the trophic niche (calculated by the same method) of fathead minnows (*Pimephales promelas*) was smaller in sympatry with two other competing fish species (finescale dace, *Phoxinus neogaeus*, and northern redbelly dace, *Phoxinus eos*) in a small Canadian lake, as compared with the allopatric situation.

However, there were diverging impacts of pikeperch introduction on the residential piscivores with respect to the intraspecific niche. The size classes of the piscivorous specialist pike were already strongly separated in the period before pikeperch introduction, mainly due to a separation of the smallest size class from the two bigger ones. Accordingly, there were only weak modifications in the indicators of niche overlap. The proportion of diet space occupied by only one size class of pike on the TNH slightly decreased whereas the PLI increased. These patterns indicate that further intraspecific niche segregation in the pike size classes was almost impossible due to the ontogenetic diet shift towards piscivory. Comparably, in the pike population in Lake Trasimeno (Italy), diet data of different age classes indicated a low intraspecific diet overlap since the larger pike consumed more fish and less crustaceans than the smaller ones (Lorenzoni et al. 2002).

Table 6

Percentage of each species' space occupied by other species and levels of intersection in the pikeperch-free and pikeperch period.

	Pikeperch-free		Pikeperch		
	On perch	On pike	On perch	On pike	On pikeperch
Perch	–	57.6	–	36.5	No overlap
Pike	53.1	–	30.3	–	49.1
Pikeperch	–	–	No overlap	8.3	–
PLI	53.1	57.6	30.3	44.9	49.1
SLI	–	–	No overlap	No overlap	No overlap

In contrast, the effect on the intraspecific niche of perch was very large. The intraspecific overlap between size classes in perch strongly decreased or ceased completely during the pikeperch period. As a result, the diet space used by a single size class increased to almost 98%, a value comparable to that found between the pike size classes. Furthermore, the PLI decreased, and the SLI and TLI became even zero after the pikeperch introduction. These changes indicate the substantially intensified diet segregation between all perch size classes, despite of the fact that the overall trophic niche of perch became more compressed. The strong segregation was probably caused by the competitive inferiority of the smaller sizes for fish as prey that forced them to shift to a dominant invertebrate feeding mode. This trend was supported by the higher availability of small benthic invertebrates.

According to the differing type of specialisation, a weaker diet overlap of the specialist pikeperch with the generalist perch was predicted, which was corroborated by the results of our study in Lake Großer Vätersee. The low overlap was attributable to the high proportion of invertebrate prey in the diet of all perch size classes whereas pikeperch did not consume any invertebrates. Exclusive piscivory was also reported from pikeperch populations in other water bodies (Dörner et al. 2007; Kangur and Kangur 1998) and corroborates that pikeperch is a highly specialised predator. In contrast, the overlap between pikeperch and pike was high, attributable to the specialisation of both pike and pikeperch for piscivorous feeding. However, the overlap was highly asymmetric with pikeperch sharing a high degree of diet space with pike, whereas pike shared only a low amount of its diet space with pikeperch. The asymmetry in niche overlap resulted from the constant, although low, proportion of invertebrates in the diet of pike which were not consumed at all by pikeperch.

The data on interspecific niche overlap indicated that there was a ranking of niche partitioning capabilities in the predators in Lake Großer Vätersee. Pike showed a slightly weaker diet specialisation than the strictly piscivorous pikeperch. Perch was the species with the highest diet plasticity and showed the strongest diet modifications. The correspondence between the degree of diet modifications and competitive ranking becomes obvious when growth is impaired, since growth retardation of fishes at coexistence is a sensitive indicator whether competition occurs (Bergman and Greenberg 1994; Forrester et al. 2006). For both perch and pike in Lake Vätersee, individual growth rates were measured in marked fish at consecutive recapture dates for both the pikeperch-free and the pikeperch periods. Due to strong differences between the individuals and a high variability of repeated weight estimates, these individual growth rates did not change significantly in response to pikeperch stocking (Schulze et al. 2006a). However, bioenergetics estimates of energy acquisition of predators revealed that perch had to face a reduction in specific consumption rates by 22% (Schulze et al. 2006a), indicating competitive inferiority of perch after pikeperch introduction. In contrast, the energy acquisition of pike increased by 19% from 1997 to 2002 (Schulze et al. 2006a). This would indicate that pike even profited from pikeperch stocking, probably due to the higher abundance of prey fish in the littoral zone resulting from avoidance reactions to the higher density of pelagic predators (Hölker et al. 2007).

According to the strong asymmetry in diet overlap between pike and pikeperch, also the exclusively piscivorous pikeperch was competitively inferior against the less specialised resident predator pike. Indeed, empirically derived consumption rates showed that pikeperch had the lowest specific consumption rates of the three investigated species in Lake Großer Vätersee (Schulze et al. 2006a). So, the species with intermediate specialisation, pike,

seems to be the strongest competitor in Lake Großer Vätersee. In a similar study on the niches of three cyprinid species, the species with the medium proportion of PLI on total niche space (like pike in Lake Großer Vätersee) had the largest population (Litvak and Hansell 1990b). Comparably, pike had the highest biomass among all predator populations in Lake Großer Vätersee. Therefore, the present study supports Litvak and Hansell (1990b) hypothesis that the competitive squeeze rather comes from the intermediately specialised competitor than from the edges of the specialisation continuum. In a further study using Litvak and Hansell (1990a) niche concept, the piscivore community in the oligotrophic Long Lake (USA) was investigated (Hodgson et al. 1997). The asymmetry in niches between largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*) and smallmouth bass (*Micropterus dolomieu*) was mostly due to the ability of largemouth bass to utilise terrestrial prey more effectively than its competitors. Accordingly, the less specialised largemouth bass performed better than the strictly specialised smallmouth bass.

Our study confirms that the effect of introductions on the receiving community depends on the trophic specialisation of both introduced and resident species. If an invading specialist is confronted with the niche of a resident specialist species, strong interactions must be expected (Bohn and Amundsen 2001). Consequently, for successful establishment, an invading specialist must find either a biotic vacancy or a place only weakly held by a displaceable species such that the resident specialist may ultimately disappear (Cowx 1997; Craig 1992; Welcomme 1992). Alternatively, coexistence of all resident and the introduced species may be facilitated by resource segregation (Adams and Maitland 1998; Baxter et al. 2004; Vander Zanden et al. 1999), if some of the competing species are flexible enough with respect to their diet composition and thus do not show strict specialisation. In the case of Lake Großer Vätersee, niche partitioning did occur, since pike was more flexible in the diet composition and less specialised than the introduced pikeperch. Further, the generalist resident perch responded strongest through a severe change of its intraspecific niche overlap.

Our data do not allow predicting whether long-term coexistence of all three-predator populations in Lake Großer Vätersee was possible. Stably coexisting populations of perch and pikeperch or pike and perch were found in a large number of waters (Dörner et al. 1999; Fedorova and Drozhina 1982; Popova and Sytina 1977). However, coexistence of pike and pikeperch is less frequent, and in only 2 of 67 north-German lakes all three species coexist (see Diekmann et al. 2005; Mehner et al. 2005). This suggests that the species with strongest diet specialisation, pikeperch or pike, may coexist only with a generalist and highly flexible species such as perch. A successful introduction or invasion of a diet specialist seems to be possible only if its diet niche is not at all occupied by resident species, or if the residents belong rather to the generalists along the specialisation continuum. In contrast, the introduction of a generalist predator to a set of specialised residents may result in stable coexistence.

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