

Determinants of habitat use in large roach

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(Received 20 April 2005, Accepted 11 May 2006)

In this study gillnet catches of large roach *Rutilus rutilus* and their potential predators, large perch *Perca fluviatilis*, pikeperch *Sander lucioperca* and pike *Esox lucius*, in combination with data on food resources and abiotic variables were used to reveal the variables influencing the habitat use of large roach in Lake Großer Vätersee. The occurrence of large roach was negatively coupled with the occurrence of potential predators. Although almost all roach studied were larger than those actually fed on by the predators, high roach catches never coincided with high predator catches. Since the overall habitat-specific distribution of roach and its predators was nevertheless highly similar, this indicated that large roach obviously avoided the immediate vicinity of the predators without being forced to a full habitat shift. The behavioural response to predators of roach in Lake Großer Vätersee was clearly length dependent, since the patterns of diel habitat use differed between large and small roach. For lake-wide estimates of trophic interactions, size groups of prey should be separated, since size-dependent trait changes may impact habitat-specific resources in a contrasting way. © 2006 The Fisheries Society of the British Isles

Key words: activity; diel patterns; habitat use; predation; resources; roach.

INTRODUCTION

The influence of predation risk on habitat use and foraging behaviour of individuals has been studied repeatedly during recent years (Lima & Dill, 1990; Werner & Peacor, 2003). Migrations and a temporally variable habitat use were often discussed as being the consequence of the trade-off between habitat-specific resource profitability and the risk of predation (Gilliam & Fraser, 1987; Sih, 1997; Skalski & Gilliam, 2002). In fishes, habitat use, migrations and activity patterns are highly adaptive behavioural traits and have been shown to depend on several biotic and abiotic factors. The spatial and temporal dimensions of this behavioural pattern include both diel and seasonal horizontal and vertical migrations (Jacobsen & Perrow, 1998; Scheuerell &

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Schindler, 2003). There is high consensus that the proximate trigger of, *e.g.* diel migrations, is the change in illumination strength during the transition phases between day and night (Reeb, 2002). In contrast, ultimate (evolutionary) explanations of habitat use are more variable and cover predator avoidance during daylight (Jacobsen & Perrow, 1998), maximization of food uptake by following prey availability (Radke *et al.*, 2003; Lewin *et al.*, 2004) and bioenergetic optimization as a consequence of temperature differences between the habitats (Fisher *et al.*, 1987; Sogard & Olla, 1993). Further, in some cases, the oxygen demand of fishes may influence their habitat use and prevent the use of habitats with low oxygen concentration (Eby & Crowder, 2002).

The variability of habitat use has been studied intensively in small roach *Rutilus rutilus* (L.), a common fish species in north-east German lakes (Mehner *et al.*, 2005a). Roach is mainly planktivorous, but larger roach may ingest algae and macrozoobenthos as well (Persson, 1983; Haertel & Eckmann, 2002). Accordingly, their preferred lake habitat is the pelagic zone where high zooplankton abundances can be found. The habitat use of roach, however, is also strongly influenced by the presence of predators (Eklöv & Persson, 1996; Jacobsen & Berg, 1998; Okun & Mehner, 2005). Brabrand & Faafeng (1993) showed that roach more frequently occurred in the littoral zone in response to stocking the lake with the pelagic and night active piscivorous pikeperch *Sander lucioperca* (L.). Similarly, according to an individual-based modelling study, roach were assumed to stop their diel horizontal migration (DHM) in response to the experimental introduction of pikeperch into a small lake in north-east Germany (Lake Großer Vätersee) (Hölker *et al.*, 2002; Hölker & Mehner, 2005). First empirical data from this whole-lake experiment showed that small roach (6–15 cm total length, L_T) indeed stopped their DHM and were thus more frequently caught in littoral areas during the night after pikeperch stocking as compared with the predominant use of pelagic habitats in the previous pikeperch-free period (Haertel *et al.*, 2002; H. Dörner, unpubl. data). The situation, however, may be different in large roach (>15 cm L_T) since the predation risk of these larger fish may be substantially lower due to the gape limited feeding of the predators and a resulting potential size refuge for the larger roach (Lammens *et al.*, 1992; Mittelbach & Persson, 1998). Consequently, the study of habitat use of large roach in comparison to the smaller fish in Lake Großer Vätersee may elucidate the length dependency of this behavioural strategy.

In this study, large roach and predatory fish species were sampled in both littoral and pelagic areas of Lake Großer Vätersee during day and night over two seasons. The habitat-specific differences of the main food resources for roach, zooplankton and benthic organisms were determined as well. Based on stomach analyses of predators, the upper risk length threshold for the roach to be fed on was calculated. By using a binary logistic regression approach, the occurrence of roach in relation to their predators, their food and two abiotic variables (water temperature and oxygen) was predicted. It was hypothesized that the occurrence of large roach was predicted better by predator density, than by zooplankton or benthos abundances in case that the predators represent a potential risk to large roach. This may be independent of the real capability of predators to include large roach in their diet but be related to the

predation risk anticipated by large roach. Alternatively, if predators fed mainly on small roach, and large roach were aware of a low risk, habitat use was hypothesized to be predicted exclusively by the differential diet availabilities and abiotic factors in both lake habitats.

MATERIAL AND METHODS

Lake Großer Vätersee (12 ha, maximum depth 11.5 m, mean depth 5.2 m; 60 m a.s.l.) is situated *c.* 70 km north-east of Berlin, Germany (53°00' N; 13°33' E). The mesotrophic lake has no inflow or outflow and the catchment is mostly covered by forest (Kasprzak *et al.*, 2000). Most of the lake's shore and the adjacent littoral zones are covered by reed beds (*Phragmites australis*) and *Chara* spp. There is no commercial fishery at the lake, and angling was forbidden for the duration of the investigation.

The non-piscivorous fish guild in Lake Großer Vätersee was dominated by roach and small perch *Perca fluviatilis* L. (<16 cm L_T). Further non-piscivores were rudd *Scardinius erythrophthalmus* (L.) and bleak *Alburnus alburnus* (L.) (H. Dörner, unpubl. data). Lake-wide biomasses of non-piscivores (6–16 cm L_T) in 2002, estimated by a multiple mark-recapture census (perch, roach and rudd; H. Dörner, unpubl. data) and from purse seine hauls (bleak), were 124.8 kg for perch, 176.6 kg for roach, 4.8 kg for rudd and 25.5 kg for bleak (Mehner *et al.*, 2005b; H. Dörner, unpubl. data). The piscivorous fish guild consisted of pike *Esox lucius* L. and large perch (>20 cm L_T). Pikeperch was experimentally introduced by stocking juvenile fish (length range 17.0–39.0 cm L_T) in spring 2001. To compensate for post-stocking mortality, a further stocking was performed in spring 2002 (23.0–43.5 cm L_T). Lake-wide biomasses of piscivores, estimated by multiple mark-recapture census, were 134 and 236 kg for pike (12.5–92.0 cm L_T), 88 and 48 kg for perch (20.5–37.0 cm L_T) and 98 and 82 kg for pikeperch (28.0–55.0 cm L_T) in 2001 and 2002, respectively (size ranges for fishes present in the lake are given for both years; T. Schulze, unpubl. data).

Two rows of four gillnets, each with 25, 32, 40 and 50 mm mesh-size (knot to knot; length of net *c.* 25 m, height of nets *c.* 2 m) 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 2001 and 2002. Nets were set during the day (after sunrise and until sunset) and night (after sunset and until sunrise) for short time intervals (40–170 min, depending on water temperature) to minimize mortality and to prevent net visibility due to catch saturation effects. If possible, all fishes were released after recording and processing. All fish (roach only in 2002) were measured to the nearest 0.5 cm L_T . The catch per unit effort (cpue, individuals h^{-1} per 100 m² net) of each fish species caught on a row of nets was calculated. These data were not normally distributed (Kolmogorov–Smirnov statistics), such that for comparisons, non-parametric tests were used.

Piscivorous fishes were anaesthetized (MS 222) and their diet obtained by stomach flushing. Further diet analyses were conducted on predators caught by additional electrofishing in both years. Stomach contents were examined under a stereoscopic microscope. Prey fishes were determined to species level and in case of advanced digestion, identified from remaining hard structures. Prey fish L_T was measured or backcalculated from hard part and length relationships. Diet analyses of large roach were based on fish, which were caught in July and September 2001, and September and October 2002. The guts were dissected and preserved in 4% formaldehyde solution (2001) or stored in ice immediately (2002). In the laboratory, per cent composition of the diet by volume was assessed for the first third of the intestine. Four categories of diet were distinguished: zooplankton, benthic prey, algae and detritus.

Benthic organisms (gastropods, chironomids and other insect larvae) were sampled monthly with an Ekman-Birge grab (15 × 15 cm; depth of grab *c.* 2–3 cm) at three sites (one sample per site) each in the littoral (3 m) and pelagic (6 m) zones. Samples

were sieved through 1 mm mesh, pooled and organisms counted. Pelagic zooplankton (*Daphnia* sp. and other cladocerans) was sampled with a cone-shaped plankton net (90 µm mesh-size). Triplicate vertical hauls from the bottom to the surface were taken biweekly. Littoral zooplankton was collected monthly with a Schindler trap at four sampling sites at a water depth of 3 m and mixed samplings were analysed. Water temperature and oxygen concentrations were measured by a multiprobe in 0.5 m steps from the surface to the bottom of the lake in biweekly intervals. Averages were calculated for the depth zones 1–3 m (littoral zone) and 4–6 m (pelagic zone) according to the position and height of the gillnets. When required for statistical analyses, abundances of invertebrates, temperature and oxygen concentrations were linearly interpolated to match the fish sampling dates.

To estimate the influence of predators on the spatial occurrence of large roach, a binary logistic regression was calculated by the inclusion method. Each row of gillnets containing at least one roach or one of the predators was treated as an independent sampling unit, whereby both littoral and pelagic catches were combined. The dependent variable was 'roach caught' (coded 1, independent of the actual cpue) or 'not caught' (coded 0) on this row. Predictors (independent variables) were the cpue of perch, pike-perch and pike per row of nets as an estimate of predation risk. Further independent variables were habitat-specific densities of benthic organisms and zooplankton as an estimate of food availability, habitat-specific oxygen concentrations and water temperatures, and the time of day (categorical variable, day coded 1 and night coded 0, reference: night). This procedure predicted the probability of catching a roach as a function of biotic and abiotic variables in both habitats, but did not make the deterministic prediction that a roach not caught by the gillnet in the one habitat must have been occurring in the other one. All statistical analyses were performed by SPSS 9.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

In total, 238 rows of gillnets were set of which 151 caught at least one roach or piscivorous fish. Of the total catch, 59% were roach, 32% perch, 8% pike-perch and 1% pike (Table I). The median (maximum) numbers of individual fishes caught on the single nets were 1 (22) in perch, 1 (3) in pikeperch, 1 (1) in pike and 1 (7) in roach. The habitat use (percentages of gillnet catches in the littoral and pelagic zone) of all investigated species was not significantly different between day and night indicating no strong diel migrations between the littoral and the pelagic habitats [Mann–Whitney *U*-test: perch ($n_{\text{day}} = 40$, $n_{\text{night}} = 23$), pikeperch ($n_{\text{day}} = 7$, $n_{\text{night}} = 19$), pike ($n_{\text{day}} = 2$, $n_{\text{night}} = 3$) and roach ($n_{\text{day}} = 31$, $n_{\text{night}} = 42$) all $P > 0.05$; Fig. 1]. Percentages of cpue per habitat were not significantly different between all species (Kruskal–Wallis, d.f. = 3; night, $P > 0.05$; day, $P > 0.05$), indicating a similar habitat use of all species and therefore no strong separation of roach from its predators between littoral and pelagic areas. Overall, roach used the pelagic zone more often than the littoral zone during the whole sampling period in 2001 and 2002 (Fig. 2).

Absolute cpue was higher during the day than during the night in perch, higher during the night than during the day in roach and pikeperch, and not different in pike [Mann–Whitney *U*-test ($n_{\text{day}} = 73$, $n_{\text{night}} = 78$): roach, $P < 0.001$; perch: $P < 0.01$; pike, $P > 0.05$; pikeperch, $P < 0.05$]. Roach and pikeperch were therefore more active during the night, whereas perch showed higher activity and thus capture rates during the day (Fig. 3).

TABLE I. Numbers and total length (median and range) of piscivorous fishes caught and analysed, and of roach caught and consumed by piscivorous fishes in Lake Großer Vätersee

	Perch	Pikeperch	Pike	Roach
<i>n</i> of fish caught in gillnets	168	41	5	307
L_T (cm) of fish caught in gillnets	28.0 (17.5–36.5)	35.5 (28.0–49.0)	43.5 (37.5–73.0)	29.0 (18.0–37.0)
<i>n</i> of stomachs analysed	429	173	210	
<i>n</i> of stomachs with roach	16	12	10	
L_T (cm) of predators with roach consumed	23.0 (18.0–35.0)	37.0 (34.0–43.5)	40.0 (25.5–50.5)	
<i>n</i> of roach consumed	19	15	12	
L_T (cm) of roach consumed	9.0 (2.2–13.8)	7.7 (3.3–10.6)	11.7 (4.5–20.0)	

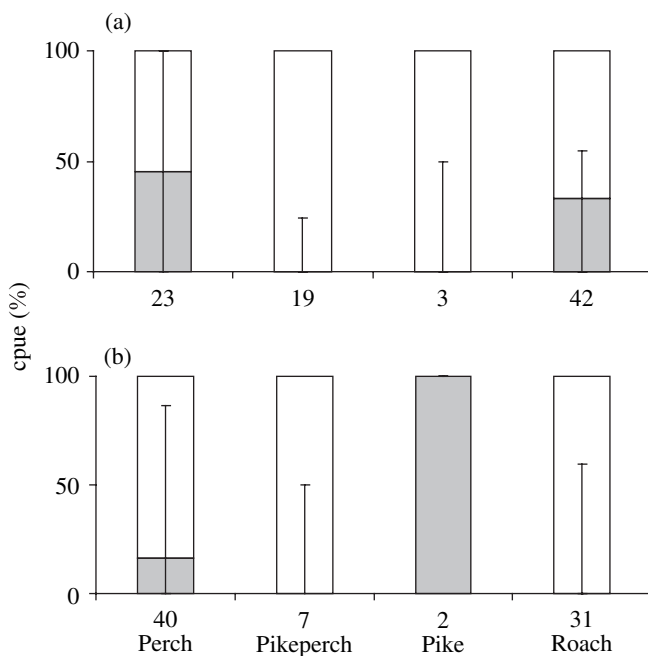


FIG. 1. Median per cent cpue (□, pelagic and ■, littoral zones) of perch, pike, pikeperch and roach in Lake Großer Vätersee during (a) night and (b) day. Whiskers indicate the 25 and 75% quartiles. The numbers below the columns indicate the number of sampling occasions when a species was caught. The proportions of the littoral and pelagic zones always sum up to 100%, the whiskers indicate the same deviation in either habitat.

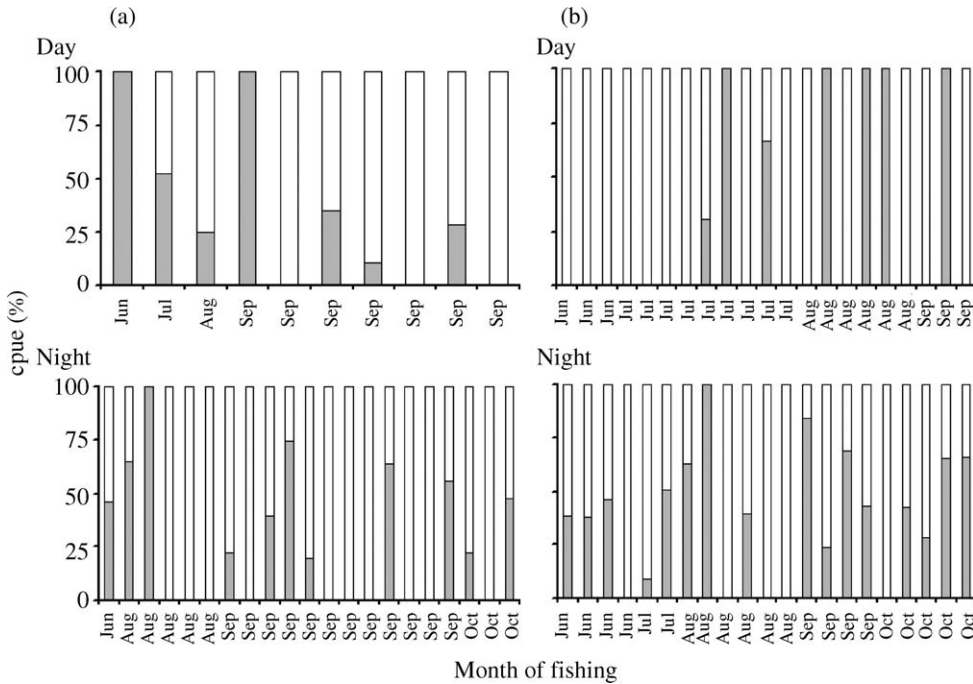


FIG. 2. Habitat use (□, pelagic and ■, littoral zones) of roach (per cent cpue) at all fishing occasions in Lake Großer Vätersee during day and night in (a) 2001 and (b) 2002.

The cpue values for each piscivorous species were always higher when no roach was caught. This was not significant in pike, but significant during the night in perch and pikeperch and during the day in perch, and indicated that roach never co-occurred with high perch densities at any time of the day and

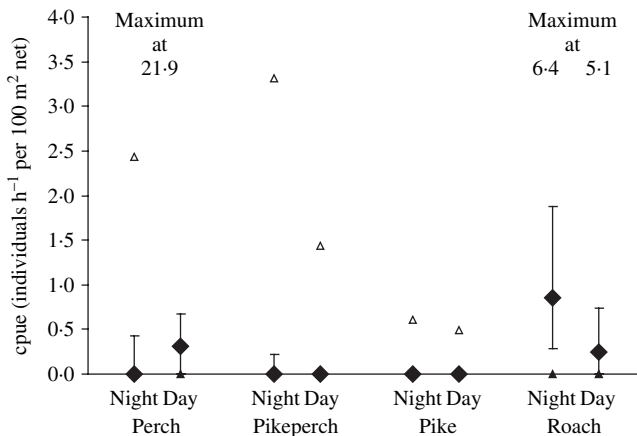


FIG. 3. Median cpue (◆) of perch, pike, pikeperch and roach in Lake Großer Vätersee during the night and day. Whiskers indicate the 25 and 75% quartiles. △, Maximum values; ▲, minimum values.

with high pikeperch densities during night [Fig. 4; Mann–Whitney U -test, night ($n_{\text{no roach}} = 11$, $n_{\text{roach caught}} = 67$): perch, $P < 0.05$; pike, $P > 0.05$; pikeperch, $P < 0.01$; day ($n_{\text{no roach}} = 35$, $n_{\text{roach caught}} = 38$): perch, $P < 0.001$; pike, $P > 0.05$; pikeperch, $P > 0.05$].

The L_T of roach (total $n = 249$) did not differ between the pelagic and the littoral catches during the day or night [Mann–Whitney U -test, day ($n_{\text{Lit}} = 8$, $n_{\text{Pel}} = 66$), $P > 0.05$; night ($n_{\text{Lit}} = 48$, $n_{\text{Pel}} = 127$), $P > 0.05$]. The L_T of roach caught in the nets in 2002 were greater than those of roach consumed by pike, perch and pikeperch [Table 1; Mann–Whitney U -test ($n_{\text{roach caught}} = 249$, $n_{\text{roach fed}} = 46$) $P < 0.001$]. The L_T ranges of those predators which had consumed roach were limited in comparison with the overall size range of the predators in the lake

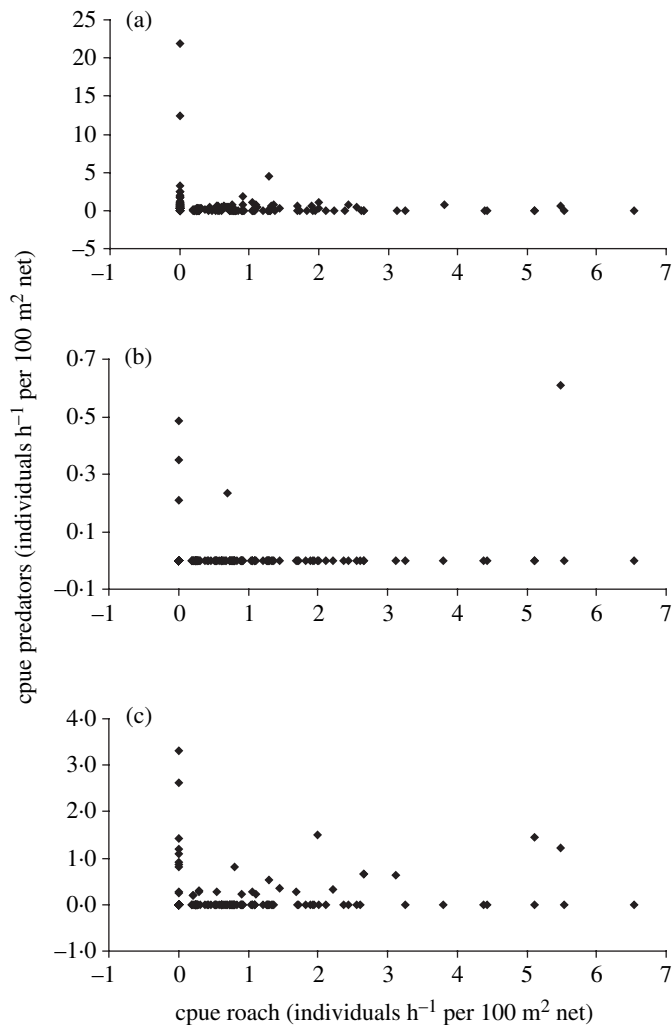


FIG. 4. The cpue of (a) perch, (b) pike and (c) pikeperch in relation to cpue of roach. Note the different scales on the y-axes.

(Table I). Large roach fed on a mixture of algae, zooplankton, benthic prey and detritus (Table II).

Temperature and oxygen levels were almost always lower in deeper area of Lake Großer Vätersee over both years (Fig. 5). Abundances of zooplankton were always higher in the pelagic than in the littoral zone, whereas abundances of benthic organisms were similar in both habitats in 2001 and almost always higher in the littoral zone in 2002 (Fig. 5).

The binary logistic regression model significantly predicted the occurrence of roach (Hosmer-Lemeshow statistics, $c^2 = 4.9405$, d.f. = 8, $P = 0.7639$; in this case a high error probability indicates good fit as this statistic tests the null hypothesis that there is no difference between the observed and the predicted value; Backhaus *et al.*, 2000) and the model represented >45% of variance (Nagelkerke $r^2 = 45.6\%$). The classification table indicated that 82.8% (78.3% for non-occurrence and 84.8% for occurrence; cut value set to 0.59) of all predicted cases were correctly classified. Both the cpue of pikeperch and perch had significant effects on the occurrence of large roach and the e^{β} values <1 indicated that with increasing cpue values of the predators, the probability of catching a roach decreased (Table III). No correlation between the occurrence of roach and the cpue of pike was found. Further significant negative influences were found for the time of day with a higher probability to catch a roach during night than during day. The temperature effect was not significant ($P > 0.05$ but the P -value was close to the significance level) indicating a higher probability of roach being caught in colder, *i.e.* deeper pelagic areas. Neither the abundance of benthic organisms or zooplankton, nor the oxygen concentration had significant effects on the occurrence of large roach (Table III).

DISCUSSION

The results of the study indicated that the catch of large roach by gillnets in both habitats of Lake Großer Vätersee was negatively coupled to the catch of potential predators. Although almost all roach studied were larger than those actually fed on by the predators, high roach catches never coincided with high predator catches. Since the overall habitat-specific distribution of all species was nevertheless largely similar, this indicated that roach obviously avoided

TABLE II. Per cent diet composition by volume, sample sizes, and total length (median and range) of large roach from gillnet catches in Lake Großer Vätersee in July and September 2001, and September and October 2002

	July 2001	September 2001	September 2002	October 2002
Zooplankton (%)	39	1	31	0
Benthic prey (%)	10	7	7	0
Algae (%)	47	76	52	87
Detritus (%)	5	17	9	13
n of diet inspections	44	15	8	5
Median L_T (cm)	26.5	25	25	28.5
L_T range (cm)	18.5–33.5	22.5–34.0	24.0–32.0	28.0–34.0

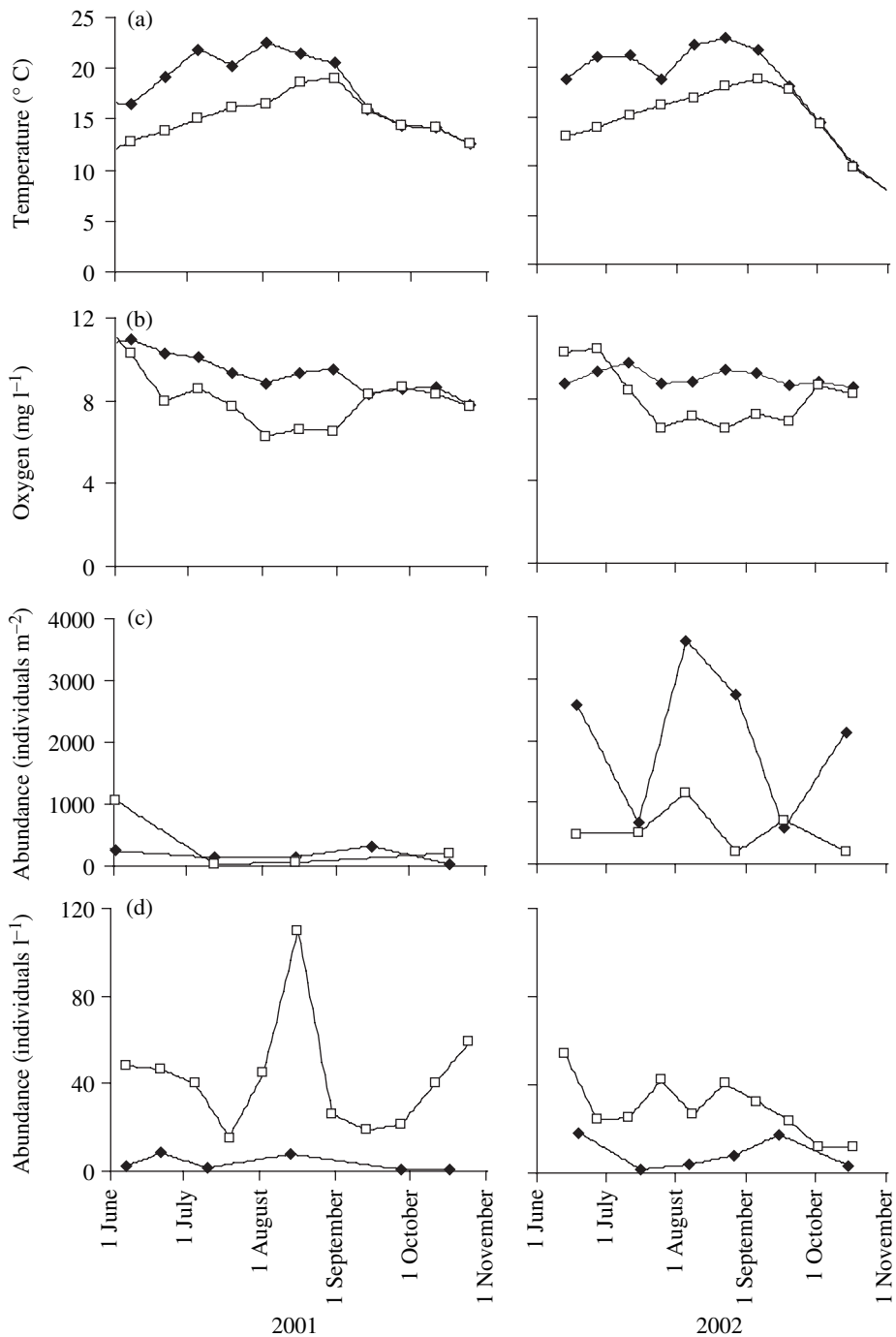


FIG. 5. (a) Temperature, (b) oxygen concentration, and abundance of (c) benthic organisms and (d) zooplankton (*Daphnia* spp. and other cladocera) in the littoral (◆; 3 m depth) and pelagic (□; 6 m depth) zones in Lake Großer Vätersee in 2001 and 2002.

TABLE III. Summary of statistics of the logistic regression to predict the occurrence [0, no roach caught (reference); 1, roach caught] of large roach in Lake Großer Vätersee

Variable	β	Wald	d.f.	<i>P</i>	<i>r</i>	e^{β}
Time of day	-1.8893	13.41	1	0.0003	-0.25	0.1512
Pikeperch cpue	-1.7885	9.81	1	0.0017	-0.21	0.1672
Perch cpue	-1.1056	6.55	1	0.0105	-0.16	0.3310
Temperature	-0.1766	3.41	1	0.0650	-0.09	0.8381
Oxygen	0.4342	2.85	1	0.0911	0.07	1.5437
Pike cpue	-2.9955	1.34	1	0.2479	0.00	0.0500
Benthic organisms abundance	-0.0003	0.85	1	0.3577	0.00	0.9997
Zooplankton abundance	0.0068	0.34	1	0.5626	0.00	1.0068
Constant	2.3975	0.72	1	0.3958		

the immediate vicinity of the predators without being forced to a full habitat shift, as was found for the small roach (6–16 cm L_T , Haertel *et al.*, 2002; H. Dörner, unpubl. data).

For example, even if pikeperch and perch preferred to stay in the pelagic zone during the day, large roach did not migrate into the littoral zone, but remained in the pelagic area at some spatial distance from the larger predator concentrations. Further, large roach showed the same diel activity peak as the introduced pikeperch and used the pelagic zone together with perch and pikeperch during the night. This clearly separated the behaviour of the large roach from that of the smaller roach in Lake Großer Vätersee. For the latter size class (6–16 cm L_T), it was shown that they performed a regular DHM in response to the differing habitat-specific predator activities before the introduction of pikeperch, and exclusively used the littoral zone during all times of the day after the introduction of pikeperch (Haertel *et al.*, 2002; H. Dörner, unpubl. data).

Large roach used the pelagic habitat with its higher zooplankton densities to a greater proportion than the littoral zone. Nevertheless, the catch of large roach was not significantly predicted by the zooplankton abundances. Instead, a declining catch was weakly related to increasing water temperature indicating that roach preferred the deeper and colder areas of the pelagic zone. Also the benthic resources, whose biomasses were higher in the littoral areas, did not predict the occurrence of roach. The benthos biomass in Lake Großer Vätersee was highly variable from month to month. The benthic communities were dominated by high densities of insect larvae (mostly chironomids) in early June 2002 and high densities of *Potamopyrgus* sp. at the beginning of August (H. Dörner, unpubl. data). Highly variable densities of benthic organisms were also found in the littoral of other lakes in Europe (*e.g.* Lake Esrom, Sweden: six-fold decline in benthos densities from June to the beginning of July and an increase in August at the depth of 2 m) and North America (*e.g.* Lac La Ronge, Canada: two peaks of chironomids, the May peak and the August peak) and were explained with different live cycles and emergence of species such as *Chaoborus*, chironomids or other organisms that dominate the benthos

in a given lake (Brinkhurst, 1974). Also, strong seasonal variation of *Potamopyrgus antipodarum* was found in the Madison River basin, Yellowstone National Park, U.S.A., with declining densities during winter (September to March) and a c. 10-fold increase from March to July (Kerans *et al.*, 2005). In Lake Großer Vätersee, however, the distribution of large roach seemed to be almost independent of the habitat profitability and this lack of coincidence may be attributable to the opportunistic feeding of large roach which ingest zooplankton, benthic food, submerged macrophytes and algae (Persson, 1983; Hölker & Breckling, 2001; Haertel & Eckmann, 2002) instead of being strictly planktivorous such as smaller roach. Indeed, also in Lake Vätersee, roach >12 cm have been shown to feed on a mixture of zooplankton, benthic prey, algae and detritus (Radke & Eckmann, 2001). Since the 'Lake Großer Vätersee project' focused on behavioural interactions, reducing the stock of large roach to inspect their diet would have compromised the experiment. Thus, the number of samples was limited. The results of the diet analyses nevertheless corroborate that large roach were opportunistic feeders. Since macrozoobenthos density was higher in the littoral zone, but zooplankton density was higher in the pelagic area, large roach probably move between both habitats such that a significant prediction of the habitat use by resource densities was impossible. Further, oxygen levels which were >6 mg l⁻¹ in both habitats at all times, had no significant influence on the occurrence of roach, and therefore did not restrict roach from using the pelagic zone up to the depth of 6 m. Anoxic conditions were found only <8 m during summer (T. Schulze, unpubl. data).

A better explanation for spatial differences in catch of roach was found if the distribution of potential predators was considered. The probability of catching large roach declined with increasing predator catches, mainly attributable to high densities of perch and pikeperch in the pelagic area. Interestingly, however, cpue of pikeperch was negatively correlated to roach occurrence only at night. This indicates that roach anticipated a higher predation risk at night than during the day in response to higher activity and the good adaptation of pikeperch to low light conditions (Craig, 1987; Maitland & Campbell, 1992). The negative prediction of roach catch by predator cpue was not significant for the third predator, pike. This might be due to the reason that less mobile species like the sit-and-wait predator pike are generally under-represented in gillnet catches. Alternatively, it is possible that the perception of predator presence is mainly visual in roach, such that the densely structured littoral habitats are not perceived as being risky even if pike hide there.

There was no evidence of large roach performing DHM between littoral and pelagic habitats, as it was observed for the smaller roach. Instead, the large roach were more often caught in the pelagic area, but avoided close vicinity to the predators. It was similarly observed in Lake Tjeukemeer, The Netherlands, that large roach co-occurred with pikeperch in the middle of the lake, and only the distribution of roach <20 cm fork length was negatively related to the distribution of pikeperch (Lammens *et al.*, 1992). Also in Lake Gjersjoen, Norway, only the density of juvenile roach decreased in the pelagic areas after the introduction of pikeperch, whereas larger roach continued to utilize the pelagic zone (Brabrand & Faafeng, 1993). In contrast to the above-mentioned studies, however, the analysis of the single catches like in this study

nevertheless revealed a separation of large roach and its predators, but on a smaller spatial scale than that of the regular habitat shifts.

The strong avoidance of large roach to predator occurrence was somewhat surprising since most of the roach caught by gillnets were larger than those found in the predator stomachs. Therefore, although large roach may have reached a size refuge in Lake Großer Vätersee, their behaviour was still strongly predictable by the predator distribution. The estimate of the size refuge, however, is based only on the length of the few roach actually fed by a restricted length range of the predators. Pike and pikeperch with roach in their stomachs were smaller than the maximum length of those species caught by the gillnets. Furthermore, pike and pikeperch caught by additional electrofishing and fyke nets in Lake Großer Vätersee were even larger (92.0 and 55.0 cm L_T , respectively). Thus, there may be still a risk to be preyed on even for the largest roach sampled and large roach may anticipate this risk. In a laboratory experiment, fathead minnows *Pimephales promelas* Rafinesque distinguished between small and large pike by chemical cues alone, and thus were able to assess their predation risk (Kusch *et al.*, 2004). Therefore, if large roach, like fathead minnows, are able to distinguish between predators of different sizes, and if this mechanism also works in whole lakes, roach may possess complete information on their actual predation risk. Alternatively, even if roach were already within a size refuge, but had incomplete information on their actual predation risk, they could also respond to the presence of a wider range of predator sizes. In either case, large roach would avoid the close vicinity of its potential predators as indicated by this study.

In fishes, spatially and temporally structured predator avoidance strategies were often discussed as a trade-off between optimal feeding places and predation risk (Gilliam & Fraser, 1987; Diehl & Eklöv, 1995; Skalski & Gilliam, 2002). In small roach, a proximate factor like the change in illumination strength may trigger the reaction to the predator presence leading to diel habitat shifts between the safe littoral by day and a nightly occurrence in the more profitable pelagic area of lakes (Hölker *et al.*, 2002; Lewin *et al.*, 2004; Okun & Mehner, 2005). This regular migration is probably genetically fixed and the presence of predators is directly perceived either visually and chemically (Eklöv & Persson, 1996), or indirectly *via* alarm substances of injured conspecifics (Gliwicz *et al.*, 2001). As a consequence, large roach may also perceive their predators by the same cues, for example, by alarm substances released by injured or eventually ingested small roach. This is corroborated by the frequently found avoidance behaviour of other prey species after addition of predators, even if predators had disabled feeding organs or were displayed even within cages (Lima, 1998). These experimental observations make information by chemical cues very likely, and chemical signalling may have triggered predator perception of large roach at least in the pelagic area of Lake Großer Vätersee. Consequently, large roach would indeed possess a good risk evaluation system and were therefore keeping a safe distance to the hazard. This idea is in accordance to Lima & Dill (1990) who argued that a lack of predation does not imply a lack of behavioural sensitivity to the risk of predation.

In this case, it remains to be discussed why large roach, in contrast to their small conspecifics, did not migrate between the littoral and pelagic habitats on

a diel scale, but only avoided a too close proximity to predators. There are two non-exclusive explanations. Firstly, the pelagic zooplankton resource is more profitable, whereas feeding on macrozoobenthos in the littoral during daytime would not cover the energetic requirements of the larger roach to a further extent than it was calculated for smaller individuals (Hölker & Mehner, 2005). Secondly, small and large roach may differ with respect to their escape capabilities to predators. Large roach can achieve higher swimming speeds than the smaller roach (Ohlmer & Schwartzkopf, 1959; Lightfoot & Jones, 1996). Furthermore, since handling time increases with prey size (Nilsson & Brönmark, 2000), the chance of an escape even after initial capture by a predator is higher for large than for small roach. Thus, a large roach is at a lower risk being actually killed in the pelagic zone of Lake Großer Vätersee.

In summary, it was shown that the behavioural response to predators in roach of Lake Großer Vätersee was clearly length dependent. Patterns of habitat use differed between large and small roach. For lake-wide estimates of trophic interactions, it is highly recommended to separate such size groups of prey, since size-dependent trait changes may impact habitat-specific resources in a contrasting way (Werner & Peacor, 2003; Hölker & Mehner, 2005).

We wish to thank C. Helms and A. Türc for supporting all kind of labour intensive fieldwork. We thank all members of the Department of Biology and Ecology of Fishes and the colleagues of the Lake Vätersee Project for their support during the stocking, larger fishing programmes and regular samplings, and for valuable discussions. J. Gladitz gave valuable statistical advice and D. Beare checked the language. The study was mainly financed by the German Research Council (DFG, ME 1686/4-1+2).

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