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Realistic variations in substrate composition affect spawning preference and egg retention in river lamprey (*Lampetra fluviatilis*)

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Abstract

Egg drift from the nest is clearly an important cause of mortality in lithophilic species; however, the effect of substrate composition on this process has been overlooked. Here, we investigated the role of substrate on the spawning preference and egg retention of river lamprey (*Lampetra fluviatilis*) during a whole breeding season in a two-option experimental setting. Despite no initial preference, the lamprey eventually favoured the most efficient substrate for egg retention. The pebbly substrate hosted 12 times as many matings as the sandy one, while blurting 20% fewer eggs.

Keywords: spawning habitat, reproduction, habitat choice, South-West France

Among the 41 lamprey species (order: Petromyzontiformes; Potter et al., 2015), the European river lamprey *Lampetra fluviatilis* (Linnaeus, 1758), also known as the river lamprey, is a parasitic anadromous species that is widespread throughout Europe (Hardisty, 1986; Maitland, 1980). Although the river lamprey has been globally considered Least Concern according to the IUCN Red List of Threatened Species, the species is considered endangered in the Iberian Peninsula. In Spain, *L. fluviatilis* is considered Regionally Extinct (Doadrio, 2001) while in Portugal it is included in the Critically Endangered category of the red list of endangered species (Cabbral et al. 2005). One of the main reasons for the general drop in population size is the loss of spawning and larval habitat due to river fragmentation induced by dredging, engineering works or impoundments (Lucas et al., 2020). Lampreys being lithophilic (i.e. they deposit eggs and sperm within the substrate in shallow water) (Jang and Lucas, 2005; Nika and Virbickas, 2010), such anthropic disturbances make the accessibility to suitable spawning grounds challenging. The river lamprey spawns in nests built by removing coarse substrate (pebbles) with their oral disc and fine substrate (sand and gravel) with their tail (Jang and Lucas, 2005).

Egg drift from the nest is a major cause of mortality for rheophilic fishes (e.g. Gauthey et al., 2017), especially for lampreys. By comparing the number of eggs in nests of sea lamprey (*Petromyzon marinus* L.) with the number expected from the number and size of females, Manion and Hanson (1980) estimated that 86% of the eggs were washed from the nest. In another study, Silva et al. (2015) placed drift nets downstream from nests of river lamprey in which dyed eggs were inserted, and caught from 1.5% to 86% of the inserted eggs, increasing with higher current speed to which the nests were exposed and decreasing with the distance from the spawning habitat (depth effect not considered here). Since egg survival is very high in the nest and virtually nil out of it, mainly because of predation (Manion and Hanson, 1980: survival rate in nest = 90%; Smith and Marsden, 2009: no viable egg outside of nest), the ability of lamprey to choose nesting conditions that reduce the likelihood of egg drift must be under strong selection. Silva et al. (2015) highlighted an egg hatching success of solely 52.0% downstream from the nests with silt beds, generally found downstream of spawning areas. However, as their observation was made in the laboratory without egg predation, we therefore suspect that this percentage is overestimated.

Of all the environmental factors that could affect egg retention in the nest, substrate is probably, alongside current speed where the nest is built (Silva et al. 2015, Dhamelincourt et al. 2022), one of the most significant. Indeed, freshly laid lamprey eggs are coated with an adhesive structure that aggregates sand grains (Yorke and McMillan, 1979). Thus ballasted, the eggs sink in cavities between pebbles, where they nestle safe from drift and predators. Consistently, lampreys typically spawn in stream beds covered with a mixture of sand, gravel and pebbles (Jang and Lucas, 2005; Johnson et al., 2015). Although Smith and Marsden (2009) showed that egg retention was better in gravel than in silt, lampreys rarely, if ever, spawn in silt, and one can wonder if more realistic variations in substrate composition can affect egg drift. If so, one would expect lampreys to prefer the substrate that better retains the eggs. Such assessment may help to understand the effects of substrate subtle modifications within spawning grounds.

Hence, the objective of the present study was to accurately determine the role of the relative proportion of sand and pebbles on both the choice for spawning microhabitat and the retention of river lamprey eggs during a whole breeding season. A gradual change from one substrate type to another may occur more frequently than a total switch, as such variation is prone to be found within real spawning grounds affected by environmental variations. To do this, we placed 35 adults of river lamprey in a large fish tank with two spawning patches containing a mixture of gravel (50%) and a large proportion of either sand or pebbles (40% and 10%). The number of spawning acts performed on both substrate patches, and the number of eggs drifting from them was compared. If the factor limiting egg retention is the ballasting sand grains, egg drift should be less likely from the sandy patch, and lamprey should prefer to spawn on it. The expected outcome would be reversed if cavities between coarse particles are the limiting factor.

The *L. fluviatilis* used in this study were captured with drift nets in early spring 2019 (between March 15th and 26th) during their upstream migration on the Garonne river (South-West France) by professional fishermen. A total of 35 individuals (15 males, total length: 28.3 ± 2.1 cm and mass: 45.2 ± 8.3 g; 20 females, total length: 28.4 ± 1.7 cm and mass: 51.6 ± 7.5 g) were sampled and transferred in an oxygenated and temperature-controlled tank with Garonne water (13°) to the INRAE experimental facilities in Saint-Pée-sur-Nivelle, France (ECP, 2018). Individuals were acclimated for a few days in tanks (between 8 and 19 days depending on the capture date, 13.8 ± 0.8 °C in tanks) supplied with water from the Nivelle River (France) to avoid behavioural changes due to transportation and/or differences in water properties during the course of behavioural observations. The day before the experiment, we tagged each lamprey with a unique combination of three spots of UV-fluorescent visible implant elastomer (VIE) injected in the posterior dorsal fin to allow individual recognition under both white light and UV light. Tagging was performed after fish were anaesthetised with benzocaine (0.3ml/L).

The experiment took place in a 4 m^3 (10 x 1 x 0.4 m) linear section of a 25 metres long circular aquarium, supplied with water from the Nivelle River in a semi-open circuit, with water replacement of 6 litres per minute. To define whether egg drift from nests was influenced by substrate size and the degree of activity of the spawners, spawning substrate was limited to two 0.48 m^2 (0.8 x 0.6 x 0.1 m) boxes placed 5 meters from each other, and filled with a mixture of sand, gravels and pebbles corresponding to the spawning habitat selected by river lampreys (Jang and Lucas, 2005; Figure 1).

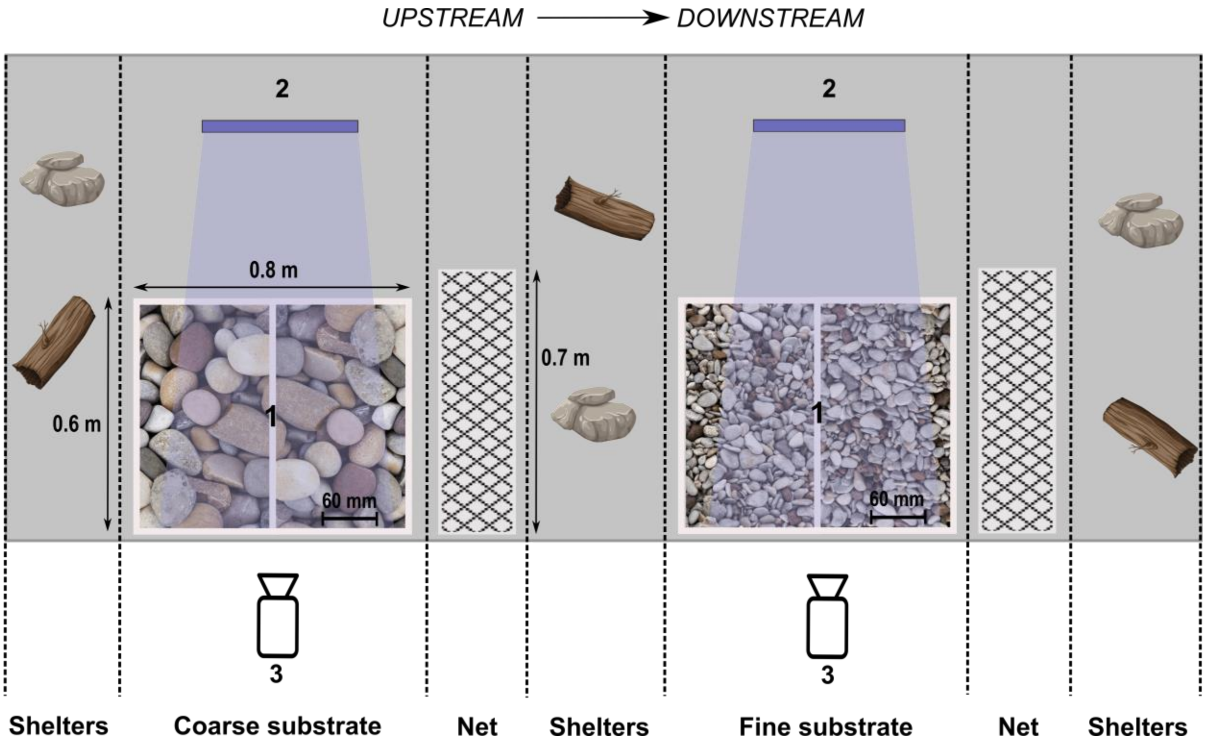

Figure 1. Experimental setup used for the experiment. 1: substrate boxes (0.8 x 0.6 x 0.1 meter) with either fine or coarse substrate; 2: UV light used during the night, replaced by white light during the day; 3: cameras recording spawning activity. Current speed was set to 0.6 m/s on both substrates. The scale in each box refers only to the substrate size.

The first box, referred to as the "sandy patch", was filled with 50% (in volume) gravels (= 2-4 mm), 10% pebbles (4-64 mm) and 40% sand (0.125-2 mm) while the second box, referred to as the "pebbly patch" was filled with 50% gravels, 40% pebbles and 10% sand. Current speed was set to 0.6 m/s on both substrates and water temperature was monitored daily and followed that of the river (15.87 ± 0.95 °C). A net with a 0.5 mm nylon mesh size and 70 cm width was placed immediately downstream of each substrate box and covered the entire water column while being larger than the boxes. Nonetheless individuals could easily move around as the nets left a gap on the left side of the boxes. Eggs were recovered from nets at the same time each day and stored in Falcon® tubes with 90° ethanol up to the exhaustive count. Two video cameras (Basler acA1920-40gc) continuously recorded lampreys' activity in each spawning substrate throughout the experiment. The aquarium was lighted with white neon bulbs (1800 lx delivered at the water level) following the natural photoperiod (12:12 with 30 minutes of "dawn" from 8 to 8:30 AM and 30 minutes of "dusk" from 8:00 to 8:30 PM), but since river lamprey is also active at night during the spawning period (Sjoberg, 1977), we positioned UV light above each substrate box (20 lx delivered at the water level). Individuals were placed in the experimental tank on the 3rd of April and the experiment ended on the 3rd of May, at the death of the last individual. Individuals were only removed from the aquarium once they died. Recorded videos were analysed using BORIS software (Friard and Gamba, 2016) and the number of spawning acts occurring each day during the entire spawning season was exhaustively noted by the observer. A spawning act was identified as body entwinement and vibration (Hardisty and Potter, 1971) of at least one male and one female, the species being polygynandrous (Jang and Lucas, 2005). During the spawning act, the female is usually attached to a pebble with her oral disk, and her cloaca is in contact with the substrate in order to lay the eggs in it, so the body vibration associated with spawning often results in substrate movement. The first and last mating acts occurred on April 9th and 30th respectively, making the spawning season 22 days long.

All analyses were performed using R software version 4.1.0 (R Core Team, 2020) and using a significance level of 0.05. Non-parametric Kruskal-Wallis test was used to test whether the daily recorded number of spawning acts differed between the coarse and fine substrate patches. A binomial test was used to test whether the first spawning act performed by each individual was more likely to occur on either substrate. A Generalized Linear Model (GLM) was applied to test whether the number of eggs caught downstream from a spawning patch on a given day depended on 1) substrate size, 2) the number of spawning acts performed on it on that day, and 3) the cumulated number of spawning acts performed on it over the last twelve days. While the number of spawning acts on a given day is an indicator of both the number of eggs laid on that day, the cumulated number of spawning acts over the last twelve days was used to indicate the number of eggs buried in the substrate and possibly dislodged from it. Indeed, eggs of river lamprey hatch after 200 degree.days (Moser et al., 2019), which corresponded to twelve days in our experimental conditions. The GLM assumed a negative binomial distribution to account for data overdispersion, and a Log link function. The three independent variables and their interactions were included in an initial full model, which was reduced through a model selection procedure based on the minimization of Akaike Information Criterion (function stepAIC in MASS package for R; Venables and Ripley, 2002).

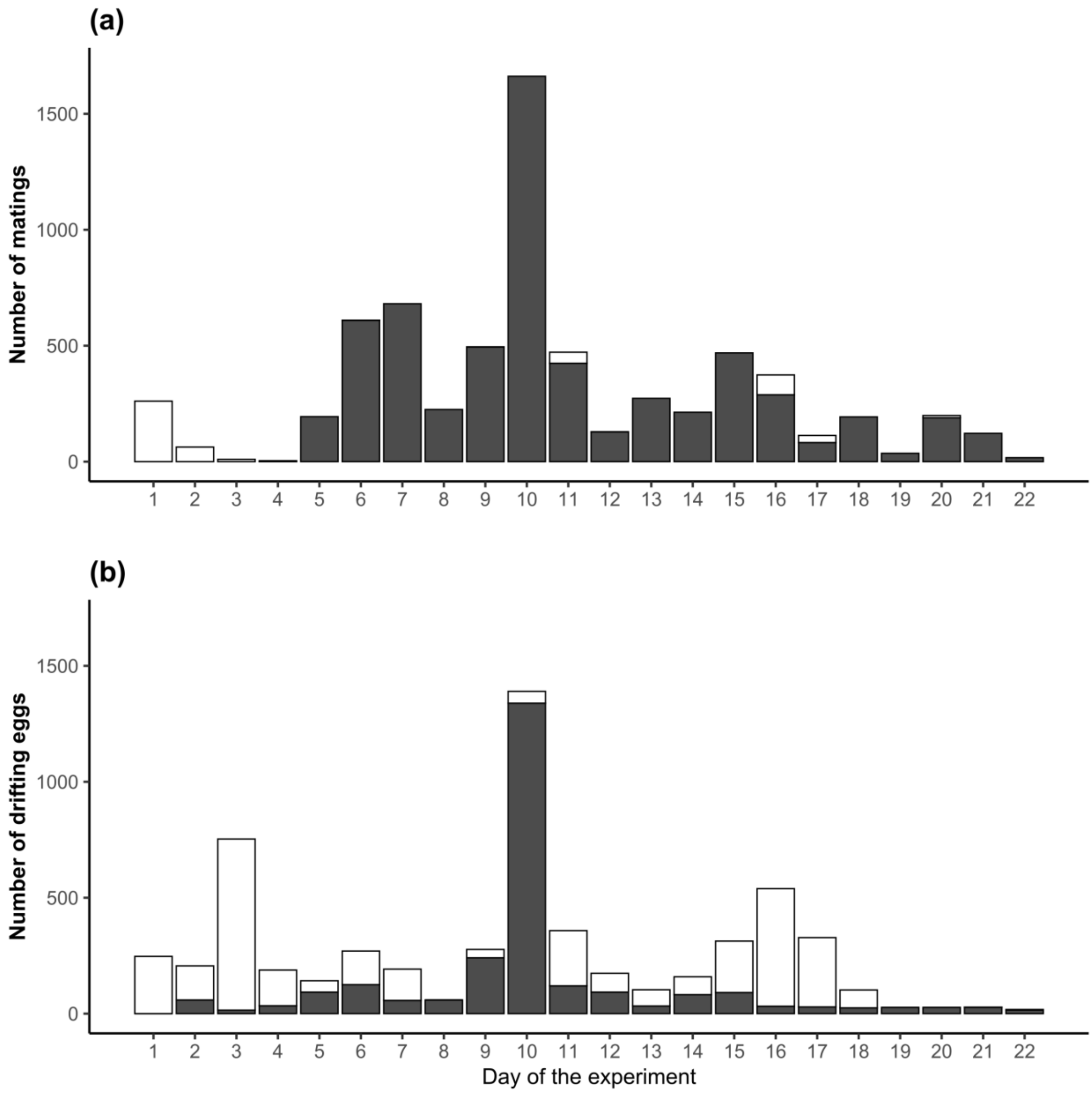

Figure 2. Daily number of mating acts (a) and eggs drifting (b) from the pebbly (grey bars) and sandy (white bars, stacked on grey bars) substrate patches, placed in an aquarium containing 20 females and 15 males of river lamprey (*Lampetra fluviatilis*). The first and last mating acts occurred on April 9th and 30th respectively, making the breeding season 22 days long.

A total number of 6815 matings occurred during the breeding season, among which 515 (7.5%) took place on the sandy patch and 6300 (92.5%) on the pebbly patch. An average (± SD) of

23.41 (± 58.11) matings per day occurred on the sandy patch while an average of 286.36 (± 367.76) took place on the pebbly patch (Figure 2a). The number of mating acts differed significantly between the substrate types (Kruskal-Wallis test: $\chi^2 = 15.51$, $P < 0.001$). A total of 16 females and 14 males spawned at least once on the sandy patch (between 1 and 149 acts per female; between 1 and 93 acts per male), whereas 18 females and all 15 males spawned at least once on the pebbly patch (between 2 and 803 acts per female; between 10 and 1054 acts per male). Six (30%) females and 10 (67%) males spawned first on the sandy patch, indicating no initial preference for either substrate (Binomial test; $P = 0.1153$ for females, $P = 0.3018$ for males, $P = 0.7353$ for pooled females and males), when individuals did not experience any patch by digging on it.

Overall, 5900 eggs drifted during the experiment, among which 3277 (55.5%) were found downstream of the sandy patch and 2623 (44.5%) downstream of the pebbly patch. An average (±SD) of 148.95 (±180.49) eggs drifted per day on the sandy patch while an average of 119.23 (±277.59) eggs drifted from the pebbly patch (Figure 2b). The final model after the AIC-based selection procedure indicated a negative effect of pebbly patch (z value = -3.862, $P < 0.001$) and a positive effect of the number of spawning acts observed during the current day (z value = 3.731, $P < 0.001$) on egg drifting from the spawning patch. Hence, the sandy substrate and an increase in the number of spawning acts influence negatively the retention in the nest. Table 1 summarizes all the results.

Table 1. Comparison of the results for the number of mating acts and the number of eggs that drifted between pebbly and sandy substrate.

Variable	Sandy substrate	Pebbly substrate
Number of matings	515 (7.5%)	6300 (92.5%)
Matings per day	23.41 ± 54.66	286.36 ± 370.19
Number of females	16	18
Number of males	14	15
Number of mating acts (range) for females	1-149	2-803
Number of mating acts (range) for males	1-93	10-1054
First spawning act (females)	6 (30%)	14 (70%)
First spawning act (males)	10 (67%)	5 (33%)
Total egg drift	3277 (55.5%)	2623 (44.5%)
Daily egg drift	148.95 ± 180.49	119.23 ± 277.59

The pebbly substrate was clearly better at retaining eggs, and river lamprey clearly preferred to spawn on it. Their preference seems to emerge from a sampling process, as the probability of choosing either substrate on the first spawning occasion was balanced considering the binomial test results - showing no preference of one substrate for each sex independently or with all individuals pooled - whereas the proportion of total spawning acts performed on the pebbly substrate was 12 times higher than on the sandy substrate. Lampreys are certainly able to assess substrate composition during nest-building, using their mouth and tail to build the nest. Moreover, lampreys can spawn hundreds of times (here, on average 341 for females and 454 for males) within a few days in the same or different sites (Dhamelincourt et al., 2021; Jang and Lucas, 2005), reinforcing the idea that they may be able to sample their environment and choose their spawning site accordingly. Gardner et al. (2012) observed a negative association between the abundance of sea lamprey nests and substrate cover by fine sediment, and suggested that this result could be due to lampreys either preferring coarser substrate, or coarsening the substrate through repeated nest-building in the same spots, or both. Here, we showed that river lamprey deliberately selected a suitable spawning habitat by preferring pebbly substrate over sandy substrate, from which eggs were more likely to drift, suggesting that an excess of fine particles on nesting sites was detrimental to egg retention in the substrate. The coarsening effect of spawning activity on substrate size suggested by Gardner et al. (2012) is unlikely to have occurred in our study: *a priori*, heavy scouring was prevented by the moderate current speed and the containment of substrate in boxes; *a posteriori*, no accumulation of substrate was observed on the bare concrete surrounding the boxes. Substrate size in the nest may affect egg survival through exposure to low-oxygenated water, fungal contamination or predators (Silva et al., 2015; Smith and Marsden, 2009). While coarse particles offer shelter from predators, fine particles may cause suffocation but also limit the contact surface for fungus propagation. The optimal response to this trade-off certainly depends on the prevalence of each source of mortality at the spawning site, and echoes the trade-off faced by all nest-building animals when choosing a nesting site (Lissåker and Kvarnemo, 2006; Mayer et al., 2009; Tieleman et al., 2008).

Although the great risk of egg drift documented in the field was not even approached in our experimental setup, our results highlight substrate composition and over digging as two realistic sources of variation in the risk of egg drift. Assuming that female fecundity ranges from 16 000 to 37 000 eggs (Docker et al., 2019), the 5 903 eggs that drifted from both substrate patches only represent 0.8% to 1.8% of the number of eggs produced. Several features of our setup could explain this low proportion, among which the constant and moderate water flow (0.6 m/s) and the fact that the substrate was contained in boxes that prevented heavy scouring.

However, one commonality between our setup and natural conditions in the field was that lamprey repeatedly spawned on the same patch, so eggs previously laid on it could have been resuspended and drift downstream. However, the number of eggs drifting on a day was positively linked to the number of matings occurring on that day, not on the twelve previous days. This initial failure to sink in the substrate may be the main cause of drift, and eggs that managed to sink in the substrate may be not disturbed by subsequent spawning activity. The deleterious effect of overdigging documented in salmonids (Fleming, 1996), can however not be completely ruled out: Although we were not able to determine the precise age of eggs to check if eggs older than one day still drifted, some prolarvae (from stages prior to their natural downstream migration; Piavis, 1961) were caught in the nets. In the field, overdigging can be accentuated by obstacles to migration and habitat loss that lead to spawning aggregation in suboptimal (e.g. sandy) habitat.

Overall, our results confirm the necessity to consider the spawning-site substrate as an important factor influencing lamprey egg retention in the nest and therefore egg survival and larvae hatching. As advocated by Lucas et al. (2020), attention should be paid to the preservation or restoration of adequate substrate in areas suitable for lamprey spawning.

Conflicts of interest

The authors declare that they are not aware of any competing interests.

Ethical statement

The care and use of experimental animals complied with the French animal welfare laws, guidelines and policies as approved by the ethical committee for birds and fishes in the French region Nouvelle Aquitaine (authorization #2019021009248986).

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Author contributions

L.D. and M.D. equally contributed to this work. L.D., M.D. and C.T. were involved in the video analysis, statistical analysis and in writing and editing the manuscript. C.T. contributed to the initial idea and to the experimental design. J.R. conceived the experimental design. A.M. and M.D. collected the data. A.M. and S.S. helped with the video analysis.

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