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Article

Movements of Non-Migrant European Eels in an Urbanised Channel Linking a Mediterranean Lagoon to the Sea

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Abstract: Transitional ecosystems and, particularly, Mediterranean lagoons represent important habitats for the European eel (*Anguilla anguilla*) population. In these habitats many anthropogenic pressures can disturb eel movements and, in turn, negatively affect the population. Despite the importance of movements during the non-migrant growing stage in eels, this topic is understudied in Mediterranean lagoons. We thus aim to describe the diel and seasonal phenology and the effect of environmental drivers on non-migrant eel movements. Videos obtained from an Adaptive Resolution Imaging Sonar (ARIS) acoustic camera that continuously recorded from October 2018 to April 2020 were processed to evaluate the daily number of eels swimming toward the lagoon. More than 60% of the 7207 eels observed were females with a size >45 cm. Movements were year-round and predominantly during the night. A Boosted Regression Tree analysis demonstrated that, among the 10 environmental drivers studied, flow velocity, water temperature, discharge of the main tributary, wind velocity and atmospheric pressure, had the strongest influence on eel movement activity. Non-migrant eel movements should be better incorporated into lagoon management plans through actions such as limiting dredging activities from 18:00 to midnight, especially when the water flows toward the lagoon and when the water temperature is higher than 12 °C.

Keywords: acoustic camera; *Anguilla anguilla*; behaviour; diadromy; dual-frequency sonar; migratory fish



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1. Introduction

Transitional ecosystems such as coastal lakes, wetlands and lagoons are highly valuable ecosystems with elevated ecological, biodiversity and socio-economical values [1]. Within these transitional ecosystems, Mediterranean lagoons are particularly important for biodiversity with more than 700 macrophyte taxa, 900 invertebrate taxa, and almost 400 fish taxa recorded [2,3]. Among fish species, the European eel (*Anguilla anguilla*, referred as eel hereafter) is among the most abundant. For example, the eel biomass in Mediterranean lagoons was estimated to range from seven to more than 30 kg·ha^{−1} [4–6] which is greater than most biomasses reported in other habitats such as rivers or freshwater lakes [4]. However, a drastic decline in eel catches has been observed since the mid-1970s in Mediterranean lagoons [7,8], that coincide with the severe decline of the eel population reported throughout Europe [9]. Consequently, *A. anguilla* was listed in Annex II of the Convention on International Trade in Endangered Species [10] in 2007 and as critically endangered in the International Union for Conservation of Nature Red List in 2010 [11]. The high number of eels in Mediterranean lagoons and the alarming decrease in the population

highlight the need to develop specific management and conservation measures for eels in these ecosystems.

As for many diadromous and/or potamodromous migratory fish species, movements and migrations are key elements of the eel life cycle as they are critical to its reproduction, growth and dispersal [12,13]. Eels are presumed to spawn in the Sargasso Sea [14,15], and after hatching, the leptocephali larvae migrate to the coasts of Europe and northern Africa [16] where they colonise coastal and inland waters, including Mediterranean lagoons, to grow. At the end of their growing period, eels escape their growing habitat to migrate back to the Sargasso Sea [17,18]. Most studies concerning eel movements were focused on their diadromous migration, when glass eels arrive from the sea to their continental growing habitat [19,20], or when silver eels migrate seaward to return to the Sargasso Sea [4,18,21,22]. Beyond these migratory movements, non-migrant eels also move within their growing habitat [23–25] and/or between freshwater and brackish or marine habitats [26–28]. Non-migrant eels usually spend several years in their growing habitats [29], and consequently performed numerous movements within and/or between habitats. These movements are pivotal to their life cycle as they allow eels to seek refuge [30] or to forage for food [31,32]. However, during their movements non-migrant eels are exposed to harmful impacts such as predation [33] or anthropogenic habitat degradations and loss of connectivity between habitats [34]. Expanding our knowledge of non-migrant eel ecology, specifically with respect to their movements, is thus important to improve management and restoration measures targeting this species. In particular, the description of the different habitats used by non-migrant eels and the timing of their movements between or within habitats can help to protect critical areas and/or periods for this stage.

Despite the importance of Mediterranean lagoons for the eel population, non-migrant eel movements in these habitats have received little attention (but see [28,35]). In particular, the seasonal and diel movement phenology of non-migrant eels in Mediterranean lagoons and how environmental drivers influence these movements is largely unknown. This information is critical to predict the spatio-temporal occurrence and abundance of non-migrant eels in different areas of the lagoons and, ultimately, to design suitable management and restoration plans [13]. Mediterranean lagoons are linked with the sea by channels in which the physico-chemical conditions gradually change from the lagoon to the sea environment. These habitats are often highly anthropised with, for example, harbours located along the channels or sluice gates which limit water and sediment exchanges between the lagoon and the sea. In this context, we aimed to study the seasonal and diel phenology of non-migrant eel movements between an anthropised channel and a Mediterranean lagoon and describe the influence of several environmental drivers on the dynamics of non-migrant eel movements. Finally, we provide recommendations to improve management and conservation measures in Mediterranean lagoons to better incorporate the non-migrant eel stage.

2. Material and Methods

2.1. Overall Sampling Strategy and Study Site

The instruments used to measure environmental parameters and eel movements in this study were installed in the channel that links the Bages-Sigean lagoon with the Mediterranean Sea (Figure 1a–c). The lagoon area is 38 km² with a mean depth of 1.3 m, a maximum depth of 2.9 m [36] and a watershed area of 460 km². The Bages-Sigean lagoon hosts an important population of eels which support an ancestral and traditional fishery that harvests tens of tons each year [4]. The two main freshwater inputs in the lagoon are the Berre river in the south-west and the Robine navigation channel in the north-east (Figure 1b). The discharge of the latter was not monitored during the study but it rarely exceeds 1 m³·s^{−1} (A. Seguy, Voies Navigables de France com. pers.). The discharge of the Berre river was recorded at the Ripaud gauging station (Figure 1b). The channel is 50–150 m wide with a depth ranging from 3 to more than 10 m. No sluice gate or other man-made structure influences the hydraulic communication between the lagoon and

the sea. Consequently, the substrate is similar between the lagoon, the channel and the coastal area in front of the channel and is dominated by sandy-mud. The channel is heavily anthropised as it is used as a commercial harbour and the city of Port la Nouvelle is located on its south bank.

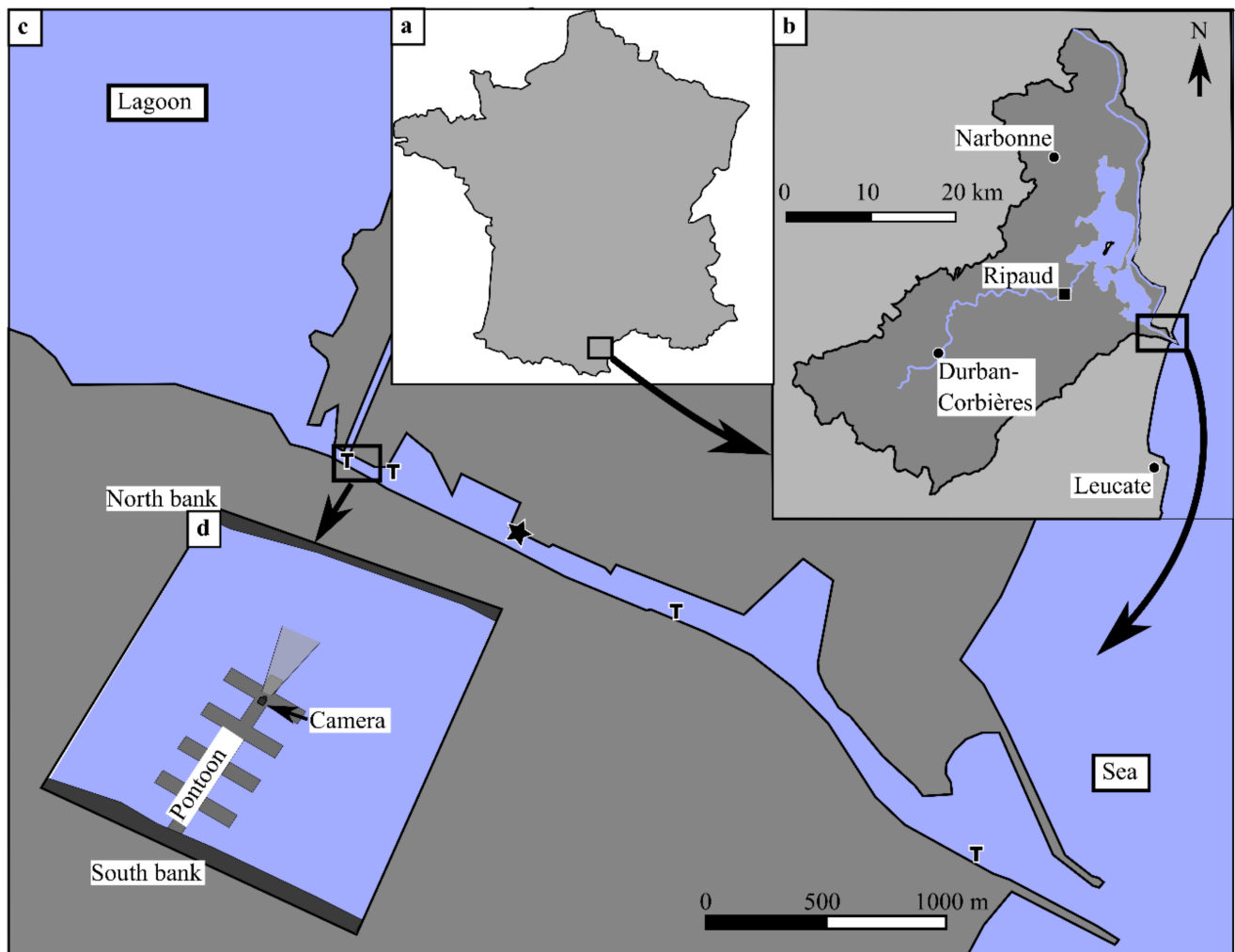


Figure 1. Location of the studied Bages-Sigean lagoon in southern France (a), the channel linking the lagoon with the sea (b) and the pontoon where the Adaptive Resolution Imaging Sonar (ARIS) camera was attached (c–d). The black circles represent the locations of the three meteorological monitoring stations and the black square indicates the location of the gauging station on the Berre river (b). The name of each station is specified on the map. The black star represents the location of the Horizontal Acoustic Doppler Current Profilers (H-ADCPs) and Conductivity–Temperature–Depth (CTD) probe and the black “T” marks the location of each temperature logger (c). The grey shaded area represents the estimated field of view of the camera in aerial view (d).

2.2. Acoustic Camera

An Adaptive Resolution Imaging Sonar (ARIS, Explorer 1800, Sound Metrics) acoustic camera was used to monitor eel movements in the channel. The acoustic camera was positioned in the narrowest part of the channel which is 53 m wide with a mean depth of 3.5 m (Figure 1c). It was fixed at a pontoon pillar at a depth of 3 m and at a distance of 20 m from the closest bank in order to film horizontally toward the opposite bank and perpendicularly to the flow direction. It was set at a frequency of 1.8 MHz which provides a range of images at a distance of only 14–15 m but facilitates the identification of eels based on their behaviour and morphology. At this frequency, the camera field of view covered approximately 10% of the surface of the channel at this section (Figure 1d). The

camera continuously recorded successive videos of 15 mn each, 24 h a day from 26 October 2018 to 30 April 2020 (18 months, 553 days) except for a period of 45 days due to technical issues (power outage, hard drive failure).

All videos from the 18:00–midnight period, hypothesised as the most active period for eel movements, were processed by one of two experienced operators who manually counted and measured the Length acoustic video (L_{AV} cm) of each eel identified based on its shape and swimming behaviour using ARIS fish software (Sound Metrics). The swimming direction of the eels (seaward, toward the lagoon or unknown when eels turned around in the camera field of view) was also recorded. Fifteen videos lasting 24 h (from 00:00 to midnight) were also analysed. These videos were selected for the high number of eels counted during the 18:00 to midnight period for the same day and also because together, they cover every calendar month of the year.

A previous study demonstrated that the two operators who analysed the videos counted an equivalent number of eels per video but the L_{AV} estimated by each operator underestimates the real size of eels [37]. As a consequence, the error distribution made by the two operators for three different size classes (i.e., $L_{AV} < 45$ cm, $45 \text{ cm} \leq L_{AV} < 60$ cm and $L_{AV} \geq 60$ cm) described in Lagarde et al. [37] was used to correct the L_{AV} estimates. To do so, a correction factor ranging from -30% to $+20\%$ was assigned to each L_{AV} estimate made by each operator in accordance with the error distribution of the concerned operator for the given L_{AV} class [37].

2.3. Environmental Parameters

The effect of 11 environmental parameters on eel movement activity was investigated. The parameters were selected as they are known to influence eel movements [25,38–41]. Six variables were obtained from the three closest Météo France meteorological stations (Narbonne, Durban-Corbière and Leucate, Figure 1b): rain fall ($\text{mm}\cdot\text{h}^{-1}$), air temperature ($^{\circ}\text{C}$), atmospheric pressure (hPa), nebulosity (qualitative scale from 0 clear sky to 9 fully cloudy), wind velocity ($\text{m}\cdot\text{s}^{-1}$) and direction ($^{\circ}$). The two latter variables were aggregated into one by attributing a positive value to the wind velocity when the wind direction was between 20° and 200° (blowing seaward) and a negative value otherwise. The discharge of the Berre River ($\text{m}^3\cdot\text{s}^{-1}$) was obtained from the Ripaud gauging station (available at www.hydro.eaufrance.fr (access on 6 July 2020), Figure 1b) and the moon phase was expressed as a percentage of the full moon (0% new moon, 100% full moon) using the *lunar* package [42] in the open source R software (version 3.5.1 [43]). Finally, five environmental parameters were measured in the channel (Figure 1c): flow velocity ($\text{m}\cdot\text{s}^{-1}$) and direction ($^{\circ}$) at 1.5 m and 4.5 m depths using two Horizontal Acoustic Doppler Current Profilers (H-ADCP, Channel Master, RDI-Teledyne) which were also used to estimate the suspended solids concentration (SSC, $\text{g}\cdot\text{L}^{-1}$) at each depth. SSC was derived from the intensity of the acoustic echoes using the sonar equation [44]. Next, backscattered intensities were first corrected from geometrical corrections and sound absorption, and then converted into SSC using 19 water samples from the channel ($R^2 = 0.63$). The flow velocity was estimated using the mean across-channel velocities measured by the two H-ADCPs following the methodology of Fiandrino et al. [45]. The flow velocity and direction were aggregated into a single variable with positive values for along-channel flow velocity when the water flowed seaward and negative values otherwise. The water temperature ($^{\circ}\text{C}$) and salinity were measured using a Conductivity–Temperature–Depth (CTD) probe (6600 or EXO2, YSI). Salinity was also measured manually with a refractometer each morning from 19 December 2018 to 16 March 2020. Temperature was monitored in four other locations in the harbour (Figure 1c) using temperature loggers (PLUG & Track, iBcod). Finally, 11 environmental parameters were kept for the analysis: rain fall, air temperature, atmospheric pressure, nebulosity, wind velocity, discharge of the Berre river, moon phase, flow velocity, SSC, water temperature and salinity (Table 1).

Table 1. Summary of environmental parameters obtained or measured during the study (Oct 2018–April 2020). The number of instruments used to measure the parameters and the type of instruments are specified. When more than one instrument measured the same parameter, the mean values measured by the different instruments were kept in the analyses.

Environmental Parameter	Mean	Min–Max	N of Measurements
Rain fall ($\text{mm}\cdot\text{h}^{-1}$)	0.08	0–4.5	3 (climate monitoring stations)
Air temperature ($^{\circ}\text{C}$)	13.5	2.4–31.5	3 (climate monitoring stations)
Atmospheric pressure (hPa)	1017.4	988.2–1034.7	3 (climate monitoring stations)
Nebulosity	1.7	0–9.0	3 (climate monitoring stations)
Wind velocity ($\text{m}\cdot\text{s}^{-1}$)	2.5	−12.9–12.9	3 (climate monitoring stations)
Berre river discharge ($\text{m}^3\cdot\text{s}^{-1}$)	0.6	0.01–21.5	1 (Ripaud gauging station)
% of the full moon	50.0	0.0–100.0	1 (lunar package)
Flow velocity ($\text{m}\cdot\text{s}^{-1}$)	0.01	−0.31–0.58	2 (1.5 m and 4.5 m depth H-ADCP)
SSC ($\text{g}\cdot\text{L}^{-1}$)	0.02	0.002–0.07	2 (1.5 m and 4.5 m depth H-ADCP)
Water temperature ($^{\circ}\text{C}$)	15.3	4.4–28.8	5 (CTD probe and 4 PLUG&Track loggers)
Water salinity	36.7	22.1–43.0	1 (CTD probe of manual measurements)

3. Statistical Analysis

The corrected L_{AV} distributions were compared between each calendar month. This comparison was performed using kernel density estimates [46]. The bandwidth of the corrected L_{AV} was selected using the procedure described by Sheather and Jones [47]. The statistical difference of corrected L_{AV} was tested with a permutation test that compared the kernel frequency distributions with a null model of no difference among months [46].

All the environmental parameters of the study were measured at a frequency ranging from 5 min to one hour. In order to be consistent with the period when eels were counted in the study, the mean of each environmental parameter over the 18:00–midnight period was used in the analyses. The manual estimates of salinity collected in the morning were used when the CTD measurements during the 18:00–midnight period the day before were missing due to technical issues. To identify the redundant parameters among environmental variables, a correlation analysis was performed. The environmental parameters measured by several instruments were correlated with a Pearson correlation coefficient $r > 0.8$. Consequently, the mean value of the parameter measured by all instruments was used in the analyses. Additionally, as the air and water temperatures were correlated with a $r > 0.8$, only the water temperature, more representative of the eel's habitat condition, was included in the analyses.

The effect of the 10 remaining environmental parameters on the number of eels swimming toward the lagoon was analysed using Boosted Regression Tree (BRT). BRT is suited to selecting the most relevant predictors from a large set of candidate variables, does not depend on the normality and homoscedasticity of the data, and integrates non-linear responses [48]. A BRT model was fitted to model the number of eels swimming toward the lagoon using the 10 environmental parameters as predictors. The number of eels was log transformed to limit the influence of data collected for a few specific dates where eel count numbers were exceptionally high, on the total deviance. The BRT was fitted with a learning rate of 0.005 and a tree complexity of three as recommended for a small dataset (250–500 lines, [48]). The BRT performance was assessed via the amount of deviance explained and the cross-validated correlation [49]. The partial dependence plots for parameters with a contribution $>10\%$ were used to visualise the effect of a parameter on the number of eels swimming toward the lagoon. In dependence plots, the fitted function value superior to zero indicates a positive effect of the variable on the number of eels swimming toward the lagoon compared to the average effect of all other parameters [48] and vice versa for negative values.

All statistical analyses were conducted using the open source R software (version 3.5.1 [43]). It was implemented with the *Kernsmooth* [50] and *sm* [51] packages for comparison of corrected L_{AV} frequency distributions and the *gbm* [52] and *dismo* [53] packages for BRT analyses.

4. Results

4.1. Eel Movement Phenology

Videos of the 18:00–midnight period were analysed from 26 October 2018 to 30 April 2020 (508 days). A total of 19,689 eels were observed and measured. Among these eels, 12,461 (63%) were swimming seaward and 7207 (37%) were swimming toward the lagoon. Only 21 eels (<1%) with an unknown swimming direction were observed, and these individuals were not considered in the following analyses. The difference in eel counts between individuals swimming seaward and toward the lagoon is probably due to the high levels of escape for silver eels swimming seaward. Consequently, only the eels swimming toward the lagoon are further analysed in this study. The results concerning the eels swimming seaward are provided in supplementary materials for information only (Figures S1 and S2). The linear relationship between the total number of eels swimming seaward and the total number of eels swimming toward the lagoon is weak ($N = 508$, $F_1 = 30.4$, $p < 0.001$, $R^2 = 0.05$). Interestingly, this relationship fairly improved when the main escape period for silver eels (October–December) was removed from the analyses ($N = 353$, $F_1 = 161.7$, $p < 0.001$, $R^2 = 0.31$). For the 15 days for which videos were analysed from 00:00 to midnight, a total of 960 eels swimming toward the lagoon were counted. The majority (86%) of these eels were counted at night, from 18:00 to 6:00 mostly during the 18:00–midnight period and before dawn, from 04:00 to 05:00 (Figure 2).

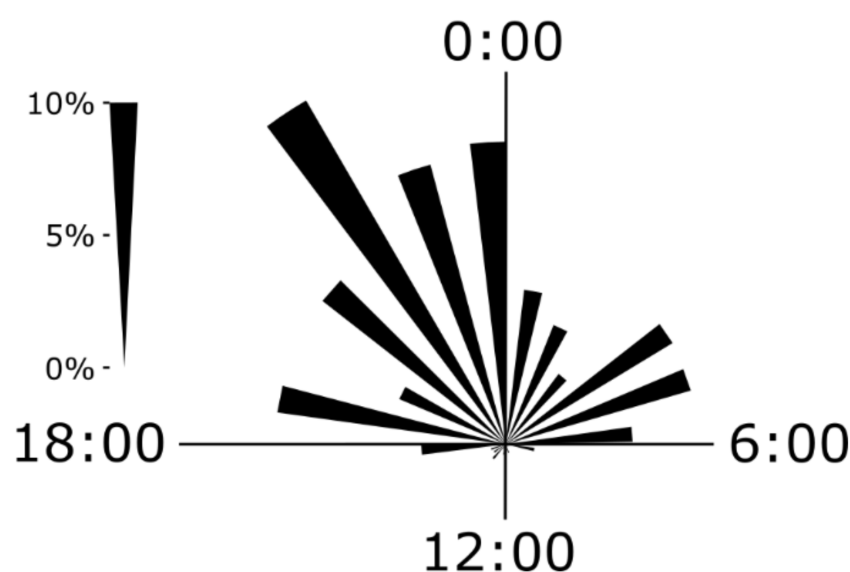


Figure 2. Circadian repartition of eels ($N = 960$) swimming toward the lagoon counted over the 15 days for which videos were analysed from 00:00 to midnight. For each hour (black triangle), the percentage was calculated as the number of eels counted during this hour divided by the total number of counts in 24 h.

The daily number of eels swimming toward the lagoon ranged from 0 to more than 200 (Figure 3). Peaks in daily number of eels swimming toward the lagoon were observed throughout the year but were less common and had a lower amplitude in January.

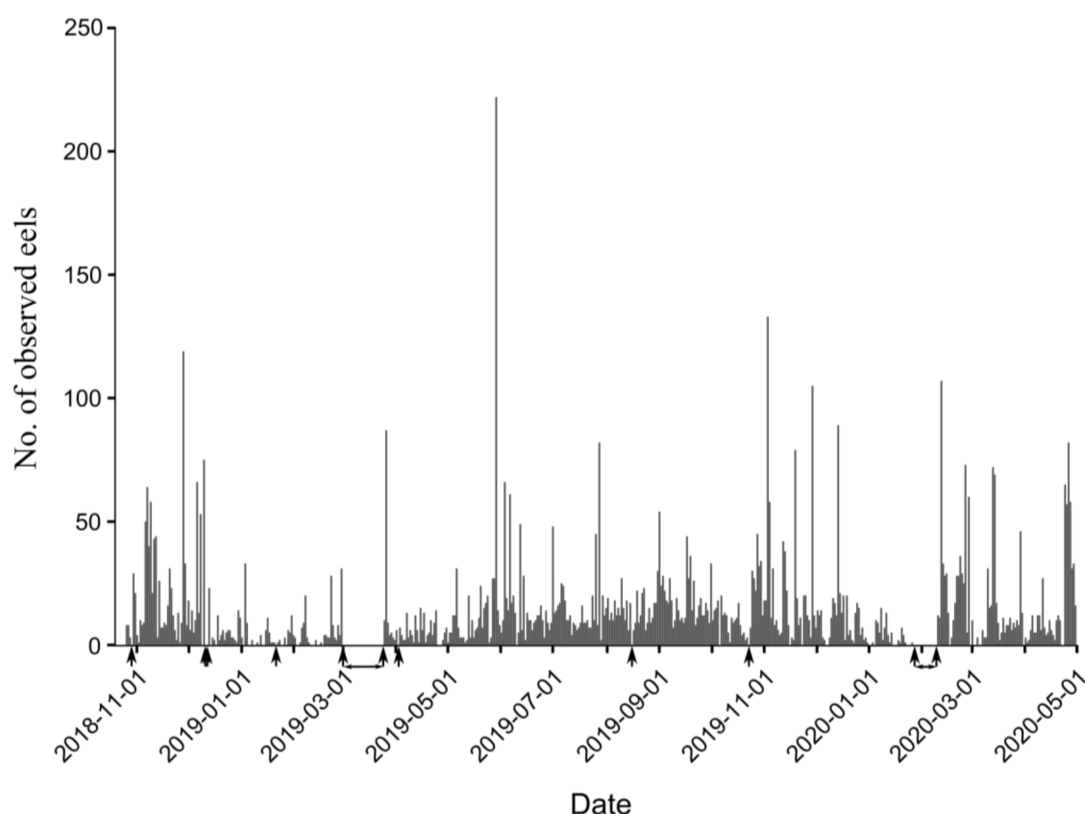


Figure 3. Daily counts of eels swimming toward the lagoon during the 18:00–midnight period. The black arrows indicate the periods when videos were not recorded during the 18:00–midnight period due to technical issues (45 days in total).

4.2. Size Frequency Distributions

The corrected L_{AV} for eels swimming toward the lagoon ranged from 20 cm to 114 cm (Figure 4). Approximately 66% of the eels measured more than 45 cm. More than 62% of the eels measured between 45 and 75 cm from January to October and almost 50% measured between 25 cm and 45 cm in November and December (Figure 2). The L_{AV} frequency distribution was significantly different between months (kernel density estimate, band width = 2.0 cm, $P < 0.001$).

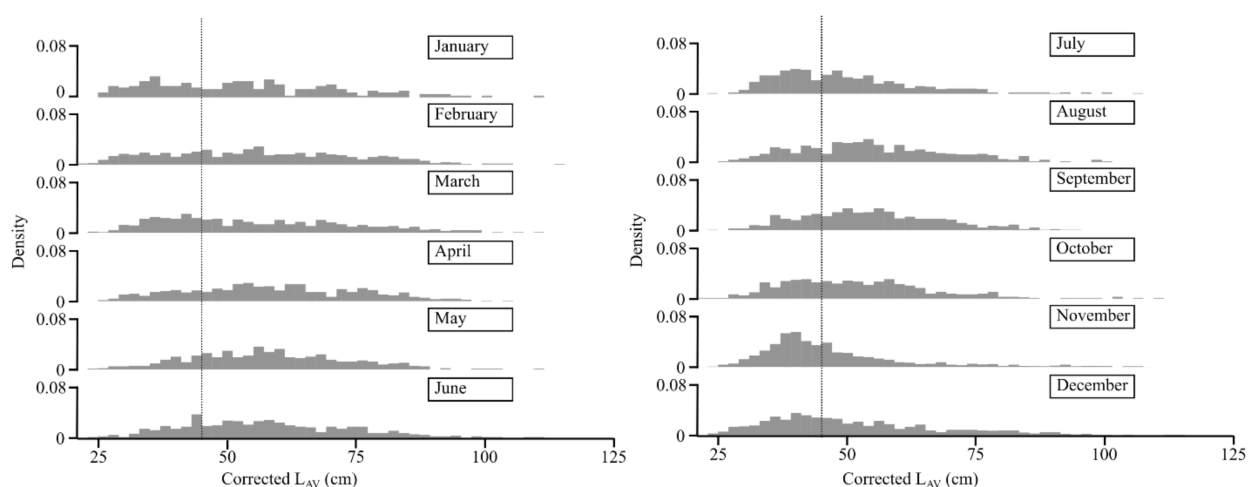


Figure 4. Monthly size (corrected L_{AV}) frequency distribution of eels swimming toward the lagoon. The black line represents the corrected L_{AV} of 45 cm above which eels are considered as females.

4.3. Effect of Environmental Parameters on Eel Movements

The BRT analysis was performed for 429 dates where both eel counts from 18:00 to midnight and environmental parameters were available together. The BRT explained 63% of the total deviance and had a cross-validated correlation of 0.59, and thus its performance was evaluated as very good. The five environmental parameters for which the relative contribution was >10% were the flow velocity, water temperature, the Berre river discharge, wind velocity and atmospheric pressure (Table 2).

Table 2. Relative importance of the 10 environmental parameters explored in order to explain the number of eels swimming toward the lagoon over the 18:00–midnight period from the Boosted Regression Tree (BRT). The bold values highlight the parameters with a relative importance >10% for which the dependence plots were displayed.

Environmental Parameter	Relative Importance
Flow velocity	27.7%
Water temperature	19.9%
Berre river discharge	11.0%
Wind velocity	10.6%
Atmospheric pressure	10.1%
% of the full moon	7.2%
SSC	5.8%
Water salinity	5.4%
Rain fall	1.3%
Nebulosity	1.1%

The number of eels swimming toward the lagoon was higher when the water was flowing toward the lagoon (Figure 5a) and when the water temperature was higher than 12 °C (Figure 5b). This number increased for Berre river discharge ranging from 0 to 2 m³·s^{−1}, decreased for discharges up to 3 m³·s^{−1} and remained stable for higher discharges (Figure 5c). Finally, the number of eels swimming toward the lagoon is more elevated when the wind blew toward the sea and for an atmospheric pressure lower than 1005 hPa (Figure 5d–e).

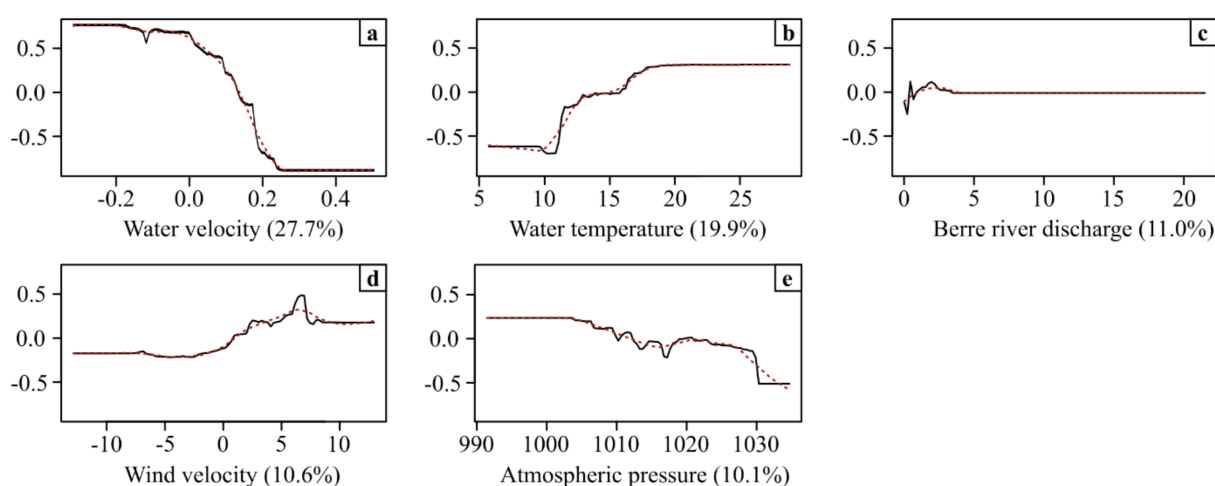


Figure 5. Partial dependence plots of the five most important environmental parameters influencing the number of eels swimming toward the lagoon: (a) water velocity (m·s^{−1}), (b) water temperature (°C), (c) Berre river discharge (m³·s^{−1}), (d) wind velocity (m·s^{−1}) and (e) atmospheric pressure (hPa). The percentage indicates the relative contribution of each environmental parameter in the BRT. Black lines represent the raw results whereas dashed red lines represent the smoothed results.

5. Discussion

5.1. Is the Number of Eels Swimming toward the Lagoon a Good Proxy for Non-Migrant Eel Movement Activity?

Acoustic cameras are well-adapted to monitor eel movements and migration as they are non-invasive and can be used during the night and/or with excessive turbidity [54]. However, the frame resolution does not allow for skin colour and detailed anatomical features such as eye diameter or fin length, which are commonly used to differentiate migratory silver eels from non-migrant eels, to be distinguished [55,56]. Consequently, to distinguish migratory silver eels from non-migrant eels using acoustic camera videos relies exclusively on behavioural interpretations. In our study, several behavioural observations (see below) such as the diel and seasonal movement phenology or the size structure of eels suggest that the observed eels swimming toward the lagoon are non-migrant individuals and that the daily numbers observed could be used as a proxy for the intensity of their movement activity.

First, while the correlation between the number of eels swimming seaward and toward the lagoon is generally weak ($R^2 = 0.05$), it is fairly improved when the main period of silver eels escape (i.e., October–December, [4]) is not considered in the analysis ($R^2 = 0.31$). When the migrant silver eels are removed from the analysis, there is an acceptable correlation between the numbers of non-migrant eels swimming seaward or toward the lagoon. This observation could be explained by round trip movements and/or by a similar daily number of eels swimming seaward and toward the lagoon. Consequently, the number of eels swimming toward the lagoon may be a fair estimation of the non-migrant eel movement activity including during the main period of escape for silver eels.

The diel and seasonal phenology of eels swimming toward the lagoon during the entire monitoring period in this study is consistent with the known behaviour of non-migrant eels. The nocturnal peak in activity of non-migrant eels was previously described for many habitats such as the Shelde river Polders system in the Netherlands [25], the Awirs river in Belgium [23] and several lagoons of the French Mediterranean coast, including the Bages-Sigean lagoon [31]. These authors usually attributed the nocturnal peak in activity of non-migrant eels to their foraging activity in relation to their feeding behaviour. The secondary peak for eels swimming toward the lagoon before dawn is comparable with the non-migrant yellow eel behaviour in the Poole Harbour in England [24], where one of the two main movement periods is two hours before sunrise. The seasonal phenology of eels swimming toward the lagoon with the lowest numbers observed in January is consistent with observations made for non-migrant yellow eels in different habitats such as the Shelde polders [25], the river Itchen [57] in England and the Grand Lieu lake [39] on the French Atlantic coast. Costa-Dias and Lobon-Cervia [32] and Lecomte-Finiger [31] observed that eels captured in the Llorin river in Spain and in French Mediterranean lagoons had a higher abundance and occurrence of food items in the stomach during the spring and summer compared to autumn and winter. It is thus likely that the lower number of eels swimming toward the lagoon in January and February is related to their reduced foraging activity during the cooler months.

The monthly size class distribution is dominated by eels with a corrected L_{AV} of more than 45 cm which are mostly females [58], as males are usually smaller than 45 cm [59]. This observation is not consistent with the known size structure of the Bages-Sigean lagoon eel population which is dominated by individuals smaller than 45 cm [4]. While the detection of smaller eels may have been lower due to the use of an acoustic camera, the pattern most likely reflects an ecological process. The size of the non-migrant eel home range usually increases with individual size as described in Lough Finn in Ireland [60] or in Hanningfield Reservoir in England [40]. These authors argue that because larger individuals require a greater quantity of food resources, they therefore need to forage over a larger area. If larger non-migrant eels have a larger home range they are more likely to swim in the camera field of view during their foraging movement which makes them more likely to be observed. The higher proportion of individuals with a $L_{AV} < 45$ cm in November and December may

be explained by a higher number of silver eels for this period [4,36]. During their seaward migration, some individuals may disrupt their migration and swim back to the lagoon. This behaviour was previously described by Bultel et al. [61] in the Loire river estuary in France. This hypothesis is also consistent with the results of an acoustic study carried out in the Bages-Sigean channel where several tagged silver eels swam back in the direction of the lagoon before escaping to the sea (Mercader et al. in prep).

5.2. Effect of Environmental Drivers on Non-Migrant Eel Movement Activity

Environmental drivers can have a direct effect on non-migratory eel movement activity such as facilitating the motion or limiting energy expenditure due to swimming [62], or an indirect effect when influencing other drivers such as food availability or habitat conditions [30,57]. The number of non-migrant eels swimming toward the lagoon was higher when the water flowed toward the lagoon (negative values of flow velocity) and sharply decreased when the water flowed seaward. Even if tide has a limited impact on the flow velocity in the Bages-Sigean channel compared to other drivers such as the wind and the discharge of the tributaries, our results are in accordance with Barbin [63] who described movements of *A. rostrata* at the yellow stage (non-migrant eels) following the tide (selective tidal stream transport) in the Penobscot estuary in the USA. Conversely, more yellow eels tended to swim against the flow in the Poole Harbour [24]. These authors hypothesised that their results were biased by the complexity of the diel tidal cycle in Pool Harbour with two periods of high water and a single period of low water. Temperature is frequently described as one of the main drivers of intensity for non-migrant eel movements. In our study, the number of non-migrant eels swimming toward the lagoon is low when the water temperature is lower than 12 °C and greatly increases when the temperature is 12–13 °C or higher. Our observations are consistent with the results of Baras et al. [23] and Verhelst et al. [25] who described an increase in non-migrant yellow eel activity when the water temperature was higher than 10–13 °C. This behaviour is probably related to the increase in metabolic activity with higher temperatures that drives non-migrant eels to forage more frequently and over a larger home range to find more prey items [32]. The higher number of non-migrant eels swimming toward the lagoon when a strong wind was blowing seaward (positive values of wind velocity) may also be related to their foraging behaviour. The strong wind likely promotes the resuspension of nutrients and small organisms due to the shallowness of the lagoon [64]. Accordingly, the availability of prey items such as oligochaetes, crustaceans and insects [31,65] is probably higher during these windy conditions, enhancing the foraging behaviour of non-migrant eels. This hypothesis may also explain the increase in the number of non-migrant eels swimming toward the lagoon when the Berre river discharge increases, as the river could also be a source of prey items in the lagoon [66]. However, this effect is weakened when the Berre river discharge is high. The associated high discharge in the Berre river with strong flood conditions and a strong current flowing toward the sea (personal observation, [45]) may prevent the movement of non-migrant eels toward the lagoon. Finally, the observed positive effect of low atmospheric pressures on the number of non-migrant eels swimming toward the lagoon may be explained by their capacity to sense the decrease in atmospheric pressure. Although it has not been documented for eels, other animal biota such as the white-crowned sparrow (*Zonotrichia leucophrys*) and the blacktip shark (*Carcharhinus limbatus*) were documented to have behavioural responses associated with the decrease in atmospheric pressure [67,68]. Similarly, low atmospheric pressure could be sensed by the eels and may indicate the onset of rainy conditions, leading to an increase in the allochthonous input of prey in the lagoon, similar to the increase in the Berre river discharge.

5.3. Management Implications

Lagoons and other transitional ecosystems such as estuaries and coastal wetlands represent an important fraction of eel habitats [7,69]. Understanding how eels use these habitats during their continental growing period is thus essential to develop specific management measures. Our study demonstrated that many eels in a lagoon population extensively move between the lagoon and the channel linking it to the sea. This result highlights that these areas merit specific management and conservation efforts [30]. Channels linking transitional ecosystems to the sea are often extensively urbanised, especially for harbour activity [70,71] that requires regular dredging for navigation purposes. The dredging activity disturbs and may impair the behaviour of non-migrant eels moving between the harbour and the lagoon or other transitional ecosystems for foraging. Consequently, one way of reducing the impact of dredging activity on eel foraging behaviour would be to avoid conducting this activity at night, especially from 18:00 to midnight as shown in this study. As non-migrant eel movements between the lagoon and the harbour were observed year-round, seasonal regulation of the dredging activity would probably have a limited effect on their behaviour. However, regulation of dredging activity could also be improved if the effect of environmental drivers was taken into account. Dredging should be avoided when the water flow is directed toward the lagoon and when the water temperature is more than 12 °C, as these are the conditions when non-migrant eels move the most. However, areas in the channel and/or harbour can also be used for daytime refuge habitats for non-migrant eels as observed for *A. rostrata* yellow eels in the river York estuary, Canada [30]. Further studies, such as those based on fixed array acoustic telemetry, could help to locate these refuge habitats to limit the dredging activity in these zones. This study highlights the importance of understanding eel behaviour in modified and/or urbanised habitats that link the sea to transitional ecosystems, in order to implement efficient/appropriate management measures.

Supplementary Materials: The following are available online at <https://www.mdpi.com/2073-4441/13/6/839/s1>, Figure S1: Daily counts of eels swimming seaward during the 18:00–midnight period. The black arrows indicate the periods when videos were not recorded during the 18:00–midnight period due to technical issues (45 days), Figure S2: Circadian repartition of eels (N = 2328) swimming seaward counted over the 15 days for which videos were analysed from 00:00 to midnight. For each hour, the percentage was calculated as the number of eels counted during that hour divided by the total number of counts in 24 h.

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