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Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake

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Abstract The objective of this study was to contrast movement rates and habitat choice of pike (*Esox lucius* Linnaeus) in mid-summer and mid-winter in a 25-ha lake (Kleiner Döllnsee, northeastern Germany) using radio-telemetry. Positional telemetry for consecutive 96-h was conducted by boat in July 2005 and by walking on surface ice in January/February 2006. Positions of pike ($N = 11$) were recorded with a GPS unit corrected by a reference station. Movement rates, distance to shore and habitat use were compared between summer and winter and relative to daytime and fish length. Pike moved significantly more in summer, and during summer had activity peaks in twilight periods. In winter, pronounced activity peaks at specific daytime periods were missing and pike chose habitats significantly closer to shore. In summer, submerged macrophyte beds were positively and pelagic areas negatively selected. In winter, pike negatively selected shallow open water in the littoral zone, and there was a tendency to avoid the pelagic. Movement rate and distance to shore were significantly and positively related to the size of pike.

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Introduction

Pike (*Esox lucius* Linnaeus) is a top predatory species occurring naturally or due to stocking programs in many freshwater and brackish ecosystems in the northern hemisphere (Raat, 1988; Craig, 1996). It is a keystone predator able to control fish community composition through predation (Prejs et al., 1994; Berg et al., 1997). Due to its importance as top predator and fisheries resource for commercial and recreational fisheries (e.g. Arlinghaus & Mehner, 2004), an understanding of the behaviour and habitat choice of pike is paramount for effective conservation and fisheries management.

Positional telemetry by either radio or acoustic transmitters is suited to analyze behaviour and habitat choice in fish (Lucas & Baras, 2000). Several studies have applied telemetry to investigate the ethology of pike in freshwater systems (e.g. Diana et al., 1977; Rogers, 1998; Jepsen et al., 2001; Beaumont et al., 2005; Koed et al., 2006). A great versatility of pike in habitat use and behaviour was observed in these studies, which was related to size (Masters et al., 2005; Vehanen et al., 2006), sex (Jepsen et al., 2001), season (Rogers, 1998; Jepsen et al., 2001) and environmental conditions, e.g. water clarity (Jepsen et al., 2001).

There is some considerable consensus on several aspects of the behavioural ecology of pike. For example, pike are known to be most active during the spawning period (Cook & Bergersen, 1988; Koed et al., 2006), to display their highest levels of activity at twilight (Cook & Bergersen, 1988; Rogers, 1998; Beaumont et al., 2005), and to prefer the littoral zone (Chapman & Mackay, 1984b; Cook & Bergersen, 1988) and structurally diverse vegetated habitats (Cook & Bergersen, 1988; Casselman & Lewis, 1996; Grimm & Klinge, 1996; Jepsen et al., 2001). Size-specific differences have been observed in the utilization of vegetation cover, with larger fish more likely to choose lesser-vegetated sublittoral or pelagic areas (Chapman & Mackay, 1984a; Rosell & MacOscar, 2002).

Contrasting results have been reported with regard to the influence of temperature and season on movement rates. For example, Jepsen et al. (2001) and Koed et al. (2006) found increased movement of pike in winter, while Cook & Bergersen (1988) and Rogers (1998) reported less activity in winter than in summer. In contrast, Diana et al. (1977) found no differences in movement of pike in summer and winter. Different study results might not only reflect variations in pike behaviour in different ecosystems, but also occur due to differences in methods and study design (Jepsen et al., 2001). For example, most of the available telemetry studies on pike used landmarks and maps to define the position of a single pike by triangulation (Diana et al., 1977; Rogers, 1998; Jepsen et al., 2001). This kind of measurement becomes increasingly inaccurate with increasing distance of the pike's position to shore (Rogers, 1998). Application of locally referenced geographic positioning systems (GPS) can minimize the positioning error. However, no study of pike behaviour and movement was found that used GPS for an accurate localisation of a specimen, with Rogers & Bergersen (1996) as a notable exception. Also, analyses of diurnal activity patterns and more accurate estimates of movement rates such as minimal displacement per hour require 24-h trackings and repeated locations of individual fish throughout the day at small time intervals (Rogers & White, 2007). Such estimates are lacking in many previous studies or have been sporadically conducted in weekly (Jepsen et al., 2001) or monthly (Rogers, 1998) intervals and at rather broad time intervals between locations (e.g. every 6-h). Moreover, most research on movement rates of pike reported rather broad estimates of minimal movement per day (Diana et al., 1977) instead of focusing on smaller time intervals such as movement rate per hour that is a better indictor of movement pattern in fish (Rogers & White, 2007).

The objective of the present study was to contrast movement rate and habitat choice of the same pike individuals in a small lake assessed over four consecutive 24-h trackings in mid summer and mid winter. This study improved the accuracy in pike location by applying a 3-h time interval between trackings and GPS techniques, and by calculation of dusk and dawn times on a precise hourly level. Behaviour of pike at highest annual water temperature in summer was compared with behaviour and habitat use beneath a 40-cm thick ice layer in very cold nights in winter. This exploratory study was conducted to improve the basic ethological knowledge of a keystone species in the aquatic system. Its aim was to contribute to the limited literature on the behaviour and habitat choice of pike in lakes.

Study area

The study was conducted on the natural lake Kleiner Döllnsee, a 25-ha dimictic, shallow (mean depth 4.1 m, maximum depth 7.8 m) and mesotrophic to slightly eutrophic lake (P concentration at spring overturn of 28 $\mu g\ l^{-1}$) with a mean Secchi depth of 3.5 m in 2005. It is located 80 km northeast of Berlin in the northeastern lowlands of Germany (N 52° 59′ 32.1″, E 13° 34′ 46.5″). The entire lake shoreline was surrounded by dense, 2–55 m wide reed belts

(*Phragmites australis, Typha latifolia, T. angustifolia*). In total, 14% of the lake surface was covered by emerged macrophytes, and further 27% of the lake bottom by submerged macrophytes (mainly *Potamogeton* spp., *Ceratophyllum* spp., *Najas* spp., *Myriophyllum* spp.) with varying degrees of cover and structural complexity during the summer months. No commercial or recreational fishing was allowed on this lake. The lake had a natural, self reproducing pike population slightly exploited by experimental fishing. The fish community comprised 12 fish species according to recent surveys (unpublished data). The natural top predators were pike and perch (*Perca fluviatilis* Linnaeus). Eel (*Anguilla anguilla* Linnaeus) and European catfish (*Silurus glanis* Linnaeus) were also present, albeit at lower abundances and stocked.

Table 1 Individual data of radio-tagged pike in Lake Kleiner Döllnsee. The pike tagged on July 3 was supplied with a tag retrieved from a dead fish tagged in April 2005. Due to a number of reasons mentioned in the text, only $N = 11$ out of 20 pike originally tagged were used for the present study. All pike were females

Fish ID	Length (mm)	Weight (g)	Date of tagging (2005)
150.023	560	1104	April 21
150.052	522	845	April 21
150.110	493	768	April 21
150.181	630	1555	April 26
150.219	688	2170	July 3
150.238	733	2287	April 28
150.341	543	1064	April 28
150.372	515	976	April 28
150.391	488	816	April 28
150.412	462	640	April 28
150.431	450	580	April 28

Material and methods

Capture and tagging

Twenty adult pike were caught using a battery-powered DC electro-fishing unit (Type EFGI 4000, 4 kW, Brettschneider Spezialelektronik, Chemnitz, Germany) with a 40-cm diameter ring anode between April 21 and April 28, 2005 and radio tagged at the day of capture. Holohil SB-2 transmitters with a length of 20 mm, a diameter of 9 mm, a weight of 5.2 g in air, a battery life of 10 month and frequencies ranging from 150.023 to 150.431 MHZ were used. Relative transmitter weight was ≤0.8% of pike's body mass (Table 1).

Pike were anaesthetised using a 100 mg l^{-1} solution of MS 222 until fish lost equilibrium and opercular rate became slow and irregular. The radio transmitters were implanted into the body cavity through a 2–3 cm incision 3 cm behind the base of the left pectoral fin as outlined in Fredrich et al. (2003). A lateral body wall exit site was made for the transmitter antenna between the ventral and anal fin using a 15-cm long needle. The incision was closed up with two individual stitches circa 10 mm apart. The duration of the operation ranged between 2 and 3 min and recovery time was between 3 and 5 min. After tagging the fish were measured to the nearest mm (total length) and weighed to the nearest g. Average length of the pike was 577 mm (range 450–755 mm) and average weight was 1402 g (range 580–2679 g, Table 1). An external sex determination was conducted following Casselman (1974). All of the pike used in the present study were females (Table 1). Water temperature at the time of tagging was 11°C measured in 1.8 m water depth. After tagging the recovered fish were released close to their individual capture point. Fish tracking started after a two weeks post operation recovery period.

Tracking

Radio tracking was performed manually from an electro-powered boat in July 2005 and by walking on ice in January/February 2006 using a handheld receiver (Lotek SRX 400 Telemetry Receiver, Ontario, Canada) and a three-element Yagi antenna. Visual observations revealed that pike could be approached by the boat to approximately 2 m in shallow water before eliciting a flee response. In deeper water, the boat could be moved directly above a pike without eliciting a flee reaction. Once a fish was located, the position was marked by GPS unit (Garmin, etrex summit, UTM coordinates) referenced to a base station (PFCBS Version 2.12, Trimble Navigation, Sunnyvale, CA) installed immediately at the lake shore at the research station. A tracking precision of ±6 m radius was determined by analyzing the position scattering of two dead fish over two weeks. It was assumed that any tracking error would be systematic, thus affecting all fish to the same degree. Each fish was attempted to be localized once in 3-h tracking intervals for consecutive 96-h in both summer and winter. This procedure resulted in up to 8 positions per fish and 7 net movements per 24-h. Fish were excluded from further analyses when less than 6 positions were obtained per 24-h. Tracking for 96-h took place from July 18 to July 22, 2005 and from January 30 to February 3, 2006. On each of these tracking days, water temperature was measured with a multi parameter sensor (YSI 6600, YSI Corporation, Yellowstone Springs, Ohio, USA) positioned 1.8 m under water surface in the centre of the lake. Recordings were made every 15 min and later averaged.

Habitat mapping

A digital map of the available habitats in Lake Kleiner Döllnsee was created in summer to relate the habitats chosen by pike (assessed by GPS) to the available habitats. This was also done to investigate location/habitat fidelity by comparing the pike's habitat choices in summer and winter. For example, we were interested in understanding whether a potential preference for locations with vegetation during summer would also be preferred during winter when vegetation becomes procumbent on the lake bottom or dies off. However, it is important to realize that our approach to identify habitat choice of pike by overlaying the GPS location coordinates with the digital habitat map did neither allow precise identification whether a pike was located within, or above, the submerged macrophytes, nor if a pike was associated with a particular plant species. It was also not possible to precisely determine its vertical position within the water column. However, pike locations were precisely distinguished according to areas covered by submerged macrophytes, the pelagic area and emergent macrophytes.

In order to create the digital habitat map, the following four large scale habitat features were screened by boat: (1) a macrophyte-free pelagic area, which encompassed all habitats without macrophytes (typically at water depths >4 m); (2) littoral habitats with emerged macrophytes; (3) shallow open water, which also included submerged macrophytes covering the sediment $\leq$30 cm only, as these habitats provided similarly limited structured habitats for adult pike as open water; and (4) submerged macrophytes including all areas with submerged vegetation growing $>$ 30 cm into the water column assuming that these macrophyte stands provided significant cover and refuge for adult pike.

The occurrence of the four different habitat types in summer was assessed by scuba diving along transects. In total, 28 transects were randomly selected covering the entire shoreline. Each transect was surveyed orthogonally to the shoreline until the end of the vegetated area. Each transition zone between the different habitat categories mentioned above was marked with buoys. The buoy positions were recorded by GPS from a boat and later imported into Arc View 3.2. Habitat area polygons were created by interpolation and assigned to one of the four habitat types. Diving took place on July 23, 2005 to allow for full expression of the biomass of macrophytes. Habitat expansions were as follows: pelagic area 14.7 ha (mean depth, 5.6 m), submerged macrophytes 3.6 ha (mean depth, 3.0 m), shallow open water in the littoral zone 3.3 ha (mean depth, 2.5 m) and emerged macrophytes 3.6 ha (mean depth, 1 m). The same habitat map created in summer was used to identify habitat choice in winter bearing in mind that especially the submerged macrophyte habitat changed in winter, because of the reduced height of macrophyte stands. However, examining seasonally changing habitat choice at a site enables to distinguish between active habitat choice and site fidelity in pike behaviour, i.e., do pike actively adapt to habitat changes and select new sites or do they select the same site in winter which was attractive and positively selected during summer. The date when vegetation disappeared from the water column was assessed by sporadic echosounder surveys.

Data analysis and statistics

Movement patterns in summer and winter were evaluated using minimal displacement per hour (MDPH) as an indicator of behavioural activity (Rogers & White, 2007). MDPH was defined as the straight line distance between consecutive locations of the same fish, divided by the time elapsed between these locations (maximum 3-h). MDPH values were also separately calculated for different periods of the day: dawn, day, dusk and night. Twilight periods were calculated according to the nautical definition based on the geocentric horizon using http://www.cgi.stadtklima-stuttgart.de/mirror/sonne.exe. Dawn was defined as the time period when the centre of the sun moved from the position 12° under the geocentric horizon to sunrise, while dusk was the period when the sun centre moved from sunset to the 12° position under the geocentric horizon. Twilight lasted about 2 h in July 2005 and about 1.3 h in February 2006, which resulted in missing data points for some fish during twilight periods because of the 3-h tracking interval. Therefore, the first location shortly after twilight was used to estimate MDPH per dawn and dusk respectively.

MDPH values were ln-transformed using ln $(x + 1)$ and the transformed values tested for normal distribution using Kolmogorov-Smirnov tests. Logarithmic MDPH values were normally distributed and variances homogenous at $P > 0.05$ in both summer and winter. In order to account for the dependent samples and repeated measures, mixed model analyses of variances with Bonferroni post hoc tests were used to test for differences in MDPH for the fixed effects season, daytime, with total length of pike as a covariate. The individual fish were treated as random effect.

In order to estimate distance to shore (DTS), the shoreline was defined as the boundary of emerged macrophytes and open water. An exact positioning of a fish within the reed belt was not possible. Therefore, the exact determination of the true DTS of fish within the reed belt was not possible. DTS was set to zero in these situations. DTS of all tracking points was calculated using the software Fishtel 1.4 (Rogers & White, 2007). DTS values were ln-transformed using ln $(x + 1)$ to stabilize variances. Despite this transformation, DTS values were not normally distributed and variances inhomogeneous across factors ($P < 0.05$). Nevertheless, mixed model analysis of variance was used to model the impact of the fixed effects season and daytime on DTS, with length of fish as a covariate. Individual fish were treated as random effect. Results were compared with factor-specific non-parametric statistical analyses. The results were similar in terms of statistical significance to the results of a full mixed model analysis of variance indicating robustness of this multivariate technique against deviations from underlying assumptions of normal data distribution and variance homogeneity. Therefore, the results of the full model are presented.

Individual-based log-likelihood test statistics as described in detail by Rogers & White (2007) that accounted for the repeated location of individual fish in selected habitat structures were used to examine habitat use in summer and winter. Selection ratios and their associated Bonferroni-adjusted 95% confidence intervals were calculated according to Rogers & White (2007). Selection ratios were considered significant in summer and winter when the selection ratio together with the 95% confidence intervals were greater or smaller than 1 (Rogers & White, 2007).

All statistical analyses were conducted with the SPSS software package version 14.0.1 (SPSS Inc. 1989–2005) at a type 1-error probability of $\alpha = 0.05$ with the exception of the analyses of the selection ratio, which were calculated by the software Fishtel 1.4 (see Rogers & White, 2007).

Results

Descriptive data and abiotic conditions

In the course of the study, one pike died and another lost its transmitter shortly after tagging in April 2005. A third individual died due to an attack by a larger pike, another three due to experimental angling mortality and another three transmitters stopped working before the winter tracking in January/February 2006. Thus, 11 out of 20 originally radio-tagged pike specimens with total lengths between 450 and 735 mm were used to comparatively analyse their movement patterns in summer and winter (Table 1).

During summer trackings in July 2005, the water temperature (±SD) was 21.9 ± 0.2°C, and Secchi depth was 3.7 m. Air temperatures ranged from 11.3°C at night to 24.3°C at day. During the winter tracking in February 2006, the water temperature (±SD) was only 2.7 ± 0.1°C and the air temperature ranged from −19°C at night to 2°C at day. It started to snow on the third day of tracking. In 2006, the lake was completely ice covered from the beginning of January. Submerged macrophytes began to disappear from the water column and became procumbent on the lake sediment in mid-October 2005.

Movement rates

Pike exhibited significantly reduced MDPH in winter compared to summer (Table 2, mean of individual means MDPH ± SE (range), $N = 11$: winter 12.0 ± 2.8 m h^{-1} (2.7–24.5 m h^{-1}); summer 20.4 ± 4.4 m h^{-1} (3.2–46.9 m h^{-1})). MDPH was significantly related to the size of pike with larger pike moving significantly more (Table 2, estimate of fixed effect ± SE = 0.031 ± 0.005). Daytime had no significant influence on pike movement rates in both summer and winter as indicated by the lack of a significant daytime × season interaction (Table 2). However, during summer pronounced activity peaks occurred at twilight during dawn and dusk (Fig. 1). Movement rates in the different daytimes were more homogenous in winter (Fig. 1).

Distance to shore

Mean DTS was significantly higher in summer than in winter (Table 3, mean of individual means MDPH ± SE (range), $N = 11$: summer 51.4 ± 8.3 m (0.0–82.6 m); winter 43.8 ± 16.1 m (0.0–156.2 m)) (Table 3). Larger pike choose a significantly greater distance to the shoreline than smaller fish (Table 3, estimate of fixed effect ±SE = 0.025 ± 0.011). The DTS varied significantly between times of the day in a similar manner in summer and winter as indicated by a significant effect of daytime and a lack of a significant daytime × season interaction (Table 3).

Table 2 Results of a mixed model analysis of variance on logarithmic values of minimum displacement per hour (m h^{-1}) of pike in Lake Kleiner Döllnsee

Source	df nominator	df denominator	F	*P*
Intercept	1	269.096	2.411	0.122
Daytime	3	155.922	1.337	0.264
Season	1	268.727	28.195	0.000
Daytime × Season	3	155.912	1.596	0.193
Length	1	264.913	33.956	0.000

Daytime encompasses four diel periods, whereas season encompasses summer and winter

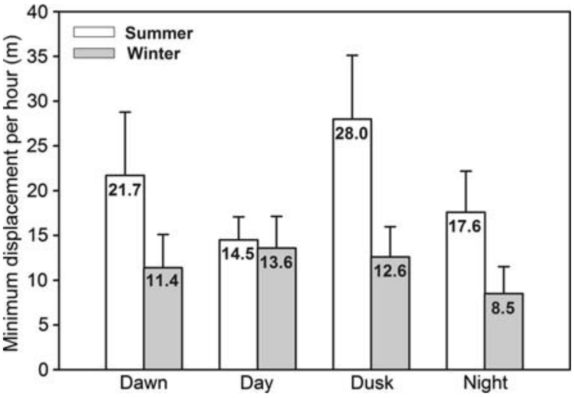

Fig. 1 Minimum displacement per hour (mean of individual means ±SE) of pike ($N = 11$) at different times of the day compared between summer and winter in Lake Kleiner Döllnsee

Table 3 Results of a mixed model analysis of variance on logarithmic values of distance to shore (m) of pike in Lake Kleiner Döllnsee

Source	df nominator	df denominator	*F*	*P*
Intercept	1	284.806	4.328	0.038
Daytime	3	129.892	2.959	0.035
Season	1	250.492	14.823	0.000
Daytime × Season	3	129.906	0.353	0.787
Length	1	282.682	4.807	0.029

Daytime encompasses four diel periods, whereas season encompasses summer and winter

Differences were significant between DTS at day compared to night, with DTS being significantly higher at night (Fig. 2). There was a trend for increasing DTS from day, through dawn until night, after which DTS decreased to reach minimum values during the day.

Habitat choice

Habitat choice by pike was not random in summer ($X^2_{likelihood} = 769.98$, df = 65, $P < 0.0001$) and winter ($X^2_{likelihood} = 627.78$, df = 55, $P < 0.0001$). Individual variability in habitat choice was high as indicated by wide 95% confidence intervals for several of the calculated selection ratios (Fig. 3). During summer, pike significantly preferred habitats in or near submerged macrophytes and negatively

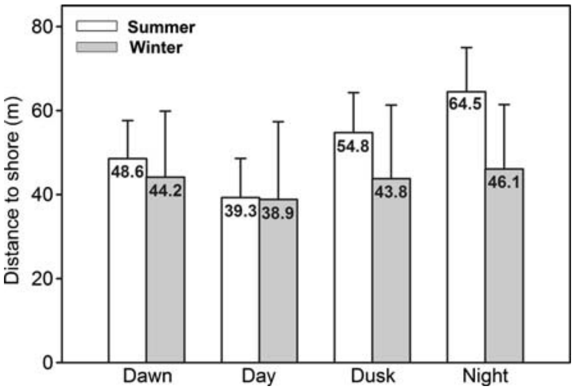

Fig. 2 Distance to shore (mean of individual means ±SE) of pike ($N = 11$) at different times of the day compared between summer and winter in Lake Kleiner Döllnsee

selected pelagic areas (Fig. 3). In winter, there was no significant selection for those habitats in which submerged macrophytes occurred during summer, and the negative selection for the pelagic was less pronounced (Fig. 3). There was a significantly negative selection for shallow open water habitats in winter. Selection for emergent macrophytes was positive, albeit not significant in both summer and winter.

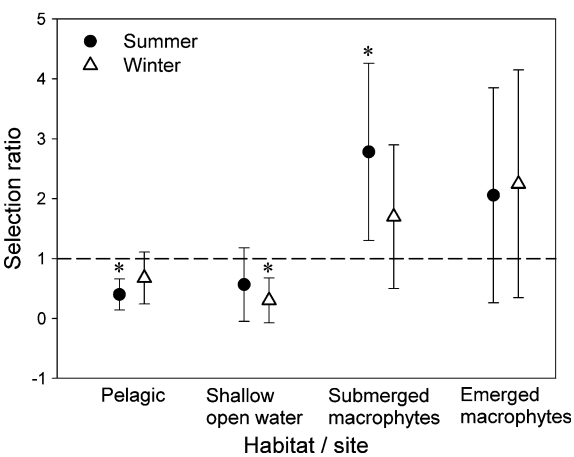

Fig. 3 Selection ratios and their associated Bonferroni adjusted 95% confidence intervals to show selection for (interval greater than one) or against (interval less than one) a given habitat type on an individual level approach for pike during summer and winter. * indicates significant selection. Note that the "submerged macrophyte" category in winter encompassed those locations (sites) where during summer submerged macrophytes were present providing structure >30 cm in the water column; during winter these submerged macrophytes were procumbent, i.e., still present but with less coverage in the water column

As mentioned before, there was a high degree of individual variation in habitat choice, which is shown descriptively for selected individuals in Fig. 4. One pike (fish ID 150.391) was almost completely sedentary and stayed in the reeds during both the summer and winter period, even when clearance between ice and lake bottom was less than 1 m. This fish only moved parallel with the shore inside the reeds. Another pike (fish ID 150.238) stayed in the reed belt during the day, moved out at dusk, swam through the pelagic area and returned back to the same reed area where the journey started at dawn. This fish repeated its behaviour every tracking day in both summer and winter. Other individuals such as pike 150.023 shifted between reed, submerged macrophytes and the pelagic area in summer and

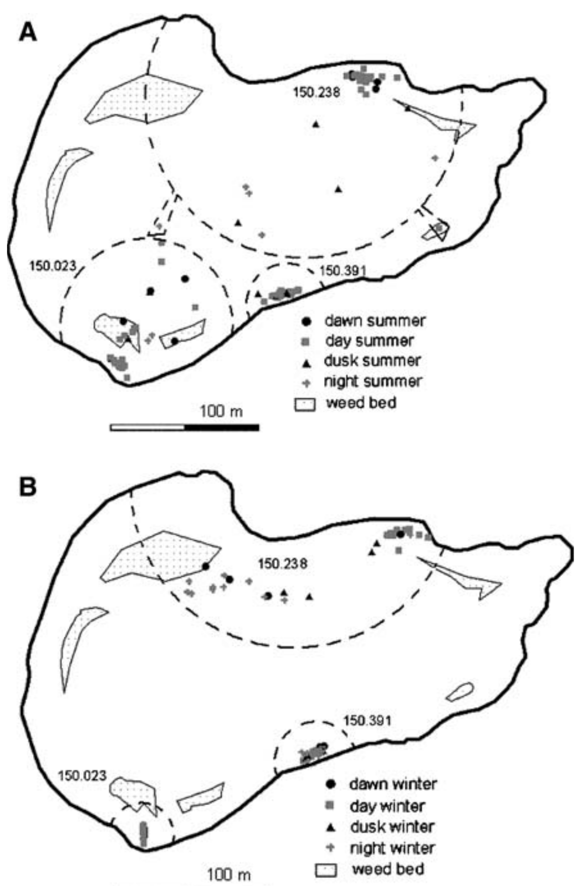

Fig. 4 Individual locations in Lake Kleiner Döllnsee shown for three pike (fish ID 150.023; 150.238; and 150.391 MHz) during summer (**A**) and winter (**B**). Circles show the approximate area that the individual used

exclusively stayed in dense reed or close to shore in winter.

Discussion

The movement rates of pike observed in the present study were significantly smaller in winter than in summer. These findings corresponded with earlier field reports by Cook & Bergersen (1988) and Rogers (1998). One obvious variable explaining reduced activity in winter is temperature as it affects all biological rates and metabolic processes, especially individual growth (Casselman, 1978), and many metabolic and physiological rates are inversely related to temperature (Charnov & Gillooly, 2004). Our study was conducted at temperature ranges that corresponded well with Casselman's (1978) laboratory studies on the temperature-dependency of swimming activity in pike. Consistent with our data, lowest swimming activity in pike can be expected at water temperatures <6°C, while activity is highest at 19–20°C (Casselman, 1978).

In contrast, Diana et al. (1977) did not find differences in movement rates in pike between summer and winter in a large lake, which might be explained by the different tracking method used (Jepsen et al., 2001) and/or the triangulation technique to locate the pikes (Rogers, 1998). Contrasting results on pike movement in lakes in winter have also been reported by Jepsen et al. (2001). These authors observed increased movement in winter and highest activity of pike due to a temperature increase from 2 to 5°C in a turbid reservoir in February. In the present study water temperatures were stable during the four day tracking period due to the ice cover, which might have prevented a possible activity peak in winter.

Movement rates were not only influenced by season, but were also related to the size of pike. Size-dependent movement rates in pike were previously reported by Jepsen et al. (2001), Masters et al. (2005) and Vehanen et al. (2006). Larger movement rates of larger individuals might be explained by reduced risk of cannibalism faced by larger fish compared to smaller individuals (Grimm & Klinge, 1996). Reduced predation risk as well as absolutely increasing food demand might be an incentive for larger fish to increase forageing activity reflected in increased movement rates.

Diel movement rates substantially varied between daytimes. In summer, highest activities were observed at dawn and dusk, however, these activity peaks were not statistically significant presumably owing to low sample size and the associated low statistical power. Previous research has reported significantly increased activity of pike at twilight (Cook & Bergersen, 1988; Rogers, 1998; Beaumont et al., 2005), consistent with laboratory studies reporting lowest activities at high light intensities (Casselman, 1978). Forageing probably explains the increasing movement at dusk and dawn. Many predatory fishes exploit the transitional nature of the twilight periods and are most active and successful during this time (Helfman, 1993). For example, Pitcher and Turner (1986) found that pike could approach their prey three times nearer in twilight than under day light. Hence, increased movement rates at twilight might be a short term behavioural response of pike to maximise food intake during a period where the probability of prey capture success is greatest.

In the present study, the activity peaks of pike at dusk during summer corresponded with an increasing DTS at dusk and night compared with daytime. These data indicated horizontal migrations of pike, preferring habitats close to shore during the day and a habitat shift from the shoreline to the open littoral and sometimes to the pelagic area at night. This finding agrees with the study by Cook & Bergersen (1988) who also observed highest distance to shore of pike at night and lowest at daytime during summer in a large reservoir. This pattern might be explained by the predator following their prey when the prey fish move out of their refuges in the vegetated littoral at night. The literature is relatively consistent concerning diurnal horizontal migrations of cyprinid species (Bohl, 1980) that are often prey for pike (e.g. Skov et al., 2003; Adamek & Opacak, 2005). For example, Jacobsen et al. (2004) showed in a clear standing water body that during summer roach (*Rutilus rutilus* Linnaeus) stayed significantly closer to the shore at day than at night. They also noticed a behavioural shift from the shoreline during dusk into the open water during night and a return to the shoreline area at dawn. Hence, during summer pike in Lake Döllnsee might match the diurnal pattern of their prey following them into the open littoral or the pelagic area at night where they presumably forage on their prey (Jepsen et al., 2001). These diurnal patterns were only pronounced in summer. In winter, prey fish should be less active, exhibit less diurnal habitat shifts and a general tendency to stay closer to the shoreline or in winter refuges (Jacobsen et al., 2004). In that case, both MDPH and DTS for pike should be less variable across the day in winter than in summer, a pattern that was found in the present study on Lake Döllnsee. An alternative explanation for the more homogenous movement rates of pike from dusk until dawn in winter might be related to lower light intensities during the day under ice. It is known that the activity of pike is lowest at high light intensities characteristic for the midday period in summer (Casselman, 1978), but during winter when light intensities are generally lower during the day, activity of pike might be less reduced (Casselman, 1978). This in turn could lead to reduced variation in MDPH from dusk until dawn during winter under ice as found in our study.

In Lake Döllnsee, pike moved significantly closer to the shoreline during winter compared to summer. This observation conflicted with findings by Diana et al. (1977), Cook & Bergersen (1988), Rogers (1998), and Jepsen et al. (2001) who reported pike to move farther from shore in winter. Rogers (1998) found pike to concentrate in the centre of the lakes and Jepsen et al. (2001) reported pike to abandon the littoral zone during winter. Distance to the shoreline might be expected to depend on lake-size. However, an evaluation of the four studies cited revealed no relation between lake size and distance to shoreline observed. Diana et al. (1977) and Cook & Bergersen (1988) examined large lakes (5700 and 1362 ha), whilst Rogers (1988) (26.7 and 29.1 ha) and Jepsen et al. (2001) investigated pike behaviour in a relatively small lake and a reservoir (58 ha and 22 ha) comparable in size to Lake Kleiner Döllnsee (25 ha). Therefore, the contrasting observations might result from differences in prey availability and shoreline structure as well as from varying availability of preferred habitats under ice. Increasing distance to shore has to be expected if ice cover prevents pike from maintaining shallow vegetated littoral areas typical for most lake shorelines. In Lake Kleiner Döllnsee, the reed belt was not avoided in winter, presumably because of the rooting depth of the reed. In this lake, the emerged vegetation covers the littoral up to a depth of 200 cm, and is therefore available as shelter habitat even under an ice layer of 40 cm.

Larger pike have been previously reported to choose the deeper littoral or the pelagic areas more often than smaller fish (Chapman & Mackay, 1984a, b; Rosell & MacOscar, 2002), and to shift more frequently between macrophyte stands and the pelagic (Chapman & Mackay, 1984a). In contrast, smaller pike (<54 cm) strictly depend on vegetation and typically avoid vegetation-free pelagic areas (Grimm & Klinge, 1996). If this size-dependent habitat choice is a general behavioural feature of pike, a positive relation between size of pike and distance to shore has to be expected. Results of our study are in agreement with this expectation as indicated by the positive relation between DTS and size of pike. However, it is well known that all size classes of pike depend on vegetated habitats for shelter and spawning (Casselmann & Lewis, 1996; Grimm & Klinge, 1996). Not surprisingly, in the present study pelagic areas were significantly avoided by pike in summer and, less pronounced, also in winter.

In Lake Kleiner Döllnsee, there were six different dense weed beds during summer that were located relatively far distance to the shoreline (Fig. 4) in water depths of 3–4 m that mainly comprised the submerged macrophyte habitat category during summer (Fig. 3). These habitats were highly attractive to pike, as indicated by a positive selection ratio for submerged macrophytes during summer time. In winter, these locations lost their attractiveness due to the disappearance of the submerged macrophytes that become procumbent on the lake sediment. The corresponding loss of significant selection ratios for this former submerged macrophyte habitat indicates active habitat choice of pike, behavioural flexibility in response to changing ecological conditions and a limited site fidelity. However, decaying or procumbent plant material was still more attractive to pike than shallow open water in the littoral during winter time, which was significantly avoided. It is also important to note that in winter the selection ratio was negative for the pelagic and positive for reed, albeit not statistically significant. This suggested that pike in both summer and winter favoured habitats that provided some degree of plant cover. During winter time, such habitats mainly comprised the emergent macrophytes in the littoral of Lake Kleiner Döllnsee. Correspondingly, Headrick & Carline (1993) observed pike moving back to shallow areas with vegetation when temperature decreased in autumn, and Grimm & Klinge (1996) observed inundated and emergent vegetation as the overwintering locations for pike, as long as oxygen concentrations are acceptable (Casselmann & Lewis, 1996).

This study provided information on the seasonal dynamics of pike behaviour in small mesotrophic lakes. Its validity is based on the assumption that the surgery did not bias the behaviour of pike or affected their condition. Previous research on pike showed only limited impacts of similar surgery procedures and transmitter implantation on pike (Jepsen & Aarestrup, 1999; Koed et al., 2006). Hence, we feel confident that there was no bias induced by surgery and transmitter implantation on the behaviour and habitat choice of pike in the present study.

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References

Adamek, Z. & A. Opacak, 2005. Prey selectivity in pike (*Esox lucius*), zander (*Sander lucioperca*) and perch (*Perca fluviatilis*) under experimental conditions. Biologia 60: 567–570.

Arlinghaus, R. & T. Mehner, 2004. A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). Environmental Management 33: 331–344.

Beaumont, W. R. C., K. H. Hodder, J. E. G. Masters, L. J. Scott & J. S. Welton, 2005. Activity patterns in pike (*Esox lucius*), as determined by motionsensing telemetry. In Spedicato, M. T., G. Lembo & G. Marmulla (eds), Aquatic telemetry: Advances and Applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9–13 June 2003. FAO/COISPA, Rome, 231–243.

Berg, S., E. Jeppesen & M. Sondergaard, 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in Lake Lyng (Denmark). Hydrobiologia 342/343: 311–318.

Bohl, E., 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44: 368–375.

Casselman, J. M., 1974. External sex determination of northern pike, *Esox lucius* Linnaeus. Transactions of the American Fisheries Society 103: 343–347.

Casselman, J. M., 1978. Effects of environmental factors on growth, survival, activity, and exploitation of northern pike. American Fisheries Society Special Publication 11: 114–128.

Casselman, J. M. & C. A. Lewis, 1996. Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53 (Suppl. 1), 161–174.

Chapman, C. A. & W. C. Mackay, 1984a. Direct observation of habitat utilization by northern pike. Copeia 1: 255–258.

Chapman, C. A. & W. C. Mackay, 1984b. Versatility in habitat use by a top aquatic predator, *Esox lucius* L. Journal of Fish Biology 25: 109–115.

Charnov, E. L. & J. F. Gillooly, 2004. Size and temperature in the evolution of fish life histories. Integrative & Comparative Biology 44: 494–497.

Cook, M. F. & E. P. Bergersen, 1988. Movements, habitat selection and activity periods of northern pike in eleven mile reservoir, Colorado. Transactions of the American Fisheries Society 117, 495–502.

Craig, J. F. (ed.), 1996. Pike: Biology and Exploitation. Chapman & Hall, London.

Diana, J. S., W. C. Mackay & M. Ehrman, 1977. Movements and habitat preference of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. Transactions of the American Fisheries Society 106: 561–565.

Fredrich, F., S. Ohmann, B. Curio & F. Kirschbaum, 2003. Spawning migrations of the chub in the River Spree, Germany. Journal of Fish Biology 63: 710–723.

Grimm, M. P. & M. Klinge, 1996. Pike and some aspects of its dependence on vegetation. In Craig, J. F. (ed.), Pike: Biology and Exploitation. Chapman & Hall, London: 125–156.

Headrick, M. R. & R. F. Carline, 1993. Restricted summer habitat and growth of northern pike in two Southern Ohio Impoundments. Transactions of the American Fisheries Society 122: 228–236.

Helfman, G. S., 1993. Fish behaviour by day, night and twilight. In Pitcher, T. J. (ed.), Behaviour of Teleost Fishes. Chapman & Hall, London, 479–512.

Jacobsen, L., S. Berg, N. Jepsen & C. Skov, 2004. Does roach behaviour differ between shallow lakes of different environmental state? Journal of Fish Biology 65: 135–147.

Jepsen, N. & K. Aarestrup, 1999. A comparison of the growth of radio-tagged and dye-marked pike. Journal of Fish Biology 55: 880–883.

Jepsen, N., S. Beck, C. Skov & A. Koed, 2001. Behavior of pike (*Esox lucius* L.) <50 cm in a turbid reservoir and in a clearwater lake. Ecology of Freshwater Fish 10: 26–34.

Koed, A., K. Balleby, P. Mejhelde & K. Aarestrup, 2006. Annual movement of adult pike (*Esox lucius* L.) in a lowland river. Ecology of Freshwater Fish 15: 191–199.

Lucas, M. C. & E. Baras, 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish and Fisheries 1: 283–316.

Masters, J. E. G., K. H. Hodder, W. R. C. Beaumont, R. E. Gozlan, A. C. Pinder, R. E. Kenward & J.S. Welton, 2005.

Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. In Spedicato, M. T., G. Lembo, G. Marmulla (eds), Aquatic Telemetry: Advances and Applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9–13 June 2003. FAO/ COISPA, Rome, 179–190.

Pitcher, T. J. & R. Turner, 1986. Danger at dawn: experimental support for the twilight hypothesis in shoaling minnows. Journal of Fish Biology 29: 59–70.

Prejs, A., A. Martyniak, S. Boron, P. Hliwa & P. Koperski, 1994. Food web manipulation in a small, eutrophic Lake Wirbel, Poland: effects on stocking with juvenile pike on planktivorous fish. Hydrobiologia 275/276: 65–70.

Raat, A. J. P., 1988. Synopsis of Biological Data on the Northern Pike *Esox lucius* Linneaus 1758. FAO Fisheries Synopsis 30 Rev 2: 178 pp.

Rogers, K. B., 1998. Habitat Use by Largemouth Bass and Northern Pike on the Rocky Mountain Arsenal, Colorado. Colorado State University Fort Collins, Colorado (PhD Thesis).

Rogers, K. B. & E. P. Bergersen, 1996. Application of geographic information systems in fisheries: Habitat use by northern pike and largemouth bass. American Fisheries Society Symposium 16: 315–323.

Rogers, K. B. & G. C. White, 2007. Analysis of movement and habitat use from telemetry data. In Brown, M. & C. Guy (eds), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland Chapter 14, 625–676.

Rosell, R. S. & K. C. MacOscar, 2002. Movements of pike, *Esox lucius*, in Lower Lough Erne, determined by mark-recapture between 1994 and 2000. Fisheries Management and Ecology 9: 189–196.

Skov, C., O. Lousdal, P. H. Johansen & S. Berg, 2003. Piscivory of 0+pike (*Esox lucius* L.) in a small eutrophic lake and its implication for biomanipulation. Hydrobiologia 506: 481–487.

Vehanen, T., P. Hyvärinen, K. Johansson & T. Laaksonen, 2006. Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river. Ecology of Freshwater Fish 15: 154–160.