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1 Early back-calculated size-at-age of Atlantic yellow eels sampled along ecological
2 gradients in the Gironde and St. Lawrence hydrographical systems

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21 **Abstract**

22 An international sampling program investigating the causes of the decline of American
23 eels (*Anguilla rostrata*) and European eels (*Anguilla anguilla*) in the St. Lawrence (Canada) and
24 Gironde (France) rivers systems provided the opportunity to compare early growth of eels of each
25 species among habitats using back-calculated size-at-age from 1 to 5 years old. Our study
26 supports previous studies showing that the early back-calculated lengths of *A. anguilla* were
27 higher in downstream and more saline Gironde system habitats than in the upstream fluvial
28 section, and provides a new indication that length at 1-year-old is twice higher than that reported
29 10 years earlier. However, our data contradict the current paradigm for *A. rostrata* by providing
30 evidence that early size-at-age of eels from the upstream St. Lawrence system, most distant from
31 the spawning area, exceeds those of eels sampled downstream, at less distant sites in the estuarine
32 section. Overall these observations are consistent with the hypothesis that the observed spatial
33 variations in early growth rate of yellow eels sampled in the St. Lawrence and Gironde systems
34 are the consequence of processes occurring in the first year of age such as genetic selection
35 and/or genetically-dependent habitat choice.

36
37 **Keywords:** *Anguilla rostrata*; *Anguilla anguilla*; back-calculated length; growth; habitat; St.
38 Lawrence River system; Gironde River system

39

List of abbreviations

Abbreviation	Signification
CER	Certes
DOR	Dordogne river
GAR	Garonne river
GIR	Gironde river
SFL	Saint François Lake
SJR	Saint Jean River
SOR	Sud-Ouest River
SPL	Saint Pierre Lake
Y	Year

40

41

42 Introduction

43 A decline of North European and American eel populations (here called “Atlantic” eels)
44 has been observed over the last 30 years (Castonguay et al. 1994; Cosewic 2012; Dekker 2003;
45 FAO/ICES 2009). Multiple factors have been evoked, including barriers to migration,
46 overfishing, parasites, pollutants and oceanographic and climate changes (Castonguay et al. 1994;
47 Couillard et al. 2014; Geeraerts and Belpaire 2010), but it remains difficult to disentangle their
48 relative contributions and they have probably acted in synergy (Jacoby et al. 2015; Miller et al.
49 2016).

50 Atlantic eels are two panmictic and catadromous species with very similar life cycles
51 (Avisé 2003). After a long trans-oceanic larval drift from their spawning grounds in the Sargasso
52 Sea to the continental shelf, glass eels penetrate into coastal areas, then they grow into elvers and
53 later into yellow eels (Tesch and Rohlf 2003). Yellow eels complete their somatic growth phase
54 in a large range of habitats (estuaries, rivers and lakes) (Daverat and Tomás 2006; Jessop 2010).
55 At the end of the yellow phase, they undergo a last metamorphosis, turn into silver eels and begin

56 their long migration to the Sargasso Sea where they reproduce and die (Tesch and Rohlf 2003).
57 The growth phase associated with lipid accumulation is a key determinant of trans-oceanic
58 migration, fecundity, and consequently of reproductive success (Belpaire et al. 2009; Svedäng
59 and Wickström 1997). Since the metamorphosis into silver eels and the success of their
60 reproductive migration are heavily dependent on body length and fat content at migration, growth
61 rate of the yellow phase directly affects reproductive success (Belpaire et al. 2009; Couillard et
62 al. 2014; Van Ginneken and Van den Thillart 2000).

63 Female American and European eels exhibit a latitudinal cline in growth rate, partly
64 explained by temperature, with lower growth rate (at the silver stage) and higher size-at-
65 metamorphosis at higher latitudes and/or longer distances from the spawning site (Jessop 2010;
66 Vélez-Espino and Koops 2009). Our current understanding is that within the St. Lawrence system
67 (Canada), the growth rate of female eels decreases and size-at-metamorphosis increases from the
68 Gulf of St. Lawrence (downstream section) to Lake Ontario (upstream section)(Jessop 2010).
69 While eel's growth rate is known to be largely plastic (Côté et al. 2014; Drouineau et al. 2008),
70 genetic/epigenetic differences linked to differential migratory patterns or to selection are
71 increasingly supported as contributing factors for the early differential growth rates observed in
72 elvers at different latitudes (Côté et al. 2009; Côté et al. 2014).

73 At the river basin scale, eels can use a wide range of habitats as demonstrated by studies
74 using otolith microchemistry (Daverat and Tomás 2006; Thibault et al. 2007). This also results in
75 variability in growth rates at this basin scale. Yellow eels with different migratory tactics have
76 different growth rates, as shown in the Gironde System (France) for *A. anguilla* (Daverat et al.
77 2012; Daverat and Tomás 2006; Edeline et al. 2007; Edeline et al. 2005a) and in various sites in
78 the St. Lawrence system for *A. rostrata* (Boivin et al. 2015; Cairns et al. 2009; Jessop et al. 2007;
79 Thibault et al. 2007). Resident freshwater eels display lower growth rates than resident brackish

80 water eels, and the growth rates of nomadic migrants vary according to habitat salinity (Daverat
81 and Tomás 2006; Thibault et al. 2007). As observed for the latitudinal variations of growth rate,
82 differential growth patterns between salinity ecotypes are detected at an early age (glass eels and
83 elvers) and appear to be related to genetic/epigenetic differences (Côté et al. 2009; Edeline et al.
84 2007; Pavey et al. 2015).

85 The present study is part of an international project examining the influence of
86 anthropogenic and environmental factors on the decline of Atlantic eels. This large-scale
87 sampling program provided a unique opportunity to investigate early size-at-age of yellow
88 Atlantic eels captured at the same time with similar protocols in different habitats of the Gironde
89 and St. Lawrence systems. Previous studies demonstrated that both species exhibited, at an early
90 age, extreme inter-individual phenotypic variance in terms of size-at-age related to
91 genetic/epigenetic differences and to the use of highly heterogeneous environments (Côté et al.
92 2009; Côté et al. 2014; Daverat and Tomás 2006; Gagnaire et al. 2012). The objective of our
93 study was to test if the current spatial patterns of early size-at-age of yellow *Anguilla sp.* in these
94 two systems are consistent with the current paradigm of higher early growth rates of eels growing
95 in habitats more saline and/or less distant from the Sargasso Sea spawning area. Early growth
96 rates of yellow eels were compared within species among habitats more or less saline and/or
97 distant from the Sargasso Sea, using back-calculated length from 1 to 5 years old. Then, we
98 carried out linear mixed effect models for each site including random effects to account for
99 possible inter-cohort's variation in lengths and individual random effects. Finally, the early size-
100 at-age of American and European eels were compared with historical data to examine the
101 temporal evolution of eel early growth in recent years.

102

103 **Materials and methods**

104 The St. Lawrence Estuary is one of the largest and most productive ecosystems in Canada
105 (Dufour and Ouellet 2007). It is 5 times longer and 9.5 times wider than the Gironde Estuary
106 (GE) (Fig. 1 and Table S1). The GE is one of the largest estuaries in Western Europe and it
107 originates from the confluence of two freshwater rivers, the Garonne and the Dordogne rivers, at
108 the Bec d'Ambès. Both systems are composed of marine, brackish and freshwater sections (Fig.
109 1).

110 For each hydrographical system during early summer in 2011 and 2012, a total of 120
111 yellow eels were collected at 4 sites along brackish and freshwater sections (Table 1). Our
112 scientific collector permits restricted the number of fish to 30 eels per site because of their
113 threatened status, a major constraint of this study. As further constraint, fish were captured in two
114 different years (15 eels per site per year) due to the low abundance of eels in several sites and the
115 requirement of our sampling design for selecting specific size ranges (see below). In Quebec, eels
116 were captured in two fluvial lakes, St. François Lake (SFL) and St. Pierre Lake (SPL) located in
117 the freshwater section and in the mouth of two freshwater tributaries of the Estuary and the Gulf
118 of St. Lawrence respectively, the Sud-Ouest River (SOR) and St. Jean River (SJR), (Fig. 1a and
119 Table 1). SFL and SPL are shallow freshwater fluvial lakes near Montréal in an urbanized and
120 industrialized region (Béguet-Pon et al. 2015; Hodson et al. 2014). Previous studies have shown
121 that the estimated average transit times of the upstream migration of early life stages of eels
122 between the Gulf and these lakes are 3 years and 5-6 years for SPL and SFL respectively (G.
123 Verreault, unpublished data; Benchetrit et al. 2017). Yellow eels from SOR and SJR typically
124 arrive at about 1 to 2 Years old (Y) and grow in running freshwater habitats, which are tributaries
125 opening into a brackish estuary (G. Verreault, unpublished data).

126 In France, eels were captured in two freshwater rivers, the Dordogne (DOR) and Garonne
127 (GAR) Rivers, one brackish site, the Gironde estuary (GIR) with a salinity gradient moving up
128 and downstream as a function of both tide and freshwater discharge (Larrose et al. 2010) and one
129 salt marsh site, Certes (CER). This site is located in the Certes marsh connected to the Arcachon
130 basin, a nearby coastal environment not influenced by water from the Gironde watershed (Fig. 1b
131 and Table 1). The GIR site is known to be contaminated by anthropic and agricultural activities
132 (Delpech et al. 2010; Tableau et al. 2013). The DOR site is considered as the least contaminated
133 site in the watershed and the GAR site is located near the city of Bordeaux in a contaminated
134 region (Tapie et al. 2011). The DOR and GAR sites are located in the tidally influenced part of
135 the rivers. In contrast to *A. rostrata* from the St. Lawrence system, the estimated transit time of *A.*
136 *anguilla* elvers from the coast to their growth habitat is very short, an average of 2-3 weeks to
137 reach the GAR and DOR sites (Beaulaton and Castelnaud 2005).

138 European and American yellow eels were captured using trap nets (mesh size of 6.4 mm),
139 trawl (mesh size of 31 mm) and electro-fishing by professional fishers or technical staff (Table
140 1). In 2011 and 2012, all eels were from a single capture in one day, except for SOR and SJR
141 sites in Quebec where eels were captured in two days due to a small sample the first day. Based
142 on existing information according to Nilo and Fortin (2001), yellow eels from a pre-defined size
143 were targeted, in order to have the same range of ages (5-10 years old) for all sites. In Quebec,
144 the selected fish ranged between 495 to 655 mm in length and in France, the selected fish ranged
145 between 433 to 578 mm. After each capture, eels were kept in tanks with aerated water from the
146 site for few hours until processing.

147

148 **Morphometric measurements and tissue sampling**

149 American and European eels were processed using the same standardized protocols in

150 France and in Quebec. Total body length (± 1 mm) and total body mass (± 0.1 g) were measured
151 and then eels were killed by decapitation. Eel manipulations were made in agreement with
152 approved protocols from animal ethics committees in both countries. Sex (undifferentiated: U;
153 Male: M; Female: F) was determined by macroscopic observation of the gonads using previously
154 described criteria (Jones and Sinha 1966). Based on calculated gonadal and pectoral fin indices
155 (Durif et al. 2000; Durif et al. 2009), all eels retained were immature yellow eels.

156

157 **Otolith processing**

158 Sagittal otoliths were extracted, cleaned with distilled water, dried and stored in plastic
159 Eppendorf tubes at ambient room temperature until processing. Otoliths were processed for age
160 determination according to Verreault et al. (2009) using a five-stage procedure: 1) cleaning with
161 sodium hypochlorite (2.5%) and rinsing with demineralized water and drying with ethanol
162 (70%); 2) embedding in epoxy resin (24h); 3) sanding on 800-grit paper and polishing with
163 aluminium oxide powder (1 μ m); 4) etching with EDTA solution, and finally; 5) staining with
164 0.01% toluidine blue. Otoliths were observed with a binocular microscope (60X) under
165 transmitted light for aging.

166

167 **Back-calculation of length**

168 Back calculation was undertaken using a relationship between body size and otolith radius
169 (Francis 1990). The biological intercept procedure proposed by Campana (1990) uses a
170 biologically-determined intercept in the back-calculation equation using the mean size of the
171 body and the otolith at the elver stage. This method is robust to any variations in the fish-otolith
172 relationship and provided from Tremblay (2009). Back-calculated body length (L_t) at age t are
173 calculated as follows:

174
$$L_t = L_c + (L_c - L_{bi}) \times (O_t - O_c) / (O_c - O_{bi})$$

175 where O_t is the measured otolith radius at age t , L_c and O_c are the body length and otolith radius
176 at capture, respectively, and L_{bi} and O_{bi} are the body length and otolith radius at the biological
177 intercept, respectively. Measurements of the radius (mm) of the t^{th} annuli (R_t), which is the
178 distance from the elver mark (the first growth check outside the nucleus from where continental
179 age determination commences) of the otolith to the t^{th} annuli (meaning: $O_t - O_{bi}$) and of the radius
180 (mm) of the otolith at capture (R), which is the distance from the elver mark of the otolith to the
181 edge ($O_c - O_{bi}$). These measurements were always made along the longest axis on the ventral side
182 of the sagittae of the otolith. In this study, the mean total body length of elvers when they recruit
183 to coasts (L_{bi}) was set to 67 mm (SD=4.5), for *A. anguilla* and 62 mm (SD=3.2) for *A. rostrata*,
184 which corresponds to the age 0 year old or continental age (ICES 2009; Lambert et al. 2003).

185

186 **Statistical analyses**

187 Statistical analyses were conducted using Prism v. 5.0 (GraphPad Software Inc., San
188 Diego, CA, USA) and R (R. 2011). Mixed models were fitted using the package lme4 (Horton et
189 al. 2011) and Tukey tests were carried out using package multcomp (Bates et al. 2014). For all
190 statistical tests, a probability of $p \leq 0.05$ was considered significant. It was not possible to collect
191 same-sized eels at each sampling site. To increase the comparability of eels among sampling
192 sites, only eels between 2 and 20 years old were considered in this analysis. The total number of
193 eels retained for statistical analyses were 102 in 2011 and 112 in 2012 (Tables 2 and 3).

194 Most analyses were conducted for each country/species separately. Firstly, biological
195 characteristics of eels at capture were statistically compared among sites within a species and
196 year. For each year, data normally distributed (using the Shapiro-Wilk test) were compared with
197 one-way ANOVA followed by a Tukey's multiple comparison test. Data not normally distributed

198 was compared among sites using non-parametric Kruskal-Wallis test (KW) followed by the
199 Dunn's multiple comparison test. The relative proportions of female and undifferentiated eels
200 were compared among sites or between sampling years in each country using a Chi-square test.

201 To compare size among sites within systems for eels of the same age, back-calculated
202 lengths from 1 to 5 Years old (Y) were compared among sites within a species using the KW test
203 as described above. Then, we carried out linear mixed effect models for each site including
204 random effects to account for possible inter-cohort variations in length and individual random
205 effects. First, we fitted a linear mixed effect model for each site to assess whether length at 1Y
206 significantly differed among sites:

$$207 \quad (1) L_1 \sim \text{Site} + (1|\text{cohort})$$

208 with L_1 , the length-at-age at 1Y, Site, the site of capture and (1|cohort), a random effect to
209 account for possible inter-cohort variations in length. Tukey multiple comparison tests were then
210 carried out to detect significant differences among sites.

211 A second analysis was performed to check whether growth rates were different among
212 sites. We first computed yearly growth increments for each fish, i.e. the difference in back-
213 calculated lengths between two successive ages. Growth increments are a linear function of initial
214 length when fish follow a Von Bertalanffy growth curve (i.e. $I_t = L_t - L_{t-1} = (L_\infty - L_{t-1}) \cdot (1 - \exp(-K))$)
215 with I_t , the growth increment between year $t-1$ and year t , L_t the size-at-age at age t , K the Brody
216 coefficient and L_∞ the asymptotic length). In view of this, we fitted a generalized linear mixed
217 model on growth increments for each species separately:

$$218 \quad (2) I_t \sim \text{Site} + L_{t-1} + (1|\text{eel}) + (1|\text{cohort})$$

219 with I_t , the vector of yearly growth increments (we used the 4 increments for each from 1Y to
220 5Y) and L_{t-1} , the vector containing the corresponding initial length. We added a cohort random

221 effect to account for inter-cohort differences and an individual random effect since each eel was
222 considered 4 times in the analysis. We used a gamma family distribution to account for
223 dissymmetry in growth increment distributions (DeLong et al. 2001; Drouineau et al. 2008), with
224 an identity link to preserve the linear relationship. Similarly, to the first model, we carried out
225 Tukey multiple tests to compare yearly growth increments among sites.

226

227 **Results**

228 **Eel biological characteristics in the St. Lawrence and Gironde systems**

229 For *A. anguilla* sampling, male eels were removed due to small sample size (n=3 in the
230 Gironde system) and for *A. rostrata* sampling, no males have been detected (n=0 in the St.
231 Lawrence system). In 2011 and 2012, body length and age of *A. anguilla* from the Gironde
232 system ranged from 278 to 825 mm and from 3 to 18 years old respectively, and differed among
233 sites (H=38.5, p<0.0001 in 2011 and H=12.8, p=0.005 in 2012 for body length; H=33.8,
234 p<0.0001 in 2011 and H=25.3, p<0.0001 in 2012 for age, Tables 2 and 3). Eels from DOR were
235 smaller and lighter than eels captured in GAR, GIR and CER with median body length and body
236 mass 1.3 and 2.8 times lower, respectively (H=37.7, p<0.0001 in 2011 and H=21.8, p<0.0001 in
237 2012 for body mass, Tables 2 and 3). In both sampling years, the proportions of undifferentiated
238 eels increased from the salt marsh habitat (CER) to freshwater habitats and the highest
239 proportions of undifferentiated eels were observed in DOR and GAR (Tables 2 and 3). No
240 significant difference was observed in biological characteristics between female and
241 undifferentiated European eels in GAR and DOR (Student t-test, Tables S2).

242 In the St. Lawrence system, the body length and age of *A. rostrata* captured in 2011 and
243 2012 ranged from 265 to 963 mm and from 5 to 19 years old respectively and both parameters

244 differed among sites ($F=174.0$, $p<0.0001$ in 2011 and $H=41.5$ $p<0.0001$ in 2012, for body length
245 and $F=13.1$, $p<0.0001$ in 2011 and $H=6.1$, $p<0.0001$ in 2012 for age, Tables 2 and 3). Eels from
246 SOR were consistently smaller and lighter than eels from SPL and SFL ($H=44.4$, $p<0.0001$ in
247 2011 and $H=40.7$, $p<0.0001$ in 2012, for body mass, Tables 2 and 3). In 2011, body length and
248 age were higher in eels from SPL and SFL compared to SJR (Table 2). In 2011 and 2012, body
249 mass was higher in SPL and SFL than in SJR (Tables 2 and 3).

250 In 2011, yellow eels captured in the Quebec sites were older than those sampled in France
251 ($U=357.5$, $p<0.0001$, Mann Whitney test).

252
253 **Comparison of back-calculated length at age 1Y to 5Y of eels from different habitats in**
254 **each species**

255 In the Gironde system, at 1Y, back-calculated lengths of eels sampled in the salt marsh
256 CER site (median of 219 mm) were higher than those of eels sampled in the estuarine GIR site
257 and in the fluvial GAR and DOR sites (medians were respectively 152, 136 and 134 mm,
258 $H=51.4$, $p<0.0001$, Fig. 2a and Table S3). At 2Y, back-calculated lengths of eels from the
259 estuarine GIR site became higher than those of eels from fluvial GAR and DOR sites and the
260 difference was maintained until 5Y ($F=51.2$, $p<0.0001$ for 2Y; $F=48.7$, $p<0.0001$ for 3Y; $F=30.6$,
261 $p<0.0001$ for 4Y and $F=16.7$, $p<0.0001$ for 5Y, Fig. 2a). From 2Y to 5Y, eels from the marine
262 CER site had the higher median of back-calculated length compared to the other sites and eels
263 from GAR and DOR sites remained with the lowest median of back-calculated length (Fig. 2a).

264 In the St. Lawrence system, at 1Y, back-calculated lengths of eels captured in fluvial SPL
265 and SFL sites (with a median length of 184 and 171 mm respectively) were higher than those of
266 eels from the estuarine SOR and SJR sites (with a median length of 134 and 142 mm
267 respectively, ($F=31$, $p<0.0001$, Fig. 2b and Table S3). The significant difference between higher

268 back-calculated length of eels from SPL and SFL and lower back-calculated length of eels from
269 SOR and SJR was maintained until 5Y (H=46.4, $p<0.0001$ for 2Y; H=50.2, $p<0.0001$ for 3Y;
270 F=31.2, $p<0.0001$ for 4Y and F=40.6, $p<0.0001$ for 5Y, Fig. 2b and Table S3).

271

272 **Linear mixed effect models**

273 In both years, for *A. anguilla*, this analysis confirmed that the length at age 1Y was higher
274 in CER than in any other site. Length at age 1Y in GIR was slightly higher than in DOR, and no
275 difference was observed between GAR and DOR. This confirmed the decreasing gradient in
276 length at age 1Y from downstream to upstream habitats (Table 4). For *A. rostrata*, length at age
277 1Y was higher in the two upstream lakes than in downstream rivers but no differences were
278 detected between the two lakes or between the two rivers (Table 4).

279 Results were rather similar regarding subsequent growth-increments (Table 5): increments
280 were higher in downstream sites than in upstream sites for *A. anguilla*, although CER and GIR
281 did not differ. Yearly growth increments from 1Y to 5Y were consistently higher in the two
282 upstream lakes than in downstream rivers for *A. rostrata*.

283

284 **Discussion**

285

286 This study confirms that the current spatial pattern of early growth rates of yellow *A.*
287 *anguilla* in the Gironde system is consistent with the paradigm of higher early growth rates of
288 eels growing in habitats more saline and/or less distant from the Sargasso Sea spawning area.
289 Moreover, comparisons with historical data in the Gironde system indicate that this spatial
290 pattern remains stable despite temporal variation in the overall growth rates. In contrast, our
291 study reveals that early growth rates of yellow *A. rostrata* in the St. Lawrence system are highest
292 in eels captured in the less saline habitats, more distant from the Sargasso Sea, in contradiction

293 with the current paradigm. This new information is useful to guide further studies on the
294 mechanisms leading to the different ecotypes of Atlantic eels in different rearing habitats.

295
296 **Spatial variations in early back-calculated length in *Anguilla anguilla***

297 At 1Y, eels from the salt marsh site CER had higher back-calculated length than eels from
298 the estuarine site GIR and from the fluvial sites GAR and DOR. From 2Y to 5Y, while eels from
299 CER maintained their higher back-calculated length, eels from the estuarine site GIR displayed
300 an increasingly faster growth rate with higher back-calculated length than those of eels from
301 freshwater sites. These results are consistent with previous studies, which demonstrated that eels
302 sampled in brackish habitats grew faster than those from riverine freshwater habitats.
303 Specifically, Daverat and Tomás (2006) have reached similar conclusions on the spatial
304 variations of early growth rates of eels sampled in 2001-2004 in the Gironde system. Since the
305 transit time of *A. anguilla* glass eels from the coast to their growth habitat was estimated to last 2-
306 3 weeks according to Beaulaton and Castelnaud (2005), it is likely that their growth was already
307 influenced by the characteristics (biological, chemical and/or physical) of the selected habitat at
308 the age of 1Y. However, laboratory (Edeline et al. 2007) and genetic studies (Pujolar et al. 2005)
309 in *A. anguilla* suggest that the ecotypic differences among eels occupying different habitats are
310 not only the effect of phenotypic plasticity. They may also be caused by functional genetic
311 differences resulting from intra-generational spatially varying selection and/or genotype-
312 dependent habitat choice (or both) of ecologically divergent habitats (Pavey et al. 2015).

313 At 1Y, no significant difference in length was detected between eels from the estuarine
314 site GIR and eels from the freshwater sites GAR and DOR. This observation could be related to a
315 high within-site inter-individual variability in back-calculated length. One factor of variability is
316 the older age of some of the eels sampled in GIR and GAR. However, results of analyses using a

317 linear mixed model integrating individual variability and cohort effect were consistent with the
318 results of the KW test indicating these sources of variability had no significant impact on the
319 results. Overall these data and the similarity with the pattern described a decade earlier by
320 Daverat and Tomás (2006) indicate a very consistent spatial pattern of higher growth at an early
321 age (from 1Y to 5Y) in yellow eels sampled in the more saline site (CER) compared to eels
322 sampled in the upstream fluvial section of the Gironde system.

323

324 **Spatial variations in early back-calculated length in *Anguilla rostrata***

325 *Anguilla rostrata* sampled in the fluvial freshwater sites (SPL and SFL) in the Upper St.
326 Lawrence River had a higher back-calculated length from 1Y to 5Y compared to same-aged *A.*
327 *rostrata* sampled downstream in tributaries opening into a brackish estuary (SJR and SOR). In
328 our study, the difference in back-calculated length in *A. rostrata* sampled in the upstream St.
329 Lawrence system and those sampled in downstream tributaries was present as early as 1Y. At this
330 early age, *A. rostrata* of the fast-growing group (LSP, LSF) have not yet reached their growing
331 habitat. It is likely that they were still migrating in the St. Lawrence system and therefore their
332 growth rate could not yet be influenced by the local conditions in the fluvial lakes (Benchetrit et
333 al. 2017).

334 The higher back-calculated length at 1Y of eels from the upstream portion of the St.
335 Lawrence system compared to more downstream populations that we report here contrasts with
336 recent literature. Based on previous studies on *A. rostrata* captured in the Gulf of St. Lawrence
337 and in tributaries of the marine portion of the St. Lawrence system, a slower growth at 1Y was
338 expected with increasing distance of the capture sites from the Sargasso Sea (Boivin et al. 2015).
339 A common garden experiment by Côté et al. (2009) suggested a genetic basis for growth
340 differences among *A. rostrata* early life stages from different geographical locations. They found

341 that *A. rostrata* elvers from the Mira River (Nova Scotia; shortest distance to the Sargasso Sea)
342 grew faster than those from Grande-Rivière-Blanche (Québec, longest distance to the Sargasso
343 Sea), a result confirmed by the study of Boivin et al. (2015). Molecular tools were used to
344 support the hypothesis that life-history traits of *A. rostrata* were influenced by spatially variable
345 genetic selection along latitudinal gradients of temperature and/or increasing distance from the
346 Sargasso Sea and by genotype-dependent habitat choice (Boivin et al. 2015; Côté et al. 2009;
347 Gagnaire et al. 2012; Pavey et al. 2015). Moreover, glass eels of *A. rostrata* from New
348 Brunswick and Nova Scotia sites (which are closer to the Sargasso Sea) translocated to Lake
349 Ontario exhibited faster annual growth and matured at smaller sizes and ages at reproductive
350 migration than wild migrating silver eels from Lake Ontario (Couillard et al. 2014; Stacey et al.
351 2014; Verreault et al. 2010). Despite some limitations in fish samplings, our study clearly
352 demonstrates an inverse pattern of early growth rate from 1Y to 5Y for *A. rostrata* with fast
353 growing eels reaching the upstream St. Lawrence system and slow growing eels remaining in the
354 downstream section. These observations question our current understanding of eels adaptation to
355 environmental heterogeneity (Mateo et al. 2016).

357 **Similarities between *A. anguilla* and *A. rostrata* and comparisons with previous studies**

358 This study is the first to use a common methodology to compare the back-calculated
359 length of the yellow stage of the two species of Atlantic eels. Given the wide range of habitats
360 covered in this study (a larger hydro-geographical scale associated with longer upstream
361 migration of early life stages, longer distance to the Sargasso Sea for Gironde system eels and
362 different temperature regimes for the two river systems), we found that from 1Y to 5Y, the back-
363 calculated length of *A. rostrata* collected in the St. Lawrence system in the northern part of their
364 distribution range presented some similarities with values from *A. anguilla* collected in the

365 Gironde system. The back-calculated length of *A. rostrata* from the upper St. Lawrence system
366 (SPL and SFL) was similar to that of eels from the downstream sites GIR (at 2Y and 3Y) and
367 CER (at 4Y and 5Y). From 1Y to 5Y, the back-calculated length of eels from the downstream St.
368 Lawrence system sites, SJR and SOR, were comparable to those of slow-growing eels from the
369 upstream sites GAR and DOR. Our study highlighted an inverse pattern of early growth rate
370 according to the upstream-downstream gradient of the location of habitats between *A. rostrata*
371 with faster growers from the upstream section of the St. Lawrence system and *A. anguilla* with
372 faster growers from the downstream section of the Gironde system.

373 In our study, median of back-calculated length at 1Y and 5Y of *A. anguilla* collected in
374 the Gironde in 2011-2012 (Table S3) were approximately twice those observed in eels captured
375 10 years earlier in the same sites in the Gironde system by Daverat and Tomás (2006). This
376 suggests an improvement in growth performance possibly related to abiotic factors (salinity,
377 temperature, productivity and habitat quality) and/or biotic factors (low density of eels, weak
378 coastal recruitment of glass eels) (Bonhommeau et al. 2008; Daverat et al. 2012; Knights 2003).
379 Despite the observed changes in growth performance in *A. anguilla*, the spatial pattern of early
380 growth rate did not change with time. However, the back-calculated length at 5Y of slow growing
381 *A. rostrata* collected in SJR in 2011-2012 are similar to those calculated for yellow eels captured
382 at the same site in 2004 by Thibault et al. (2007). These data suggest that, at least for the SJR site,
383 no significant change in growth rate up to 5Y has occurred in the last 7-8 years. Unfortunately, to
384 our knowledge, no historic data for early GR of yellow eels collected in the upper part of the St.
385 Lawrence system is available for comparison.

386

387 **Limitations and future directions**

388 The unique biology of eels, and especially their panmictic nature, the variability in their

389 migratory patterns during their growth phase and their large distribution ranges from tropical to
390 subarctic climates, makes their study a challenge in any circumstance. Population declines and
391 severe restrictions on commercial and scientific collection impose further difficulties. Sampling
392 sites in this international study were selected according to salinity, metal and organic
393 contamination gradients found in sediments and biota along the Saint Lawrence and the Gironde
394 systems (Laporte et al. 2016). Nevertheless, these sites cannot be considered to represent fairly
395 the wide range of habitats that the species occupy. Some limitations related to the sampling of
396 eels (30 eels captured in each site and in two years and the use of different fishing gear adapted to
397 each habitat) and the wide range of estimated age (2 to 18 years) may constitute biases.

398 In addition to spatially variable selection and/or genotype-dependant habitat choice,
399 several other processes could contribute to the observed growth variability in 1Y-old eels,
400 including epigenetic changes, early environment influences with carry-over effects on growth and
401 interactions between genotype and environment through phenotypic plasticity. A reduction in the
402 abundance of glass eels arriving in continental habitats associated with the low density of eels in
403 their growth habitats could have contributed to increase their length at early age (Castonguay et
404 al. 1994; Moriarty and Dekker 1997). Temporal variations in hatching times (Kuroki et al. 2017)
405 and in environmental conditions during development (Jonsson and Jonsson 2014) could also
406 affect early growth rates and behaviour. The season in which glass eels arrived on the continental
407 coasts may also affect their size (Desaunay and Guerault 1997). Local environmental factors such
408 as tidal height, water temperature, water discharges and the difference in temperatures between
409 estuarine and river habitats are known to have effects on glass eel's abundance and upstream
410 migratory behavior of migrants (Jessop 2003; Edeline et al. 2006). In addition, physiological
411 traits of eels such as body condition, endocrine system (thyroid hormones) and health status may
412 affect the locomotor activity, the migratory behavior and growth performance (Edeline et al.

413 2005b; Lefebvre et al. 2013). Further studies are needed on the interactions between genetic
414 variation and phenotypic plasticity in response to environmental variation during early
415 development of Atlantic eels and their impact on migration patterns and later-life history
416 performance. For that purpose, longer term studies focussing on variations of growth and
417 behaviour of 0-1 Y eels in relation to genotypes and/or environmental factors are recommended,
418 with larger sample sizes and greater number of sites.

419 In spite of these limitations, our study provides a new indication that for *A. rostrata*
420 sampled along the St. Lawrence system, faster growing individuals appear more likely to
421 colonize the head of the system than slower growing individuals. We have also highlighted that
422 the median of back-calculated length of *A. anguilla* at 1Y and 5Y is twice higher than that
423 reported 10 years earlier. Further studies and monitoring are clearly needed to test the hypothesis
424 of a possible increase of early growth rate in relation to the modifications of abiotic and biotic
425 factors and its consequences for age, length and lipid reserves at migration in *A. anguilla* and *A.*
426 *rostrata*.

427 Finally, whereas several studies have investigated the relationships between genetic
428 selection and growth rate characteristics of glass eels in *A. rostrata*, these studies are limited to
429 eels from tributaries of the lower St. Lawrence Estuary and Gulf and there is a need to confirm
430 these relationships in *A. anguilla*. Comparative studies of these two related Atlantic eel species
431 would help to better understand the relationship between differential growth rate, size-at-
432 metamorphosis, lipid accumulation, sexual differentiation and their genetic and environmental
433 bases in these two species. This information would facilitate prediction of the effects of global
434 environmental changes on the recruitment of these two declining species.

435

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444

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- 638
- 639

Table 1. Characteristics of sampling sites in France and in Quebec.

Site	FRANCE (<i>A. anguilla</i>)				QUEBEC (<i>A. rostrata</i>)			
	DOR	GAR	GIR	CER	SFL	SPL	SOR	SJR
Latitude (°N)	44°54'30"	44°43'51"	45°12'23"	44°41'18"	48°51'40"	48° 21' 17"	46°19'50"	45°09'18"
Longitude (°W)	0°15'01"	0°28'05"	0°43'13"	1°1'39"	64°28'47"	68°45'28"	72°32'06"	74°23'04"
Sampling period (month and years)	June 2011 May 2012	June 2011 May 2012	June 2011 May 2012	May 2011 May 2012	June 2011 May 2012	June 2011 June 2012	July 2011 June 2012	June 2011 June 2012
Fishing gear	Trap nets	Trap nets	Trawl	Trap nets	Trap nets	Electro-fishing	Trap nets	Trap nets
Habitat ¹ (Salinity)	FW	FW	BW	BW	FW	FW	BW	FW
Mean length at silvering (mm)	752 ^a	698 ^a	660 ^a	660 ^a	958 ^b	958 ^b	1043 ^b	520 ^b
Mean age at silvering (years)	>10 ^a	>10 ^a	>10 ^a	>10 ^a	20 ^b	20 ^b	21 ^b	11 ^b
Distance from the Sargasso Sea ² (km)	5612	5616	5539	5500	5467	5245	4840	4480

¹FW = Freshwater; BW = Brackish water. Salinity values of each sampling site are detailed in Baillon et al. (2015).

²Distance between the sampling sites and the Sargasso Sea spawning ground were estimated via the Google Earth web tool.

^a Reference: Tapie et al. (2011); ^b Reference: Jessop (2010).

Table 2. Biological characteristics for *Anguilla anguilla* and *Anguilla rostrata* for each sampling site in 2011. Values represent the median (Q1, Q3) of each biological variable (BL: Body Length; BM: Body Mass. Sex ratios are presented in % of the total number of eels within a site (Chi-square test). Different superscript lower case letters indicate statistically significant differences among sites within species (ANOVA or Kruskal Wallis).

Site	2011							
	<i>A. anguilla</i>				<i>A. rostrata</i>			
	DOR	GAR	GIR	CER	SFL	SPL	SOR	SJR
N total (Females and undifferentiated)	13	14	15	11	15	7	15	15
Sex ratio (%):								
Female	62	86	100	100	100	100	100	100
Undifferentiated	38 ^a	14 ^{ab}	0 ^b	0 ^b	0	0	0	0
BL (mm)	325 ^c (302, 354)	434 ^b (393, 503)	565 ^a (530, 614)	440 ^b (395, 478)	832 ^a (801, 856)	894 ^a (876, 929)	323 ^c (290, 382)	535 ^b (465, 606)
BM (g)	51 ^c (39, 69)	127 ^b (103, 202)	300 ^a (249, 424)	128 ^b (102, 167)	1254 ^a (1147, 1298)	1565 ^a (1435, 1642)	50 ^c (32, 92)	275 ^b (172, 440)
Age (year)	5 ^b (4, 5)	6 ^b (5, 7)	8 ^a (8, 12)	5 ^b (4, 5)	12 ^a (12, 13)	13 ^a (11, 16)	8 ^b (7, 10)	10 ^a (8, 12)

Table 3. Biological characteristics for *Anguilla anguilla* and *Anguilla rostrata* for each sampling site in 2012. Values represent the median (Q1, Q3) of each biological variable (BL: Body Length; BM: Body Mass). Sex ratios are presented in % of the total number of eels within a site (Chi-square test). Different superscript lower case letters indicate statistically significant differences among sites within species (ANOVA or Kruskal Wallis).

Site	2012							
	<i>A. anguilla</i>				<i>A. rostrata</i>			
	DOR	GAR	GIR	CER	SFL	SPL	SOR	SJR
N total (Females and undifferentiated)	14	14	14	14	12	14	15	15
Sex ratio (%)								
Female	25	71	71	93	100	100	100	100
Undifferentiated	75 ^a	29 ^{ab}	29 ^{ab}	7 ^b	0	0	0	0
BL (mm)	386 ^b (360, 402)	506 ^a (378, 597)	452 ^a (392, 480)	464 ^a (405, 522)	802 ^a (769, 825)	667 ^b (593, 771)	375 ^c (340, 435)	517 ^{bc} (373, 595)
BM (g)	78 ^b (69, 96)	262 ^a (94, 328)	148 ^a (116, 182)	156 ^a (111, 266)	983 ^a (895, 1076)	553 ^{ab} (386, 823)	63 ^c (50, 109)	245 ^{bc} (71, 441)
Age (year)	6 ^b (4, 8)	10 ^a (8, 14)	8 ^{ab} (4, 10)	4 ^b (4, 5)	10 (9, 14)	7 (7, 11)	9 (7, 10)	11 (7, 11)

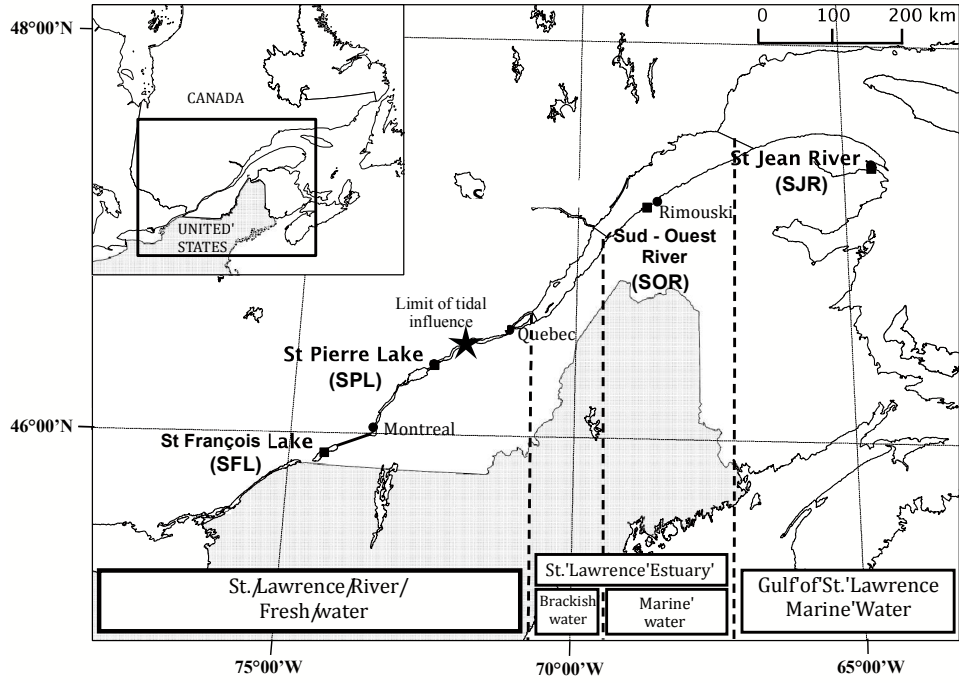
Table 4: Tukey multiple comparisons tests on the site effects in the linear mixed models on length-at-age 1. Statistical significance codes: ≤ 0.00001 ‘***’; ≤ 0.001 ‘**’; ≤ 0.01 ‘*’; ≤ 0.05 ‘.’; ≤ 0.1 ‘ns’

Species	Site 1	comparison	Site 2	significance level
<i>A. anguilla</i>				
	CER	>	GIR	***
	CER	>	DOR	***
	CER	>	GAR	***
	GIR	>	GAR	.
	GIR	>	DOR	*
	GAR	>	DOR	ns
<i>A. rostrata</i>				
	SFL	>	SPL	ns
	SFL	>	SJR	***
	SFL	>	SOR	***
	SPL	>	SJR	***
	SPL	>	SOR	***
	SJR	>	SOR	

Table 5: Tukey multiple comparisons tests on the site effects in the linear mixed models on growth increments. Statistical significance codes: ≤ 0.00001 ‘***’; ≤ 0.001 ‘**’; ≤ 0.01 ‘*’; ≤ 0.05 ‘.’; ≤ 0.1 ‘ns’

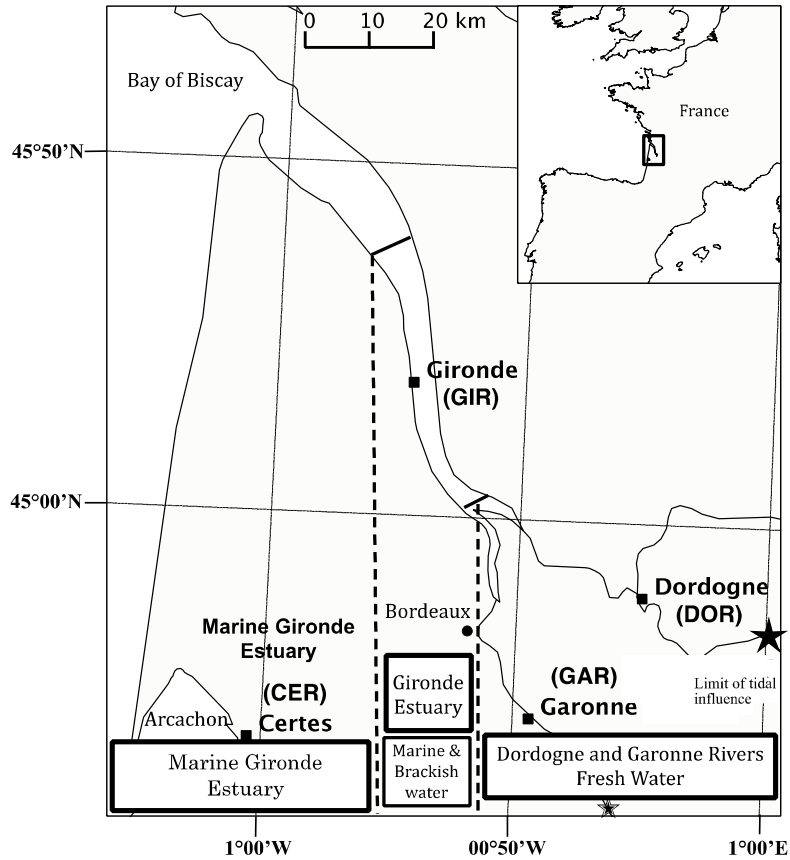
Species	Site 1	comparison	Site 2	significance level
<i>A. anguilla</i>				
	CER	>	GIR	ns
	CER	>	DOR	***
	CER	>	GAR	.
	GIR	>	GAR	*
	GIR	>	DOR	**
	GAR	>	DOR	
<i>A. rostrata</i>				
	SFL	<	SPL	ns
	SFL	>	SJR	***
	SFL	>	SOR	***
	SPL	>	SJR	***
	SPL	>	SOR	***
	SJR	>	SOR	.

1



2

(a)

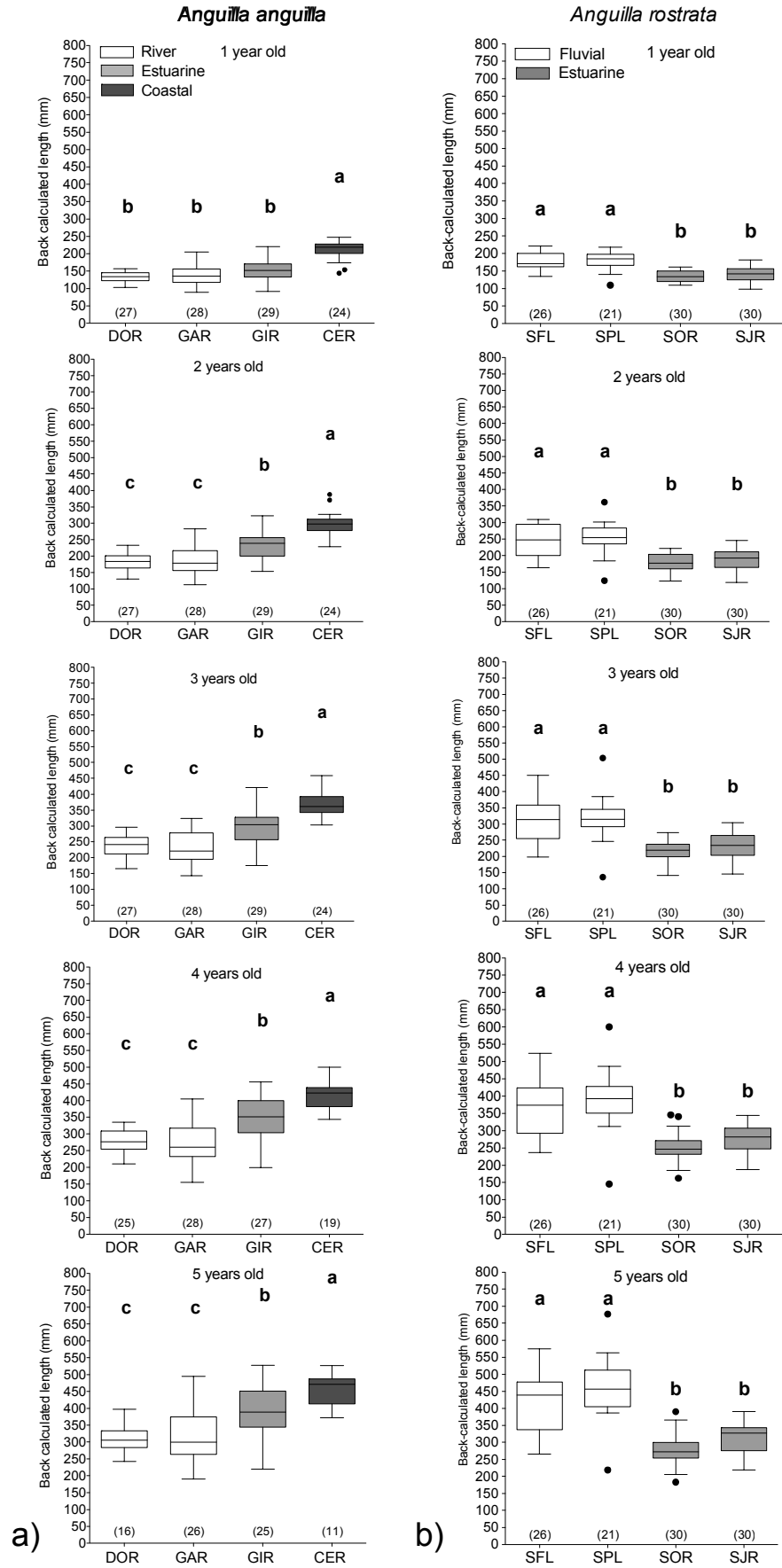


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(b)

5 **Figure 1.** Study areas and sampling sites for (a) yellow eels captured in Quebec (North
6 Eastern Canada) and (b) yellow eels captured in the Gironde region (South West France)
7 showing the separation into 3 salinity sectors (freshwater, brackish and marine sectors). Black
8 squares refer to sampling sites and black circles refer to the closest cities. The symbols (★)
9 indicate the limits of tidal influence. The map was made using QGIS project, a free and open
10 source geographic information system (www.qgis.org).



12 **Figure 2.** Back-calculated length in relation to age from 1Y to 5Y for a) *Anguilla anguilla*
13 captured in fluvial (DOR, Dordogne and GAR, Garonne), estuarine (GIR, Gironde) and
14 coastal (CER, Certes) habitats and for b) *Anguilla rostrata* captured in fluvial (SPL, Lake St.
15 Pierre and SFL, Lake St. François) and estuarine habitats (SJR, St. Jean River and SOR, Sud-
16 Ouest River). Rectangle boxes encompass the medians (horizontal line through the box), the
17 25th percentiles (Q1) and the 75th percentiles (Q3). Above and below the boxes are whiskers
18 representing the Q1-1.5 x InterQuartile Range (IQR, which is the difference with the first and
19 the third quartiles) and Q3+1.5 x IQR. Filled circles are outliers. N in parentheses are the
20 numbers of fish per site. In each species, different uppercase letters indicate differences
21 among sites (Anova or Kruskal Wallis, $p \leq 0.05$).