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Diurnal and seasonal behaviour of adult and juvenile European catfish as determined by radio-telemetry in the River Berounka, Czech Republic

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The first telemetry study analysing behaviour of the largest freshwater predator in European rivers, *Silurus glanis*, was performed bimonthly during the years 2002–2004. Movement of juveniles and adults occurred mostly in the same time intervals. The only statistical differences occurred for nocturnal activity in spring and autumn. In spring and winter, activity was low with the peaks during daylight, and in autumn, maximal movement was recorded during dusk. In summer, the European catfish were active across the whole 24 h even during high-flow conditions. During all other seasons, movement was inversely related to flow rate. Maximal home ranges occurred in summer, being larger for adults. Juveniles and adults were spatially segregated. With increasing flow, fish were displaced, and individuals from both groups got closer to each other. Only juveniles migrated downstream from the upstream isolated river stretch suggesting a negative impact of lateral obstructions on the fish population structure. © 2007 The Authors

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Key words: flow; home range; movement; siluriforms; temperature.

INTRODUCTION

European catfish *Silurus glanis* L. is the largest freshwater fish of European rivers, potentially achieving a size of 3 m total length (L_T), body mass of 320 kg (Maitland & Campbell, 1992) and with maximal recorded age of 28 years (Balon, 1966). The rare occurrence of large, trophy specimens in rivers can be explained by the effect of riverbed channelization, environmental disturbance and sport fishing (particularly large streams needed by this species). Individuals with a body mass of *c.* 50 kg, however, are regularly angled. The European catfish is predator, significantly influencing the structure of fish assemblages (Wysujack & Mehner, 2005), although it feeds on smaller prey than similarly

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large predators such as pike *Esox lucius* L. or pikeperch *Sander lucioperca* (L.). The species shows maximal movement during the warmest season (Maitland & Campbell, 1992) and has strictly nocturnal feeding activity under laboratory conditions (Boujard, 1995). Data on its behaviour in natural conditions, however, are not available. An important ontogenetic feature of the species is that only relatively large individuals (males of minimal L_T of 830 mm and mass of 3.7 kg; females of 860 mm in minimal L_T and mass of 4.4 kg) became mature (Alp *et al.*, 2004).

Fish body length tends to decrease with decreased depth of water (Mahon & Port, 1985; Harvey & Stewart, 1991), hence preference for different habitats by juvenile and adult European catfish can be expected. Spatial separation of juveniles to shallows and adults to variable types of habitats has been described for Siluriformes in South and North America (Barthem *et al.*, 1991; de Menezes & Caramaschi, 2000; Simon & Wallus, 2004). Moreover, the spatial and temporal distribution of juveniles can also be influenced by agonistic behaviour of adults. Competition for resources in space and time may divide populations into dominant and subdominant components, with different behavioural characteristics (Fausch, 1984). Resource partitioning by dominant individuals, demonstrated by their occupation of the most profitable positions and beneficial feeding times, results in spatial and temporal segregation, with subdominant individuals exploiting the resources at different times (Alanärä *et al.*, 2001; Valdimarsson & Metcalfe, 2001). Utilization of feeding resources determined by social rank was described by Hansen & Closs (2005) for the freshwater species the giant kokopu *Galaxias argenteus* Gmelin. Reduced food supply induced an increase in habitat use, home range size and aggressiveness of dominant fish simultaneously reducing spatial and temporal activity and habitat use of subdominant fish. Density-dependent competition for spatial and food resources may result in the emigration of subdominant individuals into suboptimal habitats as predicted by the 'ideal despotic distribution' theory (Fretwell, 1972). This is characterized by the greater movement and larger home range size of smaller fishes (Nakano, 1995), which are incompatible with the basic model describing a positive relationship between fish body mass and its home range size (Harestad & Bunnell, 1979).

Telemetry was used to study the movements of the European catfish in the lowland Berounka River (Central Europe) across 2 years. The influences of flow (Stalnaker *et al.*, 1989), light intensity (Hansen & Closs, 2005) and moon phase (Allen & Wootton, 1984; Fraser & Metcalfe, 1997) on behaviour of the juvenile and adult European catfish were examined across seasons.

MATERIALS AND METHODS

STUDY SITE

The study was carried out on the Berounka River (Elbe catchment area, Czech Republic). The river has a L_T of 139 km with a catchment area of 8861 km². The river stretch studied was 3.5 km long with the total area of 37 ha, maximal depth of 1.8 m and limited by lateral obstructions (weirs) without fish passes; the height of the weirs was 1 m (49°55' N; 14°14' E; upstream) and 1.4 m (49°56' N; 14°17' E; downstream).

Three types of habitat were determined within the studied river stretch: riffles, runs and pools (1273, 407 and 1850 m in length, with average width of 127, 68 and 95 m and average slope of 2.98, 1.41 and 0.53‰, respectively). The river bottom was covered by gravel and small boulders (riffles and runs) or by sand and organic sediment (pools). No submerged vegetation, floating plants or woody debris were recorded. Alder *Alnus glutinosa* L., willow *Salix alba* L. and poplar *Populus alba* L. created riparian vegetation; overhanging plants were, however, rare, and shading of the stream was minimal. Flood barriers isolate the floodplain area from the main channel.

SAMPLING PROCEDURES

A total of 17 European catfish (10 adults and seven juveniles; Table I) were caught by electrofishing (650 V, 4 A, pulsed D.C.). Fish were anaesthetized with 2-phenoxy-ethanol (0.2 ml l⁻¹), measured (standard length L_S , mm) and weighed (g). Radio transmitters (MCFT 3A, 16 g in air, 16 × 46 mm, with operational life of c. 761 days; Lotek Engineering Inc., New market, Ontario, Canada) were implanted into the body cavity through a midventral incision that was closed by three separate stitches, using 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). The fish were released at or near the point of capture after they recovered their equilibrium and showed spontaneous swimming activity (c. 5 min after surgery).

Fish were monitored during the period September 2002 to August 2004. Anglers caught one adult European catfish, and one juvenile fish died during the first 2 months of the study. Both individuals were excluded from further analyses. Individuals were tracked bimonthly during the diurnal cycle, using a radio receiver (SRX 400 W31) and a three element Yagi antenna. Fish positions were determined by triangulation (Winter, 1983) during eight subsequent 3 h intervals and recorded on a map with the help of the GPS (GPS map 76S, Garmin Ltd, Miami, FL, U.S.A.). Data on fish movements were transferred from the GPS to PC and analysed with the help of the Map Source Version 5.3 (Garmin Ltd).

In August 2003 and 2004, control samplings of the studied stretch were carried out to determine the fish community present and potential downstream immigration of other European catfish from upstream river stretches. Fish were caught by electrofishing, and 15 species were found within the study stretch. The sampled fishes were predominantly cyprinids, with five species the most numerous: chub *Leuciscus cephalus* (L.), roach *Rutilus rutilus* (L.), bleak *Alburnus alburnus* (L.), bream *Abramis brama* (L.) and gudgeon *Gobio gobio* (L.) Piscivorous fishes were represented by pike, asp *Aspius aspius* (L.) and perch *Perca fluviatilis* L. In August 2003, two untagged juvenile European catfish (120 and 130 mm L_S) were caught. Similarly, two untagged catfish (580 and 142 mm L_S) were caught in August 2004.

TABLE I. Standard length (L_S) and fish body mass (M) of the radio-tagged European catfish tracked at the studied river stretch in 2002–2004

Adults – 1070 valid detections during the study period										
L_S (mm)	1450	1130	1150*	1150	1100	950	920	910	890	850
M (g)	16	9	8.5	8	7	6.5	6	5.8	5.5	5
Juveniles – 658 valid detections during the study period										
L_S (mm)	590	620	650	550	540*	510	490			
M (g)	2.6	2.5	2.1	1.7	1.6	1.1	0.81			

*Individuals excluded from the statistical analyses.

HABITAT MEASUREMENTS

Water temperature ($^{\circ}\text{C}$; Fig. 1), dissolved oxygen (mg l^{-1}), pH and conductivity ($\mu\text{S cm}^{-1}$) were measured by microprocessors (Oxi 196 WTW, pH/Cond 340i SET) throughout the study during the days when fish were sampled. Average recorded values (minimum, maximum) of measured physicochemical variables were: concentration of dissolved oxygen 13.4 mg l^{-1} ($7.2, 16.8 \text{ mg l}^{-1}$), pH 8.0 ($7.7, 9.4$) and conductivity $409 \mu\text{S cm}^{-1}$ ($301, 482 \mu\text{S cm}^{-1}$). Measurements of the moon phase were conducted with the help of the Remote Weather Station BAR 928 H (Huger Electronics GmbH, Villingen-Schwenningen, Germany), whereas the light intensity (Ev) was measured by SECONIC Super Zoom Master L-68 (Seconic, Tokyo, Japan) being determined at the expected locations of individuals during each positioning. The Vitava River Authority measured flow ($\text{m}^3 \text{ s}^{-1}$; Fig. 1), biological oxygen demand (BOD) (mg l^{-1}) and turbidity (NTU) daily at the gauging station located within the study stretch. Long-term average flow at the study site was $Q_{330} = 36 \text{ m}^3 \text{ s}^{-1}$, and the average flow throughout the study period was $Q_{\text{local}} = 59 \text{ m}^3 \text{ s}^{-1}$. Extreme flow values in autumn 2002 were related to large floods in the region. Recorded average values (minimum, maximum) of other variables were: BOD 4.8 mg l^{-1} ($1.1, 14.2 \text{ mg l}^{-1}$) and turbidity 34.5 NTU ($8.2, 108 \text{ NTU}$).

STATISTICAL ANALYSES

Fourteen day samples were grouped into seasons: spring (21 March to 20 June), summer (21 June to 20 September), autumn (21 September to 20 December) and winter (21 December to 20 March). Home range size was determined using the minimum convex polygon method (Aebischer *et al.*, 1993). Data on light intensity were first entered as absolute values of illumination ($1 \text{ Ev} \cong 5 \text{ lx}$; $y = 0.6211e^{0.6943x}$, where $y = \text{lx}$ and $x = \text{Ev}$) referred to as 'intensity of illumination'. Four intervals with different light intensity were determined across the 24 h cycle, and dusk and dawn (light intensity ranged between 2 and 6 Ev), day ($>6 \text{ Ev}$) and night ($<2 \text{ Ev}$) were referred to as 'light intervals'. Based on the measurements of the Remote Weather Station, eight moon phases were identified and subsequently assigned a number, where 1 was a new moon phase and 5 a full moon, numbers 2–4; 6–8 indicated transitions between these two stages. The intensity of European catfish movements during 24 h was quantified as the difference (m) between the determined positions in two successive intervals and referred to 'movement'. The factor 'mutual position' expressed the position of a certain individual in relation to all other tagged specimens during each 3 h interval, being determined by

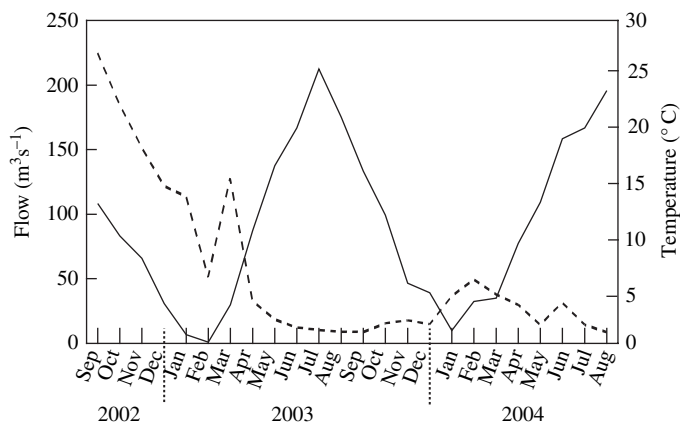


FIG. 1. Average flow (---) and water temperature (—) recorded at the locality during the study period.

distances (m) among all tagged fish. The factor 'fish size' refers to size of tagged individuals, dividing specimens into adults (850–1450 mm L_S and 5–16 kg) and juveniles (450–650 mm L_S 0.8–2.6 kg; Table I).

All data were analysed with the aid of the statistical package SAS (version 9.1; SAS Institute, Inc.). Associations between movement, home range size, mutual position of fish, fish size, temperature, flow, intensity of illumination, light intervals, moon phase and season were tested using multivariate General Linear Mixed Model (GLMM).

Separate models were applied for the following dependent variables: movement during 24 h (GLMM I), home range size (GLMM II) and mutual position of fish (GLMM III). All the data were \log_{10} transformed to achieve normality before GLMM analyses. To account for the repeated measurements on the same individuals across the period of observation, the analyses were performed with individual fish ID as a random factor, using PROC MIXED.

For the GLMM I model, fixed effects were classes: 'fish size' (juvenile and adult), 'light interval' (dawn, day, dusk and night), 'moon phase' (eight levels) and 'season' (spring, summer, autumn and winter). For the GLMM II model, fixed effects were classes: 'fish size' (juvenile and adult) and 'season' (spring, summer, autumn and winter). Continuous variables for both models were 'temperature' (0–26°C) and 'flow' (8.67–234 $\text{m}^3 \text{s}^{-1}$). For the GLMM III model, fixed effect was the class 'fish size' (juvenile and adult) and the continuous variable was 'flow' (8.67–234 $\text{m}^3 \text{s}^{-1}$).

The significance of each fixed effect in the mixed GLMM was assessed by an *F*-test, on sequential dropping of the least significant effect, starting with a full model. In the unbalanced designs with more than one effect, the arithmetic mean for a group may not accurately reflect response for that group, since it does not take other effects into account. Therefore, the least-squares-means (LSMEANS) were used. LSMEANS ('adjusted means', Adj P) are, in effect, within-group means appropriately adjusted for the other effects in the model. The Adj P were computed for each class and differences between classes were tested by a *t*-test. For multiple comparisons, the Tukey-Kramer adjustment was used. 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, predicted values were calculated for the dependent variable and plotted against the continuous variable.

RESULTS

EUROPEAN CATFISH MOVEMENT

The results of the statistical model are shown in the Table II. Movement increased with water temperature, and there was no significant difference between juveniles and adults (Fig. 2). The activity of both groups was influenced by flow, with a positive correlation in summer only, whilst during other seasons, the relationship was negative (Fig. 3). No statistically significant relationship was found for movement and the intensity of illumination during the 24 h cycle. When the relationship was evaluated in four defined light intervals across seasons, however, significance effects were noted. In spring, activity of both groups was minimal, with the peak during the day and minimum at night [Fig. 4(a)]. In summer, the activity was maximal with no significant difference among the light intervals [Fig. 4(b)]. In autumn, the lowest activity of adults was during the day, whilst the maximum occurred at dusk and night [Fig. 4(c)]; juveniles showed maximum also at dusk but minimum at night [Fig. 4(c)]. In winter, the activity was low with the peak during the day and minimum at night [Fig. 4(d)]. The only statistical difference between adults and juveniles

TABLE II. Type 3 tests of fixed effects for fish movements during 24 h, home range and spatial distribution

Effect	d.f. numerator	d.f. denominator	<i>F</i>	<i>P</i> <
GLMM I: 24 h movements				
Temperature	1	1694	4.47	0.05
Flow (season)	4	1694	16.27	0.001
Lighting interval (season)	12	1694	2.76	0.001
Moon phase	7	1694	7.60	0.001
GLMM II: home range				
Adult v. juvenile	1	1708	48.79	0.001
Mass	1	1708	11.92	0.001
Season	3	1708	37.17	0.001
Temperature × flow	1	1708	33.5	0.001
GLMM III: mutual position				
Adults v. juvenile	2	1069	8.42	0.001
Flow (adults v. juvenile)	3	1083	12.45	0.001

occurred for the night interval in spring [Adj $P < 0.001$; Fig. 4(a)] and autumn [Adj $P < 0.001$; Fig. 4(c)]. The GLMM indicated the influence of the moon phase on movements of both groups (Table II), however, differences in European catfish movements among moon phases were insignificant, and hence, the character of dependence was not possible to determine (Tukey-Kramer Adj, $P > 0.05$).

LONGITUDINAL MIGRATIONS OF THE EUROPEAN CATFISH

The average home range size was 10 871 m² being maximal in summer and minimal during spring [Fig. 5(a)]. Juveniles had smaller home ranges when

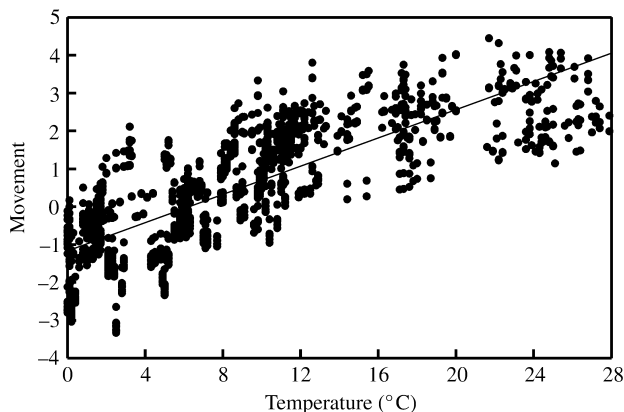


FIG. 2. The relationship between European catfish movement and water temperature. Predicted values are from \log_{10} transformed data. The curve was fitted by: $y = 0.1864x - 1.169$.

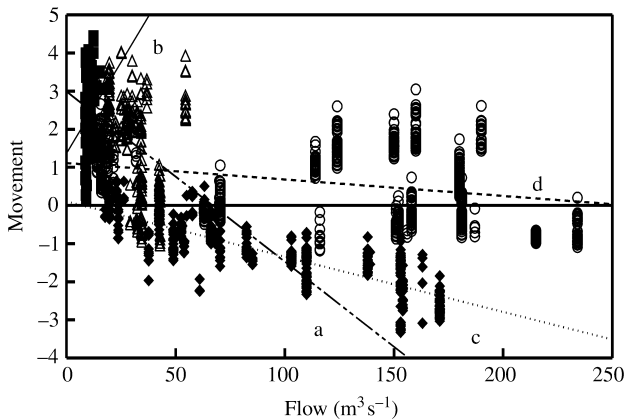


FIG. 3. The relationship between European catfish movement and flow across seasons: spring (a, Δ , \cdots), summer (b, \blacksquare , $—$), autumn (c, \circ , \cdots) and winter (d, \blacklozenge , $---$). Predicted values are from \log_{10} transformed data. The curves were fitted by: spring $y = -0.005x + 3.01$, summer $y = 0.096x + 1.37$, autumn $y = -0.0012x + 0.11$ and winter $y = -0.0043x + 1.12$.

compared with adults [Fig. 5(b)]. The average home range size of juveniles was 5604 m² (minimum 1171, maximum 14 580 m²) and of adults 15 702 m² (minimum 9519, maximum 47 136 m²). The smallest home ranges of both groups occurred at low temperatures and high flows (Fig. 6).

Distances among mutual positions of juvenile individuals were comparable with those of adult fish (Adj $P > 0.05$), whilst the distances between juveniles and adults significantly differed (Adj $P < 0.001$; Fig. 7), *i.e.* juveniles and adults were spatially separated. It changed according to increasing flow, when the distance among juveniles increased, whilst among adults and also between juveniles and adults decreased (Fig. 8).

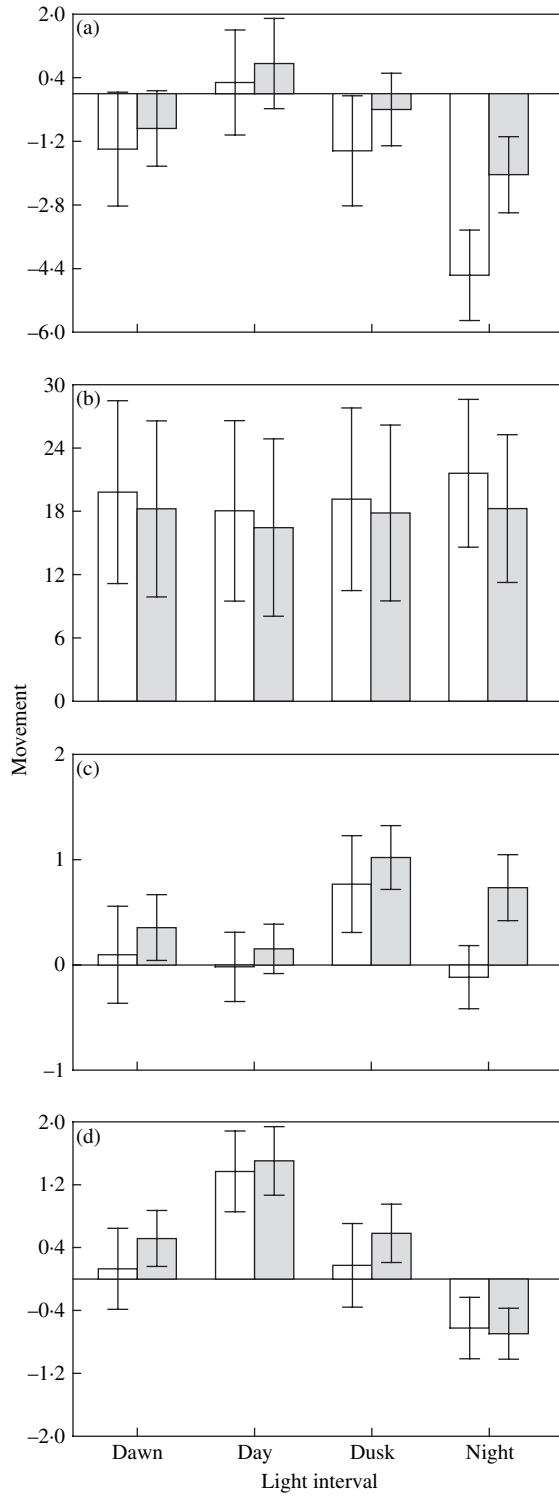
Only two juvenile fish emigrated from the upstream isolated study site. Both individuals left the area at the beginning of November, the first in 2002 and the second in 2003.

DISCUSSION

The results suggested that the European catfish in a river was not strictly nocturnal in activity. In the Berounka River, the species was active across the whole diurnal cycle. The external factors represented by temperature, flow and light intervals influenced the behaviour of juvenile and adult fish. Although the trends in behaviour of both groups were similar, differences occurred in their spatial distribution and downstream migration.

TEMPORAL DISTRIBUTION OF THE EUROPEAN CATFISH

Only minor differences in the movement of adults and juveniles during preferred time intervals suggested that agonistic behaviour of adults did not represent a key factor affecting the temporal distribution of juveniles. Although



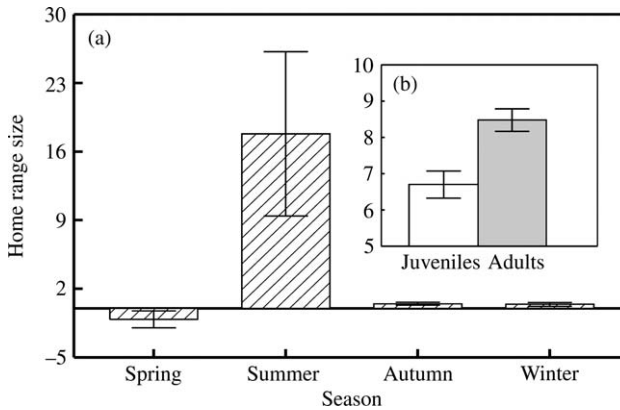


FIG. 5. (a) The predicted home range size of European catfish across seasons and (b) a comparison of the home range size between juveniles and adults during the study period. Values are means \pm s.e. of \log_{10} transformed data.

nocturnal activity of the species is usually reported for wild populations (Maitland & Campbell, 1992) and individuals under laboratory conditions (Boujard, 1995), in the Berounka River, strictly nocturnal activity occurred only for adult European catfish in autumn, whilst during winter and spring, the maximum movement was recorded during the day. The results suggested that the European catfish behaviour had a dualistic character (Eriksson, 1978; Sánchez-Vázquez *et al.*, 1998). According to Bolliet *et al.* (2001), the European catfish under laboratory conditions was able to synchronize its activity with the time when food availability was the highest. Movement of the species across all seasons strongly differed from summer when fish were highly active during the whole 24 h period. Boujard & Luquet (1996) documented the preferred nocturnal activity for the Siluriformes, however, the rhythm of feeding could alter in response to limiting values in temperature and dissolved oxygen. In the Berounka River, no relationship between movement and oxygen concentration occurred, and the preference of daylight intervals for feeding could be explained by a dependence of movement on temperature. The findings showed that low temperatures and high flows induced the smallest home range size suggesting an effort to reduce energy costs. During high flows, fishes often occupy the most profitable energetic positions within their home ranges (Harvey & Nakamoto, 1999). In contrast, a high positive correlation between movement and flow occurred in summer suggesting an attempt to optimize the utilization of spatial and feeding resources restricted during the low-flow conditions. Similarly, the eel *Anguilla anguilla* (L.) migrated to the floodplain areas during high flows following an increase in food availability and thus enlarged its home range (Tesch, 1977; LaBar *et al.*, 1987). The ability to use hydrodynamic and chemical cues for prey tracking (Pohlmann *et al.*, 2001) allows catfishes to feed

FIG. 4. European catfish predicted movements plotted against four light intervals across seasons for: juveniles (\square) and adults (\blacksquare) in (a) spring, (b) summer, (c) autumn and (d) winter. Values are means \pm s.e. of \log_{10} transformed data.

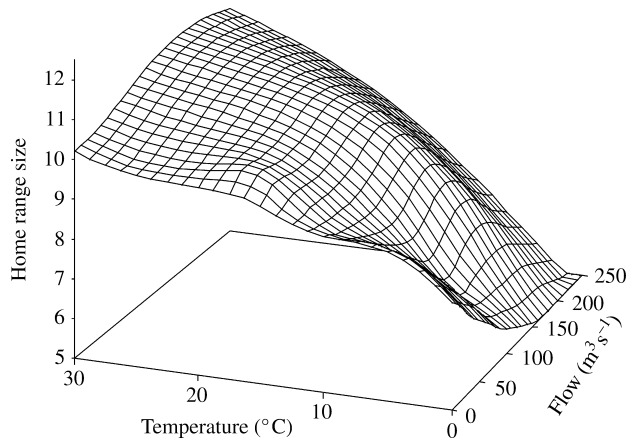


FIG. 6. Predicted values of the home range size of European catfish plotted against flow according to water temperature. Values are means of \log_{10} transformed data.

in turbid water, in contrast to, for example, salmonids with their visual feeding (Berg & Northcote, 1985). In summer, increasing food availability during the high flows is usually attended by an increase in number of invertebrates, on which the European catfish also feed (Maitland & Campbell, 1992; Dogan & Gul, 2004).

The results showed no influence of the moon phase on the movement of the fish. The absence of this relationship, *i.e.* independence from the moonlight intensity, further supported the dualistic character of the siluriform fish movement and the use of other than visual cues for prey detection (Pohlmann *et al.*, 2001).

MUTUAL POSITION OF JUVENILE AND ADULT EUROPEAN CATFISH

The results suggested significant differences in the spatial distribution of juvenile and adult fish. It was not possible to eliminate the hypotheses that

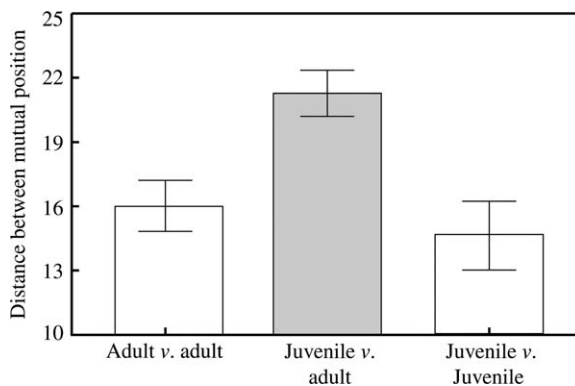


FIG. 7. Distances between mutual positions of individuals inside the groups of European catfish (juveniles and adults) and between the groups. Values are means \pm S.E. of \log_{10} transformed data.

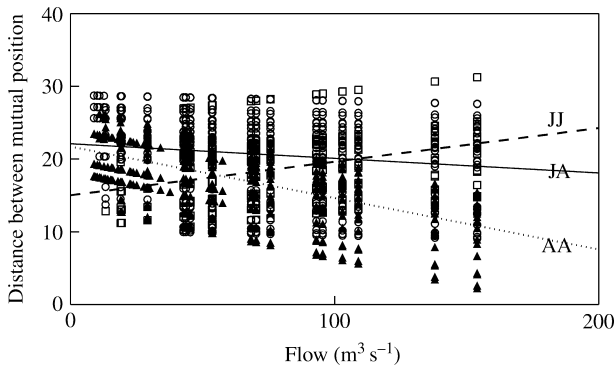


FIG. 8. Distances between mutual positions of individuals inside the groups of European catfish: juveniles (JJ; \square , ----), adults (AA; \blacktriangle ,), and between the groups (JA; \diamond , —) plotted against flow. Predicted values are from \log_{10} transformed data. The curves were fitted by: JJ $y = 0.046x + 15.04$, JA $y = -0.02x + 22.11$ and AA $y = -0.07x + 21.7$.

spatial segregation reflected aggressiveness of adults related to limited resources (Hansen & Closs, 2005), however, the results did not directly support it. Small and large individuals were spatially segregated, juveniles had smaller home ranges but distances among mutual positions inside both groups were similar. It corresponds with the findings that spatial segregation of juveniles and adults follow an ontogenetically determined pattern (Gomelyuk & Leunov, 1999; Kynard & Parker, 2005), whilst agonistic interactions are displayed most likely among related size groups of fishes (Hedger *et al.*, 2005). An increase in flow was attended by changes in mutual positions of European catfish; juveniles were more dispersed, but they got spatially closer to adults. In general, high flows reduce fish aggressiveness and disturb a dominance hierarchy (Sloman *et al.*, 2002). An increase in flow forces fishes to occupy energetically favourable positions with low velocities (Heggenes & Traen, 1998).

DOWNSTREAM MIGRATIONS OF JUVENILE EUROPEAN CATFISH

While movements of adult fish were located between the weirs, some juveniles migrated downstream from the studied river stretch. Lucas & Baras (2001) reviewed upstream reproductive migrations and lateral movements to the floodplain areas realized by the siluriforms in African rivers but downstream movements were mentioned only for juveniles. In South America, a few migratory models were described for adult and sub-adult siluriforms (Barthem *et al.*, 1991; Barthem & Goulding, 1997). In one of the models, the authors argued that eggs and larvae firstly drifted downstream, and then juvenile fishes returned upstream to areas where adults spawned. Numerous observations of drifting eggs and the larval stage of *Siluroides* suggested that downstream migrations represent an important mechanism of the population expansion (Araujo-Lima & Oliveira, 1998). Homing and a stronger association with home range of adult brown bullhead *Ameiurus nebulosus* (Lesueur) in

comparison to juvenile fishes was reported by Pellet *et al.* (1998). The present results correspond with available data about migrations of the siluriforms showing that juvenile fishes represent the migratory component of a population. It is well established that lateral obstructions without fish passes fragmentize a stream and disable upstream spawning migrations of adults and returns of juveniles displaced downstream (Lucas & Baras, 2001). When fishes relocate their home ranges (Kramer & Chapman, 1999; Crook, 2004) induced, for example, by a reduction of available habitats in response to flow decrease (Hesthagen, 1988; Young, 1994), downstream migration from the upstream isolated areas can be the only available spatial compensation. If population losses caused by downstream migration are not compensated for by upstream or downstream immigration then the population in the isolated stretch will decline (Uttinger *et al.*, 1998; Morita & Yamamoto, 2001). Hence, downstream migrations appeared to be an important factor influencing populations' development in impounded rivers with lateral obstacles.

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