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Coexistence of behavioural types in an aquatic top predator: a response to resource limitation?

**Alexander Kobler · Thomas Klefoth ·
Thomas Mehner · Robert Arlinghaus**

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Abstract Intra-population variation in behaviour unrelated to sex, size or age exists in a variety of species. The mechanisms behind behavioural diversification have only been partly understood, but density-dependent resource availability may play a crucial role. To explore the potential coexistence of different behavioural types within a natural fish population, we conducted a radio telemetry study, measuring habitat use and swimming activity patterns of pike (*Esox lucius*), a sit-and-wait predatory fish. Three behavioural types co-occurred in the study lake. While two types of fish only selected vegetated littoral habitats, the third type opportunistically used all habitats and increased its pelagic occurrence in response to decreasing resource biomasses. There were no differences in size, age or lifetime growth between the three behavioural types. However, habitat-opportunistic pike were substantially more active than the other two behavioural types, which is energetically costly. The identical growth rates exhibited by all behavioural types indicate that these higher activity costs of opportunistic behaviour were compensated for by increased prey consumption in the less favourable pelagic habitat resulting in approximately equal fitness of all pike groups. We conclude that behavioural diversification in habitat use and activity reduces intraspecific competition in preferred littoral habitats. This may facilitate the emergence of an ideal free distribution of pike along resource gradients.

Keywords Behavioural diversification · *Esox lucius* · Foraging strategy · Habitat specialization · Ideal free distribution

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A. Kobler · T. Klefoth · T. Mehner · R. Arlinghaus
Department of Biology and Ecology of Fishes,
Leibniz-Institute of Freshwater Ecology and Inland Fisheries,
Müggelseedamm 310, 12587 Berlin, Germany

A. Kobler (✉)
Department of Biology, Ethology, University of Antwerp,
Campus Drie Eiken, Universiteitsplein 1,
2610 Wilrijk (Antwerpen), Belgium
e-mail: alexander.kobler@ua.ac.be

R. Arlinghaus
Inland Fisheries Management Laboratory,
Institute of Animal Sciences,
Faculty of Agriculture and Horticulture,
Humboldt-University of Berlin, Philippstrasse 13,
Haus 7, 10115 Berlin, Germany

Introduction

Behavioural variation between individuals within a population has often been ignored by ecologists. This is reflected in the common assumption that characterizing a species by the population's average phenotype is sufficient to understand its functional role within an ecosystem (Bolnick et al. 2003; Sih et al. 2004; Réale et al. 2007). This view has been challenged through the identification of ecologically relevant variation in individual behavioural specialization unrelated to sex, size or age across a variety of taxa ranging from gastropods to mammals (Bolnick et al. 2003).

The mechanisms leading to individual behavioural specialization have only been partially understood. However, similar to the density-dependent ecological divergence between species (Rosenzweig 1991; Morris 2003), a few examples indicate that between-individual behavioural specialization within a population is also density dependent (Bolnick 2001; Swanson et al. 2003; Svanbäck and Bolnick 2007). Beyond critical density thresholds, individuals of a population might expand into unused or underused habitats (Haugen et al. 2006; Svanbäck et al. 2008), thus avoiding reductions of fitness in response to resource limitation (MacArthur and Levins 1964). For example, three-spined sticklebacks (*Gasterosteus aculeatus* L.) add alternative prey types to their diet when availability of the preferred prey is reduced due to an increase in population density (Svanbäck and Bolnick 2007). The particular configuration of the specialized behaviours that an individual expresses is referred to as a "behavioural type" (Bell 2007). However, studies examining the ecological mechanisms driving the emergence of behavioural types are lacking (De Kerckhove et al. 2006).

A species that may be suitable for the study of the coexistence of behavioural types is the top predatory fish pike (*Esox lucius* L.), which is common in waters of the northern hemisphere (Raat 1988). It has been described as a solitary sit-and-wait predator with an overall low swimming activity level (Raat 1988; Eklöv and Diehl 1994). Pike are typically bound to vegetation and other structures as foraging and shelter habitats in near-shore areas (Grimm and Klinge 1996; Kobler et al. 2008b). However, previous studies have descriptively noted high inter-individual diversity in behaviour (Rogers 1998; Masters et al. 2005; Vehanen et al. 2006; Andersen et al. 2008) and even presumed the existence of distinguishable behavioural types (Jepsen et al. 2001). This behavioural diversification may play a role in the emergence of an ideal free distribution (IFD), as pike are known to adjust habitat choice according to density of conspecifics along habitat-specific fitness gradients, resulting in an IFD across macro-scale habitats (Haugen et al. 2006). Behavioural diversification may itself emerge from density-dependent resource limitation as observed in Eurasian perch (*Perca fluviatilis* L.), stickleback or roach [*Rutilus rutilus* (L.)] (Svanbäck and Persson 2004; Svanbäck and Bolnick 2007; Svanbäck et al. 2008). Therefore, we hypothesized that prey resource limitation may create behavioural differentiation also in pike, with some individuals alternatively exploiting the open water resources, which typically constitutes the less suitable habitat due to lack of cover (Raat 1988; Grimm and Klinge 1996). However, since cover availability and prey fish densities often differ between the near-shore and open-water zones in lakes (e.g. Okun and Mehner 2005), foraging strategies and swimming activities of pike may differ accordingly (Andersen et al. 2008). The resulting energy budget requirements would differ among behavioural types, with more active fish needing higher prey consumption to maintain body growth, and hence fitness (compare Werner and Hall 1976).

In this paper, we present evidence for individually variable behaviour and coexistence of three behavioural types within a pike population in a small natural lake. We demonstrate that behavioural diversification is flexibly related to prey biomass, with only a part of the population leaving the preferred vegetated habitats in response to resource limitation. We also show that the emerging differences in habitat use and activity between groups of individual pike were not accompanied by growth rate differences in preceding years, thus pointing to the coexistence of behavioural types with approximately equal fitness. We argue that behavioural diversification is important to reduce intraspecific competition and facilitates the IFD along resource gradients.

Materials and methods

Study site

The study was conducted in the dimictic, slightly eutrophic Kleiner Döllnsee (25 ha surface area, mean depth 4.1 m, maximum depth 7.8 m) in the north-eastern lowlands of Germany (52°59′32.1″N, 13°34′46.5″E). The population abundance of adult pike, ≥45 cm total length (TL), was 91 individuals (95% confidence interval, 73–116) in the study year of 2005 (Klefoth 2007). Further predators in the lake were perch and European catfish (*Silurus glanis* L.). Potential competition between pike and the other predators influencing the behaviour of pike was assumed to be of minor importance because the pike used in this study were larger than the maximum sizes of perch, and catfish abundance is low. For a more detailed characterization of the study area, see Kobler et al. (2008b) and Klefoth et al. (2008).

Tagging

Behavioural types in pike were studied from 20 June to 15 September 2005 because submerged macrophytes were fully developed and habitat diversity reached a seasonal maximum. Furthermore, stratification, temperature and water clarity of the lake were relatively consistent during this period (Klefoth 2007; Kobler 2007). Twenty adult pike ≥45 cm (TL) representing 22% of the adult stock were caught by electro-fishing in the reed belt between 21 and 28 April 2005 and tagged at the day of capture. At this time, the spawning period of pike had just ended, and we expected the majority of pike to be still in or near the reed belt where pike usually spawn (Grimm and Klinge 1996). We therefore assumed to catch a random sample of pike individuals representing all behavioural types. Radio-transmitters (20 mm long, 9 mm diameter, weight 5.2 g in air, battery life 10 months; SB-2; Holohil Systems, Canada) were used. Transmitter weight relative to pike body mass was well below the 2% threshold where behaviour is regarded to be affected by the transmitter (Jepsen et al. 2002). Transmitters were implanted into the body cavity as described in detail by Fredrich et al. (2003). After tagging, the fish were measured to the nearest mm (TL) and weighed to the nearest gram (wet weight; WW) [electronic supplementary material (ESM) Table 1]. Ten scales were taken dorsally to the lateral line from every individual. Sex of the fish was determined externally following Casselman (1974). All pike were females, thus controlling for sex-specific behaviours.

Tracking

Radio tracking was performed manually from an electro-powered boat using a handheld receiver (SRX 400; Lotek, Newmarket, ON, Canada) and a three-element Yagi antenna. Once a fish was located, the position was taken by a GPS unit (Etrex summit; Garmin, Olathe, Kans.) referenced to a base station (PFCBS version 2.12; Trimble Navigation, Sunnyvale, Calif.) with a precision of ±1 m. Once every week (selected by systematic random sampling), a 24-h tracking session was conducted. At each tracking session, we attempted to localise each pike once in a 3-h tracking interval. This resulted in up to eight locations per pike and tracking session. One additional 96-h tracking session was conducted between 18 and 22 July 2005 (up to 32 locations per individual). If fewer than six positions were obtained per pike and tracking session, data were excluded. Due to early transmitter failure and mortality, only 17 out of 20 pike were used for analysis. For a more detailed description of the tracking procedure, see Kobler et al. (2008a, b).

Three habitat types were present in Kleiner Döllnsee, namely emergent macrophytes (mainly reed, *Phragmites australis*; 14.4% of lake surface), submerged macrophytes (mainly hornwort, *Ceratophyllum demersum*; 27.2% of lake surface), and the open pelagic area (58.4% of lake surface). Individually recorded observations were linked to the habitats using a digital three-fold partitioned habitat map in ArcView GIS 3.2 (ESRI, Redlands, Calif.) (for details see Kobler et al. 2008a). Pike habitat use was assigned to the times of the diurnal cycle, but only day and night locations were used due to low sample sizes during dusk and dawn. The displacement of an individual between two sequential tracking locations was used to calculate the minimum displacement per hour (MDPH; $\mathrm{m\,h^{-1}}$; Rogers and White 2007), and day- and night-specific arithmetic means were calculated from all MDPH values per individual.

Age and growth

Age determination and lifetime growth calculation of pike individuals were conducted with three out of ten scales. Distances between annuli and the scale centre were measured anterior to the scale centre for each recognised growth year of pike (Quick Scope manual; Mitutoyo, Japan). Results of three scales were averaged and used for fitting a von Bertalanffy growth model to estimate the individual-specific parameters growth constant (k) and asymptotic maximum length (L_∞) (von Bertalanffy 1938). For growth comparisons between individual pike, the product $k \times L_\infty = \omega$ was used since it is more robust to variations in the data than the interdependent and inversely related parameters k and L_∞ (Gallucci and Quinn 1979). Distances of the annuli to the scale centre were used to back-calculate annual growth of the individuals using a Fraser-Lee equation as described by Francis (1990). The constant (c) of the Fraser-Lee equation was defined as the intercept of the regression of TL of pike at day of capture (ordinate) on total scale radius (abscissa) from a total of 75 pike caught in spring 2005. Because recapture of tagged pike immediately after the end of the study period was not possible, growth estimates for the study year were not available. Therefore, we extrapolated the individual growth in the study year from the individual growth rates in the previous years assuming a consistent life history and behaviour between years (see Wolf et al. 2008).

Assessment of prey resource availability

To characterize the spatial distribution of potential prey for pike over the entire season, fish abundance and biomass were estimated by gill-netting (8, 12, 16 and 20-mm mesh size) in both littoral and pelagic areas during 2-h surveys at both day and night monthly between May and November 2005. These mesh sizes caught prey fish in a size range between 46 and 245 mm TL, which is a range commonly consumed by adult pike ≥45 cm (Raat 1988; Nilsson and Brönmark 2000). During each survey, three floating net fleets (each with all mesh sizes) were placed in the pelagic area (in total 317.25 $\mathrm{m^2}$ fishing area) covering the water column from 6 m to the surface, and six benthic nets were placed in the littoral zone (about 2 m deep) at the edge of the reed belts, with three nets (292.65 $\mathrm{m^2}$ total fishing area) each placed randomly on the opposite sides of the lake along its greatest dimension. Gill nets could not be placed directly within submerged macrophytes and reed belts, but were set at the outer edge of the reed close to submerged macrophytes. Species, TL (mm) and WW (g) of catch were determined, and catch per unit effort (CPUE) calculated (number or g WW $\mathrm{m^{-2}}$ gill net $\mathrm{h^{-1}}$).

Bioenergetics

The annual prey consumption by individual pike was estimated by the Fish Bioenergetics model 3.0 (Hanson et al.

1997). Water temperature was measured together with oxygen concentration at a central point in the lake at 2-m depth every 15 min (multi parameter sensor, YSI 6600; YSI, Yellowsprings, Ohio) and at 0.5-m depth intervals once during every tracking session at noon (multi parameter sensor, 4002-FST; Syland Scientific, Heppenheim, Germany). The mean water temperature at 2-m depth was 21.1°C (SD ± 1.3°C, range 19.1–24.1°C) between 20 June and 15 September 2005, and mean oxygen concentration at 2-m depth was 9.2 mg l^{-1} (SD ± 0.7 mg l^{-1}, range 7.4–10.5 mg l^{-1}). Deeper areas of the lake had oxygen concentrations below 3 mg l^{-1} during summer, and thus the longer term occurrence of pike was limited to the water layers between 0 and 5.5 m. The exact depth used by pike is impossible to be determined with radio telemetry. Instead, the depth range potentially used by individual pike was determined by relating the known position of the fish to the lake depth at this location, accounting for the oxygen-rich water layers only. The resulting depth range was converted into an approximate behavioural type-specific mean-experienced water temperature for that day, to consider the potentially lower water temperatures at deeper pelagic sites. Small-scale horizontal variation in temperature of the epilimnetic layer was considered unimportant for bioenergetics because the daily energy demands of fish are most sensitive to differences in individual swimming activity (Boisclair and Sirois 1993). Energetic densities of fish were obtained from several populations from ecosystems close to the study lake (average of four dominant cyprinid prey species, 5,255 J kg^{-1}; pike, 4,980 J kg^{-1}; Schreckenbach et al. 2001). The annual weight increment per age class of pike was estimated from length back-calculations and a TL-WW regression for the tagged pike [WW (g) = 0.0115 × TL $(cm)^{2.861}$; $n = 17$, $R^2 = 0.97$]. Fish were modelled to grow between 1 May and 31 October. Consumption, respiration, egestion and excretion rates were parameterized for pike according to the standard bioenergetics model (Hanson et al. 1997) with modifications with respect to maximum and optimum respiration temperatures (Wysujack and Mehner 2002).

In fish bioenergetics models, the energetic costs of swimming activity are accounted for by multiplying the standard metabolic rates by an activity multiplier (ACT) whereby ACT = 2 is a good approximation for costs of normally active fish (Winberg 1956). In pike, an average ACT = 1.5 has been determined, based on physiological telemetry in the natural environment (Lucas et al. 1993). However, activity costs may be individually and seasonally variable with ACT fluctuating between 1 and >4 (Boisclair and Sirois 1993; Hölker and Breckling 2002). Therefore, activity costs often constitute the dominating fraction of the individual's energy budget, making bioenergetics calculations sensitive to the choice of the ACT multiple (Boisclair and Sirois 1993; Hölker and Mehner 2005). To account for the sensitivity of bioenergetics calculations to individually differing activity rates, we assumed that the activity costs of the most inactive behavioural type of pike (see below) were appropriately modelled by ACT = 1, whereas the ACT multiples of the more active pike were adjusted according to the type-specific ratios of mean swimming distances relative to the least active pike over 24-h cycles.

Statistics

Proportion of occurrence in three main habitats during day and night (six variables) and activity (average MDPH during day or night, two variables) of the 17 tagged pike were used to discriminate between behavioural types (ESM Table 1). The 17 pike × 8 behaviour variables matrix was grouped by a hierarchical cluster analysis (Sørensen distance, linkage method flexible $\beta = -0.25$). The resulting cluster groups were tested for significant differences by a multi-response permutation procedure (MRPP). We also tested a further cluster analysis by omitting the two activity variables and found identical groups, thus suggesting that the grouping was most sensitive to the habitat use variables.

To infer whether habitat use of pike differed from habitat availability (i.e. reflecting active habitat choice), selection ratios and their associated Bonferroni-adjusted 95% confidence intervals (individual-based log-likelihood test for repeated measures) were calculated for day and night recordings (Rogers and White 2007). Habitat choice was considered to be significant if the lower confidence interval of the selection ratio was greater (preference) or the upper confidence interval was smaller (avoidance) than 1 (Rogers and White 2007).

Individual TL, age and ω were compared between the pike clusters by one-way ANOVAs. Since the analysis of growth differences between behavioural types was crucial for the present study and the sample size low, a retrospective power analysis for one-way ANOVA at unequal sample sizes and homogeneous variances (Levene-test, $P > 0.05$) between types was conducted for ω to determine the power of detecting significant differences.

Since diurnal differences in prey catch were low, averages from day and night catches for prey fish biomasses [weight per unit effort (WPUE); g WW m^{-2} h^{-1}] and abundances [number per unit effort (NPUE), n fish m^{-2} h^{-1}] were compared between littoral ($n = 12$ nets per sampling date) and pelagic zones ($n = 6$) and between the sampling months by a repeated measures ANOVA using month (May–November) as a within-subject factor. Habitat was treated as a fixed between-subject factor. WPUE and NPUE values were homogeneous in their variance (Levene-test, $P > 0.05$ in all cases). To detect responses of pike behaviour to fluctuations of prey resources, a linear regression between WPUE of prey fish (mean of littoral and pelagic catches) and relative pelagic occurrence of pike (% of locations) was calculated for all 17 pike as well as separately for each behavioural type.

Significance of all calculations was assessed at α < 0.05. Statistical analyses were conducted with SPSS 15.0 (SPSS, Chicago, Ill.). Habitat selection ratio was calculated by Fishtel 1.4 (Rogers 2002). Multivariate analyses were done by PC-ORD 5.01 (McCune and Mefford 1999). The power analysis was conducted with the UnifyPow freeware in SAS 9.0 (SAS Institute, Cary, N.C.) as described by Lewis (2006).

Results

The cluster analysis (ESM Fig. 1) identified three behavioural types of pike that exhibited differential patterns in habitat use (Fig. 1) and swimming activity (Fig. 2). These groups differed significantly in the multivariate space (MRPP, $T = -8.64$, chance-corrected within-group agreement $A = 0.52$, $P < 0.0001$).

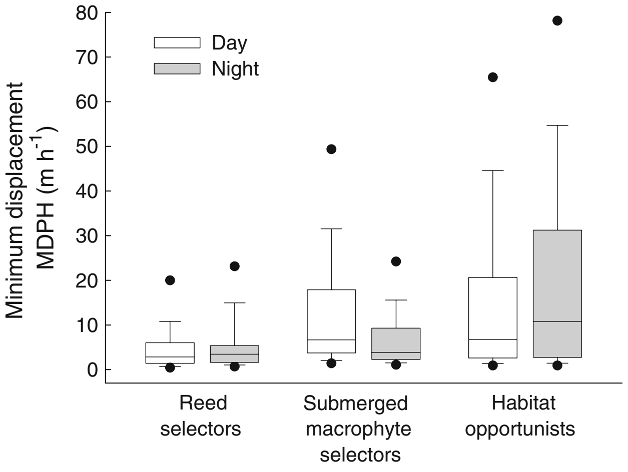

Fig. 2 Minimum displacement per hour (*MDPH*) of pike behavioural types during day and night for reed selectors ($n = 5$), submerged macrophyte selectors ($n = 4$) and habitat opportunists ($n = 8$). *Box plots* indicate medians, 75 (*box*), 90 (*whiskers*) and 95th percentiles (*dots*)

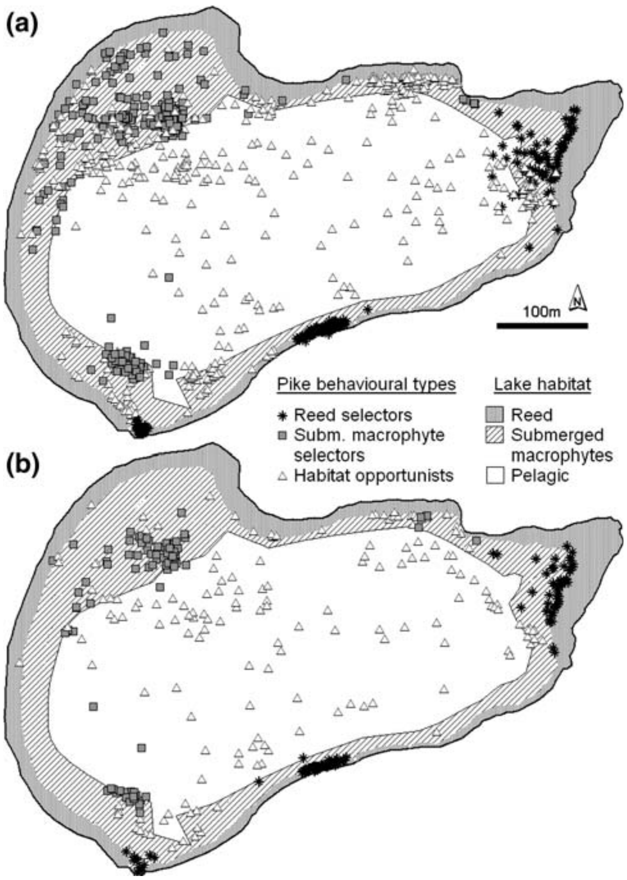

Fig. 1 Locations of three clusters of pike (*Esox lucius*, $n = 17$) in 25-ha Kleiner Döllnsee 20 June–15 September 2005 during **a** day and **b** night. Clusters of pike are based on habitat preference: reed selectors ($n = 5$), submerged macrophyte selectors ($n = 4$) and habitat opportunists ($n = 8$). Map of the lake indicates the three habitat types: reed, submerged macrophytes and pelagic area

The habitat choice of pike differed substantially between the cluster groups (ESM Table 1). Pike of cluster 1 ($n = 8$) significantly avoided the pelagic area during the day (selection ratio ± confidence interval, 0.47 ± 0.23) while showing a positive selection during the night (1.12 ± 0.11) with non-significant choices for the two vegetated habitat types. The other pike preferred only littoral areas (Fig. 1), with cluster 2 pike ($n = 5$) being found mainly in the reed (day, 5.59 ± 1.91; night, 5.56 ± 1.06) and cluster 3 pike ($n = 4$) in submerged macrophytes (day, 3.37 ± 0.13; night, 3.43 ± 0.21). Subsequently, we labelled cluster 1 pike as habitat opportunists (HO), cluster 2 pike as reed selectors (RS), and cluster 3 pike as submerged macrophyte selectors (SMS). HO were 3.7 times more active than RS (ratio of mean overall activity), and SMS were 2.2 times more active than RS. RS were similarly inactive during the day and night (Fig. 2). In contrast, HO and SMS exhibited diurnally varying swimming activity patterns. HO were more active during the night, and SMS were more active during the day (Fig. 2).

TL and age of pike did not differ between the three behavioural types (Table 1; ESM Table 1). Furthermore, the three types of pike exhibited similar lifetime growth (Fig. 3), indicated by ANOVA on the integrated growth parameter ω (Table 1). Although the power of the test was low (0.12), the retrospective power analysis revealed that the necessary sample size to detect a significant difference at $P = 0.05$ and sample size for a power = 0.8 was higher ($n = 205$) than the total abundance of pike ≥45 cm in Kleiner Döllnsee ($n = 91$). This indicated that all behavioural

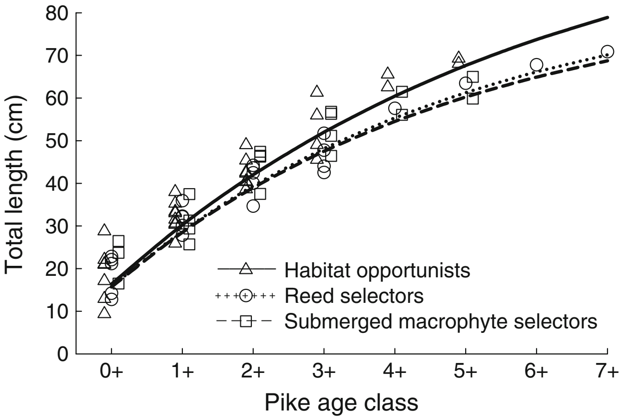

Fig. 3 Back-calculated total lengths (cm) per age class and averaged von Bertalanffy growth curves of the three behavioural types of pike from Kleiner Döllnsee; reed selectors ($n = 5$), submerged macrophyte selectors ($n = 4$) and habitat opportunists ($n = 8$)

Fig. 4 Annual consumption (grams wet weight of prey fish per season) of pike behavioural types in the age classes 1+ to 4+ from Kleiner Döllnsee, as estimated by a bioenergetics model. The differences in consumption between the three behavioural types (reed selectors, $n = 5$; submerged macrophyte selectors, $n = 4$; habitat opportunists, $n = 8$) are attributable to differing activity rates and slightly differing mean water temperatures experienced in the preferred habitats

types had similar growth trajectories in previous years, and thus similar overall net energy budgets. Nevertheless, we averaged the length and weight-at-age data separately for each behavioural type of pike, thus accounting for the non-zero probability that the slightly faster growth of HO (Fig. 3) might reflect a true difference. The bioenergetics estimates were then run with type-specific weight-input parameters.

The fish consumption rates of the three behavioural types were estimated while accounting for the differences in energy required for swimming. Accordingly, we used ACT = 1 for the almost inactive RS, and adjusted the ACT for the other types to the ratios of mean swimming distances relative to RS (ACT = 2.2 for SMS, ACT = 3.7 for HO). As to be expected, the absolute annual consumption rates were higher in older fish, and ranged between 661 (1+ RS pike) and 10.996 g season^{-1} (4+ HO pike; Fig. 4). Due to the type-specific activity differences, the consumption rates averaged over the 1+ to 4+ age classes were 2.04 times higher in a SMS pike and 3.23 times higher in a HO pike, relative to a RS pike (Fig. 4).

The gill-net catches included eight species, with roach and perch dominating. Potential prey fishes ($n = 4{,}055$) had a mean (±SD) TL of 120.6 ± 30.3 mm (range, 46–245 mm) and a mean wet weight of 21.4 ± 17.1 g (0.9–155.1 g). Prey fish biomass differed significantly between months for both littoral and pelagic sites (repeated measures ANOVA, Huynh-Feldt, type III sum of squares = 207.58, $df = 4.03$, $F = 2.85$, $P = 0.036$; no interaction of month and habitat) with an overall declining trend from spring to autumn (Fig. 6). Monthly differences were weaker for prey abundance (repeated measures ANOVA, $SS = 0.57$, $df = 3.66$, $F = 2.29$, $P = 0.084$). There were no habitat-specific differences of prey fish catches, i.e. biomass and numbers of prey fish were similar in both habitats over the season (Fig. 5; repeated measures ANOVA, WPUE, $SS = 9.46$, $df = 1$, $F = 0.21$, $P = 0.660$; NPUE, $SS = 0.08$, $df = 1$, $F = 0.06$, $P = 0.818$).

The proportional occurrence of all 17 pike in the pelagic area significantly increased with the seasonally declining overall prey biomass (mean from littoral to pelagic sites) (Fig. 6a; linear regression, $F_{1,6} = 9.16$, $r^2 = 0.604$, $P = 0.023$). However, the response differed between the behavioural types. When analysed separately for each behavioural type, it was evident that only HO significantly increased their pelagic occurrence (Fig. 6d; $F_{1,6} = 14.94$, $r^2 = 0.714$, $P = 0.008$) with decreasing prey biomass. In contrast, the percentage of pelagic locations in the other behavioural types was unrelated to prey biomass (Fig. 6b, c; RS,

Table 1 Type-specific averages ± SD, and results of one-way ANOVAs on pike total length, age and product of von Bertalanffy growth parameters (ω) between the behavioural types in Kleiner Döllnsee

Source	HO	RS	SMS	*SS*	*F*	*P*
Length (cm)	55.9 ± 4.0	54.8 ± 4.8	62.0 ± 2.9	134.325	0.632	0.546
Age (year)	4.8 ± 0.5	5.6 ± 0.8	6.0 ± 0.6	3.807	0.782	0.476
ω	1.86 ± 0.62	1.63 ± 0.56	2.00 ± 0.98	0.322	0.332	0.723[a]

$df = 2$ in all tests. *HO* Habitat opportunists, *RS* reed selectors, *SMS* submerged macrophyte selectors

[a] The power of this statistical test was 0.120 at a pooled SD = 0.63; the least significant total sample size with a power of 0.80 was $n = 205$

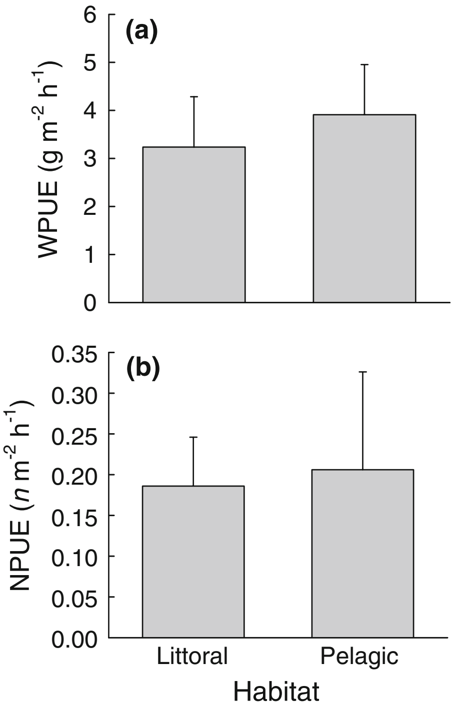

Fig. 5 Habitat-specific weight per unit effort (*WPUE*; g wet weight m^{-2} h^{-1}) and number per unit effort (*NPUE*; *n* fish m^{-2} h^{-1}) of monthly gill-netting of prey fish in Kleiner Döllnsee from May to November 2005, estimated marginal means ± SE from repeated measures ANOVA

$F_{1,6} = 1.34$, $r^2 = 0.183$, $P = 0.290$; SMS, $F_{1,6} = 0.56$, $r^2 = 0.009$, $P = 0.821$).

Discussion

Three behavioural types were found to coexist within the pike population in Kleiner Döllnsee. RS consistently preferred reed habitats and were least active, whereas the more active SMS predominantly occurred in beds of submerged macrophytes. The most active HO were located in all three lake habitats, but increased their preference for pelagic sites in response to a declining prey biomass throughout the season. Habitat specialization of fish between near-shore littoral and open water has been observed frequently, for example in bluegill sunfish (*Lepomis macrochirus* Rafinesque), Eurasian perch and roach (Ehlinger and Wilson 1988; Svanbäck et al. 2008). In most of the studies, habitat divergence was attributable to intraspecific competition (Svanbäck et al. 2008). Our study presents evidence for a similar resource-dependent habitat divergence in pike, but adds a further differentiation within the littoral habitat between RS and SMS. The behavioural flexibility shown by habitat-opportunistic pike likely reduced intraspecific competition because underused pelagic resources were exploited. This conclusion corresponds to results from a game-theoretic model and a field study with three species in three habitats where opportunists were found to reduce the overall competition between the species (Brown 1996; Morris 1996), corroborating that competition-induced ecological mechanisms seem to operate similarly within and between species.

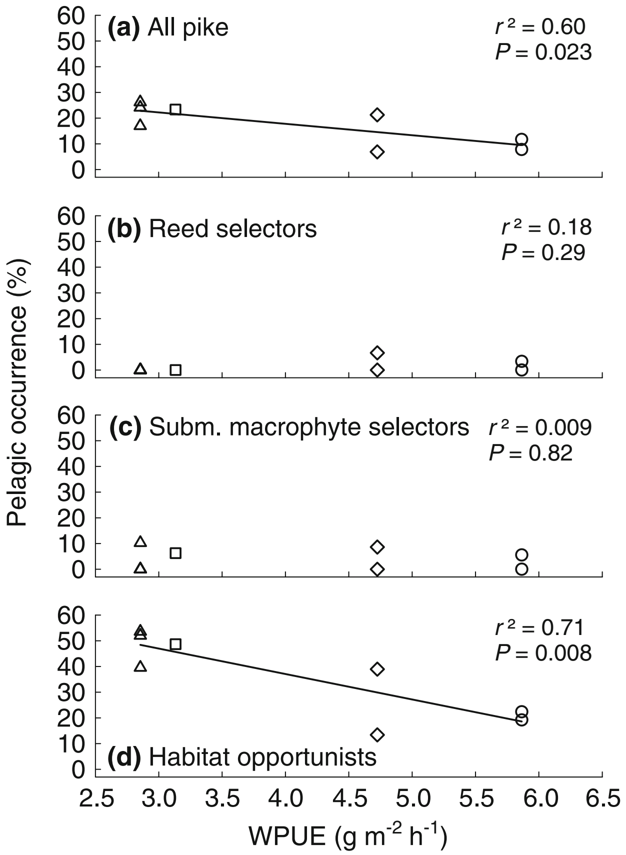

Fig. 6 Scatter plot and linear regression between biomass of prey fish (WPUE, average from monthly conducted littoral and pelagic gill-net catches, g wet weight m^{-2} h^{-1}) and proportion of locations of **a** 17 tagged pike, and separately for **b** reed selectors ($n = 5$), **c** submerged macrophytes selectors ($n = 4$) and **d** habitat opportunists ($n = 8$) at pelagic sites in Kleiner Döllnsee. Results from eight 24-h tracking periods between June and September 2005 were grouped to the least distant date of prey fishing. *open circle* June, *open diamond* July, *open triangle* August, *open square* September

It is intriguing to see that about 50% of pike (eight out of 17) regularly used pelagic habitats, whereas the other half of the individuals stayed almost exclusively in littoral areas. However, all pike exhibited equal lifetime growth, despite different activity levels and corresponding energy demands. Because growth rates in fish can be considered a good proxy for fitness (Werner and Hall 1976) and because resource densities in both habitats were similar, our findings resemble patterns to be expected from IFD theory (Fretwell and Lucas 1970). IFD predicts that individuals will distribute themselves in a way that results in equalized fitness among habitats as a result of individuals seeking to maximize their own fitness by switching to more favourable habitats until the fitness advantage of habitat switching vanishes (Fretwell and Lucas 1970). Pike have been shown to distribute in an ideal free manner according to between-habitat fitness gradients that result from density- and resource-dependent survival and fecundity (Haugen et al. 2006). The similar behavioural type-specific growth of pike found in our study suggests that pike respond with behavioural diversification to resource gradients without compromising fitness despite remarkably different habitat use and activity levels. Behavioural diversification in pike may be a mechanism equalizing fitness among types and habitats, thereby facilitating the IFD of pike populations (Haugen et al. 2006).

Two critical assumptions of IFD theory are that individuals are able to assess the quality of different habitats, and that the costs of movement between habitats are low (Fretwell and Lucas 1970). Both aspects likely hold in our study lake. In regard to ability to assess the quality of habitats, spatial distances between the habitats in the study lake were short (Fig. 1). This likely allowed individual pike to familiarize themselves with and remember different habitats including their quality in terms of resource availability. Indeed, in an accompanying study we found that all pike types exhibited precise navigational capabilities towards previously established residence areas after translocation to opposite sides of the lake (Kobler et al. 2008a). However, for HO to start engaging in exploiting prey resources in the pelagic, two aspects related to the perceived or real costs of moving appear to be critical. First, there must be a competition-driven incentive to move, which in our study was given by a drop in prey resource availability through the course of the season. Second, the costs of movement from the littoral to the pelagic areas and back must be lower than or equal to the energy gain obtained by feeding in the pelagic area. The equal lifetime growth rates of all behavioural types in our study suggest that the higher movement costs of HO were balanced by higher energy gains.

Additional non-energetic costs of leaving the safer vegetated littoral habitat, such as risk of death through cannibalism, were probably low in the study lake. The maximum victim:cannibal ratio in pike is 0.55 (Persson et al. 2006). Thus, our smallest tagged pike was under risk of cannibalism by an 82-cm-long conspecific. Because we caught only four pike $\geq$80 cm from a total capture of 318 pike in Kleiner Döllnsee in 2005 (Klefoth 2007), the HO were likely exposed to low probabilities of falling victim to cannibals.

We found that not all pike responded behaviourally to a resource decrease. For example, the RS did not sample their entire environment and were practically never located in the pelagic area over a period of 3 months. Therefore, both responsive and unresponsive pike individuals coexisted in our study lake as in other pike populations (Andersen et al. 2008). This corresponds with a recent theoretical model (Wolf et al. 2008), which suggests a frequency-dependent occurrence of individuals with different responsiveness within animal populations. While unresponsive individuals (i.e. RS and SMS) are consistent in their established behaviour whenever there is a cost associated with a behavioural change (i.e. switch from sit-and-wait foraging in the littoral zone to pursuit tactic in the pelagic, see further discussion), the responsive individuals (i.e. HO) keep changing their behaviour according to the ecological state of the environment. In our study, responsive habitat opportunistic pike were more mobile than unresponsive pike that were bound to littoral structures. Responsive pike might constitute competitively superior individuals that respond to seasonally declining resource availability by exploiting abundant prey in generally less favourable open water habitats (Andersen et al. 2008; Knight et al. 2008). An alternative perspective is that these responsive individuals are competitively inferior and are displaced from preferred vegetated habitats into open water by conspecifics due to density- and resource-dependent interference competition (Nilsson and Brönmark 1999; Nilsson 2006). Irrespective of the exact mechanism, behavioural diversification into responsive and unresponsive individuals may result in fitness optimization for all behavioural types, and substantially reduces intraspecific competition.

Pike has been described as a typical sit-and-wait predator (Raat 1988) with a morphological adaptation to transient swimming and explosive attacks on prey fish (Harper and Blake 1991). In our study lake, submerged macrophytes (mainly hornwort) are less structured than the dense reed belt, and open water habitats do not offer any cover for the predator. Because strikes of pike on prey in open water are less successful than those in structured habitats (Eklöv and Diehl 1994), a sit-and-wait tactic in open water can be expected to result in lower prey intake. If the sit-and-wait tactic is not profitable enough, a switch to a pursuit tactic might be advantageous (Davies 1977; Inoue and Matsura 1983). This switch depends on the rate of foraging profitability, which balances search efficiency and energy expenditure (Norberg 1977). When resource levels drop, search efficiency can be improved by an increased swimming activity (Vøllestad et al. 1986; Turesson and Brönmark 2007; Andersen et al. 2008), which is however, accompanied by higher energy demands. The similar growth of the three behavioural types indicates that the active opportunistic pike were able to balance their higher activity costs by a higher energy intake in the presumably less suitable open water. A reasonable assumption is that the higher energy intake might be facilitated by greater encounter frequencies with prey for the more active pike. Because gill-net catches reflect both abundances and activity of prey fish (see Hölker et al. 2007), the similar CPUE data in both habitats of Kleiner Döllnsee suggest that prey density and swimming activity of prey were comparable at littoral and pelagic sites. This should have resulted in higher prey encounters by more active habitat opportunistic pike in the open water. However, the reactive distance of a prey is likely to be higher in open water at high transparency during daytime than in turbid water and during twilight or dark conditions (Helfman 1993). Foraging success of pike hunting in the pelagic zone should therefore be higher at weak illumination (Helfman 1993). Interestingly, HO were found to be more active during the night than during the day, which could be interpreted as a behavioural response to increase prey capture success when foraging in open water (Helfman 1993).

Our assumption of equal fitness of all three behavioural types was based on retrospective analyses of growth rates. Unfortunately, direct recapture of tagged pike after termination of the study was impossible, and thus the growth rates in the study year could not be compared. Our assumption is therefore valid only if the individual pike do not switch between different behaviours from year to year. We do not have data to validate behavioural consistency across years. During the study period, however, we did not find much evidence for a switch in behavioural types, because the behaviour of the two vegetation selector groups was consistent over the sampling months. A between-year consistency of individually distinct habitat use has been demonstrated in adult lake trout (*Salvelinus namaycush* Walbaum) (Morbey et al. 2006) and in Icelandic cod (*Gadus morhua* L.) (Pàlsson and Thorsteinsson 2003). Theoretically, consistency in behaviour between years is likely because future costs of ecological adaptation can be reduced when individuals fine-tune their behaviour (Wolf et al. 2008). Such costs involve the time, energy, and mortality costs of sampling the environment, or the costs of building and maintaining the required sensory machinery (Wolf et al. 2008). Therefore, even small positive feedback between the established behaviour and fitness will induce behavioural consistency (Wolf et al. 2008). Similar growth in all pike behavioural types is suggestive of little consequence of the behavioural divergence in terms of fitness. It is an avenue for future research to investigate whether behavioural types develop due to behavioural plasticity or are a result of frequency- and density-dependent selection. We assume that the behavioural types detected in habitat choice and swimming activity correspond to individual-specific personality traits (Sih et al. 2004; Réale et al. 2007) probably reflecting differences in underlying physiology and energetics. Future studies shall elucidate if the behavioural divergence of pike from Kleiner Döllnsee can be consistently reproduced between years and from other ecosystems.

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