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Article

The Influence of Natural and Anthropogenic Environmental Pressures on European Eel Abundances in French Estuaries

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Abstract: The aim of this study was to investigate the influence of environmental characteristics and anthropogenic pressures on the abundance of estuarine European eels (*Anguilla anguilla* L.) during their continental growth phase. European eels were collected with fyke nets from spring to autumn in twenty-nine estuaries along the French English Channel and the Atlantic coast. Eel abundance (catch per unit effort, CPUE) was assessed for all eels and by size class for small (total length < 300 mm), intermediate (≥ 300 to <450 mm), and large (≥ 450 mm) eels. The environmental characteristics of the French estuaries were described by twelve descriptor variables, mainly related to hydro-morphological and sedimentary factors. Based on principal component analysis and hierarchical clustering analysis, estuary size was identified as the main explanatory variable and used to compare eel abundance. Eel abundance differed significantly according to estuary size, with higher abundances observed in small estuaries (7.22 to 13.00 ind. fyke nets 24 h⁻¹) compared to large estuaries (0.13 to 0.71 ind. fyke nets 24 h⁻¹). Spatial variation in eel abundance was correlated with differences in estuary size for all eel size classes. The influence of anthropogenic pressures on eel abundance was assessed by nine anthropogenic estuarine pressure indicators. The results indicate that high values of the anthropogenic pressure indicators were correlated with low eel abundance. This study highlights that large French estuaries subject to stronger anthropogenic pressures were less favourable habitats than small estuaries with less anthropogenic pressure.

Keywords: eel abundance; estuarine habitats; hydro-morphological and sedimentary factors; estuary size; anthropogenic pressure indicators

Key Contribution: The influence of environmental factors, including anthropogenic pressure, on the eel abundance in estuaries during the continental growth phase was investigated at a regional scale in French estuaries along the English Channel and Atlantic coasts. Our results indicated a decline in abundance that was associated with increasing estuary size and increasing anthropogenic pressure.



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1. Introduction

The European eel (*Anguilla anguilla* L.) is a facultative catadromous migratory fish that spawns in the Sargasso Sea, and the newly hatched larvae (i.e., the leptocephalus stage) migrate to the continental waters of Europe and North Africa [1,2]. Once they reach the coasts, the glass eels enter estuaries and progressively colonize the watersheds from the marine coast to the upstream parts of the rivers, where they are subject to multiple environmental and anthropogenic pressures. Eels in the yellow stage feed and grow until they mature into the silver stage before migrating to the spawning grounds to reproduce. European eel populations have declined in recent decades due to a sharp decline in glass eel recruitment in the early 1980s [3–5]. Eel populations were affected by many factors

(e.g., habitat degradation, overfishing, pollution, and migration barriers) [6] that act synergistically, especially during the continental growth phase [7]. Migration barriers, poor water quality, and habitat loss have been identified as the main causes of decline [8–10]. The European eel is considered a vulnerable species and is listed on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species [11]. Scientific research, conservation, and management efforts have been undertaken to effectively mitigate the causes of the decline and contribute to the recovery of the European eel populations through the implementation of eel management plans [12]. Conservation strategies for eels include restocking programmes, habitat restoration, eel ladders, barrier removal, and fishing regulations; however, despite the strategies put in place, the conservation status of eel remains threatened [13].

During the continental growth phase, eels occupy a wide range of marine, brackish, and freshwater habitats, from coastal marine waters to paralic, riverine, fluvial, and lacustrine environments [14–16]. Eels show behavioural plasticity in habitat use and can reside in marine, brackish, and freshwater habitats or move between them during their growth [17–20]. Their ability to tolerate and adapt to a wide range of environmental conditions results from the diversity of life history traits that this species exhibits [2]. Eels residing in estuarine habitats grow faster and in better physiological condition than those living in freshwater [21–23], probably due to higher biological productivity compared to freshwater, especially at low latitudes [24,25]. Brackish habitats such as estuaries are also important habitats for the maintaining of eel populations [17,19,26] and generally support higher densities than freshwater habitats [27]. The characteristics of the local environment, in particular the quality and size of the estuary, have been identified as the most important factor influencing eel populations [21]. Spatial variation in eel life history traits appears to be related to variation in macrozoobenthos prey availability dependent on local hydro-morphological and sedimentary characteristics [22,28]. Studies on the relationship between spatial distribution and environmental characteristics have largely been carried out for the European eel (e.g., [29–32]), but most studies have focused primarily on freshwater habitats.

The response of eel populations to the prevailing environmental gradients and anthropogenic pressures in estuarine habitats remains poorly understood and needs to be studied on a larger scale. We know that estuarine fish populations are influenced by local and regional environmental characteristics [33–35]. Abiotic and biotic factors influence estuarine habitats and associated fish assemblages [36]. For example, substrate composition, estuarine depth, estuarine surface area, and proportion of intertidal area are important predictors of total fish abundance in European estuaries (e.g., [37,38]). The intensification of local anthropogenic disturbances in estuaries is also associated with a decrease in species richness and fish abundance [39,40]. Improving our knowledge of the ecological role of European eels in marine habitats is an important contribution to their management and conservation [41]. The European eel stock is currently at its lowest historical level [13], and effective eel management is difficult, partly due to a lack of understanding of the relationship between environmental and anthropogenic factors on the estuarine eel population at the regional scale.

This study aimed to investigate the influence of environmental characteristics and anthropogenic pressures on the abundance of estuarine European eels during their continental growth phase. Eels were collected from twenty-nine French estuaries of different sizes located along the French English Channel and Atlantic coast. More specifically, this study aimed to (i) identify the main environmental characteristics structuring the twenty-nine French estuaries based on hydro-morphological and sedimentary factors and identify clusters of sites based on these factors, (ii) determine the relationship between identified clusters and eel abundance in estuaries using a comparative approach, and (iii) assess the influence of anthropogenic pressures.

2. Materials and Methods

2.1. Data Origin

Eels were collected from twenty-nine estuaries located along the French English Channel and Atlantic coast (Figure 1). For this study, two different data matrices were compiled into one database. The first dataset was a compilation of eel data collected in the 23 estuaries between 2005 and 2010 as part of the Water Framework Directive (WFD) monitoring programme. The second dataset consisted of eel data collected in 2019 and 2020 in six other French estuaries located in the eastern English Channel [21], specifically the Slack, Wimereux, Liane, Canche, Authie, and Somme estuaries.

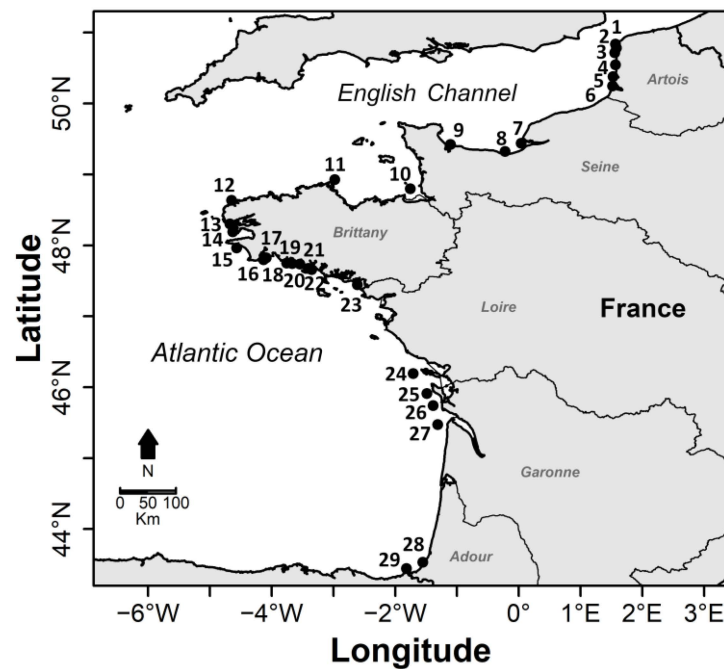


Figure 1. Location of the twenty-nine sampling estuaries along the French coast in the English Channel and Atlantic Ocean. The names of the estuaries are given in Table 1. The eel management units are also indicated in a grey colour on the map.

Table 1. List of the studied estuaries and number of conducted samples in each estuary (i.e., total number of fyke nets deployed for the entire sampling period), sampling period (years, seasons), and station location (i.e., 1: lower, 2: middle, and 3: upper estuary).

Estuary Number	Estuary	Number of Sampling	Sampling Year	Sampling Season	Station Location
1	Slack	72	2019–2020	Spring–autumn	1–2–3
2	Wimereux	72	2019–2020	Spring–autumn	1–2–3
3	Liane	56	2019–2020	Spring–autumn	1–2–3
4	Canche	72	2019–2020	Spring–autumn	1–2–3
5	Authie	72	2019–2020	Spring–autumn	1–2–3
6	Somme	96	2019–2020	Spring–autumn	1–2–3
7	Seine	80	2006	Spring, autumn	2–3
8	Orne	64	2006	Spring, autumn	3
9	Veys bay	128	2006	Spring, autumn	3
10	Mont St Michel bay	192	2006	Spring, autumn	1–2–3
11	Trieux	32	2007	Spring, autumn	2
12	Aber Wrach	32	2007	Spring, autumn	2
13	Elorn	32	2007	Spring, autumn	3
14	Aulne	32	2007	Spring, autumn	2
15	Goyen	32	2007	Spring, autumn	3

Table 1. Cont.

Estuary Number	Estuary	Number of Sampling	Sampling Year	Sampling Season	Station Location
16	Pont l'Abbe	18	2007	Summer-autumn	1–2
17	Odet	24	2007	Summer-autumn	2
18	Aven	20	2007	Summer-autumn	2–3
19	Belon	20	2007	Summer-autumn	3
20	Laita	20	2007	Summer-autumn	2–3
21	Scorff	4	2007	Spring	2–3
22	Blavet	20	2007	Spring, autumn	3
23	Vilaine	32	2007	Spring, autumn	1–2–3
24	Sevre Niortaise	32	2007	Spring, autumn	2–3
25	Charente	32	2005	Spring, autumn	2–3
26	Seudre	38	2005	Spring, autumn	2–3
27	Gironde	32	2006–2008, 2010	Summer-autumn	3
28	Adour	34	2005	Spring-summer	1–2–3
29	Bidassoa	16	2005	Spring, autumn	3

2.2. Estuarine Environmental Factors and Anthropogenic Pressures

To describe the environmental characteristics of the estuaries, 12 hydro-morphological and sedimentary variables (Table 2) measured during the study period were obtained from previously published data [35,38], from French government agencies (i.e., Service Hydrographique et Océanographique de la Marine (SHOM)), the national portal of the Service d'Administration Nationale des Données et Référentiels sur l'Eau (Sandre), Office Française de la Biodiversité (OFB), and the water agency (hydro.eaufrance.fr, accessed on 1 January 2024) or not found in the literature, using ArcGis 10.8 software and Google Earth. To characterize the hydrodynamics of each estuary, the maximum tidal range, river length, tidal influence limit, catchment area, and mean annual river discharge provided by French government agencies were retrieved. The maximum tidal range, river length, tidal influence limit, and catchment area were provided by Sandre and OFB (data exported in 2023). The mean annual river discharge was averaged over the last twelve years (i.e., from 2001 to 2021) of data collected from water agency databases (hydro.eaufrance.fr; data exported in 2023). The estuary surface area was estimated with ArcGis software as the area of the estuary from the mouth to the salinity limit of the water, measured from the polygons of the estuary surface covered by water at high spring tide, based on the SHOM limits. The depth and width of the estuarine mouth indicated the accessibility for fish [35] and were obtained from Google Earth and Marine charts (data exported in 2016). The wave exposure factor was considered to be the protection provided by these estuaries [42,43], ranging from very exposed to sheltered, and was obtained from the literature [35,38] or based on the depth and width of the estuary mouth and the tidal range obtained from the SHOM (data exported in 2023) where data were not available. The percentage of the total intertidal area within the estuary derived from the literature [35,38] was assessed to understand its role as a nursery habitat [44–46]. The substrate type was analysed to determine habitat suitability for fish and was obtained from the SHOM Marine sediment maps. The latitude of the estuary, measured using Google Earth, was used as a proxy for temperature.

In addition, anthropogenic pressures were included to assess the extent of local anthropogenic disturbance within the estuarine habitat. The CPI (cumulative pressure index) is a common anthropogenic disturbance indicator used under the WFD [47]. CPI is calculated based on eight anthropogenic indicators (see [34,48] for details) including loss of intertidal area (LIA), interference with the hydrographic regime (IH), anthropogenically affected coastline (AC), water chemical quality (WC), water quality biological effect (WB), benthos status (BS), dissolved oxygen temporal (DOT), and dissolved oxygen spatial (DOS). The severity of disturbance of each indicator was given an impact score between 0 and 9, defined from the conversion of scientific data, whether public or calculated, and expert knowledge

(Table S1). The CPI was calculated from the sum of all indicator scores, ranging from 0 for no disturbance to 72 for very high disturbance. The CPI is defined as the combined effect of several stressors, i.e., the sum of the individual effects acting in isolation.

Table 2. Hydro-morphological and sedimentary variables used to describe the environmental characteristics of the estuaries. Data sources: Service Hydrographique et Océanographique de la Marine (SHOM), national portal of the Service d'Administration Nationale des Données et Référentiels sur l'Eau (Sandre), Office Française de la Biodiversité (OFB), and water agency (hydro.eaufrance.fr).

Variables	Measurement Units or Ordinal Scores	Data Source
Catchment area	Kilometres squared	Sandre
River length	Kilometres	Sandre
Estuary surface area	Kilometres squared	ArcGis software
Tidal influence limit	Kilometres	OFB
Substrate type	1: muddy, 2: muddy/sandy, 3: sandy, 4: sandy/gravel, 5: rocky	Marine sediment maps, SHOM
Estuarine mouth width	Kilometres	Google Earth
Estuarine mouth depth	Metres	Marine Charts
Wave exposure	1: very exposed, 2: moderately exposed, 3: protected from waves	Literature [35,38], SHOM
Maximum tidal rang	Meters	SHOM
Total intertidal area	1: 0–20%, 2: 20–40%, 3: 40–60%, 4: 60–80%, 5: 80–100%	Literature [35,38]
Mean annual river discharge	Meters cube per second	Hydro.eaufrance.fr
Estuary latitude	Degree	Google Earth

2.3. Eels Sampling

For each estuary, eels were sampled between spring and autumn during one to four years (Table 1). Eels were sampled using two fyke nets, each 16 m long, with a mesh size of 15 mm at the beginning, 10 mm in the middle, and 8 mm at the cod end. The fyke nets were deployed at one to three stations along the salinity gradient (i.e., lower, middle, and upper estuary), depending on the estuary sampled. Fyke nets were deployed along the shoreline during low tide at a depth of between 0.5 and 1 m to keep the fyke net submerged, and each deployment consisted of two consecutive 24 h periods.

2.4. Eel Biological Characteristics

Captured eels were anaesthetised with eugenol solution (0.04 mL·L⁻¹; Thermo Fisher Scientific, Waltham, MA, USA) and then counted and individually measured (total length TL, with a precision of ±0.1 mm) before being released. Eel abundance was assessed using catch per unit effort (CPUE), based on the number of eels caught per gear and per unit of time (ind. fyke nets 24 h⁻¹). The number of eels caught in an estuary during the study depended on the sampling effort. To limit sampling bias, eel CPUE was standardised to the estuary surface area. Abundance values were standardised to facilitate comparisons between eel populations in estuaries of different sizes. In order to obtain a standardised CPUE (ind. fyke nets 24 h⁻¹ km⁻²), the eel abundance of each estuary was divided by sampling area (km²). Eel abundances were averaged per estuary to account for the number of sampling stations established in each estuary, which showed no significant difference in eel abundance between station locations (i.e., lower, middle, and upper estuary) in the estuary (Kruskal–Wallis test, $p = 0.649$), the number of seasons (Kruskal–Wallis test, $p = 0.107$), and years sampled (Kruskal–Wallis test, $p = 0.065$). During the continental phase, eel growth lasts several years and varies according to sex, with males generally being smaller and younger than females [49]. Eel abundance was calculated for three size classes

based on their TL with the small (<300 mm), intermediate (≥ 300 to <450 mm), and large (≥ 450 mm) eels. Small eels are considered to be yellow eels, intermediate eels are male silver eels or female yellow eels, and large eels are female silver eels.

2.5. Statistical Analyses

Principal component analysis (PCA) was used to describe and identify the main estuarine environmental characteristics and to determine the similarities between the twenty-nine estuaries according to twelve hydro-morphological and sedimentary explanatory variables (i.e., maximum tidal range, tidal influence limit, catchment area, estuary surface area, estuarine mouth depth and width, river length, wave exposure, total intertidal area, substrate type, mean annual river discharge, estuary latitude; Table 1). Variables were normalised by log transformation ($\log(x + 1)$) to reduce the skewness of the distribution, then centred and reduced before analyses. A hierarchical clustering analysis (HCA) was performed on the PCA scores for each estuary based on the first two selected PCA axes that explained at least 60% of the total variance, in order to classify the estuaries by size according to their hydro-morphological and sedimentary factors. To determine the number of PCA to select, the ordination eigenvalues were compared with the broken-stick eigenvalues [50] (Figure S1a). The aim of this analysis was to identify estuary clusters by grouping together estuaries with similar environmental characteristics. The Euclidean distance metric was applied and the estuaries were grouped according to the Ward criterion. The optimal number of significant groups was determined by maximising the Spearman coefficient between the original distance matrix and the binary matrix calculated for each section of the dendrogram [51] (Figure S1b). The combination of PCA and HCA resulted in latent variables describing trends in estuarine environmental characteristics, which were then used in subsequent analyses to assess relationships between eel population characteristics (i.e., eel abundance and TL) and the latent variables (i.e., first two PCA axis site scores and estuary clusters, see Section 3). Since the data satisfied the parametric hypotheses of normality (Shapiro–Wilk test) and homoscedasticity of variance (Levene’s F test), two-way analysis of variance (ANOVA) and multiple Tukey tests (HSD Tukey) were used to compare the explanatory variables between the estuary clusters and thus relate them according to their environmental characteristics, except for the ranges or classes of exploratory variables (i.e., wave exposure, substrate type, and total intertidal area), for which the non-parametric Kruskal–Wallis test and Dunn’s multiple comparison test were used. The sample size for all analyses was 29. The PCA, HCA, Spearman rank correlation test, Shapiro–Wilk test, Levene F test, ANOVA, HSD Tukey, Kruskal–Wallis test, and Dunn’s multiple comparison test were performed using the `pca`, `hclust`, `cor`, `shapiro.test`, `leveneTest`, `aov`, `TukeyHSD`, `kruskal.test`, and `dunn.test` functions in the FactoMineR [52], vegan [53], stats [54], car [55], and dunn.test [56] packages in R 4.0.2 software [54], respectively.

We compared the proportion of eel size classes among estuary clusters using the Chi-square test and its post hoc test. As the data did not satisfy the parametric hypotheses of normality and homoscedasticity of variance, eel abundance for all size classes was also compared between estuary clusters using the non-parametric Kruskal–Wallis test and Dunn’s multiple comparison test. Correlations between eel abundance of all size classes and latent variables (i.e., first two PCA axis site scores and estuary clusters), the eight anthropogenic disturbance indicators, and CPI were examined using the Spearman rank correlation test. The Chi-square test and post hoc test were performed using the `chisq.test` and `chisq.posthoc.test` functions in the stats [54] and `chisq.posthoc.test` [57] packages in R 4.0.2 software [54], respectively.

3. Results

3.1. Estuarine Environmental Characteristics

The first two axes of the PCA explained 44.63 and 19.39% of the total variance in the hydro-morphological and sedimentary factors of twenty-nine estuaries, respectively (Figure 2). The first PCA axis was highly correlated ($r > 0.70$) with six variables (i.e., catch-

ment area, river length, estuary surface area, tidal influence limit, mean annual river discharge, and estuarine mouth width) that are all indicators of estuary size (Figure 2a). The second axis was mostly correlated with variables indicating a marine influence, such as total intertidal area, estuarine mouth depth, estuary latitude, and maximum tidal range ($r > 0.55$), while substrate type was correlated with the third axis ($r = 0.88$).

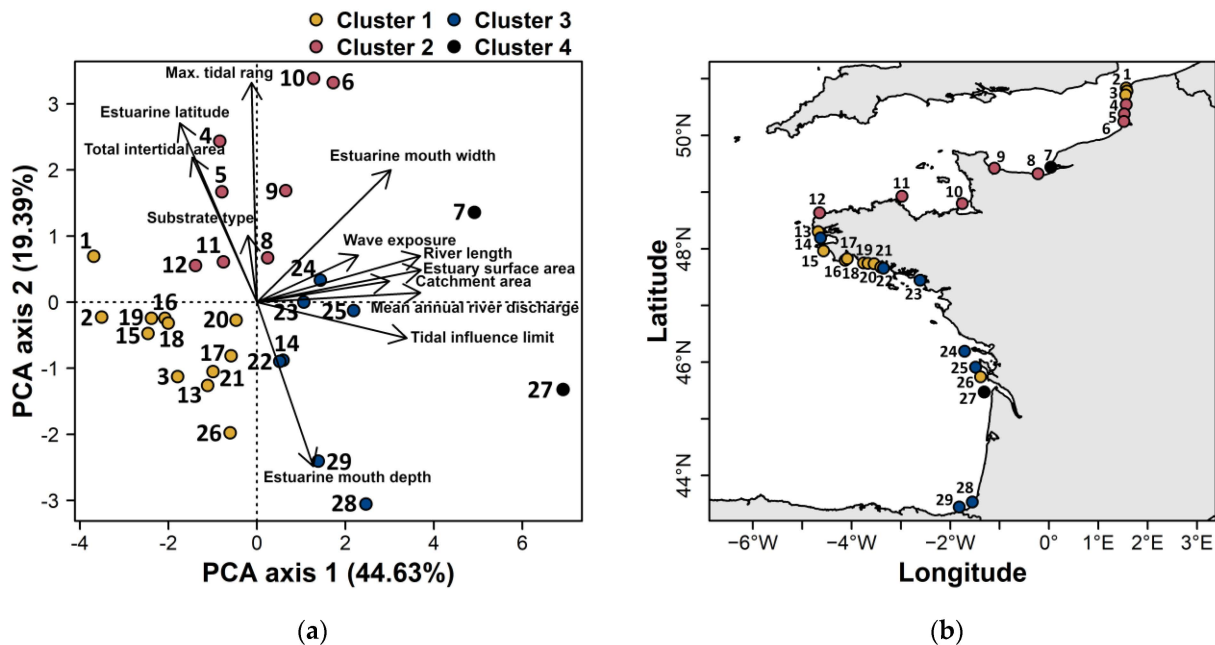


Figure 2. (a) Plot of the first two principal component analysis (PCA) axes and the biplot showing the associations of the 12 hydro-morphological and sedimentary variables (black) with each axis and the 29 French (Table 2) and (b) geographical distributions of the four estuary size clusters obtained by the hierarchical clustering analysis (HCA). The names of the estuaries are given in Table 1.

The HCA grouped the estuaries into four clusters distributed along the first two axes selected by the PCA (Figure 2b and Figure S1). The estuary clusters were significantly related to estuary size variables (ANOVA, $p < 0.001$; Figure 3), with cluster 1 including small estuaries such as the Slack, Wimereux, Liane, Elorn, Goyen, Pont l'Abbe, Odet, Aven, Belon, Laita, Scorff and Seudre; cluster 2 included eight medium estuaries at higher latitudes, including the Canche, Authie, Somme, Orne, Veys bay, Mont St Michel bay, Trieux, and Aber Wrach; cluster 3 included medium estuaries at lower latitudes with Aulne, Blavet, Vilaine, Sevre Niortaise, Adour, and Bidassoa estuaries; and cluster 4 included the large estuaries of the Seine and Gironde. The first PCA axis was correlated with the estuary clusters, confirming that estuary size clusters and PCA axis 1 site scores can be used as independent variables in subsequent analyses to assess the relationships between eel population characteristics and anthropogenic disturbance indicators, with these latent variables reflecting estuary size. The second PCA axis was considered to be a covariate for marine influence.

3.2. Eel Abundance and Total Length in Estuarine Habitats

A total of 3636 eels ranging in length from 160 to 968 mm were collected from the twenty-nine French estuaries. Mean eel abundances ranged from 0.50 ± 0.25 to 13.00 ± 0.01 ind. fyke nets 24 h^{-1} (Table 3). The highest mean CPUE values were observed in the Wimereux, Liane, Odet, Laita and Scorff estuaries, while the Trieux, Aber Wrach, and Gironde estuaries had the lowest values.

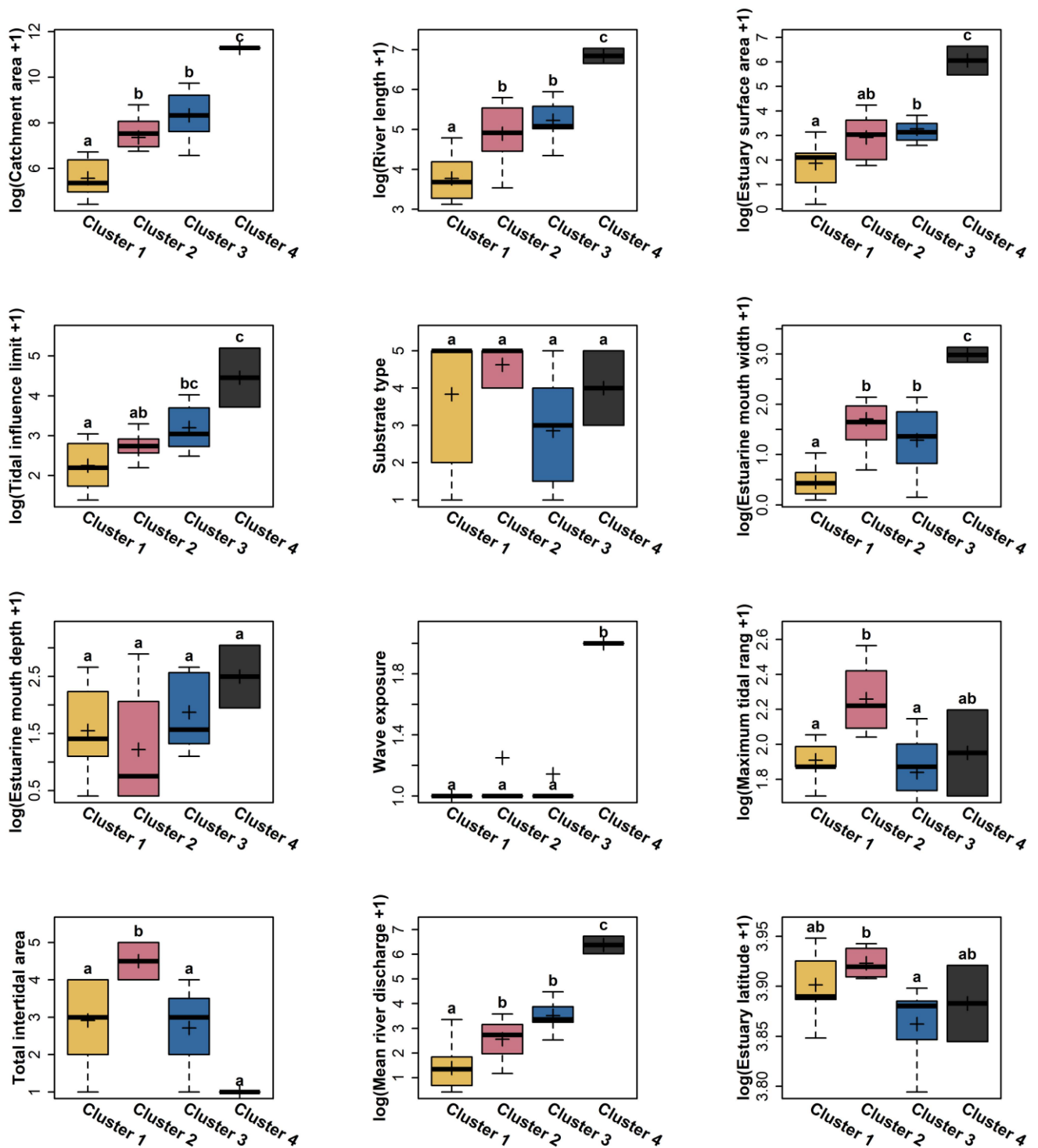


Figure 3. Boxplots of the twelve hydro-morpho-sedimentary variables (see Table 2) of the twenty-nine estuaries located along the French English Channel and Atlantic coasts according to four estuary size clusters obtained by HCA (see Figure 2). The cross represent the mean values. Different letters above each boxplot show significant differences ($p < 0.05$) assessed by ANOVA followed by HSD Tukey or Kruskal–Wallis test followed by Dunn’s multiple comparison test.

Table 3. Mean \pm standard deviation of CPUE (ind. fyke nets 24 h⁻¹) and standardized CPUE (ind. fyke nets 24 h⁻¹ km⁻²) in the twenty-nine French estuaries along the English Channel and Atlantic coasts. Also indicated is which of the four HCA-derived estuary size clusters each estuary belongs to (see Figure 2).

N° Estuary	Estuary	Estuary Clusters	CPUE	Standardized CPUE
1	Slack	1	2.29 \pm 1.52	1.77 \pm 1.17
2	Wimereux	1	7.22 \pm 11.96	32.83 \pm 54.35
3	Liane	1	8.68 \pm 7.86	0.39 \pm 0.36
4	Canche	2	1.85 \pm 1.58	0.35 \pm 0.30
5	Authie	2	2.64 \pm 2.13	0.22 \pm 0.18
6	Somme	2	2.74 \pm 3.64	0.07 \pm 0.09
7	Seine	4	1.38 \pm 0.71	0.01 \pm 0.01
8	Orne	2	7.38 \pm 4.77	1.51 \pm 0.97
9	Veys bay	2	0.81 \pm 0.31	0.02 \pm 0.01
10	Mont St Michel bay	2	0.69 \pm 0.01	0.01 \pm 0.01
11	Trieux	2	0.25 \pm 0.01	0.03 \pm 0.01
12	Aber Wrach	2	0.13 \pm 0.01	<0.01 \pm 0.01
13	Elorn	1	1.19 \pm 0.27	0.19 \pm 0.04
14	Aulne	3	0.69 \pm 0.44	0.04 \pm 0.02
15	Goyen	1	1.75 \pm 1.59	0.63 \pm 0.57
16	Pont l'Abbe	1	3.50 \pm 0.01	0.05 \pm 0.01
17	Odet	1	10.75 \pm 0.01	1.16 \pm 0.01
18	Aven	1	2.31 \pm 3.09	0.28 \pm 0.38
19	Belon	1	5.00 \pm 0.01	0.61 \pm 0.01
20	Laita	1	8.00 \pm 0.01	29.63 \pm 0.01
21	Scorff	1	13.00 \pm 0.01	4.39 \pm 0.01
22	Blavet	3	0.88 \pm 0.88	0.07 \pm 0.07
23	Vilaine	3	2.25 \pm 1.24	0.10 \pm 0.06
24	Sevre Niortaise	3	0.88 \pm 0.88	0.02 \pm 0.02
25	Charente	3	1.13 \pm 0.71	0.05 \pm 0.03
26	Seudre	1	1.42 \pm 0.47	0.17 \pm 0.06
27	Gironde	4	0.50 \pm 0.25	<0.01 \pm 0.01
28	Adour	3	0.71 \pm 0.12	0.06 \pm 0.01
29	Bidassoa	3	3.25 \pm 3.54	0.03 \pm 0.04

Of the total of 2289 eels measured, the size class with the greatest proportion of captures (>55%) was the intermediate eels (≥ 300 to <450 mm) with mean total lengths ranging from 332 ± 66 mm to 489 ± 125 mm (Figure 4). A higher frequency of eels < 300 mm was observed in the small Goyen and Belon estuaries (29–30%), the medium Sevre Niortaise, Adour, and Bidassoa estuaries (22–29%) and the large Gironde estuary (29%), whereas eels ≥ 450 mm were caught in the small Liane, Elorn, and Odet estuaries (56–63%) and the medium Charente estuary (56%). No significant difference in the frequency of eel size classes occurred among the estuary size clusters (Chi-square test, $p = 0.678$).

3.3. Influence of Estuary Size on Eel Abundance

Mean eel abundances varied significantly among the estuary size clusters, both for intermediate (≥ 300 to <450 mm), large (≥ 450 mm), and all eels (Kruskal–Wallis test, $p < 0.001$; Figure 5). Only small eels (<300 mm) exhibited no significant difference between estuary size clusters (Kruskal–Wallis test, $p = 0.929$). Eel abundance for all size classes exhibited a significant negative correlation with the estuary size clusters (Spearman rank correlation test, $r = -0.79$ to -0.71 , $p < 0.001$; Figure 6), indicating that estuary size had a significant impact on eel abundance. Eel abundance was higher in the small estuaries (cluster 1) of the Wimereux, Goyen, Belon, Scorff, and Odet (0.56 ± 0.57 to 10.5 ± 0.01 ind. fyke nets 24 h⁻¹) and lower in the large estuaries (cluster 4) of the Seine and Gironde (0.13 ± 0.01 to 0.71 ± 0.47 ind. fyke nets 24 h⁻¹). In the medium estuaries (clusters 2 and 3), eel abundances ranged from 0.13 ± 0.18 to 5.50 ± 0.01 ind. fyke nets 24 h⁻¹, except in the

Somme estuary and the Veys and Mont St Michel bays for the small eels (<0.09 ind. fyke nets 24 h⁻¹).

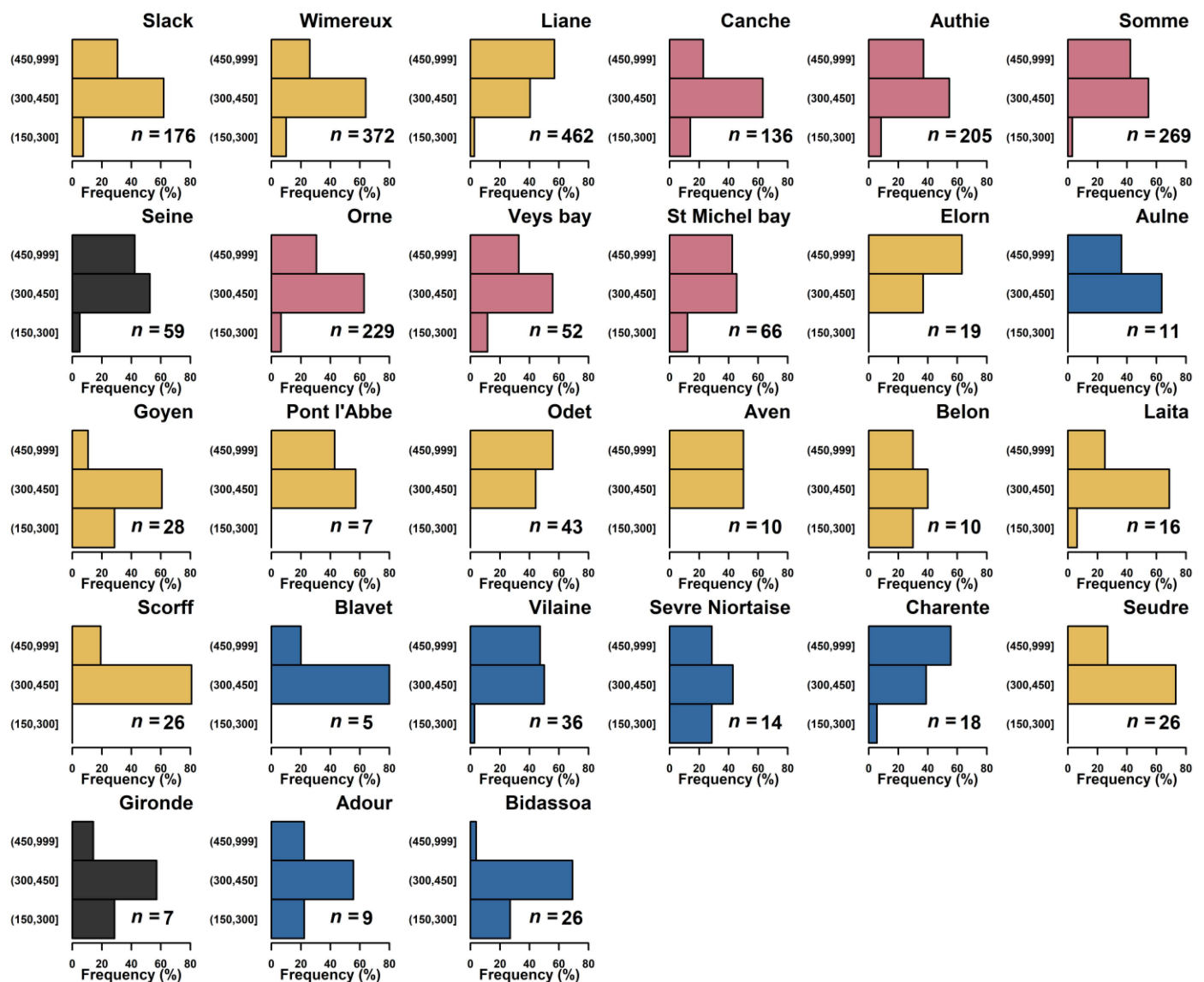


Figure 4. Frequency of small (<300 mm), intermediate (≥300 to <450 mm), and large (≥450 mm) eels in the French estuaries located along the English Channel and the Atlantic coasts. The different colours refer to the four estuary size clusters obtained by the HCA (see Figure 2).

Spearman rank correlation tests indicated a negative correlation between eel abundance and the first axis of the PCA for small, intermediate, large, and all eels ($p < 0.01$; Figure 6). The standardized mean eel abundance decreased with increasing estuary size from 2.53 ± 2.61 to 20.37 ± 23.19 ind. fyke nets 24 h⁻¹ km⁻² in the small estuaries to less than <0.01 ind. fyke nets 24 h⁻¹ km⁻² in the large estuaries (Table 3). The second PCA axis was not correlated with abundances (Spearman rank correlation test, $p > 0.05$), indicating that marine influence did not significantly affect eel abundance.

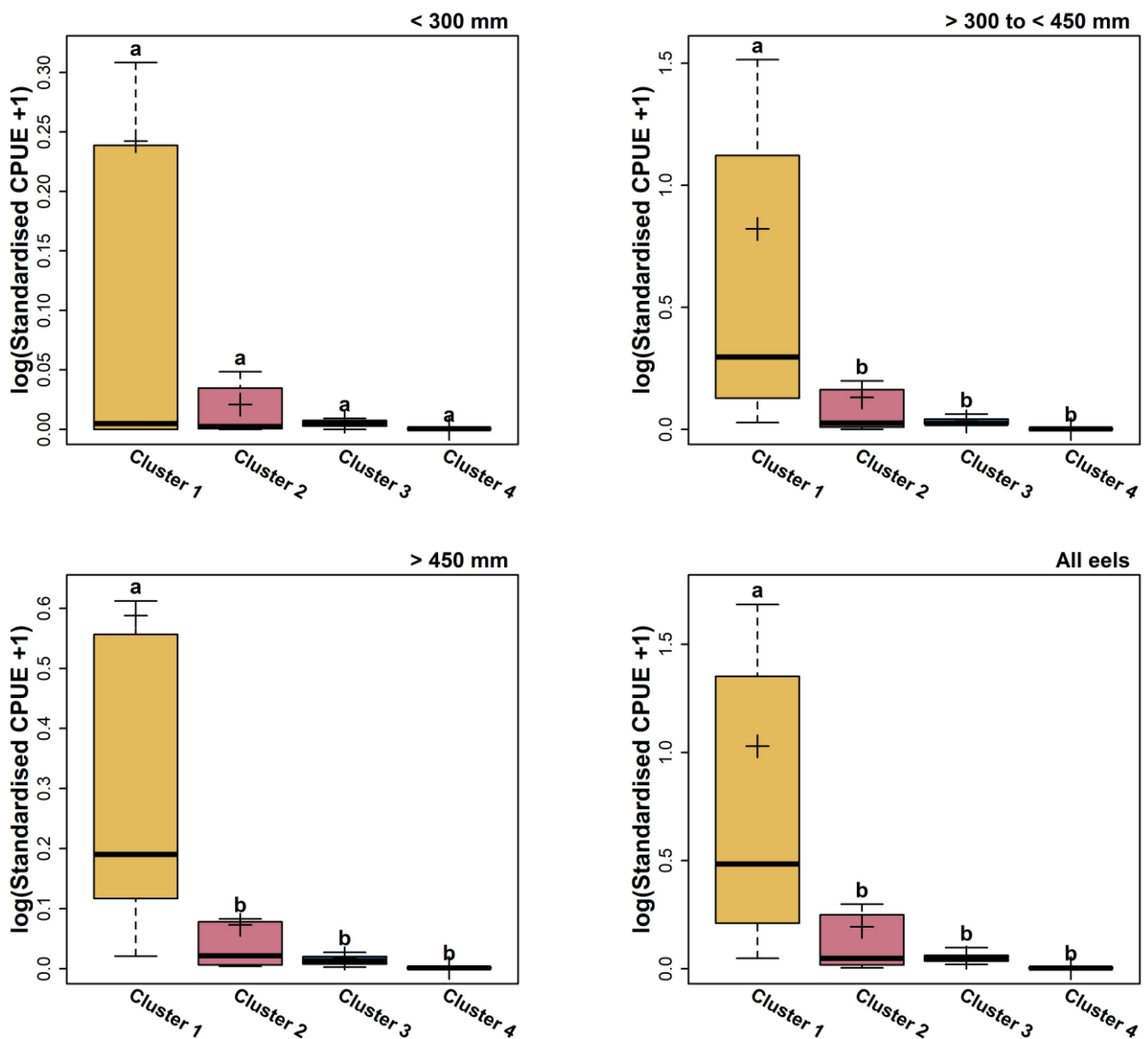


Figure 5. Boxplots of the standardized CPUE ($\log(x + 1)$) of the small (<300 mm), intermediate (≥ 300 to <450 mm), large (≥ 450 mm), and all eels in the twenty-nine estuaries located along the French English Channel and the Atlantic coasts according to four estuary size clusters obtained by HCA (see Figure 2). The cross represent the mean values. Different letters above each boxplot show significant differences ($p < 0.05$) assessed by Kruskal–Wallis test followed by Dunn’s multiple comparison test (see the Section 2.5 above).

3.4. Relationship with Anthropogenic Pressures

The anthropogenic disturbance indicators, which represent the anthropogenic impact, varied between the estuaries (Table 4). The cumulative pressure index (CPI) ranged from 7 to 27 in the small estuaries, from 21 to 44 in the medium estuaries, except the Canche and Authie estuaries (i.e., 16 and 13), and from 50 to 56 in the large estuaries. In general, the small estuaries had anthropogenic disturbance indicators with lower impact scores, with the exception of the Seudre, which had a very high impact for loss of intertidal area (LIA). For most of the medium estuaries, high impact scores were observed for LIA, hydrographic regime disturbance (IH), and anthropogenic affected coastline (AC), whereas the two large estuaries had very high impacts on almost all anthropogenic disturbance indicators.

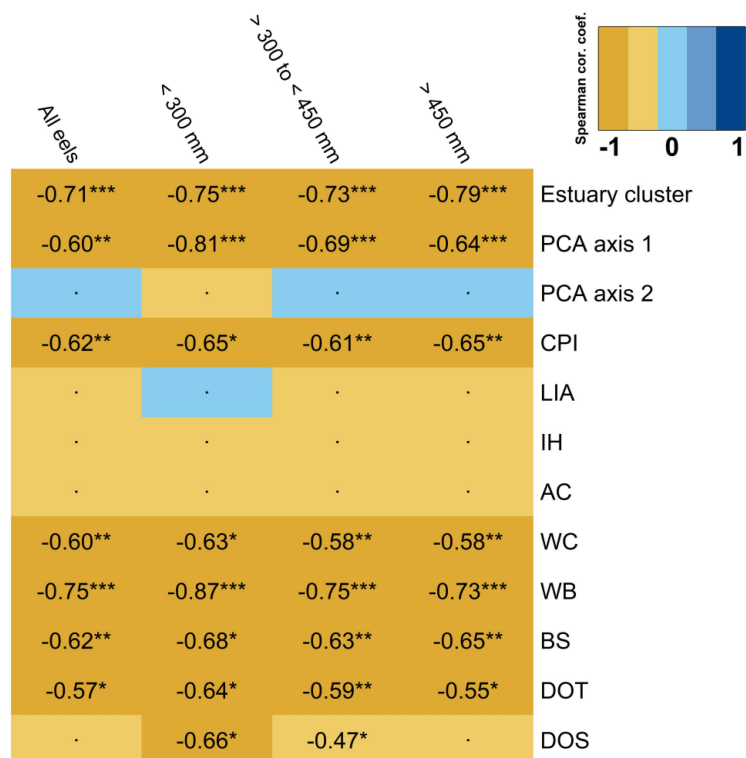


Figure 6. Spearman rank correlation coefficients (r) and significance levels ($p < 0.05$ *, $p < 0.01$ ** and $p < 0.001$ ***) between the standardized abundance of small (<300 mm), intermediate (≥ 300 to <450 mm), large (≥ 450 mm), and all eels in the twenty-nine estuaries with the estuary size clusters, the two first PCA axis site scores, and the anthropogenic disturbance indicators. Abbreviations: CPI—cumulative pressure index, LIA—loss of intertidal area, IH—interference with the hydrographic regime, AC—anthropogenically affected coastline, WC—water chemical quality, WB—water quality biological effect, BS—benthos status, DOT—dissolved oxygen temporal, and DOS—dissolved oxygen spatial.

Table 4. Impact scores of the anthropogenic disturbance indicators. Abbreviations: CPI—cumulative pressure index, LIA—loss of intertidal area, IH—interference with the hydrographic regime, AC—anthropogenically affected coastline, WC—water chemical quality, WB—water quality biological effect, BS—benthos status, DOT—dissolved oxygen temporal, and DOS—dissolved oxygen spatial for each estuary. Impact score ranged from 0 (no change) to 9 (very high) for the level of anthropogenic disturbance indicators, except for the CPI, which ranged from 0 (no disturbance) to 72 (very high disturbance). It is also indicated which of the four HCA-derived estuary size clusters each estuary belongs to (see Figure 2).

Estuary	Estuary Clusters	CPI	LIA	IH	AC	WC	WB	BS	DOT	DOS
Canche	2	16	9	3	1	0	1	1	1	0
Authie	2	13	9	1	0	0	1	1	1	0
Somme	2	25	5	5	7	3	3	1	1	0
Seine	4	56	9	9	5	9	7	5	5	7
Orne	2	29	9	9	7	1	1	1	1	0
Trieux	2	21	5	5	7	1	1	1	1	0
Goyen	1	27	7	7	7	5	0	0	1	0
Odet	1	22	3	5	7	3	1	1	1	1
Aven	1	10	5	1	3	0	0	0	1	0
Belon	1	10	3	1	5	0	0	0	1	0
Laita	1	7	3	1	1	0	0	1	1	0

Table 4. Cont.

Estuary	Estuary Clusters	CPI	LIA	IH	AC	WC	WB	BS	DOT	DOS
Scorff	1	18	5	7	5	0	0	0	1	0
Blavet	3	13	3	5	3	0	0	1	1	0
Sevre Niortaise	3	33	9	7	7	5	3	1	1	0
Charente	3	26	7	3	7	1	1	3	3	1
Seudre	1	29	9	3	7	3	1	5	1	0
Gironde	4	50	5	7	9	7	9	3	3	7
Adour	3	44	9	5	9	5	5	5	3	3
Bidassoa	3	35	9	9	7	3	3	3	1	0

A positive correlation was observed between the anthropogenic disturbance indicators and the estuary size (i.e., estuary size clusters and PCA axis 1), signifying a positive relationship between the disturbance indicators (Spearman rank correlation test, $p < 0.01$; Figure 7). There was also a significant relationship between estuary size and anthropogenic disturbance (Spearman rank correlation test, $p < 0.05$), and with CPI ($r > 0.44$), water quality (WC and WB; $r > 0.43$), benthic status (BS; $r > 0.48$), and hypoxia (DOS; $r > 0.45$). Estuary disturbance increased with increasing estuary size, such as a CPI of 10 for the small estuaries to values > 50 for the large estuaries (Table 4). Abundance in three size classes and all eels related to the estuary size showed a significant negative correlation with the same anthropogenic disturbance indicators (Spearman rank correlation test, $r = -0.47$ to -0.87 , $p < 0.05$), indicating that eel abundances were negatively affected with increasing anthropogenic pressure (Figure 6).

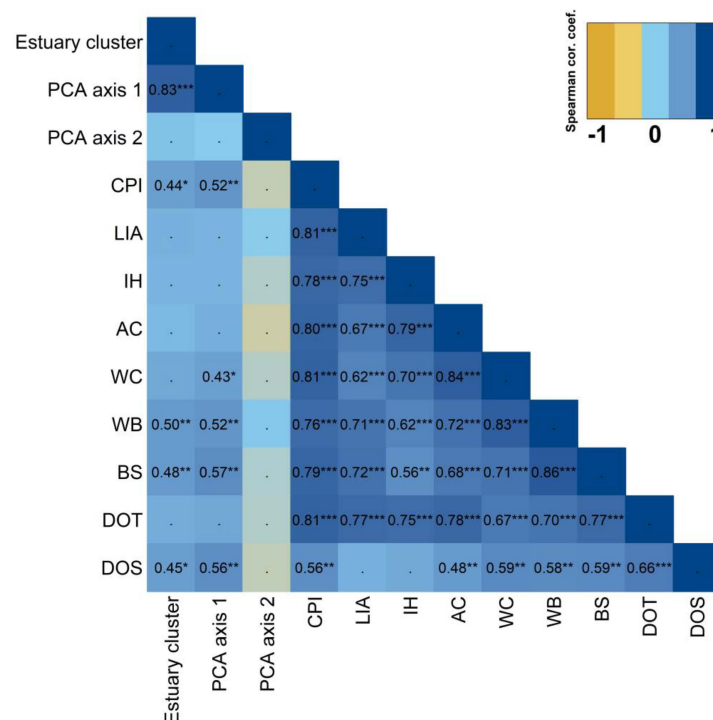


Figure 7. Pairwise Spearman rank correlation coefficients (r) and significance levels ($p < 0.05$ *, $p < 0.01$ ** and $p < 0.001$ ***) between the estuary size clusters, the two first PCA axis site scores, and the anthropogenic disturbance indicators. Abbreviations: CPI—cumulative pressure index, LIA—loss of intertidal area, IH—interference with the hydrographic regime, AC—anthropogenically affected coastline, WC—water chemical quality, WB—water quality biological effect, BS—benthos status, DOT—dissolved oxygen temporal, and DOS—dissolved oxygen spatial.

4. Discussion

4.1. Spatial Variation in Eel Abundance in Estuarine Habitats

Eel abundance exhibited clear differences among the estuaries, with lower abundance recorded in the Wimereux, Liane, Odet, Laita, and Scorff estuaries, while the lowest eel abundance was observed in the Seine and Gironde estuaries. The interactions between estuarine environmental characteristics and eel abundance are complex to identify and little studied. Our results indicate that eels had a significantly higher mean abundance in most small estuaries compared to medium and large estuaries. The Spearman rank correlation test indicated a negative correlation between eel abundance and estuary size. Several studies have shown that local environmental characteristics, in particular habitat size, productivity, and anthropogenic pressure, remain the main factors affecting eels [58–60]. Furthermore, recent studies suggest that small local estuaries are habitats capable of supporting high densities of European eels [21,26]. For example, the WARENNE, a small coastal river (i.e., a short river with a total length of 3.4 km, a narrow width not exceeding 1 m, a shallow depth not exceeding 0.5 m, and a low maximum flow of $5 \text{ m}^3 \cdot \text{s}^{-1}$) in north-eastern France, had mean CPUE eels similar to the highest densities reported in the International Council for the Exploration of the Sea (ICES) Working Group on Eels (WGEEL) database, which includes the largest rivers in the UK, France, and Spain in the Atlantic and North Sea Interreg areas [26]. Our results are consistent with these observations and highlight the effect of estuary size (i.e., hydro-morphological characteristics) on eel abundance at a regional scale of French estuaries. These observations cannot be confirmed on a larger scale (e.g., in Europe) due to a lack of available data on eels in other estuaries, which should be the subject of future research.

Smaller habitats have a different hydro-morphology compared to larger ones, in particular a slower flow with less influence from the sea. Variations in the influence of the sea lead to changes in macroinvertebrate taxa composition, in particular a lower abundance of marine macroinvertebrates in the estuaries least exposed to the sea [61,62]. Conversely, the large surface area of the estuary, the high degree of connectivity with the marine environment, and the predominantly sandy sediments result in a higher density and diversity of marine macrozoobenthos in the larger estuaries than in the smaller ones [63,64]. The European eel is considered to be an opportunistic forager [65–67]. It has a preference for macrozoobenthos as a food source, except when these prey are in low abundance, at which point the eel will switch to a piscivorous diet [68]. The availability of benthic prey induces dietary changes [28] and thus alters the growth and condition of eels [21,22]. These differences in prey composition with estuary size may have an influence on abundance that should be further investigated in future studies.

4.2. The Influence of Anthropogenic Pressures

The anthropogenic disturbance, indicators of anthropogenic pressure, showed a positive relationship with estuary size, suggesting that larger estuaries are subject to greater anthropogenic pressure than smaller estuaries. Eel abundance showed a significant negative correlation with anthropogenic disturbance indicators such as the cumulative pressures index (CPI), water quality, and benthic status, highlighting the negative impact of anthropogenic pressure on estuarine eel populations. A reduction in fish abundance due to anthropogenic disturbance has also been observed for benthic fish in estuaries [39] and coastal zones [40,69], suggesting that benthic fish are highly sensitive to stressors despite their high abundance [34]. Anthropogenic impacts on fish populations can be additive, antagonistic, or synergistic [70]. As a species sensitive to the quality of its environment, the European eel is considered to be an indicator species for the state of the environment [71], and the state of its population reflects the quality of its habitat [72]. The fish population is sensitive to the quality of the aquatic environment which, if degraded, will impoverish its diversity and reduce its abundance by favouring certain species and age classes [73]. For example, the loss of essential habitats is the main factor affecting fish populations as it reduces fish abundance [74]. A large intertidal zone in the estuarine habitat has been shown

to support high fish abundance. The presence of dikes, dams, or harbours reduces the availability of habitats and food sources for fish species. This is particularly true for the French estuaries, where larger estuaries with human activities have been shown to have a greater impact than smaller estuaries. Bank structures can prevent lateral ecological continuity between the watercourse and the submerged zone (e.g., mudflats, sandbanks) [75]. The presence of artificial lateral structures leads to the disappearance and fragmentation of the intertidal habitat in the estuary, creating barriers that are more or less difficult to overcome if not properly managed. These barriers have a direct impact on the distribution of eel populations in estuaries [76,77]. However, our results do not indicate a clear relationship between eel abundance and the loss of habitat (LIA), but rather the status of the benthos (BS), which reflects the quality of benthic habitats and indicates any changes to the seabed. Future research should focus on macroinvertebrates' composition and abundance rather than habitat loss.

Eel abundance was significantly correlated with water quality (WC, WB, DOT, and DOS) in the estuaries studied. The impact of pollutants on European eel populations has been widely reported in several studies [78,79], suggesting a higher influence on eel populations than environmental factors [80]. Several pollutants have been identified as affecting the physiology of European eels, including heavy metals [81–83], polychlorinated biphenyls (PCBs; [84,85]), and pesticides [86,87]. Heavy metals such as mercury and copper mainly bioaccumulate in the lipid metabolism of eels and alter their physiological state [88,89]. PCBs disrupt the endocrine system and bioaccumulate in eels, posing a long-term threat [85]. Pesticide loads in the ecosystem from industry, agriculture, and urbanization also affect the health of eels, affecting their growth, development, and reproductive capacity [79,90]. Eels exposed to pollutants are more susceptible to parasites such as the parasite *Anguillicola crassus*, a non-native species that infects eels and causes pathological damage to the swim bladder, impairing their ability to cope with hypoxic conditions [91,92]. Larger estuaries, such as the Seine and the Gironde, have higher concentrations of pollutants [93,94] and exhibit poor water quality, which we found to be associated with low eel abundances. The contaminants may affect the reproductive success of eels, exacerbating population decline. Thus, our results suggest that it is also essential to consider the effects of contaminants to ensure the conservation and management of European eel populations [79].

Other factors that could potentially affect eel abundance, such as commercial fishing and restocking, were not included in our analyses. Eel overfishing has had a significant impact on European eel stocks and is partly responsible for their decline in recent decades [3,95]. Fishing was very important in the 1970s, targeting both glass eels, especially in the estuarine habitat, and eels in the yellow and silver stages during their continental growth phase [96]. As the stock has declined dramatically since the 1970s, landings of yellow and silver eels have gradually decreased [13] from an average of 2000 tonnes in 1980' to 654.4 tonnes in 2023 in France. This trend can be observed for yellow and silver eels in all regions of the French English Channel and the Atlantic coasts (i.e., eel management unit; Figure 1) from 2008 to 2023 (Figure S2). In the Brittany, Loire, and Garonne regions, landings of yellow and silver eels were higher from 2012 to 2014 (mean 17.7, 19.9, and 11.0 tonnes per year; respectively) and much lower in 2022 (<4 tonnes), except in the Loire region (11 tonnes). In contrast, estuarine glass eel landings were relatively stable (between 28.4 and 53.4 tonnes per year), except for in 2008 (71.4 tonnes). In the Loire and Garonne regions, landings of estuarine glass eels were higher (mean 24.1 and 10.8 tonnes per year, respectively) than in the other regions (mean < 5 tonnes per year). Commercial landing data were not available for the 29 French estuaries studied and should be considered in future studies to better understand the impacts of commercial fishing pressure on eel abundance. It should be noted that in accordance with the Council Regulation (EU) 1100/2007 of the European Union establishing measures for the recovery of the stock of European eel and Council Regulation (EU) 2023/194 fixing the fishing regulations for 2023, eels under 12 cm are subject to fixed quotas allocated by region for commercial fishing and a prohibited

fishing period of at least six months. Unlike the glass eel fishery (<12 cm), the yellow eel fishery is not limited by quotas but fishing is only allowed during a period set by the management unit. Recreational fishing in the maritime area below the salinity limit of the water is prohibited for all life stages of eels (with certain exceptions). France's national eel management plan sets a target to reduce the fishing mortality of these eels by commercial fishing. The ICES recommends zero catches of European eels in all habitats, including glass eels for restocking and aquaculture, and zero mortality from all non-fishing human impacts [13]. The ICES scientific advice recommends that catches for restocking purposes should be stopped as they increase eel mortality without any proven net benefit for the species' reproduction. The European Council of Ministers has decided to maintain fishing quotas for 2024 at the same level as in 2023 and to continue the six-month closure of all commercial eel fisheries.

Restocking is the transfer of glass eels or elvers from estuarine areas to host sites considered to be the most favourable habitats. It can be an effective measure for re-establishing European eel populations and promoting successive spawning stocks within the target populations [97]. Glass eel restocking in continental freshwater areas is a conservation measure that has the potential to boost local eel stocks, thereby maintaining the species in aquatic habitats where it might otherwise disappear. The restocking programme started in France in 2011 and involves a series of 19 rivers in western France mainly along the Atlantic coast [98], 4 of which discharge into our 29 studied estuaries (i.e., Somme, Vilaine, Charente, and Sevre Niortaise) and only 1 during the period in question (i.e., the Somme estuary). About 28 tonnes of glass eels, i.e., around 88 million individuals, have been released since 2011 [99]. Eel abundance in the Somme estuary in our study was slightly higher than the average for estuaries of a similar size not concerned by restocking. A recent study analysing data from 10 years of eel restocking in France (i.e., from 2011 to 2021) found that the relative contribution of transferred eels to the existing eel population varies between 10 and 90% of the population [99]. This study showed that the eel restocking programme is an effective measure to introduce eels into river sections where they are not present. The restocking sites are mainly in freshwater, several kilometres away from the estuaries (i.e., 7 to 263 km upstream), e.g., 131 km from the sea in the Vilaine. Although eels have a plasticity in habitat use that allows for a wide geographic distribution of the species [100–102], most eels rapidly adopt a sedentary lifestyle during the continental growth phase [22,103,104] and may limit their dispersal to a few kilometres upstream and downstream of the restocking locations. The proportion of silver eels reaching estuaries as a result of restocking is unknown. Ongoing research suggests that the first silver eels from the 2018 Loire restocking programme have begun to migrate downstream and could represent between 5 and 10% of the silver eel population [99]. However, further research is needed to assess the effectiveness of restocking programmes on the number of silver eels produced from glass eels released into rivers compared to eel populations by analysing the proportion of marked eels (e.g., with alizarin red S [105]) resulting from restocking at the catchment scale.

The effectiveness of restocking is highly variable [106] and does not appear to have had a significant impact on the general trends of stock and fishery decline [5,107,108]. However, little is known about the fate of these restocked eels and the early ecological behaviour of young eels transferred to rivers. Restocking can only be considered an appropriate tool for stock recovery if it results in a higher escapement biomass of silver eels than would have occurred if glass eels had not been removed from their natural (donor) habitat in the first place [109].

4.3. Potential Sampling Biases

This study highlights the need to continually refine sampling techniques, considering the unique dynamics of estuarine ecosystems, in order to improve our knowledge of the role these environments play in sustaining eel populations. The use of fyke nets highlights certain advantages and limitations of their use. The advantage of using fyke nets is that

they are effective in catching eels at night when they are most active [110]. The use of fyke nets for sampling may exclude eels in certain areas, particularly hard substrates which are not favoured by eels that prefer fine gravel substrates [111]. The use of fyke nets near the banks of the estuary does not allow eels swimming in the main channel to be captured. However, eels tend to frequent banks where the water speed is lower, perhaps because of their limited swimming ability [112].

Other sampling methods (i.e., beam trawls, environmental DNA, electrofishing) are currently used to monitor migratory fish and fish in estuaries. Fyke nets used in estuaries have been shown to be more selective for eels than beam trawls [113]. It is important to note that electrofishing is not practiced in estuaries due to factors such as high salinity, depth, and hydrodynamics. Environmental DNA (eDNA) analysis is more sensitive than traditional sampling techniques for detecting the presence of eels in low abundance habitats [114]. It is proving to be a non-invasive tool for monitoring eel distribution. The application of eDNA methods in estuaries has enabled the identification of a wider range of marine and estuarine fish species than traditional methods [115,116]. However, the complexity of the relationship between eDNA copy number and abundance needs to be further elucidated. Therefore, eDNA read abundance as an indicator of species abundance must be interpreted with caution to avoid over-interpretation of the results [117]. The transport and dispersal of eDNA by freshwater inputs and tidal action in estuaries complicates the determination of its origin and poses problems for the accurate interpretation of detected eDNA. Indeed, the use of eDNA remains a major challenge to understanding and interpreting results. Further research could focus on small estuaries, which are characterized by reduced freshwater inflow, especially during the summer season, and less exposure to marine inputs, resulting in longer water residence times [118]. Consequently, the fyke net appears to be the most suitable gear for sampling eels in estuaries compared to the other sampling methods listed above.

5. Conclusions

These results highlight the crucial role of small estuaries in supporting European eel populations in French estuaries. Small estuaries with their specific hydro-morphological characteristics can provide favourable conditions for eel abundance. The negative correlation between eel abundance and anthropogenic pressures highlights the vulnerability of eel populations to human disturbance. These anthropogenic impacts are significantly increased in large estuaries, which suggests that the accumulation of pressures needs to be considered when developing eel conservation efforts.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fishes9020044/s1>. Table S1: Description of eight anthropogenic pressure indicators and impact score guidelines (see [34,48] for further details); Figure S1: (a) Scree plot and broken stick model of the Principal Component Analysis (PCA) performed on twelve hydro-morphological and sedimentary explanatory variables of the twenty-nine estuaries located along the French English Channel and Atlantic coasts (see Table 1), and (b) the Hierarchical Clustering Analysis (HCA) with the Ward method and Euclidean distance on the principal component scores for each estuary based on the first two selected PCA axes that explained at least 60% of the total variance. The four estuary size clusters obtained by HCA (see Figure 2). The names of the estuaries are given in Table 1; Figure S2: Time series of declared commercial landings (in tonnes) of (a) glass eels and (b) yellow and silver eels in estuary and freshwater from 2008 to 2023 by eel management unit in France (see Figure 1), from the WGEEL database updated to 2023.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Data available upon request. Data are contained within the article and Supplementary Materials.

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