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80's population-specific compositions of two related anadromous shad species during the oceanic phase determined by microchemistry of archived otoliths

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Manuscripts

1   **80's population-specific compositions of two related anadromous shad**

2   **species during the oceanic phase determined by microchemistry of**

3   **archived otoliths**

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Abstract

The specific stock composition and dispersion of anadromous fish species aggregations in the marine environment are poorly known, while they can play a major role in the metapopulation dynamics. Otolith microchemistry has proven to be a powerful tool to address natal origins of anadromous fish. We used archived otolith microchemistry to investigate the population-specific composition of European shads (*Alosa alosa* and *Alosa fallax*) subadults in the ocean during the 80's. The allocation of natal origin was addressed relying on contemporary water and juveniles signatures within a Bayesian model. A great discrimination of natal origin was obtained at the Biscay Gulf scale. However, the discrimination of 80's natal origin for the southern rivers with similar geology based on 2013 water and juveniles baselines was doubtful. Our results showed that the most abundant southern populations were dominant, suggesting that population-specific composition was related to population relative abundance. The dispersion in the marine environment was plastic; alternatively shads were found large distances away from their natal rivers, while others remained in the vicinity of their natal river plume.

Introduction

Anadromous fish species, such as salmons and shads, share a complex life cycle where reproduction and early life are undertaken in freshwater habitats, whereas growth and maturation are achieved in oceanic habitats. Many anadromous fishes tend to return to spawn to their natal river -a behaviour named homing-, with varying degrees of fidelity, albeit few individuals stray to spawn in a different river than their natal one (Walther et al. 2008; Martin et al. 2013; Martin et al. 2015). While a large amount of information is available concerning the use of freshwater habitats, only few reports are available on how anadromous fishes use the oceanic environment. When oceanic distribution is defined, often with a poor spatial resolution, little is known about the stock-specific ocean migration or the mixing of the fish originating from different rivers (Walther and Thorrold 2010; Loewen et al. 2015; Johnson et al. 2016).

Over the last decades, it has been generally accepted that the return of anadromous fishes to their natal river is influenced by the combination of geomagnetic and olfactory cues (Lohmann et al. 2008; Bandoh et al. 2011; Putman et al. 2013). Recently, it has been suggested that social interactions and collective behaviour could also play an important role in the return of salmons to the river of origin (Berdahl et al. 2016). That is, there is evidence that collective navigation and group effect could facilitate decision-making to find correct migration pathways from the ocean to the native rivers. This group effect could reduce dispersal, which would most likely occur if one individual moved away from the group. In fact, a recent study has shown that although small-scale Chinook salmon *Oncorhynchus tshawytscha* aggregations in the sea are not entirely uniform, they tend to be composed of individuals from the same natal origin (Johnson et al. 2016). Whether fishes segregate following their natal origin or form mixed stocks at sea has consequences on the possibility

66   of exchanges between populations, and more generally demonstrates their dispersal ability at

67   sea (Walther and Thorrold 2010; Loewen et al. 2015; Johnson et al. 2016). Disentangling the

68   habitat occupation and migration patterns at sea of the main source populations in a meta-

69   population dynamic can provide insight on the relevant management scale and priorities.

70   However, identifying the natal origin of wild anadromous fishes during the ocean growth

71   phase constitutes a real challenge.

72   Natural tags contained in certain tissues, such as otoliths (calcified structures of the inner ear

73   of teleost fish), could be a good approach to obtain information about the natal origin and

74   subsequent population marine mixing of anadromous species (Hobson 1999; Turner et al.

75   2015). Otoliths are acellular metabolically inert materials, which grow continuously

76   throughout the life of the fish. The concentration of certain accreted elements in the

77   successive growth layers is largely correlated with their concentration in the ambient water,

78   especially in freshwater (Campana and Thorrold 2001; Walther and Thorrold 2006; Morais

79   and Daverat 2016). Therefore, if there are natal habitats with significant difference in

80   chemical composition, otoliths core from fish hatched in each of them will record for life the

81   unique signatures of each particular natal area, enabling the retrospective identification of

82   natal origin (Campana and Thorrold 2001; Walther et al. 2008; Morais and Daverat 2016).

83   Thus, the unique properties of these calcified pair structures make them especially useful to

84   unravel the life-history features and movement patterns of diadromous fishes at fine spatial

85   scales, such as dispersal capacities, patterns of population connectivity and natal origin of

86   fish (Daverat et al. 2011; Nachón 2017; Randon et al. 2018). Anadromous fishes are often

87   caught as bycatch in coastal fisheries, particularly shads because of their school-forming

88   behaviour (Taverny and Elie 2001; Hasselman et al. 2015; Nachón et al. 2016). These

89   opportunities are usually capitalized to collect various organs or tissues in order to study the

90   life history of the fish caught (Taverny and Elie 2001; Walther and Thorrold 2010;

91   Hasselman et al. 2015). Scales and mostly otoliths are thus collected routinely for age

92   determination purposes. After age estimation, these tissues are usually archived in research

93   institutions or museums. Historical otolith collections are precious sources of retrospective

94   information. However, to the best of our knowledge, studies analysing the microchemistry of

95   historical archived otoliths have rarely been addressed (Gao and Beamish 2003; Munro et al.

96   2005; Loewen et al. 2015).

97   In the present study, we used natural chemical tags recorded in historical archived otoliths to

98   assess the natal origins of subadults of European shad species collected in the marine

99   environment in the 80's. The European shads, Allis shad (*Alosa alosa*) and Twaite shad

100   (*Alosa fallax*), are a complex of two sympatric sister species of anadromous Clupeidae

101   species. Juveniles develop in freshwater and migrate to the sea during their first year of life

102   (Taverny 1991; Taverny et al. 2000*a*; Taverny and Elie 2001). During their growth phase,

103   shads aggregate in coastal habitats and undertake back-and-forth movements between the

104   marine and estuarine environments, especially Twaite shad for their first two years of life

105   (Taverny 1991; Taverny and Elie, 2001; Nachón 2017). Then, the growth phase is completed

106   in oceanic habitats until they reach sexual maturity (generally between 3 to 6 years of age)

107   and migrate back to the rivers to spawn (Aprahamian et al. 2003*a*, 2003*b*; Baglinière et al.

108   2003). Both shad species were originally distributed along the Northwest Atlantic coast, from

109   Scandinavia to Morocco as well as in the western Mediterranean (Allis shad) or throughout

110   the Mediterranean (Twaite shad) (Baglinière 2000). Like other diadromous species, the

111   European shads have suffered major declines as their life cycle, using both freshwater and

112   marine ecosystems, exposed them to a suite of accumulation of possible impacts, such as

113   damming of rivers, overfishing, bycatch, deterioration of spawning habitats, etc. (Taverny et

114   al. 2000*b*; De Groot 2002; Limburg and Waldman 2009). The deleterious effects of these

115   impacts began to be significantly apparent from the late 19th century and intensified during

116   the 20th century, leading to considerable extinctions, especially at the extremes of their

117   distribution range, and declines in abundance levels throughout the range of distribution

118   (Baglinière 2000; Taverny et al. 2000*b*; Aprahamian et al. 2003*a*). Shad populations were

119   still abundant in France at the end of the 20th century, even though some populations had

120   already suffered significant reductions in the population numbers, such as the Adour and

121   Loire populations, and others had already collapsed or even disappeared, such as the Seine,

122   Brittany and Normandy populations (Taverny 1991; Baglinière 2000; Bruslé and Quignard

123   2013). During this period, the Gironde system (Dordogne and Garonne rivers) Allis shad

124   populations were the most abundant in Europe (Martin–Vandembulcke 1999; Baglinière

125   2000; ICES 2015). However, from the year 2000 onwards, the Garonne and Dordogne Allis

126   shad populations collapsed (Rougier et al. 2012) and the abundance of other French shad

127   populations has also decreased dramatically (Cellule Migrateurs Charente Seudre 2017;

128   Legrand and Besse 2018).

129   During their oceanic phase, the habitats used by subadults of both species are located in the

130   vicinity of the river mouths of most important spawning grounds, such as Gironde system,

131   Charente, Loire and Vilaine rivers, along the French Atlantic coast of the Bay of Biscay

132   (Taverny 1991; Taverny and Elie 2001). The presence of subadults in marine habitats

133   connected to an estuary would suggest that fishes stay close to their natal river basin

134   (Taverny 1991; Taverny and Elie 2001). Recent studies that have revealed that Allis shad

135   formed a meta-population where exchanges of adults primarily occurred between

136   neighbouring rivers (Martin et al. 2015; Randon et al. 2018), would support this hypothesis.

137   Genetic tools suggested that Twaite shad formed more structured populations than Allis shad

138   populations, meaning that exchanges between populations should be more intense for the

139   latter (Jolly et al. 2012). So far, there is no knowledge on whether straying is favoured by a

140   mixing of the populations of shads from different natal origin at sea or if shads are straying

141   from distinct marine habitats. Understanding the population-specific dispersal capacities in

142   the ocean is thus required. Allis shad juveniles from a Moroccan population displayed

143   migrations of 600 km along the coast between their natal river and their marine habitats,

144   demonstrating the dispersion ability of the species (Sabatié 1993). In addition, some Allis

145   shad adults would be able to enter rivers for spawning at a distance of more than 700 km

146   from their natal river (Martin et al. 2015). Marine bycatches of both species have been

147   documented several hundred kilometres away from their most likely rivers of origin (La

148   Mesa et al. 2015; Nachón et al. 2016).

149   In the present study, the goals were first, to address the utility of archive otoliths in assigning

150   the natal origin of European shads captured 30 years ago in the marine environment, when

151   the Gironde shad populations were still abundant, and second, to investigate the distribution

152   of Allis shad and Twaite shad subadults at sea following their natal origin in order to

153   understand the extent of mixing or segregation of European shad populations. For that

154   purpose, we coupled the otolith elemental and isotopic microchemistry with a Bayesian

155   mixing model following Martin et al. (2015) and Randon et al. (2018).

Material and methods

Study area

158   The Bay of Biscay is a large open oceanic area located at the east of the North Atlantic Ocean

159   (western part of Europe), which expands from north coast of Spain (from Cape Ortegal,

160   ~42°N, -9°W), to the west coast of France (up to Finistère in Brittany, ~48°N and 1°E). This

161   bay has a contrasted morphology as the continental shelf (depths < 200 m) is very narrow in

162   the south, along the coast of Spain (10–65 km wide), whilst widens northward along the

163   French coast, from 20 km in the southern part (Capbreton Canyon) to over 200 km in the

164   northern part (Koutsikopoulos and Le Cann 1996; Le Pape et al. 2003; Bertin et al. 2012).

165   Our study focused on the French part of the Bay of Biscay (Fig. 1). Surface coastal waters of

166   this area receive a strong freshwater run-off from outflow plumes of the main rivers, with

167   Loire River and Gironde system providing 75% of the freshwater input (Ayata et al. 2010;

168   Laiz et al. 2014; Costoya et al. 2017). Other rivers along the coast as Vilaine, Sèvre Niortaise,

169   Charente, Adour and Nivelle rivers have more limited contributions in terms of freshwater

170   run-off. The strong density gradients, which occurred in the vicinity of the outflow plumes of

171   the Loire River and Gironde system, lead to extensive density currents over the shelf,

172   essentially in a northwards direction (Koutsikopoulos and Le Cann 1996; Ayata et al. 2010).

173   The regions under the influence of the river plume, especially those around the Vilaine River,

174   Loire River and Gironde system, are highly productive pelagic areas, mainly for plankton

175   (both phytoplankton and zooplankton) and small pelagic fishes (Motos et al. 1996; Irigoien et

176   al. 2008).

177   **Source of available shad samples**

178   Archived otoliths from subadults of both shad species captured as bycatch in the late 1980s

179   during research campaigns of "Institut Français de Recherche pour l'Exploitation de la Mer"

180   (IFREMER) throughout the French continental shelf of the Bay of Biscay were selected as

181   biological material (Taverny 1991; Taverny and Elie 2001). Bottom trawl scientific surveys

182   (RESSGASC and SOLDIF) were conducted using random stratified sampling designs and

183   targeting demersal or benthic species rather than pelagic species.

184   RESSGASC campaign (from August 1986 to Mars 1989) covered practically the entire coast,

185   approximately 430 km (from the Morbihan Cape at 48°N to the North of the Arcachon Basin

186   at 45°N), in a range of depths between 11 m and the 100 m isobaths (Fig. 1). The gear used in

187   this campaign was a Vendée bottom trawl net of 25 m of headline and a 55 mm stretched

188   mesh in the cod end. Of the 427 completed stations over all period, Allis shad and Twaite

189   shad were captured in 59 and 55 locations respectively, with 18 shared locations. Catches

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190   averaged 4 fishes per trawl date for both species, with the largest collections accounting 21

191   and 45 individuals of Allis shad and Twaite shad respectively (total n = 254 Allis shad; n =

192   224 Twaite shad).

193   SOLDIF campaign (from May 1988 to February 1989) was limited to a smaller sampling

194   area, both with respect to the length, around the mouth of the Vilaine and Loire rivers

195   (47°17'N), and the depth, from outside the coastal zone to depths of less than 50 m (Fig. 1).

196   Two gears were used in this sampling campaign: a 25 m double bottom trawl with 20 mm

197   stretched mesh in the cod end and a 3 m long beam trawl of 1 mm stretched mesh in the cod

198   end. Of the 168 completed stations over all period, Allis shad and Twaite shad were captured

199   in 16 and 15 locations respectively, with 6 shared locations. Catches in these campaigns

200   averaged 3 and 2 individuals per day for Allis shad and Twaite shad respectively, with the

201   largest collection of 15 and 5 individuals of Allis shad and Twaite shad respectively (total n =

202   51 Allis shad; n = 31 Twaite shad).

203   The identification of the species was carried out by Taverny (1991) based on the relationship

204   between total length and gillrakers number along the first gill arch. All captured individuals

205   were in the sub-adult phase (Taverny 1991; Taverny and Elie 2001). The age ranged from 2

206   to 5 years for Allis shad and from 2 to 6 years for Twaite shad, with more than 80% of Allis

207   shad individuals aged between 2 and 3 years, and more than 80% of Twaite shad aged

208   between 3 and 4 years (Taverny 1991; Taverny and Elie 2001). Full details of the sampling

209   campaigns carried out in marine environments together with biometrical and demographic

210   characteristics of all individuals are given in Taverny (1991) and Taverny and Elie (2001).

211   In total, sagittal otoliths of 209 Allis shad (RESGASC, n = 160; SOLDIF, n = 49) and 166

212   Twaite shad (RESGASC, n = 140; SOLDIF, n = 26) were selected from the overall archives

213   (1986–1989, Fig. 1). Samples selection was based on biometry and location catch data

214   availability. Allis shad subadults belonged to 1982-1986 cohorts while Twaite shad subadults

215   belonged to 1982-1987 cohorts. More than 80% of the samples from both species belonged to

216   the 1985 year class (see online supplementary Table S1[3]).

Otolith preparation and microchemistry analysis

218   The archived otoliths from Taverny works (Taverny 1991; Taverny and Elie 2001) have

219   previously been used *in toto* for age reading. Untreated otoliths have been stored dry in

220   individually labelled paper envelopes since then. Thus, the absence of chemical or physical

221   treatments on the otolith ensured the integrity of otoliths chemical composition. Furthermore,

222   targeted elements of this study ($^{87}Sr{:}^{86}Sr$, Sr:Ca and Ba:Ca ratios) should be stable over 30

223   years of time in archived otoliths under correct storage conditions, as strontium and barium

224   substitute calcium in otoliths (Kennedy et al. 2000; Campana and Thorrold 2001).

225   Consequently, one sagittal otolith from each pair was randomly selected for microchemistry

226   purposes. Selected otoliths were rinsed with ultrapure water and air-dried during 24h under a

227   laminar flow hood. This process and the following ones were carried out in class 10 000

228   clean room, in order to avoid any possible contamination. Posterior otolith preparation was

229   carried out according to Martin et al. (2015). To analyse $^{87}Sr{:}^{86}Sr$, Sr:Ca and Ba:Ca ratios,

230   two C-shaped ablation trajectories of 60 μm thick were performed 40 μm away from the core.

231   A High Resolution (Thermo Scientific, USA) inductively coupled plasma quadrupole mass

232   spectrometer (HR-ICP-MS) was used to analyze Sr:Ca and Ba:Ca ratios. The HR-ICP-MS

233   was coupled to a UV high-repetition-rate femtosecond laser ablation (fs-LA) system (Nexeya

234   SA, Canejan, France). A Nu-Plasma multicollector inductively-coupled-plasma mass-

235   spectrometer (MC-ICP-MS, Nu Instruments, UK) coupled to a UV high-repetition-rate

236   femtosecond laser ablation (fs-LA) system (Nexeya SA, Canejan, France) was used to

237   analyze $^{87}Sr{:}^{86}Sr$. Analytical process can be found in Martin et al. (2015).

238   [3]Supplementary data are available with the article.

Baseline samples and statistical analyses

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240   The natal origin of each individual caught at the sea during the 1980s was assigned using a

241   Bayesian mixing model relying on a water and otolith chemical database (^{87}Sr:^{86}Sr, Sr:Ca and

242   Ba:Ca ratios), from water samples and juvenile otoliths of Allis shad, as well as both adults

243   collected in 18 rivers throughout its 2000s distribution range (Randon et al. 2018). Since no

244   model of microchemical data was available for Twaite shad, the same Allis shad model was

245   also used for this species. This was justified by the fact that there was no ^{87}Sr:^{86}Sr biological

246   fractionation (Kennedy et al. 2000; Walther and Thorrold 2008; Pouilly et al. 2014). In

247   consequence, the otoliths of both shad species from a given system would share the same

248   ^{87}Sr:^{86}Sr ratios. In addition, Strontium incorporation rate was found to be the same for both

249   species (Lochet 2006). Because of the close phylogenetic relationship of both species, we can

250   assume that it would be similar for Ba (Bentzen et al. 1993; Alexandrino et al. 2006; Chang

251   and Geffen 2013). According to the available literature, both species occupied to a large

252   extent the same rivers in the 1980s as in the 2000s (Taverny 1991; Baglinière 2000; Bruslé

253   and Quignard 2013). Thus we can assume that our model includes all natal river populations

254   that could most likely be found in the marine stock mix during the 1980s.

255   In our work, the sea caught subadults were grouped according to the proximity to the river

256   plumes. Thus, our samples were grouped into two zones that mimic two new capture rivers.

257   A Bay of Biscay Center (BBC) group was created for each species (Allis shad, $n = 64$;

258   Twaite shad, $n = 127$). It included all the catches located between 45–46º N, likely originating

259   from the Charente River and the Gironde system. Although located in the southern Bay of

260   Biscay where there were no marine catches, the rivers of the Adour basin and the Nivelle

261   River could also potentially contribute individuals to the mixture of marine individuals

262   located in the Bay of Biscay Center. The second group, the Bay of Biscay North (BBN)

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263 included all individuals caught between 46–48º N (Allis shad, n = 145; Twaite shad, n = 39),

264 which would likely originate from Brittany and Normandy rivers and from Loire River.

265 The model was run with all available samples, i.e., using baseline datasets (Allis shad

266 juveniles, n = 61 and water, n = 61), otolith microchemistry of Allis shad adults with

267 unknown origins (n = 615) from Randon et al. (2018) and the addition of 209 Allis shad and

268 166 Twaite shad sea samples grouped following their capture zone. We established a period p

269 (before 1990, after 2005) effect in the probabilities of origin to account for a possible

270 modification of the homing dynamics along the time. The model was carried out employing

271 the software JAGS and was run by runjags package (Plummer 2003; Denwood 2013), which

272 promotes the communication between JAGS and R statistical software (R Development Core

273 Team, R.3.1.1, 2014). Three independent Monte Carlo Markov Chain (MCMC) chains were

274 run in parallel for 20 000 iterations after a burn-in period of 10 000 iterations to draw

275 simulations from Bayesian posterior distributions. A vector $\{\theta c,p\}$ denoting the probabilities

276 that a given fish captured in a river (c) during each period (p) was born in each of the kb river

277 of the water baseline was included for each catch river and period. Each subadult caught in a

278 marine region during the period < 1990 was reassigned to one or more natal rivers, among the

279 18 possible natal rivers included in the baseline dataset, at the end of the iterative process.

280 Thus, the frequency of reassignment of a fish f in a source k was defined as the number of

281 iterations of the MCMC in which the fish f was reassigned into a source k, divided by the

282 total number of iterations produced during the MCMC. As a result a reassignment probability

283 of f in k is obtained. This probability was calculated for each of the fish and sources, in such

284 a way that each fish has at the end an Ff vector containing the kb reassignment probabilities

285 (one for each river of the baseline). Finally, each fish was assigned to its natal origin based on

286 the maximum posterior classification probability. We then calculated the proportional

287 representations of each identified source stock to the marine sectors defined. A matrix

13

288 containing the Ff of each fish in rows and natal river in columns was created. Thus, we used

289 Spearman's correlation test (threshold 0.05) to calculate the correlation between each of the

290 pairs of columns. There is confusion during the process of reallocation if there is a strong and

291 positive correlation between the corresponding rivers, while the rivers are well discriminated

292 if there is a strong and negative correlation. For more detailed descriptions about statistical

293 calculations of the Bayesian model see Randon et al. (2018).

294 **Results**

295 **Model requirements and probabilities of reallocation**

296 The model satisfied all the requirements, such as convergence under the Gelman-Rubin

297 diagnostic (see Randon et al. 2018 for more details about model requirements), in order to

298 provide estimates of the proportion of individuals in each marine region according to their

299 natal origin. Maximum posterior conditional assignment probabilities (i.e., the probability of

300 assignment to each natal river) from the Bayesian mixing model were greater than 0.7 for

301 92.3% ($n = 193$ of 209 individuals) and 81.3% ($n = 135$ of 166 individuals) for Allis shad and

302 Twaite shad respectively. Thus, the majority of subadults caught in the marine environment

303 were assigned to a natal river with high degrees of confidence. Slight confusions were found

304 as shown by the correlation matrix (Fig. 2). Confusions occurred usually between

305 neighbouring rivers as between the Nive and Saison rivers, although there were also some

306 confusions between rivers from distant basins (Charente-Saison or Vire-Vilaine).

307 Nevertheless, northern French rivers (from Loire River upwards) were well discriminated

308 from southern French rivers (from Charente River downwards).

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311 **Stock composition**

312 Chemical signatures from the otoliths revealed that Allis shad and Twaite shad subadults

313 caught in the Bay of Biscay originated from Southern rivers (Figs. 3, 4 and 5). The rivers in

314 the Northern part of our study area (Loire River, Brittany and Normandy rivers) did not

315 provide any fish of both shad species to the samples in the marine environment.

316 **Allis shad subadults**

317 When analysing all the probabilities of assignment of each fish we observed a clear

318 dominance of assignment of the individuals to the Adour River in both marine regions (Fig.

319 3). With respect to the maximum probabilities of assignment of each individual the

320 dominance of the Adour River was certified, with a percentage of 95.69% (n = 200

321 individuals), and the remaining individuals originated from the Charente (3.35%, n = 7

322 individuals), Nivelle (0.48%, n = 1 individual) and Aveyron rivers (0.48%, n = 1 individual).

323 Slight differences in the stock composition were detected according to the geographical

324 region (Fig. 4). In the Bay of Biscay North, 97.24% of individuals (n = 141 individuals) were

325 assigned to the Adour River, while in the Bay of Biscay Center 92.19% of individuals (n = 59

326 individuals) were assigned to the Adour River. In Bay of Biscay North, the Aveyron (0.7%, n

327 = 1 individual) and the Charente River (2.07%, n = 3 individuals) natal origins were observed

328 while in Bay of Biscay Center, Charente (6.25%, n = 4 individuals) and the Nivelle River

329 (1.56%, n = 1 individuals) individuals completed the specific composition.

330 **Twaite shad subadults**

331 Similarly to Allis shad, all the probabilities of assignment of each fish showed that almost

332 every individual originated from one source, in this case the Oloron River (Fig. 3). Oloron

333 river also belongs to the Adour basin to the south of the study area. Maximum probabilities of

15

334   assignment of each individual showed that a percentage of 95.78% of individuals ($n = 159$

335   individuals) were assigned to the Oloron River. The remaining individuals originated from

336   the Charente River (4.22%, $n = 7$ individuals). In both marine regions, individuals were

337   mostly assigned to the Oloron River Twaite shad population (Fig. 5). In the Bay of Biscay

338   North all individuals originated from the Oloron River ($n = 39$ individuals). In Bay of Biscay

339   Center, 94.49 % of individuals ($n = 120$ individuals) were assigned to the Oloron River,

340   while the rest of the individuals came from the Charente River (5.51%, $n = 7$).

Discussion

341

Population-specific proportions at sea

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343   Despite the vast spatial coverage of the sampled area (525 sampling stations in a stratified

344   random fashion), the data collection was not exhaustive (especially in the Southern area)

345   which could have biased the stock composition estimates. However, the access to any shad

346   data at sea was and is still nowadays a major challenge that deserves to be fully addressed

347   with an appropriate sampling plan.

348   In the northern region of the Bay of Biscay, where a large proportion of the samples were

349   located (especially for Allis shad), the absence of individuals native of northern French rivers

350   was observed. This result was consistent with the relative abundance of shad populations

351   along the Bay of Biscay in the 80's. Vire and Brittany rivers shad populations were nearly

352   extinct and Loire River shad populations had very low abundance compared to the Southern

353   rivers shad populations (Taverny 1991; Baglinière 2000; Bruslé and Quignard 2013). The

354   very contrasted geologic and chemistry differences between Northern granitic French rivers

355   (Loire and northwards) and Southern sedimentary French rivers (Charente and southwards)

356   enabled a robust and accurate discrimination of natal origins between these two main groups

357   of rivers (Martin et al. 2015; Willmes et al. 2018). While Northern granitic French rivers have

358   high $^{87}Sr:^{86}Sr$ ratios between $0.71160 \pm 1.00E\text{-}04$ and $0.71429 \pm 1.01E\text{-}04$, Southern

359   sedimentary French rivers have low Sr values between $0.70823 \pm 5.70E\text{-}05$ and $0.71037 \pm$

360    $1.22E\text{-}04$ (Martin et al. 2015). Our Bayesian model of natal origin was mainly driven by

361    $^{87}Sr:^{86}Sr$ ratios, while Sr:Ca and Ba:Ca ratios complemented the discrimination (Martin et al.

362   2015). $^{87}Sr:^{86}Sr$ ratios were considered as "ideal" spatial markers for characterizing natal

363   sources since they reflect the different bedrock geologies and tended to be stable over

364   ecological timescales (Kennedy et al. 2000; Zimmerman et al. 2013; Loewen et al. 2015).

365   Therefore, populations of the Southern sedimentary French rivers undoubtedly supplied both

366   species in the marine areas.

367   **Interpretation of natal origin of shad and metapopulation dynamics at sea**

368   Looking at a finer geographical scale, our results showed that an overwhelming majority of

369   Allis and Twaite shad subadults caught at sea were assigned to only two natal sources of the

370   Southern sedimentary French rivers group, identified by the model as the Adour River and

371   Oloron River for Allis shad and Twaite shad respectively. The dominance of a limited

372   number of river populations in the mixed stock at sea was already observed for a closely

373   related species, the American shad, *Alosa sapidissima* (Walther and Thorrold 2010).

374   Although a wider range of ages were considered in the present study, European shads and

375   American shad showed the same metapopulation dynamics with few source populations and

376   several sinks. This similarity of dispersal and behavioural capabilities during immature stages

377   could be related to the phylogenetic proximity between American shad and European shads

378   (Bentzen et al. 1993).

379   Unexpectedly, only a small percentage of Allis shad subadults were assigned to the

380   populations of the Gironde system, which was considered to be the most important Allis shad

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381   populations in Europe in the 80's (Martin–Vandembulcke 1999; Baglinière 2000; ICES

382   2015). In the same way, a low abundance of Twaite shad subadults originating from

383   populations of the Gironde system was observed. Although the available data on the

384   abundance of Twaite shad in freshwater during the 1980s were scarce, the reported 13-15

385   tonnes of commercial catch of Twaite shad adults and an estimated recruitment of 9.5-22.5

386   millions of Twaite shad juveniles in the Gironde system, suggested that Twaite shad

387   populations in this system were also abundant (Taverny, 1991; Baglinière et al. 2001). The

388   subadults samples from the present study belonged to a reduced numbers of cohorts (1982-

389   1986 and 1982-1987 for Allis shad and Twaite shad respectively), 1985 being the dominant

390   cohort for both species. The dominance of subadults Adour and Oloron origin for Allis shad

391   and Twaite shad respectively could be explained by a difference in abundance and

392   recruitment success between populations of Adour and Oloron rivers and Allis shad and

393   Twaite shad populations from Gironde system during 1982-1986 period of time. Despite the

394   fact that Allis shad total commercial catches were 30 times greater in the Gironde system

395   (708.4 metric tons, 1983-1987 period) than in the Adour River (24.3 metric tons, 1985-1987

396   period, see Elie et al. 2000; Baglinière et al. 2003 and references therein), the relative fishing

397   effort would rather result in only a factor 4 relative shad abundance between both River

398   systems (Albiges et al. 1985; Prouzet et al. 1994; Castelnaud et al. 2001). There was no

399   available catch data for the Twaite shad in the Oloron River, and therefore no conclusions

400   could be drawn about the difference in relative abundance between Oloron River and the

401   Gironde system Twaite shad abundances. Juvenile shad abundance index in the Gironde

402   estuary showed considerable fluctuations between cohorts, with lowest values in 1983 and

403   1986 and in 1984 for Allis shad and Twaite shad respectively (Lambert et al. 1997).

404   Anthropogenic juvenile mortality was particularly high in the Gironde system during 1985,

405   when most of our samples were hatched, as it was estimated that 1.2 million individuals of

406   Allis shad juveniles and 880 000 individuals of Twaite shad juveniles died from water intake

407   from the nuclear power plant of Blayais (Taverny, 1991). Thus, the hypothesis of a greater

408   abundance of Adour origin Allis shad 1982-1986 cohorts and Twaite shad 1982-1987 cohorts

409   could be explained by the chaotic dynamics of shad populations, a clupeid species (Sabatié

410   1993; Rougier et al. 2012; Nachón et al. 2016). However, data on juvenile abundance was

411   totally lacking for the Adour estuary (common estuary to Adour River and Oloron River),

412   which did not allow us drawing a final conclusion on the relative abundance of juveniles of

413   both species between the two main natal rivers (Adour River for Allis shad and Oloron River

414   for Twaite shad) and Gironde systems for studied cohorts. Alternatively, a great recruitment-

415   stock relationship and high survival for Allis shad and Twaite shad individuals originating

416   from Adour River and Oloron River respectively and the opposite situation for shad

417   populations of the Gironde system could drive to a situation in which Allis shad population

418   from Adour River and Twaite shad population from Oloron River acted as a source and Allis

419   shad and Twaite populations from the Gironde system as a sink. Unfortunately, homing

420   behaviour in these rivers during the 80's was not available to discuss this hypothesis.

421   An alternative hypothesis to explain the dominance of Adour River and Oloron River natal

422   origin in the marine samples would be the allocation confusion between these rivers and

423   rivers from Gironde system. The allocation of 80's fish natal origins in the present study was

424   based on contemporary references (water and juveniles) because of the lack of available 80's

425   references. The chemical baselines used in previous studies were adapted to the

426   contemporary context of the Allis shad populations and the hydromorphological

427   characteristics of the rivers, and based on discrete samples collected during the spawning

428   period in the known spawning grounds (Martin et al. 2015; Randon et al. 2018). Although

429   European shads exhibited a high interannual fidelity to spawning grounds, interannual

430   hydrological fluctuations and density-dependent processes could induce changes in the

431   selection of spawning grounds (Cassou-Leins et al. 2000). Hence, the number and spatial

432   coverage of spawning areas in the 1980s were likely different in the Adour system and the

433   Gironde system than in recent years, mainly due to hydrological and abundance changes

434   between the two periods. In fact, considerable inter-annual fluctuations have been detected in

435   the occupation of the spawning grounds by Allis shad over time in the Gironde system

436   (Cassou–Leins and Cassou–Leins 1981; Belaud et al. 2001; Taverny 1991). This situation

437   was more confusing for the Twaite shad all the more because Twaite shad spawning grounds

438   were found more downstream, where the homogeneity of water signatures increased as the

439   mix of tributaries contribution increased. Yet, the knowledge of the different spawning

440   grounds occupied during the 80's in the French Southern Rivers was not available.

441   Adour and Garonne Rivers chemical signatures could be discriminated considering a recent

442   period of a few years, however, Martin et al. (2015) already pointed that differences between

443   Sr isotopes, Sr:Ca and Ba:Ca water composition among Southern sedimentary French rivers

444   group were tiny (Table 1 and Fig. 6). More specifically, close values of water composition

445   were measured for Adour River, Garonne River and Dordogne River (see online

446   supplementary Table S2[3]). Randon et al. (2018) observed slight allocation confusions for

447   origin allocations of contemporary samples, being greater between Garonne River and Adour

448   River or between Adour River and Oloron River, while Dordogne and Charente showed very

449   slights confusions issues. But ultimately, allocations confusions should remain low enough to

450   discriminate Adour River and Garonne River origins for contemporary shads according to

451   Randon et al. (2018). Strontium isotopes values for the river main stretches could be affected

452   by the relative contribution of the tributaries flow to the total flow. Factors such as rock type,

453   weathering velocities, or the magnitude of flow variation between sessions were found to

454   affect the composition of strontium isotopes water values (Walther and Limburg 2012).

455   Rivers from Gironde system have suffered a flow decrease (especially the Garonne River), a

456   systematically increase of water uptake for agricultural irrigation, granulate extraction and

457   damming (Jalón–Rojas et al. 2015; Schmidt et al. 2016). There anthropogenic pressures

458   might have slightly modified Sr isotopes values to the extent to add confusion in the

459   discrimination between Southern sedimentary French rivers chemical signatures. We cannot

460   exclude the hypothesis that the present study might have failed to discriminate precisely

461   shads natal origins provided the lack of 80's references such as exhaustive water composition

462   of all potential spawning grounds and juvenile fish otolith chemical composition. However,

463   the allocation of natal origin was very accurate between northern and southern Rivers,

464   allowing the interpretation of stock mixing at sea.

465   In conclusion, given the uncertainties to accurately discriminate individual originated from

466   the Southern sedimentary French rivers group to a more finer scale (specific river), from now

467   on we will refer to southern populations of Allis shad.

468   **Population-specific dispersal capacities at sea**

469   Our results overall suggested that large populations resulted in large dispersion of individuals

470   at sea. Marine habitat occupation was plastic, with a proportion of Allis shad and Twaite shad

471   subadults from Southern rivers populations remaining in the vicinity of their natal river

472   estuary plume and other subadults using marine habitats further away, covering distances up

473   to 400–600 km. The pattern and distances travelled were identical to those shown by the

474   predominant one-year-old population American shad along the North American east coast

475   (Walther and Thorrold 2010), reinforcing the similar dynamics functioning hypothesis

476   through the phylogenetical similarity between these species.

477   Based on our results we suggested a modification of a previous hypothesis stating that

478   European shads would aggregate following natal origin in the vicinity of their natal river

479   estuary (Taverny and Elie 2001; Lassalle et al. 2008; Rougier et al. 2014). An alternative

480   hypothesis consistent with our results would be two population-specific dispersal behaviours.

481   The first type of behaviour could be called resident gregarious, formed by individuals with

482   the same natal origin and remaining in the vicinity of the natal estuary. The second type of

483   behaviour could be called dispersive gregarious, formed by individuals with the same natal

484   origin but travelling longer distances away from their natal estuaries. The underlying

485   mechanism driving the existence of two types of behaviours or ecotypes should be explored

486   in future studies. Both abiotic factors, such as the predominant northward currents

487   (Koutsikopoulos and Le Cann 1996), and biotic factors such as density-dependent processes,

488   genetic components, or foraging may be involved (Taverny and Elie 2001; Johnson et al.

489   2016; Huntsman et al. 2017). The discovery of this type of important latitudinal

490   displacements contrasted with a previous study carried out in the Bay of Biscay, which

491   suggested that both shad species primarily performed seasonal longitudinal movements and

492   barely performed latitudinal displacements (Trancart et al. 2014).

493   Our results supported the first description of the population-specific dispersal capabilities of

494   European shads subadults at sea. A previous study showed that juveniles Allis shad from the

495   Sebou River in Morocco migrated southwards for about 600 km until they reached the

496   upwelling areas rich in nutrients (Sabatié 1993). However, Sabatié (1993) did not carry out

497   any specific studies on natal origin and suggested that the Allis shad individuals present in

498   these upwelling areas would most likely originated from the only river (Sebou River) with a

499   stable and abundant presence of Allis shad along the Atlantic coast of Morocco. Marine by-

500   catches of European shads have also been documented several hundred kilometres from the

501   most likely source rivers (La Mesa et al. 2015; Nachón et al. 2016). Based on natal origin

502   determined by otolith microchemistry, Allis shad individuals were also found to migrate

503   considerable distances along the marine environment from their natal origin river to their

504   spawning river (Martin et al. 2015). Similarly, genetic studies suggested that Twaite shad

505   individuals could cover distances of hundreds of kilometres between their natal rivers and

506   their spawning river (Jolly et al. 2012).

507   **Implications of the population-specific composition at sea on the metapopulational**

508   **dynamics at continental scale**

509   Whether the population specific dominance of Southern rivers populations in the Bay of

510   Biscay promoted straying and subsequent colonization of some rivers remains to be tested. In

511   the 80's, Brittany Allis shad populations were nearly extinct, but since the 2000s, small

512   populations started to establish again. Recent studies showed that Allis shad populations in

513   Brittany exhibited a high degree of homing, with small exchanges of spawners (Randon et al.

514   2018). The recovery of a depleted population is driven by two different processes: the

515   increase of abundance of residual populations that had remained in the considered rivers

516   and/or coastal nearby areas, or alternatively by immigration of strayers originating from

517   nearby populations (Belliard et al. 2009; Perrier et al. 2009; Andrée et al. 2011). The

518   reintroduction success by straying relied on the proportion of strayers provided to the

519   depleted population as well as on the proximity of neighbouring populations (Hamann and

520   Kennedy 2012; Keefer and Caudill 2014). The colonisation of Brittany Rivers in the 1980s

521   by Allis shads from Southern Rivers, located at sea in vicinity of river plumes, could explain

522   the recovery of Brittany Rivers.

523   In the hypothesis of a composition of marine stocks linked to the abundance of shads in the

524   continental environment, the dispersal capacities in the marine environment could have

525   changed in the current context of the collapse of the Gironde system populations and

526   generalised French populations abundance decrease (Rougier et al. 2012; Cellule Migrateurs

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527 Charente Seudre 2017; Legrand and Besse 2018). Weak dispersion in the marine

528 environment would explain why straying behaviour was mainly observed between

529 neighbouring rivers nowadays (Randon et al. 2018). Even the Dordogne River, which has

530 been identified as the main source river in the metapopulation dynamics of Allis shad,

531 produces strayers that mostly enter in other river (Garonne River) of the same basin (Randon

532 et al. 2018). The virtual absence of strayers from southern rivers in northern rivers (Randon et

533 al. 2018), was consistent with the hypothesis of a lesser dispersal capacities at sea. It would

534 be interesting to find out if the dispersion of Southern rivers populations has changed over

535 time. Whether dispersion at sea is determined by abundance (density dependence) or another

536 factor remains to be tested. Therefore, future studies on stock-composition at sea are

537 necessary to understand how erratic individuals exchange between the different local

538 populations forming Allis shad metapopulation occurs. Regarding Twaite shad, it is also

539 essential to carry out studies on the natal homing to elucidate if this species shows

540 metapopulational behaviour similar to Allis shad.

541 In conclusion, the results of this paper show that the subadults of the European shads

542 captured at sea presented a limited diversity of natal origins. Most of the Allis shad subadults

543 came from the Adour River while most of the Twaite shad subadults originated from the

544 Oloron River. There were two hypotheses to explain the results: either the results reflected

545 the reality of the populations and expressed differences of survival between the populations

546 of the Southern Rivers or the alternative hypothesis was that it resulted from a confusion of

547 allocation between the rivers of the South due to the lack of references to the chemistry of the

548 water and the otoliths of the juveniles during the 80's. A robust discrimination of Northern

549 and Southern rivers suggested that the population-specific composition of European shads at

550 sea was influenced by abundance in the continental environment. As a result of this

551 abundance, there was a great diffusion in the marine environment, with most abundant

552 populations dispersing from areas close to the native river to areas hundreds of kilometres

553 away. Stock specific composition at sea is important for management and may be useful to

554 prioritize protection of main population sources of shads.

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865

866   **Table captions**

867   Table 1. Total canonical structure coefficients for canonical discriminant analysis performed

868   on elemental and Sr isotopic ratios in water samples. Taken from Martin et al. (2015).

Figure captions

Fig. 1. Sampling surveys campaigns and collection locations of the Allis shad and Twaite shad subadults retained for this study. Marine catches were grouped into two marine regions, Bay of Biscay North (BBN) and Bay of Biscay Center (BBC). The French rivers where water and Allis shad otoliths samples were collected to build the Bayesian model of attribution to the river of origin, as described in Randon et al. (2018), are also shown. Only the lowermost sections of the main rivers are showed.

Fig. 2. Confusion matrix of reallocation between rivers. If the correlation is positive there is confusion while if the correlation is negative it means that there is a good discrimination between rivers. Colours (or shades of grey) as well as the size of the circles provide information about the intensity and direction of the correlations. Only significant correlations (p-value < 0.05) are shown.

Fig. 3. Summary of all reallocation probabilities for each river separated by species and marine region. Rivers were ordered from north to south. Each boxplot represent the first quantile (25%), the median (50%) and the last quantile (75%) of the distribution. The segments are the 95% credibility intervals.

Fig. 4. Most probable natal river assignations for Allis shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Allis shad are color-coded for the identification of the natal origin of individuals.

Fig. 5. Most probable natal river assignations for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.

892   Fig. 6. Canonical discriminant plot of isotope (^{87}Sr:^{86}Sr) and elemental (Sr:Ca and Ba:Ca)

893   signatures from water samples collected from 17 rivers in 2013. Symbols represent water

894   samples, and ellipses are 95% confidence intervals around each group. Grid scale is given (d

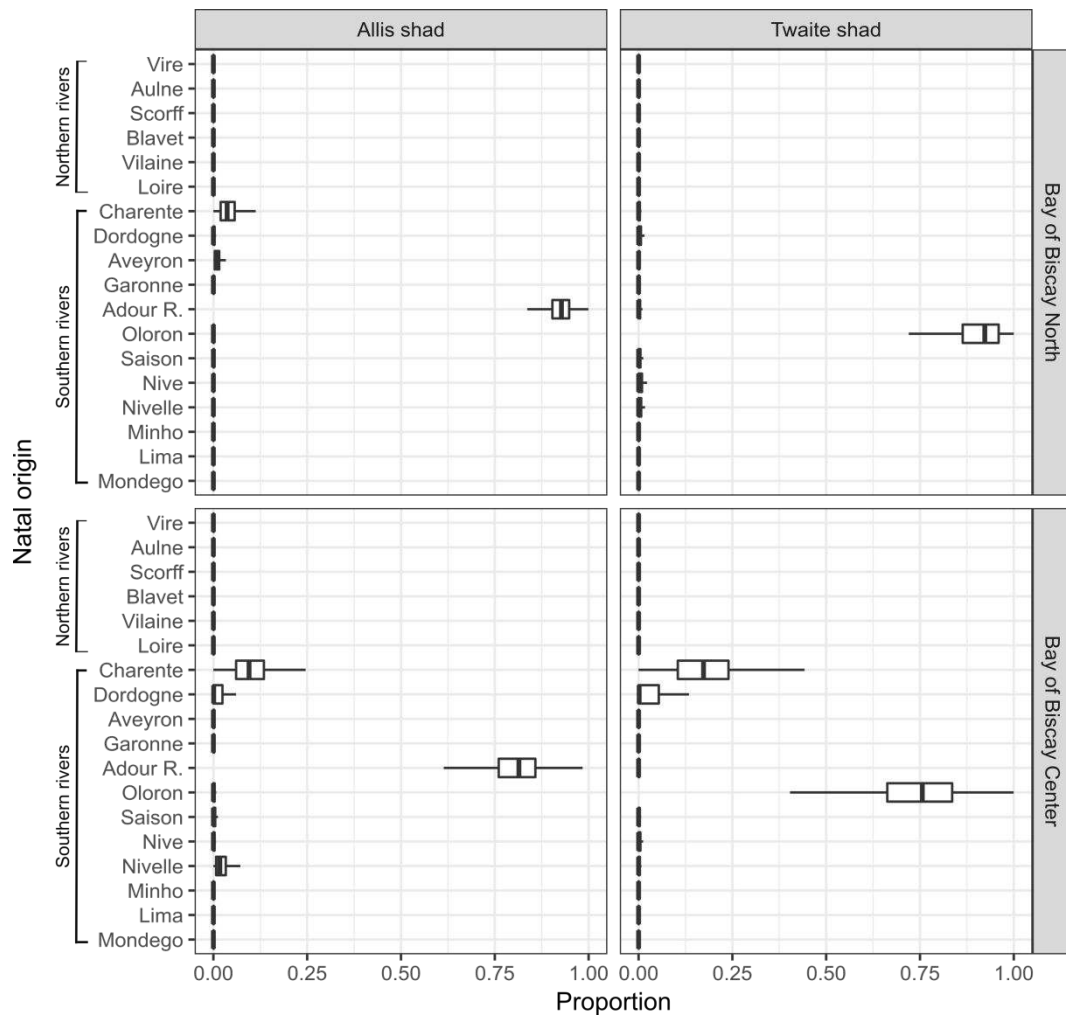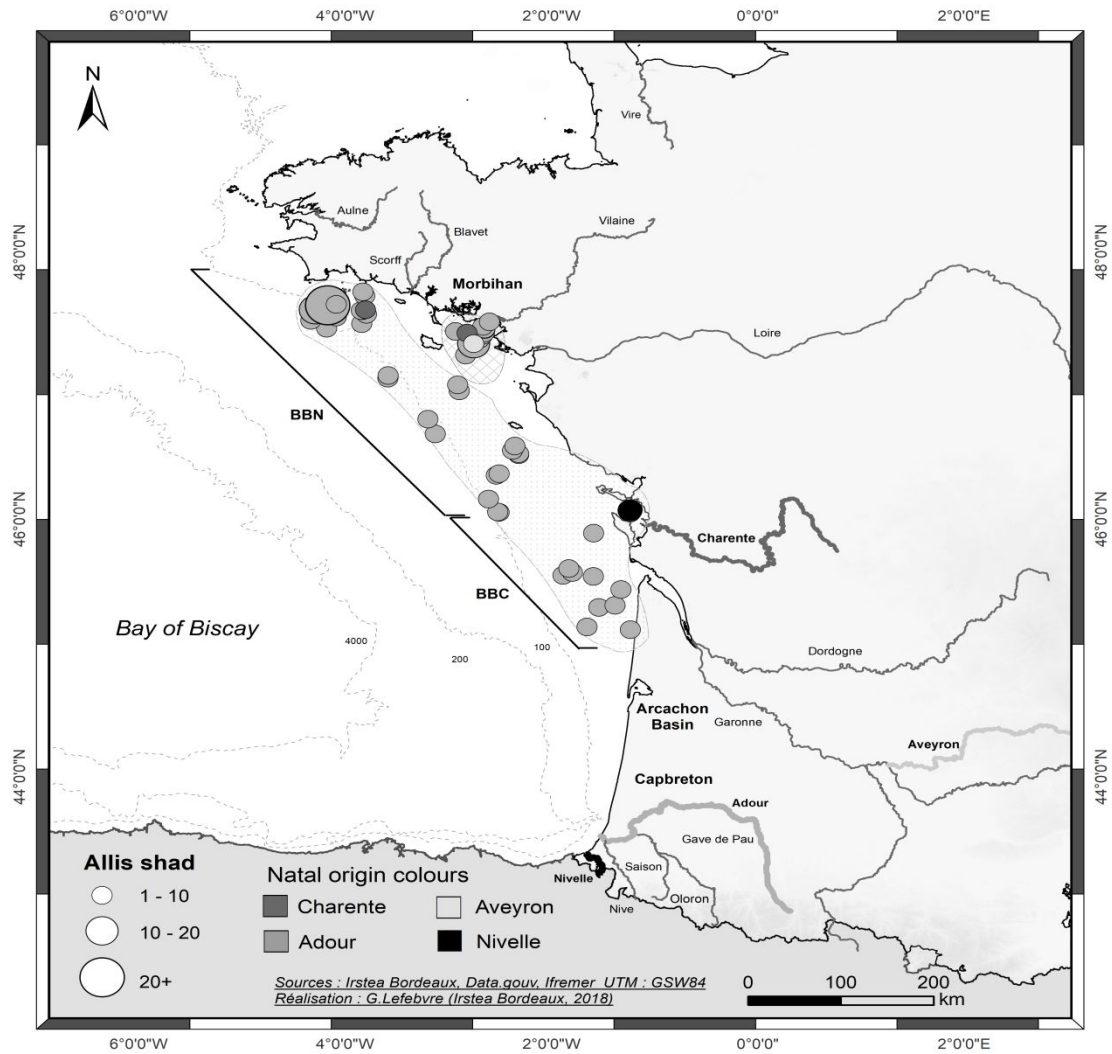895   = 1). Taken from Martin et al. (2015).

896

897   **Tables**

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Ratios	CV1	CV2
$^{87}Sr:^{86}Sr$	-0.880	0.362
Sr:Ca	0.151	-0.518
Ba:Ca	0.034	-0.205

901   **Figures**
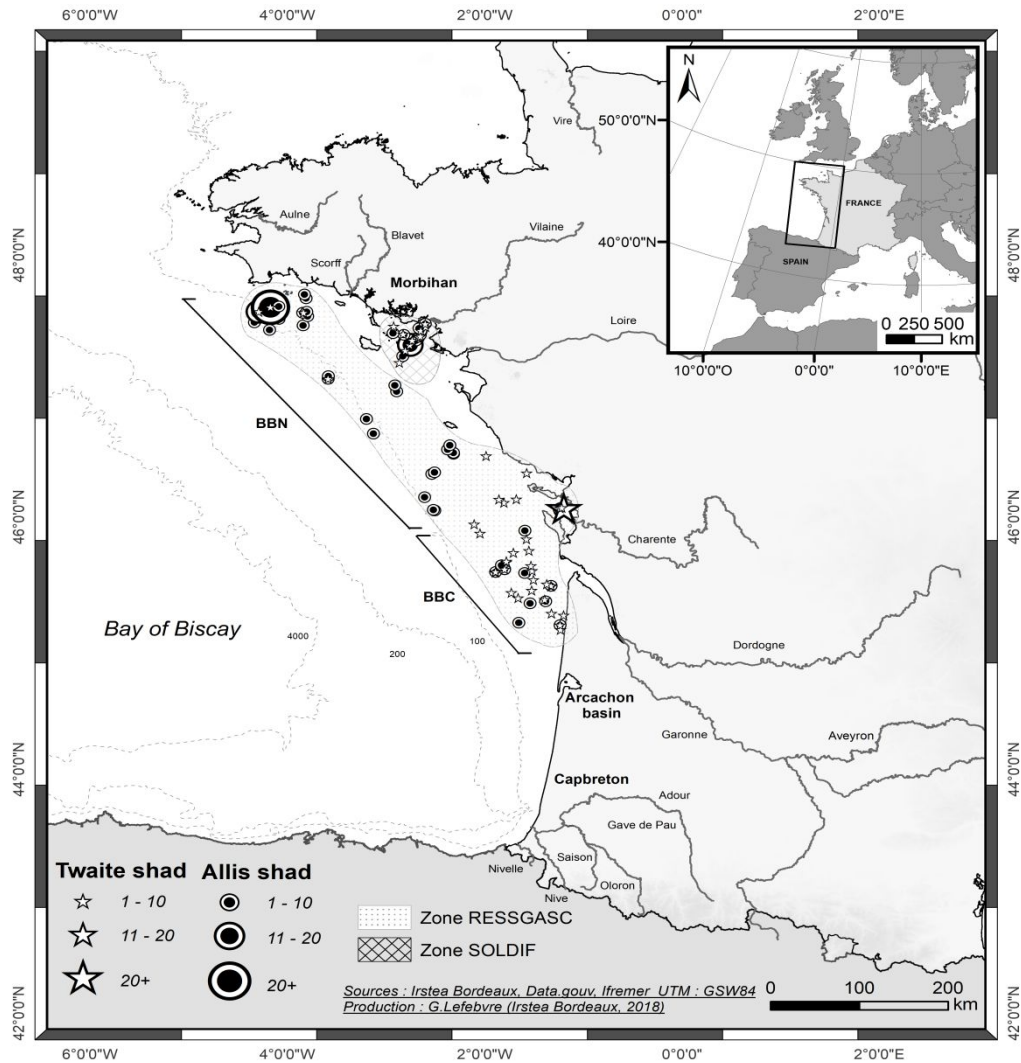
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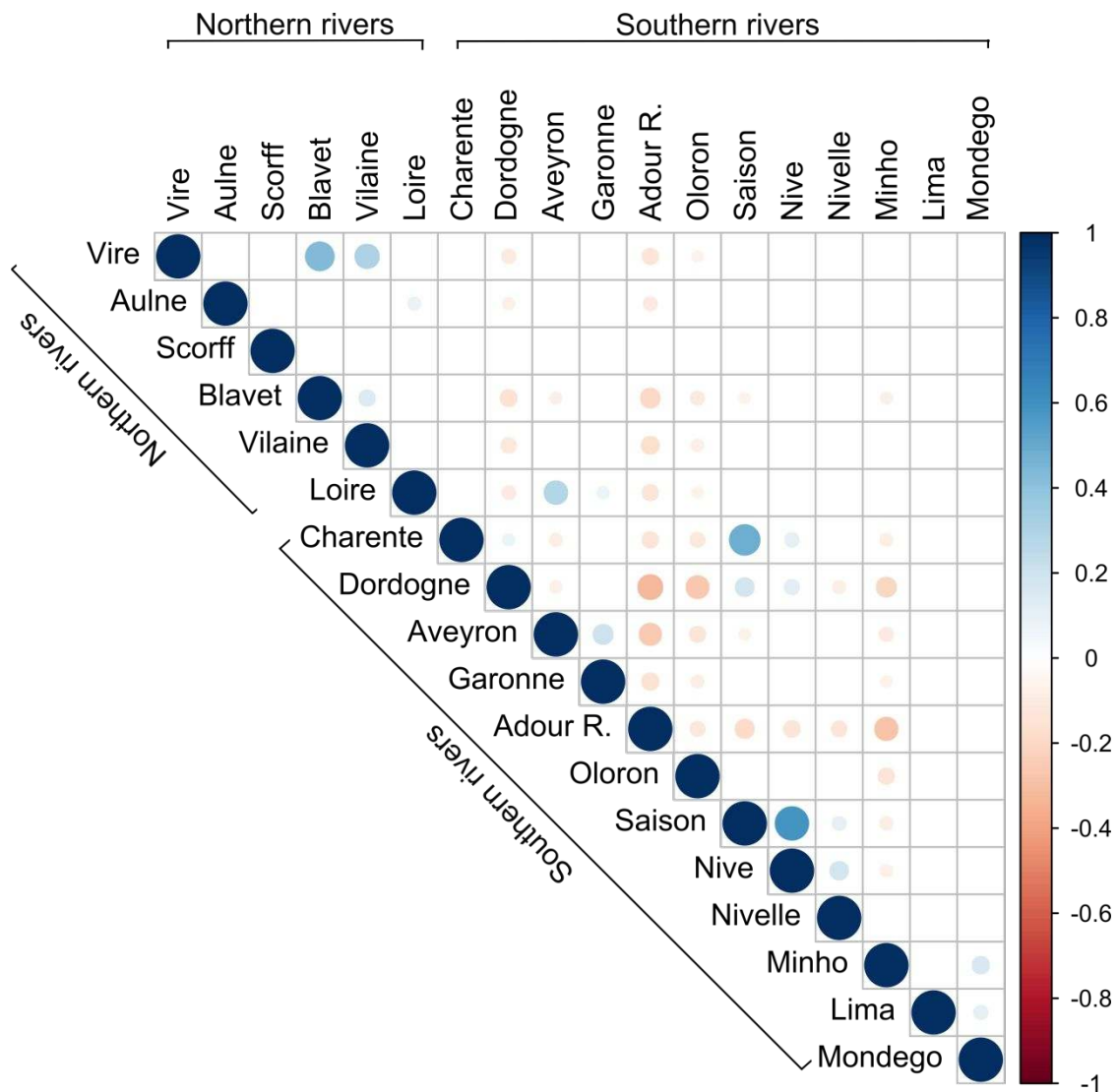
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Fig.5. Most probable natal river assignations for Twaite shad subadults. The map shows all

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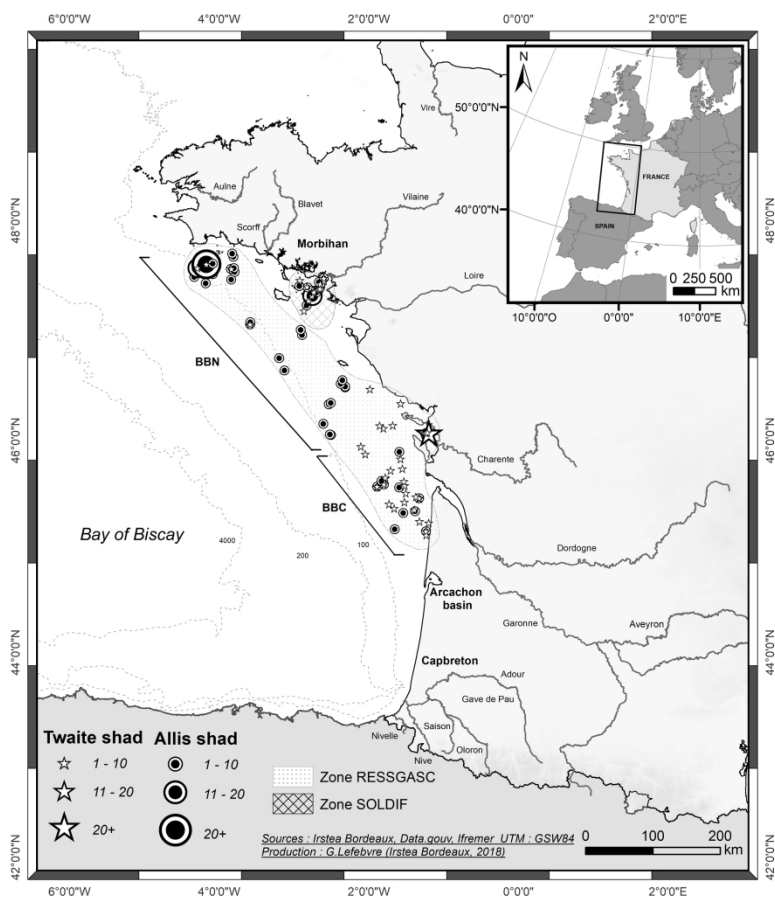
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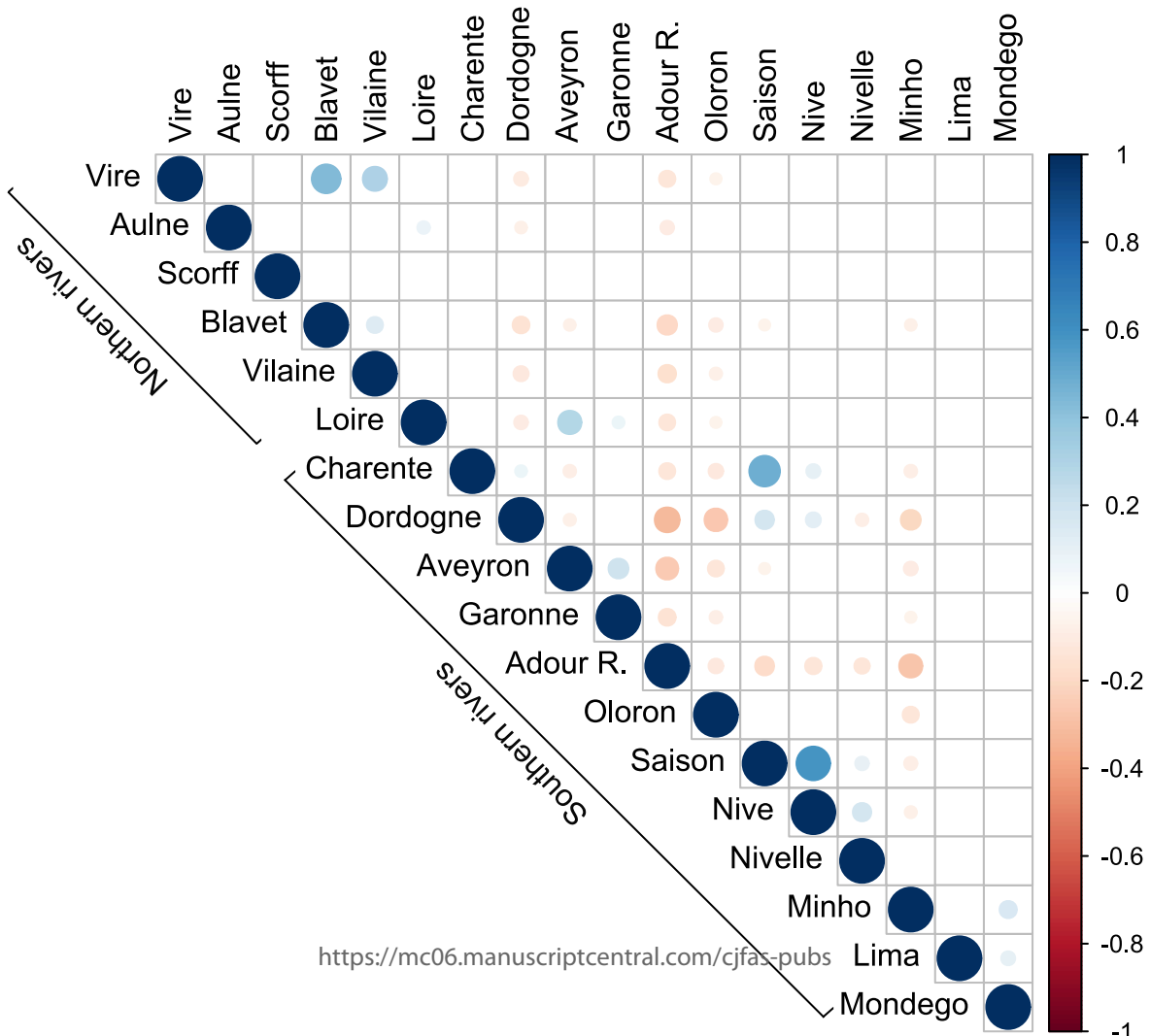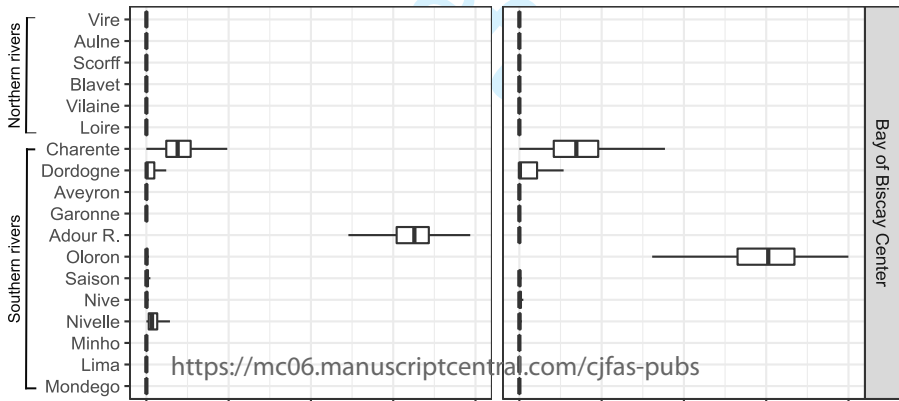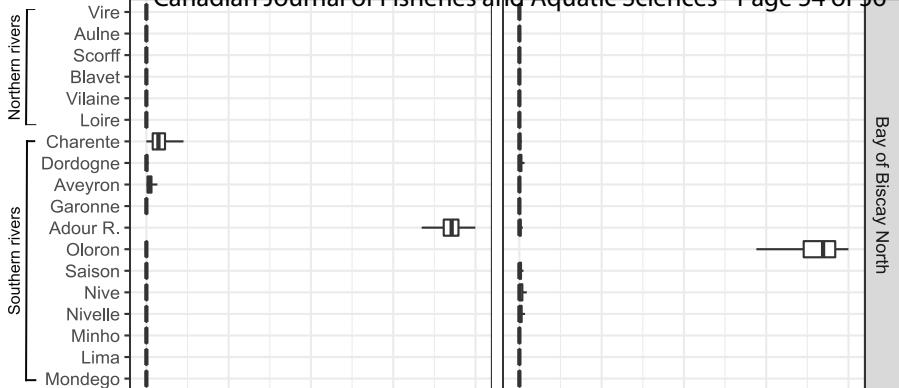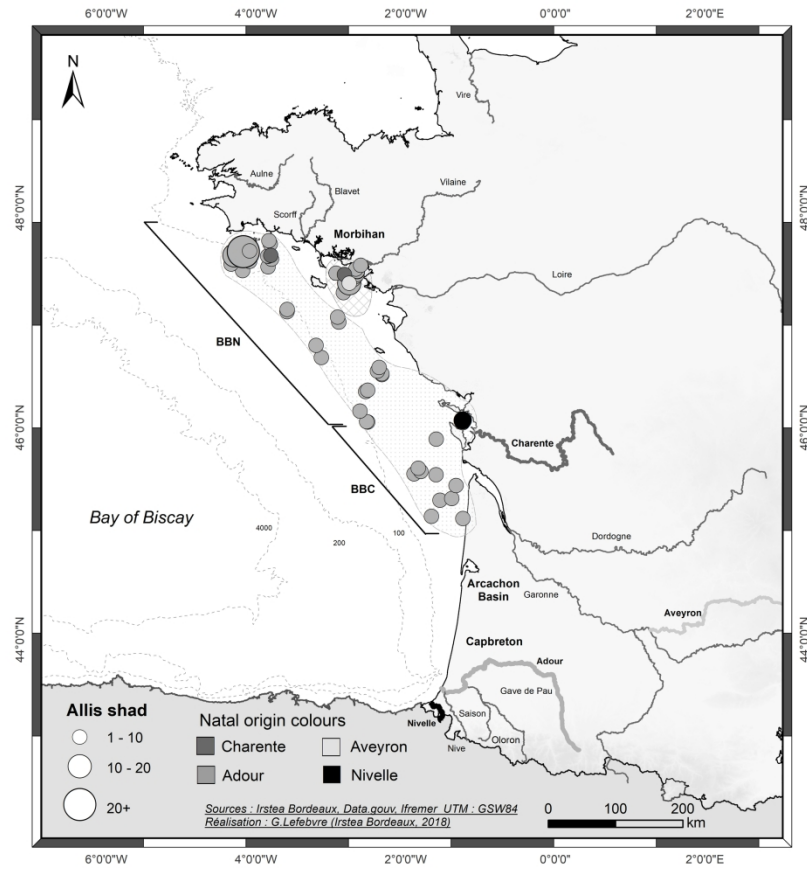
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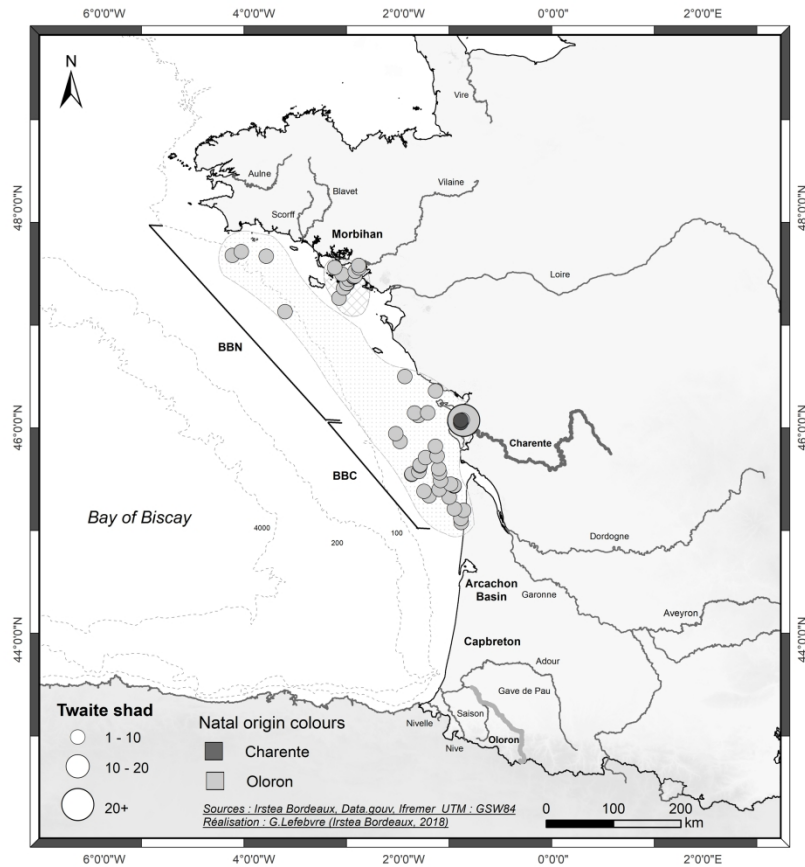
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Fig. 5. Most probable natal river assignations for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.
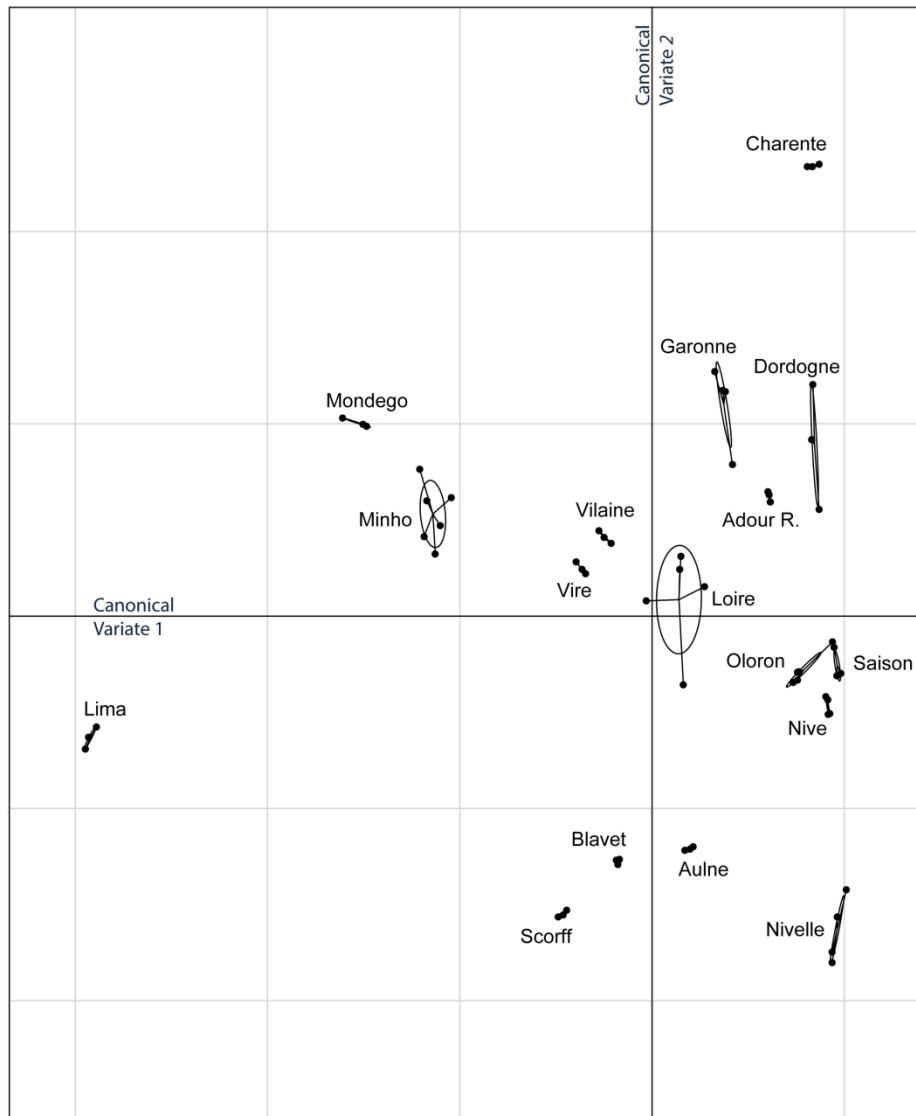
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