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**Benthic habitat selection in juvenile European eel *Anguilla anguilla*:
implications for coastal habitat management and restoration**

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ABSTRACT

The critically endangered European eel *Anguilla anguilla* is dependent on suitable habitat qualities over a vast geographic area. Even though a significant proportion of the population never enters fresh water, the preferred benthic habitat is largely unknown in the marine environment. Examining substratum selection in *A. anguilla* reveals that elvers prefer coarse gravel, suggesting that conservation efforts may benefit from targeting this type of substratum in marine coastal areas.

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KEYWORDS

Anguilla anguilla, coastal management, elvers, European eel, habitat selection, marine sediment

Marine habitat selection and burrowing behaviours by *Anguilla anguilla* L. 1758 elvers were examined in the laboratory. Specifically, it was hypothesized that *A. anguilla* actively selects between four different marine substrata. Previous studies, mostly conducted in the freshwater environment, have indicated that *A. anguilla* selects a diversity of habitats that are usually dependent on the body size (stage) of the eels (Westerberg *et al.*, 1993; Laffaille *et al.*, 2003; Pedersen, 2009). During the daytime and during winter, yellow-stage *A. anguilla* often shelter in sand, mud, fine gravel or in the interstitial spaces between coarse gravel and cobble to avoid predation (Tomie *et al.*, 2017). In contrast, substratum preference of *A. anguilla* elvers is largely unknown. The elver life stage follows metamorphosis of the glass eels, resulting in a miniature version of the adult *A. anguilla*. Knowledge on marine benthic habitat selection in *A. anguilla* elvers is an important step towards understanding the behaviour and ecology of this life stage, which may contribute to coastal management and the preservation of this species.

Many marine coastal habitats are degraded by anthropogenic activities including dredge fisheries, *e.g.*, trawling (Jennings & Kaiser, 1998; Freese *et al.*, 1999; Gage *et al.*, 2005), extractions of marine sand and gravel in coastal areas (de Groot 1986, 1996, Desprez 2000; ICES 2015), or affected by frequent and severe occurrences of hypoxia (Schmidtke *et al.*, 2017; Breitburg *et al.*, 2018), phytoplankton blooms (Diaz & Rosenberg, 2008; Chapman, 2016) and pollution (Sühling *et al.*, 2016; Vince & Hardesty, 2016). Multiple concurrent pressures have altered the type and spatial distribution of vegetation in coastal areas as well as resulting in changes in sediment type (ICES, 2015).

In mid-June 2015, elvers ($n = 129$, mean \pm SD total body length (L_T) = 10.8 ± 1.2 cm) were collected in a trap situated in the Hellebækken Brook ($56^\circ 03' 54.53''$ N; $12^\circ 33' 14.78''$ E) in north-eastern Denmark. The trap was situated 2 m from the sea and emptied every 48 h. Therefore, elvers were in fresh water for a maximum of 48 h before they were collected. Fish were kept in a flow-through holding tank ($T = 17 \pm 1^\circ\text{C}$; salinity 14 ± 1 ; photoperiod 8L:16D) and fed dry pellets every second day for 3 weeks prior to experimentation. Following Carl *et al.* (2008), two identical experimental tanks ($75 \times 15 \times 40$ cm, L \times W \times D) were each divided into four equal squares ($18.75 \times 15 \times 40$ cm, L \times W \times D), separated by 15 cm high Plexiglas walls. A basket made of fine plastic mesh ($18.5 \times 14.75 \times 39.75$ cm, L \times W \times D) was placed in each of the four squares.

Four different substrata were prepared for the experiment, one substratum in each mesh basket. Substrata were retrieved at the end of each trial by lifting the basket to examine for the presence of elvers. The Plexiglas separation and the top of the substratum were level, ensuring that the substratum separation did not interfere with substratum selection.

Tested substrata included fine gravel (FG; $\varnothing = 8\text{--}12$ mm), medium gravel (MG; $\varnothing = 12\text{--}32$ mm), large gravel (LG; $\varnothing = 32\text{--}64$ mm) and sand ($\varnothing = 0.25\text{--}0.50$ mm) combined with vegetation (SV). Sand was collected from a nearby beach, while the other substrata (FG, MG and LG) came from a commercial gravel supplier. As with previous studies (Carl *et al.*, 2008; Jepsen *et al.*, 2008), vegetation was simulated using strands of plastic ribbon, imitating eelgrass *Zostera marina*. In each SV square, *c.* 150 strands (25 cm high) simulated an eelgrass meadow, with height and density similar to natural habitats (Short *et al.*, 1995). Water variables in the two experimental tanks were the same as in the holding tank.

Elvers were transferred to the experimental tanks without air contact (Poulsen *et al.*, 2010, 2012). Preliminary experiments indicated that elvers spent 30 min searching for

favourable substrata after the transfer. Elvers were therefore acclimated for 30 min prior to data collection similar to previous studies (Poulsen *et al.*, 2010, 2012).

Data collection included 12 trials (replicates) in total, with elver groups consisting of 9–13 individuals. Individuals were introduced simultaneously to the tank to avoid any confounding influence of introduction order (Svendsen *et al.*, 2003) and were distributed evenly over the four squares. After 30 min acclimation, data collection comprised observing the individual habitat use every 30 min for 2 h (*i.e.* five measures of habitat selection after acclimation (at 0, 30, 60, 90, 120 min). For each individual, habitat use was divided into three categories: Category 1, elvers with $> 80\%$ of their body covered by the substratum; Category 2, elvers with their body $\leq 80\%$ covered by the substratum; Category 3, elvers swimming in the water column. The 80% threshold was arbitrarily chosen but appeared to be a useful measure to separate different behaviours. After data collection, all *A. anguilla* were retrieved alive from the experimental tanks and returned to the brook. No fish were used more than once.

To analyse the habitat preference of elvers, X_{ij} was the observed number of elvers in habitat i in the j th trial $i = \text{FG, MG, LG, SV}$ and $j = 1, \dots, 12$. The simple multinomial model states that the vector: $x_j \sim \text{multinomial}(N_j, P_j)$, where N_j is the number of elvers in the j th trial and $P_j = (p_{\text{FG}j}, p_{\text{MG}j}, p_{\text{LG}j}, p_{\text{SV}j})$ is a probability vector describing the preferences for each substratum in the j th trial. However, the individual trials revealed that a simple multinomial model, with a common P vector for all trials ($P_j = P$), was insufficient due to over dispersion. To account for this, the model was extended such that $P_j = q_j(\sum q_j)^{-1}$, where $q_{ij} = \exp(\alpha_i + z_{ij})$. Here, α_i is the unbounded parameters describing the common (across trials) part of the probability vector and z_{ij} are mean zero random deviations describing the variation between trials $z_{ij} \sim N(0, \sigma^2)$. This allows the model to capture the variation between the individual trials, but at the same time gives an estimate of the overall preference across experiments.

To analyse behaviour across time, we compared the distribution of *A. anguilla* elvers > 80% covered in sediment, ≤ 80% covered in sediment, or swimming at the five different observation times (*i.e.* 0, 30, 60, 90, 120 min after acclimation). The analysis was performed using a χ^2 -test, but as it was not possible to observe the trend per trial, so for this analysis, data from all 12 trials were summed.

The results showed that, on average, 44%, 30%, 14% and 12% of the elvers were found in MG, LG, SV and FG, respectively (Figure 1). The hypothesis that the elvers selected habitats randomly was rejected (likelihood ratio test $P < 0.001$). Instead, a hypothesis that only two levels of preference existed, one for habitats LG and MG (both with a probability = $37 \pm 2\%$) and one for habitats SV and FG (both with a probability = $13 \pm 2\%$), was accepted (likelihood ratio test $P > 0.05$). Results indicated that elvers exhibited an almost three-times greater preference for LG compared with FG and SV.

No significant difference was found in the distribution of *A. anguilla* > 80% covered, ≤ 80% covered or swimming between the five different observation times (Pearson's χ^2 -test, $\chi^2 = 11.3$, $P > 0.05$). This showed that behaviours did not change over time, indicating that the acclimation time used in the present study (30 min) was adequate (Table 1).

To the authors' best knowledge, this is the first study to document habitat selection and burrowing behaviour by *A. anguilla* elvers in a marine setting. The results show that elvers prefer coarse benthic habitats ($\emptyset = 12\text{--}64\text{mm}$). Most studies on *A. anguilla* habitat selection and substratum preference, have only investigated the freshwater environment (Daverat & Tomas, 2006; Pedersen, 2009). However, Nyman (1972) documented substratum preference of young yellow *A. anguilla* ($L_T = 13\text{--}37$ cm) in a coastal environment. He found that in cold ($5\text{--}8^\circ\text{C}$) water, *A. anguilla* is inactive and hidden in mud, protected from predators. In warmer ($> 9^\circ\text{C}$) water, *A. anguilla* migrates from mud to rocky areas and more *A. anguilla* are swimming freely. Importantly, at temperatures comparable with the present study (16–18

°C), sheltering individuals appeared to favour rocks over sand (Nyman, 1972), which is in accordance with our observations.

The availability of shelters between tree roots and similar crevices in streams (Pedersen, 2009) and in vegetated areas in the coastal zone, partly explains the carrying capacity for *A. anguilla* elvers in these habitats (Westerberg *et al.*, 1993). Field observations in Danish coastal gravel areas have also revealed high densities of elvers when stones are upturned (M. Christoffersen, unpubl. data). Along with the observed preference for coarse gravel (MG and LG) in the present study, this indicates that *A. anguilla* elvers prefer spatially complex habitats. Many biological factors (*e.g.* presence of food and predators) were excluded in the present experiment, indicating that the substratum selection of elvers was determined mainly by the physical attributes of available substrata. The gravel substratum provides shelter without the need for burrowing and is therefore a quickly available refuge. An elevated shelter availability, provided by coarse gravel, might increase the carrying capacity for *A. anguilla* elvers in the marine environment. This would resemble the observations in freshwater environments and in vegetated areas in the coastal zone (Westerberg *et al.*, 1993; Laffaille *et al.*, 2003; Pedersen, 2009).

The body form and behaviour of anguillids suggests that they are adapted for using many different types of shelter, including the need for burrowing (Gans, 1975). Indeed, anguillids inhabit a variety of habitats (Tesch, 2003). In the marine environment, Tomie *et al.* (2017) found that yellow-stage American eels *Anguilla rostrata* (Lesueur 1817) (> 30 cm) prefer mud substrata during most of the year, except in the winter periods (< 2°C) when preference shifts more towards cobble substrata. At lower temperatures, the metabolic rate of *A. rostrata* is depressed (Walsh *et al.*, 1983) and perhaps this is part of the reason that anguillids in cold water seem to hide in cobble interstitial spaces, instead of actively burying. Moreover, elevated sheltering as well as reduced burying and swimming at low temperatures

(< 2–8° C) could be responses to increased predation risk by homoeothermic predators that may have an advantage over heterothermic prey in cold water (Heggenes *et al.*, 1993; Svendsen *et al.*, 2004). The study by Tomie *et al.* (Tomie *et al.*, 2017) was conducted on yellow eel and although no similar studies are available on elvers in the marine environment, burrowing behaviour may be similar in the different life stages. Burrowing in the SV substratum was not observed in the present study, but elvers could use the same burrowing behaviours in the medium (MG) and large (LG) gravel as observed by Tomie *et al.* (Tomie *et al.*, 2013). The authors indicate that *A. rostrata* commonly burrow in soft-bottomed habitats, but also discuss a potential bias because the greater part of their study area consisted of soft bottom. Aoyama *et al.* (2005) suggested that Japanese eels *Anguilla Japonica* Temminck & Schlegel 1846 construct mud burrows only when other more spatially complex habitats are unavailable and further suggested that *A. japonica* may not be morphologically adapted to perform well in burrows.

Many *A. anguilla* are estuarine-dependent (Tzeng *et al.*, 2000) and a large proportion of glass-eel larvae end the journey from the Sargasso Sea in the coastal areas of northern Europe and never enter freshwater systems (Tsukamoto *et al.*, 1998). Elvers of *A. anguilla* typically arrive in inner Danish waters in late spring when water temperatures and salinities resemble the experimental conditions used in the present study. Inner Danish waters and estuaries represent a transition area, between the brackish Baltic Sea and the more saline Kattegat and North Sea. The bottom salinity in inner Danish waters varies a lot, with salinities approaching 30 in the northern Kattegat region (57° 30' N; 11° 00' E) and 10 in the Arkona Basin (55° 00' N; 13° 00' E) (Zervoudaki *et al.*, 2009). A salinity of 14 was chosen in the present study to simulate a typical estuarine system. As the elvers used in this experiment were collected in a trap (emptied every 48 h) positioned about 2 m from where the Hellebækken Brook drains into the Kattegat and the elvers were acclimated for 3 weeks before beginning the

experiments, we assume little or no effects from the transfer between salinities on the results of the experiments. Nevertheless, further studies are needed, but our results indicate that preservation of coarse marine substrata should be taken into consideration while planning future management initiatives and restoration projects. An elevated availability of marine coarse substrata is probably beneficial to the coastal population of *A. anguilla* elvers.

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Figure 1. Mean (\pm 95% CI) probability of *Anguilla anguilla* ($n = 129$) found in four different substrata: large gravel (LG; $\varnothing = 32$ –64 mm), medium gravel (MG; $\varnothing = 12$ –32 mm), fine gravel (FG; $\varnothing = 8$ –12 mm) and sand ($\varnothing = 0.25$ –0.50 mm) combined with vegetation (SV).

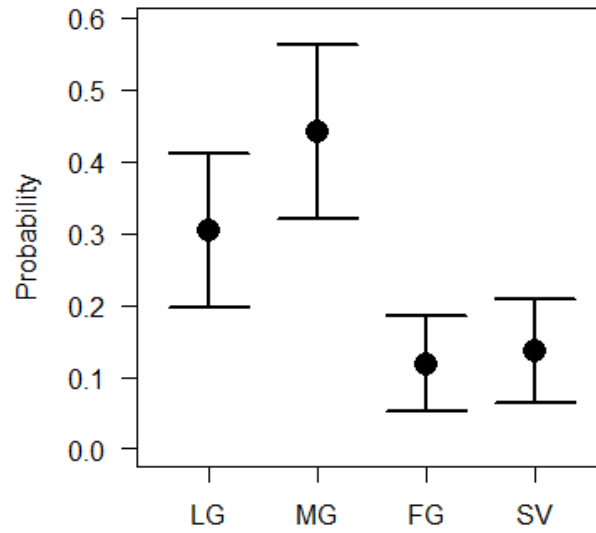


Table 1. Number of *Anguilla anguilla* elvers with different behaviours observed every 30 min until the end of experiment (120 min)

Observation (min)	Coverage		Swimming (n)
	> 80% (n)	≤ 80% (n)	
0	115†	7	7
30	108†	10	11
60	103†	19	7
90	112†	11	6
120	111	14	4

†Elvers that were > 80% covered could not be registered before the end of the experiment; calculated from; $n = 129 - \Sigma(\leq 80\% + \text{swimming})$.