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Abstract: 17 individuals of ide Leuciscus idus were radio-tracked weekly from September 2003 to September 2004 in the Elbe River, Czech Republic to examine migration patterns and the influence of environmental factors on the diurnal behaviour. Of the 10 environmental factors measured, ide were significantly influenced by turbidity, which increased diurnal movement and the home range size of the species. The peak of longitudinal movement occurred in the spring, indicating pre-spawning migration. Migrating fish moved downstream and later returned upstream to the vicinity of their original locations, displaying a homing behaviour.

Factors influencing movement behaviour and home range size in ide *Leuciscus idus*

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Running title: Behaviour of ide

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INTRODUCTION

It has been suggested that the daily activity rhythms of fish are the result of a complex trade-off between growth and survival, which takes into account diel fluctuation in food availability, food capture efficiency and predation risk (Metcalfe *et al.,* 1999). Usually such diel activity patterns are closely related to variations in the physical environment. For example, a temperature-dependent shift in diel activity is supposed to be a consequence of higher predation risk in cold water (Webb, 1978; Fraser *et al.,* 1995). Changes in diel activity patterns have been related to the light intensity and duration corresponding with the daytime (Harvey & Nakamoto, 1999), season (David & Closs, 2003) or the moon phase (Horký *et al.,* 2006). However, other environmental conditions, such as the influence of water turbidity (Benfield & Minello, 1996; Sweka & Hartman, 2003) and water flow conditions, may have an effect (Harvey & Nakamoto, 1999; Slavík *et al.,* 2007).

Ide, *Leuciscus idus* (L.), is a species of benthopelagic, riverine cyprinid inhabiting deeper, slower flowing reaches of lowland middle-sized rivers east of the Rhine basin in Europe to Siberia (Maitland & Campbell, 1992). It achieves a maximum size of 53 cm total length (L_T), a body mass of 2.0 kg, and a recorded age of 14 years. Ide are visually oriented feeders and predominantly consumes insects, although coarse fish or plant material might be occasionally consumed (Cala, 1970). Ide spawn in spring and belonging to the phyto-lithophilic spawning group (Balon, 1975). Their migratory pattern has been described as potamodromous with a prevailing upstream migration (Cala, 1970; Müller, 1986). According to Winter & Fredrich (2003), who observed migrations of ide in the middle reaches of the River Elbe in Germany and the River Vecht in the Netherlands, ide is a flexible species capable of adapting its movement pattern to different conditions of river systems. To investigate within catchment variation in the migratory patterns of ide we tracked the movements of individuals in a low stream order, upstream section of the Elbe River, closer to the source than previous investigations (Winter & Fredrich, 2003). To assess which environmental factors influence the migration and diurnal behaviour of ide, 17 specimens were radio-tracked weekly from September 2003 to September 2004 in the Elbe River, Czech Republic.

MATERIALS AND METHODS

STUDY AREA

The study was carried out on the upper part of the River Elbe, Czech Republic. The river rises at 1383 m above sea level. It has a total length of 1091 km with a catchment area of 148,268 km^2. The Czech portion of the river is 368 km long and has a catchment area of 51,394 km^2. The primary river stretch studied was about 40 km long, from the weir at Střekov (distance from the source 320 km; 50°38′ N; 14°03′ E) to the frontier with Germany (Fig. 1). During spawning migrations, the stretch studied was extended as far as Meissen, Germany (distance from the source 410 km; 51° 81' N; 13° 28' E) as fish were followed. The river width in the area studied was 100 to 150 m, and the riverbanks have little aquatic vegetation and are reinforced with rocks and concrete. The water was up to 6 m deep and no submergent vegetation or floating plants were recorded. Across the whole study period, the average flow was 293 m^3 s^{-1}, with the maximum in winter (748 m^3 s^{-1}) and the minimum in early autumn (79 m^3 s^{-1}).

FISH CAPTURE AND TAGGING

Fish were sampled by electrofishing (650 V, 4 A, pulsed D.C.) and seventeen individuals were radio tagged. All fish were caught and released at 5 km long river stretch

(Fig. 1). The individuals were measured to the nearest mm (mean standard length 378 mm L_S, ranging from 285 to 450 mm) and weighed to the nearest g (mean fish body mass 755 g, ranging from 450 to 1240 g). Fish were anaesthetized with 2-phenoxy-ethanol (0.2 ml l^{-1}). Radio transmitters (MCFT 3B, 11 g in air, 14 x 43 mm, with an operational life estimated to be 399 days; MCFT 3EM, 8.9 g in air, 11 x 49 mm, with an operational life estimated to be 278 days; Lotek Engineering, Inc., Canada) were implanted into the body cavity through a midventral incision that was closed by three separate stitches, using a sterile, braided, absorbable suture (Ethicon Coated Vicryl). The mass of the transmitter never exceeded 2 % of the fish body mass in the air (Winter, 1983). Fish were held until they had recovered their equilibrium and showed spontaneous swimming activity (*c*. 5 min. after surgery), then released close to the site of capture. The transmitters had external antennae and their potential range was approximately 300 m depending on the gain of receiver and tracking conditions.

SAMPLING PROCEDURES

All fish were tracked from a boat weekly during the period from 11 September 2003 to 21 September 2004. Once all the fish were positioned, one individual was randomly chosen for a 24h tracking cycle. Fish positions were determined once in each three-hour period over a diel cycle (0600 – 0859, 0900 – 1159, 1200 – 1459, 1500 – 1759, 1800 – 2059, 2100 – 2359, 2400 – 0259, 0300 – 0559 hours) using a GPS receiver. The interval between measurements varied slightly depending on the tracking conditions (3 hours ± 20 min.). The fish were located using landmarks and positioned with the help of a GPS (GPS map 76S, Garmin Ltd., USA) using two radio receivers (Lotek SRX_400 receiver firmware versions W5 and W31) and three-element Yagi antennas equipped with a compass. The fish direction was determined by the double lateral extinction technique (bearing on the bisecting line of the two extinction axes; Winter *et al.,* 1978). A computer program was developed to obtain fish position coordinates and plot them on the map using the biangulation method proposed by White & Garrot (1990).

HABITAT MEASUREMENT

Water temperature (°C), dissolved oxygen concentration (mg l^{-1}), conductivity (μS), pH, and turbidity (NTU) were measured by microprocessors (Oxi 196; pH/Cond 340i/SET; TURB 355 T; WTW, Germany). Light intensity (Ev) was measured by a SECONIC Super Zoom Master L-68 (Seconic, Tokyo, Japan) at the expected locations of individuals during each positioning. Measurements of the atmospheric pressure and the moon phase were conducted with help of the Remote Weather station BAR 928 H (Huger Electronics, Germany). The Elbe River Authority measured water flow daily at a gauging station located within the study stretch.

DATA ANALYSES

Short term movements were defined as the distance (m) between the fish positions determined in two subsequent three-hour intervals over a 24 hour cycle and are henceforth referred to as "diurnal movements". Although the fish were located every time, in several cases the signal was so weak that triangulation could not be precise: These occasions were excluded from further analysis. Longer term movements were determined from the difference (m) between the locations of a fish in two successive week intervals and, henceforth, are referred to as "longitudinal movements". Data on fish movements were analyzed using Map Source Version 5.3 (Garmin Ltd., USA). The sizes of home ranges were determined using the Minimum Convex Polygon method (Mohr, 1947). Fish that were used for home range analyses were suggested to occupy home range; i.e. fish could not move during two subsequent weeks in the longitudinal direction more than its usual extent of diurnal movements across the twenty-four-hour cycle. Furthermore, fish that moved for the whole twenty-four-hour cycle in only one direction (upstream or downstream) was suggested to exhibit a mobile or emigration phase of a home range shift and was subsequently excluded from the analyses. Data concerning light intensity were first entered into the analysis as the absolute values of illumination (1 Ev ≅ 5 lx; $y = 0.6211e^{0.6943x}$, where y = lx, x = Ev), referred to as 'intensity of illumination'. Furthermore, three intervals with different light intensity were determined across the twenty-four-hour cycle: twilight (light intensity ranged between 1 – 6 Ev), day (above 6 Ev), and night (below 1 Ev); in further analysis, these categories will be referred to as 'light intervals'.

STATISTICAL ANALYSES

Associations between the variables were tested using the Linear Mixed Model (LMM). Separate models were applied for the following dependent variables: diurnal movements (LMM I), home range size (LMM II) and longitudinal movements (LMM III). All of the data were square root transformed to achieve normality before analyses. To account for the repeated measurements of the same individuals across the period of observation, analyses were performed using mixed model analysis with individual fish and date nested within individual fish (LMM I, II) and individual fish and date nested within individual fish (LMM III) a**s** a random factors, using PROC MIXED (SAS, version 9.1).

PROC MIXED is the way to cope with repeated-measures experiments with people or animals as subjects, where subjects are declared random because they are selected from the larger population to which you want to generalize (SAS Institute Inc., 2004). For the LMM I model, fixed effect used were the classes 'moon phase' (8 levels), 'season' (spring, summer, autumn, winter), and 'light interval' (day, night, twilight), and the continuous variables were 'turbidity' (range 5.5 – 44 NTU), 'fish mass' (1293–3946 g), 'water temperature' (0–24 ºC), 'water flow' (79–748 $m^3 s^{-1}$), 'atmospheric pressure' (992–1033 hPa), 'conductivity' (332–

425 μS), ‘light intensity’ (0 – 15.1 Ev), and ‘dissolved oxygen’ (5.5–12.9 mg l^{-1}). For the LMM II - III models, fixed effects used were the same as for the LMM I model except for the ‘light interval’ (day, night, twilight) and ‘light intensity’ (0 – 15.1 Ev) that were excluded from the analyses. The significance of each fixed effect (including interactions) in the analyses was assessed by the F-test, upon sequential dropping of the least significant effect, starting with a full model. Fixed effects and their interactions that were not statistically significant are not discussed further. In unbalanced designs with more than one effect, the arithmetic mean for a group may not accurately reflect the response for that group, since it does not take other effects into account. Therefore, the least-squares-means (LSMEANs) were used. LSMEANs (further referred to as ‘adjusted means’) are, in effect, within-group means appropriately adjusted for the other effects in the model. Adjusted means (Adj P) were computed for each class; differences between classes were tested by the *t*-test. For multiple comparisons, we used the Tukey-Kramer adjustment. Associations between the dependent variable and other continuous variables were estimated by fitting a random coefficient model using PROC MIXED as described by Tao *et al.* (2002). With this random coefficient model, we calculated predicted values for the dependent variable and plotted them against the continuous variable with predicted regression lines. The degrees of freedom were calculated using the Kenward-Roger method (Kenward & Roger, 1997).

RESULTS

Final LMM models contained the fixed factors ‘turbidity’ for diurnal movements (LMM I), ‘turbidity’ and ‘season’ for home range area size (LMM II), and ‘season’ for longitudinal movements (LMM III). Details of the models are shown in Table I. Descriptive data of the extent of diurnal movements, longitudinal movements, total distance migrated during spawning and home range per individual are provided in Table II. The other environmental variables tested (water temperature, dissolved oxygen, conductivity, pH, atmospheric pressure, moon phase and light intensity) were not found to have a significant effect.

DIURNAL MOVEMENTS AND HOME RANGE SIZE OF IDE

During the whole study fish did not remain at one exact position, however they occupied defined home ranges between which they relocated (e.g. during spring migration). Mean home range size was 19,495.8 ± 13,890.9 m^2 (Table II), but both diurnal movement and home range size appeared to vary in a consistent manner. Repeated measurements indicated that both diurnal movement [Fig. 2(a)] and the home range size [Fig. 2(b)] of ide increased with increasing turbidity. The relationship between flow and turbidity was not statistically significant; increased turbidity was a consequence of both surface run-off and phytoplankton growth. Home range size was significantly smaller (Tukey-Kramer Adj. $P < 0.05$) during winter than other seasons [Fig. 3(a)].

Final GLMM I model indicated the influence of the light interval nested within season on the diurnal movements of ide (Table I); however, differences among classes were insignificant, and hence the character of dependence was not possible to determine (Tukey-Kramer Adj. $P > 0.05$).

LONGITUDINAL MOVEMENTS OF IDE

Longitudinal movements of the ide were significantly larger (Tukey-Kramer Adj. $P < 0.01$) in the spring, with non-significant differences among other seasons [Fig. 3(b)]. Almost all individuals, with one exception, displayed downstream spring migrations, most of them remaining within Czech part of Elbe River (40 km long; Fig. 1). Six individuals moved to near the confluence of the River Bílina at Ústí nad Labem, including one individual that moved 19 km upstream to reach this spot (the only upstream migrating individual). Four individuals moved downstream to near the town of Malé Březno and a further two to near the border with Germany. Five individuals undertook longer migrations (68 – 100 km) to reach spawning sites near Dresden and Meissen in the German part of River Elbe (Fig. 1). The individuals that undertook longest migration started their run earliest, at the end of February. All final destination of migration were shallower riffles with a gravel substrate. Later in the season, ide displayed homing behaviour and returned to within 0.5 – 2 km of the starting position.

DISCUSSION

Behaviour of visually oriented animals is known to be affected by visibility, as they rely on visual cues for orientation and feeding. In aquatic ecosystems, the visibility is determined not only by the light intensity but also by the water turbidity (Benfield & Minello, 1996). Turbidity imposes a considerable environmental constraint with a potential to affect whole fish communities (Colby *et al*., 1972; Diehl, 1988). It may shape the habitat choice patterns (Miner & Stein, 1996), social interactions (Valdimarsson & Metcalfe, 2001) or reproductive behaviour of the fish, in terms of reduced sexual selection (Järvenpää & Lindström, 2004; Heubel & Schlupp, 2006). Increased turbidity influences visually-oriented fish by decreasing their visual range (Utne-Palm, 2001), typically affecting foraging efficiency by reducing the distance at which a predator detects prey (Benfield & Minello, 1996; Sweka & Hartman, 2003). Benfield & Minello (1996) evaluated the influence of turbidity on predation rates of gulf killifish, *Fundulus grandis* Baird and Girard, and that significantly fewer prey were consumed in tanks containing turbid water. Brook trout, *Salvelinus fontinalis* L., become more active in higher turbidity, thus increasing the chance of encountering potential prey by enlarging the total volume of water searched (Sweka & Hartman, 2001a). Hence, we suggest that ide extend their diurnal movements and home range size as a result of the reduced foraging success in turbid water.

In riverine systems, increased turbidity is usually associated with increased flow during hydrologic events (Sahoo *et al.,* 2006). However, low discharge may have the opposite effect: increased water residence time during low water flow may allow the buildup of phytoplankton biomass (Lane *et al.,* 2007). Here there was no significant relationship between discharge and turbidity, suggesting both potential sources and that the behaviour of ide was influenced by the water turbidity per se. Home range size varied consistently with season and turbidity. The influence of turbidity is likely to due to its effect on visibility. Reduced diurnal movement in winter may be due to lower food availability and/or temperature related metabolism.

The winter season is a period of reduced activity in cyprinid fish (Bauer & Schlott, 2004). They tend to remain in areas with the most appropriate conditions for wintering, as was shown for example in bream *Abramis brama* L. migrating into lentic refugia (Molls & Neumann, 1994). A restricted home range may be a direct consequence of a reduced metabolic rate linked to low temperatures as well as a result of efficient energy conservation or the use of locally restricted refuge during harsh conditions (Brown & Mackay, 1995; Hiscock *et al.,* 2002).

Many freshwater fish species, including cyprinids, undertake long distance migrations during the breeding season (Baras & Cherry 1990; Lucas 2000). Previous reports of ide indicated an upstream pre-spawning migration followed by downstream movement after spawning (Cala, 1970; Müller, 1986), including studies in the middle reaches of the River Elbe (Winter & Fredrich, 2003). In contrast, we observed that ide undertook similar long distance migrations in spring but in the opposite direction, i.e. downstream during spring and returning upstream towards formerly occupied areas later in the season. These findings are partly consistent with Cala (1970) from Kävlingeån in Sweden, where ide also displayed large downstream migration in spring. However, the latter case is more complicated as the fish migrated downstream to coastal waters in the spring, where they remained for the consecutive summer, only returning to the river in autumn (Cala *op. cit.*). Such inconsistency in the direction of migration may indicate that the movements of fish are shaped by multiple factors that vary even within river systems. An obvious constraint is the presence of lateral obstructions that hamper fish migration (Lucas & Frear, 1997; Horký *et al.,* 2007), although in our study no fish were observed to move to the vicinity of the weir at Strekov during spring migration. The location of suitable spawning areas (Pollux *et al.,* 2006) and channel morphology (Lau *et al.,* 2006) may also be essential.

Although ide are declining in numbers, classified as vulnerable by IUCN Red List criteria (2001) and protected as an endangered species (Lusk *et al.,* 2004), few references regarding its behaviour exist (Cala 1970; Winter & Fredrich 2003). Our data demonstrate that the turbidity may substantially influence the movement patterns of this species. As turbidity is influenced by both eutrophication and changes in land-use (Duchrow & Everhart, 1971), and increased turbidity has a negative effect on foraging success and growth of fish (Sweka & Hartman 2001a; Sweka & Hartman 2001b), eutrophication of the river catchment could be an important negative influence on ide abundance and distribution.

Our findings further indicate that their migratory behaviour is shaped by multiple factors that vary even within river systems. Whilst encouragingly this may indicate a degree of plasticity in the species, more work is needed to understand the factors influencing these migrations and hence direct conservation efforts to improve the breeding success of the remaining populations.

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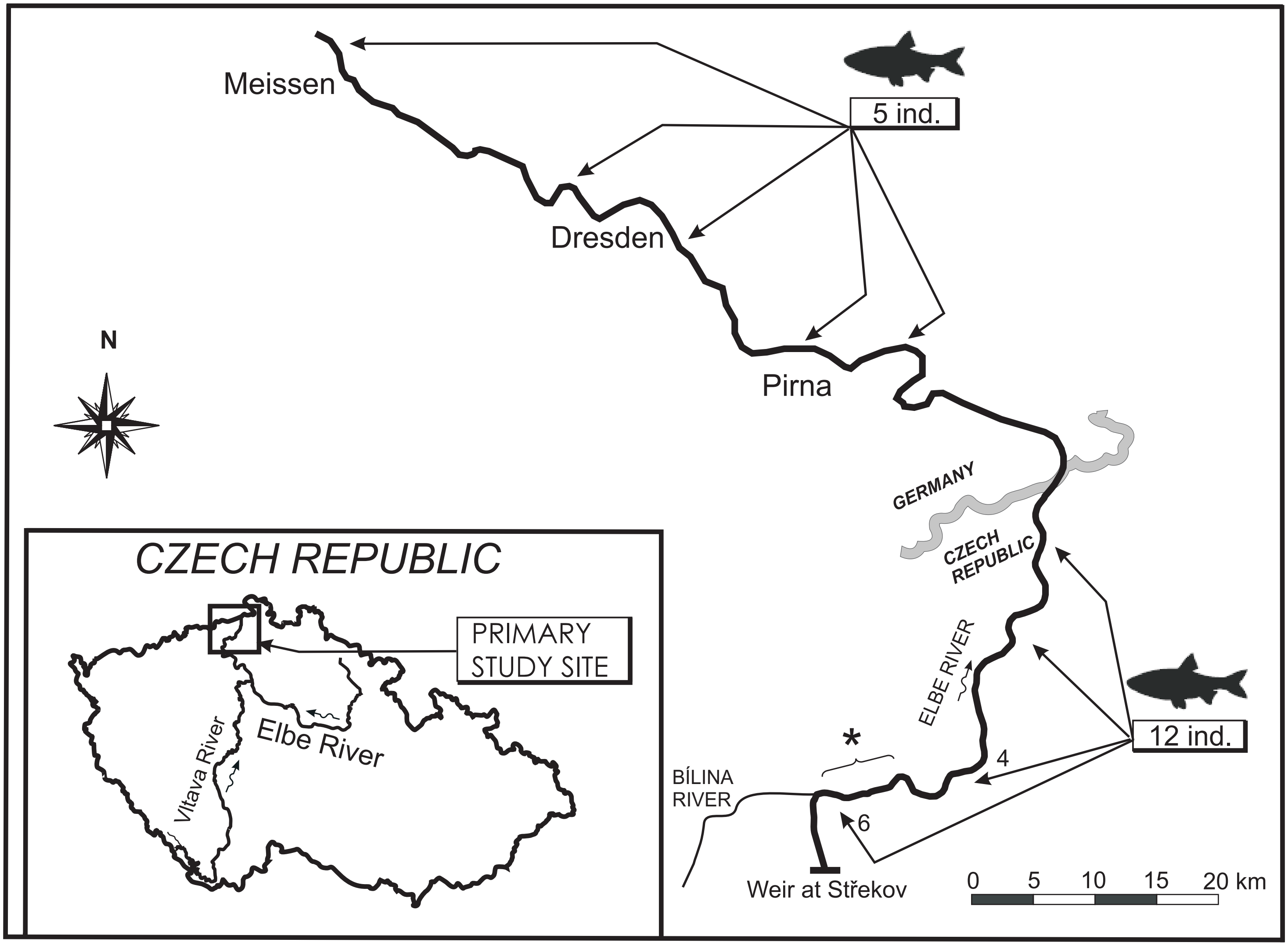
Figure Captions

Fig. 1 Map showing the location of the study site with highlighted distances of spring downstream migrations and number of individuals (ind.) migrating within Czech and German part of River Elbe. Bracket with asterisk indicate the river stretch where the fish were caught and released after tagging. Arrow (↝) indicates the direction of river flow.

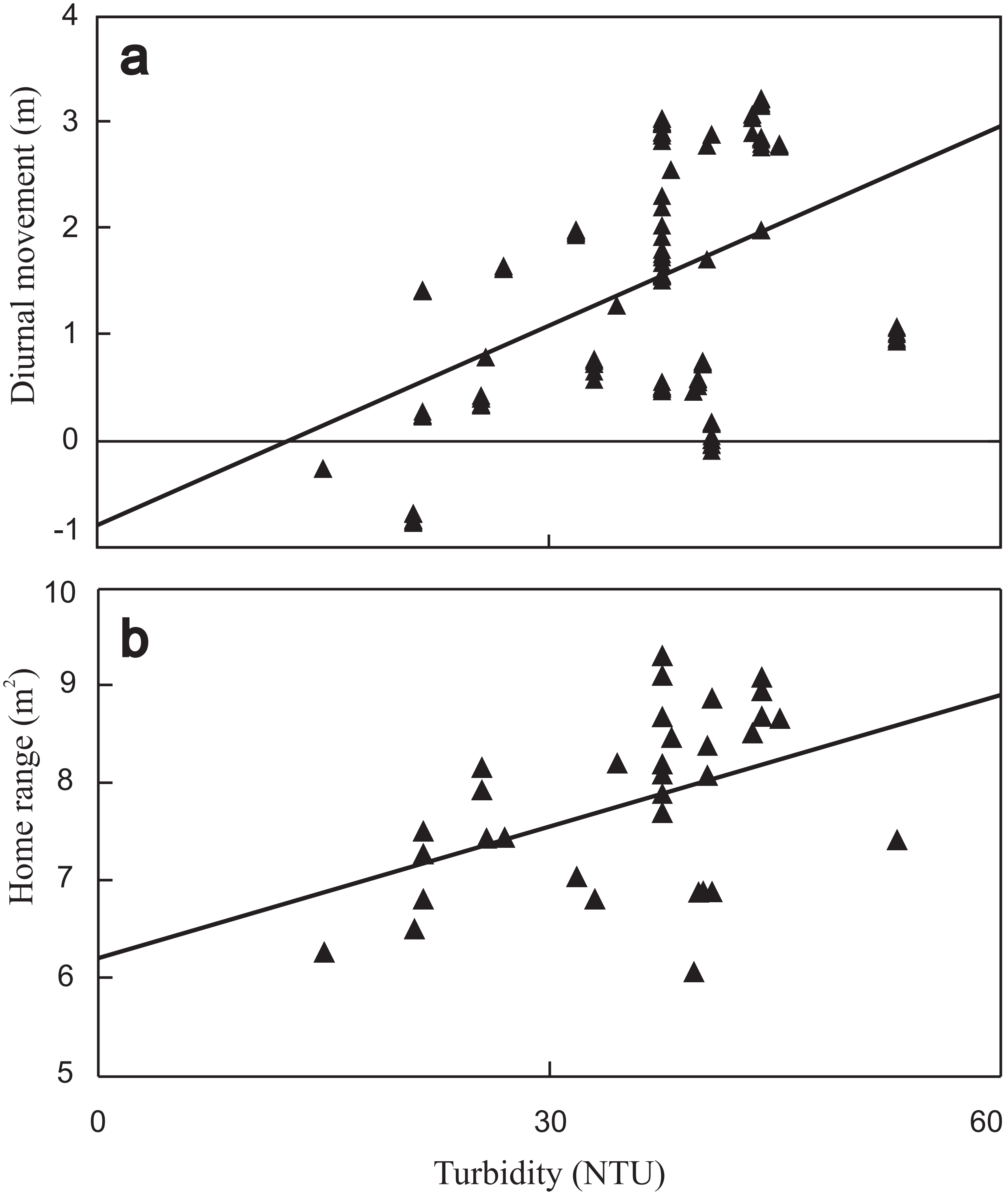
Fig. 2 Relationship between diurnal movements (a) and home range size (b) of ide and turbidity. Predicted values are from square root transformed data. The curves were fitted by: $y = 0.0188x - 0.0395$, ($r^2 = 0.38$) for diurnal movements and $y = 0.0189x + 7.4581$, ($r^2 = 0.34$) for home range size.

Fig. 3 Home range size (a) and longitudinal movements (b) of ide across seasons. Asterisks indicate significant differences between groups (* $P < 0.05$; ** $P < 0.01$). Values are adjusted means ± S.E. of square root transformed data.

Figure

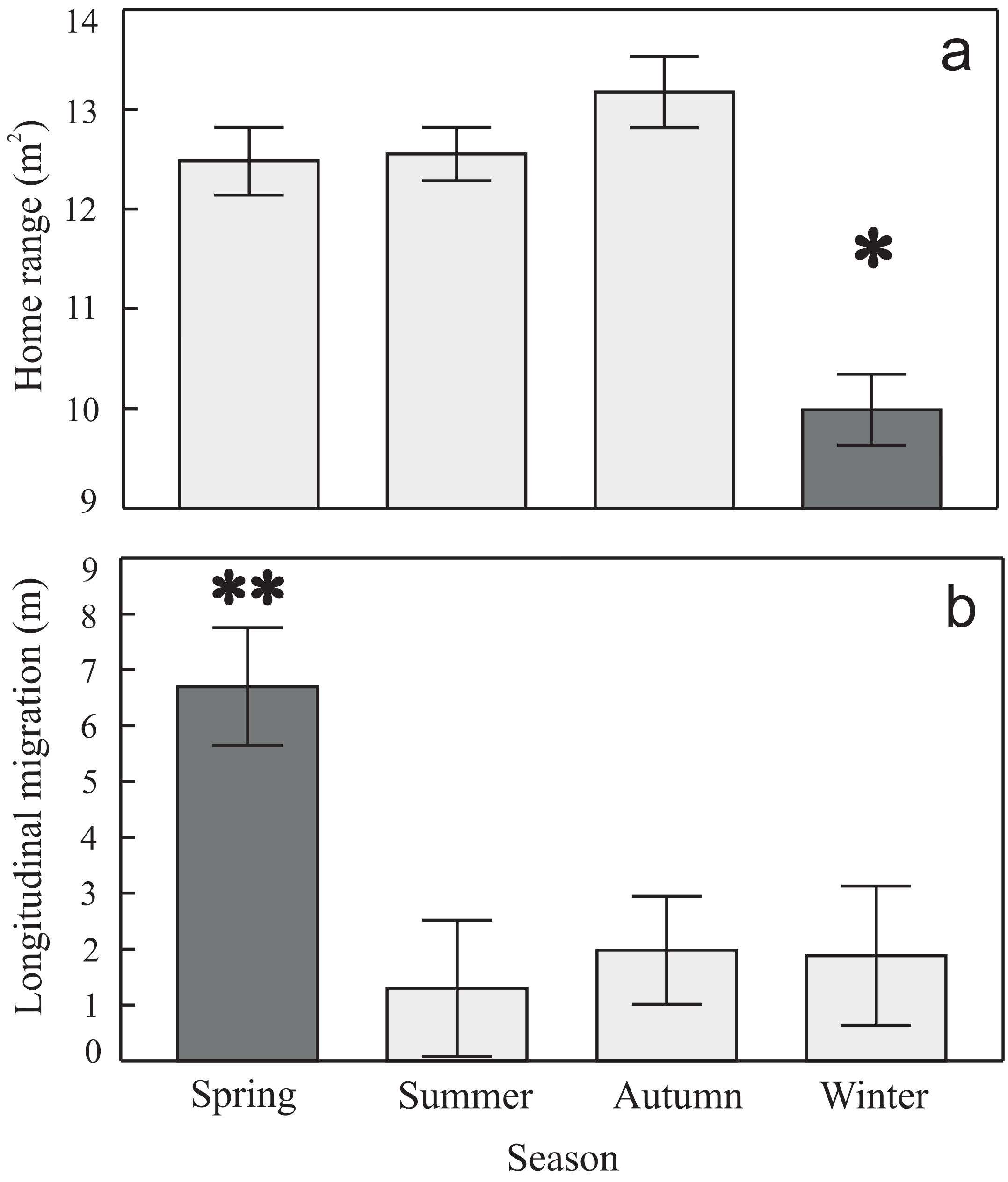

Meissen
5 ind.
Dresden
Pirna
N
GERMANY
CZECH REPUBLIC
ELBE RIVER
12 ind.
4
*
BÍLINA RIVER
6
Weir at Střekov
0 5 10 15 20 km
CZECH REPUBLIC
PRIMARY STUDY SITE
Vltava River
Elbe River

Figure



a
b
Diurnal movement (m)
Home range (m^2)
Turbidity (NTU)
4
3
2
1
0
-1
10
9
8
7
6
5
0
30
60

Figure



a
Home range (m^2)
14
13
12
11
10
9
*
b
Longitudinal migration (m)
9
8
7
6
5
4
3
2
1
0
**
Spring
Summer
Autumn
Winter
Season

TABLE I. Type 3 tests of fixed effects for diurnal movements, home range area size, and longitudinal movements.

Effect	**Num DF**	**Den DF**	**F**	**P<**
LMM I *(diurnal movement)*				
turbidity	1	256	7.82	0.0056
light interval(season)	11	256	3.20	0.0004
LMM II *(home range size)*				
turbidity	1	255	68.37	0.0001
season	3	255	56.12	0.0001
LMM III *(longitudinal movement)*				
season	3	255	5.79	0.0008

TABLE II. Tagged individuals of ide with mean (± S.D.) of their recorded diurnal movements, longitudinal movements (LM), total distance migrated during spawning (TD) and home range (HR).

Individual code	**DM (m)**	**LM (m)**	**TD (m)**	**HR (m^2)**
12	50.1 ± 100.5	1 824.8 ± 5 168.2	13 649	29 817.6 ± 23 924.05
14	24.8 ± 68.2	4 908.7 ± 13 711.2	99 729	19 506.4 ± 14 325.2
16	39.4 ± 89.7	6 372.6 ± 6 803.6	13 284	23 465.8 ± 12 698.7
17	15.6 ± 24.2	135.6 ± 361.8	3 882	7 400.4 ± 4 441.02
18	45.7 ± 95.8	5 510.2 ± 10 119.3	54 160	11 342.1 ± 8 432.6
24	32.8 ± 84.3	1 447.8 ± 3 193.4	18 633	36 157.5 ± 22 001.1
28	77.8 ± 120.1	6 238.5 ± 13 801.3	85 505	24 158.2 ± 17 325.8
40	21.1 ± 54.3	1 710.7 ± 1 909.6	2 908	8 352.1 ± 5 368.3
43	65.7 ± 118.6	2 811.3 ± 5 122.2	18 284	25 931.0 ± 18 963.2
44	34.3 ± 40.5	5 517.6 ± 12 024.6	37 406	13 700.2 ± 7021.4
45	38.1 ± 81.6	982.5 ± 3 421.7	4 145	27 536.5 ± 19871.8
46	20.4 ± 53.8	1 628.1 ± 4 236.9	9 380	23 658.8 ± 21 879.6
47	43.2 ± 94.4	2 874.3 ± 3 465.5	26 089	17 502.3 ± 13 468.2
48	37.3 ± 71.1	1 382.4 ± 2 678.6	4 332	19 875.4 ± 13 489.7
49	19.2 ± 52.9	1 348.2 ± 1 825.1	3 546	26 849.7 ± 21 487.2
50	28.4 ± 65.3	2 949.5 ± 8 236.4	67 946	13 672.3 ± 9 237.4
51	30.2 ± 41.5	2 131.4 ± 5 628.5	13 680	2 502.7 ± 2 030.6

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