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A multi-approach study to reveal eel life-history traits in an obstructed catchment before dam removal

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Abstract River fragmentation is expected to impact not only movement patterns and distribution of eels within catchment, but also their life-history traits. Here, we used otolith multi-elemental signatures to reconstruct life sequences of European silver eels within an obstructed catchment, just before the removal of hydropower dams. Beyond providing an initial state, we hypothesized that otolith signatures can provide crucial information on the way eels use the watershed. Indeed, their spatial distribution is

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expected to shape life-history traits, including condition coefficient, trophic level, growth rate, or infection by metazoan parasites. While Sr:Ca and Ba:Ca ratios were complementary in tracing fish movements between freshwater and estuary, the Ba:Ca variations allowed to discriminate three freshwater sectors. The eels assigned to the midstream sector were more mobile and exhibited lower growth rates, probably in response to higher competition at the vicinity of dams. While most eels are currently produced by downstream and midstream sectors, eels assigned to upper reaches of connected tributaries generally

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M. Druet INRAE U3E "Experimental Unit on Ecology & Ecotoxicology", Rennes, France display higher richness in native parasite and higher body condition and lipid reserve, known to promote the success of migration and reproduction. In the near future, the dam removals will represent an outstanding experimental framework for evaluating impacts of catchment reconnection.

Keywords Phenotypic plasticity \cdot Life-history trait \cdot River barrier \cdot Otolith microchemistry \cdot LA-ICP-MS \cdot Metazoan parasites

Introduction

Fragmentation of aquatic systems is a major threat for biodiversity of continental ecosystems, and thus remains a priority issue for conservation and restoration actions (Nilsson et al., 2005; Reid et al., 2019). In Europe, at least 1.2 million instream barriers were recently recorded (Belletti et al., 2020), and more than 8700 additional hydropower plants are planned or under construction (WWF et al., 2019). For migratory fish, the loss of connectivity, caused by river barriers, heavily restricts access to spawning or growth habitats, and can lead to the confinement of populations in bounded sub-optimal areas (Drouineau et al., 2018; Forget et al., 2018; Verhelst et al., 2021). The decline of available habitats and the fish accumulation downstream of barriers promote over-density conditions, enhancing intra-specific competition and spread of some pathogens, which can ultimately affect growth and survival (Laffaille et al., 2003; Machut et al., 2007; Thielen et al., 2007; Costa et al., 2008). Notwithstanding the growing scientific literature, the impacts of dams on life-history traits of migratory fish remains poorly understood, despite their importance for river basin management (e.g., Pess et al., 2014; Lin and Robinson, 2019; Righton et al., 2021). This is especially important for catadromous fish because their growth within the river is determinant for their marine migration and future reproductive success (McCleave, 2001).

The European eel is a facultative catadromous species, widely distributed throughout a range of aquatic ecosystems, including lakes, rivers, brackish waters, or small coastal streams (Daverat et al., 2005; Daverat & Tomas, 2006; Tabouret et al., 2010). Once reaching the continental shelf, glass eels progressively settle in continental habitats (Feunteun et al., 2003) for three to sometimes more than 30 years 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). In addition to a strong sexual dimorphism, where migrating females are larger and older than males (Tesch, 2003), environmental conditions and thus aquatic habitats encountered during the continental stage critically influence the life-history traits (Vøllestad, 1992; Jessop, 2010; Daverat et al., 2012; Boulenger et al., 2016a, b). Such changes in life-history traits are generally driven by multifaceted mechanisms, involving density- and resource-dependent processes (Feunteun et al., 2003), which in turn can impact survival and reproductive success of eels (Mateo et al., 2017).

Silver eel body condition and life-history traits are determinant for their reproductive success, since eels have to travel more than 5000 km before breeding (Belpaire et al., 2009; Clevestam et al., 2011). For example, the size- and age-at-silvering greatly fluctuate along river catchments, with lower growth rates and older eels observed in upper reaches (Daverat et al., 2012), as opposed to eels residing in brackish waters, with earlier maturation and higher growth rates (Cairns et al., 2009). The condition of eels is also closely related to variation in their diet across different habitats, leading to changes in overall condition between marine, brackish, and freshwater habitats (Parzanini et al. 2021). Additionally, eel life-history traits are affected by contamination and parasitism, which are locally diverse (e.g., Palstra et al., 2007; Belpaire et al., 2009; Geeraerts and Belpaire, 2010; Amilhat et al., 2014). For instance, the overall body condition of silver eels is generally reduced when contaminated by metallic compounds (Maes et al., 2005) as well as when infected by parasites, such as the invasive species of monogenean infecting gills Pseudodactylogyrus sp., or the trophically transmitted swimbladder nematode Anguillicoloides crassus (Kuwahara, Niimi & Itagaki, 1974) (Palstra et al., 2007; Gérard et al., 2013). The sexual determinism is another peculiarity of eels as environmental conditions play a decisive role in the produced sex-ratio (Geffroy & Bardonnet, 2016). Indeed, low density conditions observed in headwater streams promote the production of female eels, whereas lower reaches or areas located downstream barriers tend to produce a majority of males (Feunteun et al., 2003; Costa et al., 2008).

At catchment scale, eel life-history traits such as sex determination, age-at-silvering, fecundity, lipid reserves, or health status are thus expected to be highly sensitive to disruption of river connectivity. The continental phase of eels ends with the silver stage where eels having accumulated enough resources to quit the river and migrate back to their maritime reproductive place (seaward migration). Therefore, focusing on the silver stage appears particularly relevant as the life-history traits of silver eels integrate the various conditions encountered during their continental stage. Beyond direct parameters measured on fish (e.g., size, lipid reserves), analysis of otolith can provide additional information on the past conditions encountered by eels (Campana, 1999). Otolith macrostructures can be investigated to estimate the age of eels, as well as their growth rates during the continental stage (Daverat & Tomas, 2006). Moreover, otolith elemental composition can yield powerful indications to reconstruct the movement patterns, providing there is sufficient heterogeneity in ambient water chemistry to discriminate habitats crossed by fish (Secor et al., 1995). Although a large panel of trace elements can be tracked using LA-ICP-MS (laser ablation-inductively coupled plasma mass spectrometry), not all elements provide information on the surrounding habitats and some of them are more influenced by the fish physiology than by its environment (e.g., Mg, Limburg et al., 2018). Strontium:Calcium (Sr:Ca) and Barium:Calcium (Ba:Ca) elemental ratios are known to reflect changes in ambient water while poorly influenced by physiological regulation pathways (Daverat et al., 2005; Hüssy et al., 2021). Modifications in Sr:Ca and Ba:Ca ratios along an otolith transect are thus commonly used to trace fish migration in relation to salinity ambient conditions (Tsukamoto & Nakai, 1998; Daverat et al., 2006; Tabouret et al., 2010), as well as movements along freshwater catchments (Teichert et al., 2018). Accordingly, otolith elemental signatures can provide crucial information on the way in which eels moved in and used a water catchment, and how their spatial distribution shapes their life-history traits. In complement, metazoan parasites of eels may also give information on host (e.g., diet, movements, condition), and more generally on free-living biodiversity and changes in ecosystems (e.g., Marcogliese, 2004; Hudson et al., 2006 for reviews).

Here, we provide an overview of movement patterns, metazoan parasites, and life-history traits of the European eel, *Anguilla Anguilla* (Linnaeus, 1758), within an obstructed catchment, the Sélune River (Lower-Normandy, western France), to get an initial state before the complete removal of two large hydropower dams. More precisely, otolith microchemistry signatures (i.e., Sr:Ca and Ba:Ca ratios) were used to reconstruct life sequences of migrating silver eels and investigate their movement patterns, to measure how their spatial distribution impacts the life-history traits in a fragmented catchment.

Materials and methods

Study area and fish sampling

The Sélune River flows over 91 km from the source to the English Channel in the Mont Saint-Michel Bay, Lower-Normandy, France (Fig. 1). While the watershed covers 1106 km², its upper part is disconnected (827 km²) by two large hydroelectric power dams (La Roche-qui-Boit (H=16 m) in downstream and Vezins (H=36 m) in upstream) that disrupt the ecological continuity. Accordingly, the distribution of migratory fish, including eels, is currently limited to lower reaches of the Sélune River (279 km²), from the estuary to the La Roche-qui-Boit dam (Forget et al., 2018). Nevertheless, the three tributaries located downstream the dam (i.e., Moulinet, Oir, and Beuvron Rivers) are freely accessible and currently colonized by eels till their upper reaches. Recently, environmental authorities and local operators decided to remove the two dams to restore continuity in compliance with the EU Water Framework Directive. Upper reaches of the Sélune River will thus be reconnected and freely accessible to migratory fish by 2022 (Fig. 1). Although the first dam located upstream of the Sélune (i.e., La Roche-qui-Boit) was teared down in 2019–2020, the removal of the second dam, which constitutes the main barrier, will only be effective in late 2022.

To provide an overview of the life-history traits of eels produced by the whole Sélune catchment, migrating silver stage eels were collected at a fishery



Fig. 1 Location of the six sampling sites within the Sélune catchment, Western Europe, France. The green area highlights the river reaches currently accessible for eels, whereas the red indicates the inaccessible ones, obstructed by the dams (*RQB*)

specifically set up for catching migratory eels (site 1), located downstream of the Sélune River and its main tributaries (Fig. 1). This site is located in a freshwater estuary but is subjected to tidal influence during spring tides. Silver eels were caught at night during two migration seasons (autumn 2019 and autumn 2020) while upper reaches of the Sélune River were still inaccessible for them. A stow net (L=20 m,W=6 m, H=3 m) was used to sample eels during their seaward migration (Durif et al., 2008). In order to optimize sampling efforts and ensure high capture rates, the net was placed in the main stem of the river when night high discharge conditions were met, since major migration runs mostly occur during these flows (Teichert et al., 2020). Silver stage of eels was visually assessed following previously defined criteria (Acou et al., 2005), such as the color of the back and

Roche-qui-Boit, *Vez* Vezins). St 1 to St 6 indicate the different sites where yellow eels were caught, while silver eels were collected at St 1

belly, the presence of a well-defined lateral line, and a high Pankhurst ocular index (OI > 6.5) (Pankhurst, 1982). A total of 35 (Total Length, min-max TL: 370—862 mm) and 39 silver eels (TL: 321–946 mm) were collected during first (2019) and second migration seasons (2020), respectively.

Additionally, changes in otolith elemental signatures along the Sélune catchment were also assessed in yellow stage eels, collected in six freshwater locations distributed on the Sélune catchment (Fig. 1). For each site, 5 yellow eels (N=30; TL: 199–536 mm) were caught by electrofishing in September 2019. It was assumed that yellow eels were residents (Laffaille et al., 2005), so that otolith signature was used as spatial references to describe the chemical signature of the sites where they were caught (see thereafter for method details).

All collected eels (yellow and silver stage) were anesthetized with a Benzocaine solution (15 mg. L^{-1}) before being euthanized with an overdosed solution of Benzocaine (400 mg. L^{-1}), and then frozen (-20 °C) until dissections at the laboratory. This study was approved by the Cuvier Ethic Committee (project n°68–106), the local representative of the French national ethic committee for animal in research.

Description of life-history traits

For each silver eel, a range of life-history traits were investigated. These life-history traits can be pooled in three main categories according to (1) the river life conditions encountered by eels (i.e., trophic level, growth, age-at-silvering), (2) the genitor quality when migrating back to their spawning ground (i.e., size-atsilvering, condition coefficient, lipid reserve, gonads maturation), and (3) the metazoan parasite community associated with eels (Tables 1 and 2).

Eel biometry

Eels were measured (Total Length, TL, mm) and weighed (Total Weight, TW, g) to calculate the Fulton (1904) condition coefficient (K) according to the following formula: $10^5 \times TW/TL^3$. Individuals were then dissected to determine their sex through macroscopic observations of the gonads (Colombo et al., 1984), and the gonads (Gonad Weight, GW, g) and the liver (Liver Weight, LW, g) were weighted. The gonadosomatic (GSI, %) and hepatosomatic (HSI, %) indices were calculated as the ratio of organ weight to body weight: GSI=GW/TW×100, and HSI=LW/ TW×100, respectively. GSI provides insights on the level of gonad maturation and individual reproductive investment, whereas HSI is a proxy of lipid reserves, which are involved in gonad maturation and sea migration.

Muscle stable isotope

For each eel, one muscle tissue sample was dissected just below the dorsal fin to determine the ratio of carbon relative to nitrogen (C:N ratio). This ratio was then used as a proxy of lipid content stored in silver eels' muscle (McConnaughey & McRoy, 1979; Post et al., 2007). Nitrogen isotopic signature was used to estimate eel trophic level and was expressed in the delta unit notation as deviation from standard

Table 1 Summary of life- history traits and parasite	Life-history traits	Females	Males	<i>p</i> -value				
The means \pm standard error are presented along with the significance of deviance reduction tests investigating differences between sexes	River life condition							
	Trophic level	11.93 ± 0.29	13.14 ± 0.30	0.008				
	Growth (mm year $^{-1}$)	36.23 ± 1.72	37.78 ± 1.77	0.534				
	Age (year)	15.32 ± 0.76	9.10 ± 0.40	< 0.001				
	Spawning migration							
	Size (mm)	586.18 ± 19.71	380.20 ± 5.60	< 0.001				
	Condition-K	0.19 ± 0.00	0.18 ± 0.00	0.028				
	Lipids-C:N	7.65 ± 0.19	7.48 ± 0.24	0.613				
	Lipids-HSI (%)	1.64 ± 0.04	1.52 ± 0.04	0.046				
	Gonads-GSI (%)	1.80 ± 0.07	0.39 ± 0.06	< 0.001				
	Spawning migration							
	Total prevalence (%)	70.59 ± 7.81	90.00 ± 4.74	0.032				
	Total abundance	8.71 ± 2.05	8.05 ± 2.04	0.331				
	Species richness	1.35 ± 0.21	1.50 ± 0.14	0.598				
	Anguillicoloides crassus (prev)	58.82 ± 8.44	82.50 ± 6.01	0.024				
	Anguillicoloides crassus (abd)	3.44 ± 0.72	3.28 ± 0.46	0.697				
	Pseudodactylogyrus sp. (prev)	29.41 ± 7.81	40.00 ± 7.75	0.34				
<i>abd</i> abundance, <i>prev</i> prevalence (%)	Pseudodactylogyrus sp. (abd)	1.68 ± 0.75	2.15 ± 0.92	0.142				
	Acanthocephalus spp.(prev)	14.71 ± 6.07	12.50 ± 5.23	0.782				
Significant effects ($p < 0.05$) are indicated in bold	Acanthocephalus spp. (abd)	2.88 ± 1.66	0.28 ± 0.13	< 0.001				

Table 2 Community of the ten metazoan parasite taxa found in 74 European silver eels collected in the Sélune catchment

Parasite taxa	Habitat	Sector	Diet	Prevalence	Abundance	Infection pathway
MYXOZOA						
Myxidium giardii (Cepede, 1906)	G	DMU	-	9.46 ± 3.40	0.96 ± 0.53	Ingestion of spores released by oligochaete HI
MONOGENA						
Pseudodactylogyrus sp. Gusev, 1965	G	EDMU	Surface browser	35.14 ± 5.55	1.93 ± 0.60	Active attachment on gill lamellae
CESTODA						
Bothriocephalus claviceps (Goeze, 1782)	Ι	М	Osmotrophic	1.35 ± 1.34	0.01 ± 0.03	HI or HP ingestion (copepods, fish)
NEMATODA						
Anguillicoloides crassus (Kuwahara et al., 1974)	S	DMU	Hematophagous	71.62 ± 5.24	3.35 ± 0.41	HI or HP ingestion (copepods, ostracods, gastropods, fish)
Paraquimperia tenerrima (Linstow, 1878)	Ι	DU	Chyle feeder	4.05 ± 2.29	0.15 ± 0.09	HI ingestion (unknown)
Raphidascaris acus (Bloch, 1779)	Ι	D	Chyle feeder	1.35 ± 1.34	0.01 ± 0.01	HI or HP ingestion (<i>Gammarus</i> , fish)
Spinitectus inermis (Zeder, 1800)	Ι	U	Chyle feeder	2.70 ± 1.89	0.46 ± 0.45	HI or HP ingestion (mayflies, fish)
ACANTHOCEPHALA						
Acanthocephalus anguillae (Müller, 1780)	Ι	MU	Osmotrophic	2.70 ± 1.89	0.07 ± 0.05	HI or HP ingestion (Asellus, fish)
Acanthocephalus clavula Dujardin, 1845	Ι	DMU	Osmotrophic	9.46 ± 3.40	0.89 ± 0.50	HI or HP ingestion (Asellus, fish)
Acanthocephalus lucii (Müller, 1776)	Ι	MU	Osmotrophic	5.41 ± 2.63	0.51 ± 0.33	HI or HP ingestion (Asellus, fish)

Species are listed along with their microhabitat (G Gills, I Intestine, S Swimbladder), main sector (E estuary, D downstream, M midstream, U upstream), diet prevalence ($\% \pm$ se), abundance (mean abundance \pm se), and infection pathway (HI intermediate host, HP: paratenic host) (Kennedy et al., 1992; Benajiba & Marques, 1993; Moravec & Scholz, 2015)

(atmospheric nitrogen (N)) following the formula: $\delta^{15}N = ((\text{Rsample/Rstandard}) - 1) \times 1000)$, where R is the ratio ${}^{15}\text{N}:{}^{14}\text{N}$ in the sample and in the standard. For each muscle sample, nitrogen and carbon total quantities, and the ${}^{15}\text{N}:{}^{14}\text{N}$ ratios were measured by continuous flow isotope mass spectrometry (CF-IRMS) using a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Thermo Scientific Flash 2000 elemental analyzer. Analytical precision (standard deviation) was $< \pm 0.15\%$ of reference material.

Age estimate

Sagittal otoliths of eels were extracted and embedded in epoxy resin (Araldite 2020, Huntsman Corporation), then grounded along the longitudinal plane and polished until the primordium was reached (Acou et al., 2013). The age-at-silvering of eels (AGE, y) was estimated from a visual count of annuli (rings) on the otolith section, beginning from the first growth check outside the elver mark, which reflects the beginning of continental phase (Daverat & Tomas, 2006). Readings were conducted independently by two operators to avoid bias, and when age estimates differed, a simultaneous reading was performed to define a consensual age estimate. The age reading was carried out along the longest transect of otolith, between the nucleus and the outer edge. The distance separating each annuli was then measured (µm) on a micrograph picture using the ImageJ software v. 1.53e (Rueden et al., 2017). Finally, the mean annual growth rate (Gr, $mm.y^{-1}$) of eel during their continental phase was calculated following the formula: Gr = (TL-65)/AGE, where 65 mm is the mean size at recruitment (Durif et al. 2020).

Metazoan parasites

The presence of metazoan parasites was meticulously checked in each silver eel to determine the parasite constraint and provides information on host and environment (Gérard et al., 2013). The gills, the heart, the digestive tract, the liver, and the swimbladder were dissected using a binocular stereomicroscope. All the metazoan parasites were counted per organ and per fish and morphologically identified based on Fomena and Bouix (1997) for Myxozoa, Ogawa and Egusa (1976) for Monogena, Khalil et al. (1994) for Cestoda, Golvan (1969) and Brown et al. (1986) for Acanthocephala, and Moravec (1994) for Nematoda. The parasitological parameters used to describe the parasite community were the prevalence (i.e., number of fish infected with a particular taxon / number of fish examined), the taxa richness (i.e., number of parasite taxa infecting eels), and the abundance (i.e., number of individuals of a particular parasite taxon in/on a single fish) (Bush et al., 1997).

Analysis of otolith microchemistry

The elemental composition of otoliths (Sr and Ba) was quantified using femtosecond laser ablation (LA, IR 1030 nm; Alfamet-Novalase, France) coupled to an ICP-MS (DRCII; Perkin Elmer, Shelton). The ablation was performed with a raster scanning strategy along the longest transect of each otolith with a laser beam of 15 µm of diameter, at a frequency of 20 Hz, moving forward at 5 μ m s⁻¹ as previously described (Tabouret et al., 2011). The resulting elementary profile consists of successive measures taken every 5 µm along the otolith. The external calibration was done by using the international reference materials NIST614, NIST612, and NIST610 (National Institute of Standards and Technology, USA). Calcium was used as an internal standard to account for variations in the amount of ablation material and laser energy in ablation efficiency. Analytical precision was measured using the otolith certified reference materials: fish NIES22 (National Institute for Environmental Studies, Japan; Yoshinaga, Nakama, Morita, & Edmonds, 2000) and FEBS-1 (National Research Council Canada, Canada). Elementary compositions were expressed in elementary mass ratios, so that lifetime movements of eel were inferred from Sr:Ca and Ba:Ca elemental ratios.

Reconstruction of life sequences

Habitat changes during the eel continental life were inferred from otolith elementary profiles by considering only elemental values recorded outside the glass eel mark (Daverat & Tomas, 2006). Firstly, bivariate time series based on Sr:Ca and Ba:Ca ratios were screened to identify change points, and then partitioned to produce segments (Lavielle, 1999; Patin et al., 2020), each homogeneous in their elemental concentration, and therefore assumed to represent sedentary phases in distinct habitats. A minimum segment length of four measurements (i.e., length of 20 µm on the otolith) has been specified for the segmentation process to avoid over-segmentation. A segment of 20 µm of the otolith approximately represents one month of an eel life at the beginning of its continental phase but may reflect nearly three months of its life when older due to slower growth.

Then, means of elemental ratios were calculated for each otolith segment, and a k-means clustering method was applied to determine clusters of segments with similar Sr:Ca and Ba:Ca signatures, representing eel residing in the same environment. By contrast, variations in Sr:Ca and Ba:Ca signatures correspond to eel that moved from one habitat to a distinct one. The optimal number of clusters was selected based on the total within sum of squares (TWSS). The ecological interpretation of clusters was supported by the projection of marginal signatures (recorded on terminal otolith segments) of resident eels (yellow stage) on the bivariate plan. This approach assumes that the signature at the otolith edge, which is the last period of a fish life, indicates the chemical signature of the last living habitat before being caught. To improve the interpretation of elemental signatures, relationships between marginal signatures of resident eels and the distance from the river mouth were investigated using Pearson correlation tests. Significant relationships suggest gradual changes in elemental ratios along the Sélune catchment. Based on these indications and the knowledge on Sr:Ca and Ba:Ca responses to salinity variations (e.g., Tsukamoto and Nakai, 1998; Daverat et al., 2005; Tabouret et al., 2010), elemental signatures of clusters were used to assign the otolith segments to broad sectors of the Sélune catchment.

Finally, eel successions of movements during their continental phase were defined from sector-assigned segments. Age-related changes in eel habitat were investigated through a linear interpolation of annual rings (i.e., otolith macrostructures) along the ablation transect to infer time series to the eel life sequence (Fablet et al., 2007). As we focused on the continental phase, the elver mark was defined as the origin of time series, so that eel age thereafter refers to eel 'continental age'.

Life transitions and spatial changes in life-history traits

Life sequences were used to determine the sector where each eel spent the maximum of time (thereafter referred as 'main resident sector') and the number of different sectors crossed during the continental phase, which was thereafter used as an indicator of eel mobility. A transition matrix, detailing when transitions from one sector to another occurred, was calculated to estimate the proportion of moving eels for each continental age-class. Proportions of both transitions between sectors, and directional movements toward upstream or downstream were calculated to summarize the overall movement patterns of eels in the Sélune catchment.

Spatial changes of life-history traits were quantified using linear mixed models (LMMs). LMMs were independently adjusted for 14 individual traits as response variables (i.e., mobility, trophic level, continental growth, age-at-silvering, size-at-silvering, K, C:N, RHS, RGS, parasite taxa richness, total parasite abundance, Anguillicoloides crassus, Pseudodactylogyrus sp. and Acanthocephalus spp. abundances), while the main residence sector inferred from otolith microchemistry was used as explanatory categorical variable. Models were adjusted using an identity link function and a Gaussian error distribution. The abundance variables were log(x+1)-transformed to meet normality assumptions. Response variables were standardized to have a mean of 0 and a variance of 1 to obtain standardized regression coefficients, which were interpreted as effect sizes. This approach allows to directly compare model outcomes as they are expressed in a similar range of magnitude. Eel sex and sampling season were included as random effects to account, respectively, for the influence of sexual dimorphism and the two-year sampling procedure on the variable response. Accordingly, effect sizes reveal consensual trends among sex and seasons when the other sources of variability are considered by a random intercept. The statistical significance of main residence sector in models was assessed based on deviance reduction tests (*F*-tests). The direction and magnitude of spatial changes in life-history traits were then assessed from the sign and value of the effect sizes. Finally, changes in the prevalence of parasites (i.e., total parasite prevalence, *A. crassus, Pseudodactylogyrus* sp. and *Acanthocephalus* spp. prevalences) were investigated using binomial Generalized Linear Mixed Models (GLMMs). Eel sex and sampling season were included as random effects and the significance of main residence sector was assessed based on deviance reduction tests (*Chi*-square tests).

All statistical analyses were performed in the R environment v. 4.0.5 (R Core Team, 2018), using the base package for standard analysis (i.e., mean comparisons and proportion tests) and "segclust2d" for elemental profile segmentation (Patin et al., 2019). LMMs and GLMMs were fitted using the "Ime4" package (Bates et al., 2014) and parameters standardized with the "effectsize" package (Ben-Shachar et al., 2020). The statistical significance of changes in the proportions between groups (i.e., sex-ratio, ageclass) was tested using either binomial or Chi-square tests. Differences in life-history traits between males and females were tested using Generalized Linear Models (GLMs). GLMs were adjusted using an identity link function and a Gaussian error distribution for the life-history traits, while binomial or poisson distributions were used for, respectively, testing changes in prevalence and abundance of metazoan parasites. The statistical significance of sex in models was then assessed based on deviance reduction tests (Chisquare tests).

Results

Life-history traits and metazoan parasites

For the 74 silver eels collected in autumn 2019 (n=35) and 2020 (n=39), the sex-ratio did not significantly differ from 0.5 (54% males; binomial test, n=74, P=0.561). As expected, the age- and size-at-silvering were higher for females than males, as well as the body condition, the liver lipid reserves and the gonadosomatic index (Table 1). Contrastingly, male trophic levels were significantly higher than female ones. The mean annual growth over the continental

phase and the lipid content in muscle did not significantly differ between sexes (Table 1).

In total, $81.08 \pm 4.55\%$ of the 74 silver eels were infected by one to four metazoan parasite species among the ten identified (i.e., nine helminths and one myxozoan, Table 2), with an average richness of 1.43 ± 0.12 parasite species per eel and a mean abundance of 8.35 ± 1.43 parasites per eel (range: 0–69). Except the monogenean Pseudodactylogyrus sp., all the parasite species found were heteroxenous, involving various invertebrate and fish species as intermediate and paratenic hosts (Table 2). The total prevalence was significantly higher in males than in females, even if species richness and total abundance of metazoan parasites were unaffected by sex (Table 1). Three taxa dominated the parasite community whatever the sex (in decreasing order): the non-native swimbladder Anguillicoloides crassus, the non-native gill Pseudodactylogyrus sp., and the native intestinal Acanthocephalus spp. (Table 2), but the prevalence of A. crassus and the abundance of Acanthocephalus spp. significantly differed between sexes (Table 1).

Reconstruction of life sequences

The number of segments identified from otolith elementary profiles for silver eels (n=74) and resident eels (n=30) ranged from 2 to 8 depending on individuals (on average 3.6 ± 0.11 segments). In resident eels, the Ba:Ca signatures recorded in the marginal segments were significantly correlated with the distance to the sea (Fig. 2a; n=6, r=0.98, t=11.8, P < 0.001), which highlights the relevance of the Ba:Ca ratio to indicate habitat changes along the downstream-upstream gradient. On the contrary, Sr:Ca signatures did not vary significantly with the distance to the sea (Fig. 2b; n=6, r=0.40, t=-0.88, P=0.42), but ratio values typically fit with range recorded for eels living in freshwater environment (Sr:Ca signatures between 1.05×10^{-3} and 2.74×10^{-3} for resident eels; Daverat et al., 2005; Tabouret et al., 2010).

The k-means method applied to otolith segments of silver eels resulted in four clusters with distinct ranges in Sr:Ca and Ba:Ca signatures (Fig. 3a). One cluster contrasted from others because of its high Sr:Ca signatures (Sr:Ca > 3.15×10^{-3}), hereafter assigned to the 'estuary sector' because such signatures are similar to the ones retrieved in eels involving in brackish water. For the three other clusters, the observed ranges of Sr:Ca ratio were comparable to freshwater signatures $(0.97 \times 10^{-3} < \text{Sr:Ca})$ $< 3.21 \times 10^{-3}$), but clusters differed in their Ba:Ca signatures. The first freshwater cluster showed the lowest Ba:Ca ratios (Ba:Ca $< 2.12 \times 10^{-5}$) and gathered the resident eel signatures from sites 1, 4, and 5, located less than 15 km from the river mouth, hereafter assigned to the 'downstream sector'. The second freshwater cluster featured intermediate Ba:Ca ratios $(2.14 \times 10^{-5} < Ba:Ca < 3.72 \times 10^{-5})$ ⁵) and included sites 2 and 3 located downstream from the first dam, between 15 and 23 km from the river mouth, hereafter assigned to the 'midstream sector'. The third freshwater cluster showed



Sr:Ca -Marginal segment (x10⁻³) 2.0 (b) st 5 1.8 st 1 st 3 1.6 st 4 st 2 st 6 1.4 30 10 20 40 Distance from the sea (km)

Fig. 2 Relationships between the distance from the sea and otolith signatures recorded in the marginal segments of resident eels. The mean elemental ratios of Sr:Ca (a) and Ba:Ca





Fig. 3 Reconstruction of silver eel life sequences based on otolith elemental signatures. a Clustering of otolith segments based on Sr:Ca and Ba:Ca elemental signatures of silver eels collected in the Sélune catchment. The optimal number of clusters was defined from the Total Within Sum of Squares (TWSS). The full yellow dots denote the otolith signatures recorded in the marginal segments of resident yellow eels

(mean \pm se). **b** Individual life sequences of silver eels inferred from the otolith elemental signatures (n=74). Eels were grouped according to the main resident sector during their continental phase: upstream-dominated (n=11), midstream-dominated (n=27), downstream-dominated (n=34), and estuary-dominated (n=2) life sequences

the highest Ba:Ca ratios $(Ba:Ca > 3.76 \times 10^{-5})$ and included the site 6, which was located over 38 km from the river mouth, hereafter assigned to the 'upstream sector'. As the upper reaches of the Sélune River were inaccessible for eels, this sector only refers to upstream areas of the connected tributaries with confluences located downstream of the Sélune dams (i.e., the Beuvron and the Oir). Finally, the assigned segments were then used to reconstruct life sequences of the 74 silver eels and to estimate the amount of time spent in each sector of the Sélune catchment (Fig. 3b).

Residence sectors and life transitions

Over the continental phase, 34 eels predominantly resided in the downstream sector (46%), 27 in the midstream sector (36%), 11 in the upstream sector (15%), and 2 in the estuary sector (3%). Once in the catchment, the number of sectors crossed by eels ranged between 1 and 5 depending on individuals. Whereas 24.3% of individuals were briefly assigned to the estuary sector once entering the catchment, the others were directly assigned to

the downstream (27.0%), midstream (39.2%) or upstream (9.5%) sectors (Fig. 3b).

The proportion of eels that moved between the different catchment sectors were over 20% for the three first continental age-classes (Fig. 4a), then it significantly dropped to 5-10% for the older ageclasses ($X^2 = 65.8$, df = 14, P < 0.001). This mobility pattern was essentially shaped by a significant decrease in the proportion of movements toward upstream with the age of eels ($X^2 = 84.5$, df = 14, P < 0.001), whereas the proportion of movements toward downstream remained unchanged with age $(X^2 = 14.4, df = 14, P = 0.41)$. These results suggest that eels actively colonized and exploited the catchment during the first three years of their continental life, then a more resident behavior was adopted with punctual returns downstream. Indeed, 55% of eels reaching the upstream sector and 76.9% of eels reaching the midstream sector ultimately returned further downstream for the rest of their continental life. Interestingly, almost 40% of the transitional movements reported for the 74 eels involved individuals leaving the midstream sector to the downstream sector (Fig. 4b).

Spatial changes in life-history traits

The main residence sector of eels in the Sélune catchment was not significantly related to the sex-ratio of eels (i.e., 50, 53, 55, and 54% of males in estuary, down-, mid-, and up-streams sectors, respectively; $X^2 = 0.05$, df = 3, P = 0.99), but it significantly shaped some life-history traits related to the river life condition, the spawning migration, and the metazoan parasite community (Fig. 5, Table 3). The two eels that mainly resided in estuaries exhibited a sedentary lifestyle associated with the highest levels of trophic status and somatic growth. However, their body condition and lipid storage were lower than those of freshwater eels. Eels from the estuarine sector were also poorly infected with only four *Pseudodactylogyrus* sp. parasites retrieved on the gills of one eel.

Individuals from the downstream sector showed the lowest trophic level in comparison with the other freshwater sectors (Fig. 5; Table 3), which suggests a low proportion of fish in the eel diet. The highest degree of mobility was observed for the eels predominantly residing in the midstream sector and was associated with the lowest grow rates. Although differences in age-at-silvering was not significant between sectors, eels of the midstream sector tended to be older than those residing in the other sectors (Fig. 5). Overall, eels



Fig. 4 a Annual proportion of eels moving between sectors of the Sélune catchment depending on their continental ageclass (i.e., from recruitment in the catchment). b Overall pro-

portion of transitions between sectors of the Sélune catchment recorded for the 74 silver eels collected in 2019 and 2020. The direction of movement is detailed





Fig. 5 Overview of the influence of the main sectors of the Sélune catchment on river life condition, genitor quality for the spawning migration, and metazoan parasites of silver eels. The

Significant effect of the main resident sector

standardized marginal means are effect sizes that reflect intensity of deviations for each sector from the population mean. Statistical significance of tests is detailed in Table 3

living upstream displayed highest values of life-history traits related to the migration and reproduction success (Fig. 5; Table 3), whereas eel body condition was lower in downstream, as well as muscle lipid contents in both downstream and midstream sectors. On the contrary, the size-at-silvering and the GSI did not differ significantly between the residence sectors (Table 3).

The mean species richness and abundance of eel parasites significantly changed along the Sélune catchment (Fig. 5; Table 3), with the highest values recorded for eels living in the upstream sector. Interestingly, the eel parasitic community observed in the upstream sector differed from the rest of the catchment, mainly because of both higher abundance and prevalence of *Acanthocephalus* spp. (Table 3). By contrast, no significant differences occurred for the two non-native species except the abundance of *Anguillicoloides crassus* lower in upstream compared to the other freshwater sectors (Table 3).

Discussion

Lifetime movements in the Sélune catchment

In this study, eel life sequences were reconstructed based on the segmentation of otolith elementary profiles following the method proposed by Patin et al. (2020). While this method was initially developed to identify transition phases in record time series from telemetry studies, our results demonstrate that it can successfully integrate otolith microchemistry records. Compared to classic visual interpretations of otolith elemental composition, taking into account the temporal dimension of otolith not only provides new insights on but also allows non-subjective and quantitative reconstruction of fish movements (Fablet et al., 2007; Vignon, 2015). Fluctuations of elemental ratios (Sr:Ca and Ba:Ca) in otoliths have been previously used to trace eel migration between marine, estuarine,

Life-history traits	Catchment sectors					
	Estuary	Downstream	Midstream	Upstream		
River life condition						
Mobility (nb sectors)	1.50 ± 0.50	2.12 ± 0.18	2.56 ± 0.19	2.18 ± 0.33	< 0.001	
Trophic level	13.96 ± 0.36	11.80 ± 0.28	13.64 ± 0.34	12.94 ± 0.65	< 0.001	
Growth (mm year $^{-1}$)	39.25 ± 3.53	38.51 ± 2.11	34.39 ± 1.82	38.75 ± 2.33	< 0.001	
Age (year)	11.50 ± 2.50	11.53 ± 0.71	12.81 ± 1.04	11.27 ± 1.43	0.182	
Spawning migration						
Size (mm)	502.5 ± 57.5	471.71 ± 19.68	465.81 ± 22.32	501.64 ± 64.79	0.15	
Condition-K	0.15 ± 0.00	0.18 ± 0.00	0.19 ± 0.00	0.19 ± 0.01	< 0.001	
Lipids-C:N	6.56 ± 1.16	7.49 ± 0.24	7.36 ± 0.24	8.57 ± 0.38	< 0.001	
Lipids-HSI (%)	1.28 ± 0.13	1.59 ± 0.04	1.59 ± 0.05	1.57 ± 0.08	< 0.001	
Gonads-GSI (%)	0.90 ± 0.75	1.05 ± 0.14	1.02 ± 0.15	1.09 ± 0.23	0.426	
Metazoan parasites						
Total prevalence (%)	50.00 ± 35.36	76.47 ± 7.27	81.48 ± 7.48	100.00 ± 0.00	0.09	
Total abundance	2.00 ± 2.00	8.18 ± 1.83	5.44 ± 1.00	17.18 ± 7.11	0.025	
Species richness	0.50 ± 0.50	1.29 ± 0.18	1.41 ± 0.18	2.09 ± 0.37	0.002	
Anguillicoloides crassus (prev)	0	70.59 ± 7.81	77.78 ± 8.00	72.73 ± 13.43	0.220	
Anguillicoloides crassus (abd)	0	3.85 ± 0.71	3.26 ± 0.59	2.64 ± 0.77	0.033	
Pseudodactylogyrus sp. (prev)	50.00 ± 35.36	35.29 ± 8.20	33.33 ± 9.07	36.36 ± 14.50	0.162	
Pseudodactylogyrus sp. (abd)	2.00 ± 2.00	2.56 ± 1.22	1.74 ± 0.57	0.45 ± 0.21	0.297	
Acanthocephalus spp. (prev)	0	2.94 ± 2.90	18.52 ± 7.48	36.36 ± 14.50	< 0.001	
Acanthocephalus spp. (abd)	0	0.47 ± 0.47	0.33 ± 0.17	7.64 ± 4.76	0.042	

Table 3 Changes in life-history traits and parasite descriptors of silver eels (n=74) depending on the main sectors of the Sélune catchment

The mean \pm standard error are presented, along with the significance of mixed models investigating differences between catchment sectors

abd abundance, prev prevalence (%)

Significant effects (p < 0.05) are indicated in bold

and freshwater habitats (e.g., Tsukamoto and Nakai, 1998; Daverat et al., 2006; Tabouret et al., 2010). While Sr:Ca and Ba:Ca ratios simultaneously changes in eel otoliths along the salinity gradient (e.g., Tabouret et al. 2010), our results also demonstrated a longitudinal gradient of the Ba:Ca ratio in the Sélune catchment, which can be used to infer habitat shifts within the freshwater environment. Such variation of Ba:Ca ratios in fish otolith can be related to different ambient water chemistry influenced by the substratum composition and physical erosion process (Elsdon and Gillanders, 2005).

Although our clustering approach was conducted with no a priori knowledge regarding salinity or geographical gradients, the threshold value identified for segregating freshwater from estuarine habitats (Sr:Ca > 3.15×10^{-3}) is congruent with those reported in other water catchments (e.g., Daverat et al., 2005; Tabouret et al., 2010). Moreover, otolith marginal signatures of resident eels reveal a decreasing gradient of Ba:Ca ratios along the longitudinal profile of the Sélune catchment (i.e., Ba:Ca signatures ranged between 1×10^{-5} and 7×10^{-5}). Even though such gradual changes do not allow strict assignations to specific tributaries (Teichert et al., 2018), the clustering method we used properly segregates three broad freshwater sectors. Our method, based on a higher spatial resolution than a classic discrimination of saline areas, allows to both reconstruct consistent life sequences along the upstream-downstream gradient, and assesses the contribution of the main catchment sectors. In the Sélune catchment, silver eel production is essentially supported by the downstream (46%) and midstream (36%) sectors, whereas the upper connected reaches appear less productive (15%). This result underlines the impact of connectivity loss, as only the upstream areas of the two main tributaries with confluences located downstream of the Sélune dams (i.e., the Beuvron and the Oir) are currently colonized by eels.

Our results also clearly emphasize the temporal dynamic of eel catchment colonization, as featured by an active upstream migration during the first three years following the glass eel stage. Similar observations have been reported in the Gironde watershed (France), where the number of transitions between different habitats decreasing as eels aged (Fablet et al., 2007). After the settlement phase, eels of the Sélune catchment become more sedentary and upstream movements are rarer, as previously reported for yellow eels > 300 mm TL (Daverat & Tomas, 2006). Although the proportion of eels moving downstream is low, it remains constant between age-classes (6.1% on average), which indicates that a substantial proportion of individuals reaching upstream finally returns downstream. Similar behavior, named "downstream nomad", has been reported for eels of the Gironde watershed, where migration from freshwater to the estuary occurred during the second and third years of continental life (Daverat & Tomas, 2006). Such downstream movements have been attributed to an optimization tactic aiming to maximize the size-at-age, which is advantageous for eels settling in lower habitats, where strong intra-specific competition occurs (Daverat & Tomas, 2006). In the Sélune catchment, downstream movements occurred independently of eel age, and they predominantly involved eels leaving the midstream sector to the downstream one. This could be due to dams in the midstream sector that restrict access of young eels to upper reaches and artificially increase the density of migratory fish downstream to the barriers (Feunteun et al., 2003; Hitt et al., 2012). In this midstream sector, we observed greater mobility of eels compared to other sectors, which could be explained by inter- and intra-specific competition for habitat and resources induced by barriers.

Spatial changes in life-history traits

The areas currently colonized by eels are restricted within the Sélune catchment, but our results highlight significant variations in eel movement patterns as well as in their life-history traits according to their growth sectors. Although we observe high growth rate and trophic level for estuarine eels, the condition coefficient and lipid store contents are lower than for freshwater eels. Similar results were reported for eels in Norway (Parzanini et al. 2021), but diverge from other watersheds where eels caught in brackish areas exhibited better body condition (Cairns et al., 2009; Daverat et al., 2012; Kaifu et al., 2013). One potential explanation is that sandy areas covering most of the Sélune estuary are poorly suitable for eel settlement, which is traduced by low body condition of eels living there. Estuarine silver eels also appear less parasitized than freshwater eels, with both smaller parasite abundance and richness, a single parasite species (Pseudodactylogyrus sp.) being recorded, versus 6 to 8 species in freshwater sectors. It may be due to the higher salinity which is known to influence prevalence and abundance of metazoan parasite species in A. anguilla (e.g., Køie, 1988; Jakob et al., 2008). However, as most parasite species found in the Sélune catchment [i.e., Anguillicoloides crassus, Pseudodactylogyrus sp., Acanthocephalus spp., Myxidium giardia Cépède, 1906, Bothriocephalus claviceps Goeze, 1782, Raphidascaris acus (Boch, 1779)] have already been recorded in both fresh and brackish waters (Køie, 1988; Jakob et al., 2008), the occurrence of a single parasite species in the two estuarine eels may be related to low sampling size. To conclude, although our results show that life-history traits of the two estuarine eels are highly dissimilar from the ones observed in freshwater eels, sampling effort in the estuarine area should be increased to confirm this trend.

In the Sélune catchment, our results indicate that the eel trophic level is influenced by their spatial distribution. As previously reported for eel, the trophic level appears higher in saline water (Parzanini et al. 2021), but a gradient in $\delta^{15}N$ was also observed between freshwater sectors, with a higher propensity to piscivory in the midstream and upstream sectors than in the downstream. This gradient probably reflects a specialization of eels in relation to prey availability (Cucherousset et al., 2011). Additionally, silver eels living in the upstream reaches of connected tributaries had greater body condition and lipid reserve than eels living in other freshwater sectors. As previously indicated, the midstream sector located just downstream of the dam appears to be less suitable for growth even though eels had been feeding in higher tropic level compared to other freshwater sectors. In midstream, eels were generally highly mobile and the lipid reserves in muscles were relatively low compared to the upstream sector. This might be due to high density and related intraspecific competition for resources that have been reported in fragmented rivers (Feunteun et al., 1998; Costa et al., 2008), which promote increased nomadism in eels (Feunteun et al. 2003). Accordingly, the connected headwaters of the Sélune catchment appear more beneficial for eel growth and should produce genitors with higher fitness than downstream areas. Indeed, energy reserves and the health state of individuals play a crucial role in gonad maturation and in the success of migration to spawning grounds (Van den Thillart et al., 2007; Belpaire et al., 2009; Clevestam et al., 2011). Although the richness and abundance of metazoan parasites were higher in eels living upstream of the Sélune catchment, abundances of pathogenic non-native species were lower compared to other sites. Most upstream metazoan parasites were heteroxenous (i.e., life cycle involving various intermediate or paratenic hosts) and trophically transmitted. The high diversity of upstream parasitofauna suggests a greater free-living biodiversity and thus healthier environmental conditions (Marcogliese, 2004; Hudson et al., 2006). Native parasites, such as Acanthocephalus spp., which are more prevalent and abundant in upper reaches, share a common evolutionary history with A. anguilla and have generally less negative impact on host fitness (Gérard et al., 2013).

Our results indicate that eel sex-ratio does not vary over the Sélune catchment, which contrasts with studies usually reporting increased female proportion with the distance to the sea (Vollestad et al., 1986; Acou et al., 2009; Geffroy & Bardonnet, 2016). Downstream reaches typically produce a majority of males, while females grow slowly in upstream reaches where they reach larger size (Tesch, 2003). Moreover, previous studies conducted in the Oir tributary reported a female biased sex-ratio as expected in low-density conditions (Acou et al., 2009). These inconsistencies can be explained by the spatial heterogeneity of eel densities between the main river course of the Sélune and its tributaries (Druet et al., 2021). Water flow attraction is crucial for young eel orientation during their freshwater migration (Harrison et al., 2014), so eel density is much higher in the main river course currently impaired by dams than in the river tributaries. However, our overview of the longitudinal gradient of the whole Sélune catchment does not allow to conclude on the spatial distribution of male and female eels over the catchment tributaries.

Conclusion

In this study, we demonstrate that eel life sequence reconstruction based on otolith elemental signatures provides valuable information on eel ecology within an obstructed catchment context. Despite a restricted network of connected rivers, the heterogeneity in elemental ratios was sufficiently contrasted to trace fish movements across four catchment sectors. Lifehistory traits and movement patterns of eels, constrained by the dams, significantly varied along the upstream-downstream gradient. Eels assigned to the midstream sector were more mobile and exhibited low growth rates, probably in response to higher density-dependent competition at the vicinity of the dams. While most eels are currently produced by the downstream and midstream sectors, eels assigned to upper connected reaches generally displayed a superior richness in native parasites, higher body condition, and lipid reserve, which are known to promote the success of migration and reproduction. In the near future, the complete dam removals, leading to the reconnection of upper reaches, will represent an outstanding experimental framework for evaluating impacts of reconnection of an entire catchment on the life-history traits of catadromous species such as eels. We can expect that the upper reach reconnection will strongly modify eel spatial distribution within the catchment while reducing intra-specific competition, with corollary effects on growth, age and size at silvery, and sex-ratio of eels migrating to the sea to reproduce (e.g., Hitt et al., 2012; Watson et al., 2018). Hence, medium- and long-term monitoring of silver eels in this catchment appears essential after dam removal to fully assess dam effects on eel life-history traits and distribution and accurately highlight ecological benefices.

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

Declarations

Conflict of 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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