

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

Géraldine Patey^{1,2}, Catherine M. Couillard², Hilaire Drouineau³, Guy Verreault⁴, Fabien Pierron^{5,6}, Patrick Lambert³, Magalie Baudrimont^{5,6} and Patrice Couture¹

¹Institut National de la Recherche Scientifique (INRS), Centre Eau Terre Environnement, 490 De La Couronne, Québec, QC G1K 9A9, Canada. Tel: +1 418 654 3825; e-mail: patrice.couture@ete.inrs.ca

² Fisheries and Oceans Canada, Maurice Lamontagne Institute, 850 Route de la Mer, Mont-Joli, G5H 3Z4, Québec, Canada, Tel: +1 418 775 0681; Fax: 418 775 0718; e-mail: catherine.Couillard@dfo-mpo.gc.ca

³Institut national de Recherche en Sciences et Technologies pour l'Environnement et l'Agriculture (IRSTEA), équipe Poissons Migrateurs Amphihalins (PMA), 50 avenue de Verdun Gazinet, 33612 CESTAS, France. Tel: +33 5 57 89 08 09; e-mail: patrick.lambert@irstea.fr

⁴Ministère des Forêts, de la Faune et des Parcs, 186 rue Fraser, Rivière-du-Loup, G5R1C8, Québec, Canada. Tel: +1 418 862 8213 poste 306; email: guy.verreault@mffp.gouv.qc.ca

⁵Univ. Bordeaux, UMR EPOC CNRS 5805, F-33400 Talence, France

⁶CNRS, EPOC, UMR 5805, F-33400 Talence, France. Tel: +33 5 56 22 39 27; Fax: +33 5 40 70 85 04; e-mails: f.pierron@epoc.u-bordeaux1.fr; magalie.baudrimont@u-bordeaux.fr

* Corresponding author: Tel: +1 418 261 8906; email: geraldine.patey@gmail.com

Abstract

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

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

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

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

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

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

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

Materials and methods

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

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

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

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

Morphometric measurements and tissue sampling

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

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

Otolith processing

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

Back-calculation of length

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

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

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

Statistical analyses

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

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

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

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

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

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

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

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

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

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

Results

Eel biological characteristics in the St. Lawrence and Gironde systems

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

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

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

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

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

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

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

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

Linear mixed effect models

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Limitations and future directions

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

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

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

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

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

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

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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

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

² Distance 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)

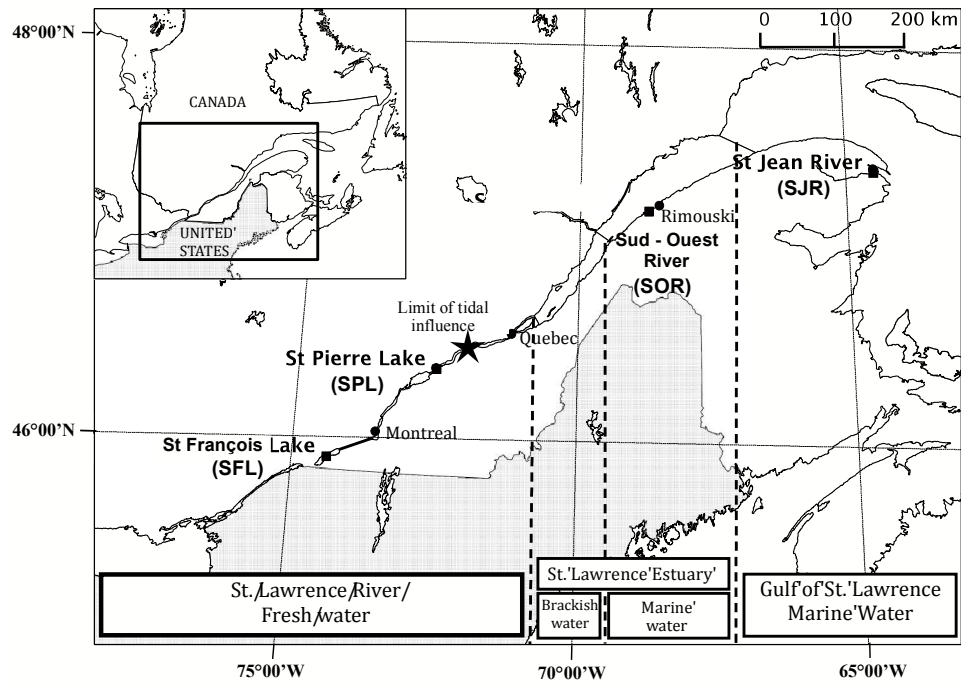
Table 4: Tukey multiple comparisons tests on the site effects in the linear mixed models on length-at-age 1. Statistical significance codes: ≤ 0.00001 ‘***’, ≤ 0.001 ‘**’, ≤ 0.01 ‘*’, ≤ 0.05 ‘.’, ≤ 0.1 ‘ns’

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’

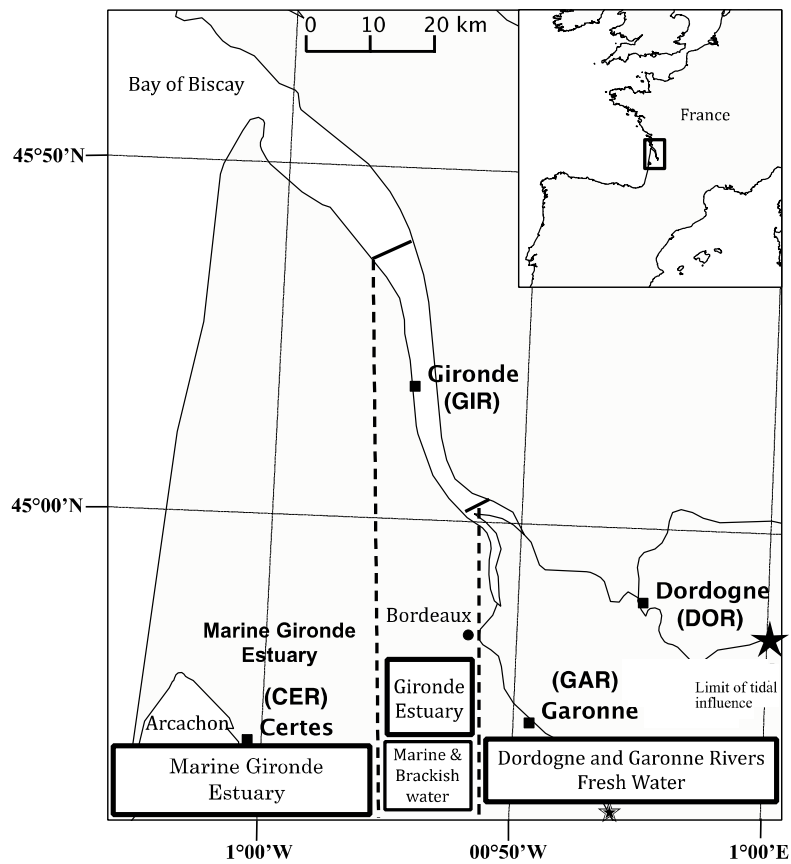
Species	Site 1	comparison	Site 2	significance level
<i>A. anguilla</i>	CER	>	GIR	ns
	CER	>	DOR	***
	CER	>	GAR	.
	GIR	>	GAR	*
	GIR	>	DOR	**
	GAR	>	DOR	
<i>A. rostrata</i>	SFL	<	SPL	ns
	SFL	>	SJR	***
	SFL	>	SOR	***
	SPL	>	SJR	***
	SPL	>	SOR	***
	SJR	>	SOR	.

1



2

(a)

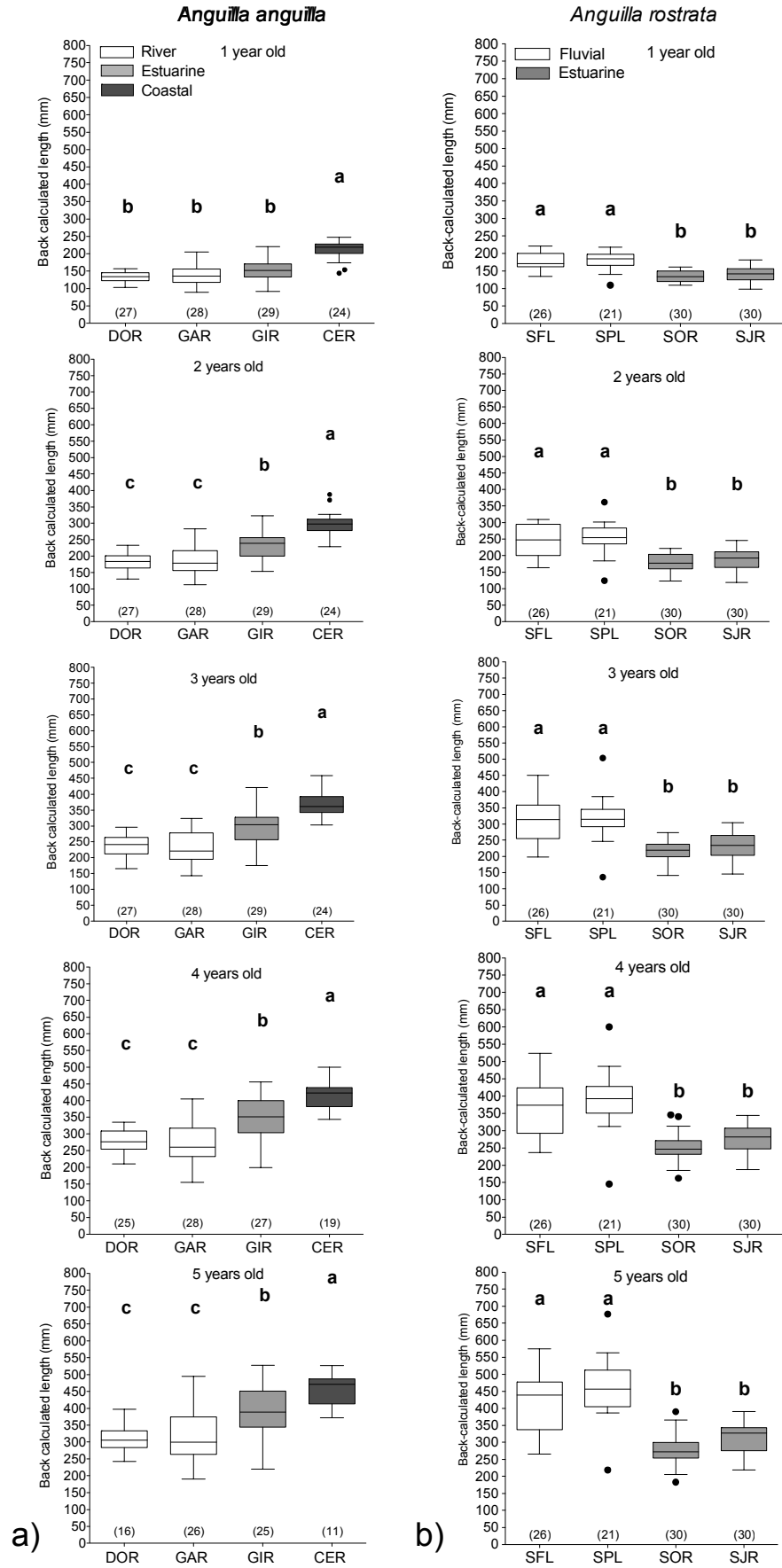


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4

(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, $p \leq 0.05$).