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Site fidelity and seasonal changes in activity centre size of female pike *Esox lucius* in a small lake

A. Kobler*†, T. Klefoth* and R. Arlinghaus*‡

**Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, 12587 Berlin, Germany and ‡Humboldt-University of Berlin, Faculty of Agriculture and Horticulture, Institute of Animal Sciences, Philippstrasse 13, Haus 7, 10115 Berlin, Germany*

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The object of this study was to test site fidelity of female pike *Esox lucius* and to contrast the activity centre size in summer and winter in a 25 ha lake in north-eastern Germany using radio telemetry. Weekly 24 h tracking and two 96 h tracking exercises were conducted by boat from June to December 2005 and by walking on surface ice from January to February 2006. Positions of 12 *E. lucius* [total length (L_T) = 450–733 mm] were recorded every 3 h within a 24 h tracking cycle. Site fidelity to individual summer activity centres was tested by translocating eight *E. lucius* away from their activity centre. All translocated *E. lucius* returned to their summer activity centre within 6 days, which provided evidence of site fidelity of *E. lucius*. There was no relation between *E. lucius* L_T or the translocation distance and return time to the activity centre after translocation. In winter, the activity centre size of *E. lucius* was significantly larger than in summer, but there was considerable overlap between the sites chosen in winter and those in summer. The seasonal variation in activity centre size possibly reflected changes in habitat structure (*e.g.* collapse of structured vegetated habitats in winter) or prey fish distribution.

Key words: home range; interindividual variation; kernel density estimation; radio telemetry; translocation; winter.

INTRODUCTION

Pike *Esox lucius* L. is a sporadically active (Diana *et al.*, 1977), ambush, sit-and-wait predator (Raat, 1988) that is common in lakes and slow flowing rivers in the northern hemisphere (Craig, 1996). It is a cannibalistic species preferring structured vegetated habitats that are used for shelter and foraging (Grimm & Klinge, 1996). Due to the low activity level of *E. lucius*, their morphological adaptation allowing rapid attacks on prey fishes (Webb & Skadsen, 1980), their dependence on structured habitats and the formation of spatially segregated, size-structured populations (Nilsson, 2006), it can be expected that *E. lucius* establish well-defined, restricted activity centres along shorelines of lakes and

†Author to whom correspondence should be addressed at present address: University of Antwerp, Department of Biology–Ethology, CDE, Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium. Tel.: +32 38202286; fax: +32 38202271; email: alexander.kobler@ua.ac.be

rivers to minimize intraspecific competition, risk of cannibalism and maximize hunting success (Grimm & Klinge, 1996).

In the fish biology literature, the term activity centre is less common than the term home range when describing an area or territory used by an individual. The home range concept was originally developed for mammals defined as the area traversed by the animal during its normal activities of food gathering, mating and caring for young (Burt, 1943). Rogers & White (2007) stated that the home-range concept is not well fitted for fish and fishery research because fishes, in contrast to mammals, seem to display more transitory ranges. Indeed, *E. lucius* has been reported to switch selected habitats repeatedly on a yearly basis (*e.g.* during the spawning period; Karas & Lehtonen, 1993; Miller *et al.*, 2001; Rosell & MacOscar, 2002), or even on daily time scales (Diana *et al.*, 1977; Cook & Bergersen, 1988). Therefore, in the present study the term home range was replaced by the term activity centre.

Various field studies conducted in static water bodies using telemetry techniques have reported that *E. lucius* populations exhibit an unrestricted spatial distribution pattern. In fact individual fish have been found to switch routinely between several core activity centres or use almost the entire system throughout the year (Diana *et al.*, 1977; Cook & Bergersen, 1988; Jepsen *et al.*, 2001). Comparable results were found using mark–recapture methods (Moen & Henegar, 1971; Kipling & Le Cren, 1984; Miller *et al.*, 2001; Rosell & MacOscar, 2002). In contrast, lentic *E. lucius* were observed to exhibit a narrow activity centre by Grimm & Klinge (1996) in a small lake (4·5 ha) and by Vostradovsky (1975) in a large reservoir (4650 ha). It is therefore a matter of debate if *E. lucius* develop well-defined, restricted activity centres as would be expected based on their morphology and foraging behaviour.

A goal of this study was to test if the activity centre of *E. lucius* exists due to a preference for a specific site or if it is only the result of random or restricted dispersal (Rogers & White, 2007). Most studies which tested for fish site fidelity have the shortcoming that the individual was translocated away from the point of capture which was assumed to lie within the activity centre of that individual. A preferred approach is to observe the fish before the translocation experiment is conducted and then translocate the individual out of this area (Hert, 1992; Ridgway & Shuter, 1996). With the collection of sufficient data on the spatial distribution of the individual before translocation, the positions of the individual after translocation can then be objectively judged to lie within or outside the quantitatively estimated activity centre established prior to translocation. Therefore, in the present study, the individuals were observed over a prolonged time period before and after translocation to determine site fidelity and quantify changes in spatial behaviour after a translocation event.

Little is known about the changes in *E. lucius* activity centre location and extent during the course of the season. Masters *et al.* (2005) observed seasonal changes in the spatial behaviour of lotic *E. lucius* that were not necessarily related to spawning activity. Individual *E. lucius* had two activity centres, which changed twice a year in May and January. Seasonal variation in activity centres of other aquatic top predators has also been observed. For example, Savitz *et al.* (1993) observed that smallmouth bass *Micropterus dolomieui* Lacepède had several activity centre locations (partly differing diurnally) during the summer. In winter as macrophytes died-off, *M. dolomieu* established new activity centre locations and abandoned the sites from summer. These seasonal differences, which were possibly connected with the seasonal occurrence and collapse of submerged macrophytes, could also exist for *E. lucius*.

The objectives of the present study were : (1) to investigate site fidelity of *E. lucius* based on a translocation experiment and (2) to quantify summer and winter activity centre size in a lentic *E. lucius* population using radio-telemetry.

MATERIAL AND METHODS

STUDY AREA

The study was conducted at Lake Kleiner Döllnsee, a 25 ha dimictic, shallow (mean depth 4·1 m, maximum depth 7·8 m) and mesotrophic to slightly eutrophic natural lake (P concentration at spring turnover of 28 μg l^{-1}) with mean ± S.D. Secchi depth of 3·4 ± 0·7 m (in 2005). The lake is located 80 km north-east of Berlin in the north-eastern lowlands of Germany (52°59′ N; 13°34′ E). In 2005, the entire lake shoreline was covered by dense, 2–55 m wide reed belts (*Phragmites australis, Typha latifolia* and *Typha angustifolia*). In July 2005, emergent macrophytes covered 14% of the lake surface, and further 27% of the lake bottom was covered by submerged macrophytes (maximum depth: 4·5 m; mainly *Ceratophyllum demersum*, *Najas minor*, *Potamogeton crispus* and *Myriophyllum alterniflorum*). No commercial or recreational fishing was allowed on the lake. The lake had a natural, self-reproducing *E. lucius* population slightly exploited by experimental fishing. In spring 2005, abundance of age 1 year and older *E. lucius* was estimated to be 544 individuals (95% CI: 194–1088), based on Petersen single-census method (Chapman modified; Ricker, 1975) using capture–mark–recapture data from two electrofishing events. The fish community consisted of 12 fish species according to recent surveys (Klefoth *et al*., 2008; Kobler *et al*., 2008). The top predators in the system were *E. lucius* and perch *Perca fluviatilis* L. European eel *Anguilla anguilla* (L.) and European catfish *Silurus glanis* L., which were stocked into the lake, were also present, albeit at lower abundances.

CAPTURE AND TAGGING

Twenty adult *E. lucius* were caught using a battery-powered DC electrofishing unit (Type EFGI 4000, 4 kW; Brettschneider Spezialelektronik, Chemnitz, Germany) with a 400 mm diameter ring anode, between 21 April and 28 April 2005. Fish were tagged on the day of capture with radio transmitters (SB-2; Holohil Systems Ltd, Carp, Ontario, Canada) that had a length of 20 mm, a diameter of 9 mm, a mass of 5·2 g in air and a battery life of 10 months. Relative transmitter mass was ≤0·8% of *E. lucius* body mass (Table I), which is in the acceptable range in terms of having negligible influence on the fish's behaviour post tagging (Jepsen *et al*., 2002). Pike were anaesthetized using a 100 mg l^{-1} solution of MS 222. The transmitters were implanted into the body cavity through a 20–30 mm incision 30 mm behind the base of the left pectoral fin, the antenna was directed outwards between the ventral and anal fin (Fredrich *et al*., 2003). The incision was closed with two stitches 10 mm apart using sutures of 3/0 non-absorbable braided silk (Ethicon Inc., Somerville, NJ, U.S.A.) and then secured with Vetbond (3M Inc., St Paul, MN, U.S.A.). The operation took 2–3 min and the recovery time ranged between 3 and 5 min. After tagging, the fish were measured to the nearest mm [total length, L_T] and weighed to the nearest g (Table I). An external sex determination was conducted following Casselman (1974). All of the *E. lucius* used in the present study were females. This was because the largest 20 individuals caught by electrofishing, which were selected for the experiment all turned out to be female and was not the result of artificial selection based on sex. After tagging, the recovered fish were released close to their individual capture point.

TABLE I. Individual data from radio-tagged *Esox lucius* in Lake Kleiner Döllnsee. Summer activity centre: 20 June to 31 August 2005 winter activity centre: 23 November 2005 to 3 February 2006. Only eight out of 12 monitored *E. lucius* were translocated. The activity centre size with 95 and 50% kernel density probability (Kernel prob.; summer and winter), distance of translocation and the minimum time required for *E. lucius* to return to its previously established activity centre after translocation are also shown. All *E. lucius* were females

Esox lucius identity number	L_T (mm)	Mass (g)	Summer 95%; 50% kernel prob. (m^2)	Winter 95%, 50% kernel prob. (m^2)	Translocation (m)	Time to return (h:min)
1	560	1104	3370; 570	90;10	—	—
2	522	845	510; 50	8910; 1390	—	—
3	511	912	830; 60	200; 30	542	42:05
5	493	768	1660; 260	5770; 610	541	143:00
8	630	1555	2630; 190	4980; 800	500	68:04
10	688	2170	290; 60	6900; 1290	510	4:47
11	733	2287	650; 250	6360; 480	550	109:30
16	543	1064	190; 30	1490; 280	326	94:07
17	515	976	80; 20	200; 50	392	74:25
18	488	816	70; 10	400; 80	377	123:50
19	462	640	3360; 540	2380; 310	—	—
20	450	580	3070; 250	5670; 620	—	—

L_T, total length.

TRACKING

Radio tracking was performed manually using an electro-powered boat from June to December 2005 and by walking on ice from January to February 2006 using a hand-held receiver (SRX 400, Lotek, Newmarket, Ontario, Canada) and a three element Yagi antenna. Visual observations revealed that, in shallow water, *E. lucius* could be approached by the boat to within *c.* 2 m before eliciting a flee response (Klefoth *et al.*, 2008; Kobler *et al.*, 2008). In deeper water, the boat could be positioned directly above a *E. lucius* without eliciting a flee reaction. The transmitter signal was still detectable in the deepest water layers (7·8 m) when approached by boat within a radius of *c.* 7 m. Once a fish was located, the position was recorded using a GPS unit (Etrex summit, Garmin, Olathe, KS, U.S.A.) referenced to a base station (PFCBS Version 2.12; Trimble Navigation, Sunnyvale, CA, U.S.A.) installed at the research station on the lake shore (up to 1 m precision). A tracking precision of ±6 m was determined by tracking the locations of two dead fish accidentally tracked for a period of 2 weeks (Klefoth *et al.*, 2008; Kobler *et al.*, 2008). An attempt was made to locate each individual *E. lucius* once in a 3 h tracking interval in 24 h tracking sessions, which were conducted every week. In addition to the weekly 24 h sessions, a 96 h tracking session was conducted in both summer and winter. The result of 24 h tracking was up to eight positions per fish. If less than six positions of an individual fish were obtained per 24 h tracking, the sampling day of the individual was excluded from analysis. Due to early transmitter failure of *E. lucius* ID 4, 6 and 14 (signal changed tone pitch, became weak and irregular and finally stopped), mortality shortly after tagging of *E. lucius* ID 7 and 13 (verified by scuba diving after lack of movement for several consecutive trackings), and angling mortality of ID 9, 12 and 15 (death shortly after capture verified by scuba diving) resulting from a parallel recreational fishing study (Klefoth, 2007; Klefoth *et al.*, 2008) only 12 out of 20 *E. lucius* were used for the activity centre analysis.

TRANSLOCATION

The goal of the translocation experiment was to determine the site fidelity of *E. lucius* to their summer activity centre. Attempts were made to recapture radio-tagged *E. lucius* at the end of the summer observation period by rod and reel using artificial and natural baits. Individual *E. lucius* were tracked and approached by boat to within a few metres and the bait was then presented as close as possible to the target fish. With this method, eight of the 12 *E. lucius* were recaptured (Table I). After capture (28 August to 20 September 2005), *E. lucius* ($n = 8$) were placed in a live well and transported to the opposite side of the lake where they were released (mean $\pm$ S.E. distance from capture point 467·0 $\pm$ 31·2 m; Table I). Based on the positions observed prior to the translocation event, it was feasible to quantitatively evaluate if an individual *E. lucius* returned to its summer activity centre after translocation. *Esox lucius* were tracked several times in the first 24 h after release and at a minimum once a day in the days that followed until they returned. After the *E. lucius* returned to their previously established summer activity centre (to 95% or 50% kernel density probability), they were again routinely tracked on a weekly basis.

TIME-FRAME DEFINITIONS AND ABIOTIC CONDITIONS

The summer time was defined as the period with mean daily water temperatures >19° C and full development of submerged macrophytes (20 June to 31 August 2005). The winter time was defined as the period with mean daily water temperatures <6° C and when macrophytes had died off (23 November 2005 to 3 February 2006 including complete ice cover in January and February). Both time periods were of comparable duration (73 days). In summer, the mean $\pm$ S.D. water temperature was 21·1 $\pm$ 1·4° C (range 19·1–24·0° C) and the mean $\pm$ S.D. oxygen concentration was 9·1 $\pm$ 0·7 mg l^{-1} (range 7·4–10·5 mg l^{-1}), measured at the deepest point in the lake at 2 m water depth: multi parameter sensor YSI 6600 (YSI Corporation, Yellow Springs, OH, U.S.A.). In winter, the mean $\pm$ S.D. water temperature was 3·1 $\pm$ 1·1° C (range 2·0–5·9° C) and mean $\pm$ S.D. oxygen concentration was 12·3 $\pm$ 1·0 mg l^{-1} (range 10·5–13·8 mg l^{-1}). In 2006, *E. lucius* spawned in the middle of April.

ACTIVITY CENTRE ESTIMATIONS

For comparisons of activity centre sizes between summer and winter, it was necessary to base activity centre calculations on the same number of locations (Seaman & Powell, 1996). Due to a lack of tracking in the period between open water and ice formation from 15 December 2005 to 16 January 2006, the data density differed between summer and winter. To keep sample sizes comparable between summer and winter, nine (the same amount as in winter) out of twelve 24 h trackings from the summer period were randomly chosen.

The kernel density probability estimate of home range (activity centre) size is more suitable over other estimation procedures as it is efficient, robust and unbiased (Börger *et al.*, 2006). This estimate was used in the present study. Calculations of activity centre size using the kernel density estimation method with a sample size of <50 locations has lead to overestimation (Seaman & Powell, 1996). In this study, however, the summer sample size per individual varied between 67 and 72 tracking locations, and in winter it ranged between 57 and 72 locations, meeting the threshold sample size in every case (Table I). As recommended by Seaman & Powell (1996), the fixed kernel estimate procedure with least squares cross validation was used to calculate density probabilities of 95 and 50% for both summer and winter. Calculations were done with the same individuals in summer and winter ($n = 12$) using the home range extension module (Rodgers & Carr, 1998) in Arc View GIS 3.2 (ESRI, Redlands, CA, U.S.A.). An overlap of the calculated activity centre with the outer shape of the lake surface was eliminated by bounding the activity centre by the lake limits.

STATISTICS

The time *E. lucius* needed to return to the previously established summer activity centre after translocation was tested for correlations with the distance between capture and release points as well as with L_T of the *E. lucius* using Spearman rank correlation (r_s; non-normality of data according to Kolmogorov–Smirnov, $P < 0{\cdot}05$). The correlation between L_T of *E. lucius* and either summer or winter activity centre size (95 and 50% probability) was also tested by r_s.

The locations of four weekly 24 h trackings, after the translocation and successful return of *E. lucius* to their summer activity centre, were used to analyse if *E. lucius* use of the summer activity centre was the same prior to and post-translocation. This was done by determining the percentage of locations after return, which were found within the 95% kernel density probability obtained from locations prior to translocation. The same procedure was also used to quantitatively compare the overlap between the summer and winter activity centres.

Due to the sample dependency of individual activity centres in summer and winter, these centres were compared using a Wilcoxon signed rank test. Comparisons were conducted for the 95 and 50% kernel density probability for 12 *E. lucius*. Due to small sample size and the associated lack of statistical power, significance was assessed at $\alpha < 0{\cdot}1$. Statistical analyses were conducted with the software package SPSS version 14.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

TRANSLOCATION

All translocated *E. lucius* ($n = 8$) returned into their previously established summer activity centre (mean ± S.E. time to return 82·5 ± 15·9 h; range 4·8–143 h; Table I). There was neither a correlation between time of return and translocation distance (Spearman's rho, $n = 8$, $r_s = -0{\cdot}10$, $P > 0{\cdot}1\%$) nor between time of return and L_T of *E. lucius* (Spearman's rho, $n = 8$, $r_s = -0{\cdot}47$, $P > 0{\cdot}1$). Within the 4 weeks after *E. lucius* returned to their summer activity centre, seven out of eight *E. lucius* used the area of the summer activity centre, which they had established before translocation in a comparable way. A mean ± S.E., 82·1 ± 5·8% of tracking locations were recorded inside the summer activity centre [Table II; compare Fig. 1(a–h)]. The only exception was one individual (ID 5) which first returned to its summer activity centre but after a week established a new centre in the direct vicinity of the 95% kernel density probability of its previously established summer activity centre [Table II and Fig. 1(b)].

COMPARISON OF SUMMER AND WINTER ACTIVITY CENTRE EXTENSION

In summer, *E. lucius* exhibited a mean ± S.E. activity centre size at 95% kernel density probability of 1392·5 ± 389·0 m^2 and at 50% probability of 190·8 ± 56·4 m^2. In winter, the mean ± S.E. activity centre size at 95% probability was 3612·5 ± 909·6 m^2 and at 50% probability 495·8 ± 136·4 m^2. Overall, in winter, the mean activity centre was *c.* 2·6 times greater than in summer (Table I). This difference was significant for the 95% kernel density probability (Wilcoxon signed rank test, $Z = -1{\cdot}883$, $P < 0{\cdot}1$) as well as for the 50% kernel density probability (Wilcoxon signed rank test, $Z = -1{\cdot}884$, $P < 0{\cdot}1$) (Fig. 2). Interindividual differences in activity centre size in both summer and winter

TABLE II. Tracking locations of *Esox lucius* in Lake Kleiner Döllnsee during different observation periods. The number of points and the per cent that were located within the area of the summer activity centre (at 95% kernel density probability) are presented. *Esox lucius* that were translocated and not translocated are included

Esox lucius identification number	Summer locations and percentage within summer activity centre	Locations 4 weeks after translocation and return and percentage within summer activity centre	Winter locations and percentage within summer activity centre
1	70; 99%	—	69; 100%
2	67; 96%	—	71; 6%
3	72; 100%	32; 100%	72; 100%
5	68; 91%	31; 3%	57; 14%
8	72; 100%	32; 91%	69; 30%
10	72; 100%	32; 78%	66; 3%
11	71; 76%	32; 72%	68; 47%
16	72; 100%	32; 75%	70; 31%
17	72; 96%	32; 100%	71; 51%
18	72; 100%	32; 59%	71; 63%
19	70; 100%	—	64; 31%
20	68; 100%	—	69; 14%

were high (Table I and Fig. 2). In the majority of cases (75%), however, the activity centre size was greater in winter than in summer (Table I).

Although most *E. lucius* had greater activity centres in winter, generalizations about activity centre site changes from summer to winter were not possible. Five out of 12 *E. lucius* (*c.* 42%) established winter activity centres in the same area as in summer (ID 1, 3, 11, 17 and 18; Fig. 1(a), (e), (g), (h) and Table II). A greater fraction of the tagged *E. lucius* (ID 2, 5, 8, 10, 16, 19 and 20, 58·3% of total sample size) used small parts of the summer activity centre in the beginning of winter but dispersed to different sites towards the end of the winter tracking period [Fig. 1(b), (c), (d), (f) and Table II]. There was no relation between L_T of *E. lucius* and activity centre size for both summer kernel density probabilities (95%: Spearman's rho, $n = 12$, $r_s = -0{\cdot}18$, $P > 0{\cdot}1$; 50%: $n = 12$, $r_s = -0{\cdot}049$, $P > 0{\cdot}1$) and both winter density probabilities (95%: Spearman's rho, $n = 12$, $r_s = 0{\cdot}178$, $P > 0{\cdot}1$; 50%: $n = 12$, $r_s = 0{\cdot}12$, $P > 0{\cdot}1$).

DISCUSSION

In the present study, all *E. lucius* returned after translocation within a short time frame to their previously established summer activity centres. This indicates pronounced site fidelity and a non-random formation of the activity centre of individual *E. lucius*. The existence of site fidelity has already been shown for other fish species (Hert, 1992; Ridgway & Shuter, 1996) and translocation experiments from capture locations (without previous observation on spatial distribution) indicated that site fidelity probably also exists in the closely related species muskellunge *Esox masquinongy* Mitchill (Crossman, 1977; Margenau,

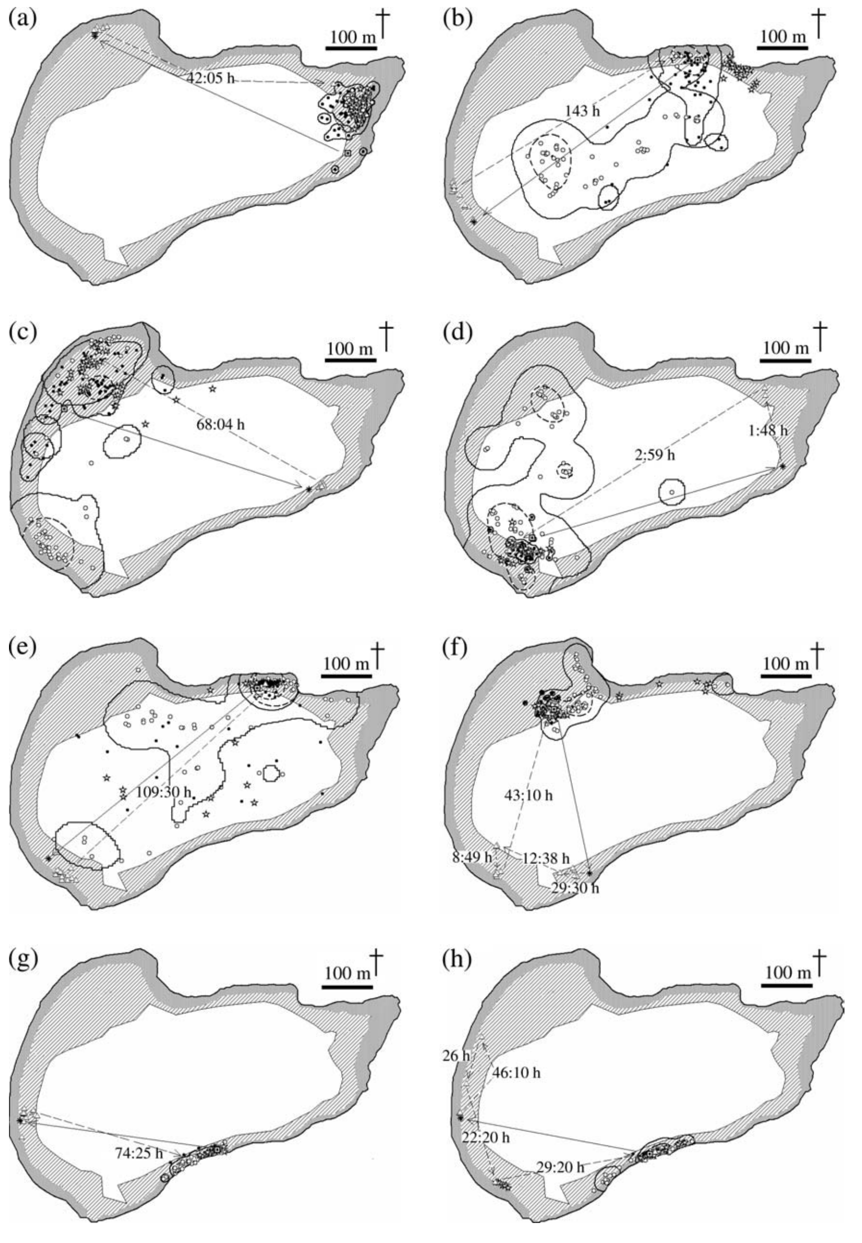

FIG. 1. Summer (●) and winter (○) tracking locations of translocated *Esox lucius* (every figure represents single *E. lucius*) ID: (a) 3, (b) 5, (c) 8, (d) 10, (e) 11, (f) 16, (g) 17, (h) 18 (for number of tracking locations see Table II). Shapes around points are activity centre estimates (around ● are summer and around ○ are winter activity centre estimates). Shapes are distinguished by line type to indicate the 95% kernel density probability (⬭) and 50% kernel density probability (⬭). Catch location of the fish (▣), the translocation (⊛), the locations from translocation to return to the activity centre (△) and the locations of four weekly 24 h trackings after the return (☆), including return time are also illustrated. ▒, emergent macrophytes; ▨, submerged macrophytes; □, pelagic.

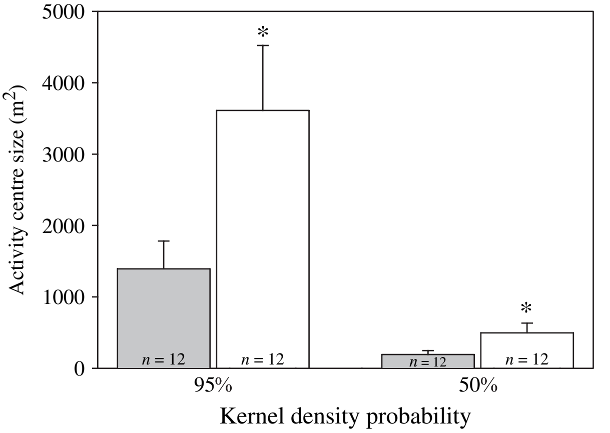

FIG. 2. Differences between mean + S.E. ▢, summer and ▢, winter activity centre size of *Esox lucius* ($n = 12$) for both 95 and 50% kernel density probability (fixed kernel estimate). *, significance was set at $P < 0{\cdot}1$.

1994). What are the ecological factors prompting *E. lucius* to return to their activity centre after translocation? In line with the hypotheses that an animal never acts implicitly and that every decision should provide the greatest possible benefit, an accepted assumption is that the benefit of returning after translocation to the former established activity centre must outweigh the risk involved in making the journey (Switzer, 1993; Marnane, 2000). Presumably, in the present study, the risk of making the journey was low as *E. lucius* was the dominant top predator in the system and these fish were probably too large to fear cannibalism as large *E. lucius* >800 mm L_T were rare in Lake Kleiner Döllnsee (Kobler, 2007). In addition, there might have been multiple benefits associated with returning to a previously established activity centre, including spatial segregation from conspecifics to avoid superior competition, predation and aggressive attacks (Nilsson, 2006). Thus, the net benefit of returning also depends upon the choices made by competing conspecifics (Kramer & Chapman, 1999). The agonistic behaviour of a conspecific at the translocation site could have forced the displaced *E. lucius* to leave that habitat and to return into their former activity centre.

In this study and in agreement with previous research from static water bodies (Jepsen *et al.*, 2001), there was no relation between activity centre size and *E. lucius* L_T. In contrast, Minns (1995) reported a positive relation between home range (in this study termed activity centre) size and L_T in a meta-analysis in fishes. Specific for *E. lucius*, Grimm & Klinge (1996) showed that *E. lucius* <540 mm L_T exhibited a more restricted home range (activity centre) than larger conspecifics. The low sample size and the overall limited size variation of *E. lucius* in the present study might have influenced the non-significant relationship between *E. lucius* L_T and activity centre size.

Quantitative calculations of activity centre size for lentic *E. lucius* populations are not available in the literature. There were estimates from Grimm & Klinge (1996) from a 4·5 ha lake, however, in which 80% of *E. lucius* recaptures were made within 100 m of the release site. These estimates are comparable to the present findings, where the average 95% probability activity centre size was only 1392·5 m^2 in summer and 3612·5 m^2 in winter, and suggest a very restricted activity centre. Diana *et al*. (1977) and Vostradovsky (1975) reported greater extents of the activity centre of lentic *E. lucius* with total displacements of 1–5 km (Diana *et al*., 1977) and up to 3 km (Vostradovsky, 1975) in radius. These studies, however, were also conducted in much larger standing water bodies compared to Lake Kleiner Döllnsee (5700 and 4650 ha compared to 25 ha). Based on the results presented above, there is therefore some indication that the extent of activity centres in lentic *E. lucius* populations might be related to the lake size. Interestingly, Vehanen *et al*. (2006) who used methods of activity centre estimation similar to those of the present study reported a mean activity centre size (with 95% probability) of only 157 m^2 in *E. lucius* in a regulated river stretch of 9 km. Hodder *et al*. (2007) reported similarly small activity centre extents in a different river system (median of 2580 m^2). The latter value was intermediate to the 95% summer and winter kernel probability estimate in the present study and was found in a small stream stretch of 2 km length. Therefore, the activity centre estimates of the present study are in agreement with previous studies from rivers, which used comparable estimation methods. The latter studies and the present study suggest that *E. lucius* indeed establish very restricted activity centres, but generalizations about the activity centre size across different ecosystems seem to be rather vague.

A finding of the present study was that the activity centre size in winter was greater than in summer. Moreover, it was found that in the winter *E. lucius* dispersed over a greater area and exploited sites, which were located outside their summer activity centre. The greater dispersion of *E. lucius* throughout the lake during winter could be indicative of a potential spawning migration towards natal sites (Karas & Lehtonen, 1993; Miller *et al*., 2001; Rosell & MacOscar, 2002). This explanation, however, is unlikely because the end of the winter observation period of the present study was in the beginning of February, but *E. lucius* spawned shortly after ice melt in April. One likely explanation for the greater dispersion of *E. lucius* across the lake in winter and the associated larger activity centres is the loss of structured vegetated habitats typically used by *E. lucius* for refuge and shelter (Grimm & Klinge, 1996). Submerged macrophytes collapsed at the end of October in 2005. As a result, some *E. lucius*, particularly those largely associated with submerged macrophytes during summer time dispersed throughout the lake in winter [Fig. 1(c), (d), (f)]. The distribution of prey fishes was also probably influenced by the collapse of submerged macrophytes and reduced temperature during the winter (Garcia-Berthou, 1999; Jepsen & Berg, 2002), which presumably influenced the spatial distribution of *E. lucius* as well. The redistribution and more clumped occurrence of prey fishes in winter (Garcia-Berthou, 1999; Jepsen & Berg, 2002) may have driven the *E. lucius* to exploit increasingly greater areas of the lake and consequently establish a greater activity centre in winter.

In conclusion, the present study provides evidence of *E. lucius* site fidelity after translocation. It was shown that *E. lucius* establish pronounced activity centres, which clearly differ in size between individuals. Furthermore, it was shown that *E. lucius* are flexible in their space use as indicated by the increasing activity centre size in winter compared to summer. It is hypothesized that seasonal difference in space arrangement was a response to the altered availability of structured habitats and prey fish distribution.

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