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An assessment of the upstream migration and reproductive behaviour of allis shad (*Alosa alosa* L.) using acoustic tracking

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We provide a detailed description of the migratory and reproductive behaviour of allis shad (*Alosa alosa* L.), a species that is in decline in Europe. Adult swimming behaviour during the last part of upstream migration and on a spawning ground downstream of an insurmountable dam was studied in detail and its main features identified, "characterized" in this context. Mobile telemetry and a fixed telemetry system were used to record fish positions and to monitor 23 acoustically tagged individuals (17 females and six males) during the 2001 and 2002 reproductive seasons. Allis shad showed considerable exploratory behaviour, and a rest area was observed 1.5 km downstream of the spawning ground. Thirteen individuals were observed on the spawning area, though both males and females spent most of their time (70–99%) away from it. Male and female residency times on the spawning area were, respectively, 1–11 days and 1–7 days, and females were observed during both day and night on the spawning ground. In 2002, an analysis of the 3D swimming behaviour on the spawning ground of six individuals allowed us to estimate the number of spawning events per fish. Males participated in more spawning acts (up to 60) than females (0–2).

Keywords: *Alosa alosa*, anadromous migration, behavioural ecology, reproduction, telemetry.

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Introduction

Allis shad (*Alosa alosa* L.) are anadromous, and have a pelagic-sea life mainly inshore along the coast migrating to the higher, middle watercourse of rivers to spawn. They are also semelparous: reproduction in large rivers being characterized by an upstream, spring migration and nocturnal spawning (Cassou-Leins *et al.*, 2000). Spawning occurs at the water surface and involves a fast, circular swimming movement during which gametes are released (Cassou-Leins *et al.*, 2000). Usually, there are several spawning grounds for populations in large river systems. Currently, this species is classified as vulnerable in Europe because of the reduction in its distribution and the threats to its freshwater habitat due to dams, pollution, and the deterioration of the spawning grounds (Baglinière *et al.*, 2003). In France, research on the biology and conservation status of allis shad has mainly focused on populations in large river systems, such as the Loire (Mennesson-Boisneau and Boisneau, 1990), the Garonne (Cassou-Leins *et al.*, 2000), the Gironde (Taverny *et al.*, 2000), and the Adour (Prouzet *et al.*, 1994). More recently, investigations of allis shad from small French rivers of the Atlantic coastal zone (Véron *et al.*, 2001) have revealed perennial populations and functional spawning grounds. Studies on the migratory behaviour have focused only on the first phases of upstream migration and no work has been carried out on the last phase, namely the arrival of spawners on the spawning

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grounds (Mennesson-Boisneau *et al.*, 2000) until relatively recently.

The allis shad population in the River Aulne (Brittany, France) congregates in one area to spawn, and the last phase of migration and spawning has been studied here since 1997. Early results showed that the spawners have similar ecological characteristics (demography, migratory, and reproductive activity) to the populations observed on large rivers (Véron, unpublished data). Population-level reproduction was studied by counting night acts of spawning (Cassou-Leins *et al.*, 2000). This method is used on all the rivers colonized by the species, but allows only an approximation of the reproductive potential of a population. In addition, it provides little information on the other aspects of the allis shad's reproductive behaviour, such as the time spent on the spawning grounds, the number of spawning events per female, and the number of males and females taking part in one spawning event. Such information is essential to evaluate the number of spawners present on a spawning area as well as the reproductive potential of a population.

To investigate these points, a detailed study of the breeding behaviour of shad on the Aulne using acoustic telemetry was conducted at the same time as a biological and ecological study of the population, the aim being to establish patterns of activity during the final stage of upstream migration, to determine residency time on the spawning ground, and to estimate the number of spawning events.

Material and methods

Study site

The catchment of the River Aulne (1875 km^2 in surface) is the third largest of the coastal rivers of Brittany. The source is on granite, and the river then penetrates the schist of Châteaulin before arriving at the roadstead of Brest after vast meanders for 145 km, of which 70 km are channelled and have 28 dams. The first dam met by upstream-migrating fish (Gilly Glas) is about 30 km from the river mouth and can be crossed by a fish pass at high tides (Figure 1). The second dam is Châteaulin at the limit of tidal influence. This sill has a fish pass with vertical slits that allow the passage of migrating fish species, such as allis shad, eels (*Anguilla anguilla* L.), sea lamprey (*Petromyzon marinus* L.), Atlantic salmon (*Salmo salar* L.), and sea trout (*Salmo trutta* L.). The pass is also equipped with a video system that allows the number of migrating fish to be counted.

The study area comprises 2.3 km of channelled river located between the dams of Châteaulin and Koatigrac'h, the latter being insurmountable by allis shad because of an unsuitable fish pass (Figure 1). The study area was divided into four subsections. Sector B was the deepest (>3 m deep) while sectors A, C, and D had average depths that varied between 1.80 m and 2.15 ± 0.30 m according to water-discharge levels. The upstream end above sector D was the most important spawning ground for allis shad (Figure 2). The physical habitat of this spawning area was similar to that described for larger rivers, with a coarse gravel bar below a deep pool (Boisneau *et al.*, 1990; Cassou-Leins *et al.*, 2000). Water-current speeds observed during the two years of our study (0.1–1.2 $m\ s^{-1}$) were low compared with those characteristic of other natural spawning grounds (1.5–2 $m\ s^{-1}$) on large rivers (Cassou-Leins *et al.*, 2000). The spawning area was not followed downstream, as is usual, by a shallow, fast-running zone, a fact which underlines the artificial nature of this spawning site. Its area, estimated by visual localization of spawning events, was 3000 m^2. Depths ranged between 0.1 and 1.9 m. In the zone covered by the fixed acoustic system, depths were between 1.3 and 1.7 m with variations of ±0.30 m related to water flow.

Water flow was measured by DIREN Brittany, Direction Régionale de l'Environnement, a national agency. Water temperature on the spawning area was recorded hourly by a datalogger (Minilog, Vemco Ltd.).

Fish capture and tagging

Allis shad are regarded as being very sensitive to handling (Larinier *et al.*, 2000), and so great care was taken to optimize fish survival at all stages. Fish were taken out of the trap at Châteaulin with a landing net and anaesthetized in a 60-l tub with 2-phenoxy-ethanol (0.2 $ml\ l^{-1}$) in 2001 and clove oil (0.5 ml of clove oil diluted in 0.8 ml of alcohol for 10 l of water) in 2002. For each fish, the sex was determined by applying gentle pressure on the abdomen (males were all ripe, with running milt), total and fork length were measured (Lt and FL, ±5 mm), and the fish were weighed (Mf ± 50 g, Table 1). A scale sample was taken to estimate age (Baglinière *et al.*, 2001). The fish were tagged internally by gently sliding the acoustic tag through the mouth into the stomach while they were held underwater. This was an adaptation of the method used by Steinbach *et al.* (1986) and Moser *et al.* (2000), illustrated in Bridger and Booth (2003). Handling of fish under anaesthesia never took more than 2 min before they were transferred into a second tub that received freshwater via a pump. The shad were held for 40 min on average to be sure that the transmitter was not regurgitated, and when they adopted a normal posture and swimming behaviour they were released upstream of the dam.

We tagged ten shad (eight females and two males) in 2001 and 13 (nine females and four males) in 2002. The pressure-sensing acoustic transmitters used (IBDT-97, Sonotronics, Tucson, Arizona, USA) were 6 cm long × 0.6 cm wide, weighed 7–8 g in air, and had an approximate lifespan of 15 days (Table 1). Each transmitter emitted at a unique frequency (69–83 kHz), which was used to identify individuals. The range for manual tracking

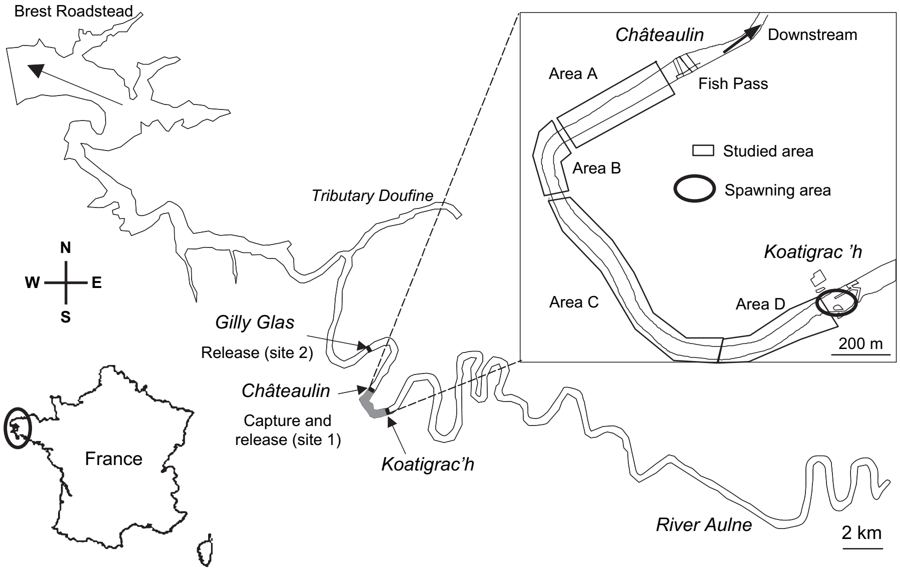

Figure 1. Map of study site within the River Aulne, western France. Areas A, B, C, and D refer to specific sections of the channel. (The coordinates of the Brest roadstead are 48°23′N 04°29′W.)

was measured at 150 m (±5 m) for this study area. This was done by progressively moving an immersed tag away from the acoustic manual receiver and measuring the distance of the farthest point that allowed signal reception. This estimation was made in both years, at the beginning of each study in the River Aulne. The accuracy of depth data was ±0.5 m for manual tracking in 2001 and ±0.1 m for manual and fixed tracking in 2002. Accuracy was checked

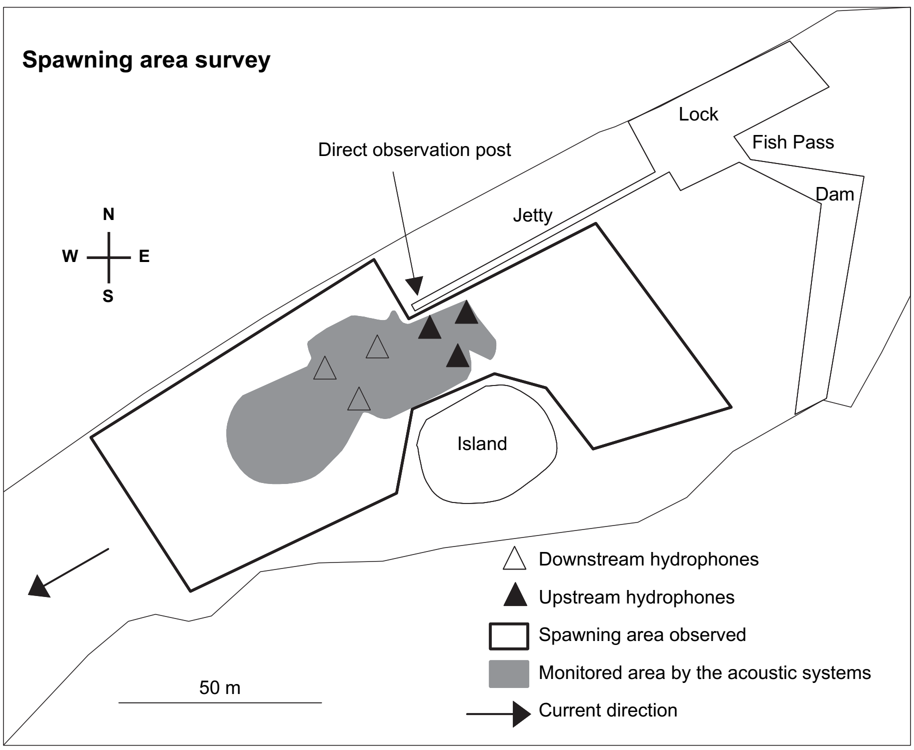

Figure 2. Location of the fixed acoustic-positioning system on the spawning ground. Overall, the two fish-positioning systems covered 21% of the spawning area, including approximately half of the most active spawning activity.

Table 1. The characteristics of tagged allis shad and report of the time spent per fish in the channel and on the spawning area in 2001 and 2002.

Year and shad number	Tagging date	Sex	Total length Lt (cm)	Standard length FL (cm)	Mass of the fish Mf (g)	Condition factor K = Mf/FL^3	Estimated age (year)	Ratio Mt/Mf (%)	Released site	Active tracking (day)	Time spent between Châteaulin & Koatigrac'h (Tc) (days)	Time spent on the spawning area: Total of days	Number of daylights (day, hours) Nd	Number of nights (day, hours) Nn	Nd/Tc (%)	Nn/Tc (%)	Total time on the spawning ground (%)
2001																	
1	23 May	F	54.5	e48.7	1 396	2.03	NA	0.50	1	4	17						
2	30 May	F	58	e51.6	1 660	2.32	5	0.42	1	7	13						
3	4 June	F	59	e52.4	1 200	1.66	6	0.75	1	6	10	7	7(50 h)	4(22 h)	20.8	9.2	30.0
4	6 June	F	53.5	e47.9	1 370	2.01	5	0.66	1	8	11	1	1(15 h)	1(3 h)	5.7	1.1	6.8
5	9 June	F	51	45.5	900	0.98	5	1.00	1	13	14						
6	12 June	F	51.5	47	950	1.01	5	0.95	1	6	7						
7	12 June	F	58.5	52	1 260	1.21	5	0.56	1	7	11	4	4(19 h)	4(18 h)	7.2	6.8	14.0
8	16 June	M	51	46	850	0.92	4/5	1.06	1	11	14	1	1(2 h)	0	0.6		0.6
9	16 June	F	51.5	46	900	0.97	5	0.78	1	5	4						
10	18 June	M	51.5	45	1 000	1.11	4/5	0.70	1	8	12	1	1(4 h)	0	1.4		1.4
2002																	
11*	22 April	F	65	57	1 600	1.40	5	0.44	2	8	8	5	5(28 h)	4(25 h)	14.6	13.0	27.6
12*	22 April	F	61.5	54	1 800	1.66	4	0.39	2	7							
13*	22 April	M	57	52	1 400	1.34	5	0.50	2	7							
14*	22 April	F	61	54	2 000	1.84	4	0.35	2	4							
15*n	30 April	F	64	56	2 450	2.18	5	0.34	1	7							
16n	30 April	M	51	47	1 250	1.32	4	0.66	1	17	24	11	8(26 h)	10(65 h)	4.5	11.3	15.8
17nb	6 May	M	55	48	1 450	1.50	4	0.57	1	7	9	3	3(11 h)	3(6 h)	5.1	2.8	7.9
18nb	6 May	M	49	43	1 050	1.22	5	0.79	1	15	19	10	1(2 h)	10(51 h)	0.4	11.2	11.6
19nb	13 May	F	62	56	2 200	1.96	5	0.38	1	0							
20nb	13 May	F	59	53	2 300	2.16	4	0.36	1	4	4	1	1(3 h)	1(2 h)	3.1	2.1	5.2
21nb	20 May	F	54	47	1 650	1.75	5	0.50	1	11	16	2	2(5 h)	1(2 h)	1.3	0.5	1.8
23nb	27 May	F	56	50	1 700	1.69	5	0.49	1	2							

"n" indicates allis shad tagged with a high, depth-sensitive transmitter (±0.1 m compared to ±0.5 m for the others); "b" indicates external tagging with Betalights®; "*" indicates a shad followed by active tracking downstream of Châteaulin; F: female; M: male; NA: data not available; "e": shows fork lengths that have been estimated from the total length measured according to the linear regression obtained from the other individuals (FL = 0.81Lt + 4.06; $R^2 = 0.97$, n = 13).

Age has been evaluated by scale reading. Mt stands for tag mass in the air and is used to calculate the ratio in the air between tag mass and fish body mass (Mf).

for each tag by progressively immersing the tag, recording the signal every 0.1-m depth increment, and calibrating each tag based on the resulting data.

External luminous tags were attached to some individuals in 2002 to provide additional information on shad reproductive behaviour during night-time (after Clough *et al.*, 2000). Tags (Betalight®, 30 mm in length by 2 mm in diameter) were attached with Kevlar line to the base of the dorsal fins of 47 individuals: seven (two males and five females) already tagged with acoustic transmitters and 40 others (20 males and 20 females). Those 40 individuals were tagged between 13 May and 17 May 2002.

Fish monitoring

All fish tagged in 2001 and nine fish (six females and three males) in 2002 were released upstream of the Châteaulin dam (site 1, Figure 1). In 2002, four individuals were released just upstream of the Gilly Glas dam (site 2, Figure 1) to examine the migratory behaviour between dams. During both years, fish were tracked using a portable receiver and directional hydrophone (receiver VR60; hydrophone VH10, Vemco Ltd.). In addition, a fixed telemetry system (VRAP, Vemco Ltd.) was used to obtain precise and semi-continuous positioning of fish on the spawning area (Klimley *et al.*, 2001). The system comprised three buoys, each equipped with an omni-directional hydrophone and a radio operator modem for transmitting data to a base station. Each immersed hydrophone was located using a differential GPS and triangulation method to later reference fish position on a map. The system successively monitored each frequency for 10 s, thus providing consecutive data on each fish's position and depth (two to six individuals tracked at the same time). In 2001, the fixed-telemetry system covered a surface area of approximately 400 m^2 (13.3% of the spawning ground). In 2002, a first positioning system ran from April 24 to May 22 and then from June 1 to June 5, and a second system was deployed upstream between May 16 and May 24. The two acoustic-positioning systems did not operate between May 25 and June 1 because of high flows ($>30\ m^3\ s^{-1}$). These systems surveyed areas of 520–640 m^2, corresponding to 13–21% of the spawning area, and included 50% of the most active spawning sites identified by direct night counting of spawning events (Figure 2). The upstream acoustic system functioned less well than the downstream system because it was placed in a zone with a stronger current.

Experimental set-up and acoustic data analysis

Protocol and data analysis procedure for active tracking in the channel

Tagged fish were manually tracked immediately after their release for 2–5 h in 2001 and 4–9 h in 2002. For the remainder of the study period, tracking was carried out daily (approximately every 3 h) between Châteaulin and Koatigrac'h from 06:00 to 01:00 (U.T. +2) at a rate of five diurnal and two nocturnal locations per fish per day. In 2002, tracking was extended downstream of the Châteaulin dam. Fish positions were located by taking reference points identified by differential GPS on the edges of the river and swimming depth was noted. Positions were integrated in a geographical information software (GIS, Arcview 3.2, ESRI) in order to visualize channel use, with associated depth, and to estimate differences the area frequented. Because of the non-normality of the data, a non-parametric statistical test (Kruskal–Wallis) was used to compare day–night and gender differences in water-column utilization.

Protocol and data analysis procedure for fixed tracking on the spawning area

Based on the quality of the received signals, the coordinates of each fish position were converted to Lambert II coordinates and integrated in the GIS. Then each fish position was visualized on the study-area map, and a second data selection, carried out manually with GIS and Excel, checked for aberrant values of swimming speed ($>6\ m\ s^{-1}$) and depth (>2.5 m) due to altered acoustic signals. The data collected allowed the presence of individuals on the spawning ground to be determined by day and by night. Night was defined as between 22:00 and 08:00 (U.T. +2) according to direct observations of the spawning activity in 2001. Data relating to depth and swimming speed on the spawning ground were available for 2002 only.

General reproductive activity was defined as the number of nights spent on the spawning ground. In 2002, the number of spawning events was estimated on the basis of distinctive "swimming depth" and "swimming speed".

The fixed-telemetry system provided a depth for each fish for each 10-s scan period. That depth value corresponded to an average of all the depth values (accuracy $\pm$ 0.1 m) received by the system during each 10-s scan; there was approximately one position recorded per second but only one depth value accessible to the operator for the whole scan period. A spawning event lasted on average 4 s according to direct observation and time keeping of a fraction of spawning acts (9.6% and 1%, respectively, in 1999 and 2001). Knowing that during a 10-s scan a fish could carry out the act of reproduction for 4 s at the surface (0–0.2 m) then go deeper (up to 1–1.4 m) for the 6 s following and *vice versa*, we calculated that the maximum average depth for an act of 4 s would be 0.9 m. Thus, sequences that lasted between 4 and 10 s at average depth 0–0.9 m were retained as one criterion for characterizing an act of reproduction. It neglected a proportion of reproduction acts shorter than 4 s that were followed or preceded by a deeper fish position.

The range of swimming speeds during spawning events was estimated according to the characteristics defined in the literature (Cassou-Leins *et al.*, 2000) and by direct observation and timing of the spawning act in the River Aulne. As the average diameter of a spawning event in this area was 1 m (0.8–1.2 m) (Cassou-Leins *et al.*, 2000), its average duration 4 s (2–10 s) and the numbers of circles carried out by the spawners averaged 2 (1–3) (Cassou-Leins *et al.*, 2000), the speed of a spawning event was calculated to be between 0.6 and 2.7 $m\ s^{-1}$ (1.5 $m\ s^{-1}$ on average). Swimming speed included in this range had to be maintained during at least 4 s in succession to be considered distinctive. Thus, shad that maintained at the same time a depth and a swimming speed in these ranges were regarded as having participated in a spawning event.

Results

Environmental conditions and tagged fish behaviour

In 2001, the start of the study was delayed until May 23 because of high flows ($> 11\ m^3\ s^{-1}$), and the study ended on July 2. During this period flows ranged between 3 and 11 $m^3\ s^{-1}$, and water temperatures ranged between 17.2°C and 22.9°C. This period coincided with the second peak of the migration, which lasted from April 16 to July 3, and by May 23, 50.6% of the spawners (2188 out of a total of 4326 counted at Châteaulin pass) had migrated upstream (Figure 3). The population spawning activity began on May 12 and ended on July 12, with the number of spawning events counted every night (16 851 spawning events in total).

In 2002, the acoustic study lasted from April 22 until June 5. The weather was cool and rainy with water temperature ranging between 12.6°C and 17.8°C. The study covered the entire migration period which started earlier than in 2001 but with fewer migrating shad (2315 compared to 4326 in 2001, Figure 3). Thus, fish tagging was spread over the entire period of migration, with the first tagged shad released and tracked on April 22 when 102 individuals had entered the river. The population spawning activity began between April 21 and May 1 and ended on July 11; the number of spawning events for the population was counted on three nights each week between May 6 and July 11 (6310 spawning events estimated in total).

During both years, there was no immediate mortality following tagging. In 2001, no downstream swimming behaviour or regurgitation were observed but still half the tagged fish were never found on the spawning ground

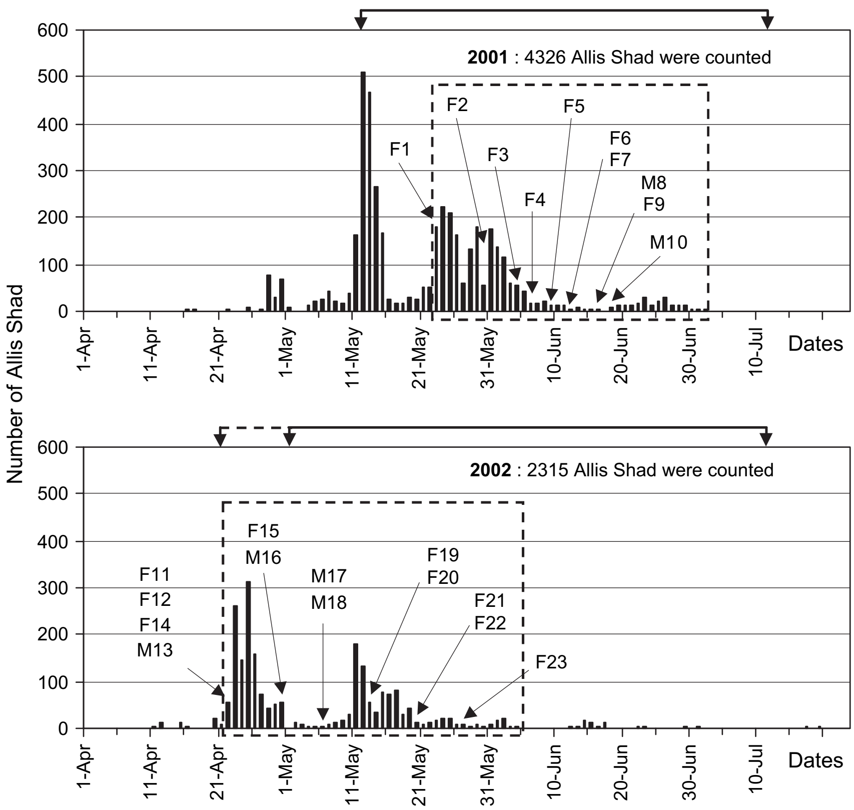

Figure 3. The number of allis shad counted by video monitoring at the Châteaulin fish pass in 2001 and 2002 in relation to time. The study period is outlined (dashed line) and the dates of fish tagging (M = male, F = female followed by the fish identity number) are noted. The population's reproduction-activity period is delimited with arrows.

(Table 1). We believe that the eventual arrival of females 1 and 2 on the spawning ground were not recorded by the fixed acoustic system for technical reasons. In 2002, three of the four fish released at site 2 reached the Châteaulin dam in less than 24 h. Male 13 and female 14 were located close to the dam of Châteaulin but remained downstream for periods of 10 and 4 days, respectively, until the end of their transmitter's lifespan. Female 11 crossed the Châteaulin dam and reached the spawning ground after one day. Among the nine individuals released at site 1, two females moved downstream, either immediately (female 23), or after 24 h (female 15) and died below the Châteaulin dam, after one and eight days, respectively. Female 19 regurgitated its transmitter. In total, the migration and reproduction behaviour of 17 allis shad was studied between the Châteaulin and Koatigrac'h dams, and 12 of these fish were observed on the spawning ground.

Fish activity in the channel

In 2001, the analysis of the condition factor did not show any intra-sex or intersex differences (males $P_{KW} = 0.32$, n = 2, d.f. = 1, females $P_{KW} = 0.43$, n = 8, d.f. = 7, males–females $P_{KW} = 0.19$, n = 10, d.f. = 1). In 2002, the comparison of tagged-fish condition factor highlighted gender differences with a condition factor in favour of females (males $P_{KW} = 0.39$, n = 4, d.f. = 3, females $P_{KW} = 0.43$, n = 9, d.f. = 8, males–females $P_{KW} = 0.009$, n = 13, d.f. = 1) (Table 1). Comparing years, no difference between females ($P_{KW} = 0.25$, n = 17, d.f. = 1) or males ($P_{KW} = 0.06$, n = 6, d.f. = 1) was underscored. However, if the four females from 2001 whose fork length (FL) was estimated were removed from the statistical analysis, then females in 2002 had a better condition factor than in 2001 ($P_{KW} < 0.01$, n = 13, d.f. = 1).

During the first hour after release, none of the tagged shad moved more than 200 m. After this time, movement rates within the channel were highly variable with the first significant movement after 4–9 h.

Over both spawning seasons, between 30–80% of fish positions were located in area A, which extended 400 m upstream the Châteaulin dam and area B, which formed the first meander (Figure 4). Time spent in the channel did not differ between males and females (males = 15.6 ± 5.9 days; females = 10.5 ± 4.2 days; $P_{KW} = 0.10$, n = 17, d.f. = 1) (Table 1).

In 2002, no differences in the depth distribution of shad were observed between day and night ($P_{KW} = 0.771$, n = 404, d.f. = 1), and so data were pooled to examine gender differences. Males were found at shallower depths in the water column than females (males = 1.16 ± 0.49 m; females = 1.37 ± 0.48 m; $P_{KW} < 0.01$, n = 404, d.f. = 1). For example, 20% of the time males were found at depths ranging from the surface (0 m) to 0.8 m below the surface (±0.1 m), compared to less than 8% for females for the same depth range.

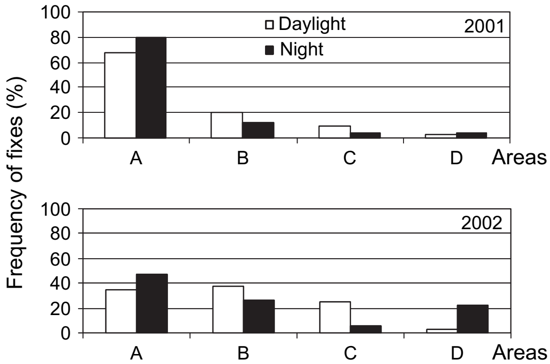

Figure 4. The frequency of fish fixes recorded by active tracking, by section of the stream channel, (Figure 1) in 2001 and 2002. The number of positions recorded (N) by daylight (d) and by night (n): Nd = 181, Nn = 25 in 2001; Nd = 248, Nn = 58 in 2002.

Fish activity on the spawning ground

Of the 20 tracked fish, we were able to document the movements of ten individuals (three in 2001 and seven in 2002) at night on the spawning ground (Table 1) when the water temperature was equal to or higher than 14 °C (Figure 5). The percentage of time that individual shad spent at night on the spawning area varied from 2.8 to 11.3% for males and from 0.4 to 13.0% for females (not significantly different: $P_{KW} = 0.21$, n = 10, d.f. = 1, Table 1).

In 2001, males 8 and 10 were tagged towards the end of the spawning run (Figure 3) and were recorded on the spawning ground only once and during daylight hours (Table 1, Figure 5). In contrast, three female shad (3, 4, and 7) attended the spawning ground during both day and night and their total residency time on the spawning ground was between one and seven days (Table 1). Forays to the spawning ground for some portion of the night were observed for two females (3 and 7) on four nights. Female 4 spent only the beginning of one night (from 22:00 to 01:00 U.T. +2) on the spawning ground after having spent all the day there.

In 2002, time spent by females and males on the spawning area at night was very variable (females: 1–25 h, mean = 7.5 ± 11.6 h; males: 6–65 h, mean = 40.6 ± 30.8 h) (Table 1, Figure 5). Four females (11, 20, 21, and 22) attended the spawning area both by day and night and their total residency time there was between one and five days (Table 1). Female 11, tagged at the beginning of the spawning run and at the early beginning of the reproduction activity (Figure 3), visited the spawning grounds on four nights, including two complete nights, and five times during the day. Female 20, one of the youngest and showing one of the highest condition factors (Table 1), was observed on the spawning ground only for a few hours during the day and night on the same day. Females 21 and 22 were twice observed on the spawning ground with night visits only at the beginning (F21) or at the end (F22) of the night. During this time, the flow abruptly increased and very few

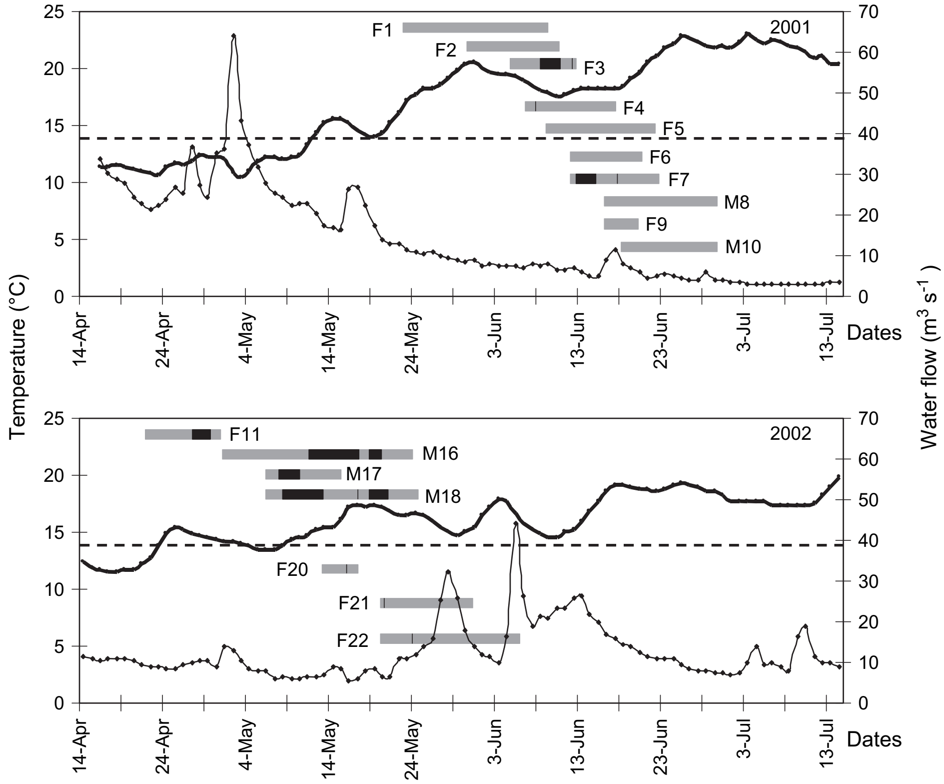

Figure 5. The nocturnal fixed-tracking observations (black) for tagged females (F) and males (M) on the spawning ground in relation to temperature and water flow. The duration of active tracking in the channel between Châteaulin and Koatigrac'h is represented in light grey.

spawning events were observed directly. The three tracked males reached the spawning ground when the water temperature exceeded 14°C (Figure 5), during three (M17) and ten nights (M16 and M18) for the whole season. The presence of males 16 and 18 at night on the spawning area was 3−28 times longer than during daylight hours (Table 1). In spite of a presence in the channel four days after its arrival on the spawning ground, male 17 did not return. Males 16 and 18 were no longer found in the study area after an abrupt increase in flow ($>15\ m^3\ s^{-1}$).

Diurnal and nocturnal swimming depths on the spawning grounds were significantly different within sexes (females: day $P_{KW} < 0.01$, $n = 266$, d.f. = 2; night $P_{KW} < 0.01$, $n = 144$, d.f. = 2; males: day $P_{KW} < 0.01$, $n = 3305$, d.f. = 2; night $P_{KW} < 0.01$, $n = 8191$, d.f. = 2); these large intra-sex differences did not allow us to carry out statistical comparisons between sex. However, for three males and two females (F20 and F21), more than 50% of the swimming activity at night happened between the surface and 1 m deep (Figure 6A). During daylight, this depth range accounted for more than 50% of the swimming activity for two males (M16 and M18) and two females (F20 and F21) (Figure 6A). Indeed, average swimming depth was close to 1 m at night for all the fish except F21 (0.74 ± 0.5 m) and it was more variable during daylight (between 0.67 ± 0.3 and 1.45 ± 0.2 m) (Figure 6B).

In 2002, shad tagged with Betalight® were observed on the spawning ground from three days to more than one month after the date of last tagging. Direct night observations, without lighting or disturbance, on shad participating in 12 spawning events over 65 observations (Figure 7), allowed their movements close to the surface and their extremely jerky trajectories to be observed. Such behaviour was also seen on the swimming trajectories recorded by the acoustic system. Direct observation allowed the measurement of the maximum swimming speed on two individuals during a straight trajectory, which peaked at $6\ m\ s^{-1}$.

Identification of spawning events

In 2001, two males (8 and 10) that attended the spawning ground only by daylight, probably did not spawn since allis shad are described as night spawners by Cassou-Leins *et al.* (2000). The three tagged females (3, 4, and 7) were present at night, and they could have reproduced on this site during four nights (F3 and F7) and a few hours in one night (F4).

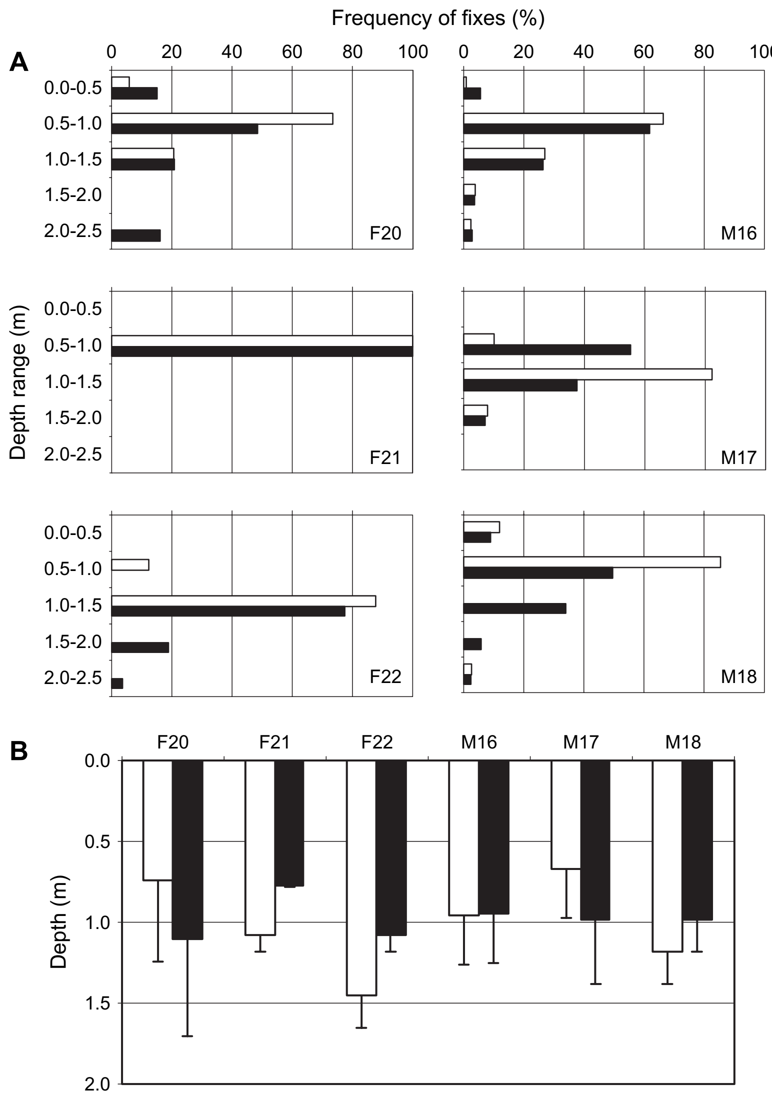

Figure 6. A histogram of individual swimming depth on the spawning area in relation to day (white bars) and night (black bars) (2002 records). (A) Frequency of fixes per depth class for each fish. (B) Average swimming depth and standard deviation per fish. (The number of fixes recorded (N) by daylight (d) and by night (n): F20: Nd = 68, Nn = 87; F21: Nd = 22, Nn = 8; F22: Nd = 196, Nn = 49; M16: Nd = 2806, Nn = 7176; M17: Nd = 347, Nn = 141; M18: Nd = 152, Nn = 4634.)

In 2002, information regarding depth and swimming speeds on the spawning ground was used to supplement the "presence/absence" data to characterize spawning events. Using our criteria, no spawning events occurred during daylight. The three females in which spawning activity could be assessed spent only one partial night on the spawning ground. One female (F20) was estimated to have participated in two spawning events, reinforced by the direct observation of two spawning events located at the same time and in the same sector. The analysis of the swimming behaviour of female 21 suggested only one probable spawning act at the beginning of the night (22:00 U.T. +2). For female 22, no spawning act could be detected. In fact, this female came on the spawning ground for only 1 h at the end of the night (06:00–07:00) (U.T. +2). Swimming depths of female 11 were not available because it was equipped with the same type of transmitter used in 2001 (depth decoding only during active tracking). However, it was observed for four successive nights, including two complete nights, on the spawning grounds and may have spawned during this period.

According to the selected criteria, male 17 could have taken part in three acts of reproduction during three successive partial nights on the spawning ground (one participation per night). A possible participation in spawning at the beginning of night (21:00 U.T. +2) was

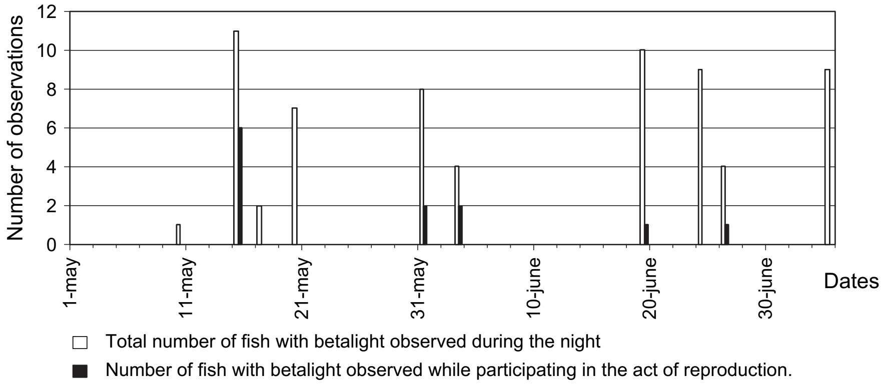

Figure 7. The number of nocturnal observations on the spawning ground of Betalight®-tagged fish in relation to time.

noted twice. For the two other males (18 and 16), their participation was estimated at 38 and 60 acts, respectively, for the ten nights spent on the spawning ground. Participation in spawning events during a single night was variable, with a maximum of 16 and 12 acts for the two males (M18 and M16), respectively.

Discussion

This study has recorded allis shad activity patterns during the last phase of the spawning migration. It shows the existence of a rest area away from the spawning ground. Furthermore, it indicated that the actual time spent by tagged fish on the spawning area was quite limited in duration. Acoustic telemetry showed individual variability in behaviour, but also highlighted differences in the pelagic distribution of males and females outside the spawning area and a higher level of participation in spawning events by males as compared to females.

Methodological aspects: tagging and acoustic system

This is the first telemetry study to be carried out on this species, though radio tracking has been employed to study migratory behaviour near dams in Europe (Steinbach *et al.*, 1986; Travade *et al.*, 1989). Acoustic-telemetry studies on homing and the effects of dams on the upstream progression have been carried out on the American shad (*Alosa sapidissima*, Wilson) in North America (Dodson and Leggett, 1973; Beasley and Hightower, 2000; Moser *et al.*, 2000). More recently, a hydroacoustic technique was developed to quantify and assess the ecological requirements for the spawning migration of twaite shad (*Alosa fallax*, Lacépède) in a shallow river (Gregory and Clabburn, 2003). During this acoustic study, of the 23 allis shad tagged, 12 were actually observed spawning, and it is possible that capture and tagging as well as the tagging dates, at the beginning or at the end of the spawning activity period, may have had some impact on the behaviour observed on the spawning ground. Two females died after moving downstream, possibly due to handling stress (Dodson and Leggett, 1973; Steinbach *et al.*, 1986) and increase in flow just after tagging and release. The large body size of allis shad and the high condition factor of one female might have caused it to regurgitate the tag, as observed by Steinbach *et al.* (1986). These observations suggest a greater sensitivity of females to handling compared to males, as a consequence perhaps of their higher condition factor. However, the high success rate for tracking fish (17/23) suggests that the care taken during capture and handling (Larinier *et al.*, 2000) and the low ratio of the mass of the transmitter to fish was not a problem, being much lower than the 2% recommended by Ross and McCormick (1981). This study highlighted some recommended procedures for handling shad viz.

(i) time in the trap should be as short as possible because fish concentration during the peaks of migration increases the risks of wounds,

(ii) the use of light anaesthesia may reduce handling stress and recovery time after tagging, and,

(iii) a 30-min period of recovery time in a constant, circular water current may avoid tag regurgitation and limit confinement stress.

The movement of individual shad released upstream of Châteaulin was restricted to an area of 200 m upstream of the dam during the first hours after release and suggested a recuperation period that varied among individuals (1−10 h) due to the stress caused by handling and by the crossing of the fish pass. This period of behavioural and physiological adjustment following tagging, which includes time of hydrostatic-balance recovery following the addition of the transmitter mass, was documented by Arnold and Holford (1978). Whereas previous studies have shown that shad tend to descend rivers following similar tagging stress (Dodson and Leggett, 1973; Steinbach *et al.*, 1986), the limited downstream movement of shad in our study was probably due to the presence of relatively calm water conditions upstream of the dam and the fact that individuals were probably physiologically ready to reproduce: the males had running milt and both sexes were caught whilst migrating upstream to the spawning area. In the Loire study (Steinbach *et al.*, 1986), allis shad were captured in the middle reaches of the river, well below their spawning ground, and at a less advanced stage of sexual maturation. Thus, the imminence of reproduction may overcome the disturbances induced by the handling and stomach tagging. The same observation was made for the Atlantic salmon during a radio-tracking study undertaken at the time of the upstream migration to the spawning ground (Baglinière *et al.*, 1990).

The use of the external tags (Betalight®) gave complementary information on the duration of the presence of fish in the channel which was up to 6 weeks for some individuals, on their participation in spawning events, and on their general swimming trajectories during spawning.

The positioning of the acoustic antenna on the spawning ground was crucial because the acoustic-wave propagation was disturbed by the speed and turbulence of the currents (Winter, 1983). Thus, the definition of a threshold value for the correct operation of this technique is particular to each site. This threshold value was determined during technical testing at the beginning of the study in 2001, when the water flow was high and did not allow the acoustic-positioning system to operate. The tracking system was disabled in conditions of flow higher than $11\ m^3\ s^{-1}$ ($55-95\ cm\ s^{-1}$ in 2002) at the study site, where the river is 25–50 m wide with a depth ranging between 1 and 3 m.

Fish behaviour in the channel

In 2001, three tagged females did not reach the spawning ground. Their poor condition (condition factor ≤ 1) and their arrival at the end of the migration suggested that they had previously spawned. Indeed, during the migration peak, we did occasionally observe in 2001 concentrations of allis shad downstream of Châteaulin dam and acts of reproduction were noticed. Moreover, Cassou-Leins *et al.* (2000) noticed that the average spawners' age, length, weight, and condition factor tend to decrease in the course of migration and that in some years, depending on the spawners' abundance or environmental conditions, a temporary spawning ground can be observed. Nevertheless, the absence of these females on the spawning ground suggested that the crossing of Châteaulin dam, in addition to the stress of handling, was sufficient to reduce their reproduction capacities in spite of a partial maturation of the ovaries (Cassou-Leins *et al.*, 2000) which might have allowed spawning at different favourable areas along the river.

In 2002, results for four individuals released downstream of Châteaulin dam showed the problem of such obstacles impeding upstream progression of allis shad in rivers (Larinier *et al.*, 2000). Only one tracked individual returned across the Châteaulin dam in less than 15 days, the lifespan of the transmitter. Nevertheless, spawning in the River Aulne was not observed downstream of Châteaulin that year, and the other tagged fish could have crossed the pass after the end of the lifespan of the tag.

The large number of fish located in the deepest area of the channel (an old pit 1.5 km below the spawning ground) and the small number of appearances at the spawning ground in time (both day and night) suggested that this was a rest area. When allis shad could not be located either by active tracking or by the fixed system, we believed them to be in areas inaccessible to acoustic tracking located just downstream of Koatigrac'h dam. This site could also be used as a rest area by actively migrating individuals at the time of their exploration of the dam of Koatigrac'h before trying to cross it. Such fish-concentration areas during migration have been observed on the River Loire, particularly downstream from sites of crossing of obstacles (Steinbach *et al.*, 1986). Further, the physiological state of allis shad, that deteriorates over the breeding season, and results in many of them dying (Mennesson-Boisneau *et al.*, 2000), will make them passive to the current.

Fish behaviour on the spawning ground

In both years, tagged fish were present at night on the spawning area when the water temperature rose over 14°C. Such a temperature influence on reproductive activity has been already highlighted for allis shad populations in a larger river (Cassou-Leins *et al.*, 2000).

We observed three important findings with respect to allis shad reproductive behaviour not previously documented. First, shad were observed on the spawning ground during both day and night. Second, time spent on the spawning grounds was limited and, at most, accounted for 30% of the total time shad were resident in the river between the Châteaulin and Koatigrac'h dams. Finally, there were sex differences in reproductive behaviour. Though the daytime presence on the spawning ground was extremely variable, the females seemed to spend more time on the spawning ground during day than at night. Two of three tagged males in 2002 spent more time on the spawning grounds at night than all the females. This is in accordance with previous findings of a highly skewed sex ratio of spawning shad in favour of males (25:1; Le Clerc, 1941). Differences in the nocturnal use of the spawning ground by females (one or four nights) might be linked to the rhythm of egg expulsion. Thus, females may have attended the spawning ground only when they were fully ripe (ovulated stage), whereas all males in the river were fully mature and could be on the spawning ground as soon as the environmental conditions (i.e. temperature, flow) were favourable. Our observation of four individual females on the spawning grounds on several nights over a period of 4–7 days supports the idea of a partial maturation of ovaries and that eggs are spawned in three to seven batches over a few days (Sabatié, 1993; Cassou-Leins *et al.*, 2000). In the case of females that spent one night on the spawning ground, the explanation is less clear and may differ from year to year. Females in 2001 were tagged at the end of the spawning run and reproduction activity was observed at a temporary downstream spawning ground. These fish had a lower condition factor than those in 2002, suggesting that they may have spawned some batches of eggs before being tagged. In 2002, it would imply that they only reproduced once despite their high condition factor (1.4–2.1). In that case, it could mean:

(i) that their split maturation was very short and that they expelled most ovules during only a few hours in one night or,
(ii) that the dam stopped the upstream progression of the spawners and disturbed the partial maturation of ovaries for some individuals, thus inducing a massive loss of eggs for the population.

At the end of the period of migration, males attended the spawning ground only during daytime. This might reflect an exploratory phase in front of the obstacle more than reproduction attempts. However, the low number of tagged males (two per eight females) did not allow us to collect night data on the spawning ground.

Estimation of spawning events

Although we used swimming-activity characteristics to estimate the number of spawning events, it is necessary first to underline the limits of the results obtained. Observations were limited by:

(i) the number of fish followed and the associated sampling rate;
(ii) the possibility of recording partial spawning events linked to the period of scanning; and
(iii) the fact that only half of the most active spawning ground was surveyed by the acoustic system.

Tracked females and males displayed spawning behaviour before total darkness (between 19:00 and 22:00 TU +2). This twilight spawning was also directly observed during the spawning survey of the whole population, but they represented only 5% of the total counts of spawning events at the time of our 2001 study. This behaviour could be a result of both individual variation and the presence of a large number of spawners on the spawning ground at the time of the migration peak, which would cause a spreading out of the spawning timing towards twilight conditions.

Three females were estimated to have participated in 0, 1, and 2 spawning events occurring during a few hours in the same night, with the last two acts spaced 7 min apart. These observations did not support current assumptions that only one laying of eggs would happen per night per female and that one spawning act would involve only one female (Cassou-Leins *et al.*, 2000). The estimation of the spawning events of the Aulne shad population based on sex ratio and on the counting of spawning events (6310 in the whole of 2002) showed that, on average, seven acts of reproduction were carried out by each female during the breeding season. While this is close to values reported elsewhere (Cassou-Leins *et al.*, 2000), it does not give any information on the number of spawning events over one night. If we apply the principle of only one spawning event per night for each tagged female, we would obtain up to four acts of laying per female during the spawning season, whereas the estimation method based on the swimming behavioural characteristics for all fish suggests more than one spawning act per night per female which spent only a few hours on the spawning ground. These observations showed the difficulty of using the number of spawning events per female as a standard method to estimate the number of females participating in spawning or present on the spawning ground.

The three males reaching the spawning ground showed a large disparity of temporal frequentation and participation in spawning. One male spent three nights with an estimated three participations in spawning events. The extended night frequentation of the spawning ground (ten nights) for the two other males suggested that they tried to participate in many more spawning events. As males are sexually active during all the spawning season, one male can presumably spawn with several females successively. For these two males, estimates of spawning activity were very high (38–60 events), although this does not necessarily imply fertilization by the emission of gametes. Between three and eight individuals were involved in half of the spawning events directly observed for the whole population. It was also reported on the River Loire that a considerable proportion of spawning events involved several pairs (Boisneau *et al.*, 1990). The high level of participation in reproduction by tagged males suggests that males attempt to maximize reproductive success through spawning frequency. High levels of participation in reproduction by males were also observed in other migratory and freshwater fish species (Baglinière *et al.*, 1991; Beall, 1994; Poncin, 1996; Mjølnerød *et al.*, 1998).

In conclusion, the present study has added greatly to the knowledge of allis shad behaviour in the final stage of migration and during reproduction. In particular, it showed the existence of a separate resting/prespawning area away from the spawning ground. Thereby, this study has raised the question of whether the requirement for a separate "resting", prespawning area away from the actual spawning ground is critical for shad to sustain populations in rivers. It would be interesting to look for the presence of such resting areas in larger rivers and to implement habitat management that takes this into account. Further, identification of a spawning event using spatial data remains a challenge. Although acoustic telemetry proved to be a useful tool, it was limited by the precision of the technique and the necessary compromise between the number of fish followed and the sampling rate. The high inter-individual and intersex variability observed in our study made it difficult to extrapolate the number of spawning acts to the whole population. However, it indicated the need to focus reproduction research on the identification of environmental factors governing shad presence on the spawning ground and of rhythms and capacities for egg laying by females.

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