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Biogeographical snapshot of life-history traits of European silver eels: insights from otolith microchemistry

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Abstract

Life-history traits of eels display a high level of phenotypic plasticity in response to large-scale biogeographical drivers, as well as local conditions encountered during the continental phase. Here, we provided a biogeographical snapshot of the variability of life-history traits of eels (*Anguilla anguilla*), across a large proportion of their natural distribution range. Silver eels ($n = 99$) were collected across eleven European catchments to investigate how life-history traits vary along geographical and saline habitats, as it was inferred from the Sr:Ca ratio in otoliths. Among 13 life-history traits tested, 3 of them such as total length, body or liver weight were related to geographical coordinates. Overall, eels grow faster in southern Europe and migrate earlier suggesting that the silvering process is related to the local growth conditions more than fish age. The salinity profiles revealed by the otoliths' Sr:Ca ratios indicate that eels with a brackish life-history generally grow faster, reach larger size-at-age, and have a better condition than eels living in freshwater. This observation associated with the lower abundance of the sanguivorous swimbladder nematode, *Anguillicola crassus*, confirms the importance of brackish areas for sustaining the eel production. A large proportion of the observed variation of life-history traits remained unexplained by the biogeographical trends and salinity condition, which suggests that other drivers act at the catchment scale.

Keywords: *Anguilla anguilla*; phenotypic plasticity; otolith; Sr:Ca ratio; biogeography; brackish habitat

Introduction

The European eel, *Anguilla anguilla*, is a facultative catadromous species, widely distributed throughout European and Mediterranean coastal and inland regions. Reproduction takes place in the tropical North Atlantic convergence zone, where adults spawn from December to mid-May (Miller et al. 2019). Eggs and leptocephali larvae are then transported by oceanic currents across the Atlantic Ocean (Miller et al. 2015; Chang et al. 2020). Glass eels reach the continental shelf of Europe from October to March and progressively settle in their continental habitats (Feunteun et al. 2003). While some individuals migrate upstream into rivers, others remain in transitional waters, such as brackish estuaries, lagoons or salt marshes (Daverat et al. 2005; Daverat and Tomas 2006; Tabouret et al. 2010), but also in very small coastal streams (Copp et al. 2021). Juveniles (yellow eels) spend from three to 30 years or more in growing areas before initiating their puberty toward the silver stage (Aroua et al. 2005) and starting their migration back to the spawning ground (Tesch 2003; Righton et al. 2016). When sub-adults leave the continental areas, the gonads remain poorly developed and the final maturation only occurs during the seaward migration (Dufour et al. 2003). Eels do not feed during their trans-Atlantic migration and, as a result, fat stores are crucial for sustaining the energy costs of migration and completing the maturation of gametes (Van den Thillart et al. 2007). Accordingly, key life-history traits, such as overall condition or energy reserves, are expected to exert a great effect on the reproductive success of silver eels that have to travel > 5000 km before breeding (Belpaire et al. 2009; Clevestam et al. 2011).

Silver eels are characterized by a strong dimorphism between the sexes, particularly in terms of age and size at silvering (Vøllestad 1992). Males can begin their reproductive migration at three years of age and rarely measure more than 45 cm long, whereas females can reside for more than 30 years in their growing areas and reach more than one metre in length (e.g. Acou et al. 2003; Tesch 2003; Durif et al. 2020). This sex-related difference in length at silvering reflects a size-maximizing strategy for females that optimize their absolute fecundity, whereas males tend to reduce the continental phase duration (Helfman et al. 1987; Oliveira 1999; Durif et al. 2020). Beyond sexual dimorphism, a great variability in fat condition, size and age at silvering is reported between and within river catchments (Svedäng and Wickström 1997; Vélez-Espino and Koops 2010; Mateo et al. 2017; Teichert et al. 2022). Eels residing in the upper reaches generally exhibit lower growth rates and metamorphose older than the individuals living downstream (Daverat et al. 2012). The highest growth rates are commonly observed for eels living in brackish environments (Acou et al. 2003; Cairns et al. 2009; Denis et al. 2022). These eels generally mature earlier and have higher condition coefficients than individuals captured in fresh waters.

Using the strontium:calcium (Sr:Ca) elemental ratios in otoliths, Daverat and Tomas (2006) demonstrated that some freshwater residents can move downstream into brackish waters during their continental phase, which helps to optimize their fitness and increase their energy reserves before migration. This high behavioral plasticity in habitat use helps to explain the variability in silver eel traits (Daverat et al. 2006). For example, Edeline (2007) proposed that colonisation process of river catchments by glass eels depends on their bioenergetic status, with individuals with high energetic status migrating upstream to avoid competition and maximize their fitness, even if the growth rate was lower. Drouineau et al. (2014) suggested that phenotypic variation in sex determination, length at silvering, and growth habitat selection can be interpreted as adaptive response to the highly variable and spatially structured environmental conditions encountered by eel. However, other biotic and abiotic factors are involved, such as temperature, productivity, or density of resident eels (Acou et al. 2009; Vélez-Espino and Koops 2010). Moreover, the human-generated pressures and infection by endogenous parasites can also substantially affect key life-history traits, such as energy stores or swimming performance (Palstra et al. 2007; Belpaire et al. 2009). For example, organic contaminants are expected to affect the lipid reserves and endocrine process, which in turn impact the reproductive success (Robinet and Feunteun 2002; Belpaire et al. 2019; Bourillon et al. 2022). Similarly, the overall body condition of silver eels is generally reduced when contaminated by metallic compounds (Maes et al. 2005) and when infected by the parasite *Anguillicola crassus*, which damages the swim bladder (Palstra et al. 2007; Gérard et al. 2013). Accordingly, local conditions, including alterations of water quality, act in combination with habitat and large-scale processes for shaping life-history traits of silver eels (Bourillon et al. 2022).

At large scales, silver eels exhibit high variability in the expression of life-history traits when starting their migration (Vøllestad 1992). Temperature and productivity gradients have been reported as major drivers of eel life-history (e.g. Vøllestad 1992; Jessop 2010; Vélez-Espino and Koops 2010; Daverat et al. 2012). For example, the decrease in annual mean temperature along the latitudinal gradient is associated with lower body growth and higher age at silvering (Vøllestad 1992), as was also reported for American eel, *Anguilla rostrata* (Jessop 2010). Also, MacNamara et al. (2016) reported spatial changes in female fecundity at given size across the eel's distribution area, with greater reproductive investment in Greece (eastern Mediterranean) and Sweden (northeast Europe) lakes than in Ireland (northwest Europe). Such geographically-related variations in life-history traits are commonly interpreted in relation to the distance that separates the spawning and growing-on areas. For American eel, individuals that grow on further from their spawning areas have been suggested to mature at larger size in order to sustain the energetic requirement of longer migration and and maximize their absolute

fecundity (Helfman et al. 1987). Larger body size is expected to favour swimming performances and to be associated with higher fat reserves (Clevestam et al. 2011). Nevertheless, Daverat et al. (2012) demonstrated that, while yearly sum of temperature is an important parameter, the local conditions, e.g. salinity, depth, or catchment position, greatly contribute to explain changes in eel growth at the scale of the distribution area. Although a complex task, disentangling the effects of geographical and local habitat conditions is thus an important step to understand European eel ecology to support management measures in the context of the significant decline of the stock.

In the present study, silver eels were collected from eleven widely distributed European catchments to investigate how life-history traits vary along geographical and saline habitats. More precisely, we attempted to determine whether some eel traits were predominantly shaped by large scale geographical constraints, continental habitat type (inferred from Sr:Ca ratios in otoliths rather than simply by capture locations) or local basin-scale characteristics. When multiple drivers act in combination, identifying the main influencing factors is particularly relevant for management purposes to understand which restoration actions are most appropriate, and at which spatial scale to act.

Materials and methods

Study area and fish sampling

Silver eels were collected within the EELIAD international project in the early winters of 2008, 2009 and 2010 across eleven European catchments (Fig. 1, Table 1). Sampled sites were featured by contrasting salinities (fresh- to brackish-water conditions), upstream catchment sizes (between 60 and 117 000 km²), human induced alterations (Bourillon et al. 2020, 2022), as well as abundance of the parasite *A. crassus* (Gérard et al. 2013). Silver eels of the freshwater sites were sampled by eel traps, fyke nets, coghill nets or electrofishing, whereas eels in the brackish sites were caught using fyke nets or pound nets (Table 1). All these techniques enable sampling of eels in the downstream part of the catchments during their seaward migration. Silver eels were identified visually based on the criteria defined by Acou et al. (2005): colour of the back and belly, presence of a well-defined lateral line, and a high Pankhurst eye index (OI > 6.5). Each fish was euthanised with different methods according to the country legislations (clove oil, benzocaine, 2-phenoxyethanol, chlorbutol or metomidate) prior to dissection and measurement of life-history traits.

Description of life-history traits

A range of life-history traits were investigated to describe the overall condition state of eels when migrating to their oceanic spawning area. Each eel was measured for total length (TL) and total weight (TW) to the nearest mm and g, respectively, with which to calculate the Fulton (1904) condition coefficient (K) according to the following formula: $10^5 \times TW/TL^3$. Eels were then dissected to determine sex via macroscopic gonad examination (Colombo et al. 1984), with individual gonad weight (IWG) and liver weight (IWL) measured to the nearest g. Gonado-somatic index (GSI) and hepato-somatic index (HSI) were calculated as the ratio of organ weight to body weight: $GSI = IWG/TW \times 100$, and $HSI = IWL/TW \times 100$, respectively. The GSI provides insights into the level of gonad maturation and of reproductive investment, whereas the HSI is a proxy of lipid reserves, which are involved in gonad maturation and oceanic migration. Nevertheless, inter-individual change in gonad maturation can induce extra variation in GSI and HSI depending on their silvering stage (Durif et al. 2005). The age of silver eels (AGE) was estimated from a visual count of annuli (rings) on the sagittal otoliths (see below), beginning from the first growth check outside the zero band, which is assumed to reflect the beginning of the continental phase. Nevertheless, the widespread distribution of the sampling sites may induce variability in age estimations because the growth patterns of eel otolith may differ between the northern part and the southern part of the distribution area (ICES 2020). The annual growth rate in body mass (AMIR, Annual Mass Increase Ratio = TW/AGE) and in continental length (ALIR, Annual Length Increase Ratio = $(TL-65)/AGE$, where 65 mm is the mean size at recruitment) were then calculated. For each individual, the level of infection by *A. crassus* was assessed by counting the total number of nematodes present in the eel's swim bladder (i.e. *A. crassus* abundance).

Otolith preparation and analysis

The sagittal otoliths of eels were extracted and embedded in epoxy resin (Araldite 2020, Hunstmann), then ground along the longitudinal plane and polished until the primordium was reached (Acou et al., 2013). A wave-length dispersive, X-ray electron microprobe analyzer (JXA-8230R, JEOL) was used at the AORI (Atmosphere and Ocean Research Institute, University of Tokyo) to measure strontium (Sr) and calcium (Ca) concentrations in the otoliths in a transect along the longest axis of each otolith from the core to the edge (Itakura et al., 2020). The standards were $CaSiO_3$ and $SrTiO_3$. The accelerating voltage and beam current were 15 kV and 12 nA, respectively. The electron beam was focused on a point 10 μm in diameter, with measurements spaced at 15 μm intervals. The Sr:Ca ratio was calculated as a weight percent ratio. The resulting elemental profiles consisted of successive measures distributed each 15 μm along the otolith transect. For each profile, the outliers were removed using an additive outliers

detection process for time series in order to smooth the Sr:Ca extreme values induced by analytic artifacts (López-de-Lacalle 2016).

Reconstruction of lifetime sequences

The elemental ratios of Sr:Ca recorded along the otolith transects were used to deduce the habitat changes in response to salinity variation (SW, BW and FW), following three successive steps: 1) segmentation of elemental profiles, 2) clustering and interpretation of segments, and 3) attribution of habitat types along the otolith transects.

First, elemental profiles were segmented to produce homogeneous segments that are assumed to represent non-moving phases in specific habitats (Teichert et al. 2022). For each eel, the univariate Sr:Ca time series was segmented following the Lavielle's (1999) method as implemented by Patin et al. (2020) to infer individual behavioral modes. This approach detects change points in time series to identify stationary phases, which were here interpreted as resident phases during the eel's life. The segmentation is performed through a dynamic programming algorithm that finds the changes in the mean and variance of segments using Lavielle's (2005) procedure based on locating rupture in the penalized likelihood. A minimum segment length of four measures (i.e. 60 μm length) was specified for the segmentation process to prevent over-segmentation. This length represents around three months at the beginning of the continental phase, but can reflect almost one year at the life end of oldest eels (when sampled).

In a second step, a K-means clustering method was used to determine clusters of segments with comparable Sr:Ca signatures, which were defined as the mean and SD of Sr:Ca values recorded in segments. The variance was used as descriptor of segments to account for the influence of environmental variability on otolith signature. Indeed, an individual can remain in given habitat but its Sr:Ca signature changes because of environmental fluctuation, such as hydrological season or tidal cycle in brackish water. The optimal number of clusters was selected based on the total within sum of squares. The segment signatures of the edge of otoliths were then projected in the bivariate plan (mean and SD of the Sr:Ca ratio) to aid in the interpretation of clusters. This approach assumes that the signature at the otolith edge, which is the last period of the eel's life, indicates the chemical signature of the habitat type where the eel was living at the moment it was caught. Accordingly, some inconsistencies are expected for silver eels because some individuals that lived in the upstream reaches can be caught in downstream brackish sites during their seaward migration. Nevertheless, the clusters interpretation can

also be supported by previous knowledge demonstrating the decreasing trend of Sr:Ca ratio in response to salinity gradient (e.g. Tsukamoto and Nakai 1998; Arai et al. 1997).

Finally, the habitat clusters were used to reconstruct the successive lifetime movements of eels along the otolith transects. Individuals were assigned to three main profiles depending on their growing-on habitat during the continental life-phase: freshwater, brackish or mixed profiles. Eels included in the freshwater and brackish profiles were sedentary, whereas the mixed-profile group combined individuals that moved between the two habitats at least once during their continental phase. For each silver eel, the proportion of time spent in a brackish-water habitat during the continental phase (thereafter called 'brackish life ratio') was estimated by dividing the otolith length corresponding to the brackish cluster by the otolith length of the continental phase. Although this approach assumes a uniform growth rate of the otolith during the eel's life, it is assumed to provide a proxy of time spent in different salinity environments.

Hierarchical Partitioning

To disentangle the effects of geographical and habitat conditions on silver eel traits, hierarchical partitioning analysis was used. This statistical approach is useful for distinguishing: a) the independent contribution of each predictor from its joint contribution with all other predictors (Mac Nally and Walsh 2004); and b) the predictors with strong independent effects from those that influence the response variable because of their correlations with the other predictors (Walsh et al. 2004). In such analytical approach, all possible models in a multiple regression setting are jointly considered to determine the independent contribution of each variable, while the influence of other predictors and their shared contributions were removed (Mac Nally 2000, 2002). The independent contribution was estimated by comparing goodnesses-of-fit (R^2) for all possible models involving the target variable, and reflected the part of variance not explained by the other predictors and their shared contributions.

For the 13 life-history traits, a hierarchical partitioning was conducted using the brackish lifetime ratio, the geographical coordinates (latitude and longitude in decimal degrees), and the sampling site as predictor variables. The correlation between continuous predictors did not exceed 0.42, which remains below the typical threshold of $|r| < 0.7$ used to prevent problem of multicollinearity (Dormann et al. 2013). The sampling site was included in models to accommodate any variability in life traits related to local characteristics of the catchment (e.g. catchment size, productivity, human induced alterations). Accordingly, the independent contributions of the brackish lifetime proportion and geographical coordinates reveal specific trends that are not explained by the other sources of variability were taken

into account by the site effect. Before analysis, both response and predictor variables were standardized to have a mean of 0 and a variance of 1 to improve convergence of models. Finally, the statistical significance of the independent contributions was assessed using randomization tests for hierarchical partitioning analysis (1000 permutations) based on Z-scores (Mac Nally and Walsh 2004).

All analyses were conducted using R (R Core Team 2018, version 3.5.1) supplemented with the package {tsoutliers} for time series outliers detection (López-de-Lacalle 2016), the package {segclust2d} for the segmentation of elemental profiles (Patin et al. 2019) and the package {hier.part} for the hierarchical partitioning analysis (Walsh and Mac Nally 2013).

Results

Reconstruction of lifetime profiles

A total of 99 silver eels were collected from the 11 sites, with a minimum of three eels from the River Frémur site and a maximum of 12 individuals from the rivers Corrib and Avon (Hampshire) sites (Fig. 1). The segmentation of otolith transects based on Sr:Ca values resulted in one to 11 homogenous segments (mean: 2.79 segments/otolith) depending on the individual. For some eels, only one segment was identified because the electron beam transect did not exactly cross the otolith core (i.e. marine larval phase). However, in this case, it is assumed that all the continental stages were properly described because visual inspection revealed that the distance from the larval marine stage was limited to a few microns. The segments were then classified into three clusters using the K-means method according to the mean and SD of Sr:Ca values recorded in otolith segments (Fig. 2a). Overall, the three clusters reflected the three main growing habitats used by eels during their larval and continental phases: sea, brackish and fresh waters. The projection of edge segments in the bivariate plan (mean and SD of the Sr:Ca ratio) indicated that the eels collected in freshwater sites were clearly segregated from those caught in brackish waters. Nevertheless, two eels collected in brackish water were classified within the freshwater cluster, but it is possible that these individuals migrated from the upper reaches of the catchment. Similarly, one eel caught in the River Loire's freshwater site was grouped in the brackish cluster probably because of an upstream movement during the late part of eel's life before capture. The segments included in the seawater cluster always corresponded to the first segment identified from the otolith core and they were characterized by high Sr:Ca values associated with large SD. The inclusion of SD as a discriminant parameter appeared especially relevant for segregating brackish from seawater

segments, because some edge segments of eels collected in brackish water were featured by Sr:Ca values as high as those recorded in the marine environment.

Finally, the three habitat clusters were used to reconstruct the lifetime movements of eels along the otolith transects (as defined here above): freshwater, brackish or mixed (Fig. 2b). Among the 99 silver eels, 63 were classified in the freshwater profile, 19 in the brackish profile and 17 in the mixed profile (Fig. 3). At least one mixed profile was observed for each site with the exception of the rivers Avon (Hampshire), Scheldt and Valencia. For most of the freshwater sites, the brackish phase occurred at the beginning of the continental phase, before eels settled in freshwater areas.

Analysis of life-history traits

All silver eels were females except the 10 individuals collected in the Esva site in which only males were caught (Table 2). Among these males, six were assigned to freshwater profiles and four to mixed profiles. Nevertheless, to avoid bias induced by sexual dimorphisms in life-history traits, because the number of males was insufficient to conduct a comparative analysis between sexes, they were excluded from the following investigations.

The variance partitioning of life-history traits conducted on the 89 females revealed a dominant effect of sampling site, with an independent contribution ranging from 0.16 to 0.42 (Fig. 4). The brackish life ratio, reflecting the time spent in a brackish environment, significantly influenced eight life-history traits: AMIR, ALIR, TW, K, LW, GW, TL and abundance of *A. crassus* in the swim bladder (Z-scores, all P s < 0.05; Fig. 4). These traits are essentially related to the growth rates during the continental phase and the overall condition of silver eels when initiating their migration. For example, the condition factor increased with the time spent in brackish water (Fig. 5a, Z-score, $P = 0.007$), whereas the abundance of *A. crassus* in the swim bladder dropped when eels lived in a brackish environment (Fig. 5b, Z-score, $P = 0.032$). Some traits were influenced by the combination of both geographical position and brackish life ratio. For example, the annual growth in length increased with the time spent in brackish water (Fig. 6a, Z-score, $P < 0.001$), but decreased with the latitude of sampling sites (Fig. 6b, Z-score, $P < 0.001$). Interestingly, some traits were essentially influenced by geographical position. Despite a large within-site variation, the age of silver eel and the hepato-somatic index significantly increased along with the latitude gradient independently from the life profile (Fig. 4, Fig. 7a, b, Z-scores, all P s < 0.001). Similarly, the gonado-somatic index tended to decrease along the longitude gradient (Fig. 7c, Z-score, $P < 0.001$).

Discussion

Although both the number of eels (n=99) and sampling sites (n=11) are relatively limited and the results should be confirmed by larger samplings, the present study provides a biogeographical snapshot of variability in the life-history traits of European eels across a large proportion of the species' natural distribution range. The Sr:Ca signatures obtained were found to reflect the three main aquatic environments (marine, brackish, fresh water) inhabited by eels. As reported in previous studies, the Sr:Ca ratios close to the central core of the otolith were higher than those recorded after the metamorphosis mark (Tsukamoto and Arai 2001) – this is probably due to the accumulation of sulfated glycosaminoglycans at the leptocephalus stage (Otake et al., 1994). The pelagic larval stage was thus clearly discriminated from the continental phase. Although the Sr:Ca ratios remained lower after the metamorphosis, the influence of salinity conditions was also identified on otolith transects. For eels collected in brackish water, the Sr:Ca signatures of edge segments was relatively variable (Sr:Ca ratios between 3 and 10), which suggests that eels were exposed to different salinity ranges, probably because of connectivity disparity with the marine environment. In contrast, the Sr:Ca ratios of eels collected in fresh water remained <3.

As often emphasised in the literature, a number of life-history traits of anguillid eels vary with latitude and longitude (e.g. Vøllestad 1992; Oliveira 1999; Jessop 2010; Daverat et al. 2012). In the present study, the investment in gonad development at similar weight, i.e. the gonado-somatic index GSI, tended to be higher in the most easterly sites independently from the salinity profile. Similar observations have been reported by MacNamara et al. (2016) by comparing fecundity of silver eels across different salinity zones and areas. Although this trend remains to be confirmed with larger sample sizes (of waters and eels, particularly in central Europe), such observations suggest that fecundity of eels should differ across geographical regions. In the present study, several morphometric measures were related to geographical coordinates, such as TL, TW or liver weight. In northern Europe, the HSI values of female eels were larger, indicating that their energy reserves were in general higher than those measured in eels collected in southern locations. This observation can be interpreted as a regional response to offset the higher energetic cost required for reaching the far-off spawning area. Previous studies demonstrated that the size and/or age at silvering of anguillid eels were significantly related to latitude or distance from the spawning ground (e.g. Vøllestad 1992; Jessop 2010). Similarly, the annual growth in length was higher in southern latitudes than in northern ones because of biogeographical trends in water productivity and temperature (e.g. Jessop 2010; Daverat et al. 2012). The present results support these earlier findings, as female eels are known to grow faster in southern Europe and migrate earlier, which suggests that the silvering process was more related to the local growing conditions than fish age. Accordingly, the females of European eel tend to favour a size-maximising strategy to increase their

absolute fecundity (Vøllestad 1992; Durif et al. 2020), whereas males favour a time-minimising strategy because their reproductive capacity was less affected by size (Helfman et al. 1987; Geffroy and Bardonnnet 2016).

Beyond large-scale processes, eels display a high level of plasticity in habitat use during their continental phase that usually influences the life-history traits and, ultimately, the migration success of silver eels toward their spawning areas (Vélez-Espino and Koops 2010; Marohn et al. 2013). In the present study, saline habitats and local conditions that occur in water systems were found to have a significant effect on life-history traits, which can overrule the biogeographical trends (Fig. 4). The life-history profiles revealed from otolith Sr:Ca records indicate that eels with a brackish life-history generally grow faster, reach largest sizes at age, and have a better condition than eels with a freshwater profile. Similar results have been reported for *A. anguilla* (e.g. Daverat et al. 2005; Daverat & Tomas 2006; Denis et al. 2022) and for other anguillid eels (e.g. Jessop 2010). Nevertheless, Parzanini et al. (2021) reported that the overall condition of freshwater eels in Norway were better compared to individual living in seawater. In contrast with the observations reported on American eels (Jessop et al. 2008), the age at silvering of female eels was not affected by the time spent in brackish water. Although eels grow faster in saline environments (Denis et al. 2022), they did not seem to leave them earlier, which suggests that females maximise growth when living in estuarine and brackish areas. Nevertheless, other studies highlighted that silvering occurs at younger ages in lower reaches than in the upstream parts of the catchments (e.g. Daverat et al. 2012).

Interestingly, the salinity conditions predominantly affected life-history traits associated with the fish condition (e.g. annual growth, total weight, condition factor) and sometimes overruled the biogeographical trends. Eels with brackish life-histories also had a lower abundance of the swimbladder nematode, *A. crassus*, that confirms previous records (Sauvaget et al. 2003; Palstra et al. 2007) and could contribute to a better growth and higher final fitness of eels (Marohn et al. 2013). Such statements suggest that brackish waters provide suitable conditions for eels, as previously concluded by Tsukamoto and Nakai (1998). Moreover, although the GSI was not influenced by saline habitats, the absolute weight of gonads was higher for female eels that resided in brackish areas, due to the positive relationship with fish size and weight (MacNamara and McCarthy 2012). Therefore, the fecundity-at-age is expected to be higher for females living in saltwater than those colonising freshwater areas. However, future studies should focus on investigating survival in brackish environments to support this statement, because the size-maximising strategy results from a trade-off between growth and survival.

This high variability shows the outstanding ability of eels to adjust their life-history traits to environmental conditions (Vélez-Espino and Koops 2010). Most life-history traits result from complex interactions between environmental local and large-scale parameters, so that determining the dominant drivers remains a complex task. Although sample selection in the present study was opportunistic (e.g. sampling dependant on fisheries or trap locations), and as such not designed to measure how local conditions control life-history traits, site location represented the most structuring predictor. Accordingly, most of the variations in life-history traits remained unexplained by the analysed environmental variables, which suggests that other, as yet unidentified drivers are acting at the catchment scale. Given that silver eels were caught at the onset of their breeding migration to the ocean, they might come from anywhere within the river basin. Therefore, the site-location effect hides a number of larger-scale variables, including natural drivers such as catchment size and characteristics, productivity, proportion of lentic vs lotic habitats and lakes. It also hides human-generated alterations to the environment, including fragmentation of the river continuum and resulting habitat availability, poor water quality, and pollutant loads (e.g. Robinet & Feunteun 2002 ; Acou et al. 2008 ; Belpaire et al. 2019; Bourillon et al. 2020, 2022). The effects of catchment feature clearly overrule the biogeographical trends and the influence of saline habitats on eel traits at silvering. The primary control of catchment conditions is particularly important for guiding management actions, because it supposes that local efforts for improving environmental availability and quality should produce direct outcomes on the fitness of females. Reducing the impact of human activities at the catchment scale is thus required for improving the quality of the spawning stock of European eel (Belpaire et al. 2019).

Future research should now focus on disentangling how human-generated factors and biological traits control the life-history of silver eels. Interestingly, by using a single elemental ratio, Sr:Ca, it was possible to attribute three contrasted life-histories to silver eels. Using a larger number of trace elements and isotope ratios (e.g. $^{87}\text{Sr}/^{86}\text{Sr}$ ratio) could enable a better understanding of catchment compartmentalisation as well as the extent to which eels have moved from one compartment to another as they grow prior to the silvering process. Moreover, the use of trace elements (human-origin and natural) and organic pollutants may serve as environmental tracers (Bourillon et al. 2020) but also as factors that influence the life-history traits of silver eels.

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CRedit authorship contribution statement

Nils Teichert: Methodology, Formal analysis, Visualization, Writing - original draft. **Bastien Bourillon:** Data curation, Methodology, Writing - review & editing. **Kyoko Suzuki:** Investigation, Data curation, Writing - review & editing. **Anthony Acou:** Methodology, Data curation, Validation, Writing - review & editing. **Alexandre Carpentier:** Writing - review & editing. **Mari Kuroki:** Resources, Writing - review & editing. **David Righton:** Conceptualization, Funding acquisition, Writing - review & editing. **Thomas Trancart:** Writing - review & editing. **Laure-sarah Virag:** Methodology, Investigation, Data curation. **Alan Walker:** Resources, Investigation, Writing - review & editing. **Tsuguo Otake:** Resources, Writing - review & editing. **Éric Feunteun:** Conceptualization, Supervision, Project administration, Validation, Writing - review & editing.

Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table 1: Details on the locations and main features of the nine European sites sampled for collecting silver eels in freshwater.

ID	Sampling site	Sampling gear	Latitude	Longitude	Catchment area (km ²)	Distance from the sea (km)
STO	Stockholm archipelago	Pound net	58°57'30.82"	18°02'05.09"	467	0
GUD	Gudenå	Eel trap	55°58'01.31"	09°42'16.64"	2684	148
COR	Corrib River	Coghill net	53°16'32.05"	09°03'21.71"	3167	1
WAR	Warwickshire Avon	Eel trap	52°10'00.46"	01°47'27.39"	4588	181
SCH	Scheldt River	Fyke net	51°03'58.53"	04°23'19.97"	20282	111
HAM	Hampshire Avon	Fyke net	50°44'41.56"	01°46'57.18"	2993	6
FRE	Frémur River	Eel trap	48°34'39.80"	02°06'13.10"	60	5
LOI	Loire River	Stow nets	47°22'59.80"	00°50'07.10"	116962	126
ESV	Rio Esva	Electrofishing	43°34'09.00"	06°28'11.00"	464	2
BAG	Bages-Sigean Lagoon	Fyke net	43°03'39.61"	02°59'38.06"	411	9
VAL	La Albufera de Valencia	Fyke net	39°20'59.58"	00°20'44.82"	886	3

Table 2: Summary of the life history traits of silver eels collected in the 11 water catchments in Europe. Mean, minimum and maximum of trait values are presented for males and females.

Life history traits	Males (n = 10)			Females (n = 89)		
	mean	min	max	mean	min	max
Total length (mm)	344.5	292.0	480.0	692.7	470.0	1005.0
Total weight (g)	71.4	39.5	193.3	684.2	145.8	2420.0
Liver weight (g)	0.8	0.4	2.5	9.3	1.8	29.3
Gonad weight (g)	0.4	0.1	1.7	11.7	1.0	42.0
Age estimate (year)	9	7	12	11	6	20
Condition factor (K)	0.2	0.1	0.2	0.2	0.1	0.3
Annual growth - mass (g.year ⁻¹)	7.8	4.4	16.1	70.1	9.6	269.7
Annual growth - length (mm.year ⁻¹)	38.9	30.2	49.4	72.1	24.1	144.0
Hepato-somatic index (%)	1.2	0.8	1.8	1.4	0.9	1.9
Gonado-somatic index (%)	0.5	0.2	1.0	1.7	0.7	2.3
<i>A. crassus</i> abundance (n)	1.0	0.0	5.0	5.1	0.0	31.0

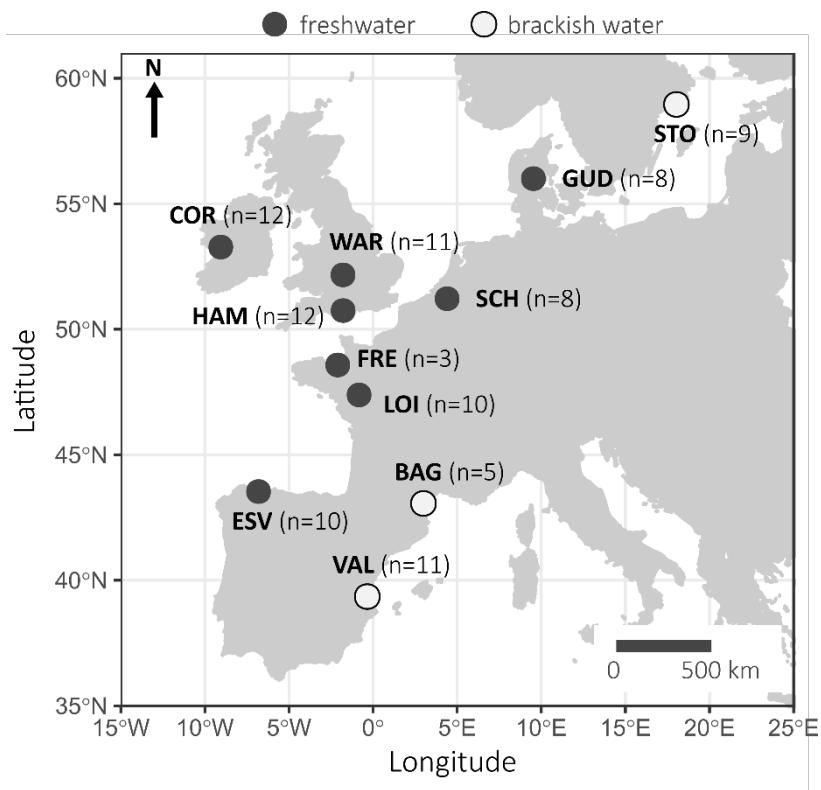


Figure 1: Locations of the nine European sites sampled for collecting silver eels in freshwater (black dots) and in brackish water (open dots). LOI : Loire River, HAM : Hampshire Avon, GUD : Gudenå, BAG: Bages-Sigean Lagoon, COR : Corrib River, ESV : Rio Esva, VAL : La Albufera de Valencia, FRE : Frémur River, STO : Stockholm archipelago, SCH : Scheldt River, WAR : Warwickshire Avon.

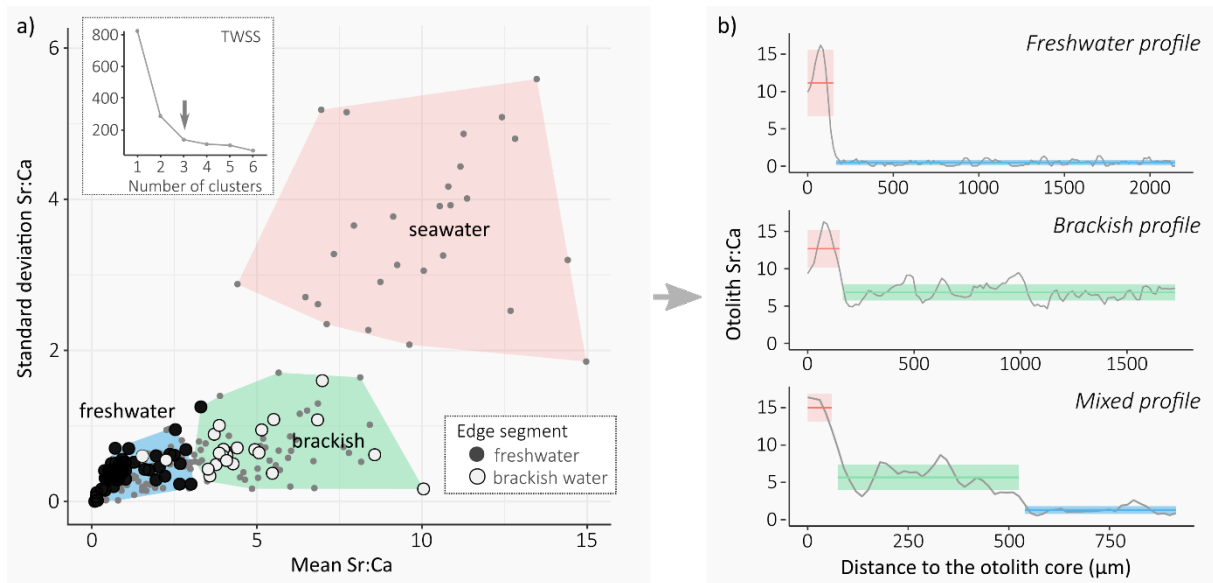


Figure 2: Clustering of the Sr:Ca segments and attribution of growth habitats along otolith transect of silver eels. a) Illustration of the three clusters determined by the K-means method according to the mean and standard deviation of Sr:Ca values in the otolith segments. Large full and open dots denote segments at the otolith edge, while other segments are symbolized by grey dots. TWSS: total within sum of squares. The arrow in the panel indicates the TWSS for three clusters. b) Examples of three profiles of life-history inferred from otolith microchemistry: freshwater, brackish and mixed profiles.

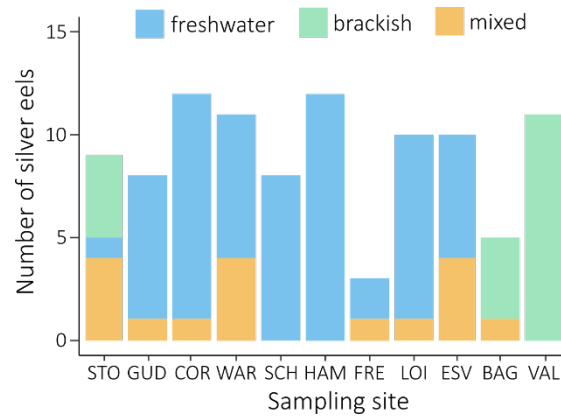


Figure 3: Life-history profiles of the 99 silver eels collected in the eleven European river sites: freshwater, brackish and mixed profiles. Sites were ordered according to their latitude positions.

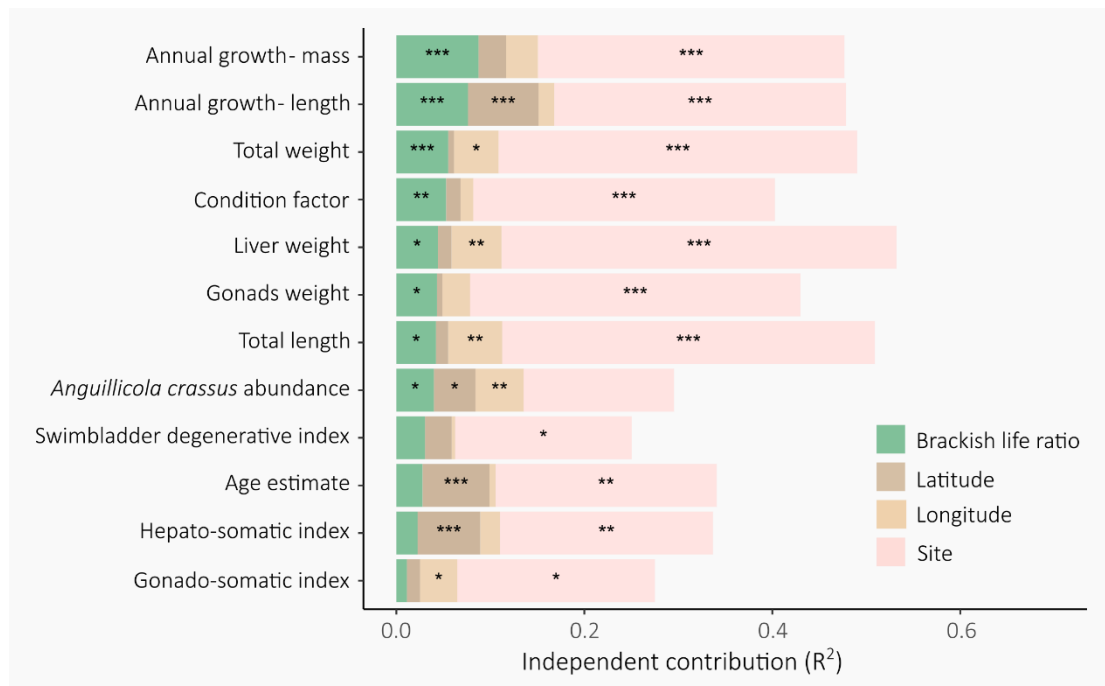


Figure 4: Variance partitioning of life-history traits according to proportion of time that silver eels spent in brackish water, river coordinates (latitude and longitude) and the sampling site. Asterisks indicate the independent contributions that significantly differ from random expectations (n=1000 permutations). The sum of independent contributions equals the goodness of fit measure of the full model minus the goodness of fit measure of the null model. * p<0.05, ** p<0.01, *** p<0.001

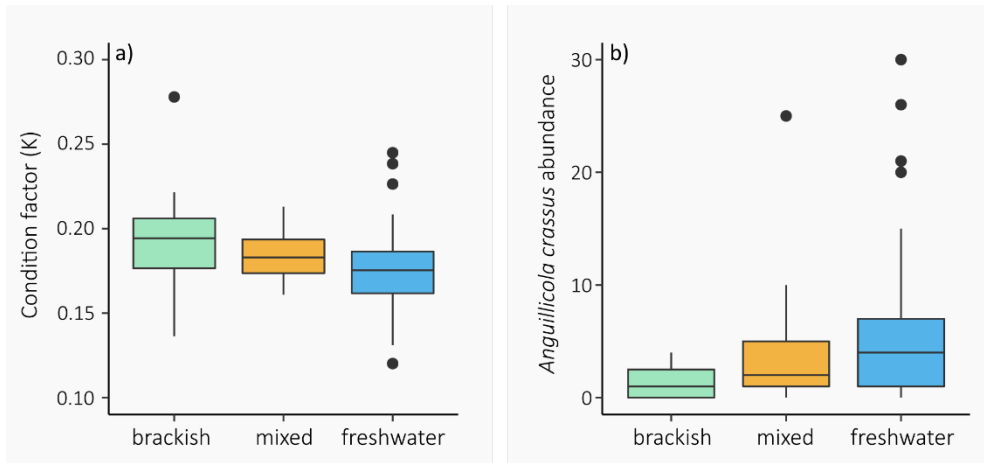


Figure 5: Examples of silver eel ecological traits influenced by the life-history profiles: a) condition factor (Fulton k coefficient) and b) number of *Anguillicola crassus* in the swimbladder.

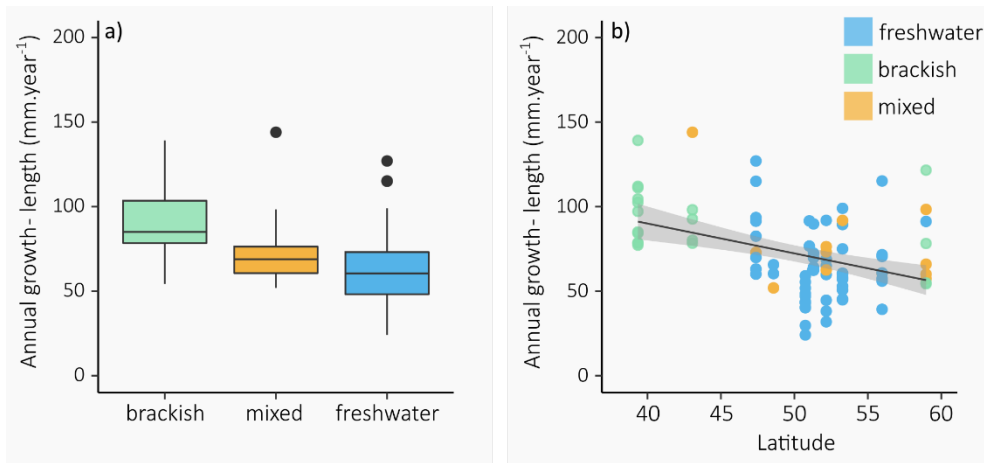


Figure 6: Annual growth of eels (mm.year⁻¹) depending on a) the life history profiles and b) the latitude of sampling sites (with linear regression, \pm standard error). Colors indicate the life history profile of individuals.

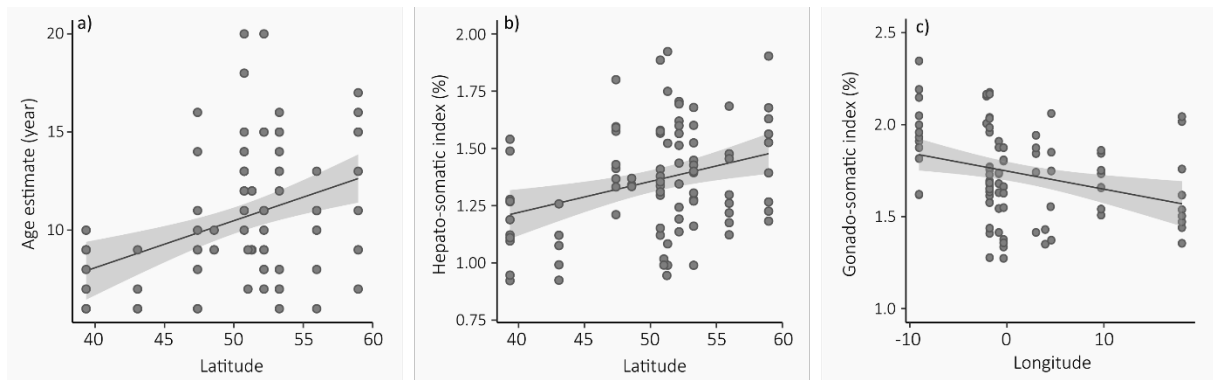


Figure 7: Examples of silver eel ecological traits influenced by the site geographical positions: a) age estimate (year), b) hepato-somatic index (HSI, %) and c) gonado-somatic index (GSI, %). Linear regressions are displayed (\pm standard error).