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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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26 Abstract

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

42 **Introduction**

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

54 Over the last decades, it has been generally accepted that the return of anadromous fishes to
55 their natal river is influenced by the combination of geomagnetic and olfactory cues
56 (Lohmann et al. 2008; Bando et al. 2011; Putman et al. 2013). Recently, it has been
57 suggested that social interactions and collective behaviour could also play an important role
58 in the return of salmon to the river of origin (Berdahl et al. 2016). That is, there is evidence
59 that collective navigation and group effect could facilitate decision-making to find correct
60 migration pathways from the ocean to the native rivers. This group effect could reduce
61 dispersal, which would most likely occur if one individual moved away from the group. In
62 fact, a recent study has shown that although small-scale Chinook salmon *Oncorhynchus*
63 *tshawytscha* aggregations in the sea are not entirely uniform, they tend to be composed of
64 individuals from the same natal origin (Johnson et al. 2016). Whether fishes segregate
65 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. 2000a; 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. 2003a, 2003b; 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. 2000b; 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 Twaité 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).

156 **Material and methods**

157 **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

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 ($47^{\circ}17'N$), 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 S1³).

217 **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 ($^{87}\text{Sr}:$ ^{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 $^{87}\text{Sr}:$ ^{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 $^{87}\text{Sr}:$ ^{86}Sr . Analytical process can be found in Martin et al. (2015).

238 ³Supplementary data are available with the article.

239 **Baseline samples and statistical analyses**

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 ($^{87}\text{Sr}:$ ^{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 $^{87}\text{Sr}:$ ^{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 $^{87}\text{Sr}:$ ^{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 $45\text{--}46^\circ\text{N}$, 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)

263 included all individuals caught between 46–48° 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 k_b 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 F_f vector containing the k_b 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

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).

309

310

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

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%, $n = 7$).

341 **Discussion**

342 **Population-specific proportions at sea**

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 $^{87}\text{Sr}:^{86}\text{Sr}$ ratios between $0.71160 \pm 1.00\text{E-}04$ and $0.71429 \pm 1.01\text{E-}04$, Southern
359 sedimentary French rivers have low Sr values between $0.70823 \pm 5.70\text{E-}05$ and $0.71037 \pm$
360 $1.22\text{E-}04$ (Martin et al. 2015). Our Bayesian model of natal origin was mainly driven by
361 $^{87}\text{Sr}:^{86}\text{Sr}$ ratios, while Sr:Ca and Ba:Ca ratios complemented the discrimination (Martin et al.
362 2015). $^{87}\text{Sr}:^{86}\text{Sr}$ 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

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 S2³). 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 slight 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). These 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 shad 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 Twaité 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 metapopulation**
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

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 metapopulation 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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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).

870 **Figure captions**

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

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

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

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

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

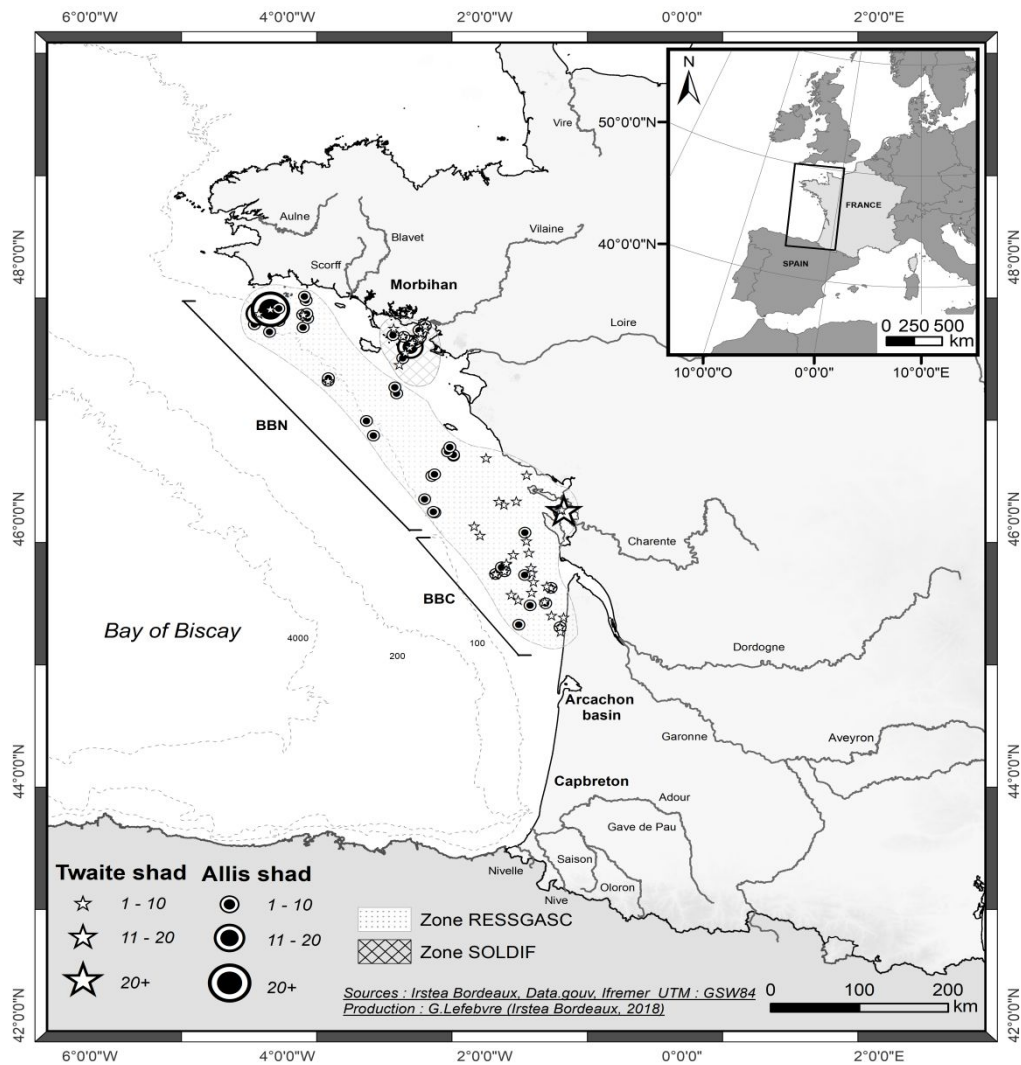
892 Fig. 6. Canonical discriminant plot of isotope ($^{87}\text{Sr}:^{86}\text{Sr}$) and elemental (Sr:Ca and Ba:Ca)
893 signatures from water samples collected from 17 rivers in 2013. Symbols represent water
894 samples, and ellipses are 95% confidence intervals around each group. Grid scale is given (d
895 = 1). Taken from Martin et al. (2015).

896

897 **Tables**

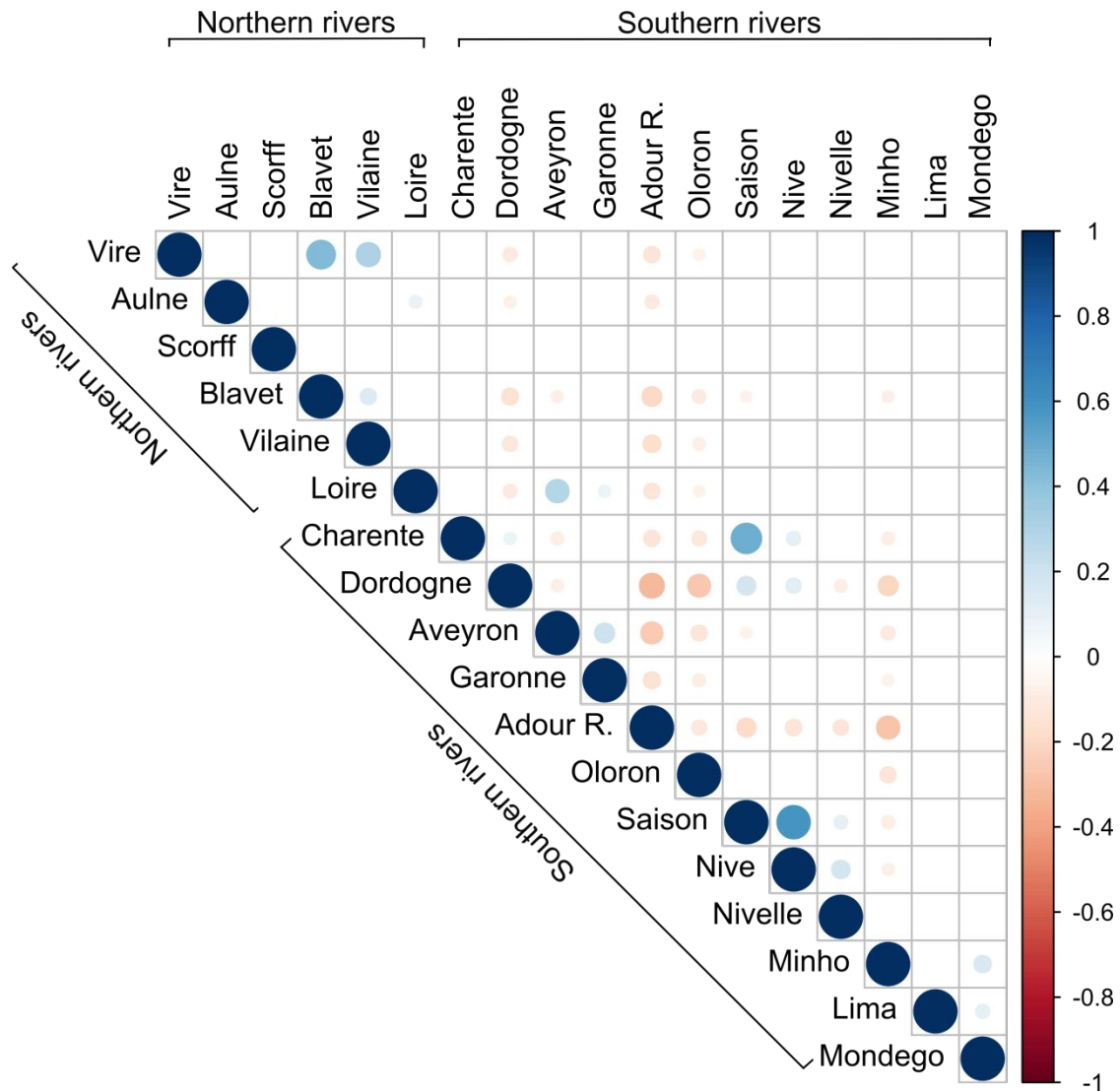
898 Table 1. Total canonical structure coefficients for canonical discriminant analysis performed
899 on elemental and Sr isotopic ratios in water samples. Taken from Martin et al. (2015).

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

901 **Figures**

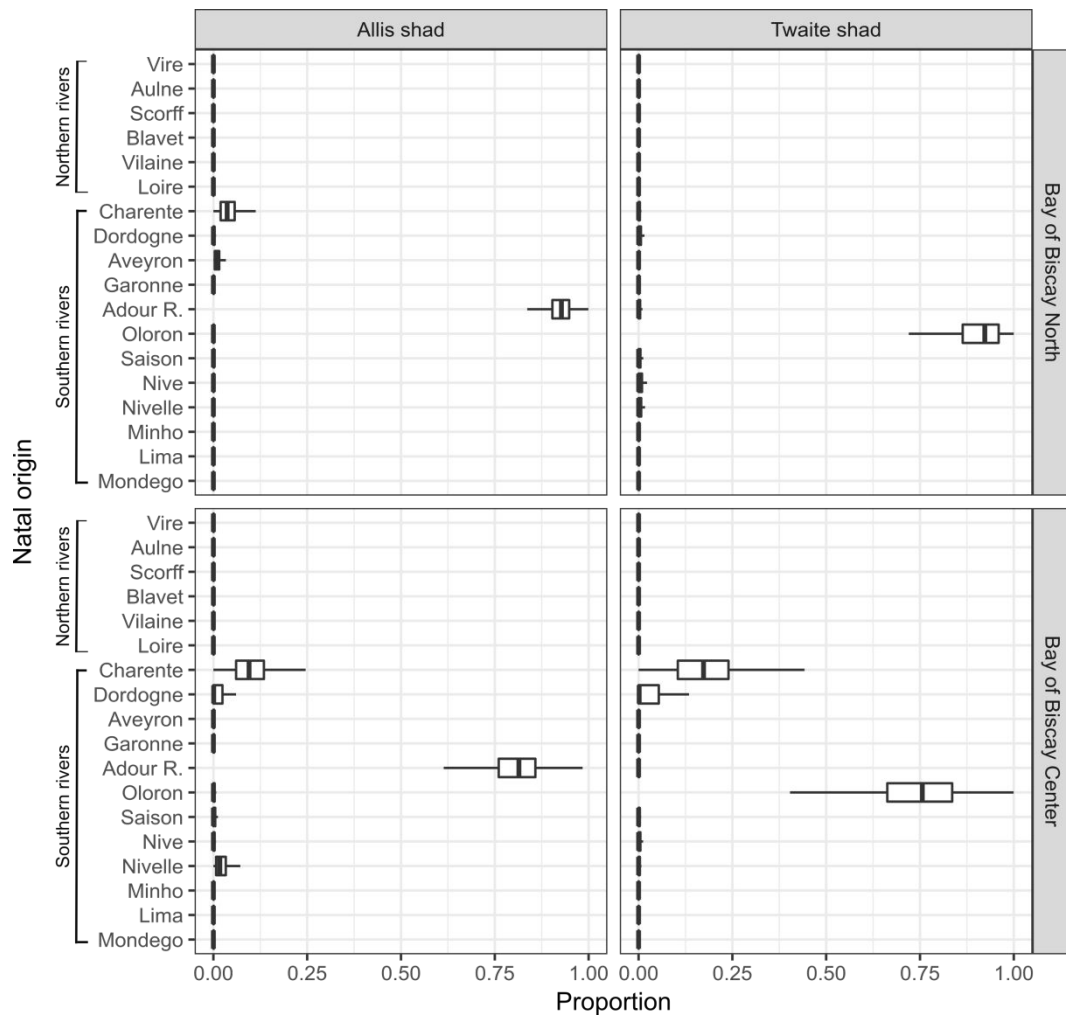
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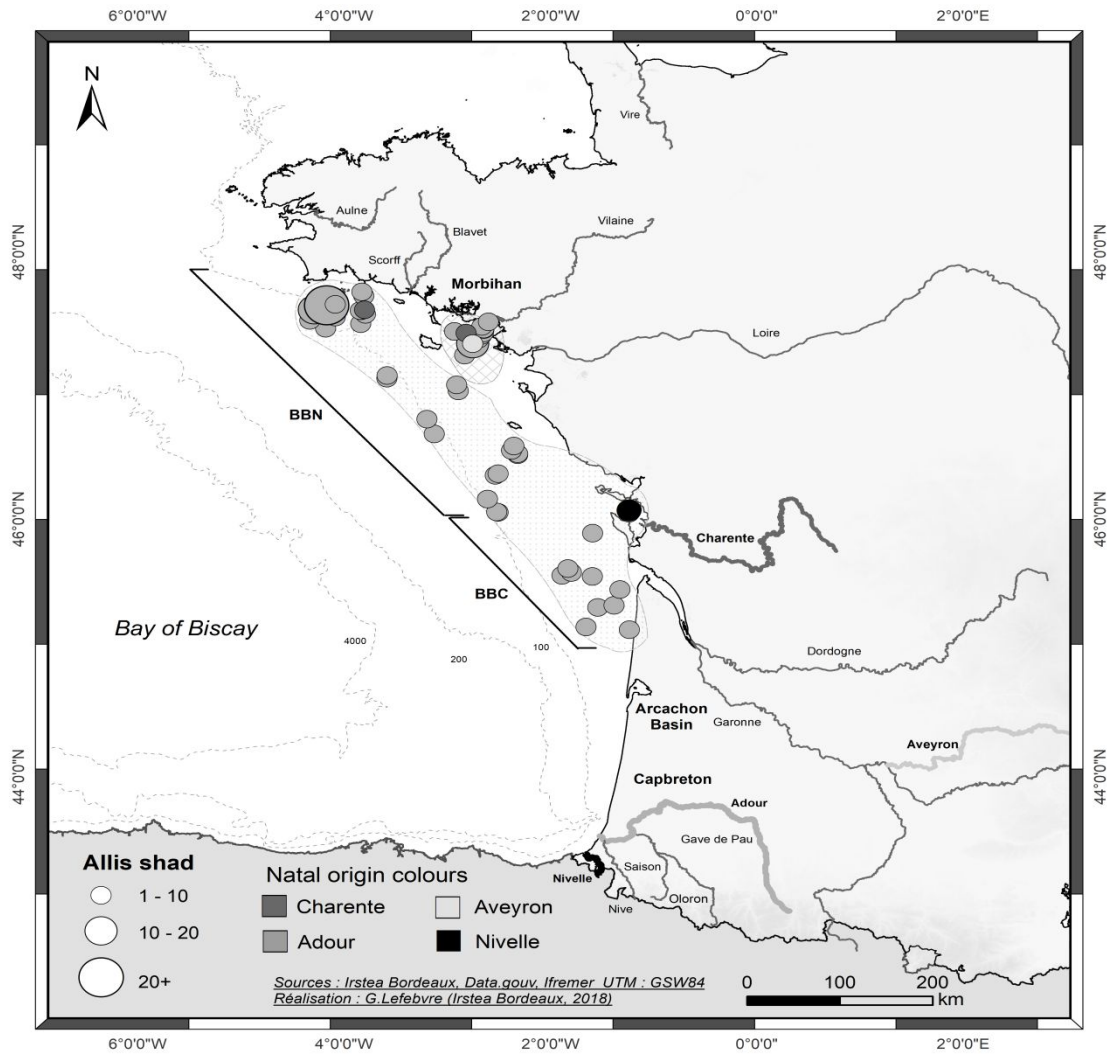
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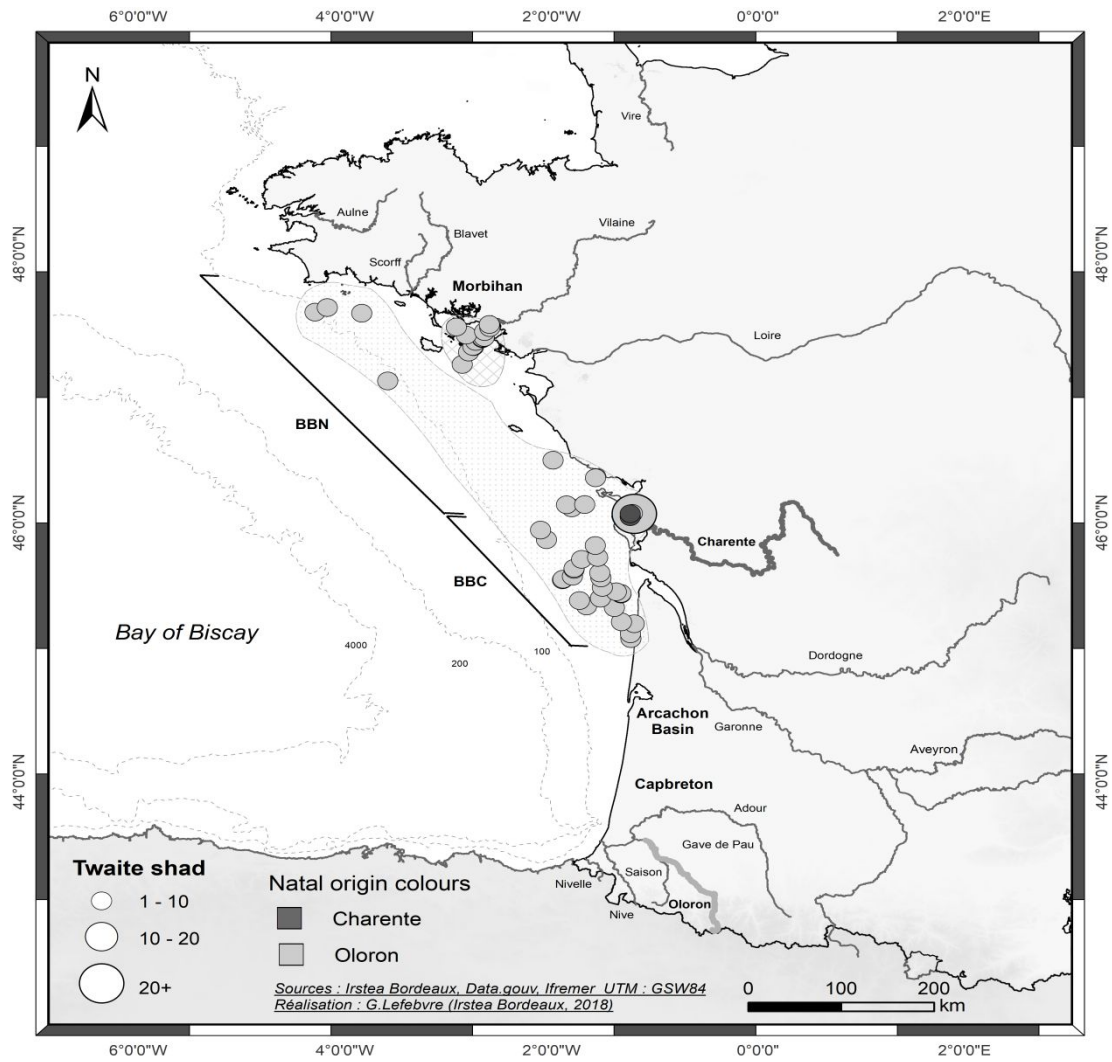
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916 Fig.3. Summary of all reallocation probabilities for each river separated by species and
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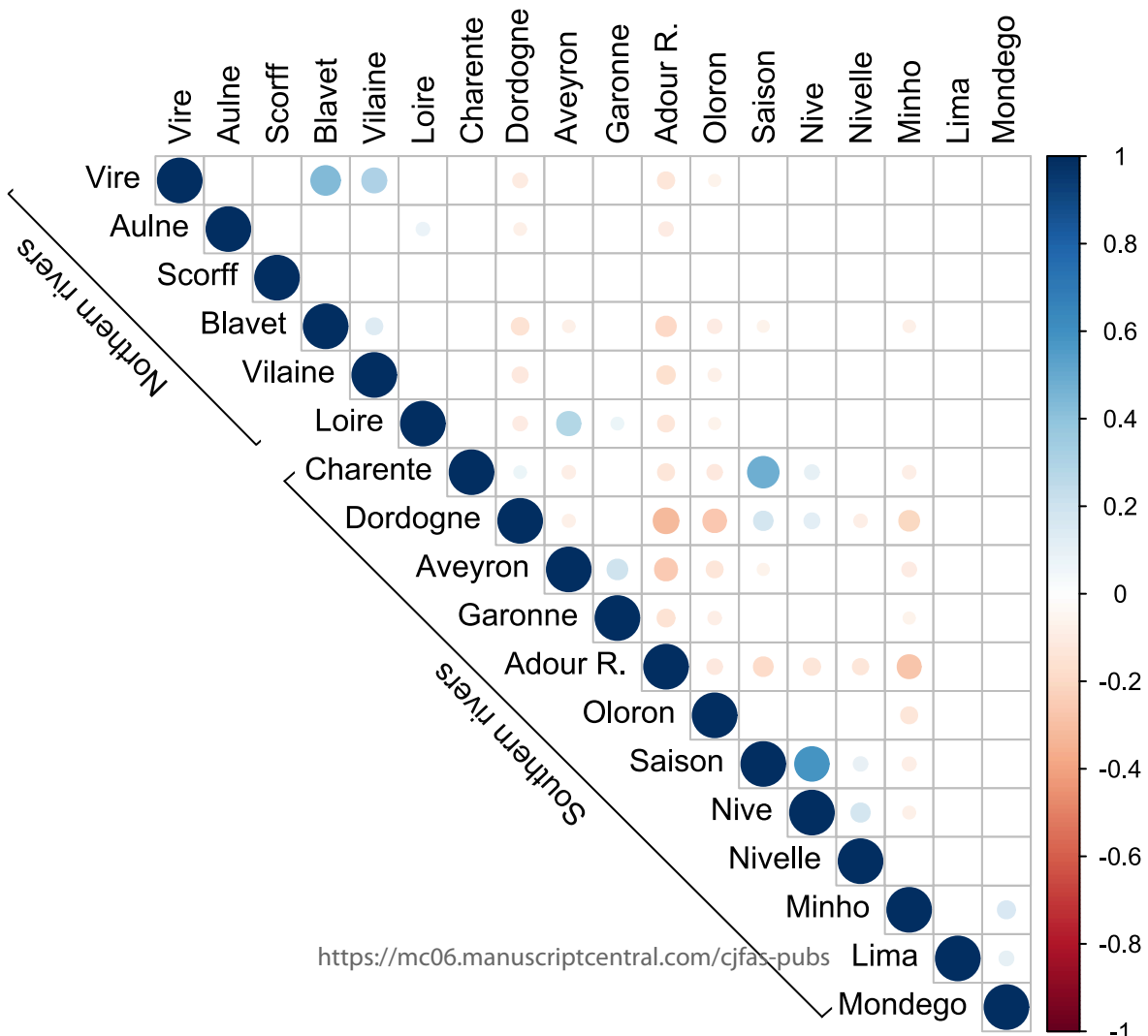
929 Fig. 6. Canonical discriminant plot of isotope ($^{87}\text{Sr}:^{86}\text{Sr}$) and elemental (Sr:Ca and Ba:Ca)
 930 signatures from water samples collected from 17 rivers in 2013. Symbols represent water
 931 samples, and ellipses are 95% confidence intervals around each group. Grid scale is given (d
 932 = 1). Taken from Martin et al. (2015).

933

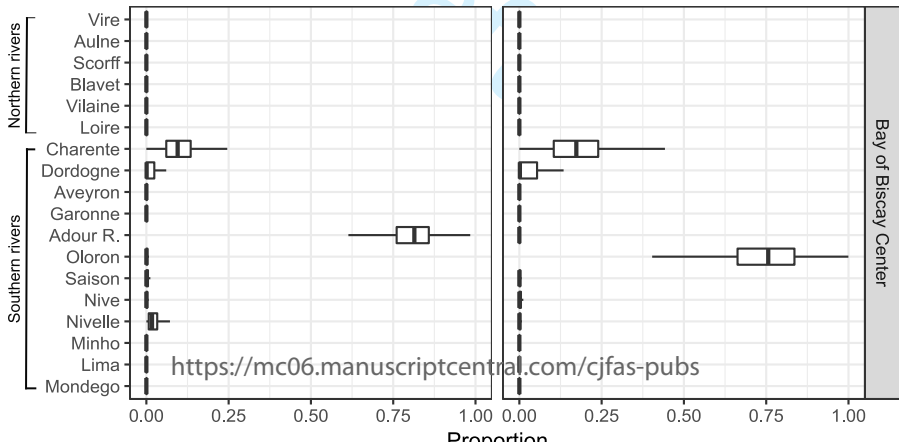
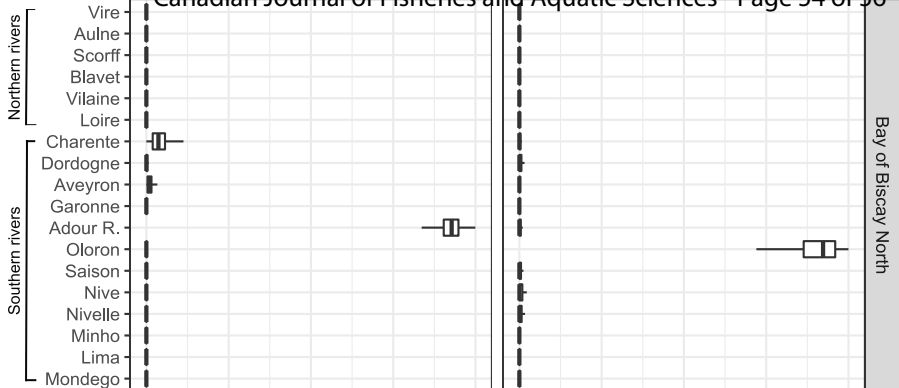
Table 1. Total canonical structure coefficients for canonical discriminant analysis performed on elemental and Sr isotopic ratios in water samples. Taken from Martin et al. (2015).

Ratios	CV1	CV2
$^{87}\text{Sr}:^{86}\text{Sr}$	-0.88	0.362
Sr:Ca	0.151	-0.518
Ba:Ca	0.034	-0.205

Draft



Natal origin



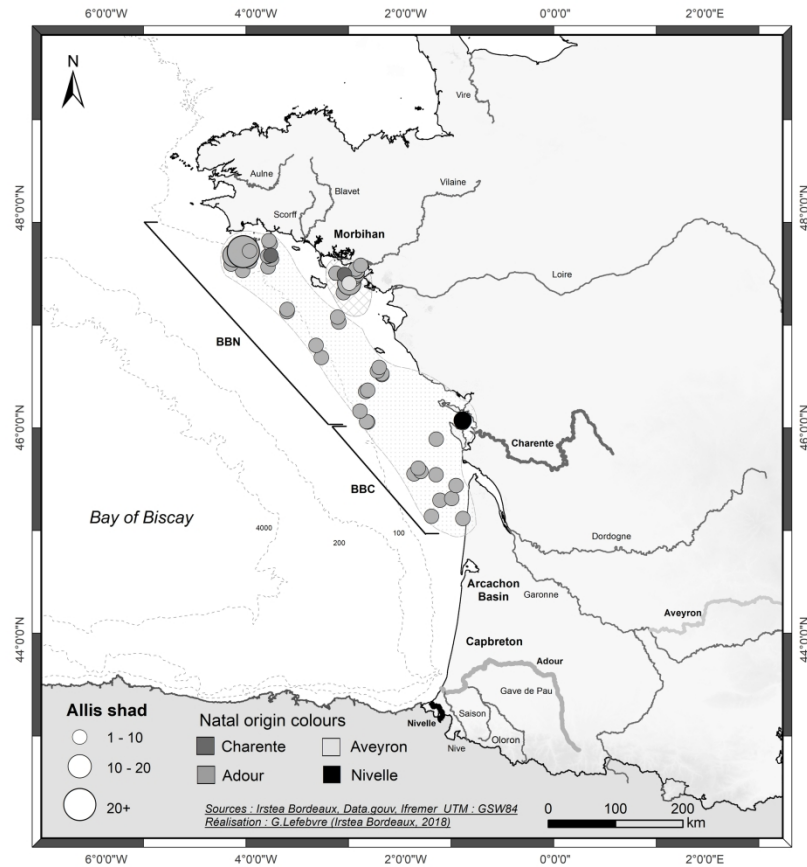


Fig. 4. Most probable natal river assignments for Allis shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Allis shad are color-coded for the identification of the natal origin of individuals.

210x297mm (300 x 300 DPI)

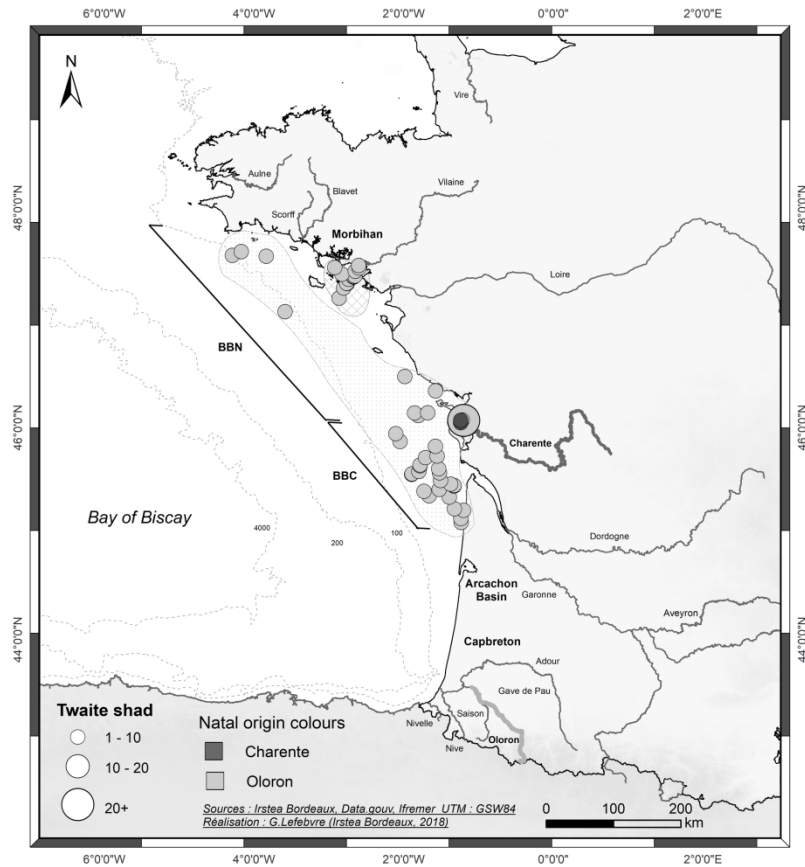


Fig. 5. Most probable natal river assignments for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.

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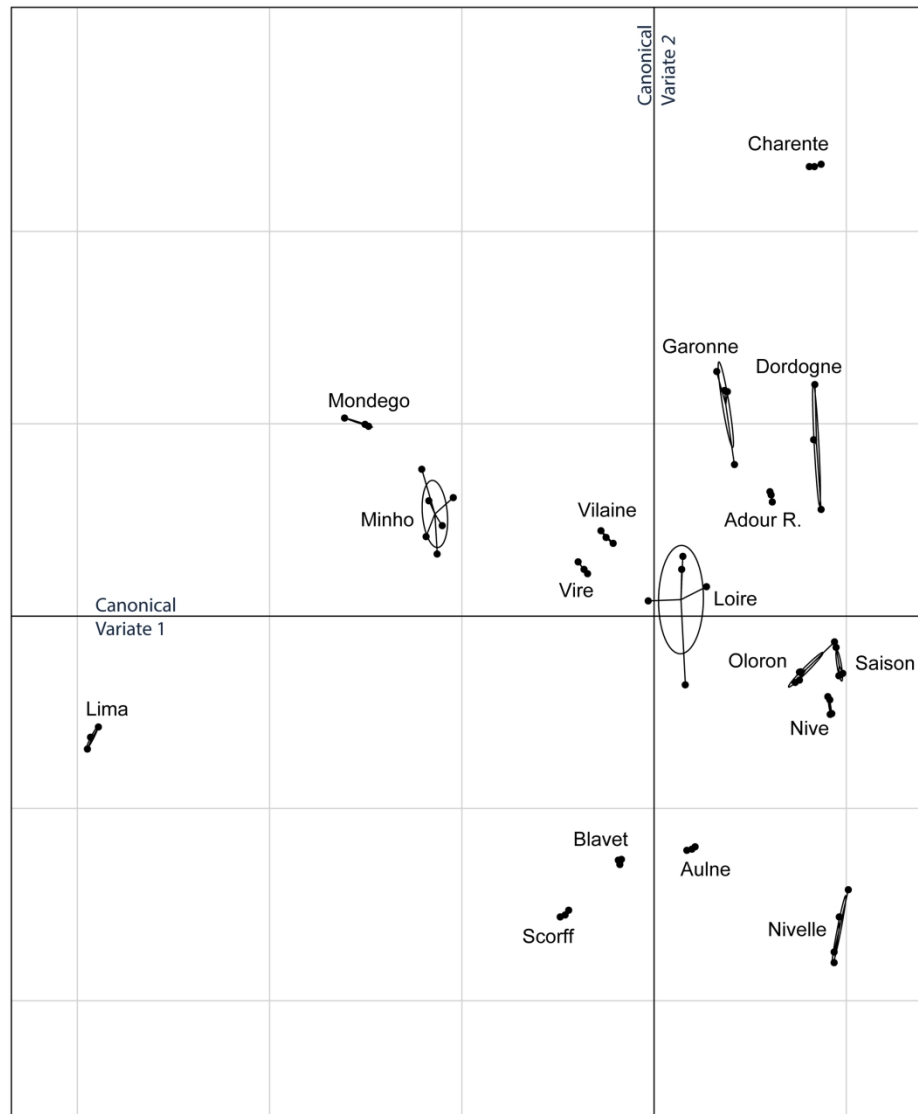


Fig. 6. Canonical discriminant plot of isotope ($^{87}\text{Sr}:^{86}\text{Sr}$) and elemental ($\text{Sr}:\text{Ca}$ and $\text{Ba}:\text{Ca}$) signatures from water samples collected from 17 rivers in 2013. Symbols represent water samples, and ellipses are 95% confidence intervals around each group. Grid scale is given ($d = 1$). Taken from Martin et al. (2015).

214x239mm (300 x 300 DPI)