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FISH TELEMETRY

Sea lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds

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Abstract Historical spawning grounds for sea lampreys (*Petromyzon marinus* L.) in most Portuguese river basins are becoming inaccessible due to the construction of impassable dams and/or weirs. Studies like the one described in this paper are particularly important in areas like the Vouga river basin, where there is a considerable fishing effort from both professional fishermen and poachers. In fact, for management and conservation purposes, it is important to clarify several aspects of the sea lamprey spawning run in this particular watershed. Therefore, a total of 30 radio tagged, migrating sea lampreys were released in the River Vouga and some of its main tributaries during 2004 and 2005. Results from the tracking sessions were used to determine the effect of poaching on the spawners' population and the characteristics of the resting sites used during the upstream movement. The rivers' stretches were also characterized according to the type of substrate present in the riverbed and flow type, in order to determine its aptitude to constitute appropriate spawning habitats for sea lampreys. We have identified in the upstream stretches of River Vouga, and in the tributary River Caima, characteristics that are particularly suitable for the construction of nests by the spawners. Presence of larvae provided evidence that spawners migrated into the River Vouga's upper reaches. However, abundance and age class diversity appeared to be higher downstream of Sernada and Carvoeiro weirs, corroborating the telemetry data which suggested difficulty in passing these obstacles during low precipitation years. In the River Caima, migration was most predictable, which might be related to daily water releases from a small hydropower dam at dusk, that stimulated the lampreys to resume migration. Poaching has had a considerable negative effect on the success of the tagged lampreys' migration: 76% of the animals released during 2005 were captured.

Keywords *Petromyzon marinus* · Radio telemetry · Resting sites · Spawning migration · Poaching

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Introduction

The sea lamprey (*Petromyzon marinus* L.) is an anadromous species that spawns in the main Portuguese River basins. Sea lamprey spawners initiate their migration in the Portuguese rivers in the middle of December, with the migration peaking between February and April and spawning usually taking place between May and June, depending on the meteorological conditions (Almeida et al., 2000). Studies carried out with holobiotic specimens showed no evidence of homing behaviour (Bergstedt & Seelye, 1995). Other authors suggest that some environmental factors such as the water temperature, the type of substrate and river flow (Morman et al., 1980; Young et al., 1990) or the release of a migratory pheromone by stream-dwelling larval lamprey (Teeter, 1980; Li et al., 1995; Vrieze & Sorensen, 2001; Sorensen & Vrieze, 2003; Fine et al., 2004; Sorensen et al., 2005) may act as a fundamental stimuli to the adult sea lamprey, guiding them to spawning streams. Mature, spermiated, male sea lamprey also release a potent sex pheromone that induces preference and searching behaviour in ovulated female lampreys (Li et al., 2002). During this period, sea lampreys exhibit a prominent pattern on the migratory activity, being active invariably through the night period and seeking rocky substrates for shelter at dawn (Hardisty & Potter, 1971; Stier & Kynard, 1986; Kelso & Gardner, 2000; Almeida et al., 2000; Almeida et al. 2002a; Quintella et al., 2004).

The gastronomic importance of sea lampreys is reflected by their high commercial value, which can easily reach € 45 per animal during the peak of the season. The high economic value of the sea lamprey in Portugal, and particularly in the Vouga River basin, makes them preferred target of both professional fishermen and poachers, creating a major threat to the sustainability and conservation of Vouga's sea lamprey population. Gravel extraction, dredging, pollution and habitat destruction resulting from the river regulation create additional threats to the survival of this species in the Portuguese rivers (Assis, 1990; Almeida et al., 2000; Almeida et al., 2002a; Rogado et al., 2005). In particular, the interruption of the Vouga's longitudinal continuity has clearly contributed to significant reduction in the habitat available to both spawners and ammocoetes. There are already several physical obstacles that interrupt the migratory path of the sea lampreys and a dam is also projected to be built soon in the River Vouga, an enterprise that will promote additional alterations in the aquatic community equilibrium, particularly for diadromous species present in this basin (i.e. sea lamprey; river lamprey *Lampetra fluviatilis*, L.; European eel *Anguilla anguilla*, L.; allis shad *Alosa alosa*, L.; twaite shad *Alosa fallax*, Lacépède, 1803).

Since the available spawning grounds for this species in most of the Portuguese river basins is quite limited due to the construction of impassable dams, it seems extremely relevant to clarify some aspects concerning the sea lamprey spawning run in the Vouga river basin. Therefore, the goal of this study was to determine the effect of poaching on the migrating sea lamprey in the Vouga river basin, to identify the main obstacles to the migration of adult sea lamprey spawners in the River Vouga and its main tributaries, and to identify and characterize the sites where the sea lampreys rest during their spawning migration. Additionally, a characterization and evaluation of these rivers' aptitudes according to the river bed flow type and the existing substrate type as appropriate spawning grounds for this species was also performed. This study assumes particular importance in rivers like Vouga, where there is a considerable fishing effort from both professional fishermen and poachers. During the 2004/05 spawning season, this situation was aggravated by an abnormally dry winter season, with extremely low precipitation.

Study area

The River Vouga is a medium size Portuguese river (148 km) whose basin covers an area of 3,635 km^2 in the northern part of the country (Fig. 1), being limited by the Douro and the Mondego river basins to the North and to the South, respectively (Loureiro & Macedo, 1986). It drains into the Atlantic Ocean in the Ria de Aveiro (45 km^2), an extremely productive estuary with an important fishing industrial activity.

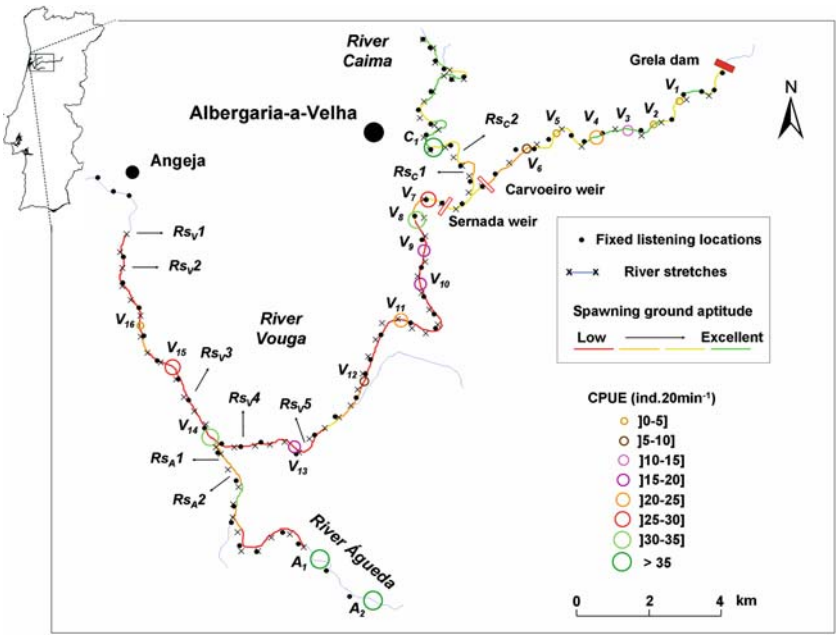

Fig. 1 Map of the Vouga river basin and results from the 2004 electrofishing campaign represented in captures per unit of effort (CPUE–individuals captured in 20 min fishing) in selected sampling sites along the studied watercourses. River stretches limits and their aptitude as spawning grounds are also represented. RS_Vn, Release sites in River Vouga; RS_Cn, Release sites in River Caima; RS_An, Release sites in River Águeda; V_n, Sites electrofished in River Vouga; C_n, Sites electrofished in River Caima; A_n, Sites electrofished in River Águeda

Sea lampreys are captured in the estuary with trammel nets, and in the river with a type of fyke net that is locally called a ''gamboa.'' Besides hundreds of professional fishers, poaching also has great relevancy in the River Vouga and its tributaries, the Caima (196 km^2) on the northside of the basin and the River Águeda (972 km^2) with its important tributaries, the rivers Cértima (541 km^2) and Alfusqueiro (205 km^2) in the south (Loureiro & Macedo, 1986). The River Antuã (149 km^2) belongs to Vouga's river basin but it drains directly into the northern part of the Ria de Aveiro estuary.

The Vouga's flow is controlled by the discharge from four dams, the Ribafeita and the Drizes in the River Vouga and the Padrastos and the Burgães in the upper part of the River Caima. Other enterprises planned in the River Vouga will probably also constrain anadromous species: the Ribeiradio hydroelectric power dam, to be located approximately 15 km upstream of the Grela dam (53 km from the river mouth), a small hydroelectric power dam built in the 1930's that became the upper limit of the sea lamprey migration on this river (Costa et al., 2001); and the new Carvoeiro weir, 34 km from the river mouth. Several weirs were built in this river basin, most of them to power mills, but are already abandoned and partially destroyed, like the one in River Caima (8.5 km from the River Vouga and 51 km from the River Vouga's mouth) that in normal conditions is impassable for sea lampreys. There are also two large blockstone weirs in River Vouga, the Sernada (42 km), and the Carvoeiro (43.5 km), that can equally reveal themselves quite difficult to be successfully overcomed by fish.

Materials and methods

In the autumn of 2004, an electrofishing (electrofisher Hans Grassl EL62, 3.0 KW, direct current 300/600 V) campaign was carried out in the River Vouga and its main tributaries, namely, the rivers Antuã, Caima and Águeda. The main purpose of

this survey was to identify both ammocoete beds and areas of the river that were used by the sea lampreys to spawn in former years in order to avoid releasing tagged sea lampreys in rivers with weak attractive chemical stimuli from larval population to spawners (Sorensen et al., 2005). Captured ammocoete age classes were defined according to Quintella et al. (2003).

Radio tracking telemetry procedures

In the spawning season of 2004, five sea lampreys were purchased from local fishermen in the area near the village of Angeja (c. 16 km from the mouth of River Vouga). These animals were tagged and released between February and April in the River Vouga and used as a preliminary approach to the study of sea lamprey up river spawning migration in this watershed. During 2005, 25 sea lampreys caught in the fishing area near Angeja were purchased from local fishermen and then tagged and released in several locations of the rivers Vouga ($n = 13$), Caima ($n = 8$) and Águeda ($n = 4$) from mid January to mid April (Fig. 1).

In both seasons, the tagging procedure was carried out in situ using externally mounted radio transmitters from ATS (model type F2020). These tags were cylindrical, with dimensions of 12×39 mm, weighing 8.6 g in air (transmitter plus wires, discs and sleeves) and were powered by 3.5 V, 0.09 mA lithium batteries which guaranteed an 80-day longevity (max. 160). They operated between 150.000 and 150.990 MHz, with a pulse rate and width of 40 ppm and 20 ms, respectively. The complete procedure was adapted from Almeida et al. (2000) in order to become faster and less stressful to the animals and so it would take, roughly, 10 min for induction in a anaesthetic solution of 0.3 ml 2-phenoxyethanol per litre of water, and c. 3 min to weigh, measure and tag the animal. Before being released in the wild, lampreys were left to recover in the river margin inside a hoop net for a period of 1–2 h. In order to determine the poaching impact on the released animals a reward was offered for each recovered transmitter.

The animals were located using the R2000 receiver and a Yagi antenna (ATS) and then monitored continuously, either by car or on foot, from release at dusk until dawn or early morning. Position of tagged animals and time were recorded in previously selected, listening locations in a total of 45 sites in River Vouga, 14 in River Caima and 10 in River Águeda. The sex of the animals used could not be determined due to their early stages of gonad maturation during which spawners do not present any external sexual dimorphism.

Characterization of the resting sites and the rivers' appetence as suitable spawning grounds

During the 2005 migration season, the radio tracking telemetry was used to study not only the upstream movement, but also some aspects related to the selection of the resting sites during the migration. The variables used to characterize resting sites are shown in Table 1. On each day following a tracking session, the precise location of the tracked animal would be identified within an area of approximately 1 m^2, and its diurnal resting site (within 2 m diameter range) would be characterized according to those variables. After the continuous monitoring of any given animal, the resting sites characterization would still be done regularly even, if the lamprey changed refuge. To characterize the rivers' abilities as suitable spawning grounds the rivers were divided in 500 m long stretches, from the lower part of the study area to the upstream limit to migrants. Then, according to both the riverbed flow type and substrate type the stretches were given a value in an aptitude scale (Table 2). So, respectively, in the rivers Vouga, Caima and Águeda, 51, 18 and 10 stretches were considered and further characterized (Fig. 1).

Data analysis

The average ground speed (GS), expressed in body lengths per minute (BL min^{-1}), was determined as:

$$GS = \frac{s}{\Delta t \times L_t},$$

where s is the total distance the animal travelled during continuous monitoring and between t and

Table 1 Variables used for the characterization of the sea lamprey refuges and the river stretches aptitude for spawning grounds

Variables	Types/Definition	Classes
Rbt	Sinuate; braided; regular (natural); regular (artificial)	<30%; 30–60%; >60%
Ft	Run; riffle; pool; slack	<30%; 30–60%; >60%
Cs	Artificial; rock; stone; gravel; sand; silt	<30%; 30–60%; >60%
Cvc	Mean cover	0%; <50%; >50%; 100%
S	Mean cover	0%; <50%; >50%; 100%
Astr	Present/absent	Easy; medium; hard; impassable
Pobs	Present/absent	Easy; medium; hard; impassable
C_w	Mean width	[0–15]m; [15–30]m; [30–45]m; [45–60]m; [60–75]m
Deb	Present/absent	–
W_{depth}	Mean water depth	≤1 m; [1–3]m; [3–5]m; ≥5 m
SGdep	Present/absent	–
Temp	Mean water temperature observed during continuous monitoring sessions (°C)	

Rbt, River bed type; Ft, Flow type; Cs, Channel substrate; Cvc, Channel vegetation cover; S, Shading of channel/resting site; Astr, Artificial structures; Pobs, Physical obstacles; C_w, Channel width; Deb, Debris; W_{depth}, Water depth; SGdep, Sand/Gravel deposits; Temp, Temperature

t^{-1} (Δt in min), and L_t is the animal total length (in cm). The total distance moved (TDM) and the total time tracked (TTT) are both only associated with the continuous monitoring and not obligatory related to the final position of the animal in the end of the season.

To calculate the halting probability of the released sea lampreys when related with the TDM, a logistic expression was adjusted. The animals that behave atypically, like the lampreys that stopped shortly after being released, and those that stopped in areas with difficult obstacles to transpose were not used in this analysis.

Results

Electrofishing in 2004 revealed a clear distinction between the abundance of sea lamprey larvae downstream and upstream of the Sernada and Carvoeiro weirs (Fig. 1). Presence of larvae upstream from these obstacles provided evidence that spawners migrated into the River Vouga's upper reaches and established larvae populations. However, abundance and age class diversity appeared to be higher downstream from these obstacles, between the sampling sites V_7 and V_{15} with peaks in sites V_8, V_{11} and V_{14} (Fig. 2). The higher ammocoete abundance downstream corroborates the telemetry data which suggested difficulty in passing Sernada and Carvoeiro weirs. Downstream from V_{15}, the sediment gradually becomes siltier, and also not suitable as ammocoetes' habitat. In the lower part of the study area (i.e. sampling site V16), only sea lamprey juveniles were captured, probably during their downstream trophic migration. Upstream from the last surveyed site (V16) we found favourable envi-

Table 2 Ecological characteristics considered for the classification of the aptitude of the stretches' to sea lamprey spawners reproduction

	Aptitude			
Variables	Low	Medium	Good	Excellent
River bed flow type	Absence of riffles	Run + riffle >60%	Run + riffle >60% and presence of riffle	Run + riffle >60% and riffle >30%
Substrate type	Absence of Stone and Gravel <30%	Gravel + Stone <30% and presence of Stone	30% <Gravel + Stone <60% and presence of Stone	Gravel + Stone >60% and Stone >30% or Gravel >60%

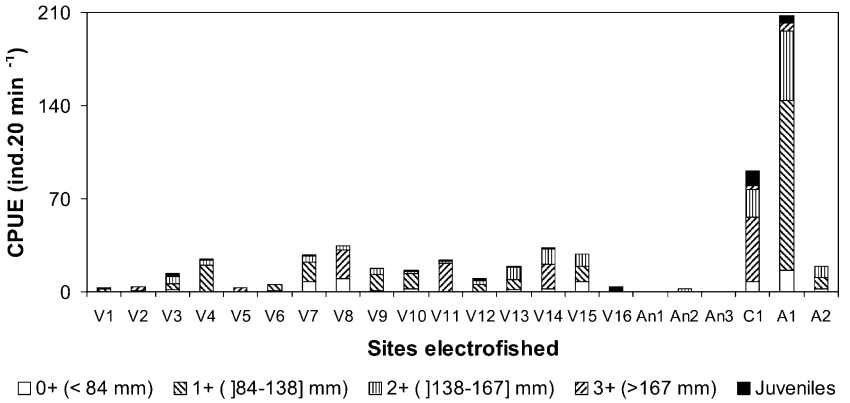

Fig. 2 CPUE of sea lamprey ammocoetes and juveniles in each electrofished site in the rivers Vouga, Antuã Caima and Águeda. V_n, Sites electrofished in River Vouga; A_n, sites electrofished in River Antuã; C_n, Sites electrofished in River Caima; A_n, Sites electrofished in River Águeda. Ammocoete age classes were defined according to Quintella et al. (2003)

ronmental conditions for these populations until, approximately, 2 km downstream from the Grela dam (V_1) constituting, roughly, 30 km of adequate habitat in River Vouga.

In tributaries Caima and Águeda, ammocoete beds were much easier to find and with much higher densities of animals. In fact, there were very good natural conditions for these animals throughout the watercourses. In River Antuã, larvae density was very low, being extremely hard to find any lamprey (i.e. *P. marinus* and *Lampetra* sp.) ammocoete whatsoever and, therefore, it was decided to exclude this particular river from the monitoring sessions in the following year, due to the fact that there would be a strong possibility that this river would not have enough pheromonal stimuli from larvae to attract spawners. Larvae and juveniles of both species were found in all rivers surveyed, a total of 741 *P. marinus* and 82 *Lampetra* sp. were collected.

The tagged lampreys released in River Vouga during 2004 spawning season had a total length (L_t) between 82 and 92 cm (mean ± SD—880 ± 40 cm) and a total weight (W_t) between 1.1 and 1.4 kg (1.3 ± 0.14 kg). The total time tracked (TTT) ranged from 10 h 05 min to 62 h 00 min and the total distance moved (TDM) in the upstream direction varied from 4.4 to 20 km. Only one of the animals released during this season showed the typical behaviour, moving upstream after release, but the rest of the lampreys either moved downstream or halted right after being released. One of them, released upstream from the Grela dam in order to assess their behaviour when migrating on a river stretch without stimuli from pheromones released neither by ammocoetes nor by other spawners, showed a peculiar behaviour moving up and downstream several times like it was somehow disoriented till it passed over this dam, remaining a few hundred meters downstream from it for several weeks.

Only one of the animals managed to overcome the Sernada and Carvoeiro weirs (at the end of the spawning season, only 33.3% of the tagged animals that reached these obstacles managed to overcome them) during continuous monitoring, taking 6 h 10 min and 4 h 20 min, respectively, to do so. Besides this animal in 2004, just two more in the 2005 spawning season successfully passed the Sernada weir, eventually residing between the rocks of the Carvoeiro weir, not being able to pass that structure. In the first year of study, two tagged sea lampreys were captured by poachers and another one that moved downstream after release was recaptured by professional fishermen.

In the 2005 spawning season, the animals used had a L_t ranging from 78 to 98 cm (mean ± SD—90 ± 5.3 cm) and the W_t varied between 0.8 and 1.9 kg (1.5 ± 0.3 kg) (see Electronic supplementary material). The TDM by the tagged sea lampreys during continuous monitoring, considering either movements done up or downstream, ranged from just 0.1 km to c. 13 km

(6.4 ± 4.8 km) and the TTT ranged between 00 h 28 min interval in the River Vouga and 11 h 52 min in the River Caima. The water temperature (T) at release ranged from 5.38°C to 15.28°C (9.88 ± 3.82°C). Both extreme values were registered in the River Caima. In the River Vouga, tagged animals were released in five locations and in the rivers Caima and Águeda in two locations (Fig. 1) in order to avoid lampreys being captured by professional fishing nets, since these entrapment gears were not consistently set in the same places throughout the spawning season.

Monitored lampreys exhibited strong diel patterns of activity in both years, moving only at night. In the night after release, most sea lampreys ($n = 6$) resumed their migration from 1 h 12 min to 3 h 15 min (2 h 01 min ± 56 min) after sunset. After this period if the lampreys had not yet commenced the upstream movement, it would not be initiated until the following night.

During continuous monitoring sessions, three tagged sea lampreys were poached in the River Vouga and one in the River Caima. In these situations, it took the poachers between 28 min and 11 h 52 min to recapture them.

In 2005, 69% ($n = 9$) of the animals released in River Vouga were poached and of those, four were captured downstream from the Sernada and Carvoeiro weirs. The signal of one of the transmitters was lost during the season, which means that it either malfunctioned or that the lamprey was caught by poachers. The latter is more probable based on returns of other tags for the reward. From the River Caima, 62.5% ($n = 5$) of tagged sea lampreys were poached and 25% ($n = 2$) were confirmed to be predated, probably by otters due to the marks of the recovered specimens. From the River Águeda, 25% ($n = 1$) of tagged lampreys were captured by poachers and the signal was lost from 75% ($n = 3$) of the animals.

Overall, 60% ($n = 15$) of the total tagged sea lampreys in the Vouga River basin were captured by poachers and the signal was lost from 16% ($n = 4$). We believe that the sum of the animals, i.e. 76% ($n = 19$) of the lampreys, represents the poaching activity during 2005. Predation occurred for 8% ($n = 2$) of total tagged lampreys and 16% ($n = 4$) were still there at the beginning of May.

The migration in River Caima was more predictable. The ground speeds (GS) observed for the animals released varied significantly between rivers (Kruskal-Wallis, $P < 0.05$). In rivers Vouga, Caima and Águeda the mean GS were respectively 25.75 ± 3.77, 15.91 ± 3.56 and 12.01 ± 7.12 BL min^{-1} (Fig. 3). In River Águeda, tagged individuals showed an atypical behaviour according to what has been previously described (Almeida et al., 2000, 2002b, 2005; Quintella et al., 2004), moving just a few hundred meters upstream and then halting for several weeks.

The sites sea lampreys selected to rest or shelter during daytime ($n = 39$) averaged 0.84 ± 0.43 m in depth, with slow current speeds (0.03 ± 0.04 ms^{-1}), and with high oxygen concentration (99.69 ± 9.28%). They also selected refuges completely shaded or darkened either by the existence of debris, rocks or vegetation (aquatic or riverbank) on 58% of occasions. Debris was found in 49% of resting sites and may be important for these animals by creating concealment and darkness. The existence of thick channel vegetation coverage (Cvc) was not an important feature for these animals; 41% of selected sites, had less than 50% Cvc. Also, 38% of the tagged lampreys chose resting sites without this type of cover. The dominant channel substrate (Cs) found in the selected resting sites was sand (39%) and the subdominant, which in this case may be a more determinant characteristic, consisted mainly of gravel (41%) and stone (27%).

Suitable spawning grounds for adult sea lampreys are just found in the upper reaches of the River Vouga (Fig. 1). Unfortunately, this area is not always reachable throughout the entire migration season, being extremely dependent on precipitation and river discharge. Punctually, some fairly suitable stretches can be found downstream and lampreys may, in alternative, spawn there (Fig. 1). This observation was strengthened by informations gathered from interviews to local professional fishermen and poachers. Bypassing the Sernada weir, River Caima also appears to be an important alternative, although in dry winter seasons such as occurred in 2004 and 2005, the river flow may be insufficient. Most of the area comprehending

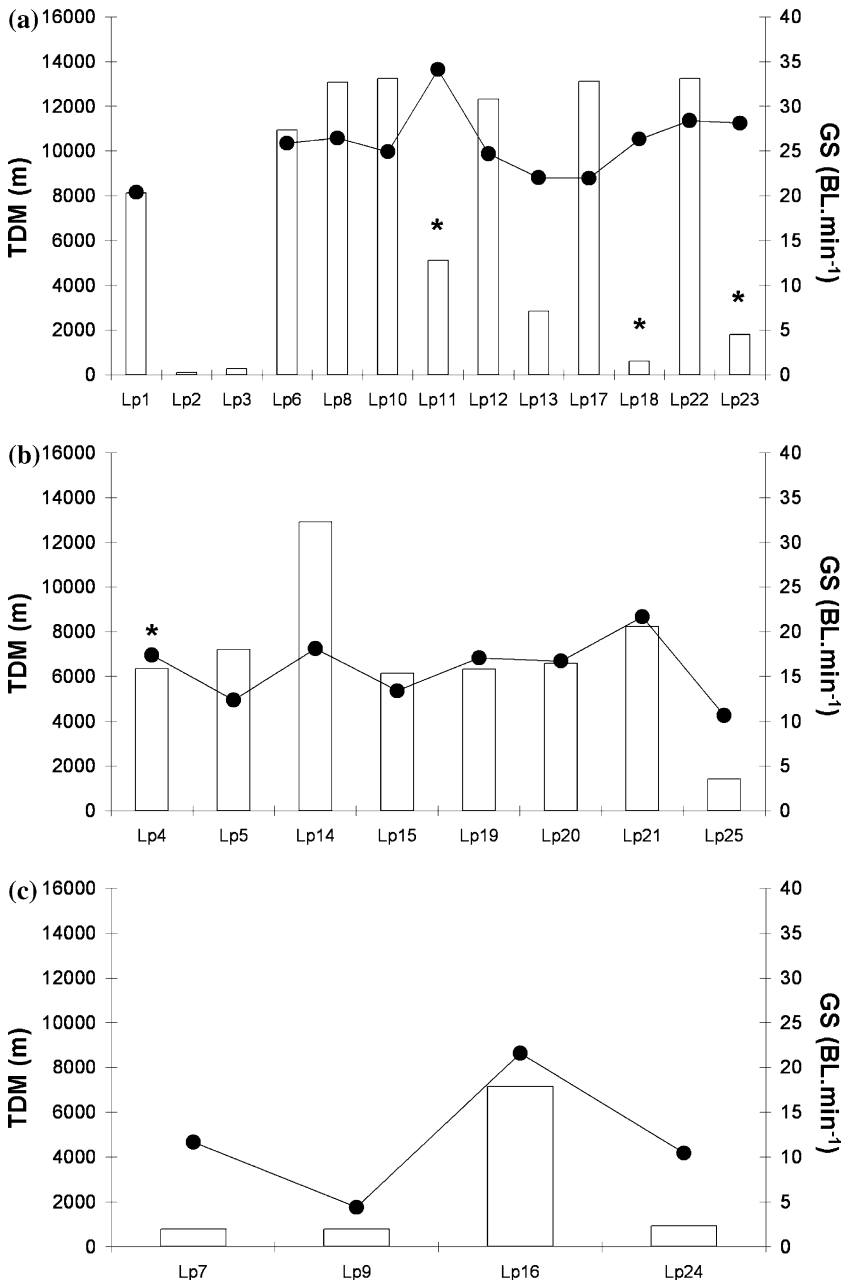

Fig. 3 Total distance moved (TDM - bars) and the mean ground speed (GS - lines) for the released tagged sea lampreys in the rivers Vouga (**a**), Caima (**b**) and Águeda (**c**) during continuous monitoring. The asterisks identify the animals captured by poachers during these sessions

the lower reaches of River Águeda is unsuited to be used by lampreys as spawning grounds since the substrate is mostly composed of sand and silt.

Excluding the animals released in River Águeda due to their atypical behaviour and those from the other studied watercourses which were in situations where they had obstacles like the existence of a difficult weir to overcome, 10 individuals were used to determine the probability of halting (CH) (Fig. 4), at the following equation:

$$CH = \frac{1}{\frac{1}{101} + 0.2427 \times 0.9995^{\mathrm{TDM}}}$$

$$(R^2 - 0.96;\ \mathrm{df} - 6;\ F - 149.32;\ P < 0.001)$$

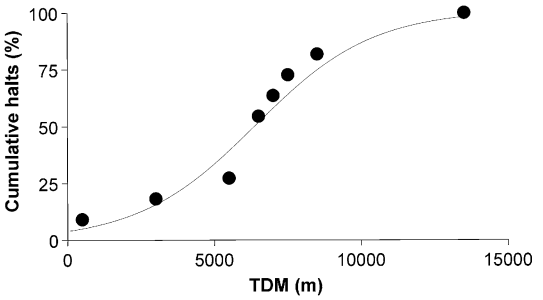

Fig. 4 Adjusted logistic expression to calculate the halting probability for sea lampreys in the rivers Vouga and Caima. TDM, total distance moved

where CH represents the probability of halting (cumulative) and TDM the total distance moved (m). According to the equation, the probability of an animal halting and looking for shelter reaches 50% when TDM reaches 6.4 km.

Discussion

The distinction in the levels of both abundance and age class diversity of lamprey ammocoetes downstream and upstream the Sernada and Carvoeiro weirs is clear. This may diminish the chemical stimuli to adults produced by resident larval lamprey that in a situation of no disturbance or when impassable obstacles are further away from the estuary would be felt from the rivers' upper reaches. However, the distribution of these animals showed a generalized occupation of the entire riverbed, unlike what has been described for the River Mondego where colonization is confined to a relatively small area downstream from the Açude-Ponte dam in Coimbra, which has been sea lamprey's natural distribution upper limit since it was built (Quintella et al., 2003).

In the River Vouga, larger ammocoete populations can be more easily found downstream from the Carvoeiro an Sernada weirs, particularly, from the sampling sites V_7–V_{15} which are, probably, preferential habitats for the establishment of ammocoetes beds since some abundance peaks were observed in these areas, mainly associated with the existence of younger individuals, belonging to the 0^+ age class. Moreover, above the Carvoeiro weir no animal belonging to this age class was captured during the electrofishing campaign. These results corroborate those obtained from the present radio telemetry studies that revealed the extreme difficulty these animals have to overcome these obstacles, which are increased in periods of low precipitation like the 2004 and 2005 spawning seasons. In the River Vouga's tributaries, rivers Caima and Águeda, ammocoete beds were easier to identify and the higher values of CPUE were also obtained in these rivers. The reasons are probably also related to the fact that these are narrower watercourses with lower depths and, therefore, being also easier to survey. They also suffer from less human interventions and both the professional fishing activity and poaching have a more reduced expression and so, the adult spawners that are able to enter into one of these rivers will probably be less likely to get caught and, consequently, will have more chance to successfully spawn.

The adequate natural conditions for the establishment of ammocoetes beds are gathered in the whole extension of the River Águeda, in the first 8 km of the River Caima and in the 30 km downstream of the Grela dam in the River Vouga.

In the spawning season of 2004, the behaviour demonstrated by these animals was atypical, at least in relation to what has been previously described for this species, particularly, in the River Mondego (Almeida et al., 2000, 2002a, b; Quintella et al., 2004; Almeida et al., 2005). Except for one of the animals, the rest of them either moved downstream or halted right after being released. The hesitation and disorientation of the animal released above the Grela dam may be explained by the more than probable lack of stimuli caused by the inexistence of both ammocoetes and other spawners upstream.

The management of the river flow downstream from the Grela dam is for now a determinant factor for the success of sea lamprey spawning migration in the River Vouga. The present data supports previous findings in which the sea lamprey spawners' cryptic pattern of behaviour is described (Hardisty & Potter, 1971; Stier & Kynard, 1986; Almeida et al., 2000; Kelso &

Gardner, 2000; Almeida et al., 2002a, b; Quintella et al., 2004), which may be considered to be a strategy developed by this species mainly to avoid predation during this sensitive period. Almeida et al. (2002b) have shown that heightened nighttime dam discharge seemed to act as a positive stimulus for the sea lamprey to migrate by promoting the increase of the animals' ground speed, but daytime releases did not influence the lampreys to move. In River Caima, an identical tendency could also be observed and the migration in this river always appeared to be much more predictable regardless of the individuals. The median GS values observed in the River Vouga (Median = 25.87 BL min^{-1}) are within those formerly obtained by Almeida et al. (2002) in the River Mondego during low (Median = 33.3 BL min^{-1}) and high (Median = 28.9 BL min^{-1}) river discharge periods. On the other hand, the mean GS observed between the lampreys released in River Caima was more similar than when considering the ones released in the other rivers and the migration was also reinitiated more often but in this case the median GS (Median = 16.88 BL min^{-1}) was much lower. The slower velocities generally observed in the River Caima are probably related to this river being shallower, much narrower and sinuate, with lower caudal and having more riffle areas and debris than the River Vouga, creating areas of difficult passage where higher ground speeds are harder to obtain.

The increase of the current velocity and level at dusk seems to have a determinant role on the physical stimulation of these animals and thus to positively influence their upstream migration (Almeida et al., 2002b). Therefore, it would be beneficial for the sea lamprey if the discharges originated by structures such as hydropower dams were coincident with its nocturnal period of activity or at least between 1 and 3 h after sunset, from the middle of December to the end of May or early June. In these circumstances, one should bare in mind the importance of the period between dusk and dawn or early morning as a fundamental aspect for the success of these animals' spawning migration. Nevertheless, more studies applied to this matter are still needed.

The fishing activity and, particularly, poaching, has an important negative effect on the number of sea lampreys that effectively spawn in the Vouga river basin. Furthermore, in such dry winter seasons with extremely low precipitation levels like 2004 and, specially, 2005, this effect is certainly more worrying and in the present situation it had a preponderant effect on the number of animals caught since it was much easier to capture these animals in a situation of low river discharge and for the lampreys was much harder to find any suitable places to shelter and spawn. In fact, in this spawning season there were 15 (60%) confirmed captures done by poachers in the three rivers and for four of the tagged animals the respective radio signal was lost, meaning that probably these have also been captured but either for being scared or just uninformed, poachers did not reclaim the transmitter recovery reward. If this hypothesis is correct, 76% (n = 19) of the released animals in 2005 in this river basin were poached. This result is quite relevant since it may have serious implications in this year's recruitment and that, associated with the progressive limitation of suitable available habitats for both ammocoetes and adults to spawn, will certainly be prejudicial for this species conservation in this river basin. It urges for more effective control of the fishing activity, both professional and illegal, by the competent authorities in this river basin along with a no fishing period during the peak migration (i.e. from February to April).

In the River Vouga, the Sernada and Carvoeiro weirs are extremely difficult obstacles to overcome and in 2005, four of the animals released in this river were captured downstream from it. Due to the extreme difficulty in bypassing this kind of obstacle, sea lampreys are usually obliged to remain downstream of these structures but, nevertheless, they still keep on trying to pass over them. In fact, all the animals that managed to overcome those weirs during the two seasons did it sometimes a month after being released. During this period of time they are quite vulnerable to poachers, who use several methods (i.e. trammel nets, lamprey-spears; underwater fishing) to capture them in these assembling areas. Additionally, suitable spawning grounds in the River Vouga are

mainly found upstream the latter weir and, therefore, whenever the river discharge is low it turns quite difficult for the animals to reach them. River Caima appears to have quite good ecological conditions for the lampreys to spawn, assuming that they manage to bypass the Sernada weir. For this reason competent authorities should consider the hypothesis of removing the Sernada and Carvoeiro weir, or at least to build effective fish passes in these structures for the target species. The design of the fishway installed in the Grela weir is clearly not appropriate to be use by migratory and potamodromous fish species present in the Vouga basin. The redesigning and transformation of the Grela fish pass would considerably increase the available habitat for sea lamprey spawners and for the growing of ammocoetes.

Sea lamprey spawners select not very deep places with very slow current velocity and high concentrations of oxygen as refuges for the daytime, dark, either due to dense aquatic vegetation, rock formations or other factors. The existence of debris is also an important feature in the riverbed creating this kind of preferential shelters. According to the present results, the probability of an animal halting and looking for shelter reaches 50% when TDM reaches 6.4 km. This means that even if there were suitable conditions for these animals to halt before that distance, it is probable that they will not do so.

Further studies regarding the sea lamprey's preferential resting sites and migratory movement should be based on the characterization of shorter river stretches considering the halting probability for these animals. The present results reinforce the idea that the river discharge, either from natural or human origin, is a factor that acts as positive stimulus in the migration of these animals. Its application is quite important to the conservation of sea lamprey populations and must be taken in consideration by the proper institutions that manage river flow related structures such as dams and barrages and when considering the construction of fish passages.

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References

Almeida, P. R., H. T. Silva & B. Quintella, 2000. The migratory behaviour of the sea lamprey *Petromyzon marinus* L., observed by acoustic telemetry in River Mondego (Portugal). In Moore, A. & I. Russel (eds), Advances in fish telemetry. CEFAS: Lowestoft, Suffolk, 99–108.

Almeida, P. R., H. T. Silva & B. R. Quintella, 2002a. The spawning migration of the sea lamprey (*Petromyzon marinus* L.), in the River Mondego (Portugal). In Pardal, M. A., J. C. Marques & M. A. Graça (eds), Aquatic ecology of the Mondego river basin. Global importance of local experience. Imprensa da Universidade de Coimbra, Coimbra, 381–386.

Almeida, P. R., B. R. Quintella & N. M. Dias, 2002b. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). Hydrobiologia 483: 1–8.

Almeida, P. R., B. R. Quintella, A. Koed & N. O. Andrade, 2005. Using electromyogram telemetry to study the spawning migration of sea lamprey (*Petromyzon marinus* L.). In Spedicato, M. T., G. Lembo & G. Marmulla (eds), Aquatic Telemetry, advances and applications. FAO-COISPA, Rome, 3–11.

Assis, C. A, 1990. Threats to the survival of anadromous fishes in the River Tagus, Portugal. Journal of Fish Biology 37: 225–226.

Bergstedt, R. A. & J. G. Seelye, 1995. Evidence for lack of homing by sea lampreys. Transactions of the American Fisheries Society 124: 235–239.

Costa, M. J., P. R. Almeida, I. M. Domingos, J. L. Costa, M. J. Correia, M. L. Chaves & C. M. Teixeira, 2001. Present status of the main shads' populations in Portugal. Bulletin Français de la Pêche et de la Pisciculture 362/363: 1109–1116.

Fine, J. M., L. A. Vrieze & P. W. Sorensen, 2004. Evidence that Petromyzontid lampreys employ a common migratory pheromone that is partially comprised of bile acids. Journal of Chemical Ecology 30: 2091–2110.

Hardisty, M. W. & I. C. Potter, 1971. The general biology of adult lampreys. In Hardisty, M. W. & I. C. Potter (eds), The biology of lampreys, Vol. I. Academic Press, London, 127–206.

Kelso, J. R. M. & W. M. Gardner, 2000. Emigration, upstream movement, and habitat use by sterile and fertile sea lampreys in three Lake Superior tributaries. North American Journal of Fisheries Management 20: 144–153.

Li, W, P. W., Sorensen & D. D. Gallaher, 1995. The olfactory system of migratory adult sea lamprey (*Petromyzon marinus*) is specifically and acutely sensitive to unique bile acids released by conspecific

larvae. The Journal of General Physiology 105: 569–587.

Li, W., A. P. Scott, M. J. Siefkes, H. Yan, Q. Liu, S. Yun & D. A. Gage, 2002. Bile acid secreted by male sea lamprey that acts as a sex pheromone. Science 296: 138–141.

Loureiro, J. & M. E. Macedo, 1986. Bacia hidrográfica do Rio Vouga. In Direcção-Geral dos recursos e aproveitamentos hidráulicos (eds). Monografias hidrológicas dos principais cursos de água de Portugal continental. Divisão de Hidrometria, Lisboa, 207–240.

Morman, R. H., D. W. Cuddy & P. C. Rugen, 1980. Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 37: 1811–1826.

Quintella, B. R., N. O. Andrade & P. R. Almeida, 2003. Distribution, larval stage duration and growth of the sea lamprey ammocoetes, *Petromyzon marinus* L., in a highly modified river basin. Ecology of Freshwater Fish 12: 1–8.

Quintella, B. R., N. O. Andrade, A. Koed & P. R. Almeida, 2004. Behavioural patterns of sea lamprey spawning migration during difficult passage areas studied by electromyogram telemetry. Journal of Fish Biology 65: 961–972.

Rogado, L. (coord.), P. Alexandrino, P. R. Almeida, J. Alves, J. Bochechas, R. Cortes, I. Domingos, F. Filipe, J. Madeira & F. Magalhães, 2005. *Petromyzon marinus* Lampreia-marinha. In Cabral, M.J., J. Almeida, P.R. Almeida, T. Delinger, N. Ferrand de Almeida, M.E. Oliveira, J.M. Palmeirim, A.L. Queiroz, L. Rogado & M. Santos-Reis (eds), Livro vermelho dos Vertebrados de Portugal. Instituto de Conservação da Natureza, Lisboa, 65–66.

Stier, K. & B. Kynard, 1986. Movement of sea-run sea lampreys, *Petromyzon marinus*, during the spawning migration in the Connecticut river. Fishery Bulletin 84: 749–753.

Sorensen, P. W. & L. A. Vrieze, 2003. The chemical ecology and potential application of the sea lamprey migratory pheromone. Journal of the Great Lakes Research 29: 66–84.

Sorensen, P. W., J. M. Fine, V. Dvornikovs, C. S. Jeffrey, F. Shao, J. Wang, L. A. Vrieze, K. R. Anderson & T. R. Hoye, 2005. Mixture of new sulfated steroids functions as a migratory pheromone in the sea lamprey. Nature Chemical Biology 1: 324–328.

Teeter, J., 1980. Pheromone communication in sea lamprey (*Petromyzon marinus*): implications for population management. Canadian Journal of Fisheries and Aquatic Sciences 37: 2123–2132.

Vrieze, L. A. & P. W. Sorensen, 2001. Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory sea lamprey (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 58: 2374–2385.

Young, R. J., K. A. Houston, J. G. Weise & J. R. M. Kelso, 1990. The effect of environmental variables on the population dynamics of sea lamprey, *Petromyzon marinus*. Canadian Technical Report of Fisheries and Aquatic Sciences 1736, 33 pp.