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

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26        **Abstract**

27        River fragmentation is expected to impact not only movement patterns and distribution of eels  
28        within catchment, but also their life-history traits. Here, we used otolith multi-elemental signatures to  
29        reconstruct life sequences of European silver eels within an obstructed catchment, just before the  
30        removal of hydropower dams. Beyond providing an initial state, we hypothesized that otolith  
31        signatures can provide crucial information on the way eels use the watershed. Indeed, their spatial  
32        distribution is expected to shape life-history traits, including condition coefficient, trophic level,  
33        growth rate, or infection by metazoan parasites. While Sr:Ca and Ba:Ca ratios were complementary in  
34        tracing fish movements between freshwater and estuary, the Ba:Ca variations allowed to discriminate  
35        three freshwater sectors. The eels assigned to the midstream sector were more mobile and exhibited  
36        lower growth rates, probably in response to higher competition at the vicinity of dams. While most  
37        eels are currently produced by downstream and midstream sectors, eels assigned to upper reaches of  
38        connected tributaries generally display higher richness in native parasite and higher body condition  
39        and lipid reserve, known to promote the success of migration and reproduction. In the near future,  
40        the dam removals will represent an outstanding experimental framework for evaluating impacts of  
41        catchment reconnection.

42        **Keywords:** phenotypic plasticity; life-history trait; river barrier; otolith microchemistry; LA-ICP-MS;  
43        metazoan parasites

## 44 Introduction

45 Fragmentation of aquatic systems is a major threat for biodiversity of continental ecosystems,  
46 and thus remains a priority issue for conservation and restoration actions (Nilsson et al., 2005; Reid et  
47 al., 2019). In Europe, at least 1.2 million instream barriers were recently recorded (Belletti et al.,  
48 2020), and more than 8 700 additional hydropower plants are planned or under construction (WWF et  
49 al., 2019). For migratory fish, the loss of connectivity, caused by river barriers, heavily restricts access  
50 to spawning or growth habitats, and can lead to the confinement of populations in bounded sub-  
51 optimal areas (Drouineau et al., 2018; Forget et al., 2018; Verhelst et al., 2021). The decline of  
52 available habitats and the fish accumulation downstream of barriers promote over-density conditions,  
53 enhancing intra-specific competition and spread of some pathogens, which can ultimately affect  
54 growth and survival (Laffaille et al., 2003; Machut et al., 2007; Thielen et al., 2007; Costa et al., 2008).  
55 Notwithstanding the growing scientific literature, the impacts of dams on life-history traits of  
56 migratory fish remains poorly understood, despite their importance for river basin management (e.g.  
57 Lin and Robinson, 2019; Pess et al., 2014, Righton et al., 2021). This is especially important for  
58 catadromous fish because their growth within the river is determinant for their marine migration and  
59 future reproductive success (McCleave, 2001).

60 The European eel is a facultative catadromous species, widely distributed throughout a range of  
61 aquatic ecosystems, including lakes, rivers, brackish waters, or small coastal streams (Daverat et al.,  
62 2005; Daverat & Tomas, 2006; Tabouret et al., 2010). Once reaching the continental shelf, glass eels  
63 progressively settle in continental habitats (Feunteun et al., 2003) for three to sometimes more than  
64 30 years before initiating their puberty toward the silver stage (Aroua et al., 2005) and starting their  
65 migration back to the spawning ground (Tesch, 2003; Righton et al., 2016). In addition to a strong  
66 sexual dimorphism, where migrating females are larger and older than males (Tesch, 2003),  
67 environmental conditions and thus aquatic habitats encountered during the continental stage critically  
68 influence the life-history traits (Vøllestad, 1992; Jessop, 2010; Daverat et al., 2012; Boulenger et al.,  
69 2016a, 2016b). Such changes in life-history traits are generally driven by multifaceted mechanisms,  
70 involving density- and resource-dependent processes (Feunteun et al., 2003), which in turn can impact  
71 survival and reproductive success of eels (Mateo et al., 2017).

72 Silver eel body condition and life-history traits are determinant for their reproductive success,  
73 since eels have to travel more than 5000 km before breeding (Belpaire et al., 2009; Clevestam et al.,  
74 2011). For example, the size- and age-at-silvering greatly fluctuate along river catchments, with lower  
75 growth rates and older eels observed in upper reaches (Daverat et al., 2012), as opposed to eels

76 residing in brackish waters, with earlier maturation and higher growth rates (Cairns et al., 2009). The  
77 condition of eels is also closely related to variation in their diet across different habitats, leading to  
78 changes in overall condition between marine, brackish and freshwater habitats (Parzanini et al. 2021).  
79 Additionally, eel life-history traits are affected by contamination and parasitism, which are locally  
80 diverse (e.g. Palstra *et al.*, 2007; Belpaire *et al.*, 2009; Geeraerts and Belpaire, 2010; Amilhat et al.,  
81 2014). For instance, the overall body condition of silver eels is generally reduced when contaminated  
82 by metallic compounds (Maes et al., 2005) as well as when infected by parasites, such as the invasive  
83 species of monogean infecting gills *Pseudodactylogyrus* sp., or the trophically-transmitted  
84 swimbladder nematode *Anguillicoloides crassus* (Palstra et al., 2007; Gérard et al., 2013). The sexual  
85 determinism is another peculiarity of eels as environmental conditions play a decisive role in the  
86 produced sex-ratio (Geffroy & Bardonnnet, 2016). Indeed, low density conditions observed in  
87 headwater streams promote the production of female eels, whereas lower reaches or areas located  
88 downstream barriers tend to produce a majority of males (Feunteun et al., 2003; Costa et al., 2008).

89 At catchment scale, eel life-history traits such as sex determination, age-at-silvering, fecundity,  
90 lipid reserves or health status are thus expected to be highly sensitive to disruption of river  
91 connectivity. The continental phase of eels ends with the silver stage where eels having accumulated  
92 enough resources to quit the river and migrate back to their maritime reproductive place (seaward  
93 migration). Therefore, focusing on the silver stage appears particularly relevant as the life-history  
94 traits of silver eels integrate the various conditions encountered during their continental stage.  
95 Beyond direct parameters measured on fish (e.g. size, lipid reserves), analysis of otolith can provide  
96 additional information on the past conditions encountered by eels (Campana, 1999). Otolith  
97 macrostructures can be investigated to estimate the age of eels, as well as their growth rates during  
98 the continental stage (Daverat & Tomas, 2006). Moreover, otolith elemental composition can yield  
99 powerful indications to reconstruct the movement patterns, providing there is sufficient  
100 heterogeneity in ambient water chemistry to discriminate habitats crossed by fish (Secor et al., 1995).  
101 Although a large panel of trace elements can be tracked using LA-ICP-MS (laser ablation-inductively  
102 coupled plasma mass spectrometry), not all elements provide information on the surrounding habitats  
103 and some of them are more influenced by the fish physiology than by its environment (e.g. Mg,  
104 Limburg et al., 2018). Strontium:Calcium (Sr:Ca) and Barium:Calcium (Ba:Ca) elemental ratios are  
105 known to reflect changes in ambient water while poorly influenced by physiological regulation  
106 pathways (Daverat et al., 2005; Hüßy et al., 2021). Modifications in Sr:Ca and Ba:Ca ratios along an  
107 otolith transect are thus commonly used to trace fish migration in relation to salinity ambient  
108 conditions (Tsukamoto & Nakai, 1998; Daverat et al., 2006; Tabouret et al., 2010), as well as

109 movements along freshwater catchments (Teichert et al., 2018). Accordingly, otolith elemental  
110 signatures can provide crucial information on the way in which eels moved in and used a water  
111 catchment, and how their spatial distribution shapes their life-history traits. In complement, metazoan  
112 parasites of eels may also give information on host (e.g. diet, movements, condition), and more  
113 generally on free-living biodiversity and changes in ecosystems (e.g. Marcogliese, 2004; Hudson et al.,  
114 2006 for reviews).

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

## 121 **Materials and methods**

### 122 *Study area and fish sampling*

123 The Sélune River flows over 91 km from the source to the English Channel in the Mont Saint-Michel  
124 Bay, Lower-Normandy, France (Fig. 1). While the watershed covers 1 106 km<sup>2</sup>, its upper part is  
125 disconnected (827 km<sup>2</sup>) by two large hydroelectric power dams (La Roche-qui-Boit (H=16m) in  
126 downstream and Vezins (H=36 m) in upstream) that disrupt the ecological continuity. Accordingly, the  
127 distribution of migratory fish, including eels, is currently limited to lower reaches of the Sélune River  
128 (279 km<sup>2</sup>), from the estuary to the La Roche-qui-Boit dam (Forget et al., 2018). Nevertheless, the three  
129 tributaries located downstream the dam (i.e. Moulinet, Oir and Beuvron Rivers) are freely accessible  
130 and currently colonised by eels till their upper reaches. Recently, environmental authorities and local  
131 operators decided to remove the two dams to restore continuity in compliance with the EU Water  
132 Framework Directive. Upper reaches of the Sélune River will thus be reconnected and freely accessible  
133 to migratory fish by 2022 (Fig. 1). Although the first dam located upstream of the Sélune (i.e. La  
134 Roche-qui-Boit) was teared down in 2019-2020, the removal of the second dam, which constitutes the  
135 main barrier, will only be effective in late 2022.

136 To provide an overview of the life-history traits of eels produced by the whole Sélune catchment,  
137 migrating silver stage eels were collected at a fishery specifically set up for catching migratory eels  
138 (site 1), located downstream of the Sélune River and its main tributaries (Fig. 1). This site is located in

139 a freshwater estuary but is subjected to tidal influence during spring tides. Silver eels were caught at  
140 night during two migration seasons (autumn 2019 and autumn 2020) while upper reaches of the  
141 Sélune River were still inaccessible for them. A stow net (L=20 m, W=6 m, H=3 m) was used to sample  
142 eels during their seaward migration (Durif et al., 2008). In order to optimize sampling efforts and  
143 ensure high capture rates, the net was placed in the main stem of the river when night high discharge  
144 conditions were met, since major migration runs mostly occur during these flows (Teichert et al.,  
145 2020). Silver stage of eels was visually assessed following previously defined criteria (Acou et al.,  
146 2005), such as the colour of the back and belly, the presence of a well-defined lateral line, and a high  
147 Pankhurst ocular index (OI > 6.5) (Pankhurst, 1982). A total of 35 (Total Length, min-max TL: 370 - 862  
148 mm) and 39 silver eels (TL: 321 - 946 mm) were collected during first (2019) and second migration  
149 seasons (2020), respectively.

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

156 All collected eels (yellow and silver stage) were anesthetized with a Benzocaine solution (15 mg.L<sup>-1</sup>)  
157 before being euthanized with an overdosed solution of Benzocaine (400 mg.L<sup>-1</sup>), and then frozen (-  
158 20°C) until dissections at the laboratory. This study was approved by the Cuvier Ethic Committee  
159 (project n°68-106), the local representative of the French national ethic committee for animal in  
160 research.

### 161 *Description of life-history traits*

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

167 **Eel biometry.** Eels were measured (Total Length, TL, mm) and weighed (Total Weight, TW, g) to  
168 calculate the Fulton (1904) condition coefficient (K) according to the following formula:  $10^5 \times TW / TL^3$ .  
169 Individuals were then dissected to determine their sex through macroscopic observations of the

170 gonads (Colombo et al., 1984), and the gonads (Gonad Weight, GW, g) and the liver (Liver Weight, LW,  
171 g) were weighted. The gonadosomatic (GSI, %) and hepatosomatic (HSI, %) indices were calculated as  
172 the ratio of organ weight to body weight:  $GSI = GW/TW \times 100$ , and  $HSI = LW/TW \times 100$ , respectively.  
173 GSI provides insights on the level of gonad maturation and individual reproductive investment,  
174 whereas HSI is a proxy of lipid reserves, which are involved in gonad maturation and sea migration.

175 **Muscle stable isotope.** For each eel, one muscle tissue sample was dissected just below the dorsal  
176 fin to determine the ratio of carbon relative to nitrogen (C:N ratio). This ratio was then used as a proxy  
177 of lipid content stored in silver eels' muscle (McConnaughey & McRoy, 1979; Post et al., 2007).  
178 Nitrogen isotopic signature was used to estimate eel trophic level and was expressed in the delta unit  
179 notation as deviation from standard (atmospheric nitrogen (N)) following the formula:  $\delta^{15}N =$   
180  $((R_{sample}/R_{standard}) - 1) \times 1000$ , where R is the ratio  $^{15}N:^{14}N$  in the sample and in the standard. For  
181 each muscle sample, nitrogen and carbon total quantities, and the  $^{15}N:^{14}N$  ratios were measured by  
182 continuous flow isotope mass spectrometry (CF-IRMS) using a Thermo Scientific Delta V Advantage  
183 mass spectrometer coupled to a Thermo Scientific Flash 2000 elemental analyzer. Analytical precision  
184 (standard deviation) was  $< \pm 0.15\%$  of reference material.

185 **Age estimate.** Sagittal otoliths of eels were extracted and embedded in epoxy resin (Araldite  
186 2020, Huntsman Corporation), then grounded along the longitudinal plane and polished until the  
187 primordium was reached (Acou et al., 2013). The age-at-silvering of eels (AGE, y) was estimated from a  
188 visual count of annuli (rings) on the otolith section, beginning from the first growth check outside the  
189 elver mark, which reflects the beginning of continental phase (Daverat & Tomas, 2006). Readings were  
190 conducted independently by two operators to avoid bias, and when age estimates differed, a  
191 simultaneous reading was performed to define a consensual age estimate. The age reading was  
192 carried out along the longest transect of otolith, between the nucleus and the outer edge. The  
193 distance separating each annuli was then measured ( $\mu m$ ) on a micrograph picture using the ImageJ  
194 software v. 1.53e (Rueden et al., 2017). Finally, the mean annual growth rate (Gr,  $mm \cdot y^{-1}$ ) of eel during  
195 their continental phase was calculated following the formula:  $Gr = (TL - 65)/AGE$ , where 65 mm is the  
196 mean size at recruitment (Durif et al. 2020).

197 **Metazoan parasites.** The presence of metazoan parasites was meticulously checked in each silver  
198 eel to determine the parasite constraint and provides information on host and environment (Gérard et  
199 al., 2013). The gills, the heart, the digestive tract, the liver and the swimbladder were dissected using a  
200 binocular stereomicroscope. All the metazoan parasites were counted per organ and per fish and  
201 morphologically identified based on Fomena and Bouix (1997) for Myxozoa, Ogawa and Egusa (1976)

202 for Monogenea, Khalil et al. (2006) for Cestoda, Golvan (1969) and Brown et al. (1986) for  
203 Acanthocephala, and Moravec (1994) for Nematoda. The parasitological parameters used to describe  
204 the parasite community were the prevalence (i.e. number of fish infected with a particular taxon /  
205 number of fish examined), the taxa richness (i.e. number of parasite taxa infecting eels), and the  
206 abundance (i.e. number of individuals of a particular parasite taxon in/on a single fish) (Bush et al.,  
207 1997).

#### 208 *Analysis of otolith microchemistry*

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

#### 222 *Reconstruction of life sequences*

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

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

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

### 252 *Life transitions and spatial changes in life-history traits*

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

260 Spatial changes of life-history traits were quantified using linear mixed models (LMMs). LMMs  
261 were independently adjusted for 14 individual traits as response variables (i.e. mobility, trophic level,  
262 continental growth, age-at-silvering, size-at-silvering, K, C:N, RHS, RGS, parasite taxa richness, total

263 parasite abundance, *A. crassus*, *Pseudodactylogyrus* sp. and *Acanthocephalus* spp. abundances), while  
264 the main residence sector inferred from otolith microchemistry was used as explanatory categorical  
265 variable. Models were adjusted using an identity link function and a Gaussian error distribution. The  
266 abundance variables were  $\log(x + 1)$ -transformed to meet normality assumptions. Response variables  
267 were standardized to have a mean of 0 and a variance of 1 to obtain standardized regression  
268 coefficients, which were interpreted as effect sizes. This approach allows to directly compare model  
269 outcomes as they are expressed in a similar range of magnitude. Eel sex and sampling season were  
270 included as random effects to account respectively for the influence of sexual dimorphism and the  
271 two-year sampling procedure on the variable response. Accordingly, effect sizes reveal consensual  
272 trends among sex and seasons when the other sources of variability are considered by a random  
273 intercept. The statistical significance of main residence sector in models was assessed based on  
274 deviance reduction tests (*F*-tests). The direction and magnitude of spatial changes in life-history traits  
275 were then assessed from the sign and value of the effect sizes. Finally, changes in the prevalence of  
276 parasites (i.e. total parasite prevalence, *A. crassus*, *Pseudodactylogyrus* sp. and *Acanthocephalus* spp.  
277 prevalences) were investigated using binomial Generalized Linear Mixed Models (GLMMs). Eel sex and  
278 sampling season were included as random effects and the significance of main residence sector was  
279 assessed based on deviance reduction tests (*Chi*-square tests).

280 All statistical analyses were performed in the R environment v. 4.0.5 (R Core Team, 2018), using  
281 the base package for standard analysis (i.e. mean comparisons and proportion tests) and “segclust2d”  
282 for elemental profile segmentation (Patin et al., 2019). LMMs and GLMMs were fitted using the  
283 “lme4” package (Bates *et al.*, 2014) and parameters standardized with the “effectsize” package (Ben-  
284 Shachar et al., 2020). The statistical significance of changes in the proportions between groups (i.e.  
285 sex-ratio, age-class) was tested using either binomial or *Chi*-square tests. Differences in life-history  
286 traits between males and females were tested using Generalized Linear Models (GLMs). GLMs were  
287 adjusted using an identity link function and a Gaussian error distribution for the life-history traits,  
288 while binomial or poisson distributions were used for respectively testing changes in prevalence and  
289 abundance of metazoan parasites. The statistical significance of sex in models was then assessed  
290 based on deviance reduction tests (*Chi*-square tests).

## 291 Results

### 292 *Life-history traits and metazoan parasites*

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

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

### 310 ***Reconstruction of life-sequences***

311 The number of segments identified from otolith elementary profiles for silver eels (n = 74) and  
312 resident eels (n = 30) ranged from 2 and 8 depending on individuals (on average  $3.6 \pm 0.11$  segments).  
313 In resident eels, the Ba:Ca signatures recorded in the marginal segments were significantly correlated  
314 with the distance to the sea (Fig. 2a; n = 6, r = 0.98, t = 11.8, p < 0.001), which highlights the relevance  
315 of the Ba:Ca ratio to indicate habitat changes along the downstream-upstream gradient. On the  
316 contrary, Sr:Ca signatures did not vary significantly with the distance to the sea (Fig. 2b; n = 6, r = 0.40,  
317 t = -0.88, p = 0.42), but ratio values typically fit with range recorded for eels living in freshwater  
318 environment (Sr:Ca signatures between  $1.05 \times 10^{-3}$  and  $2.74 \times 10^{-3}$  for resident eels; Daverat et al.,  
319 2005; Tabouret et al., 2010).

320 The k-means method applied to otolith segments of silver eels resulted in four clusters with  
321 distinct ranges in Sr:Ca and Ba:Ca signatures (Fig. 3a). One cluster contrasted from others because of  
322 its high Sr:Ca signatures (Sr:Ca >  $3.15 \times 10^{-3}$ ), hereafter assigned to the 'estuary sector' because such  
323 signatures are similar to the ones retrieved in eels involving in brackish water. For the three other

324 clusters, the observed ranges of Sr:Ca ratio were comparable to freshwater signatures ( $0.97 \times 10^{-3} <$   
325  $\text{Sr:Ca} < 3.21 \times 10^{-3}$ ), but clusters differed in their Ba:Ca signatures. The first freshwater cluster showed  
326 the lowest Ba:Ca ratios ( $\text{Ba:Ca} < 2.12 \times 10^{-5}$ ) and gathered the resident eel signatures from sites 1, 4,  
327 and 5, located less than 15 km from the river mouth, hereafter assigned to the 'downstream sector'.  
328 The second freshwater cluster featured intermediate Ba:Ca ratios ( $2.14 \times 10^{-5} < \text{Ba:Ca} < 3.72 \times 10^{-5}$ ) and  
329 included sites 2 and 3 located downstream from the first dam, between 15 and 23 km from the river  
330 mouth, hereafter assigned to the 'midstream sector'. The third freshwater cluster showed the highest  
331 Ba:Ca ratios ( $\text{Ba:Ca} > 3.76 \times 10^{-5}$ ) and included the site 6, which was located over 38 km from the river  
332 mouth, hereafter assigned to the 'upstream sector'. As the upper reaches of the Sélune River were  
333 inaccessible for eels, this sector only refers to upstream areas of the connected tributaries with  
334 confluences located downstream of the Sélune dams (i.e. the Beuvron and the Oir). Finally, the  
335 assigned segments were then used to reconstruct life sequences of the 74 silver eels and to estimate  
336 the amount of time spent in each sector of the Sélune catchment (Fig. 3b).

### 337 *Residence sectors and life transitions*

338 Over the continental phase, 34 eels predominantly resided in the downstream sector (46 %), 27  
339 in the midstream sector (36 %), 11 in the upstream sector (15 %) and 2 in the estuary sector (3 %).  
340 Once in the catchment, the number of sectors crossed by eels ranged between 1 and 5 depending on  
341 individuals. Whereas 24.3 % of individuals were briefly assigned to the estuary sector once entering  
342 the catchment, the others were directly assigned to the downstream (27.0 %), midstream (39.2 %) or  
343 upstream (9.5 %) sectors (Fig. 3b).

344 The proportion of eels that moved between the different catchment sectors were over 20 % for  
345 the three first continental age-classes (Fig. 4a), then it significantly dropped to 5-10 % for the older  
346 age-classes ( $X^2 = 65.8$ ,  $df = 14$ ,  $p < 0.001$ ). This mobility pattern was essentially shaped by a significant  
347 decrease in the proportion of movements toward upstream with the age of eels ( $X^2 = 84.5$ ,  $df = 14$ ,  $p$   
348  $< 0.001$ ), whereas the proportion of movements toward downstream remained unchanged with age  
349 ( $X^2 = 14.4$ ,  $df = 14$ ,  $p = 0.41$ ). These results suggest that eels actively colonized and exploited the  
350 catchment during the first three years of their continental life, then a more resident behaviour was  
351 adopted with punctual returns downstream. Indeed, 55 % of eels reaching the upstream sector and  
352 76.9 % of eels reaching the midstream sector ultimately returned further downstream for the rest of  
353 their continental life. Interestingly, almost 40 % of the transitional movements reported for the 74 eels  
354 involved individuals leaving the midstream sector to the downstream sector (Fig. 4b).

355 *Spatial changes in life-history traits*

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

364 Individuals from the downstream sector showed the lowest trophic level in comparison with the  
365 other freshwater sectors (Fig. 5, Table 3), which suggests a low proportion of fish in the eel diet. The  
366 highest degree of mobility was observed for the eels predominantly residing in the midstream sector  
367 and was associated with the lowest grow rates. Although differences in age-at-silvering was not  
368 significant between sectors, eels of the midstream sector tended to be older than those residing in the  
369 other sectors (Fig. 5). Overall, eels living upstream displayed highest values of life-history traits related  
370 to the migration and reproduction success (Fig. 5, Table 3), whereas eel body condition was lower in  
371 downstream, as well as muscle lipid contents in both downstream and midstream sectors. On the  
372 contrary, the size-at-silvering and the GSI did not differ significantly between the residence sectors  
373 (Table 3).

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

380 **Discussion**

381 *Lifetime movements in the Sélune catchment*

382 In this study, eel life sequences were reconstructed based on the segmentation of otolith  
383 elementary profiles following the method proposed by Patin et al. (2020). While this method was  
384 initially developed to identify transition phases in record time series from telemetry studies, our

385 results demonstrate that it can successfully integrate otolith microchemistry records. Compared to  
386 classic visual interpretations of otolith elemental composition, taking into account the temporal  
387 dimension of otolith not only provides new insights on but also allows non-subjective and quantitative  
388 reconstruction of fish movements (Fablet et al., 2007; Vignon, 2015). Fluctuations of elemental ratios  
389 (Sr:Ca and Ba:Ca) in otoliths have been previously used to trace eel migration between marine,  
390 estuarine and freshwater habitats (e.g. Tsukamoto and Nakai, 1998; Daverat et al., 2006; Tabouret et  
391 al., 2010). While Sr:Ca and Ba:Ca ratios simultaneously changes in eel otoliths along the salinity  
392 gradient (e.g. Tabouret et al. 2010), our results also demonstrated a longitudinal gradient of the Ba:Ca  
393 ratio in the Sélune catchment, which can be used to infer habitat shifts within the freshwater  
394 environment. Such variation of Ba:Ca ratios in fish otolith can be related to different ambient water  
395 chemistry influenced by the substratum composition and physical erosion process (Elsdon and  
396 Gillanders, 2005).

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

412 Our results also clearly emphasize the temporal dynamic of eel catchment colonization, as  
413 featured by an active upstream migration during the first three years following the glass eel stage.  
414 Similar observations have been reported in the Gironde watershed (France), where the number of  
415 transitions between different habitats decreasing as eels aged (Fablet et al., 2007). After the  
416 settlement phase, eels of the Sélune catchment become more sedentary and upstream movements  
417 are rarer, as previously reported for yellow eels >300 mm TL (Daverat & Tomas, 2006). Although the

418 proportion of eels moving downstream is low, it remains constant between age-classes (6.1 % on  
419 average), which indicates that a substantial proportion of individuals reaching upstream finally returns  
420 downstream. Similar behaviour, named “downstream nomad”, has been reported for eels of the  
421 Gironde watershed, where migration from freshwater to the estuary occurred during the second and  
422 third years of continental life (Daverat & Tomas, 2006). Such downstream movements have been  
423 attributed to an optimization tactic aiming to maximize the size-at-age, which is advantageous for eels  
424 settling in lower habitats, where strong intra-specific competition occurs (Daverat & Tomas, 2006). In  
425 the Sélune catchment, downstream movements occurred independently of eel age, and they  
426 predominantly involved eels leaving the midstream sector to the downstream one. This could be due  
427 to dams in the midstream sector, that restrict access of young eels to upper reaches and artificially  
428 increase the density of migratory fish downstream to the barriers (Feunteun et al., 2003; Hitt et al.,  
429 2012). In this midstream sector, we observed greater mobility of eels compared to other sectors,  
430 which could be explained by inter- and intra-specific competition for habitat and resources induced by  
431 barriers.

#### 432 *Spatial changes in life-history traits*

433 The areas currently colonized by eels are restricted within the Sélune catchment, but our results  
434 highlight significant variations in eel movement patterns as well as in their life-history traits according  
435 to their growth sectors. Although we observe high growth rate and trophic level for estuarine eels, the  
436 condition coefficient and lipid store contents are lower than for freshwater eels. Similar results were  
437 reported for eels in Norway (Parzanini et al. 2021), but diverge from other watersheds where eels  
438 caught in brackish areas exhibited better body condition (Cairns et al., 2009; Daverat et al., 2012; Kaifu  
439 et al., 2013). One potential explanation is that sandy areas covering most of the Sélune estuary are  
440 poorly suitable for eel settlement, which is traduced by low body condition of eels living there.  
441 Estuarine silver eels also appear less parasitized than freshwater eels, with both smaller parasite  
442 abundance and richness, a single parasite species (*Pseudodactylogyrus* sp.) being recorded, *versus* 6 to  
443 8 species in freshwater sectors. It may be due to the higher salinity which is known to influence  
444 prevalence and abundance of metazoan parasite species in *A. anguilla* (e.g. Kjøie, 1988; Jakob et al.,  
445 2008). However, as most parasite species found in the Sélune catchment (i.e. *A. crassus*,  
446 *Pseudodactylogyrus* sp., *Acanthocephalus* spp., *Myxidium giardii*, *Bothriocephalus claviceps*,  
447 *Raphidascaris acus*) have already been recorded in both fresh and brackish waters (Kjøie, 1988; Jakob  
448 et al., 2008), the occurrence of a single parasite species in the two estuarine eels may be related to  
449 low sampling size. To conclude, although our results show that life-history traits of the two estuarine

450 eels are highly dissimilar from the ones observed in freshwater eels, sampling effort in the estuarine  
451 area should be increased to confirm this trend.

452 In the Sélune catchment, our results indicate that the eel trophic level is influenced by their  
453 spatial distribution. As previously reported for eel, the trophic level appears higher in saline water  
454 (Parzanini et al. 2021), but a gradient in  $\delta^{15}\text{N}$  was also observed between freshwater sectors, with a  
455 higher propensity to piscivory in the midstream and upstream sectors than in the downstream. This  
456 gradient probably reflects a specialization of eels in relation to prey availability (Cucherousset et al.,  
457 2011). Additionally, silver eels living in the upstream reaches of connected tributaries had greater  
458 body condition and lipid reserve than eels living in other freshwater sectors. As previously indicated,  
459 the midstream sector located just downstream of the dam appears to be less suitable for growth even  
460 though eels had been feeding in higher trophic level compared to other freshwater sectors. In  
461 midstream, eels were generally highly mobile and the lipid reserves in muscles were relatively low  
462 compared to the upstream sector. This might be due to high density and related intraspecific  
463 competition for resources that have been reported in fragmented rivers (Feunteun *et al.*, 1998; Costa  
464 *et al.*, 2008), which promote increased nomadism in eels (Feunteun *et al.* 2003). Accordingly, the  
465 connected headwaters of the Sélune catchment appear more beneficial for eel growth and should  
466 produce genitors with higher fitness than downstream areas. Indeed, energy reserves and the health  
467 state of individuals play a crucial role in gonad maturation and in the success of migration to spawning  
468 grounds (Van den Thillart et al., 2007; Belpaire et al., 2009; Clevestam et al., 2011). Although the  
469 richness and abundance of metazoan parasites were higher in eels living upstream of the Sélune  
470 catchment, abundances of pathogenic non-native species were lower compared to other sites. Most  
471 upstream metazoan parasites were heteroxenous (i.e. life cycle involving various intermediate or  
472 paratenic hosts) and trophically-transmitted. The high diversity of upstream parasitofauna suggests a  
473 greater free-living biodiversity and thus healthier environmental conditions (Marcogliese, 2004;  
474 Hudson *et al.*, 2006). Native parasites, such as *Acanthocephalus* spp., which are more prevalent and  
475 abundant in upper reaches, share a common evolutionary history with *A. anguilla* and have generally  
476 less negative impact on host fitness (Gérard et al., 2013).

477 Our results indicate that eel sex-ratio does not vary over the Sélune catchment, which contrasts  
478 with studies usually reporting increased female proportion with the distance to the sea (Vollestad et  
479 al., 1986; Acou et al., 2009; Geffroy & Bardonnnet, 2016). Downstream reaches typically produce a  
480 majority of males, while females grow slowly in upstream reaches where they reach larger size (Tesch,  
481 2003). Moreover, previous studies conducted in the Oir tributary reported a female biased sex-ratio as  
482 expected in low-density conditions (Acou et al., 2009). These inconsistencies can be explained by the

483 spatial heterogeneity of eel densities between the main river course of the Sélune and its tributaries  
484 (Druet et al., 2021). Water flow attraction is crucial for young eel orientation during their freshwater  
485 migration (Harrison et al., 2014), so eel density is much higher in the main river course currently  
486 impaired by dams than in the river tributaries. However, our overview of the longitudinal gradient of  
487 the whole Sélune catchment does not allow to conclude on the spatial distribution of male and female  
488 eels over the catchment tributaries.

## 489 **Conclusion**

490 In this study, we demonstrate that eel life sequence reconstruction based on otolith elemental  
491 signatures provides valuable information on eel ecology within an obstructed catchment context.  
492 Despite a restricted network of connected rivers, the heterogeneity in elemental ratios was  
493 sufficiently contrasted to trace fish movements across four catchment sectors. Life-history traits and  
494 movement patterns of eels, constrained by the dams, significantly varied along the upstream-  
495 downstream gradient. Eels assigned to the midstream sector were more mobile and exhibited low  
496 growth rates, probably in response to higher density-dependent competition at the vicinity of the  
497 dams. While most eels are currently produced by the downstream and midstream sectors, eels  
498 assigned to upper connected reaches generally displayed a superior richness in native parasites,  
499 higher body condition and lipid reserve, which are known to promote the success of migration and  
500 reproduction. In the near future, the complete dam removals, leading to the reconnection of upper  
501 reaches, will represent an outstanding experimental framework for evaluating impacts of  
502 reconnection of an entire catchment on the life-history traits of catadromous species such as eels. We  
503 can expect that the upper reach reconnection will strongly modify eel spatial distribution within the  
504 catchment while reducing intra-specific competition, with corollary effects on growth, age and size at  
505 silvery, and sex-ratio of eels migrating to the sea to reproduce (e.g. Hitt et al., 2012; Watson et al.,  
506 2018). Hence, medium- and long-term monitoring of silver eels in this catchment appears essential  
507 after dam removal to fully assess dam effects on eel life-history traits and distribution and accurately  
508 highlight ecological benefices.

## 509 **CRedit authorship contribution statement**

510 **Nils Teichert:** Conceptualization, Project administration, Funding acquisition, Data curation,  
511 Methodology, Formal analysis, Writing - original draft. **Anne Lizé, H  l  ne Tabouret, Claudia G  rard,**  
512 **Alexandre Carpentier:** Methodology, Data curation, Writing - review & editing. **Gilles Bareille:** Data

513 curation, Writing - review & editing. **Anthony Acou**: Project administration, Funding acquisition, Data  
514 curation, Writing - review & editing. **Thomas Trancart**: Writing - review & editing. **Laure-sarah Virag**,  
515 **Emma Robin**: Methodology, Data curation. **Morgan Druet**, **Jordan Prod'Homme**: Data curation. **Eric**  
516 **Feunteun**: Conceptualization, Funding acquisition, Project administration, Supervision, Validation,  
517 Writing - review & editing.

## 518 **Declaration of Competing Interest**

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

## 521 **Data Availability**

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

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530 Animal Research (DAECC 68 - 0106) and comply with current laws in France.

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769 Table 1: Summary of life-history traits and parasite descriptors of females (n = 34) and males (n =  
770 40) of silver eels collected downstream of the Sélune catchment. The means  $\pm$  standard error are  
771 presented along with the significance of deviance reduction tests investigating differences between  
772 sexes. abd: abundance; prev: prevalence (%).

<b>Life-history traits</b>		<b>Females</b>	<b>Males</b>	<b>p-value</b>
River life condition	Trophic level	11.93 $\pm$ 0.29	13.14 $\pm$ 0.30	<b>0.008</b>
	Growth (mm.y-1)	36.23 $\pm$ 1.72	37.78 $\pm$ 1.77	0.534
	Age (y)	15.32 $\pm$ 0.76	9.10 $\pm$ 0.40	<b>&lt; 0.001</b>
Spawning migration	Size (mm)	586.18 $\pm$ 19.71	380.20 $\pm$ 5.60	<b>&lt; 0.001</b>
	Condition - K	0.19 $\pm$ 0.00	0.18 $\pm$ 0.00	<b>0.028</b>
	Lipids - C:N	7.65 $\pm$ 0.19	7.48 $\pm$ 0.24	0.613
	Lipids - HSI (%)	1.64 $\pm$ 0.04	1.52 $\pm$ 0.04	<b>0.046</b>
	Gonads - GSI (%)	1.80 $\pm$ 0.07	0.39 $\pm$ 0.06	<b>&lt; 0.001</b>
Metazoan parasites	Total prevalence (%)	70.59 $\pm$ 7.81	90.00 $\pm$ 4.74	<b>0.032</b>
	Total abundance	8.71 $\pm$ 2.05	8.05 $\pm$ 2.04	0.331
	Species richness	1.35 $\pm$ 0.21	1.50 $\pm$ 0.14	0.598
	<i>Anguillicoloides crassus</i> (prev)	58.82 $\pm$ 8.44	82.50 $\pm$ 6.01	<b>0.024</b>
	<i>Anguillicoloides crassus</i> (abd)	3.44 $\pm$ 0.72	3.28 $\pm$ 0.46	0.697
	<i>Pseudodactylogyrus</i> sp. (prev)	29.41 $\pm$ 7.81	40.00 $\pm$ 7.75	0.34
	<i>Pseudodactylogyrus</i> sp. (abd)	1.68 $\pm$ 0.75	2.15 $\pm$ 0.92	0.142
	<i>Acanthocephalus</i> spp. (prev)	14.71 $\pm$ 6.07	12.50 $\pm$ 5.23	0.782
<i>Acanthocephalus</i> spp. (abd)	2.88 $\pm$ 1.66	0.28 $\pm$ 0.13	<b>&lt; 0.001</b>	

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775 Table 2. Community of the ten metazoan parasite taxa found in 74 European silver eels collected in the Sélune catchment. Species are listed along with  
 776 their microhabitat (G: Gills, I: Intestine, S: Swimbladder), main sector (E: estuary, D: downstream, M: midstream, U: upstream), diet, prevalence (% ± se),  
 777 abundance (mean abundance ± se), and infection pathway (HI: intermediate host, HP: paratenic host) (Kennedy et al., 1992; Benajiba & Marques, 1993;  
 778 Moravec & Scholz, 2015).

779

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

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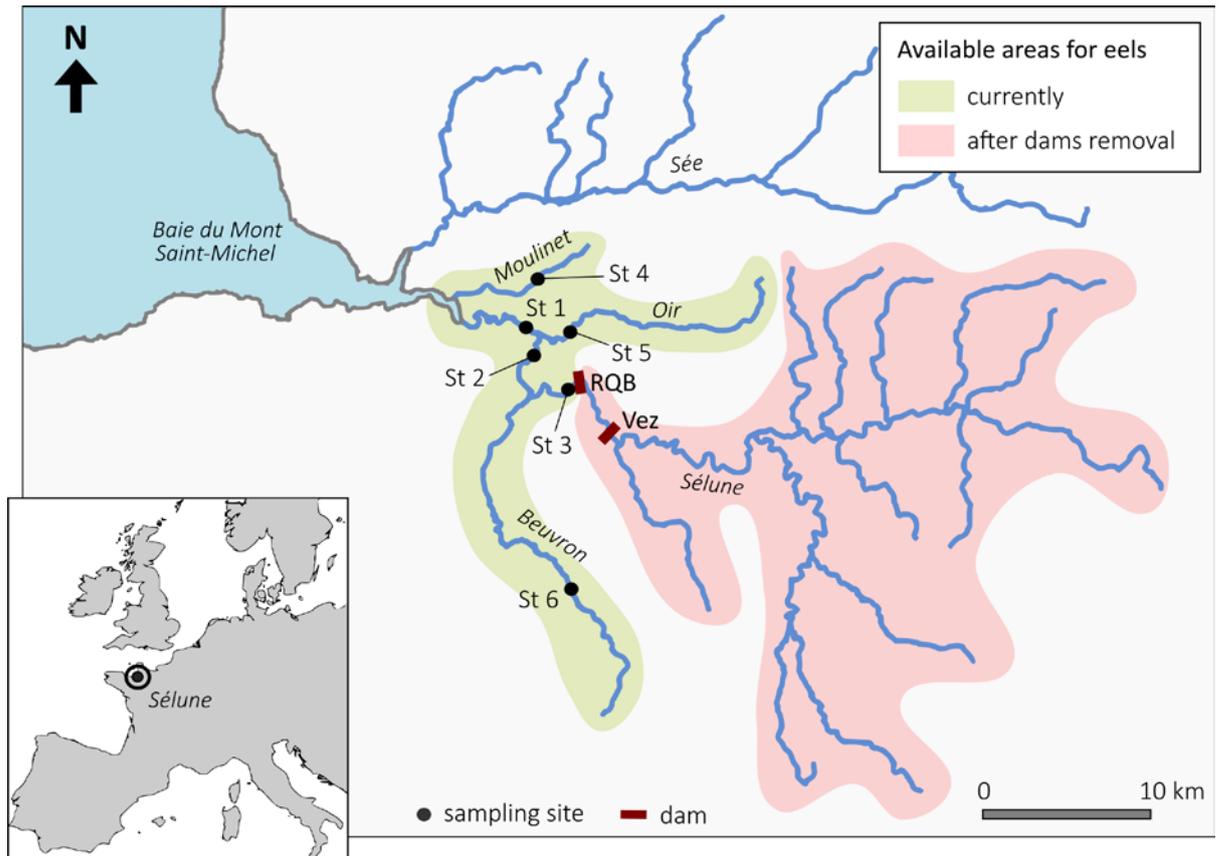
782 Table 3: Changes in life-history traits and parasite descriptors of silver eels (n = 74) depending on  
 783 the main sectors of the Sélune catchment. The mean  $\pm$  standard error are presented, along with the  
 784 significance of mixed models investigating differences between catchment sectors. abd: abundance;  
 785 prev: prevalence (%).

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

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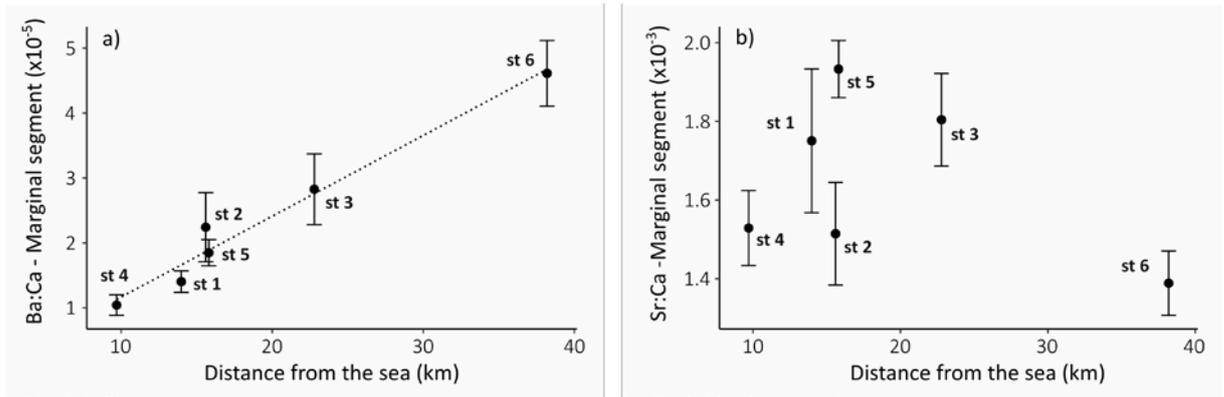
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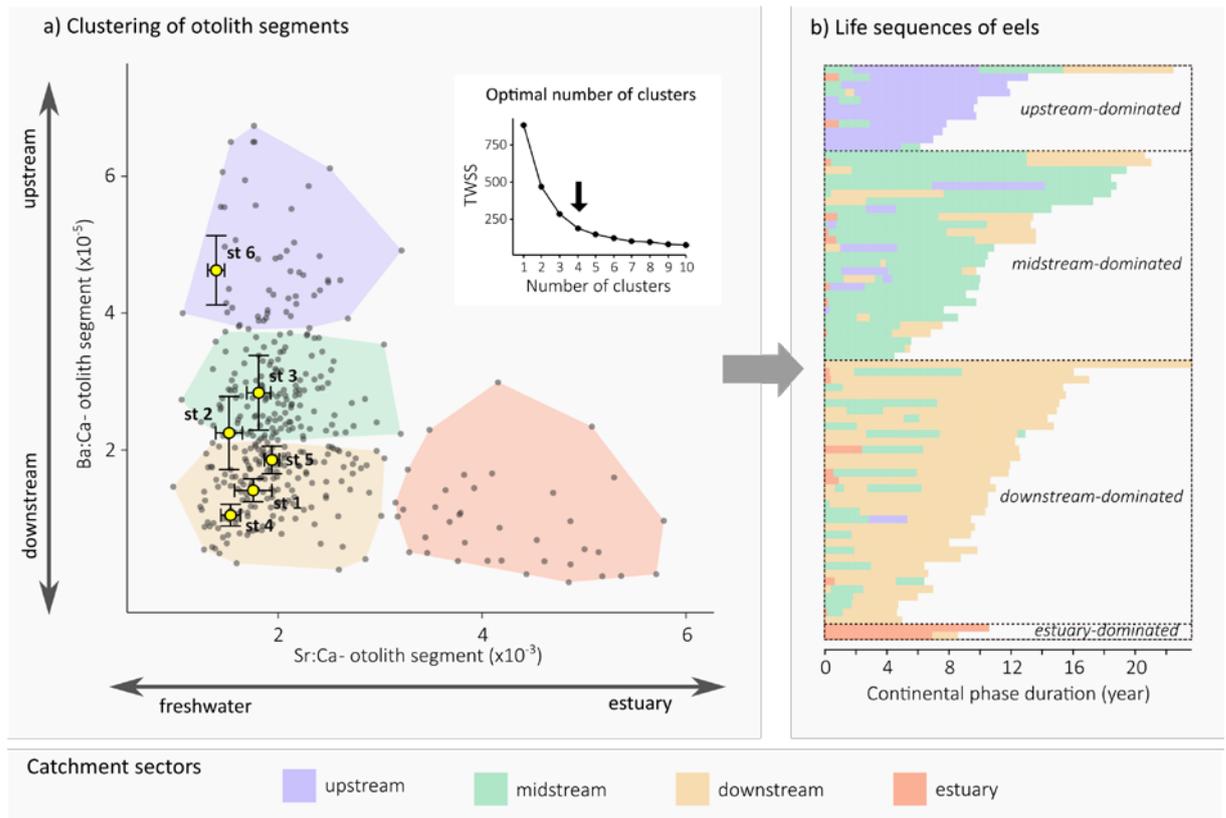
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790 **Figure 1:** Location of the six sampling sites within the Sélune catchment, Western Europe, France.  
 791 The green area highlights the river reaches currently accessible for eels, whereas the red indicates the  
 792 inaccessible ones, obstructed by the dams (RQB: Roche-qui-Boit; Vez: Vezins). St 1 to St 6 indicate the  
 793 different sites where yellow eels were caught, while silver eels were collected at St 1.



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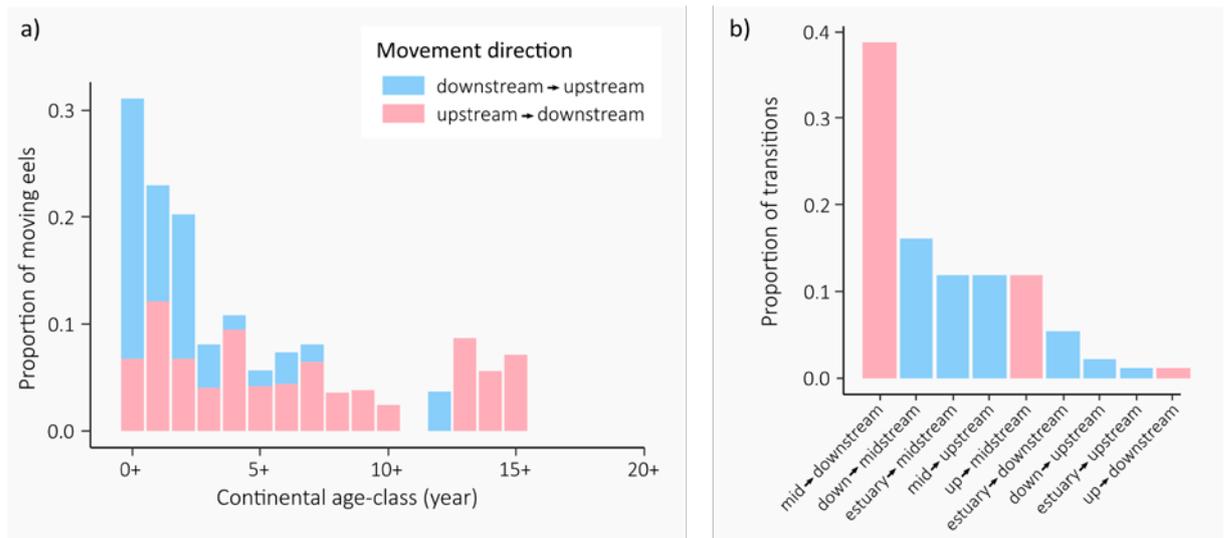
795 **Figure 2:** Relationships between the distance from the sea and otolith signatures recorded in the  
 796 marginal segments of resident eels. The mean elemental ratios of Sr:Ca (a) and Ba:Ca (b) were  
 797 provided for the six river sites (from St 1 to St 6) along the Sélune catchment. The vertical bars  
 798 represent the standard error.



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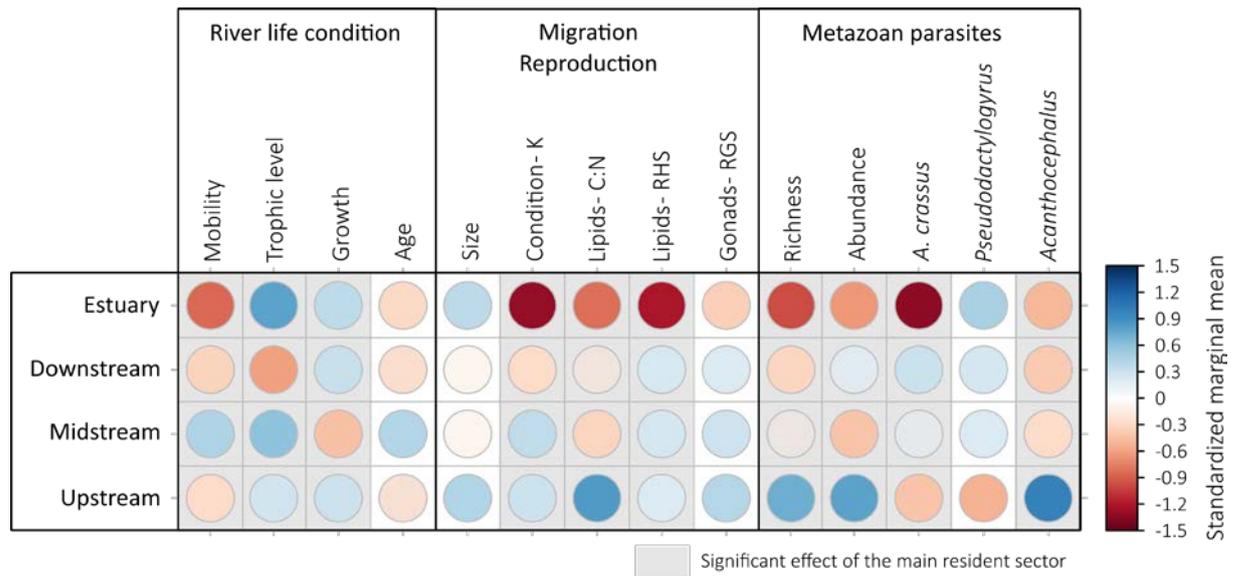
800 **Figure 3:** Reconstruction of silver eel life sequences based on otolith elemental signatures. a)  
 801 Clustering of otolith segments based on Sr:Ca and Ba:Ca elemental signatures of silver eels collected in  
 802 the Sélune catchment. The optimal number of clusters was defined from the Total Within Sum of  
 803 Squares (TWSS). The full yellow dots denote the otolith signatures recorded in the marginal segments  
 804 of resident yellow eels (mean  $\pm$  se). b) Individual life sequences of silver eels inferred from the otolith  
 805 elemental signatures (n = 74). Eels were grouped according to the main resident sector during their  
 806 continental phase: upstream-dominated (n = 11), midstream-dominated (n = 27), downstream-  
 807 dominated (n = 34) and estuary-dominated (n = 2) life sequences.

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810 **Figure 4:** a) Annual proportion of eels moving between sectors of the Sélune catchment  
 811 depending on their continental age-class (i.e. from recruitment in the catchment). b) Overall  
 812 proportion of transitions between sectors of the Sélune catchment recorded for the 74 silver eels  
 813 collected in 2019 and 2020. The direction of movement is detailed.



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815 **Figure 5:** Overview of the influence of the main sectors of the Sélune catchment on river life  
 816 condition, genitor quality for the spawning migration and metazoan parasites of silver eels. The  
 817 standardized marginal means are effect sizes that reflect intensity of deviations for each sector from  
 818 the population mean. Statistical significance of tests is detailed in Table 3.

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