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Primary Research Paper

Diel activity of adult pikeperch *Sander lucioperca* (L.) in a drainage canal in the Mediterranean basin during spring

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Abstract

Pikeperch (*Sander lucioperca* L.) is a broadly distributed fish species in Europe but little is known about its ecology in the southern part of its distribution area in warm climatic conditions. The aim of this study was to analyse pikeperch rate of movement and to assess whether it displayed a diel pattern related to temperature. Thus acoustic telemetry was used to track adult pikeperch in a drainage canal located in south of France. The survey was carried out in spring, during the spawning period. The results showed that females were more active than males. This is in accordance with previous data on the nest guardian behaviour of the males. For both genders, the activity rates increased during the study period as water temperature rose. Males and females displayed the same diel activity with a maximum at dusk, thereby confirming many indirect observations. Nevertheless, inter-individuals variations were observed. Thus, these results on diel activity are rather a general trend than a strict rule and suggest the involvement of other factors than light intensity in the control of diel activity. This diel rhythm is positively correlated to water temperature for females. Pikeperch activity may be the result of a trade-off between physiological requirements of temperature and light, satisfaction of energy needs and avoidance of predators.

Introduction

The pikeperch (*Sander lucioperca* L.) is a large piscivorous Percid fish broadly distributed in Europe. Its range extends from the Caspian Sea to the Iberian Peninsula and from the Scandinavian waters to the Mediterranean basin, as well as in the United Kingdom. Nevertheless, most of the information about its ecology and its demography comes from the northern and the eastern parts of its distribution area (e.g. Dahl, 1984; Nyberg et al., 1996) where it has an important commercial and recreational value.

Previous studies using mark-recapture methods (Goubier, 1975; Fickling & Lee, 1985) have shown that pikeperch could travel over relatively long distances (10–30 km and exceptionally >200km). Some of these movements correspond to seasonal migrations associated with stages of its life cycle. In early spring, adults migrate to reach spawning areas (Lehtonen, 1983; Lehtonen & Toivonen 1988; Koed et al., 2000) which are used every year, revealing a spawning site fidelity (Puke, 1952; Lehtonen & Toivonen 1988; Jepsen et al., 1999). In autumn, when water temperature decreases, pikeperch migrate to deeper overwintering areas (Lind, 1977; Lehtonen, 1983). Furthermore, some of these migrations (over 10 km) were attributed to the search for prey fish (Lind, 1977; Lehtonen, 1983; Fickling & Lee, 1985; Koed et al., 2000). Although the migratory behaviour of the pikeperch is generally well understood, its diel activity pattern is still poorly documented. Pikeperch is a predator considered as active during crepuscular and nocturnal periods. This was deduced from physiological considerations (Ali et al., 1977) or from other indirect observations (i.e. diet analysis see Fedorova & Drozzhina, 1982). Indeed, the pikeperch's retina possesses a *tapetum lucidum* (layer of cells reflecting and intensifying light) that enables it to navigate in turbid waters an low light conditions (Ali et al., 1977). Studies of the stomach contents at different periods of the day have shown that pikeperch exhibited crepuscular feeding patterns (Fedorova & Drozzhina, 1982). Various anecdotal observations made by anglers generally support these results (Pollet, 1959; Linfield & Rickards, 1979) but some high capture rates have also been reported in summer during periods when the daily light intensity was highest (Tarragnat, 2001).

However, this is all based on indirect evidence (i.e. tagging, diet contents, angling). To our knowledge, no studies using techniques providing direct evidence and aiming at describing the diel activity of pikeperch have been conducted or published. Using radio-telemetry, Jepsen et al. (1999) localised pikeperch every 6 h, a frequency that is sufficient neither to highlight a diel pattern nor to link it to environmental factors (Baras, 1998; Ovidio et al., 2000).

Our study lasted from March to June 2002 (i.e. during the spawning period) in a drainage canal located in the southern part of the pikeperch distribution area. We used acoustic telemetry to investigate the activity of adult pikeperch during the spawning period. The aim of the present paper was (i) to assess whether pikeperch gross rate of movement varied among month or gender and (ii) to assess whether the pikeperch displayed a diel activity rhythm and if so if this rhythm could be related to temperature conditions.

Materials and methods

Study site

The study site was located in the Rhône delta, southern France (43°34 N, 4°34 E) (Fig. 1). The Fumemorte canal collects water from a complex canal network spreading over 68 km^2 (Chauvelon, 1998). The main channel is 14.6 km long but if the largest tributaries are included, it forms a 32.5 km canal network (Fig. 1). The canal is shallow (1 m) and around 14 m wide. It drains freshwater from marshes and rice fields and flows into the Vaccarès lagoon. At its outlet, the Fumemorte canal has a raisable barrier designed to limit entrance of salt water. The barrier being submerged; most of the mobile aquatic organisms can move between the canal and the lagoon (Rosecchi & Crivelli, 1995). The Vaccarès lagoon is brackish (salinity >10 ppt), and the salinity in the Fumemorte canal varies from 0.1 ppt in summer to 5 ppt in winter depending on the agricultural activities and on the strength and direction of the wind. The water remains highly turbid throughout the year (Secchi depth >40 cm). The mean monthly water temperature ranges from 6.5 °C in January (with minima at 1.0 °C) to 23.5 °C in July (with maximum upto 27 °C). A more detailed description of the study site is provided in Poulet et al. (2004).

Pikeperch is the most abundant piscivorous fish in the Fumemorte canal. The fish community is mainly composed of topmouth gudgeon (*Pseudorasbora parva* L.), bleak (*Alburnus alburnus* L.), sand smelt (*Atherina boyeri* R.), eel (*Anguilla anguilla* L.), crucian carp (*Carassius gibelio* L.), common carp (*Cyprinus carpio* L.), pumpkinseed (*Lepomis gibbosus* L.), mullet (*Mugil cephalus* and *Liza* spp.), rudd (*Scardinius erythrophthalmus* L.), black bullhead (*Ameiurus melas* L.), wells catfish (*Silurus glanis* L.) and pike (*Esox lucius* L.). A total of 34 species occurs in the Fumemorte basin (Crivelli, Pers. com.).

Capture and tagging

Thirteen pikeperch were captured in the Fumemorte canal (Table 1) with fyke nets (mesh

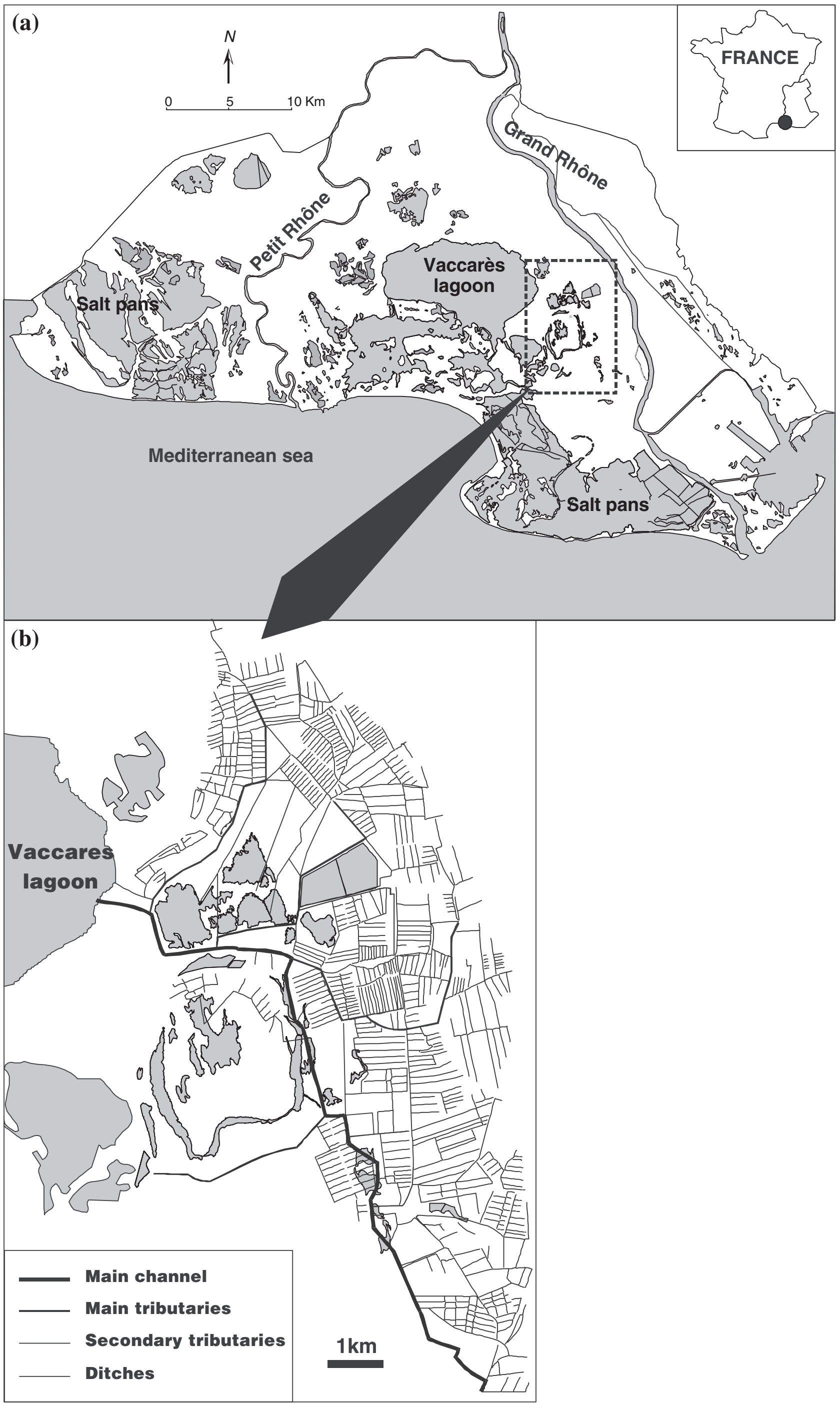

Figure 1. Study site. (a) The Rhône delta in Southern France. (b) The Fumemorte basin.

size 6 mm) and gill nets (mesh size 40, 55 and 80 mm). Most of fish were captured from late January to early March, except three in late March and one in April. Only the latter had spawned. At this period of the year, external features allow a visual determination of the gender: males exhibit a dark abdomen while that of females is white and bigger (Deelder & Willemsen, 1964).

Because of the high water conductivity (>1000 μS cm^{-1}), we used acoustic transmitters (Lotek CAFT 11_3, 40 mm × 11 mm, 9.2 g in air, 4.5 g in water) identifiable by individual code and operated at 76.8 kHz. Their life span was theoretically at least 172 days with a pulse rate of 1 beat every 5 s.

Fish were anaesthetised in a bath containing 0.5 ml l^{-1} of 2-phenoxyethanol, measured (fork length) and weighed. Internal implantation of transmitters was preferred to external attachment because Koed & Thorstad, (2001) had shown that it did not influence the swimming speed of pikeperch and the method had been employed in previous studies on pikeperch without any trouble (Jepsen et al., 1999; Koed et al., 2000; Koed & Thorstad 2001). The anaesthetised fish were placed in a V-shaped support. The transmitters were disinfected (Hibitan) and then surgically implanted into the body cavity through a ventral 20 mm incision posterior to the pelvic girdle. Antibiotic (Duphapen LA, 0.1 ml kg^{-1}) was injected in the body cavity to prevent post-surgery infections. The incision was closed with three independent sutures (Ethicon Vicryl 2/0). These sutures were absorbable, but should have lasted for about 1 month. Fish were also marked with coloured spots on the pelvic girdle using Alcian blue injected with a dermojet. This enabled anglers to identify and release them in case of capture. Each operation took about 5 min and the fish were returned to an oxygenated recovery tank. Recovery time was about 5 to 10 min but fish were maintained one night in observation and released the following morning near their capture point.

Tracking

The fish were tracked from boat using a directional hydrophone connected to a receiver (Lotek model SRX_400). Their locations were determined according to the signal strength. When a signal was first received, the motor was turned off to approach as quietly as possible. Tracking session took place monthly from March to June over 24 h with positions recorded every 2 h beginning at 06.00 h. The time reference was according to the Universal Time Coordinated (UTC) that also corresponds to the Greenwich Mean Time (GMT). The positions were recorded using a GPS receiver. Due to the length of the canal and the number of tracked individuals, tracking all of them in a single session would not have allowed a 2 h time lapse between consecutive locations. Thus, a preliminary survey was carried out the day before each session in order to choose the individuals to be tracked. Only those within a 5 km reach were tracked the next day (even if they left this perimeter). A second 24 h session was performed 1 week later (other tracking experiments for different purpose occurred in this lapse of time) to track the remaining fish. Those fish that had not been tracked by the end of the second session were considered missing for the month. Thus the selection of the tracked fish did not depend either on their activity or the easiness of positioning but on their position the day before the session. So there was no bias leading to an underestimation of the fish movements (Gowan et al., 1994).

Analysis

We used Mapinfo 6.5 (Mapinfo, 2000) to report fish position on a digitised map of the Fumemorte basin. The distance covered by a fish between two consecutive positions (i.e. 2 h interval) was assessed. This distance represented the minimal distance covered since we did not know if the fish swam in a straight-line. Then, the rate of movement was calculated by dividing this minimal distance by the time separating the two consecutive fish positions and expressed in m h^{-1}. Although this method clearly underestimates fish activity, it does provide some relevant insights into the patterns of gross activity (Cooke et al., 2001).

First of all, Pearson correlations were used to assess the relationship between mean rate activity and fish length. The distances travelled in 24 h (i.e. for a given fish, the sum of the distances measured between the successive positions), daily ranges (i.e. for a given fish, the distance between the most upstream and the most downstream positions) and rates of movement were then compared between months and between genders using non-parametric tests (Mann–Whitney and Kruskal–Wallis tests). Diel patterns were studied graphically using Lowess fitting. In order to assess

Table 1. Fork Length, weight, tag/fish mass in air ratio (%), gender and tracking session of the 13 adult pikeperch tracked

Code	FL (mm)	W (g)	Tag:Fish mass ratio (%)	Gender	Tagging date	End of tracking date	Fate	24 h tracking sessions							
								06/03	13/03	04/04	11/04	15/05	22/05	05/06	12/06
46	386	509	1.8	M	08/02	11/02	Cormorant								
50	451	770	1.2	M	19/02	09/07	Unknown	■		■		■		■	
62	472	1057	0.9	F	26/04	28/06	Unknown								
73	624	2800	0.3	F	25/02	13/06	Unknown		■		■		■		?
74	452	921	1.0	F	20/02	09/07	Recaptured		■		■		■		■
86	474	1186	0.8	F	06/02	09/07	Fisherman	■		■			■		
96	395	567	1.6	F	08/02	28/06	Angler					■			
110	605	3600	0.3	F	22/03	03/05	Dead?				■				
128	390	619	1.5	M	28/01	09/07	Unknown	■		■		■		■	
143	629	3150	0.3	M	08/02	26/04	Unknown	■		■					
152	414	612	1.5	M	08/02	11/02	Unknown								
162	385	528	1.7	M	06/02	11/02	Unknown								
170	491	1209	0.8	M	29/03	28/05	Angler				■		■		
Mean/ Total	474	1348	1.0					4	2	4	4	3	4	2	1

Black square: fish tracked and ?: fish lost due to battery failure.

the link between activity and temperature, Spearman correlations were performed between mean rates of movement by gender and by 2 h interval and mean temperature by 2 h interval.

Results

Tracking and survival of tagged fish

Thirteen fish were tagged (Table 1) during this experiment. Three individuals (N°46, 156 and 162) disappeared before the beginning of the tracking experience. Transmitter N°46 was found in the water beneath a great cormorant (*Phalacrocorax carbo*) resting place located on the canal bank. Fish N°156 and 162 were never found. Pikeperch N°143 was lost in late April. Another pikeperch (N°170) was captured by an angler in June. Fish N°110 became stationary from mid-April until the battery ran out. Attempts to make it move failed: it could have died or lost its transmitter. As the transmitter was in woody debris, we were unable to recuperate it. The battery of N°73 ran out of power during the June session.

All the fish have not been tracked each month and/or in a same 24 h session. Indeed, the canal network was very large and pikeperch did not necessarily remain in the main canal (Poulet, unpublished data). Thus in order to position fish every 2 h, a maximum of four fishes per 24 h has been tracked.

Pikeperch N°74 was recaptured on 10th July: it had a 516 mm fork length for 1370 g that is a growth of 64 mm and 449 g since its initial capture (20th of February). The scar due to transmitter implantation was completely healed and hardly visible. Pikeperch N°96 was caught by an angler on late May 2004. Its size at this time was about 800 mm, i.e. the double of its size at the tagging time, a year and a half earlier. The other individuals were not recaptured either because their transmitters were running out of power or because they were located in private parts of the canal where we did not have fishing authorisation.

Activity

There was no correlation between the mean daily rate of movement (m h^{-1}) and the length of pikeperch either for males (Pearson correlation, $R = -0.41$, $p = 0.585$, $n = 4$) or for females (Pearson correlation, $R = 0.79$, $p = 0.11$, $n = 5$) or both genders combined (Pearson correlation, $R = 0.3$, $p = 0.43$, $n = 9$). Thus, all statistical analyses were performed on all the individuals, regardless of the size.

The three highest daily ranges were 3410, 2917 and 2394 m performed by three different females. For all months pooled, the daily range was larger for females than for males (Mann–Whitney test, $U = 26.5$, $p = 0.007$). Although the mean daily range was shorter in March (Table 2), there was no difference between months regardless of the gender (Kruskal–Wallis Test, $p = 0.460$).

The three highest distances travelled in 24 h were 7561, 5284 and 4945 m, corresponding to the three females having the largest daily home ranges. Fifty-four percent of the daily distances travelled were over 1000 m and 33% over 2000 m. Both daily range and distance travelled displayed high standard variation suggesting an important individual variability (Table 2).

Table 2. Mean (± standard deviation) of daily range (DR, m) and daily distance travelled (DT, m) of pikeperch in the Fumemorte canal among genders and months

Month	Gender	Nb. of pikeperch tracked	DR	DT
March	Male	3	168 ± 116	313 ± 155
	Female	3	905 ± 1111	1769 ± 749
April	Male	4	547 ± 852	954 ± 1416
	Female	4	2010 ± 1111	3932 ± 3020
May	Male	3	426 ± 450	1476 ± 1626
	Female	4	1531 ± 1077	2820 ± 1674
June	Male	2	598 ± 554	1104 ± 685
	Female	1	22	53

The highest rate of movement recorded in a 2-h interval was 2640 m h^{-1} moved by a female in March. This speed represents 1.62 body lengths per second (bl s^{-1}). All the other rates of movement recorded were below 775 m h^{-1}. The highest movement was an outlier and therefore excluded from further analysis. During the study, the daily mean water temperature increased from 8.6 to 25.7 °C (Fig. 2). The males significantly increased their rate of movement from March to June whereas females displayed more constant rate apart from June (Table 3, Fig. 3). Within each month, males exhibited a lower rate of movement than females except in June (Table 4, Fig. 3).

Diel pattern

An important individual variability in the diel pattern was observed (Fig. 4). For example, fish N°86 moved preferentially in the morning whereas N°74 and 128 were mostly active at dusk. All of the males have remained still during at least one whole session. Several individuals, both males and females, displayed similar diel patterns among months when they were moving (N°73, 74 and 86). Conversely, pikeperch N°50, for example, displayed diurnal activity in April and May but later shifted to activity peaks in the morning and early night. Water temperature was significantly correlated to the diel activity for female ($n = 11$, $R = 0.62$, $p = 0.04$) but not for males ($n = 11$, $R = 0.28$, $p = 0.52$) (Fig. 5).

Discussion

Tracking protocol

From the 13 fish tagged initially, nine were successfully tracked. One of these pikeperch has

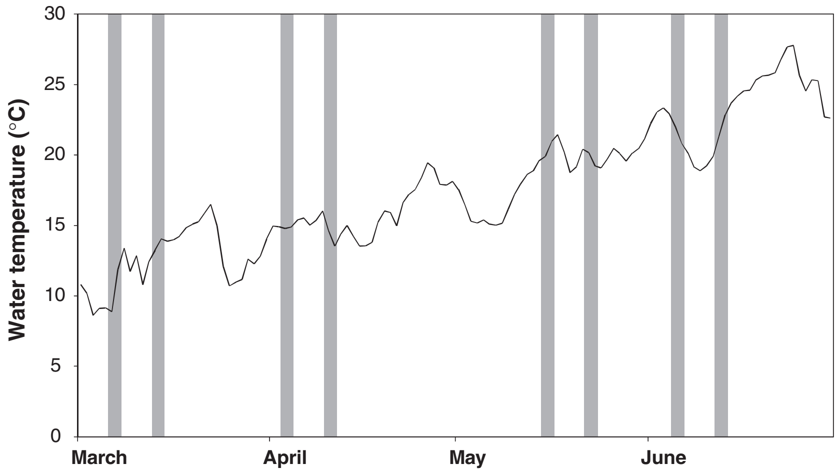

Figure 2. Water temperature in the Fumemorte canal basin within the study period. The shaded parts indicate the tracking sessions.

Table 3. Pairwise comparisons of the rate of movement between months for both gender using Mann–Whitney test

Gender	Males				Females			
Month	March	April	May	June	March	April	May	June
March		688.5	373.5	189.5		544.0	560.0	70.0
April	ns		570.5	308.5	ns		961.0	85.0
May	*	ns		337.5	ns	ns		102.0
June	**	*	ns		**	**	*	

U values are above the diagonal and *p* values below.
*$p < 0.05$; ** $p < 0.01$; ns: not significant.

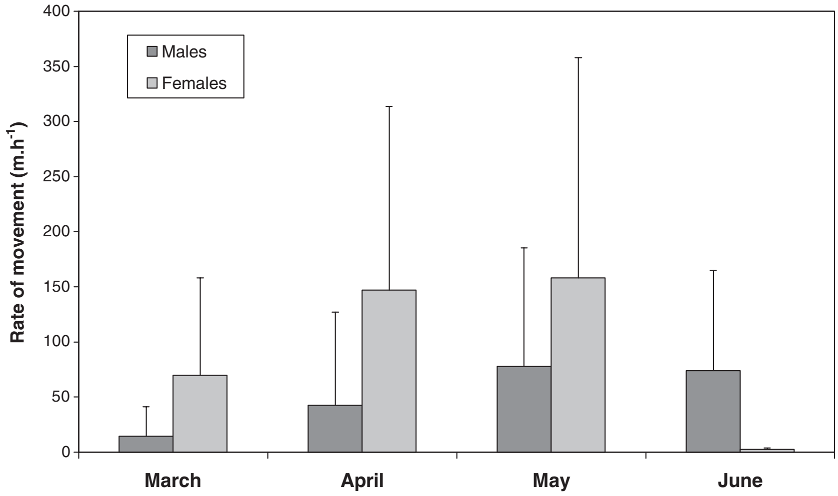

Figure 3. Pikeperch mean rate of movement (+1 standard deviation) from March to June in the Fumemorte canal.

Table 4. Pairwise comparisons of the rate of movement between genders for each month using Mann–Whitney test

Month	*U*	*p*
March	313.5	**
April	554.0	***
May	575.0	ns
June	30.0	***

*$p < 0.05$; **$p < 0.01$ ns: not significant.

probably been predated by a great cormorant, which is not surprising since it is able to swallow an adult pikeperch (Santoul et al., 2004). Indeed, many of our marked pikeperch displayed scars obviously caused by these birds. The fate of the three other missing tagged fish remained unknown. During and after the study, two pikeperch were caught by anglers and one by a fisherman: this gives some indications on the predators of pikeperch in the Fumemorte canal and on the disappearance of the other tagged fishes.

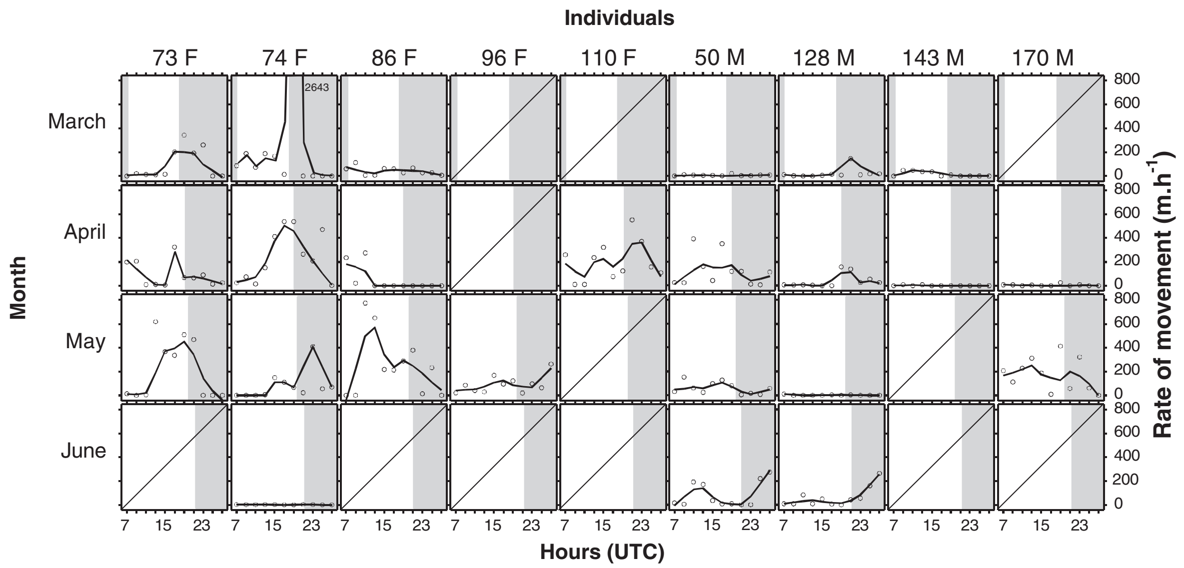

Figure 4. Rate of movement (m s^{-1}) of each tracked pikeperch (number and gender are indicated with M for male and F for female) during each 24 h session fitted according a lowess curve. The shaded parts represent low light periods.

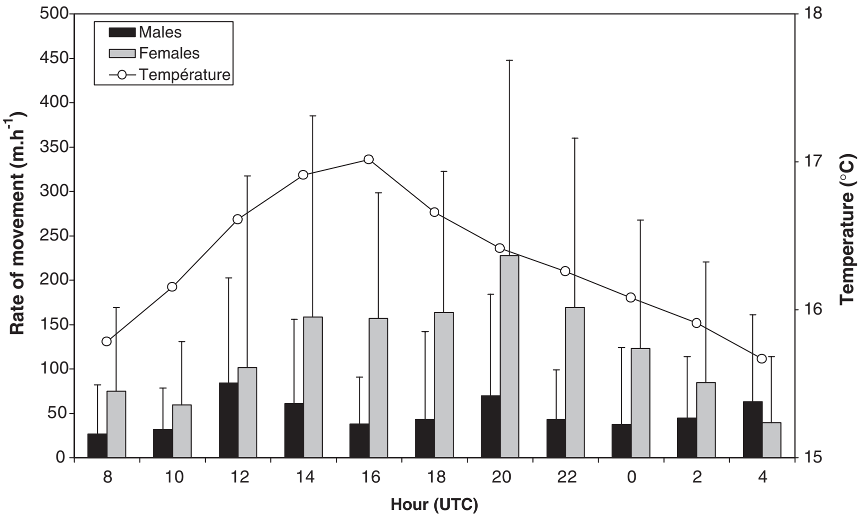

Figure 5. Diel pattern of hourly mean (± standard deviation) rate of movement (m s^{-1}) of male and female pikeperch and mean of water temperature (°C).

In our study, the tag to body mass ratios were close to the values of former successful studies on this species which did not show any trouble (Jepsen et al., 1999; Koed & Thorstad, 2001; Jepsen, 2003). The two individuals recaptured after 4 and 29 months displayed a growth in accordance with previous results for this population (Poulet et al., 2004) which confirms that pikeperch have well bear the transmitter implantation.

General behaviour

In the Fumemorte canal, pikeperch can move over quite long distances in 24 h: the majority of the observations were over 1 km with a maximum of 7.5 km. Comparison with the daily distance travelled in spring and in similar water temperature by female shows it is higher (over 3.5 km) in the Fumemorte canal than in the Bygholm reservoir (Jepsen et al., 1999) or in the River Gudenaa (Koed et al., 2000) (both 2 km) in Denmark. This could reflect a difference in the tracking protocol. Precision of positioning differed according the method and the frequency of positioning could have a major influence on the estimation of the distance travelled (Baras, 1998; Ovidio et al., 2000). When calculating the daily distance travelled on a 6-h interval basis, we found that females travel on average 2.7 km which is not so different from the results of Jepsen et al. (1999) and Koed et al. (2000). Overall, our results suggest that the pikeperch is able to exploit a large part of the Fumemorte network.

Although pikeperch is a slow swimmer like the majority of Percids (Craig, 2000; Peake et al., 2000) we observed some fast movement (1.6 bl s^{-1}). On a 6 h-interval basis, our fastest movement becomes 0.28 bl s^{-1} and the second fastest movement, 0.16 bl s^{-1} which is in the same range than the results of Jepsen et al. (1999). With an interval of 0.5 h, we might have found values as high as those found by Kelso (1976) for walleye (i.e. upto 3 bl s^{-1}).

Unlike in Jepsen et al. (1999), neither the mean rate of movements nor the mean daily range were significantly correlated to fish length. However, as far as females are concerned, the relationship between length and rate of movement displayed a high ($R = 0.79$) but not significant correlation coefficient due to the low size of the sample ($n = 5$). Thus the absence of significant correlation on the whole sample can be explained by the fact that our study was performed during the spawning period when males are less active whatever their size.

Spring activity

In March and April, males displayed a significantly lower rate of movement and daily range than females. This is consistent with the spawning behaviour previously described (Jepsen et al., 1999; Koed et al., 2000). The male prepares the nest and takes care of the eggs and the young fry (Sonesten, 1991; Craig, 2000). In this nest guarding species, although the male is less mobile, it also spends energy since parental care is costly (Cooke et al., 2002). Indeed, the males have less opportunity to feed when guarding the nest (Goncalves & Almada, 1997). On the contrary, the females spend very little time on the nest (Erm, 1981; Lappalainen et al., 2003) but invest much energy in vitellogenesis since the species displays a high fecundity (about 200 000 eggs kg^{-1}). Consequently, high female activities during the spawning period could respond to an increase in the food needs (Schlumberger & Proteau, 1996; Jepsen et al., 2000) in order to maintain energetic reserves and ensure metabolic functions.

The activity of both genders increased from March to May as the water temperature rose and day length increased. Indeed, water temperature in the Fumemorte canal had still not reached 27 °C, i.e. the physiological optimum temperature for pikeperch (Hokanson, 1977) by the end of the study in May. Therefore, we could assume that the activity will increase until the water temperature is around 27 °C. This positive relationship between temperature and pikeperch activity is consistent with previous results obtained on an annual scale (Jepsen et al., 1999; Koed et al., 2000). Nevertheless, rate of movement seemed to stabilise or even decrease in June. This suggests that other factors (e.g. dissolved oxygen) influence the activity before temperature reach pikeperch optimum. Nevertheless, too few fish have been tracked in June to be affirmative.

Diel activity

Pikeperch displayed a diel activity rhythm in the Fumemorte canal during spring. Nevertheless this diel activity was more obvious for females than for males, most of them being stationary on the nests. Our direct observations showed that during the spawning period pikeperch were mainly crepuscular, which is consistent with its status of low-light hunter (Ali et al., 1977) and confirmed the many indirect observations suggesting activity peaks during the dark hours (Fedorova & Dorzzhina, 1982; Craig, 2000). We also observed inter-individual variations: some pikeperch were rather diurnal, which has already been observed (Jepsen et al., 1999; Tarragnat, 2001). Hence, the maximum activity at dusk is rather a general trend than a strict rule. These results suggest the involvement of other factors than light intensity in the control of the activity rates. We showed that temperature was an important factor driving female diel activity. Water temperature plays a major role in swimming speed of fish (Hergenrader & Hasler, 1967) and as the water temperature in spring was below the pikeperch physiological optimum, perhaps this explains why pikeperch moved more during the warmest hours. Like many predators, pikeperch may adapt its behaviour to increase the probability of meeting its prey (e.g. Jepsen et al., 2000). The peak of water temperature occurs at dusk and most fish activity depends on temperature. Fish behaviour may also depend on predator avoidance (Metcalfe et al., 1999). The Rhône delta is an important wintering or nesting area for many piscivorous birds and this may influence fish behaviour (e.g. Allouche & Gaudin, 2001). As the Great Cormorant is diurnal (Cramp & Simmons, 1980), it could be less risky for pikeperch to move during the dark hours.

To conclude, in the Fumemorte canal, the rate of movement increased from March to May, with the females being more active than the males, travelling over quite long distances in 24 h. Both sexes displayed the same diel activity pattern between months with a maximum activity at dusk and a minimum at dawn. The diel rhythm of pikeperch may be driven by the trade-off between its physiological requirements of temperature and light, satisfying its energy needs and avoiding predators. The influence of these factors in the overall behavioural patterns of pikeperch could be assessed with telemetry experiment performed in controlled conditions (e.g. with or without predator) and using electromyogram (EMG) transmitters to quantify the activity (Cooke et al., 2004).

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