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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 monogenean 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 km², its upper part is
125 disconnected (827 km²) 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 km²), 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⁻¹)
157 before being euthanized with an overdosed solution of Benzocaine (400 mg.L⁻¹), 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 (μm) 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 μm 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 μm 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 μm on the otolith) has
229 been specified for the segmentation process to avoid over-segmentation. A segment of 20 μm 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 ± 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 ± 0.12 parasite species per eel and a mean abundance of 8.35 ± 1.43 parasites per eel
302 (range: 0-69). Except the monogenean *Pseudodactylogyus* 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 *Pseudodactylogyus* 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 ± 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 1.05×10^{-3} and 2.74×10^{-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 > 3.15×10^{-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 > 3.15×10^{-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 1×10^{-5} and 7×10^{-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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531 **References**

- 532 Acou A., Boury P., Laffaille P., Crivelli A.J., & Feunteun E. (2005). Towards a standardized
533 characterization of the potentially migrating silver European eel (*Anguilla anguilla*, L.). *Archiv für*
534 *Hydrobiologie* 164: 237–255.
- 535 Acou A., Gaele G., Laffaille P., Feunteun E., Casselman J.M., & Cairns D.K. (2009). Differential
536 production and condition indices of premigrant eels in two small Atlantic coastal catchments of
537 France. *American Fisheries Society Symposium* 58: 157–174.
- 538 Acou A., Virag L., Reveillac E., Boulenger C., & Feunteun E. (2013). Comment, à partir d'un seul
539 otolithe, âger une anguille sans exclure d'autres analyses? Colloque national de
540 Sclérochronologie, Rennes, 2 au 4 juillet 2013.

- 541 Amilhat E., Fazio G., Simon G., Manetti M., Paris S., Delahaut L., Farrugio H., Lecomte-Finiger R., Sasal
542 P., & Faliex E. (2014). Silver European eels health in Mediterranean habitats. *Ecology of*
543 *Freshwater Fish* 23: 49–64.
- 544 Aroua S., Schmitz M., Baloche S., Vidal B., Rousseau K., & Dufour S. (2005). Endocrine evidence that
545 silvering, a secondary metamorphosis in the eel, is a pubertal rather than a metamorphic event.
546 *Neuroendocrinology* 82: 221–232.
- 547 Bates D., Mächler M., Bolker B., & Walker S. (2014). Fitting linear mixed-effects models using lme4.
548 arXiv preprint arXiv:1406.5823.
- 549 Belletti B., de Leaniz C.G., Jones J., Bizzi S., Börger L., Segura G., Castelletti A., Van de Bund W.,
550 Aarestrup K., & Barry J. (2020). More than one million barriers fragment Europe's rivers. *Nature*
551 588: 436–441.
- 552 Belpaire C.G.J., Goemans G., Geeraerts C., Quataert P., Parmentier K., Hagel P., & De Boer J. (2009).
553 Decreasing eel stocks: survival of the fattest? *Ecology of Freshwater Fish* 18: 197–214.
- 554 Ben-Shachar M.S., Lüdtke D., & Makowski D. (2020). effectsize: Estimation of Effect Size Indices and
555 Standardized Parameters. *Journal of Open Source Software* 5: 2815.
- 556 Boulenger C., Acou A., Gimenez O., Charrier F., Tremblay J., & Feunteun E. (2016a). Factors
557 determining survival of European eels in two unexploited sub-populations. *Freshwater Biology*
558 61: 947–962.
- 559 Boulenger C., Crivelli A.J., Charrier F., Roussel J., Feunteun E., & Acou A. (2016b). Difference in factors
560 explaining growth rate variability in European eel subpopulations: the possible role of habitat
561 carrying capacity. *Ecology of Freshwater Fish* 25: 281–294.
- 562 Brown A. F., Chubb J.C., & Veltkamp C.J. (1986) A key to the species of Acanthocephala parasitic in
563 British freshwater fishes. *Journal of Fish Biology* 28: 327–334.
- 564 Bush A.O., Lafferty K.D., Lotz J.M., & Shostak A.W. (1997). Parasitology meets ecology on its own
565 terms: Margolis et al. revisited. *The Journal of Parasitology* 83: 575–583.
- 566 Cairns D.K., Secor D.A., Morrison W.E., & Hallett J.A. (2009). Salinity-linked growth in anguillid eels and
567 the paradox of temperate-zone catadromy. *Journal of Fish Biology* 74: 2094–2114.
- 568 Campana S.E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and
569 applications. *Marine Ecology Progress Series* 188: 263–297.
- 570 Clevestam P.D., Ogonowski M., Sjöberg N.B., & Wickström H. (2011). Too short to spawn? Implications
571 of small body size and swimming distance on successful migration and maturation of the
572 European eel *Anguilla anguilla*. *Journal of Fish Biology* 78: 1073–1089.
- 573 Colombo G., Grandi G., & Rossi R. (1984). Gonad differentiation and body growth in *Anguilla anguilla*
574 L. *Journal of Fish Biology* 24: 215–228.
- 575 Costa J.L., Domingos I., Assis C.A., Almeida P.R., Moreira F., Feunteun E., & Costa M.J. (2008).
576 Comparative ecology of the European eel, *Anguilla anguilla* (L., 1758), in a large Iberian river.
577 *Environmental Biology of Fishes* 81: 421.
- 578 Cucherousset J., Acou A., Blanchet S., Britton J.R., Beaumont W.R.C., & Gozlan R.E. (2011). Fitness
579 consequences of individual specialisation in resource use and trophic morphology in European

- 580 eels. *Oecologia* 167: 75–84.
- 581 Daverat F., & Tomas J. (2006). Tactics and demographic attributes in the European eel *Anguilla*
582 *anguilla* in the Gironde watershed, SW France. *Marine Ecology Progress Series* 307: 247–257.
- 583 Daverat F., Tomas J., Lahaye M., Palmer M., & Elie P. (2005). Tracking continental habitat shifts of eels
584 using otolith Sr/Ca ratios: validation and application to the coastal, estuarine and riverine eels of
585 the Gironde–Garonne–Dordogne watershed. *Marine and Freshwater Research* 56: 619–627.
- 586 Daverat F., Limburg K.E., Thibault I., Shiao J.-C., Dodson J.J., Caron F., Tzeng W.-N., Iizuka Y., &
587 Wickström H. (2006). Phenotypic plasticity of habitat use by three temperate eel species,
588 *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Marine Ecology Progress Series* 308: 231–241.
- 589 Daverat F., Beaulaton L., Poole R., Lambert P., Wickström H., Andersson J., Aprahamian M., Hizem B.,
590 Elie P., Yalçın-Özdilek S., et al. (2012). One century of eel growth: changes and implications.
591 *Ecology of Freshwater Fish* 21: 325–336.
- 592 Drouineau H., Carter C., Rambonilaza M., Beaufaron G., Bouleau G., Gassiat A., Lambert P., le Floch S.,
593 Tétard S., & de Oliveira E. (2018). River Continuity Restoration and Diadromous Fishes: Much
594 More than an Ecological Issue. *Environmental Management* 61: 671–686.
- 595 Druet M., Rault P., Acou A., Azam D., Bardonnnet A., Evanno G., Feunteun E., Lasne E., Launey S., Lizé A.,
596 et al. (2021). Dispersion et (re)colonisation du cours de la Sélune et de ses affluents: terminer un
597 état de référence pour les poissons migrateurs amphihalins et anticiper l’expansion spatiale de
598 l’écrevisse de Californie. Rapport final des travaux liés à la convention 1078068. Agence de l’Eau
599 Seine-Normandie: 30 p.
- 600 Durif C.M.F., Travade F., Rives J., Elie P., & Gosset C. (2008). Relationship between locomotor activity,
601 environmental factors, and timing of the spawning migration in the European eel, *Anguilla*
602 *anguilla*. *Aquatic Living Resources* 21: 163–170.
- 603 Durif C. M., Diserud O. H., Sandlund O. T., Thorstad E. B., Poole R., Bergesen K., Escobar-Lux R. H.,
604 Shema S., & Vøllestad L. A. (2020). Age of European silver eels during a period of declining
605 abundance in Norway. *Ecology and Evolution* 10(11): 4801-4815.
- 606 Elsdon T. S., & Gillanders B. M. (2005). Alternative life-history patterns of estuarine fish: barium in
607 otoliths elucidates freshwater residency. *Canadian Journal of Fisheries and Aquatic Sciences*
608 62(5): 1143-1152.
- 609 Fablet R., Daverat F., & Pontual H. De. (2007). Unsupervised Bayesian reconstruction of individual life
610 histories from otolith signatures: case study of Sr: Ca transects of European eel (*Anguilla*
611 *anguilla*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 152–165.
- 612 Feunteun E., Acou A., Guillouët J., Laffaille P., & Legault A. (1998). Spatial distribution of an eel
613 population (*Anguilla anguilla* L.) in a small coastal catchment of Northern Brittany (France).
614 Consequences of hydraulic works. *Bulletin Français de la Pêche et de la Pisciculture* (349): 129-
615 139.
- 616 Feunteun E., Laffaille P., Robinet T., Briand C., Baisez A., Olivier J.-M., & Acou A. (2003). A review of
617 upstream migration and movements in inland waters by anguillid eels: toward a general theory.
618 In *Eel biology* ed. Springer; 191–213.
- 619 Forget G., Baglinière J.-L., Marchand F., Richard A., & Nevoux M. (2018). A new method to estimate

- 620 habitat potential for Atlantic salmon (*Salmo salar*): predicting the influence of dam removal on
621 the Sélune River (France) as a case study. ICES Journal of Marine Science 75: 2172–2181.
- 622 Fomena A., & Bouix G. (1997). Myxosporea (Protozoa: Myxozoa) of freshwater fishes in Africa: keys to
623 genera and species. Systematic Parasitology 37: 161–178
- 624 Fulton T.W. (1904). The rate of growth of fishes. In Twenty-second Annual Report of the fishery board
625 of Scotland. ed. Fishery Board for Scotland, Glasgow, UK. pp. 141–241.
- 626 Geeraerts C., & Belpaire C. (2010). The effects of contaminants in European eel: a review.
627 Ecotoxicology 19: 239–266.
- 628 Geffroy B., & Bardonnet A. (2016). Sex differentiation and sex determination in eels: consequences for
629 management. Fish and Fisheries 17: 375–398.
- 630 Gérard C., Trancart T., Amilhat E., Faliex E., Virag L., Feunteun E., & Acou A. (2013). Influence of
631 introduced vs. native parasites on the body condition of migrant silver eels. Parasite 20, 38.
- 632 Golvan Y.J. (1969) Systématique des Acanthocéphales (*Acanthocephala Rudolphi* 1801). Mémoires du
633 Museum National d'Histoire Naturelle 57, Paris
- 634 Harrison A.J., Walker A.M., Pinder A.C., Briand C., & Aprahamian M.W. (2014). A review of glass eel
635 migratory behaviour, sampling techniques and abundance estimates in estuaries: implications for
636 assessing recruitment, local production and exploitation. Reviews in Fish Biology and Fisheries
637 24: 967–983.
- 638 Hitt N.P., Eyler S., & Wofford J.E.B. (2012). Dam Removal Increases American Eel Abundance in Distant
639 Headwater Streams. Transactions of the American Fisheries Society 141: 1171–1179.
- 640 Hudson P.J., Dobson A.P., & Lafferty K.D. (2006). Is a healthy ecosystem one that is rich in parasites?
641 Trends in Ecology & Evolution 21: 381–385.
- 642 Hüsey K., Limburg K.E., de Pontual H., Thomas O.R.B., Cook P.K., Heimbrand Y., Blass M., & Sturrock
643 A.M. (2020). Trace element patterns in otoliths: the role of biomineralization. Reviews in
644 Fisheries Science & Aquaculture 29: 1–33.
- 645 Jakob E., Hanel R., Klimpel S., & Zumholz K. (2008). Salinity dependence of parasite infestation in the
646 European eel *Anguilla anguilla* in northern Germany. ICES Journal of Marine Science 66: 358–
647 366.
- 648 Jessop B.M. (2010). Geographic effects on American eel (*Anguilla rostrata*) life history characteristics
649 and strategies. Canadian Journal of Fisheries and Aquatic Sciences 67: 326–346.
- 650 Kaifu K., Miller M.J., Yada T., Aoyama J., Washitani I., & Tsukamoto K. (2013). Growth differences of
651 Japanese eels *Anguilla japonica* between fresh and brackish water habitats in relation to annual
652 food consumption in the Kojima Bay-Asahi River system, Japan. Ecology of Freshwater Fish 22:
653 127–136.
- 654 Khalil L. F., Jones A., & Bray R.A. (1994). Keys to the Cestode parasites of Vertebrates. International
655 Institute of Parasitology, CAB International, 235 pp.
- 656 Køie M. (1988). Parasites in European eel *Anguilla Anguilla* (L.) from Danish Freshwater, Brackish and
657 Marine Localities. Ophelia 29: 93–118.

- 658 Laffaille P., Feunteun E., Baisez A., Robinet T., Acou A., Legault A., & Lek S. (2003). Spatial organisation
659 of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecology of Freshwater Fish* 12: 254–
660 264.
- 661 Laffaille, P., Acou, A., & Guillouët, J. (2005). The yellow European eel (*Anguilla anguilla* L.) may adopt a
662 sedentary lifestyle in inland freshwaters. *Ecology of Freshwater Fish*, 14(2), 191–196.
663 <https://doi.org/10.1111/j.1600-0633.2005.00092.x>
664
- 665 Lavielle M. (1999). Detection of multiple changes in a sequence of dependent variables. *Stochastic*
666 *Processes and their Applications* 83: 79–102.
- 667 Limburg K.E., Wuenschel M.J., Hüsey K., Heimbrand Y., & Samson M. (2018). Making the otolith
668 magnesium chemical calendar-clock tick: plausible mechanism and empirical evidence. *Reviews*
669 *in Fisheries Science & Aquaculture* 26: 479–493.
- 670 Lin H.-Y., & Robinson K.F. (2019). How do migratory fish populations respond to barrier removal in
671 spawning and nursery grounds? *Theoretical Ecology* 12: 379–390.
- 672 Machut L.S., Limburg K.E., Schmidt R.E., & Dittman D. (2007). Anthropogenic Impacts on American Eel
673 Demographics in Hudson River Tributaries, New York. *Transactions of the American Fisheries*
674 *Society* 136: 1699–1713.
- 675 Maes G.E., Raeymaekers J.A.M., Pampoulie C., Seynaeve A., Goemans G., Belpaire C., & Volckaert
676 F.A.M. (2005). The catadromous European eel *Anguilla anguilla* (L.) as a model for freshwater
677 evolutionary ecotoxicology: relationship between heavy metal bioaccumulation, condition and
678 genetic variability. *Aquatic Toxicology* 73: 99–114.
- 679 Marcogliese D.J. (2004). Parasites: small players with crucial roles in the ecological theater. *EcoHealth*
680 1: 151–164.
- 681 Mateo M., Lambert P., Tétard S., & Drouineau H. (2017). Impacts that cause the highest direct
682 mortality of individuals do not necessarily have the greatest influence on temperate eel
683 escapement. *Fisheries Research* 193: 51–59.
- 684 McCleave J.D. (2001). Simulation of the impact of dams and fishing weirs on reproductive potential of
685 silver-phase American eels in the Kennebec River basin, Maine. *North American Journal of*
686 *Fisheries Management* 21: 592–605.
- 687 McConnaughey T., & McRoy C.P. (1979). Food-web structure and the fractionation of carbon isotopes
688 in the Bering Sea. *Marine Biology* 53: 257–262.
- 689 Moravec F. (1994). Parasitic nematodes of freshwater fishes in Europe. *Academia, Praha*, 473 p.
- 690 Nilsson C., Reidy C.A., Dynesius M., & Revenga C. (2005). Fragmentation and flow regulation of the
691 world's large river systems. *Science (New York, N.Y.)* 308: 405–408.
- 692 Ogawa K., & Egusa S. (1976). Studies on eel pseudodactylogyrosis – I. Morphology and classification of
693 three eel dactylogyrids with a proposal of a new species, *Pseudodactylogyrus microrchis*. *Bulletin*
694 *of the Japanese Society of Scientific Fisheries* 42(4): 395-404.
- 695 Palstra A.P., Heppener D.F.M., Van Ginneken V.J.T., Székely C., & Van den Thillart G. (2007). Swimming
696 performance of silver eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*.
697 *Journal of Experimental Marine Biology and Ecology* 352: 244–256.

- 698 Pankhurst N.W. (1982). Relation of visual changes to the onset of sexual maturation in the European
699 eel *Anguilla anguilla* (L.). *Journal of Fish Biology* 21: 127–140.
- 700 Parzanini C., Arts M. T., Power M., Rohtla M., Skiftesvik A. B., Koprivnikar J., Browman H. I., Milotic D.,
701 & Durif C. M. (2021). Trophic Ecology of the European Eel (*Anguilla anguilla*) across Different
702 Salinity Habitats Inferred from Fatty Acid and Stable Isotope Analysis. *Canadian Journal of*
703 *Fisheries and Aquatic Sciences*, DOI: 10.1139/cjfas-2020-0432.
- 704 Patin R., Etienne M., Lebarbier E., Chamaillé-Jammes S., & Benhamou S. (2020). Identifying stationary
705 phases in multivariate time series for highlighting behavioural modes and home range
706 settlements. *Journal of Animal Ecology* 89: 44–56.
- 707 Patin R., Etienne M.P., Lebarbier E., & Benhamou S. (2019). segclust2d: Bivariate
708 Segmentation/Clustering Methods and Tools. R package version 0. 2. 0.
- 709 Pess G.R., Quinn T.P., Gephard S.R., & Saunders R. (2014). Re-colonization of Atlantic and Pacific rivers
710 by anadromous fishes: linkages between life history and the benefits of barrier removal. *Reviews*
711 *in Fish Biology and Fisheries* 24: 881–900.
- 712 Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J., & Montana C.G. (2007). Getting to
713 the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope
714 analyses. *Oecologia* 152: 179–189.
- 715 R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for
716 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 717 Reid A.J., Carlson A.K., Creed I.F., Eliason E.J., Gell P.A., Johnson P.T.J., Kidd K.A., MacCormack T.J.,
718 Olden J.D., & Ormerod S.J. (2019). Emerging threats and persistent conservation challenges for
719 freshwater biodiversity. *Biological Reviews* 94: 849–873.
- 720 Righton D., Westerberg H., Feunteun E., Økland F., Gargan P., Amilhat E., Metcalfe J., Lobon-Cervia J.,
721 Sjöberg N., Simon J., et al. (2016). Empirical observations of the spawning migration of European
722 eels: The long and dangerous road to the Sargasso Sea. *Science Advances* 2, e1501694.
- 723 Righton D., Piper A., Aarestrup K., Amilhat E., Belpaire C., Casselman J., Castonguay M., Díaz E., Dörner
724 H., & Faliex E. (2021). Important questions to progress science and sustainable management of
725 anguillid eels. *Fish and Fisheries* 22: 762–788.
- 726 Rueden C.T., Schindelin J., Hiner M.C., DeZonia B.E., Walter A.E., Arena E.T., & Eliceiri K.W. (2017).
727 ImageJ2: ImageJ for the next generation of scientific image data. *BMC bioinformatics* 18: 1–26.
- 728 Secor D.H., Henderson-Arzapalo A., & Piccoli P.M. (1995). Can otolith microchemistry chart patterns of
729 migration and habitat utilization in anadromous fishes? *Journal of Experimental Marine Biology*
730 *and Ecology* 192: 15–33.
- 731 Tabouret H., Bareille G., Claverie F., Pécheyran C., Prouzet P., & Donard O.F.X. (2010). Simultaneous
732 use of strontium: calcium and barium: calcium ratios in otoliths as markers of habitat: application
733 to the European eel (*Anguilla anguilla*) in the Adour basin, South West France. *Marine*
734 *Environmental Research* 70: 35–45.
- 735 Tabouret H., Lord C., Bareille G., Pécheyran C., Monti D., & Keith P. (2011). Otolith microchemistry in
736 *Sicydium punctatum*: indices of environmental condition changes after recruitment. *Aquatic*
737 *Living Resources* 24: 369–378.

738 Teichert N., Tabouret H., Lagarde R., Grondin H., Ponton D., Pécheyran C., & Bareille G. (2018). Site
739 fidelity and movements of an amphidromous goby revealed by otolith multi-elemental
740 signatures along a tropical watershed. *Ecology of Freshwater Fish* 27: 834-846.

741 Teichert N., Tétard S., Trancart T., de Oliveira E., Acou A., Carpentier A., Bourillon B., & Feunteun E.
742 (2020). Towards transferability in fish migration models: A generic operational tool for predicting
743 silver eel migration in rivers. *Science of The Total Environment* 739: 140069.

744 Tesch F.W. (2003). *The Eel*. Oxford, UK.

745 Thielen F., Münderle M., Taraschewski H., & Sures B. (2007). Do eel parasites reflect the local
746 crustacean community? A case study from the Rhine river system. *Journal of Helminthology* 81:
747 179–189.

748 Van den Thillart G., Palstra A., & Van Ginneken V. (2007). Simulated migration of European silver eel;
749 swim capacity and cost of transport. *Journal of Marine Science and Technology* 15: 1–16.

750 Tsukamoto K., & Nakai I. (1998). Do all freshwater eels migrate? *Nature* 396: 635–636.

751 Verhelst P., Reubens J., Buysse D., Goethals P., Van Wichelen J., & Moens T. (2021). Toward a roadmap
752 for diadromous fish conservation: the Big Five considerations. *Frontiers in Ecology and the*
753 *Environment* 19: 396-403.

754 Vignon M. (2015). Extracting environmental histories from sclerochronological structures—Recursive
755 partitioning as a mean to explore multi-elemental composition of fish otolith. *Ecological*
756 *Informatics* 30: 159–169.

757 Vollestad L.A., Jonsson B., Hvidsten N.A., Naesje T.F., Haraldstad O., & Ruud-Hansen J. (1986).
758 Environmental factors regulating the seaward migration of European silver eels (*Anguilla*
759 *anguilla*). *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1909–1916.

760 Vøllestad L.A. (1992). Geographic variation in age and length at metamorphosis of maturing European
761 eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology* 61: 41–48.

762 Watson J.M., Coghlan S.M., Zydlewski J., Hayes D.B., & Kiraly I.A. (2018). Dam Removal and Fish
763 Passage Improvement Influence Fish Assemblages in the Penobscot River, Maine. *Transactions of*
764 *the American Fisheries Society* 147: 525–540.

765 WWF, RiverWatch, GEOTA, & EuroNatur. (2019). *Hydropower pressure on European rivers: The story*
766 *in numbers*.

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768

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 (%).

Life-history traits		Females	Males	p-value
River life condition	Trophic level	11.93 \pm 0.29	13.14 \pm 0.30	0.008
	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	< 0.001
Spawning migration	Size (mm)	586.18 \pm 19.71	380.20 \pm 5.60	< 0.001
	Condition - K	0.19 \pm 0.00	0.18 \pm 0.00	0.028
	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	0.046
	Gonads - GSI (%)	1.80 \pm 0.07	0.39 \pm 0.06	< 0.001
Metazoan parasites	Total prevalence (%)	70.59 \pm 7.81	90.00 \pm 4.74	0.032
	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	0.024
	<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	< 0.001	

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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
MYXOZOA						
<i>Myxidium giardii</i> (Cepede, 1906)	G	D MU	-	9.46 ± 3.40	0.96 ± 0.53	Ingestion of spores released by oligochaete HI
MONOGENA						
<i>Pseudodactylogyrus</i> sp. Gusev, 1965	G	E DMU	Surface browser	35.14 ± 5.55	1.93 ± 0.60	Active attachment on gill lamellae
CESTODA						
<i>Bothriocephalus claviceps</i> (Goeze, 1782)	I	M	Osmotrophic	1.35 ± 1.34	0.01 ± 0.03	HI or HP ingestion (copepods, fish)
NEMATODA						
<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)
ACANTHOCEPHALA						
<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)

780

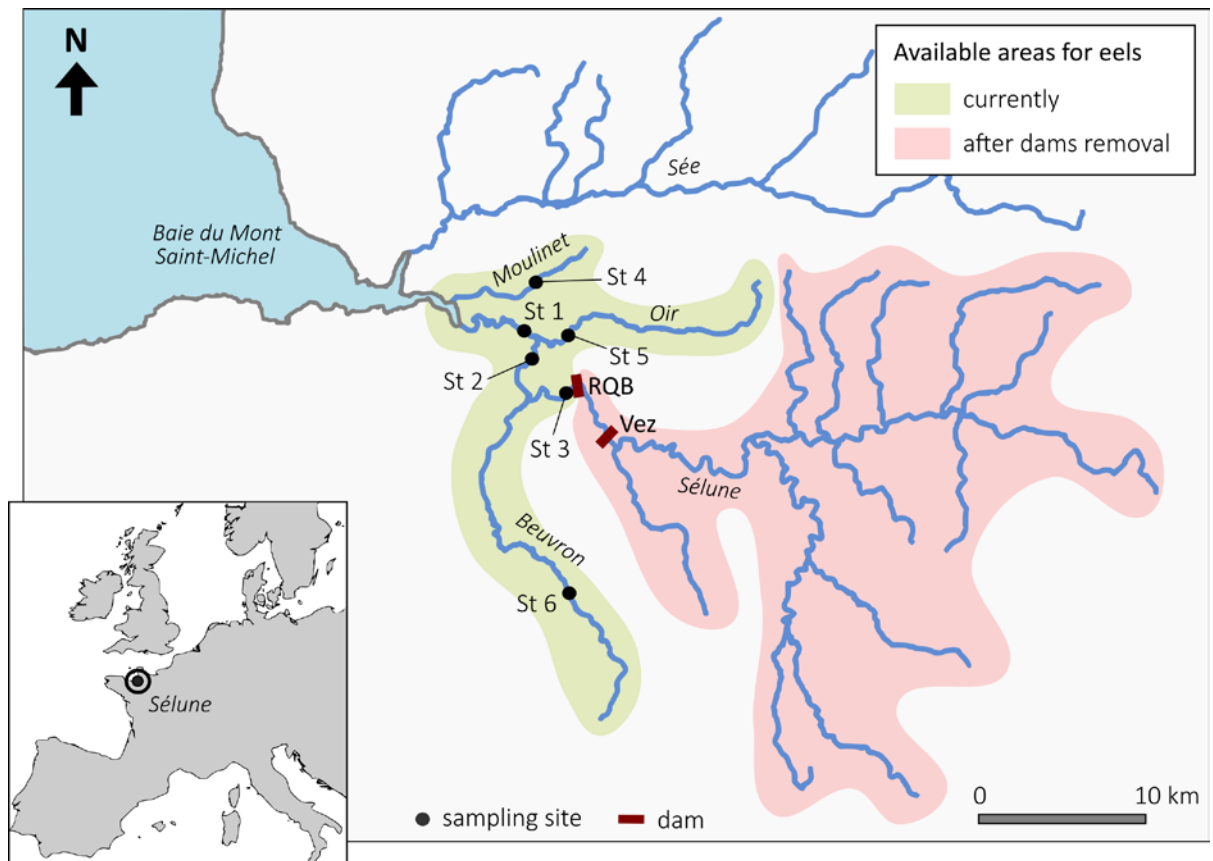
782 Table 3: Changes in life-history traits and parasite descriptors of silver eels (n = 74) depending on
 783 the main sectors of the Sélune catchment. The mean \pm standard error are presented, along with the
 784 significance of mixed models investigating differences between catchment sectors. abd: 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 ⁻¹)	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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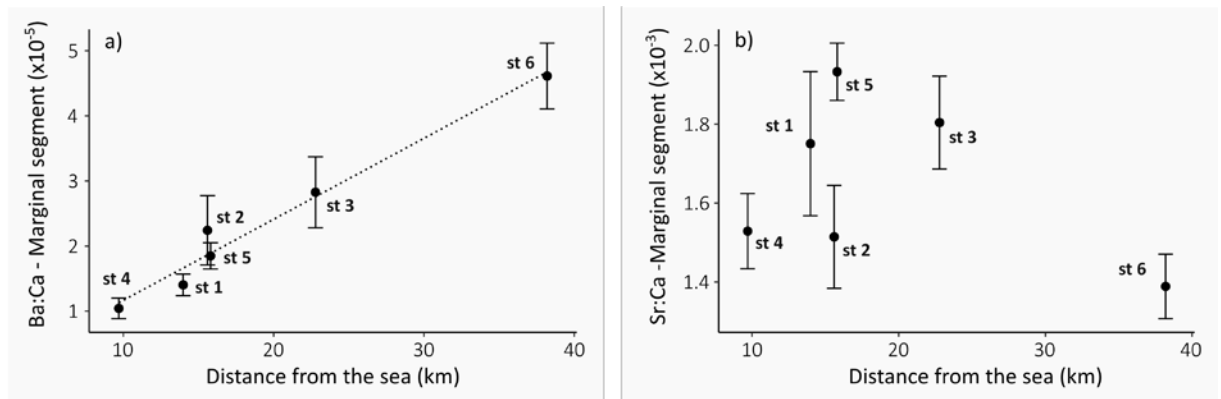
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790 **Figure 1:** Location of the six sampling sites within the Sélune catchment, Western Europe, France.

791 The green area highlights the river reaches currently accessible for eels, whereas the red indicates the

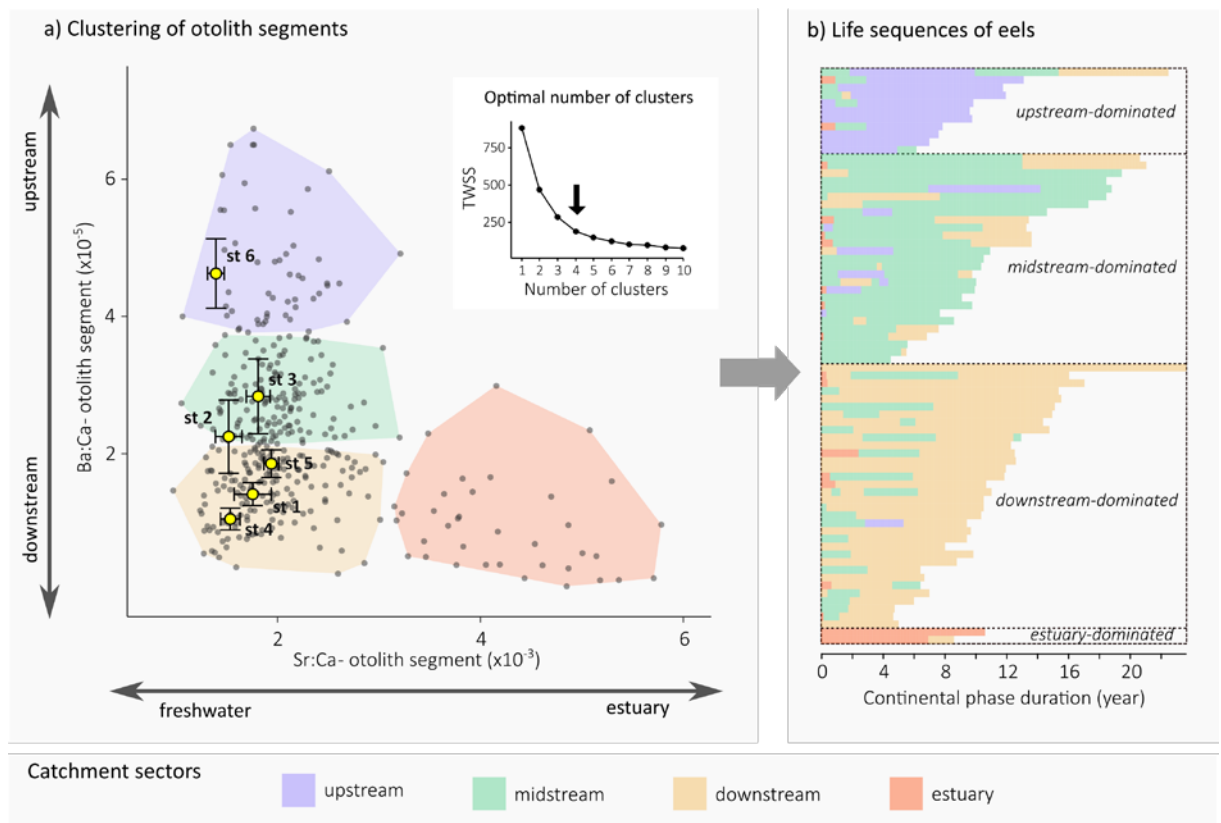
792 inaccessible ones, obstructed by the dams (RQB: Roche-qui-Boit; Vez: Vezins). St 1 to St 6 indicate the

793 different sites where yellow eels were caught, while silver eels were collected at St 1.



794

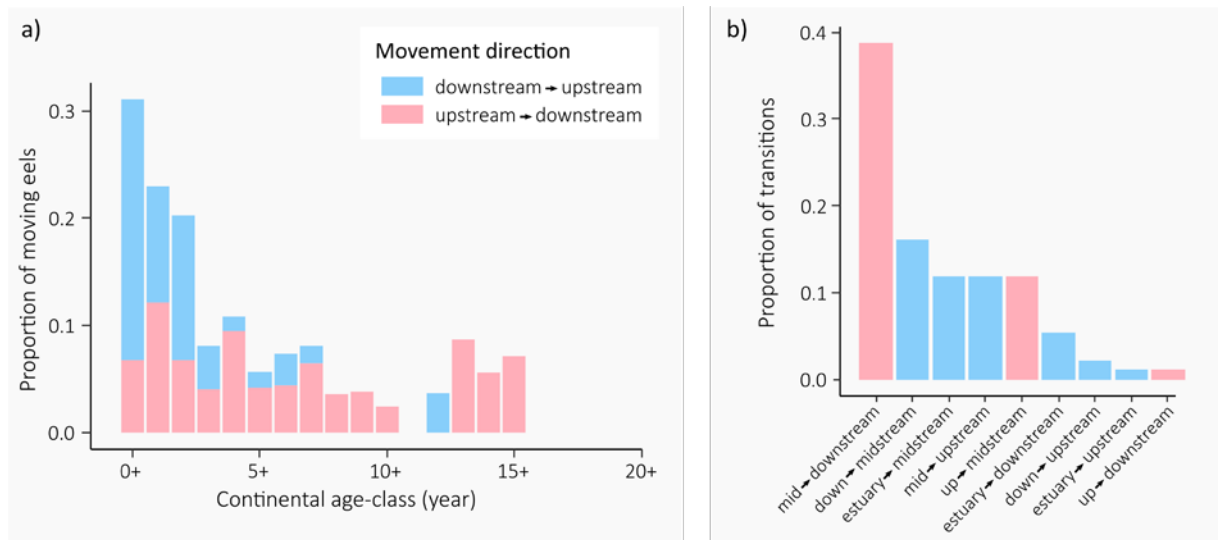
795 **Figure 2:** Relationships between the distance from the sea and otolith signatures recorded in the
 796 marginal segments of resident eels. The mean elemental ratios of Sr:Ca (a) and Ba:Ca (b) were
 797 provided for the six river sites (from St 1 to St 6) along the Sélune catchment. The vertical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



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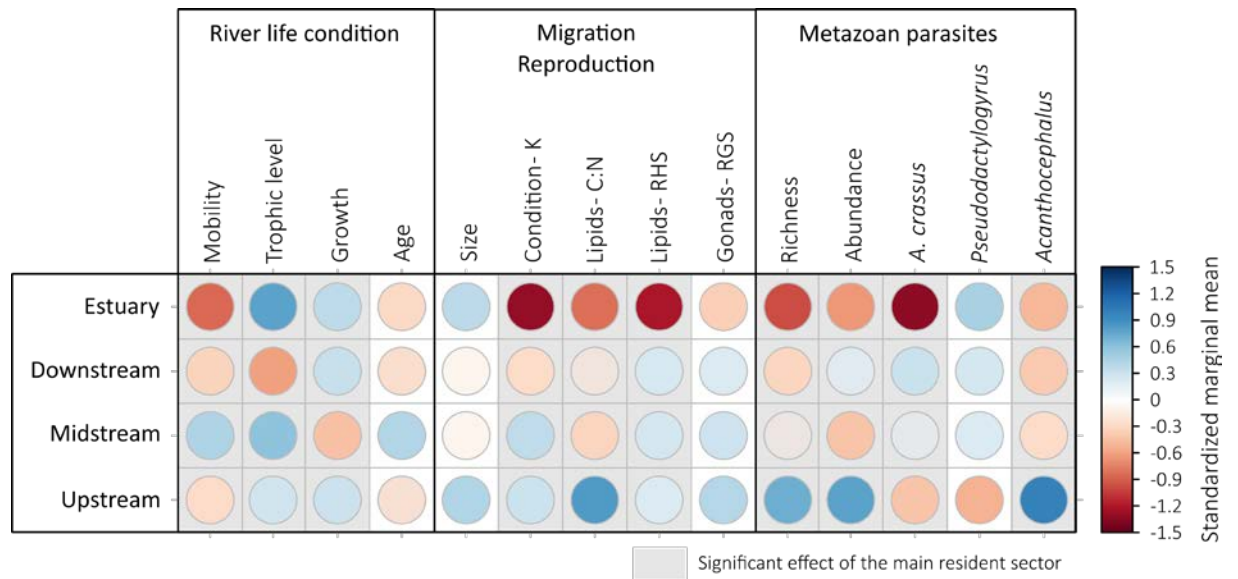
800 **Figure 3:** Reconstruction of silver eel life sequences based on otolith elemental signatures. a)
 801 Clustering of otolith segments based on Sr:Ca and Ba:Ca elemental signatures of silver eels collected in
 802 the Sélune catchment. The optimal number of clusters was defined from the Total Within 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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809

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.



814

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.

819