Estuarine, Coastal and Shelf Science
September 2023, Volume 291 Pages 108446 (14p.)
https://doi.org/10.1016/j.ecss.2023.108446
https://archimer.ifremer.fr/doc/00848/96000/

Relationship between habitat use and individual condition of European eel (*Anguilla anguilla*) in six estuaries of the eastern English Channel (North-eastern Atlantic ocean)

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Abstract :

Brackish habitats are considered important for the facultatively catadromous European eel, but knowledge of eel habitat use strategies and the consequences on their condition, particularly in the estuaries areas, is limited and yet necessary for understanding some features such as growth and maturation in the different habitats that eel inhabit during the continental phase, that might also support assessment and management of local stocks, and contribute to the stock-wide assessment of this panmictic species. This study aimed to characterise and compare the condition of European eels according to their habitat use strategies and local estuarine characteristics. Eels were collected along the salinity gradient in six small and medium-sized estuaries located along the French coast in the eastern English Channel (i.e. the Slack, Wimereux, Liane, Canche, Authie and Somme estuaries). Four condition indices (i.e. Fulton condition factor K, lipid content, hepatosomatic index and health status) were measured on 119 individuals to explore variation with habitat characteristics at the small geographical scale and their habitat use strategies. Eel condition showed clear spatial differences between the six estuaries, with better condition in smaller estuaries. The spatial differences in eel condition appear to be related to variations in their diet composition, corresponding to different availability of macrozoobenthos prey among sites, in turn due to the local hydro-morpho-sedimentary characteristics. Environmental history and movements were reconstructed from the Sr:Ca and Ba:Ca ratios of otoliths from eel samples (N = 37) in both small- and medium-sized estuaries. The Sr:Ca and Ba:Ca ratios were used to distinguish the habitat use strategies and showed that both estuaries had a high proportion of resident eels (81%). Within each estuary, the Sr:Ca and Ba:Ca ratios were sufficiently contrasted to track movements of estuarine resident eels between three resident sectors (i.e. upper, middle and lower estuary). The relationship between eel condition and habitat use showed that inter-habitat shifter eels were in poorer condition than estuarine residents. Eel condition also varied between the three resident sectors, with decreases between eels from the lower to upper estuaries.

Highlights

► Habitat use and movement reconstructed from the Sr and Ba otoliths. ► Otolith microchemistry confirms high estuarine residence. ► Otolith elemental composition to track eel movements between resident sectors. ► Estuarine resident eels were in better condition than inter-habitat shifter. ► Condition of eels declined from the lower to the upper estuary.

Keywords : Otolith microchemistry, environmental history, Fulton condition factor K, lipid content, health status, hepatosomatic index.

1. Introduction

The European eel (*Anguilla anguilla* L.) is a falcultative catadromous species (Daverat et al., 2006; Tabouret et al., 2010) that reproduces in the Sargasso Sea and grows in the continental waters of Europe and North Africa (Schmidt and Regan, 1923; Tesch, 2003). Leptocephali cross the North Atlantic through the Gulf Stream and glass eels colonise the continental waters along the European and North African coasts. Yellow eels (i.e. growing phase) remain in continental habitats for 3 years to 30 years or more (Durif et al., 2020; Poole and Reynolds, 1996), metamorphosing to the silver stage (Aroua et al., 2005) before migrating to the sea to reproduce (Righton et al., 2016; Tesch, 2003). The European eel stock declined since the early 1980s (Dekker and Beaulaton, 2016) as documented by reduced abundance and low glass eel recruitment, and the species has been listed as critically endangered by the IUCN (Pike et al., 2020). Causes of this decline are attributed to the synergistic effects of natural and anthropogenic factors, such as fishing, dams, pollution and climate changes, encountered both during their growth in continental waters and during transoceanic migrations (Morais and Daverat, 2016).

Eels have the physiological capacity to cope with environmental changes, such as colonising habitats changing salinities or moving from a freshwater to a marine environment (Lionetto et al., 2016). They have a wide range of life-history strategies for habitat use (Daverat et al., 2006; Jessop et al., 2002; Kotake et al., 2005), which allows them to occupy a wide range of marine, brackish and freshwater habitats from small streams to large rivers, lakes (Arai, 2016), estuaries (Daverat and Tomás, 2006; Harrod et al., 2005), lagoons (Capoccioni et al., 2014) and coastal waters (Arai et al., 2019; Limburg et al., 2003; Lin et al., 2012; Shiao et al., 2006; Sjöberg et al., 2017). During their continental life cycle, three main habitat use strategies have been identified: marine and brackish resident, freshwater resident and inter-habitat shifter (Daverat et al., 2005; Shiao et al., 2006; Tabouret et al., 2010; Tzeng et al., 1997). The eels remain in coastal areas (Copp et al., 2021) and estuaries (Daverat et al., 2005; Daverat and Tomás, 2006; Tabouret et al., 2010), due to higher biological productivity than in freshwater, particularly at low latitudes (Gross, 1987; Tsukamoto and Arai, 2001). It has been shown that resident eels in marine and brackish habitats grow faster and mature earlier than those in freshwater (e.g. Acou *et al.*, 2003; Cairns *et al.*, 2009; Daverat *et al.*, 2012). Inter-habitat shifters may move downstream river strietches and estuaries to take advantage of trophic resources, thereby optimising growth and increasing lipid reserves prior to breeding migration (Daverat and Tomás, 2006).

Fish habitat use and movement between habitats can be investigated using otolith microchemistry (Walther, 2019; Walther and Limburg, 2012). This approach has been applied with success to eels (e.g. Chino & Arai, 2010; Lamson *et al.*, 2006; Tsukamoto *et al.*, 1998). The chemical habitat profiles of eels can be tracked over time and their environmental history can be reconstructed from the propensity of otoliths to incorporate chemical elements into their matrix. The elemental composition of strontium (Sr) and barium (Ba) incorporated into the otolith reflects the proportion of chemical elements in the environment (Campana, 1999), whose levels in environmental water vary between marine, brackish and freshwater habitats depending on salinity gradient (Daverat et al., 2006; Tabouret et al., 2010; Tsukamoto et al., 1998). Sr and Ba are chemical markers that are unaffected by physiological processes, water temperature and food (Daverat et al., 2005; Kawakami et al., 1998), and are mainly dependent on salinity gradient, by a positive relationship with the Sr:Ca ratio and negative with the Ba:Ca ratio (Daverat et al., 2011; Rohtla et al., 2022; Tabouret et al., 2010). Otolith signatures provide valuable information on how eels have moved between habitats and can also be used to determine movement along rivers (Teichert et al., 2022), allowing to understand how their spatio-temporal distribution has shaped their life history and condition.

Environmental habitat characteristics may affect eel life history traits associated with the fish condition (Boulenger et al., 2016; Daverat et al., 2012; Jessop, 2010), but remain poorly studied (Lin and Robinson, 2019; Righton et al., 2021; Teichert et al., 2022) despite their role in understanding overall condition, in turn involved in eel survival, development and reproductive success (McCleave, 2001). The condition of a fish partly defines the health status of an individual, as it is influenced by its physiology, and by the effects of environmental factors and pressures on the individual, and this is why fish condition can be considered a measure of habitat quality (Kerambrun et al., 2013; Lloret et al., 2014). The phenotypic plasticity of eels in selecting resident habitat is an adaptation to the high variability and structure of habitat conditions (Drouineau et al., 2014). Parzanini *et al.* (2021) showed that the condition of eels is related to the variation in their diet in different habitats, leading to changes in condition between habitats of residency. Differences in trophic behavior and diet among different locations are due to local variations in availability of macrozoobenthic prey, which in turn depend on local environmental conditions (Denis et al., 2022b), thus affecting eel growth (Denis et al., 2022a), spatial use and movement patterns (Barry et al., 2016) and condition of local stocks.

The aim of this study was to evaluate the condition and the habitat use of European eels in estuarine habitats during their continental growth phase (i.e. yellow and silver eels), in order to assess how local estuarine characteristics and habitat use strategies may influence the eel condition. In this study, we focused on six small and medium-sized French estuaries, which are less studied than large estuaries (e.g. the Severn estuary; Bird *et al.* (2008) and the Gironde estuary; Daverat *et al.* (2006); Patey *et al.* (2018)), although small-sized catchments can represent a significant proportion of the overall global stock (Copp et al., 2021; Denis et al., 2022a). Specifically, we assessed the eel condition using an individual-scale multi-index approach based on four condition and health indices (i.e. Fulton condition factor K, lipid content, hepatosomatic index and health status) to explore the relationship with several factors at the local level, such as biological characteristics of eel local stock, spatial location and hydro-morpho-sedimentary features of specific estuarine habitats. We then reconstructed the environmental life history of estuarine eels using otolith microchemical analysis based on the Sr:Ca and Ba:Ca ratios to assess their habitat use and movement between habitats. Finally, we assessed the relationship between habitat use strategies and eel condition.

2. Materials and Methods

2.1. Study area

Eel sampling was carried out in three small (i.e. Slack, Wimereux and Liane) and three medium-sized (i.e. Canche, Authie and Somme) estuaries located along the French eastern English Channel coast (Fig. 1). The six estuaries are characterised by similar water temperature ranges due to their proximity (less than 20 km between two adjacent estuaries) (Selleslagh et al., 2011), but have specific local hydro-morpho-sedimentary characteristics and anthropogenic pressures (Table S1). The estuaries studied were classified as small- or medium-sized according to hydro-morpho-sedimentary characteristics, including surface area, mean annual flow, narrow mouth width, tidal action and dominant substrate (Denis et al., 2022a). The Slack and the Wimereux estuaries have a surface area (from the mouth to the desalination limit) of about 1 km^2 (IGN-F maps) and composed mainly of sandy-muddy sediments. The Liane estuary has a surface area of 22 km^2 and is mainly composed of mud. It has a dam in the lower part of the estuary which shelters it from the tides but results in greater exposure to freshwater inflow. They are small estuaries, sheltered from the tides (mouth width of about 0.1 km). The tidal range in these estuaries is 7 m and the tidal influence limit is about 3 km. The Canche, Authie and Somme are medium-sized estuaries with a surface area of 5 km^2, 12 km^2 and 41 km^2 respectively, and their sediments are composed mainly of sand and gravel (Selleslagh et al., 2009). These estuaries are more exposed to tidal action (mouth width of 3-5 km), with a tidal influence limit of 12-15 km and a tidal range of 9 m, 7 m and 10 m respectively (Nicolas et al., 2010). The water quality of the studied estuaries is classified as medium ecological status but in good chemical status (SDAGE 2016-2021), except for the Somme estuary which has poor ecological status.

2.2. Eels sampling and biological characteristcs

Eels were sampled during four sampling periods in 2019 (during March, May, July and October) using two fyke nets (mesh size of 15 mm at the entrance, 10 mm in the middle and 8 mm at the cod end) deployed for a period of 2 × 24h at three sampling stations in each estuary along the salinity gradients (i.e. lower, middle and upper estuary; Fig. 1). Permission to sample eels in the field study was obtained from the Interregional Directorate for the Eastern English Channel-North Sea (dram-npe@equipement.gouv.fr; Decision n°196/2019). This study was conducted in accordance with the European Commission Recommendation 2010/63/EU, on revised guidelines for the accommodation and care of animals used for experimental and other scientific purposes.

The eels captured were anaesthetised with eugenol solution (0.04 ml.L^{-1}; Thermo Scientific™) before being individually weighted (Total Weight, TW ± 1 g) and measured (Total Length, TL ± 0.1 mm) and the silvering stage was determined according to Durif et al. (2009, 2005). Three to six eels per sampling period and for each estuary (a total of 119 individuals) were then euthanised with a saturated eugenol solution and stored at -80°C for further analysis. The abundance of eels was calculated as catch per unit effort (CPUE) from the number of individuals caught per gear and per unit of time (ind. fyke nets 24 h^{-1}).

2.3. Condition and health indices

Fulton's (1904) condition coefficient K (mg.mm^{-3}) was calculated from the total weight and length of the eels using the formula:

$$K = \frac{TW}{TL^3} \times 10^5$$

The hepatosomatic index (HSI) was calculated to estimate the energy reserves in eels liver. Livers were removed and weighed to calculate the HSI according to the formula:

$$HSI = \frac{LW}{TW} \times 100$$

Eels body lipid content (% lipid per dry weight) was measured immediately after the capture using a fish fatmeter (FM-992, Distell Inc., West Lothian, Scotland; Pohlmann *et al.*, 2019). Lipid content was calculated from the linear relationship between fatmeter lipid content (% lipid per wet weight) and total lipid content measured in muscle (% lipid per dry weight) established from a sub sample of eels (Figure S1). Muscle lipid content was measured on a total of 50 frozen eels muscle samples using the method of Folch *et al.* (1957). Briefly, muscle samples were freeze-dried and homogenised by grinding with a glass rod, and the total lipid content was extracted from approximately 70 mg of muscle using a solvent solution of chloroform-methanol (2:1, v/v), then weighed and expressed as % dry weight.

The Eel Pathology Index (EPI ; ICES, 2015) based on the visual abundance and prevalence of anatomo-morphological lesions and external and internal parasitism (Girard and Elie, 2007) was used to assess the health status of the sampled eels. A score from 1 to 5 (from least to most) was assigned for each pathology. For each individual examined, the mean of the scores was used to classify the individual into 5 different classes according to its health status: 1 'very good health', 2 'good health', 3 'moderate health', 4 'unsatisfactory health' and 5 'poor health' (Table S2).

2.4. Otolith microchemistry

The analysis of otolith microchemistry was only carried out for eels from two contrasting estuaries: the Wimereux (small estuary) and the Somme (medium-sized estuary). Sagittal otoliths (Wimereux N = 20; Somme N = 17) were extracted, carefully cleaned with milliQ water, dried and stored individually. Otoliths were then embedded in epoxy resin (Araldite® 2020, Huntsman Corporation), and manually ground in a longitudinal plane and polished with 0.1-20.0 µm microabrasive discs (LP Unalon®) to expose the core. Otolith preparations were rinsed with milliQ water, dried and stored in individual paper bags in a dry place prior to microchemical analysis.

Otolith elemental calcium (^{43}Ca), strontium (^{88}Sr), barium (^{138}Ba) and magnesium (^{25}Mg) were measured by femtosecond laser ablation (LA, IR 1030 nm, Alfamet-Novalase, France) coupled to an ICP-MS (DRCII; Pekin Elmer, Shelton) at the IPREM of the University of Pau. An ablation transect was made along the main growth axis from the core (nucleus) to the edge of each otolith. The laser was applied as a single scan raster at a 20 Hz frequency resulting a 15 µm beam diameter and at 5 $\mu m.s^{-1}$ speed as described in Tabouret *et al.* (2010). The standard reference materials NIST 610, 612, 614 (National Institute of Standards and Technology, USA) were used to calibrate trace element concentrations. The analyses of otolith certified material NIES 22 (National Institute for Environmental Studies, Japan; Yoshinaga et al., 2000) and FEBS-1 (National Research Council Canada, Canada) ensured the analytical precision. Otolith Sr:Ca, Ba:Ca and Mg:Ca ratios were calculated as weight percent ratios and corrected from the average precision standards (Elemental ratios were expressed in $\mu g.l^{-1}$). Otolith vateritic regions were identified using otolith Mg:Ca ratios (Tabouret et al., 2010; Tzeng et al., 2007) and excluded from further analysis.

2.5. Reconstruction of environmental history

The environmental history of eels was reconstructed from otolith Sr:Ca and Ba:Ca ratios using the method described by Teichert *et al.* (2022) to infer habitat shifts during the continental growth phase in response to salinity fluctuations. Variations in ratios measured from the elver mark to the edge of the otolith were identified and divided into homogeneous segments reflecting similar chemical environments using a segmentation method (Lavielle, 1999) based on bivariate time series (Patin et al., 2020) (Fig. 2). A minimum segment length of five measurements (i.e. 25 µm length) was considered for segmentation, corresponding to an average of less than two months of life for the youngest eels and three months for the oldest eels due to lower growth. The mean values of each segment were calculated to determine clusters of segments with similar Sr:Ca and Ba:Ca ratios using a K-means clustering method and the optimal number of clusters was selected based on the Total Within Sum of Squares (TWSS). The mean ratios of marginal otolith segments were projected to environmental habitat assignment clusters, assuming that marginal otolith ratios reflect the chemical environment of the last month before the eels were caught. Otolith segments were assigned to three salinity habitats (i.e. marine, estuarine and freshwater habitat) and three sectors of estuary (i.e. lower, middle and upper estuary) after testing the relationships between otolith marginal segment ratios and eel capture habitat by Pearson's correlation tests. The age of eels along the otolith ablation transect was interpolated by observing annual growth rings under a stereomicroscope (oil-immersion, Olympus BX51) to examine time series in the life history of eels and thus occupancy time and movement between habitats.

2.6. Data and statistical analyses

As the data did not meet the parametric hypotheses of normality (Shapiro-Wilk test) and homoscedasticity of variance (Levene's F-test), TL, age, CPUE and eel condition indices were compared between estuaries using the non-parametric Kruskall-Wallis test. Dunn's test was used for post-hoc comparisons. Lipid content, percentage of eels by silvering stage and pathology index (EPI) were compared between the six estuaries studied using the chi-squared test.

Variations in eel condition were analysed using a Redundancy Analysis (RDA) performed as a constrained ordination technique to explore the influence of different factors namely eel biological characteristics, spatial location, hydro-morpho-sedimentary and anthropogenic factors. In addition, data on eel trophic status, available in Denis *et al.* (2022b), were added to the observation matrix in the RDA to explore the relationship between eel condition and their trophic status based on the predominant prey taxon in the diet (i.e. a diet based mainly on either Malacostraca or Actinopterygii prey) determined from the gut content, and the trophic position (TP) and food sources based on the stable isotope analysis $\delta^{15}N$ and $\delta^{13}C$ respectively. $\delta^{15}N$ can indicate the trophic position of an organism within a food web (Riera et al., 1999) and $\delta^{13}C$ values can be used as a tracer of trophic food sources for consumers (Peterson, 1999), thus distinguish benthic from pelagic food webs or freshwater from marine food sources (Fry, 2006). Trophic position was calculated from eel isotopic nitrogen, baseline isotopic nitrogen (set to 1) and the trophic discrimination factor (set to 3.4‰) (see details in Denis *et al.* 2022b). RDA was performed on a matrix of 4 condition and health indices (i.e. Fulton K, % lipid, HSI and EPI) and 4 trophic indicators (i.e. Malacostraca and Actinopterygii prey, TP and $\delta^{13}C$) from 119 individuals sampled in these six estuaries. Thirteen covariates were used namely eel biological characteristics (TL, age, silvering stage and CPUE), spatial location (sampling station and estuary), hydro-morpho-sedimentary (estuarine surface area, tidal range, tidal limit, tidal exposure and dominant sediment) and anthropogenic (ecological status and presence of obstacles) factors (Table S1). Data were standardised using the Hellinger distance transformation, then centred and reduced before analysis. Significant covariates were selected by forward selection using a Monte Carlo permutation test (N = 999), and their contribution to the variation in eel condition and trophic status was assessed using hierarchical and variance partitioning analysis and a permutation test (Borcard et al., 2011). Hierarchical Classification Analysis (HCA) based on the first two RDA axes (explaining at most 50% of the total inertia) was performed to identify groups of eels with similar condition based on Euclidean distance and grouped according to the Ward criterion. The number of significant groups was determined as that which resulted in the highest Spearman correlation between the euclidean distance matrix and the binary matrix calculated for each section of the dendrogram (Borcard et al., 2011). The percentages of eels for the identified HCA groups were compared between the six estuaries studied, the six silvering stages and the habitat use strategies using the chi-squared test. Only identified HCA groups with a minimum of five individuals were included in the statistical analysis to compare eel condition between habitat use strategies.

All statistical analyses were performed in R software. The Shapiro-Wilk test, Levene's F-test, Kruskall-Wallis test, Dunn's test and chi-squared test were performed using the *Stats* package of R software (R Core Team, 2020). The segmentation, K-means clustering and TWSS were performed using the *segclust2d* (Patin et al., 2019), *factoextra* and *cluster* packages of R. Finnally, the RDA, hierarchical and variation partitioning and HCA were performed using the *vegan* (Oksanen et al., 2013), *rdacca.hp* (Lai et al., 2022) and *FactoMineR* (Lê et al., 2008) packages of R.

3. Results

3.1. Eel biological characteristics

The mean total length of the 119 eel analysed was 453 ± 131 mm and the mean age 8.5 ± 3.1 years. Eel total length and age were not significantly different among the six estuaries (Kruskall-Wallis test, $p = 0.069$ and $p = 0.254$, respectively) (Table 1). A spatially significant difference was observed for CPUE (Kruskall-Wallis test, $p < 0.001$), with higher CPUE in Wimereux (12.5 ± 18.4 ind. fyke nets $24h^{-1}$) and Liane estuaries (7.4 ± 4.9 ind. fyke nets $24h^{-1}$) and lower CPUE in Canche (2.0 ± 1.1 ind. fyke nets $24h^{-1}$) and Somme estuaries (1.8 ± 1.3 ind. fyke nets $24h^{-1}$). The silvering stages were dominated by sexually undifferentiated eels (stage I, 50%), followed by females in the growth phase (FII, 18%) and pre-migrant phase (FIII, 17%). Males (MII) represented only 10% of the individuals (Table 1). In most estuaries, the silvering stages varied significantly among estuaries (chi-squared test, $p < 0.001$), with a lower abundance of sexually undifferentiated eels in the Wimereux and Liane estuaries (35% and 30% respectively), but a higher abundance of females and males (40% and 60% of females and 25% and 10% of males respectively).

3.2. Eel condition

The eels Fulton condition factor K (Fulton K) showed no significant differences among estuaries (Kruskall-Wallis test, $p = 0.423$) (Table 2). The lipid content (% lipid) also showed no significant differences among estuaries (chi-squared test, $p = 0.941$). However, the hepatosomatic index (HSI) was significantly different between the estuaries (Kruskall-Wallis test, $p < 0.05$), with lower HSI in the Liane estuary (1.6 ± 0.7). The health status varied significantly among the six estuaries (chi-squared test, $p < 0.05$). For most estuaries, the percentage of eels according to the pathology index (EPI) varied slightly, except for Authie estuary, which had the highest number of individuals in very good health (10%) and Wimereux estuary, which had the highest number of individuals in unsatisfactory health (15%) (Table 2). In total, 71.4% of the eels analysed presented internal parasites and only 11.8% anatomo-morphological lesions (Table S2). Among the internal parasites identified, the nematode *Anguillicola crassus* was observed in the swim bladder of 61.3% of eels and the cestode *Bothriocephalus claviceps* and the nematode *Contracaecum rudolphii* were observed in the digestive tract of 17.6% and 11.8% of the eels respectively. Except *A. crassus*, the prevalence of dominant parasitic species were significantly different between the estuaries (chi-squared test, $p < 0.05$). The prevalence of *C. rudolphii* was higher in the Liane and Canche estuaries (22.2%) as well as for *B. claviceps* in Wimereux and Liane estuaries (25%) (Table 3).

The selected significant covariates explained 51% (adjusted r^2) of the variance in eel condition according to tidal limit and range, silvering stage and sampling station selected covariates with 45.1%, 36.7% and 18.2% of adjusted r^2 (Fig. 3a). Analysis of variance partitioning showed that hydro-morpho-sedimentary covariate (15%) made the largest contribution to the explained variation in condition (28%), followed by biological characteristics (10%), and spatial location (6%) covariates. RDA did not select the anthropogenic covariates. Three groups of eels were identified by the HCA distributed along the first two axes of the RDA: group 1 (33% of eel) in good energy reserve with higher HSI, group 2 (39% of eel) in good condition and higher lipid content, and group 3 (28% of eel) in poor condition and health. Eels feeding mainly on Actinopterygian prey were in better condition (i.e. % lipid and Fulton K; group 2) than those feeding on marine prey (i.e. high $\delta^{13}C$), mainly Malacostraca (group 1), so these differences in eel condition may be related to differences in diet (Fig.

3a). The condition of the eels also varied according to their position in the estuary, with more eels in poor condition and health (group 3) in the upper estuary than in the lower estuary. Small estuaries with less tidal influence (i.e. tidal range and limit) had significantly more eels in good condition with higher lipid content and Fulton K (group 2) compared to medium-sized estuaries (group 1; chi-squared test, $p < 0.001$) (Fig. 3b). However, compared to small estuaries, medium-sized estuaries have significantly very few eels in poor condition and health (group 3; chi-squared test, $p < 0.001$). Silvering stages showed significantly differences in eel condition (chi-squared test, $p < 0.001$), with good condition in silver eels mainly for females (i.e. FIV and FV) (Fig. 3c).

3.3. Otolith microchemistry

Mean Sr:Ca ratios showed lower ranges for eels from Wimereux estuary (from 0.78 ± 0.19 to 2.69 ± 1.06 × 10^{-3} µg.l^{-1}) compared to the Somme estuary (from 0.78 ± 0.11 to 5.28 ± 0.81 × 10^{-3} µg.l^{-1}). Conversely, Ba:Ca ratios were similar between the estuaries, with mean values ranging from 1.96 ± 0.54 to 6.93 ± 1.52 × 10^{-6} µg.l^{-1} in Wimereux estuary and from 0.64 ± 0.47 to 6.88 ± 1.90 × 10^{-6} µg.l^{-1} in Somme estuary. Segmentation of Sr:Ca and Ba:Ca ratios measured on eel otoliths allowed the identification of 2-8 segments per eel, with an average of 4 ± 1.6 in both Wimereux and Somme estuaries. The Sr:Ca ratios of eel marginal segments were significantly negatively correlated with sampling stations along the salinity gradient in the Wimereux (Pearson correlation test, n = 13, r = -0.88, t = -6.2923, $p < 0.001$) and Somme (Pearson correlation test, n = 16, r = -0.85, t = -6.1345, $p < 0.001$) estuaries (Fig. 4). Conversely, Ba:Ca ratios were significantly positively correlated only in the Somme estuary (Pearson correlation test, n = 16, r = 0.91, t = 8.3901, $p < 0.001$). Ba:Ca ratios of eels in the Wimereux estuary did not vary significantly along the salinity gradient (Pearson correlation test, n = 13, r = 0.29, t = 1.0334, $p = 0.322$). However, the mean values of the ratios showed an increase between the lower and upper estuary (from 2.9 ± 0.4 to 3.7 ± 1.7 × 10^{-6} µg.l^{-1}) corresponding to values measured in eels in estuarine habitats (Tabouret et al., 2010). This trend highlights the importance of using Sr:Ca and Ba:Ca ratios to indicate shifts between habitats and within estuaries along the salinity gradient (Fig. 4).

For each of the two estuaries, five clusters of otolith segments with distinct Sr:Ca and Ba:Ca ratios were identified using k-means clustering method and TWSS (Fig. 5a-b). The cluster with the highest Ba:Ca ratios (> 6 × 10^{-6} µg.l^{-1} in the Wimereux estuary and > 9 × 10^{-6} µg.l^{-1} in the Somme estuary) was assigned to freshwater, whereas the cluster with the highest Sr:Ca ratios (> 6 × 10^{-3} µg.l^{-1}) was assigned to marine waters (Tabouret et al., 2010). The three other clusters were associated with different sectors of the estuary along the salinity gradient (i.e. the lower, middle and upper estuary), as these ratios are similar to those found in the marginal segments of eels caught at the three sampling stations. The cluster with high Ba:Ca ratios and low Sr:Ca ratios was associated with the mean ratios of the marginal segment of eels caught in the upper estuary, while the cluster with high Sr:Ca ratios and low Ba:Ca ratios was associated with those of eels caught in the lower estuary (i.e. near the mouth). The third cluster was associated with eels caught in the middle estuary and had intermediate Sr:Ca and Ba:Ca ratios. Although the association of the third cluster is less clear for eels from the Wimereux estuary, probably because of the proximity of the sampling stations (i.e. less than 0.5 km) compared to the Somme estuary (i.e. between 2.5 km and 6.2 km), the succession of mean ratios of the eel marginal segments along the salinity gradient confirm that this cluster corresponds to the middle sector of the estuary (Fig. 5a-b).

3.4. Habitat use and movement

During the continental growth phase of the 37 eels sampled in the Wimereux and Somme estuaries, 81% were classified as estuarine residents, with 88% in the Somme estuary (15 eels) and 75% in the Wimereux estuary (15 eels) (Fig. 5c-d). The proportions of intra-estuarine residents were similar between the Wimereux and Somme estuaries, suggesting that eels tend to occupy mainly the estuarine habitat. A total of six eels (16%) were classified as inter-habitat shifters, of which one eel spent most of its time in freshwater. Only one eel in the Wimereux estuary was classified as a freshwater resident and initially settled in the estuary (Fig. 5c). Of the estuarine resident eels (N = 30) in the Wimereux and Somme estuaries, a total of 40% were mainly in the lower estuary (40% for both), 40% in the middle estuary (53% and 33% respectively) and 20% in the upper estuary (7% and 27% respectively)

(Fig. 5c-d). Among the inter-habitat shifters (N = 6), half of the individuals initially settled in the estuaries and only one mainly resided in freshwater habitat.

Movement of eels between habitats is particularly common during the first six continental age classes (i.e. 0 to 5) (Fig. 6a). During the first continental age classes, 16% of eels moved between habitats, with 13% of movements upstream and 3% downstream. Inter-habitat movements decreased significantly after the first continental age-classes to less than 6%, mainly downstream movements, then no movement after the first six continental age classes. These results suggest that eel movements occur mainly during the first two continental age classes, corresponding to the colonisation period of continental habitats, after which eels adopt resident behaviour. More than 35% of eels showed intra-estuary movements, mainly to the upper estuary during the first life year (Fig. 6b). Eels also showed occasional movements to the lower estuary throughout their continental growth phase, mainly individuals leaving the upper estuary for the middle sector.

3.5. Relationship between habitat use and eel condition

The condition of eels compared to the habitat use strategy significantly differed between estuarine residents and inter-habitat shifter (chi-squared test, $p < 0.001$; Fig. 7). The proportion of eels in good condition and health was much higher for estuarine resident eels (ER; 69%) than for inter-habitat shifters (IHS), half of which were in poor condition and health. A significantly spatial difference in eel condition was also observed between the estuarine resident sectors (chi-squared test, $p < 0.001$), with condition and health decreasing towards the upper estuary (Fig. 7). Eels resident in the lower estuary had a higher proportion of individuals in good condition (83%) compared to those in the middle (73%) and upper estuary (33%), related to an increasingly mixed diet of high trophic position prey. These results emphasise that spatial variation in eel condition relative to estuarine residence depends on trophic status, which in turn varies with hydro-morpho-sedimentary characteristics, including tidal range. In addition, the condition of the eel inter-habitat shifters was similar to that of upper estuary residents, probably because they regularly visit this sector of the estuary (Fig. 5c-d).

4. Discussion

Located at the interface between the marine and continental environments, estuaries are known to be important areas for many organisms (Amara, 2003; Selleslagh et al., 2009). Estuaries play an essential role in the life cycle of many fish species as breeding, nursery, feeding and refuge habitats for juveniles and adults, including diadromous fish (Elliott and Hemingway, 2002). European eel is facultative catadromous species that use estuarine habitats during their continental growth phase to maximise growth and condition, and thus enable attain silvering and maturation, in order to escape to the sea and face transoceanic reproductive migration (Acou et al., 2003; Cairns et al., 2009; Daverat et al., 2012). Estuarine habitats have their own local biotic and abiotic characteristics, even within the same latitude or geographical area, which can affect the life history and condition of eels (Capoccioni et al., 2014; Teichert et al., 2023). Although eel local stocks in estuaries are important proportion of the overall global stock (e.g. Arai *et al.*, 2013; Denis *et al.*, 2022a; Kotake *et al.*, 2005), there is a lack of knowledge about eels in estuarine habitats, particularly regarding their life history (Jacoby et al., 2015; Righton et al., 2021). By combining different approaches, this study provides a better understanding of the links between habitat use strategy and eel condition during their continental growth phase.

4.1. Spatial variation of eel condition

The condition of eels in estuarine habitats showed a clear clear differences in habitat use strategies among the study sites, related to local estuarine characteristics. Eels from small estuaries had on averall higher Fulton K and lipid content, but more eels in poor condition and health compared to medium-sized estuaries. The interactions between the local environment and the condition of eels are complex. It is difficult to identify the factors that influence condition due to the ability of eels to adapt to the very wide range of marine, brackish and freshwater habitats (Vélez-Espino and Koops, 2010). The characteristics of the local environment, in particular habitat size, productivity and anthropogenic pressures (e.g. Acou *et al.*, 2008; Belpaire *et al.*, 2019; Robinet & Feunteun, 2002), remain the most important factor influencing eel condition directly and/or indirectly.

The spatial variation in the eel condition was also significantly related to the silvering stage. The lipid content and Fulton K of eels increased during silvering. Higher lipid contents are regularly reported for silver eels compared to yellow eels (Durif et al., 2005; ICES, 2020). During development, eels accumulate lipids (> 20%) up to the silver stage in order to store sufficient energy for migration to the Sargasso Sea and reproduction (Belpaire et al., 2009; Van den Thillart et al., 2007). Reproductive success therefore depends to a large extent on the lipid content previously stored because during the spawning migration, silver eels complete gonad maturation (Dufour et al., 2003) and do not feed, relying solely on energy reserves accumulated during the continental growth phase (Van den Thillart et al., 2007). The eel local stock composition in the six estuaries was not significantly different, with the exception of the Wimereux and Liane estuaries, where the abundance of silver females and males was higher, but this was not an explanation for the variation in condition. The silvering process of eels seems to be mainly related to the local environment rather than age or overall length, which is reflected in the eel condition.

Eel density can also explain variations in the condition of eel local stock (Aprahamian et al., 2007). The Wimereux and Liane estuaries had the highest CPUE compared to the other estuaries, which could lead to strong intra-competition for food (Costa et al., 2008; Feunteun et al., 1998), thus reducing eel condition. The results do not support this hypothesis as condition was higher in these small estuaries. High densities of eels can be a factor in determining the health status of eels (ICES, 2015). In the six estuaries studied, eels were mainly in good health (EPI). The parasites species found in eels are regularly observed in estuarine habitats, but high salinity can reduce the prevalence and abundance of certain parasites in eels (e.g. Jakob *et al.*, 2009; Køie, 1988). The prevalence of pathologies in fish can be directly influenced and amplified by various causes, whether environmental or anthropogenic, such as the accumulation of pollutants in eels (ICES, 2015; Patey, 2017). In the six estuaries studied, eels were mainly in good health (Eel Pathology Index EPI), but differences between estuaries and habitat use may be related to the ingestion of prey of higher trophic position, such as fish. The fish are paratenic hosts for parasite transmission, including *Anguillicola crassus* (Knopf, 2006). Eels can acquire large numbers of *A. crassus* by feeding on fish (Kirk, 2003; Pegg et al., 2015), which is an important part of their diet.

At the small geographical scale (i.e. into one sector of the estuary), environmental characteristics may be a mechanism for indirect regulation of eel condition through prey availability. Food limitation is one of the main factors affecting the condition of fish, especially juveniles in coastal nurseries (Le Pape and Bonhommeau, 2015). Eels have an opportunistic feeding plasticity with a preference for macrocrustaceans and are able to feed on other prey such as fish when benthic invertebrates are less available (Laffaille et al., 2003). In the six estuaries, eels fed more on fish in small estuaries and on macrocrustaceans in medium-sized estuaries. These inter-estuary differences in eel diet may be influenced by the availability of macrozoobenthos prey, which in turn depends on their hydro-morpho-sedimentary characteristics (Denis et al., 2022b). Dietary plasticity in eels leads to spatial differences in diet that affect eel lipid content and condition (e.g. Parzanini *et al.*, 2021a, 2021b; Vasconi *et al.*, 2019). Our results, through the relationship found between condition indices and trophic status under the influence of tides and freshwater, partially explain the spatial variation in eel condition. We have found that there is a positive relationship between eels in good condition and having eaten mainly fish. These relationships suggest that feeding on more energetic prey, such as fish, would maintain optimal condition and lipid content. Nevertheless, a high availability of macrozoobenthos prey in medium-sized estuaries, reinforced by the high tide influence would allow optimal feeding to maximise the energy reserves, thus allowing rapid silvering and reproductive success (Gross, 1987).

4.1. Habitat use and movement

The elemental Sr and Ba composition of fish otoliths allows the tracking of the movement of an individual along the temporal dimension between habitats of different salinities and reveals life history tactics for habitat (Fablet et al., 2007; Vignon, 2015). The otolith Sr:Ca ratio is the most common approach used to track eel migrations during their continental growth phase (e.g. Daverat *et al.*, 2006; Tabouret *et al.*, 2010; Teichert *et al.*, 2023). It varies with salinity and thus allows separation of habitats used along a salinity gradient (i.e. marine, estuarine and freshwater habitats). The more recently used Ba:Ca ratio allows intra-habitat movement to be inferred in an environment by dividing it into sectors along a gradient and assessing the contribution of each sector to migration (Teichert et al., 2022). In the present study, the Sr:Ca and Ba:Ca ratios of estuarine eel allowed to evidence the segregation of marine, estuarine and freshwater habitats, and also within the estuarine habitat, the segregation of three distinct sectors (i.e. lower, middle and upper estuary) along an downstream to upstream gradient. However, it is possible that the eels moved to the capture site only a few days before capture and that this time was too short to be reflected in the temporal resolution of the otolith microchemistry. The significant relationships between the mean ratios in the marginal segment and the sampling location of the eels support the view that the ratios in the marginal otoliths reflect the chemical environment. Teichert *et al.* (2022) showed that a decrease in Ba:Ca ratios of eel otoliths along the Sélune River gradient indicates intra-habitat movement in a freshwater environment, which may be related to substrate variation and erosion processes (Elsdon and Gillanders, 2005). In our study, the Ba:Ca variation allowed us to identify eels typical of the middle and upper sectors in the Wimereux and Somme estuaries, as well as the freshwater habitat, probably due to exposure of eels to different salinity ranges (i.e. distance to the sea) and different environmental conditions, and thus to reconstruct the environmental history along the salinity gradient of the estuary.

Our results confirm the plasticity of eels in habitat use, with 81% estuarine residents, 16% inter-habitat shifters and 3% freshwater resident eels in the Wimereux and Somme estuaries. Other studies have shown similar results, with more estuarine resident eels than inter-habitat shifters (e.g. Arai *et al.*, 2019; Capoccioni *et al.*, 2014; Shiao *et al.*, 2006), except in northern Europe where estuarine residents are much less common (e.g. Limburg *et al.*, 2003; Rohtla *et al.*, 2022), probably due to lower estuarine productivity than in freshwater at higher latitudes (Tsukamoto and Arai, 2001). A strong freshwater influence in estuarine habitats can also lead to an increase in the proportion of inter-habitat shifter eels (Jessop et al., 2004). Residence strategy may depend on several factors, such as prey availability, the condition of glass eels during recruitment, intra- and interspecific competition, or the water temperature of the estuarine (Edeline, 2007; Edeline et al., 2006; Imbert et al., 2008). Habitat residence is not definitive and eels, being opportunistic, may migrate between habitats to access better food resources, to escapes poor environmental conditions (e.g. hot or cold periods; Clément *et al.*, 2014), or higher intra- and interspecific competition (Edeline, 2007; Tsukamoto and Arai, 2001).

Among the inter-habitat shifter eels, movement between salinity habitats was regular at the onset of continental growth phase, then rapidly became sedentary lifestyle after the fifth year of continental life. These observations are consistent with other studies showing a decrease in the number of habitat transitions with increasing eel age (Fablet et al., 2007), particularly in the Gironde (Daverat and Tomás, 2006) and in the Sélune estuaries (Teichert et al., 2022). The high proportion of individuals moving from upstream to downstream reflects a behavioural tactic to optimise and maximise growth rate and reduce intra- and inter-specific competition (Daverat and Tomás, 2006). Half of the individuals examined were recruited to the estuary and spent most of their time in estuarine habitats, particularly in the upper estuary, suggesting that inter-habitat shifter eels rarely move upstream to freshwater but remain close to the estuary, while resident freshwater eels generally prefer a sedentary lifestyle (Panfili et al., 2012). Our results also showed that eels from the Wimereux and Somme estuaries occupied a sector of the estuary for a long periods, ranging from a few months to several years (Fig. 3). The estuarine resident eels mainly occupied the lower and middle estuary sectors (80%), whereas the upper estuary sector was much less frequently occupied, by only 20% of eels. Intra-estuarine movements were mainly downstream movements from the upper and middle estuary sectors to areas close to the sea with high salinities. The upper estuary sector was regularly occupied by inter-habitat shifter eels.

The proportions of estuarine resident eels were slightly different in the two studied estuaries (88% and 75% respectively), with a few more inter-habitat shifter eels in the Wimereux estuary. The presence of dams can restrict upstream migration and therefore the accumulation of eels in areas close to barriers (Laffaille et al., 2005), and thus reduce movement between habitats. The differences in the number of inter-habitat shifter eels between the estuaries could be partly explained by the presence of a dam upstream of the Somme estuary. The dikes, dams or harbours also reduce access to habitats and food sources for fish species (Baudoin et al., 2014), particularly in medium-sized estuaries where human activities are more important than in small estuaries. This affects the condition and reduces the growth of eels (e.g. Cairns *et al.*, 2009; Geeraerts & Belpaire, 2010; Simpson *et al.*, 2015).

4.3. Habitat use and eel condition

The results of this study also showed that estuarine resident eels presented the better condition with respect top inter-habitat shifters, in concordance with many studies showing that marine and brackish resident eels generally have a higher growth rate than inter-habitat shifters and freshwater residents (e.g. Cairns *et al.*, 2009; Daverat *et al.*, 2012; Melia *et al.*, 2006). This is probably due to the high potential of large availablility of prey and a longer growing season (i.e. high temperature) compared with freshwater habitats. Habitat selection is an opportunistic behaviour in eels due to their phenotypic plasticity (Capoccioni et al., 2014), which allows them to choose a habitat according to food availability and carrying capacity in order to maximise growth and energy reserves (Marohn et al., 2013; Vélez-Espino and Koops, 2010). Differences in eel condition between intra-estuarine residents support the hypothesis of an influence of food. Estuarine resident eels showed clear differences in condition between the three resident sectors (i.e. lower, middle and upper estuary). Eels resident in the lower estuary had a higher proportion in good condition than those in the middle and upper estuaries, with condition and health declining towards the upper estuary. The differences in condition observed according to habitat use appear to be related to differences in diet composition, from a diet of marine crustaceans to freshwater fish from downstream to upstream of the estuary, which in turn depends on local hydro-morpho-sedimentary characteristics.

The advantage of inter-habitat shifters is that they move to better environmental and trophic conditions thus improving their condition (Gross, 1987). Brackish habitats such as estuaries generally support higher densities of eel than freshwater habitats (Yokouchi et al., 2009), and the strong competition for resources can lead eels to change habitat (Feunteun et al., 2003). Inter-habitat shifter eels in the estuarine habitat were moved to to either the upper estuary or freshwater and then moved mainly between these two habitats, suggesting that they stayed close to the estuary when residing in freshwater and vice versa. The condition of the inter-habitat shifters was similar to that of the upper estuary residents, with high proportions of eels in poor condition and health. We assume that the habitat movement is not voluntary, but rather results from the influence of freshwater in the upper estuary, resulting in environmental conditions and prey availability (i.e. freshwater fish species) that are relatively comparable to those in freshwater habitat.

5. Conclusions

In this study, the combination of condition indices and otolith microchemistry analysis allowed the assessment of the relationship between habitat use and eel condition during their continental phase according to estuarine characteristics. Eel condition showed a clear spatial difference between estuaries, with better condition and health in small estuaries. The otolith elemental compositions of Sr and Ba allowed reconstruction of the environmental history and movement of estuarine eels between marine, estuarine and freshwater habitats. Results showed that eels are predominantly estuarine residents and that a small proportion of eels move between inter-habitats. The Sr:Ca and Ba:Ca ratios were sufficiently contrasted to track movements of estuarine resident eels between lower, middle and upper estuary sectors. While inter-habitat shifter eels were in poorer condition than estuarine residents, eel condition also varied between the three resident sectors. Eel condition and health decreased between eels from the lower to upper estuaries. The spatial differences in eel condition appear to be related to variations in their diet composition, corresponding to variations in the availability of macrozoobenthos prey which depends on the local hydro-morpho-sedimentary characteristics.

These results suggest that estuarine habitats provide favourable environmental conditions for eel condition, thus allowing the production of more spawners in good condition with high energy reserves and good health. These results highlight the importance to manage eels locally by preserving or restoring the quality of estuarine habitats (e.g. reducing the impact of human activities) so that eels are more likely to escape to the sea and face ocean migration with better prospects of reproductive success (Belpaire et al., 2009; Clevestam et al., 2011; Van den Thillart et al., 2007). The approach and the results of this study can also be applied to other species of Anguillidae and to other geographical areas. More generally, this study will be of interest to those who study, manage and protect other fish species that use estuaries as a dominant habitat type, and even more so to those who manage and protect estuarine environments.

Author contribution

Jérémy Denis: Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft, Visualization. **Kélig Mahé:** Methodology, Validation, Formal analysis, Writing - original draft, Visualization. **Hélène Tabouret:** Methodology, Validation, Formal analysis, Writing - original draft. **Khalef Rabhi:** Investigation, Methodology. **Kévin Boutin:** Investigation, Writing - original draft. **Mamadou Diop:** Investigation, Writing - original draft. **Rachid Amara:** Conceptualization, Methodology, Formal analysis, Supervision, Validation, Writing - original draft.

Acknowledgments: The authors would like to thank Vincent Cornille for their participation in the sampling and Alexandre Lheriau, Romain Elleboode and Antoine Dussuel for their participation in the preparation of the otoliths.

Conflicts of Interest: The authors declare no conflict of interest.

Funding: This research was funded by "Parc Naturel Marins des Estuaires Picards et de la Mer d'Opale" (DECISION N°2018-28 9 March 2018), and "European Maritime Fisheries Fund" and "Région Hauts de France" (PFEA621220CR0310022). This work also has been partially financially supported by the European Union (ERDF), the French Government, the Région Hauts-de-France and IFREMER, in the framework of the project CPER MARCO 2015–2020 (https://marco.univlittoral.fr/). This work has been partially financially supported by "ANR-21-EXES-00 11" as part of the IFSEA graduate school, which originates from National Research Agency under the Investments for the Future program.

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Tables

Table 1. Number of individuals (N) analysed for eel condition in the six estuaries (from the North with the Slack estuary to the South with Somme estuary) and their mean ± standard deviation for Total Length (TL, mm), Age (years) and CPUE (ind. fyke nets $24h^{-1}$). The percentage of individuals by silvering stage (I sexually undifferentiated growth phase, FII female growth phase, FIII female pre-migrant phase, FIV and FV female migrating phases, and MII male migrating phase) is also shown. p-value in bold indicates significant effect (p<0.05).

	Slack	**Wimereux**	**Liane**	**Canche**	**Authie**	**Somme**	**p-value**
N	20	20	20	18	21	20	
TL	414 ± 104	446 ± 121	517 ± 143	400 ± 109	439 ± 94	495 ± 174	0.069
Age	8.1 ± 3.4	9.0 ± 3.2	8.4 ± 2.8	7.2 ± 2.2	8.7 ± 2.2	9.7 ± 4.2	0.254
CPUE	3.1 ± 1.6	12.5 ± 18.4	7.4 ± 4.9	2.0 ± 1.1	3.6 ± 2.4	1.8 ± 1.3	**< 0.05**
Silvering stage							**< 0.05**
I	60	35	30	67	57	50	
FII	10	5	30	11	29	20	
FIII	15	35	15	11	10	15	
FIV			10			10	
FV			5	6	5		
MII	15	25	10	6		5	

Table 2. Mean of Fulton condition factor (Fulton K; $mg.mm^{-3}$), percentage lipid content (% lipid per dry weight) and hepatosomatic index (HSI) ± standard deviation of eels collected in the six estuaries. The percentage of individuals by eel pathology index (EPI; "very good health", “good health”, “moderate health”, “unsatisfactory health” and "poor health") is also given. p-value in bold indicates significant effect ($p < 0.05$).

	Slack	**Wimereux**	**Liane**	**Canche**	**Authie**	**Somme**	**p-value**
Fulton K	0.18 ± 0.02	0.18 ± 0.02	0.18 ± 0.04	0.19 ± 0.02	0.18 ± 0.02	0.17 ± 0.02	0.423
% lipid	13.3 ± 4.5	13.9 ± 5.4	14.0 ± 6.4	18.5 ± 8.0	15.4 ± 6.9	16.1 ± 6.3	0.941
HSI	2.0 ± 0.5	1.8 ± 0.5	1.6 ± 0.7	2.1 ± 0.5	2.0 ± 0.7	1.9 ± 0.6	**< 0.05**
EPI							**< 0.05**
Very good	20	20	35	39	10	35	
Good	15	25	25	22	24	25	
Moderate	55	40	35	33	57	40	
Unsatisfactory	10	15	5	6	5		
Poor					5		

Table 3. The prevalence of anatomo-morphological lesions and external and internal parasitism in eels collected in the six estuaries.

Names	**Anatomical locations**	**Slack**	**Wimereux**	**Liane**	**Canche**	**Authie**	**Somme**
Anatomo-morphological lesions							
Visually detectable lesions		20.0		5.0	16.7	23.8	5.0
Deformation. deformity	Mouth	5.0			5.6		
	Fin					4.8	
Gill lesions-necrosis. erosion	branchial					4.8	5.0
Eye damage-Opacity	Eye	5.0					
Haemorrhage	Gill slit				5.6		
	Pectoral fin				5.6		
	Anal orifice	5.0		5.0		4.8	5.0
Necrosis	Fin				5.6	9.5	
	Caudal fin	5.0					
External parasitism							
Visually detectable parasitism						9.5	5.0
Crustacea	Fin					9.5	5.0
	Pectoral fin					4.8	
Internal parasitism							
Visually detectable parasitism		80.0	80.0	65.0	61.1	81.0	60.0
Anguillicola crassus	Digestive tract		5.0				
Anguillicola crassus < 3 ind.	Swim bladder	40.0	40.0	45.0	33.3	42.9	40.0
Anguillicola crassus > 3 & < 6 ind.	Swim bladder	15.0	15.0	5.0	11.1	9.5	15.0
Anguillicola crassus > 6 & < 10 ind.	Swim bladder	10.0	15.0	5.0	5.6	9.5	
Anguillicola crassus > 10 ind.	Swim bladder	5.0				4.8	
Contracaecum rudolphii	Digestive tract	15.0	15.0		22.2	14.3	5.0
Bothriocephalus claviceps	Digestive tract	20.0	25.0	25.0	11.1	19.0	5.0
Ergasilus sp.	branchial	5.0					
Pomphorhynchus laevis	Digestive tract				11.1	14.3	

Figures

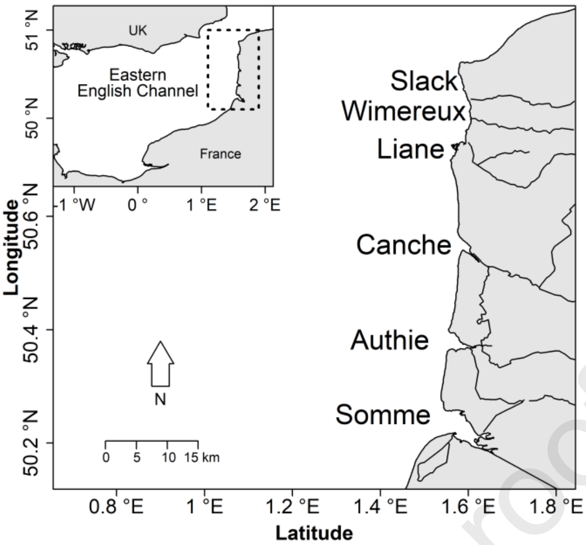


Fig. 1. Location of the six sampling estuaries along the French coast in the eastern English Channel.

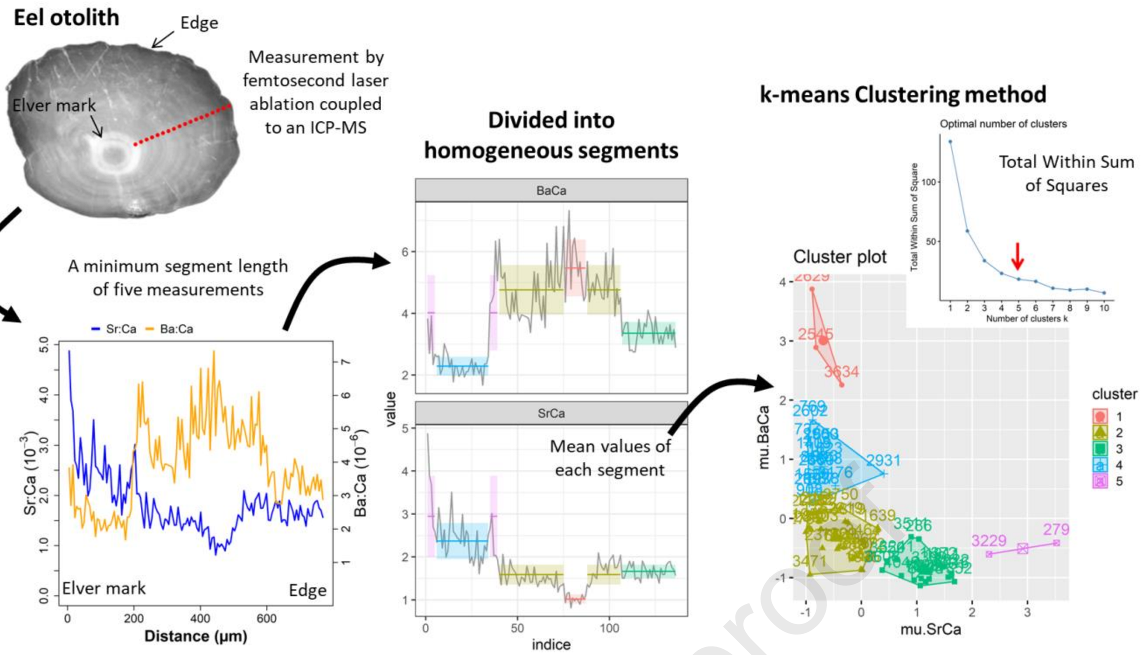


Fig. 2. Reconstruction of environmental history of eels during the continental growth phase (from the elver mark to the edge of the otolith) from otolith Sr:Ca and Ba:Ca ratios measured by femtosecond laser ablation (LA, IR 1030 nm, Alfamet-Novalase, France) coupled to an ICP-MS (DRCII; Pekin Elmer, Shelton). Variations in ratios were identified and divided into homogeneous segments reflecting similar chemical environments using a segmentation method (Lavielle, 1999) based on bivariate time series (Patin et al., 2020). The mean values of each segment were calculated to determine clusters of segments with similar Sr:Ca and Ba:Ca ratios using a K-means clustering method and the optimal number of clusters was selected based on the Total Within Sum of Squares (TWSS).

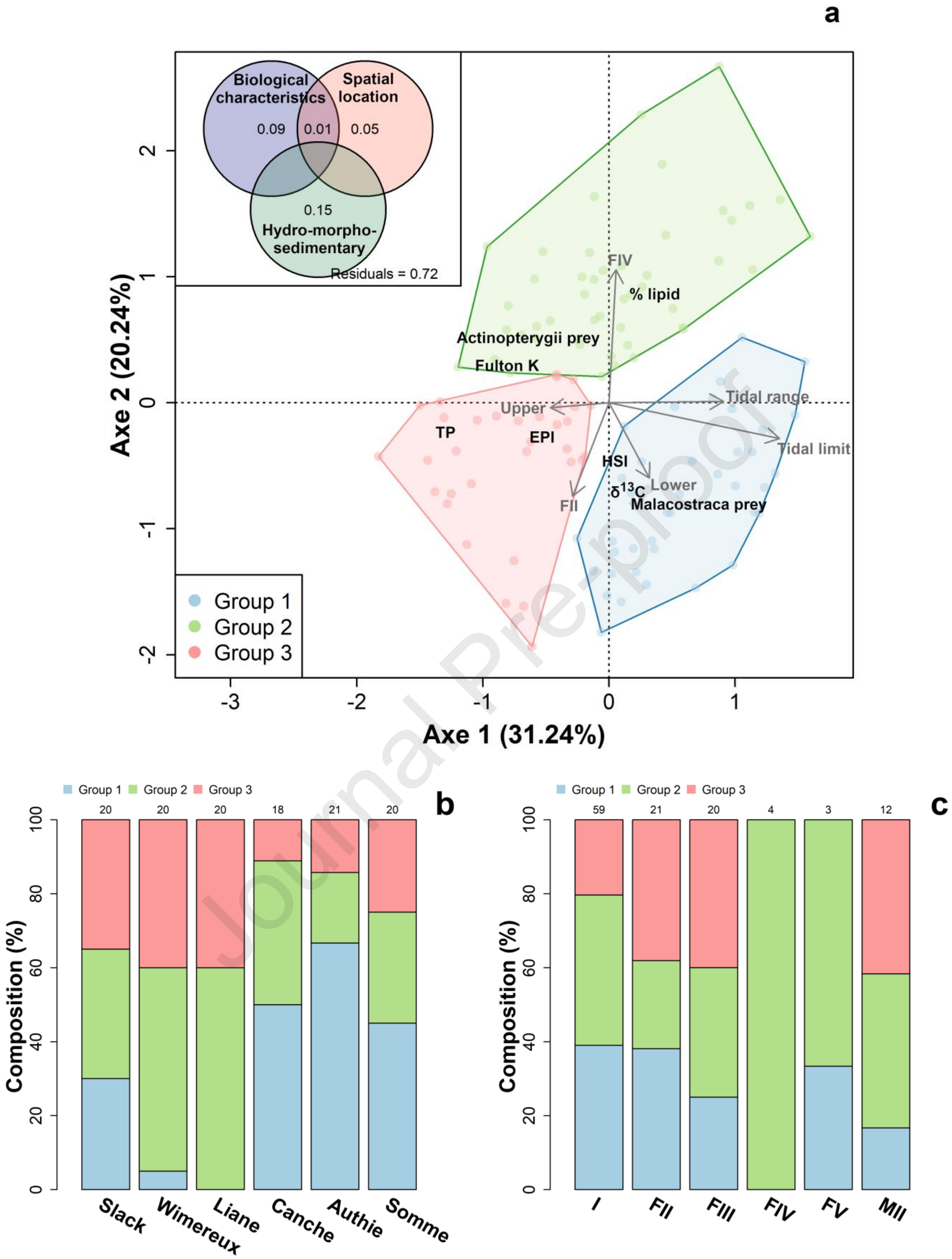


Fig. 3. Redundancy and variance partitioning (top left) analyses of condition (Fulton K, % lipid, HSI and EPI) and trophic status (Malacostraca and Actinopterygii prey, $\delta^{13}C$ and TP) of eels collected in the six estuaries constrained by selected biological structure (silvering stages: FII female growth phase; FIV female migrating phases), spatial location (sampling station: lower and upper estuary) and

hydro-morpho-sedimentary (tidal limit, tidal range) covariates (a). The three groups identified by the Hierarchical Classification Analysis (HCA) are indicated (bottom left). The numbers in the circles in the variance partitioning analysis (top left) represent the proportion of variance explained by each covariate. Variation in percentage of eels for the three identified HCA groups by six estuaries (b) and by six silvering stages (I sexually undifferentiated growth phase, FII female growth phase, FIII female pre-migratory phase, FIV and FV female migratory phases, and MII male migratory phase) (c).

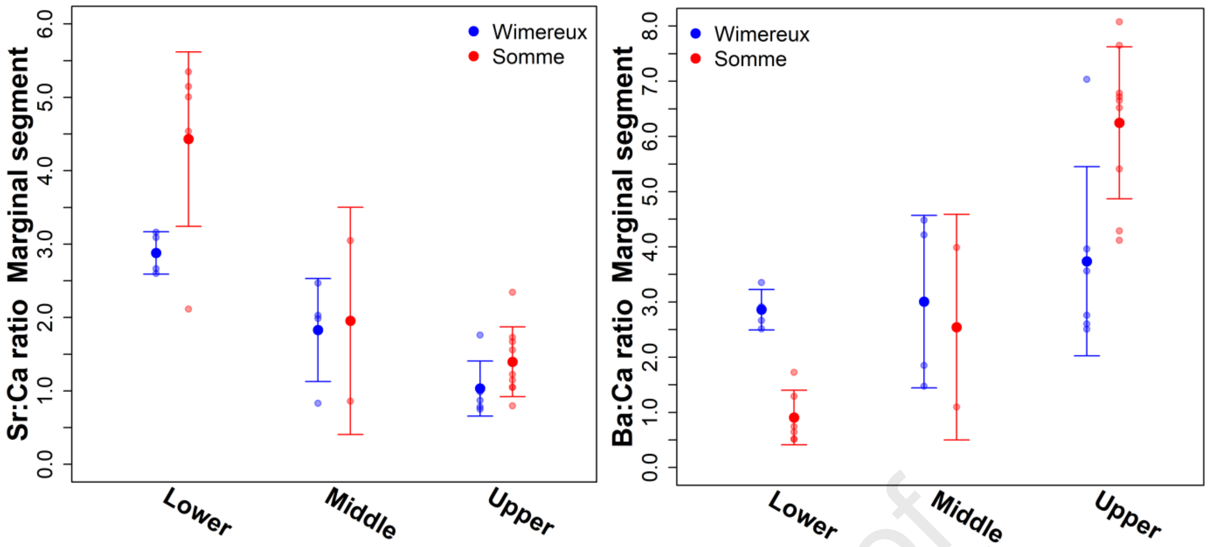


Fig. 4. Relationship between the mean ± standard deviation of Sr:Ca (left; $\times 10^{-3}$ µg.l^{-1}) and Ba:Ca (right; $\times 10^{-6}$ µg.l^{-1}) ratios in the marginal segment and eel sampling location in three estuarine sectors (lower, middle and upper estuary) in the Wimereux and Somme estuaries.

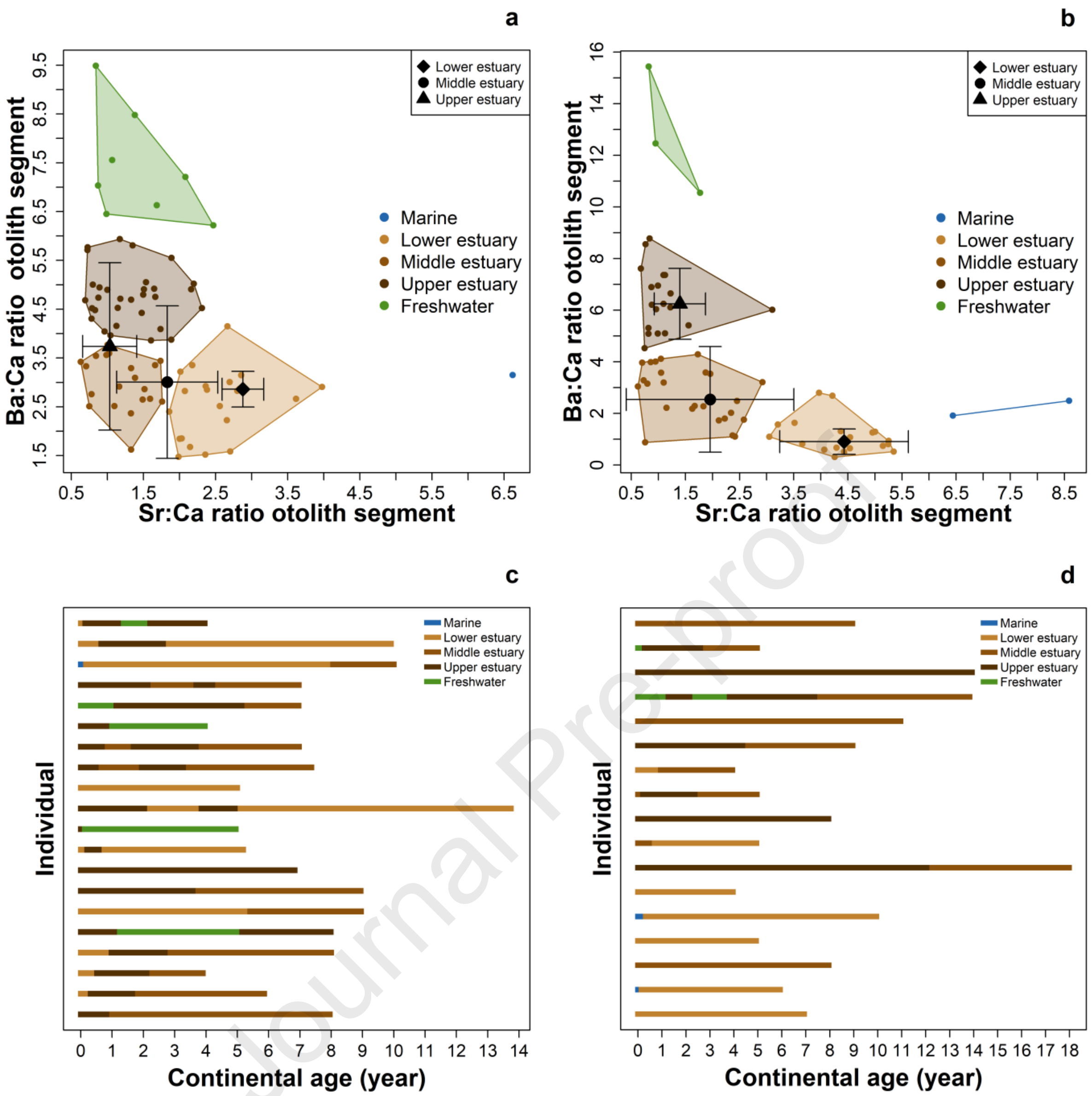


Fig. 5. (a-b) Clustering of otolith segments based on Sr:Ca (× 10^{-3} µg.l^{-1}) and Ba:Ca (× 10^{-6} µg.l^{-1}) ratios and (c-d) individual life history during the continental growth phase (year) of eels collected at three sampling stations (i.e. lower, middle and upper estuary) in the Wimereux (a-c, n = 20) and Somme (b-d, n = 17) estuaries. Mean ± standard deviation of marginal otolith segment ratios reflect the chemical environment of the month immediately preceding the capture of the eels at the three sampling stations (lower, middle and upper estuary).

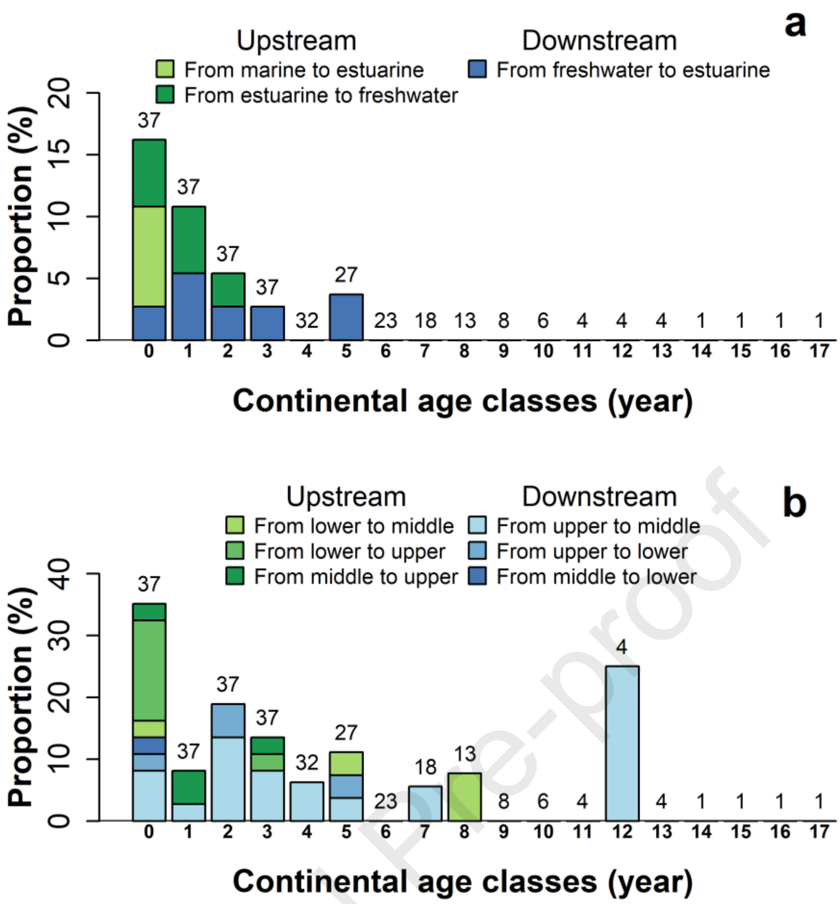
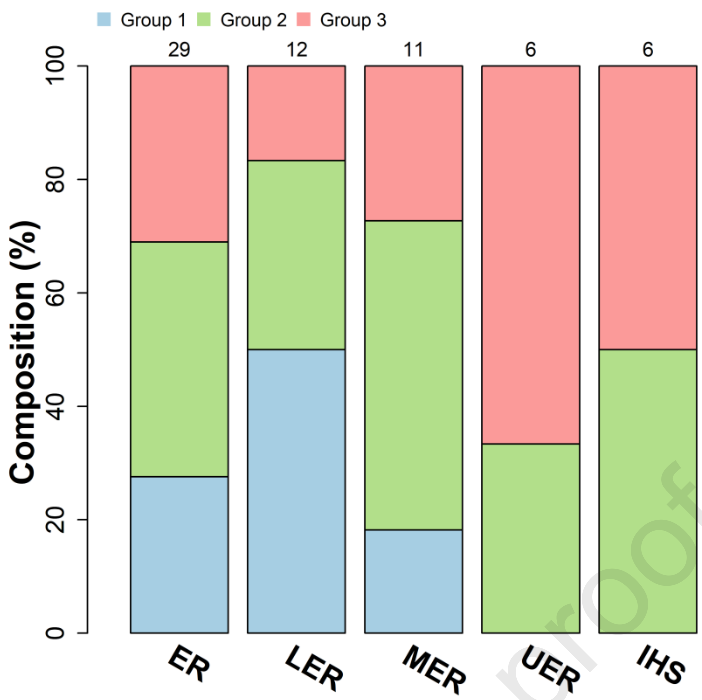


Fig. 6. Proportion of eels moving between (a) inter-habitat (marine, estuarine and freshwater) and (b) intra-estuarine (lower, middle and upper estuary) according to continental age classes (year) in the Wimereux and Somme estuaries. The number of individuals analysed is indicated above each bar.



1040
1041 Fig. 7. Variation in percentage of eels for the three identified HCA groups (see Fig. 3) by four habitat
1042 use strategies : estuarine residents (ER) with residence sectors: lower (LER), middle (MER) and upper
1043 (UER); inter-habitat shifter (IHS). The number of individuals analysed is indicated above each bar.

Supplementary

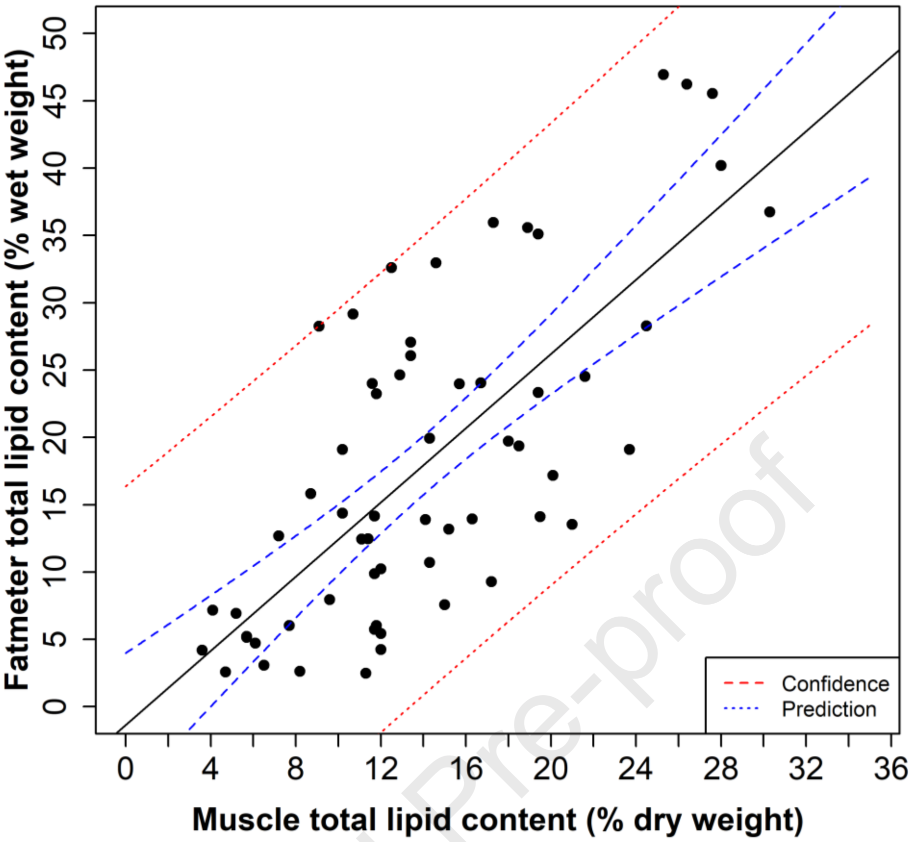
Table S1. Hydro-morpho-sedimentary and anthropogenic characteristics of the six estuaries studied: surface area (ha), tidal limit (km), tidal range (m), tidal exposure (1: sheltered; 2: exposed), dominant sediments (1: mud; 2: muddy-sand; 3: sandy-gravel), ecological status (1: very good, 2: good, 3: moderate, 4: poor, 5: bad) and number of obstacles.

	Slack	**Wimereux**	**Liane**	**Canche**	**Authie**	**Somme**
Hydro-morpho-sedimentary						
Surface area [a]	1.29	0.22	22.10	5.32	11.90	40.69
Tidal limit [b]	3	3	3	12	12	15
Tidal rang [b]	6.6	6.7	6.8	9.0	7.2	10.0
Tidal exposure [b]	1	1	1	1	1	2
Dominant sediments [b]	2	2	1	3	3	3
Anthropogenic						
Ecological status [c]	3	3	3	3	3	4
Number of obstacles [c]	1	0	1	0	0	4

[a] IGN-F maps; [b] Nicolas *et al.* (2010); [c] SDAGE 2016-2021.

Table S2. The abundance and prevalence of anatomo-morphological lesions and external and internal parasitism of eels collected in the six estuaries. Health status based on the Eel Pathology Index (EPI; 1: very good health, 2: good health, 3: moderate health, 4: unsatisfactory health, 5: poor health) are also given.

	Anatomical locations	Abundance	Prevalence (%)	EPI				
				1	2	3	4	5
Anatomo-morphological lesions								
Visually detectable lesions			11.8	×				
Deformation, deformity	Mouth		1.7		×			
	Fin		0.8		×			
Gill lesions-necrosis, erosion	branchial		1.7			×		
Eye damage-Opacity	Eye		0.8			×		
Haemorrhage	Gill slit		0.8				×	
	Pectoral fin		0.8				×	
	Anal orifice		3.4				×	
Necrosis	Fin		2.5			×		
	Caudal fin		0.8			×		
External parasitism								
Visually detectable parasitism			2.5	×				
Crustacea	Fin		2.5			×		
	Pectoral fin		0.8			×		
Internal parasitism								
Visually detectable parasitism			71.4	×				
Anguillicola crassus	Digestive tract	2	0.8		×			
Anguillicola crassus < 3 ind.	Swim bladder	1.8 ± 0.8	40.3		×			
Anguillicola crassus > 3 & < 6 ind.	Swim bladder	5.1 ± 0.7	11.8			×		
Anguillicola crassus > 6 & < 10 ind.	Swim bladder	7.9 ± 1.1	7.6				×	
Anguillicola crassus > 10 ind.	Swim bladder	12 ± 1.4	1.7					×
Contracaecum rudolphii	Digestive tract	2.4 ± 1.6	11.8			×		
Bothriocephalus claviceps	Digestive tract	1.7 ± 1.4	17.6			×		
Ergasilus sp.	Branchial	1	0.8				×	
Pomphorhynchus laevis	Digestive tract	1.8 ± 0.4	4.2			×		



1055

1056 Fig. S1. Relationship between fatmeter lipid content (% lipid per wet weight) and total lipid content

1057 measured in muscle (% lipid per dry weight).

Highlights

- Habitat use and movement reconstructed from the Sr and Ba otoliths
- Otolith microchemistry confirms high estuarine residence
- Otolith elemental composition to track eel movements between resident sectors
- Estuarine resident eels were in better condition than inter-habitat shifter
- Condition of eels declined from the lower to the upper estuary

Conflicts of Interest:

The authors declare no conflict of interest.