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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 salmon 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; Bando 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 salmon 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

of exchanges between populations, and more generally demonstrates their dispersal ability at sea (Walther and Thorrold 2010; Loewen et al. 2015; Johnson et al. 2016). Disentangling the habitat occupation and migration patterns at sea of the main source populations in a meta-population dynamic can provide insight on the relevant management scale and priorities. However, identifying the natal origin of wild anadromous fishes during the ocean growth phase constitutes a real challenge.

Natural tags contained in certain tissues, such as otoliths (calcified structures of the inner ear of teleost fish), could be a good approach to obtain information about the natal origin and subsequent population marine mixing of anadromous species (Hobson 1999; Turner et al. 2015). Otoliths are acellular metabolically inert materials, which grow continuously throughout the life of the fish. The concentration of certain accreted elements in the successive growth layers is largely correlated with their concentration in the ambient water, especially in freshwater (Campana and Thorrold 2001; Walther and Thorrold 2006; Morais and Daverat 2016). Therefore, if there are natal habitats with significant difference in chemical composition, otoliths core from fish hatched in each of them will record for life the unique signatures of each particular natal area, enabling the retrospective identification of natal origin (Campana and Thorrold 2001; Walther et al. 2008; Morais and Daverat 2016). Thus, the unique properties of these calcified pair structures make them especially useful to unravel the life-history features and movement patterns of diadromous fishes at fine spatial scales, such as dispersal capacities, patterns of population connectivity and natal origin of fish (Daverat et al. 2011; Nachón 2017; Randon et al. 2018). Anadromous fishes are often caught as bycatch in coastal fisheries, particularly shads because of their school-forming behaviour (Taverny and Elie 2001; Hasselman et al. 2015; Nachón et al. 2016). These opportunities are usually capitalized to collect various organs or tissues in order to study the life history of the fish caught (Taverny and Elie 2001; Walther and Thorrold 2010;

Hasselman et al. 2015). Scales and mostly otoliths are thus collected routinely for age determination purposes. After age estimation, these tissues are usually archived in research institutions or museums. Historical otolith collections are precious sources of retrospective information. However, to the best of our knowledge, studies analysing the microchemistry of historical archived otoliths have rarely been addressed (Gao and Beamish 2003; Munro et al. 2005; Loewen et al. 2015).

In the present study, we used natural chemical tags recorded in historical archived otoliths to assess the natal origins of subadults of European shad species collected in the marine environment in the 80's. The European shads, Allis shad (*Alosa alosa*) and Twaite shad (*Alosa fallax*), are a complex of two sympatric sister species of anadromous Clupeidae species. Juveniles develop in freshwater and migrate to the sea during their first year of life (Taverny 1991; Taverny et al. 2000a; Taverny and Elie 2001). During their growth phase, shads aggregate in coastal habitats and undertake back-and-forth movements between the marine and estuarine environments, especially Twaite shad for their first two years of life (Taverny 1991; Taverny and Elie, 2001; Nachón 2017). Then, the growth phase is completed in oceanic habitats until they reach sexual maturity (generally between 3 to 6 years of age) and migrate back to the rivers to spawn (Aprahamian et al. 2003a, 2003b; Baglinière et al. 2003). Both shad species were originally distributed along the Northwest Atlantic coast, from Scandinavia to Morocco as well as in the western Mediterranean (Allis shad) or throughout the Mediterranean (Twaite shad) (Baglinière 2000). Like other diadromous species, the European shads have suffered major declines as their life cycle, using both freshwater and marine ecosystems, exposed them to a suite of accumulation of possible impacts, such as damming of rivers, overfishing, bycatch, deterioration of spawning habitats, etc. (Taverny et al. 2000b; De Groot 2002; Limburg and Waldman 2009). The deleterious effects of these impacts began to be significantly apparent from the late 19th century and intensified during

the 20th century, leading to considerable extinctions, especially at the extremes of their distribution range, and declines in abundance levels throughout the range of distribution (Baglinière 2000; Taverny et al. 2000b; Aprahamian et al. 2003a). Shad populations were still abundant in France at the end of the 20th century, even though some populations had already suffered significant reductions in the population numbers, such as the Adour and Loire populations, and others had already collapsed or even disappeared, such as the Seine, Brittany and Normandy populations (Taverny 1991; Baglinière 2000; Bruslé and Quignard 2013). During this period, the Gironde system (Dordogne and Garonne rivers) Allis shad populations were the most abundant in Europe (Martin–Vandembulcke 1999; Baglinière 2000; ICES 2015). However, from the year 2000 onwards, the Garonne and Dordogne Allis shad populations collapsed (Rougier et al. 2012) and the abundance of other French shad populations has also decreased dramatically (Cellule Migrateurs Charente Seudre 2017; Legrand and Besse 2018).

During their oceanic phase, the habitats used by subadults of both species are located in the vicinity of the river mouths of most important spawning grounds, such as Gironde system, Charente, Loire and Vilaine rivers, along the French Atlantic coast of the Bay of Biscay (Taverny 1991; Taverny and Elie 2001). The presence of subadults in marine habitats connected to an estuary would suggest that fishes stay close to their natal river basin (Taverny 1991; Taverny and Elie 2001). Recent studies that have revealed that Allis shad formed a meta-population where exchanges of adults primarily occurred between neighbouring rivers (Martin et al. 2015; Randon et al. 2018), would support this hypothesis. Genetic tools suggested that Twaite shad formed more structured populations than Allis shad populations, meaning that exchanges between populations should be more intense for the latter (Jolly et al. 2012). So far, there is no knowledge on whether straying is favoured by a mixing of the populations of shads from different natal origin at sea or if shads are straying

from distinct marine habitats. Understanding the population-specific dispersal capacities in the ocean is thus required. Allis shad juveniles from a Moroccan population displayed migrations of 600 km along the coast between their natal river and their marine habitats, demonstrating the dispersion ability of the species (Sabatié 1993). In addition, some Allis shad adults would be able to enter rivers for spawning at a distance of more than 700 km from their natal river (Martin et al. 2015). Marine bycatches of both species have been documented several hundred kilometres away from their most likely rivers of origin (La Mesa et al. 2015; Nachón et al. 2016).

In the present study, the goals were first, to address the utility of archive otoliths in assigning the natal origin of European shads captured 30 years ago in the marine environment, when the Gironde shad populations were still abundant, and second, to investigate the distribution of Allis shad and Twaite shad subadults at sea following their natal origin in order to understand the extent of mixing or segregation of European shad populations. For that purpose, we coupled the otolith elemental and isotopic microchemistry with a Bayesian mixing model following Martin et al. (2015) and Randon et al. (2018).

Material and methods

Study area

The Bay of Biscay is a large open oceanic area located at the east of the North Atlantic Ocean (western part of Europe), which expands from north coast of Spain (from Cape Ortegal, ~42°N, -9°W), to the west coast of France (up to Finistère in Brittany, ~48°N and 1°E). This bay has a contrasted morphology as the continental shelf (depths < 200 m) is very narrow in the south, along the coast of Spain (10–65 km wide), whilst widens northward along the French coast, from 20 km in the southern part (Capbreton Canyon) to over 200 km in the northern part (Koutsikopoulos and Le Cann 1996; Le Pape et al. 2003; Bertin et al. 2012).

Our study focused on the French part of the Bay of Biscay (Fig. 1). Surface coastal waters of this area receive a strong freshwater run-off from outflow plumes of the main rivers, with Loire River and Gironde system providing 75% of the freshwater input (Ayata et al. 2010; Laiz et al. 2014; Costoya et al. 2017). Other rivers along the coast as Vilaine, Sèvre Niortaise, Charente, Adour and Nivelle rivers have more limited contributions in terms of freshwater run-off. The strong density gradients, which occurred in the vicinity of the outflow plumes of the Loire River and Gironde system, lead to extensive density currents over the shelf, essentially in a northwards direction (Koutsikopoulos and Le Cann 1996; Ayata et al. 2010). The regions under the influence of the river plume, especially those around the Vilaine River, Loire River and Gironde system, are highly productive pelagic areas, mainly for plankton (both phytoplankton and zooplankton) and small pelagic fishes (Motos et al. 1996; Irigoien et al. 2008).

Source of available shad samples

Archived otoliths from subadults of both shad species captured as bycatch in the late 1980s during research campaigns of “Institut Français de Recherche pour l'Exploitation de la Mer” (IFREMER) throughout the French continental shelf of the Bay of Biscay were selected as biological material (Taverny 1991; Taverny and Elie 2001). Bottom trawl scientific surveys (RESSGASC and SOLDIF) were conducted using random stratified sampling designs and targeting demersal or benthic species rather than pelagic species.

RESSGASC campaign (from August 1986 to Mars 1989) covered practically the entire coast, approximately 430 km (from the Morbihan Cape at 48°N to the North of the Arcachon Basin at 45°N), in a range of depths between 11 m and the 100 m isobaths (Fig. 1). The gear used in this campaign was a Vendée bottom trawl net of 25 m of headline and a 55 mm stretched mesh in the cod end. Of the 427 completed stations over all period, Allis shad and Twaite shad were captured in 59 and 55 locations respectively, with 18 shared locations. Catches

averaged 4 fishes per trawl date for both species, with the largest collections accounting 21 and 45 individuals of Allis shad and Twaite shad respectively (total $n = 254$ Allis shad; $n = 224$ Twaite shad).

SOLDIF campaign (from May 1988 to February 1989) was limited to a smaller sampling area, both with respect to the length, around the mouth of the Vilaine and Loire rivers ($47^{\circ}17'N$), and the depth, from outside the coastal zone to depths of less than 50 m (Fig. 1). Two gears were used in this sampling campaign: a 25 m double bottom trawl with 20 mm stretched mesh in the cod end and a 3 m long beam trawl of 1 mm stretched mesh in the cod end. Of the 168 completed stations over all period, Allis shad and Twaite shad were captured in 16 and 15 locations respectively, with 6 shared locations. Catches in these campaigns averaged 3 and 2 individuals per day for Allis shad and Twaite shad respectively, with the largest collection of 15 and 5 individuals of Allis shad and Twaite shad respectively (total $n = 51$ Allis shad; $n = 31$ Twaite shad).

The identification of the species was carried out by Taverny (1991) based on the relationship between total length and gillrakers number along the first gill arch. All captured individuals were in the sub-adult phase (Taverny 1991; Taverny and Elie 2001). The age ranged from 2 to 5 years for Allis shad and from 2 to 6 years for Twaite shad, with more than 80% of Allis shad individuals aged between 2 and 3 years, and more than 80% of Twaite shad aged between 3 and 4 years (Taverny 1991; Taverny and Elie 2001). Full details of the sampling campaigns carried out in marine environments together with biometrical and demographic characteristics of all individuals are given in Taverny (1991) and Taverny and Elie (2001).

In total, sagittal otoliths of 209 Allis shad (RESGASC, $n = 160$; SOLDIF, $n = 49$) and 166 Twaite shad (RESGASC, $n = 140$; SOLDIF, $n = 26$) were selected from the overall archives (1986–1989, Fig. 1). Samples selection was based on biometry and location catch data availability. Allis shad subadults belonged to 1982-1986 cohorts while Twaite shad subadults

belonged to 1982-1987 cohorts. More than 80% of the samples from both species belonged to the 1985 year class (see online supplementary Table S1³).

Otolith preparation and microchemistry analysis

The archived otoliths from Taverny works (Taverny 1991; Taverny and Elie 2001) have previously been used *in toto* for age reading. Untreated otoliths have been stored dry in individually labelled paper envelopes since then. Thus, the absence of chemical or physical treatments on the otolith ensured the integrity of otoliths chemical composition. Furthermore, targeted elements of this study (^{87}Sr : ^{86}Sr , Sr:Ca and Ba:Ca ratios) should be stable over 30 years of time in archived otoliths under correct storage conditions, as strontium and barium substitute calcium in otoliths (Kennedy et al. 2000; Campana and Thorrold 2001). Consequently, one sagittal otolith from each pair was randomly selected for microchemistry purposes. Selected otoliths were rinsed with ultrapure water and air-dried during 24h under a laminar flow hood. This process and the following ones were carried out in class 10 000 clean room, in order to avoid any possible contamination. Posterior otolith preparation was carried out according to Martin et al. (2015). To analyse ^{87}Sr : ^{86}Sr , Sr:Ca and Ba:Ca ratios, two C-shaped ablation trajectories of 60 μm thick were performed 40 μm away from the core. A High Resolution (Thermo Scientific, USA) inductively coupled plasma quadrupole mass spectrometer (HR-ICP-MS) was used to analyze Sr:Ca and Ba:Ca ratios. The HR-ICP-MS was coupled to a UV high-repetition-rate femtosecond laser ablation (fs-LA) system (Nexeya SA, Canejan, France). A Nu-Plasma multicollector inductively-coupled-plasma mass-spectrometer (MC-ICP-MS, Nu Instruments, UK) coupled to a UV high-repetition-rate femtosecond laser ablation (fs-LA) system (Nexeya SA, Canejan, France) was used to analyze ^{87}Sr : ^{86}Sr . Analytical process can be found in Martin et al. (2015).

³Supplementary data are available with the article.

Baseline samples and statistical analyses

The natal origin of each individual caught at the sea during the 1980s was assigned using a Bayesian mixing model relying on a water and otolith chemical database ($^{87}\text{Sr}:$ ^{86}Sr , $\text{Sr}:\text{Ca}$ and $\text{Ba}:\text{Ca}$ ratios), from water samples and juvenile otoliths of Allis shad, as well as both adults collected in 18 rivers throughout its 2000s distribution range (Randon et al. 2018). Since no model of microchemical data was available for Twaite shad, the same Allis shad model was also used for this species. This was justified by the fact that there was no $^{87}\text{Sr}:$ ^{86}Sr biological fractionation (Kennedy et al. 2000; Walther and Thorrold 2008; Pouilly et al. 2014). In consequence, the otoliths of both shad species from a given system would share the same $^{87}\text{Sr}:$ ^{86}Sr ratios. In addition, Strontium incorporation rate was found to be the same for both species (Lochet 2006). Because of the close phylogenetic relationship of both species, we can assume that it would be similar for Ba (Bentzen et al. 1993; Alexandrino et al. 2006; Chang and Geffen 2013). According to the available literature, both species occupied to a large extent the same rivers in the 1980s as in the 2000s (Taverny 1991; Baglinière 2000; Bruslé and Quignard 2013). Thus we can assume that our model includes all natal river populations that could most likely be found in the marine stock mix during the 1980s.

In our work, the sea caught subadults were grouped according to the proximity to the river plumes. Thus, our samples were grouped into two zones that mimic two new capture rivers. A Bay of Biscay Center (BBC) group was created for each species (Allis shad, $n = 64$; Twaite shad, $n = 127$). It included all the catches located between $45\text{--}46^\circ\text{N}$, likely originating from the Charente River and the Gironde system. Although located in the southern Bay of Biscay where there were no marine catches, the rivers of the Adour basin and the Nivelle River could also potentially contribute individuals to the mixture of marine individuals located in the Bay of Biscay Center. The second group, the Bay of Biscay North (BBN)

included all individuals caught between 46–48° N (Allis shad, $n = 145$; Twaite shad, $n = 39$), which would likely originate from Brittany and Normandy rivers and from Loire River.

The model was run with all available samples, i.e., using baseline datasets (Allis shad juveniles, $n = 61$ and water, $n = 61$), otolith microchemistry of Allis shad adults with unknown origins ($n = 615$) from Randon et al. (2018) and the addition of 209 Allis shad and 166 Twaite shad sea samples grouped following their capture zone. We established a period p (before 1990, after 2005) effect in the probabilities of origin to account for a possible modification of the homing dynamics along the time. The model was carried out employing the software JAGS and was run by runjags package (Plummer 2003; Denwood 2013), which promotes the communication between JAGS and R statistical software (R Development Core Team, R.3.1.1, 2014). Three independent Monte Carlo Markov Chain (MCMC) chains were run in parallel for 20 000 iterations after a burn-in period of 10 000 iterations to draw simulations from Bayesian posterior distributions. A vector $\{\theta_{c,p}\}$ denoting the probabilities that a given fish captured in a river (c) during each period (p) was born in each of the k_b river of the water baseline was included for each catch river and period. Each subadult caught in a marine region during the period < 1990 was reassigned to one or more natal rivers, among the 18 possible natal rivers included in the baseline dataset, at the end of the iterative process. Thus, the frequency of reassignment of a fish f in a source k was defined as the number of iterations of the MCMC in which the fish f was reassigned into a source k , divided by the total number of iterations produced during the MCMC. As a result a reassignment probability of f in k is obtained. This probability was calculated for each of the fish and sources, in such a way that each fish has at the end an F_f vector containing the k_b reassignment probabilities (one for each river of the baseline). Finally, each fish was assigned to its natal origin based on the maximum posterior classification probability. We then calculated the proportional representations of each identified source stock to the marine sectors defined. A matrix

containing the Ff of each fish in rows and natal river in columns was created. Thus, we used Spearman's correlation test (threshold 0.05) to calculate the correlation between each of the pairs of columns. There is confusion during the process of reallocation if there is a strong and positive correlation between the corresponding rivers, while the rivers are well discriminated if there is a strong and negative correlation. For more detailed descriptions about statistical calculations of the Bayesian model see Randon et al. (2018).

Results

Model requirements and probabilities of reallocation

The model satisfied all the requirements, such as convergence under the Gelman-Rubin diagnostic (see Randon et al. 2018 for more details about model requirements), in order to provide estimates of the proportion of individuals in each marine region according to their natal origin. Maximum posterior conditional assignment probabilities (i.e., the probability of assignment to each natal river) from the Bayesian mixing model were greater than 0.7 for 92.3% ($n = 193$ of 209 individuals) and 81.3% ($n = 135$ of 166 individuals) for Allis shad and Twaite shad respectively. Thus, the majority of subadults caught in the marine environment were assigned to a natal river with high degrees of confidence. Slight confusions were found as shown by the correlation matrix (Fig. 2). Confusions occurred usually between neighbouring rivers as between the Nive and Saison rivers, although there were also some confusions between rivers from distant basins (Charente-Saison or Vire-Vilaine). Nevertheless, northern French rivers (from Loire River upwards) were well discriminated from southern French rivers (from Charente River downwards).

Stock composition

Chemical signatures from the otoliths revealed that Allis shad and Twaite shad subadults caught in the Bay of Biscay originated from Southern rivers (Figs. 3, 4 and 5). The rivers in the Northern part of our study area (Loire River, Brittany and Normandy rivers) did not provide any fish of both shad species to the samples in the marine environment.

Allis shad subadults

When analysing all the probabilities of assignment of each fish we observed a clear dominance of assignment of the individuals to the Adour River in both marine regions (Fig. 3). With respect to the maximum probabilities of assignment of each individual the dominance of the Adour River was certified, with a percentage of 95.69% ($n = 200$ individuals), and the remaining individuals originated from the Charente (3.35%, $n = 7$ individuals), Nivelle (0.48%, $n = 1$ individual) and Aveyron rivers (0.48%, $n = 1$ individual). Slight differences in the stock composition were detected according to the geographical region (Fig. 4). In the Bay of Biscay North, 97.24% of individuals ($n = 141$ individuals) were assigned to the Adour River, while in the Bay of Biscay Center 92.19% of individuals ($n = 59$ individuals) were assigned to the Adour River. In Bay of Biscay North, the Aveyron (0.7%, $n = 1$ individual) and the Charente River (2.07%, $n = 3$ individuals) natal origins were observed while in Bay of Biscay Center, Charente (6.25%, $n = 4$ individuals) and the Nivelle River (1.56%, $n = 1$ individuals) individuals completed the specific composition.

Twaite shad subadults

Similarly to Allis shad, all the probabilities of assignment of each fish showed that almost every individual originated from one source, in this case the Oloron River (Fig. 3). Oloron river also belongs to the Adour basin to the south of the study area. Maximum probabilities of

assignment of each individual showed that a percentage of 95.78% of individuals ($n = 159$ individuals) were assigned to the Oloron River. The remaining individuals originated from the Charente River (4.22%, $n = 7$ individuals). In both marine regions, individuals were mostly assigned to the Oloron River Twaite shad population (Fig. 5). In the Bay of Biscay North all individuals originated from the Oloron River ($n = 39$ individuals). In Bay of Biscay Center, 94.49 % of individuals ($n = 120$ individuals) were assigned to the Oloron River, while the rest of the individuals came from the Charente River (5.51%, $n = 7$).

Discussion

Population-specific proportions at sea

Despite the vast spatial coverage of the sampled area (525 sampling stations in a stratified random fashion), the data collection was not exhaustive (especially in the Southern area) which could have biased the stock composition estimates. However, the access to any shad data at sea was and is still nowadays a major challenge that deserves to be fully addressed with an appropriate sampling plan.

In the northern region of the Bay of Biscay, where a large proportion of the samples were located (especially for Allis shad), the absence of individuals native of northern French rivers was observed. This result was consistent with the relative abundance of shad populations along the Bay of Biscay in the 80's. Vire and Brittany rivers shad populations were nearly extinct and Loire River shad populations had very low abundance compared to the Southern rivers shad populations (Taverny 1991; Baglinière 2000; Bruslé and Quignard 2013). The very contrasted geologic and chemistry differences between Northern granitic French rivers (Loire and northwards) and Southern sedimentary French rivers (Charente and southwards) enabled a robust and accurate discrimination of natal origins between these two main groups

of rivers (Martin et al. 2015; Willmes et al. 2018). While Northern granitic French rivers have 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 sedimentary French rivers have low Sr values between $0.70823 \pm 5.70\text{E-}05$ and $0.71037 \pm 1.22\text{E-}04$ (Martin et al. 2015). Our Bayesian model of natal origin was mainly driven by $^{87}\text{Sr}:^{86}\text{Sr}$ ratios, while Sr:Ca and Ba:Ca ratios complemented the discrimination (Martin et al. 2015). $^{87}\text{Sr}:^{86}\text{Sr}$ ratios were considered as “ideal” spatial markers for characterizing natal sources since they reflect the different bedrock geologies and tended to be stable over ecological timescales (Kennedy et al. 2000; Zimmerman et al. 2013; Loewen et al. 2015). Therefore, populations of the Southern sedimentary French rivers undoubtedly supplied both species in the marine areas.

Interpretation of natal origin of shad and metapopulation dynamics at sea

Looking at a finer geographical scale, our results showed that an overwhelming majority of Allis and Twaite shad subadults caught at sea were assigned to only two natal sources of the Southern sedimentary French rivers group, identified by the model as the Adour River and Oloron River for Allis shad and Twaite shad respectively. The dominance of a limited number of river populations in the mixed stock at sea was already observed for a closely related species, the American shad, *Alosa sapidissima* (Walther and Thorrold 2010). Although a wider range of ages were considered in the present study, European shads and American shad showed the same metapopulation dynamics with few source populations and several sinks. This similarity of dispersal and behavioural capabilities during immature stages could be related to the phylogenetic proximity between American shad and European shads (Bentzen et al. 1993).

Unexpectedly, only a small percentage of Allis shad subadults were assigned to the populations of the Gironde system, which was considered to be the most important Allis shad

populations in Europe in the 80's (Martin–Vandembulcke 1999; Baglinière 2000; ICES 2015). In the same way, a low abundance of Twaite shad subadults originating from populations of the Gironde system was observed. Although the available data on the abundance of Twaite shad in freshwater during the 1980s were scarce, the reported 13-15 tonnes of commercial catch of Twaite shad adults and an estimated recruitment of 9.5-22.5 millions of Twaite shad juveniles in the Gironde system, suggested that Twaite shad populations in this system were also abundant (Taverny, 1991; Baglinière et al. 2001). The subadults samples from the present study belonged to a reduced numbers of cohorts (1982-1986 and 1982-1987 for Allis shad and Twaite shad respectively), 1985 being the dominant cohort for both species. The dominance of subadults Adour and Oloron origin for Allis shad and Twaite shad respectively could be explained by a difference in abundance and recruitment success between populations of Adour and Oloron rivers and Allis shad and Twaite shad populations from Gironde system during 1982-1986 period of time. Despite the fact that Allis shad total commercial catches were 30 times greater in the Gironde system (708.4 metric tons, 1983-1987 period) than in the Adour River (24.3 metric tons, 1985-1987 period, see Elie et al. 2000; Baglinière et al. 2003 and references therein), the relative fishing effort would rather result in only a factor 4 relative shad abundance between both River systems (Albiges et al. 1985; Prouzet et al. 1994; Castelnaud et al. 2001). There was no available catch data for the Twaite shad in the Oloron River, and therefore no conclusions could be drawn about the difference in relative abundance between Oloron River and the Gironde system Twaite shad abundances. Juvenile shad abundance index in the Gironde estuary showed considerable fluctuations between cohorts, with lowest values in 1983 and 1986 and in 1984 for Allis shad and Twaite shad respectively (Lambert et al. 1997). Anthropogenic juvenile mortality was particularly high in the Gironde system during 1985, when most of our samples were hatched, as it was estimated that 1.2 million individuals of

Allis shad juveniles and 880 000 individuals of Twaite shad juveniles died from water intake from the nuclear power plant of Blayais (Taverny, 1991). Thus, the hypothesis of a greater abundance of Adour origin Allis shad 1982-1986 cohorts and Twaite shad 1982-1987 cohorts could be explained by the chaotic dynamics of shad populations, a clupeid species (Sabatié 1993; Rougier et al. 2012; Nachón et al. 2016). However, data on juvenile abundance was totally lacking for the Adour estuary (common estuary to Adour River and Oloron River), which did not allow us drawing a final conclusion on the relative abundance of juveniles of both species between the two main natal rivers (Adour River for Allis shad and Oloron River for Twaite shad) and Gironde systems for studied cohorts. Alternatively, a great recruitment-stock relationship and high survival for Allis shad and Twaite shad individuals originating from Adour River and Oloron River respectively and the opposite situation for shad populations of the Gironde system could drive to a situation in which Allis shad population from Adour River and Twaite shad population from Oloron River acted as a source and Allis shad and Twaite populations from the Gironde system as a sink. Unfortunately, homing behaviour in these rivers during the 80's was not available to discuss this hypothesis.

An alternative hypothesis to explain the dominance of Adour River and Oloron River natal origin in the marine samples would be the allocation confusion between these rivers and rivers from Gironde system. The allocation of 80's fish natal origins in the present study was based on contemporary references (water and juveniles) because of the lack of available 80's references. The chemical baselines used in previous studies were adapted to the contemporary context of the Allis shad populations and the hydromorphological characteristics of the rivers, and based on discrete samples collected during the spawning period in the known spawning grounds (Martin et al. 2015; Randon et al. 2018). Although European shads exhibited a high interannual fidelity to spawning grounds, interannual hydrological fluctuations and density-dependent processes could induce changes in the

selection of spawning grounds (Cassou-Leins et al. 2000). Hence, the number and spatial coverage of spawning areas in the 1980s were likely different in the Adour system and the Gironde system than in recent years, mainly due to hydrological and abundance changes between the two periods. In fact, considerable inter-annual fluctuations have been detected in the occupation of the spawning grounds by Allis shad over time in the Gironde system (Cassou-Leins and Cassou-Leins 1981; Belaud et al. 2001; Taverny 1991). This situation was more confusing for the Twaite shad all the more because Twaite shad spawning grounds were found more downstream, where the homogeneity of water signatures increased as the mix of tributaries contribution increased. Yet, the knowledge of the different spawning grounds occupied during the 80's in the French Southern Rivers was not available.

Adour and Garonne Rivers chemical signatures could be discriminated considering a recent period of a few years, however, Martin et al. (2015) already pointed that differences between Sr isotopes, Sr:Ca and Ba:Ca water composition among Southern sedimentary French rivers group were tiny (Table 1 and Fig. 6). More specifically, close values of water composition were measured for Adour River, Garonne River and Dordogne River (see online supplementary Table S2³). Randon et al. (2018) observed slight allocation confusions for origin allocations of contemporary samples, being greater between Garonne River and Adour River or between Adour River and Oloron River, while Dordogne and Charente showed very slight confusions issues. But ultimately, allocations confusions should remain low enough to discriminate Adour River and Garonne River origins for contemporary shads according to Randon et al. (2018). Strontium isotopes values for the river main stretches could be affected by the relative contribution of the tributaries flow to the total flow. Factors such as rock type, weathering velocities, or the magnitude of flow variation between sessions were found to affect the composition of strontium isotopes water values (Walther and Limburg 2012). Rivers from Gironde system have suffered a flow decrease (especially the Garonne River), a

systematically increase of water uptake for agricultural irrigation, granulate extraction and damming (Jalón-Rojas et al. 2015; Schmidt et al. 2016). There anthropogenic pressures might have slightly modified Sr isotopes values to the extent to add confusion in the discrimination between Southern sedimentary French rivers chemical signatures. We cannot exclude the hypothesis that the present study might have failed to discriminate precisely shads natal origins provided the lack of 80's references such as exhaustive water composition of all potential spawning grounds and juvenile fish otolith chemical composition. However, the allocation of natal origin was very accurate between northern and southern Rivers, allowing the interpretation of stock mixing at sea.

In conclusion, given the uncertainties to accurately discriminate individual originated from the Southern sedimentary French rivers group to a more finer scale (specific river), from now on we will refer to southern populations of Allis shad.

Population-specific dispersal capacities at sea

Our results overall suggested that large populations resulted in large dispersion of individuals at sea. Marine habitat occupation was plastic, with a proportion of Allis shad and Twaite shad subadults from Southern rivers populations remaining in the vicinity of their natal river estuary plume and other subadults using marine habitats further away, covering distances up to 400–600 km. The pattern and distances travelled were identical to those shown by the predominant one-year-old population American shad along the North American east coast (Walther and Thorrold 2010), reinforcing the similar dynamics functioning hypothesis through the phylogenetical similarity between these species.

Based on our results we suggested a modification of a previous hypothesis stating that European shads would aggregate following natal origin in the vicinity of their natal river

estuary (Taverny and Elie 2001; Lassalle et al. 2008; Rougier et al. 2014). An alternative hypothesis consistent with our results would be two population-specific dispersal behaviours. The first type of behaviour could be called resident gregarious, formed by individuals with the same natal origin and remaining in the vicinity of the natal estuary. The second type of behaviour could be called dispersive gregarious, formed by individuals with the same natal origin but travelling longer distances away from their natal estuaries. The underlying mechanism driving the existence of two types of behaviours or ecotypes should be explored in future studies. Both abiotic factors, such as the predominant northward currents (Koutsikopoulos and Le Cann 1996), and biotic factors such as density-dependent processes, genetic components, or foraging may be involved (Taverny and Elie 2001; Johnson et al. 2016; Huntsman et al. 2017). The discovery of this type of important latitudinal displacements contrasted with a previous study carried out in the Bay of Biscay, which suggested that both shad species primarily performed seasonal longitudinal movements and barely performed latitudinal displacements (Trancart et al. 2014).

Our results supported the first description of the population-specific dispersal capabilities of European shads subadults at sea. A previous study showed that juveniles Allis shad from the Sebou River in Morocco migrated southwards for about 600 km until they reached the upwelling areas rich in nutrients (Sabatié 1993). However, Sabatié (1993) did not carry out any specific studies on natal origin and suggested that the Allis shad individuals present in these upwelling areas would most likely originated from the only river (Sebou River) with a stable and abundant presence of Allis shad along the Atlantic coast of Morocco. Marine bycatches of European shads have also been documented several hundred kilometres from the most likely source rivers (La Mesa et al. 2015; Nachón et al. 2016). Based on natal origin determined by otolith microchemistry, Allis shad individuals were also found to migrate considerable distances along the marine environment from their natal origin river to their

spawning river (Martin et al. 2015). Similarly, genetic studies suggested that Twaite shad individuals could cover distances of hundreds of kilometres between their natal rivers and their spawning river (Jolly et al. 2012).

Implications of the population-specific composition at sea on the metapopulational dynamics at continental scale

Whether the population specific dominance of Southern rivers populations in the Bay of Biscay promoted straying and subsequent colonization of some rivers remains to be tested. In the 80's, Brittany Allis shad populations were nearly extinct, but since the 2000s, small populations started to establish again. Recent studies showed that Allis shad populations in Brittany exhibited a high degree of homing, with small exchanges of spawners (Randon et al. 2018). The recovery of a depleted population is driven by two different processes: the increase of abundance of residual populations that had remained in the considered rivers and/or coastal nearby areas, or alternatively by immigration of strayers originating from nearby populations (Belliard et al. 2009; Perrier et al. 2009; Andrée et al. 2011). The reintroduction success by straying relied on the proportion of strayers provided to the depleted population as well as on the proximity of neighbouring populations (Hamann and Kennedy 2012; Keefer and Caudill 2014). The colonisation of Brittany Rivers in the 1980s by Allis shads from Southern Rivers, located at sea in vicinity of river plumes, could explain the recovery of Brittany Rivers.

In the hypothesis of a composition of marine stocks linked to the abundance of shads in the continental environment, the dispersal capacities in the marine environment could have changed in the current context of the collapse of the Gironde system populations and generalised French populations abundance decrease (Rougier et al. 2012; Cellule Migrateurs

Charente Seudre 2017; Legrand and Besse 2018). Weak dispersion in the marine environment would explain why straying behaviour was mainly observed between neighbouring rivers nowadays (Randon et al. 2018). Even the Dordogne River, which has been identified as the main source river in the metapopulation dynamics of Allis shad, produces strayers that mostly enter in other river (Garonne River) of the same basin (Randon et al. 2018). The virtual absence of strayers from southern rivers in northern rivers (Randon et al. 2018), was consistent with the hypothesis of a lesser dispersal capacities at sea. It would be interesting to find out if the dispersion of Southern rivers populations has changed over time. Whether dispersion at sea is determined by abundance (density dependence) or another factor remains to be tested. Therefore, future studies on stock-composition at sea are necessary to understand how erratic individuals exchange between the different local populations forming Allis shad metapopulation occurs. Regarding Twaite shad, it is also essential to carry out studies on the natal homing to elucidate if this species shows metapopulational behaviour similar to Allis shad.

In conclusion, the results of this paper show that the subadults of the European shads captured at sea presented a limited diversity of natal origins. Most of the Allis shad subadults came from the Adour River while most of the Twaite shad subadults originated from the Oloron River. There were two hypotheses to explain the results: either the results reflected the reality of the populations and expressed differences of survival between the populations of the Southern Rivers or the alternative hypothesis was that it resulted from a confusion of allocation between the rivers of the South due to the lack of references to the chemistry of the water and the otoliths of the juveniles during the 80's. A robust discrimination of Northern and Southern rivers suggested that the population-specific composition of European shads at sea was influenced by abundance in the continental environment. As a result of this abundance, there was a great diffusion in the marine environment, with most abundant

populations dispersing from areas close to the native river to areas hundreds of kilometres away. Stock specific composition at sea is important for management and may be useful to 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).

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 ($p\text{-value} < 0.05$) 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 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.

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.

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).

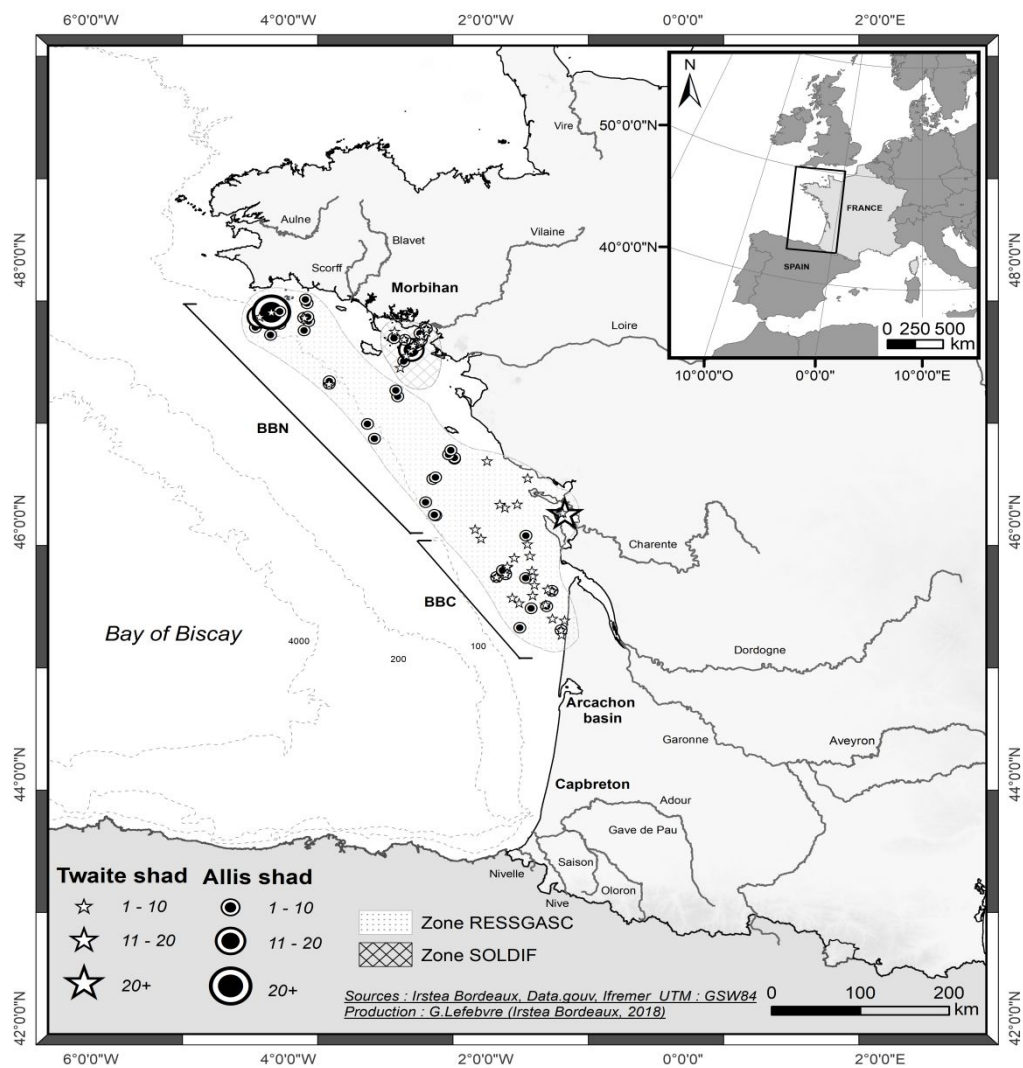
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Tables

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

901 **Figures**



902

903 Fig.1. Sampling surveys campaigns and collection locations of the Allis shad and Twaite

904 shad subadults retained for this study. Marine catches were grouped into two marine regions,

905 Bay of Biscay North (BBN) and Bay of Biscay Center (BBC). The French rivers where water

906 and Allis shad otoliths samples were collected to build the Bayesian model of attribution to

907 the river of origin, as described in Randon et al. (2018), are also shown. Only the lowermost

908 sections of the main rivers are showed.

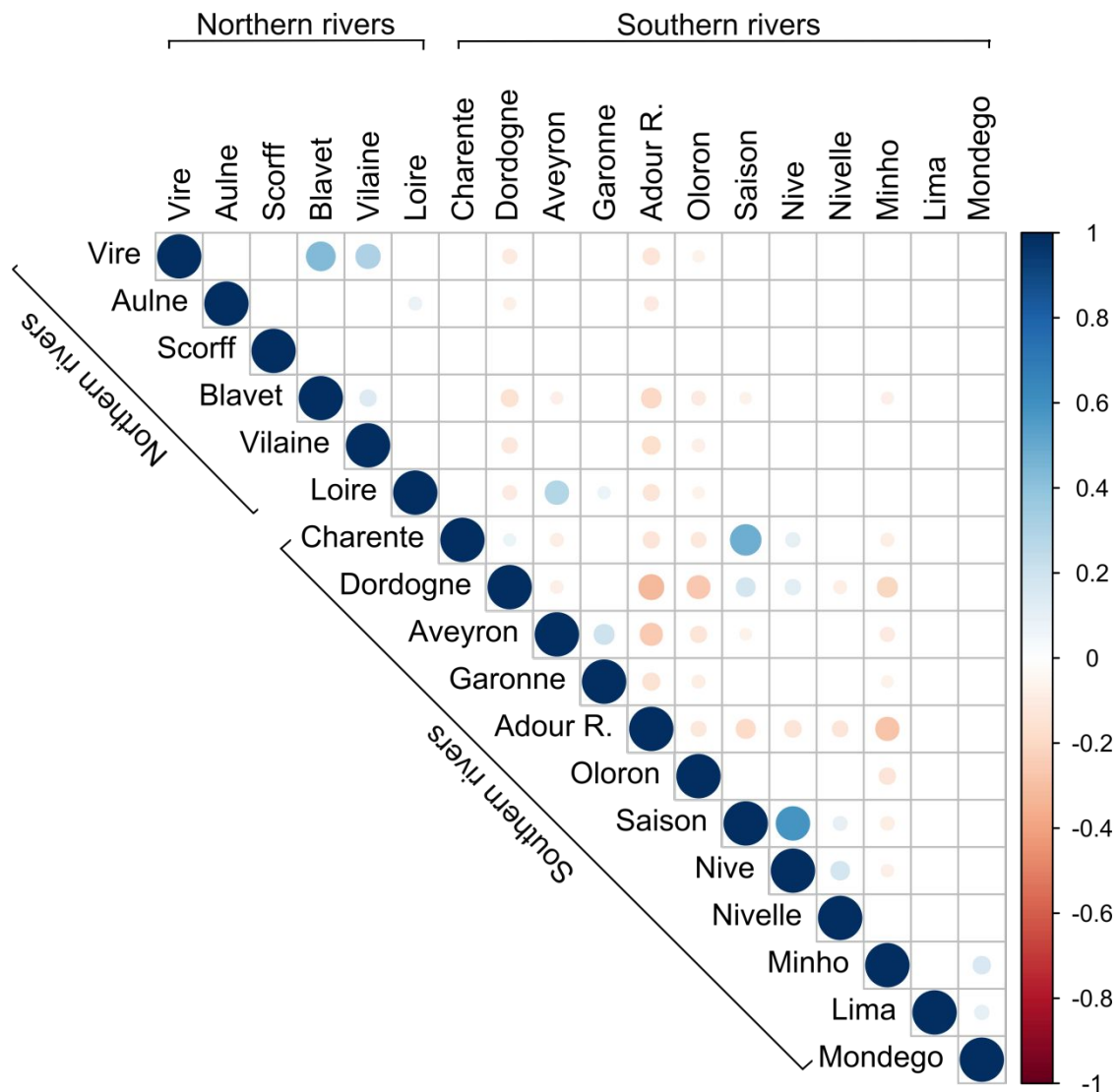
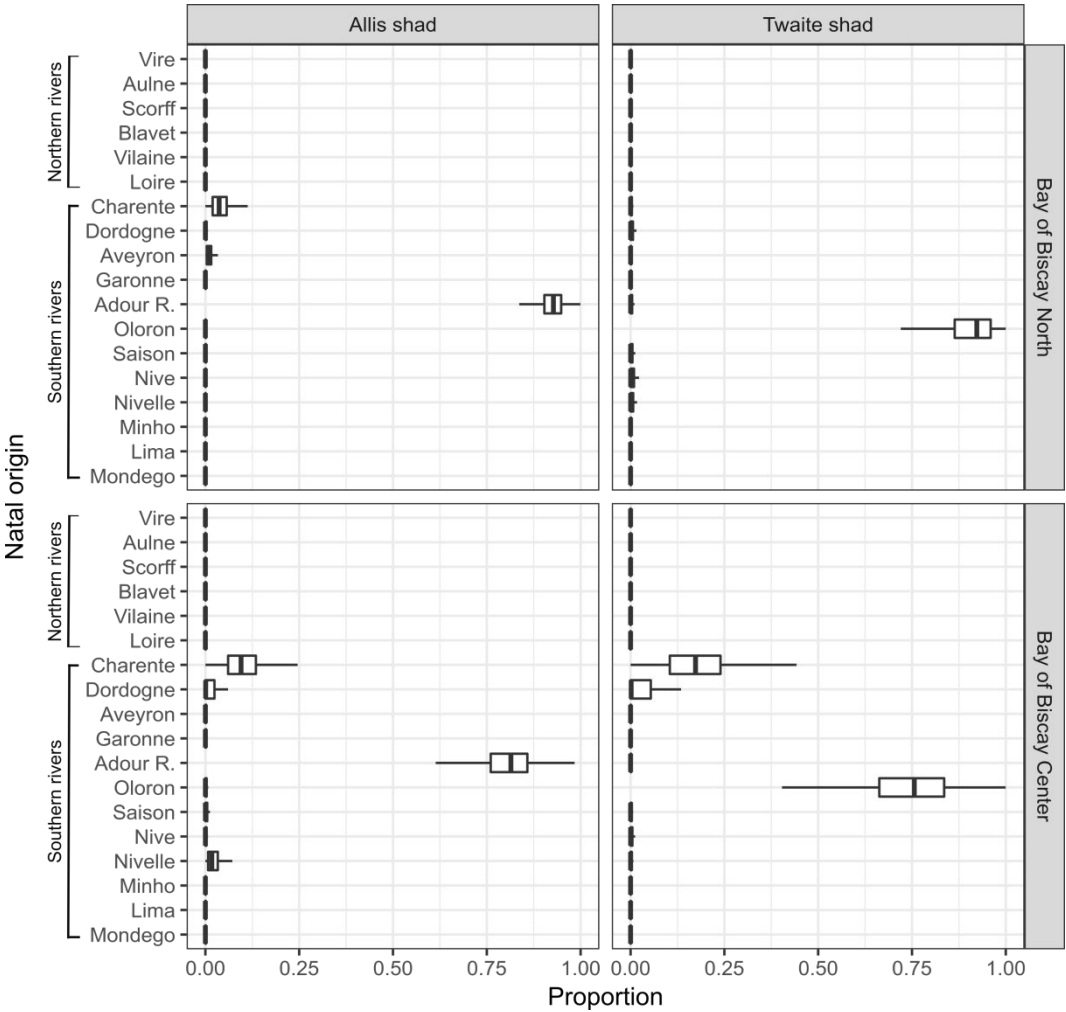
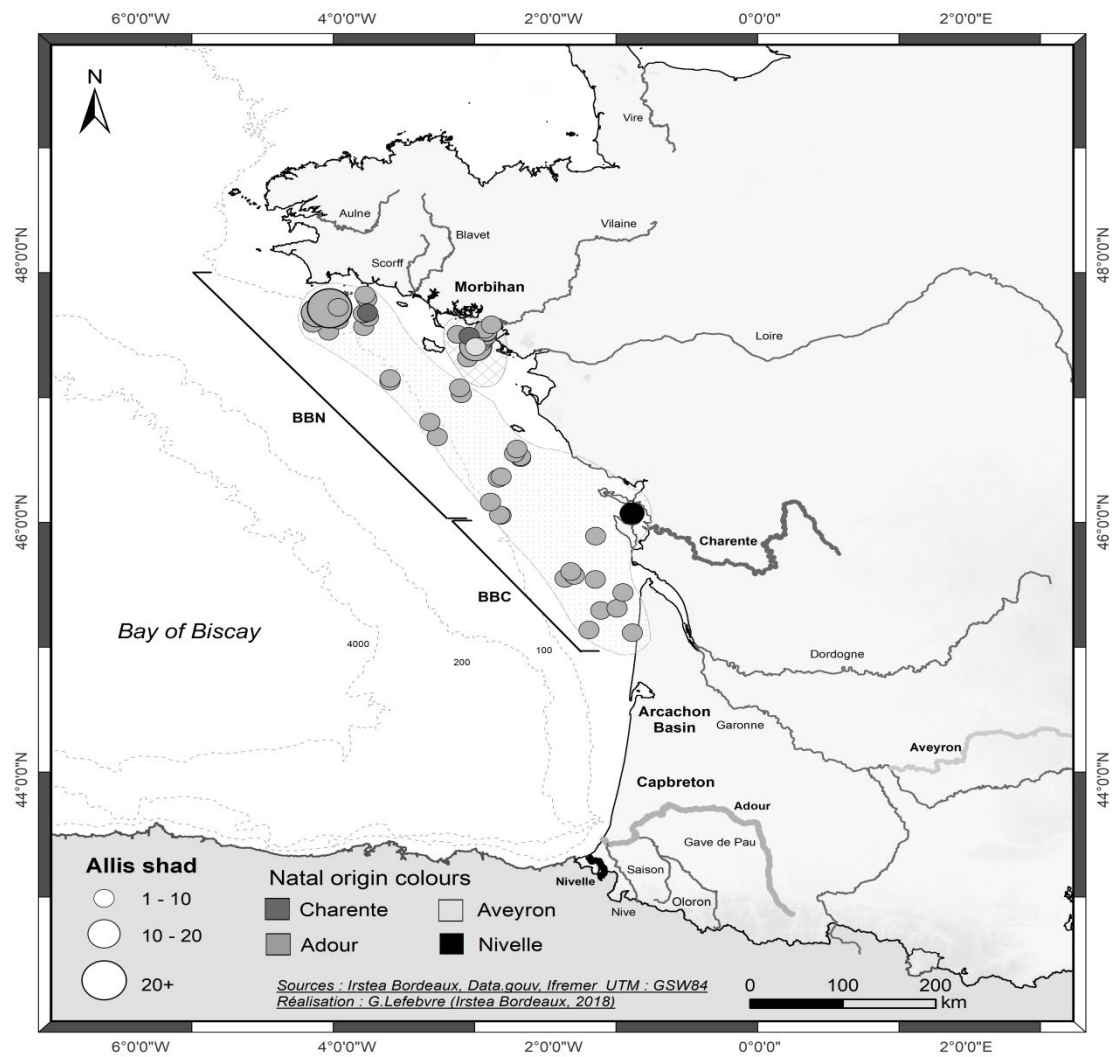


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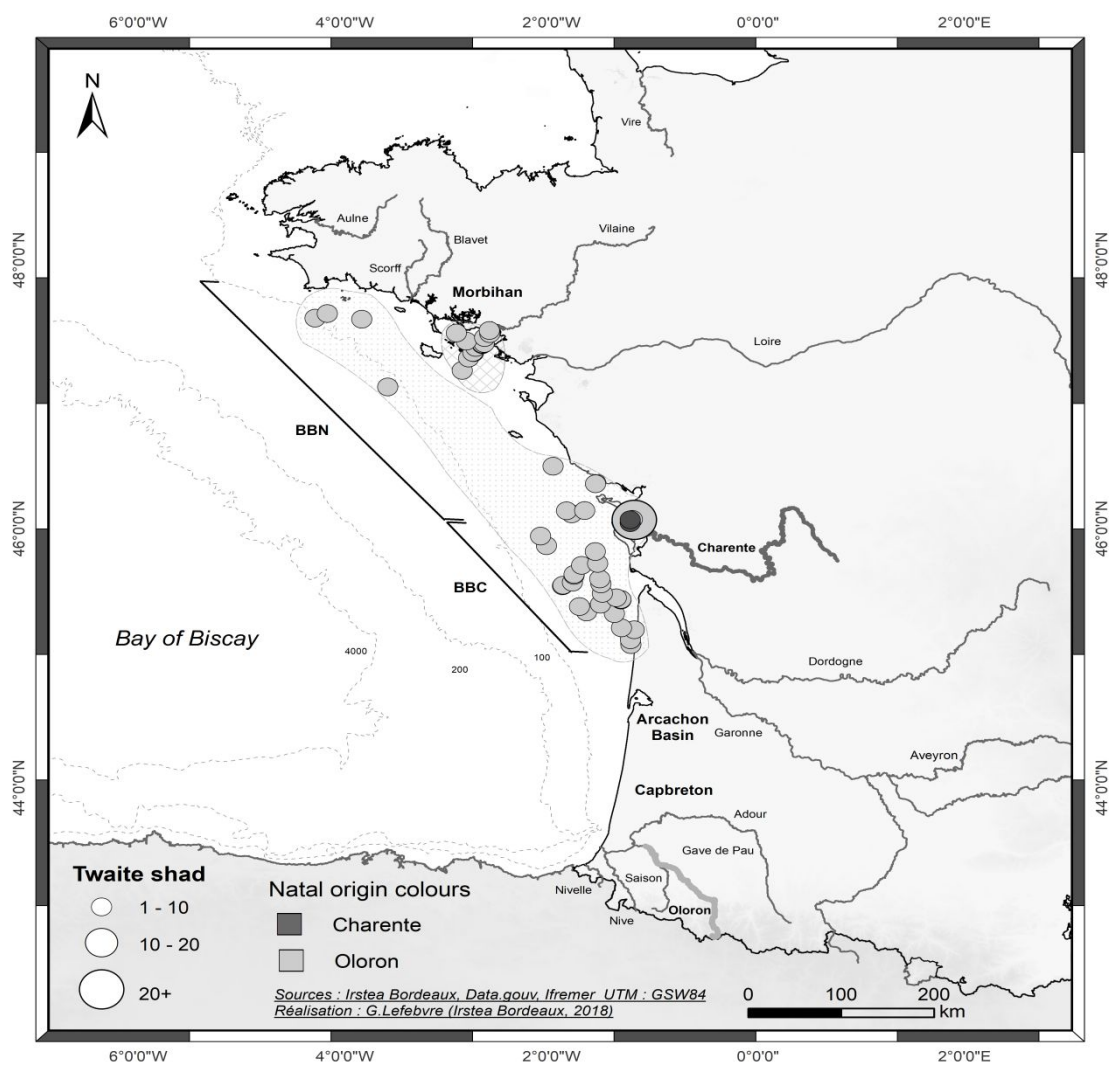
915

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



920

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



924

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

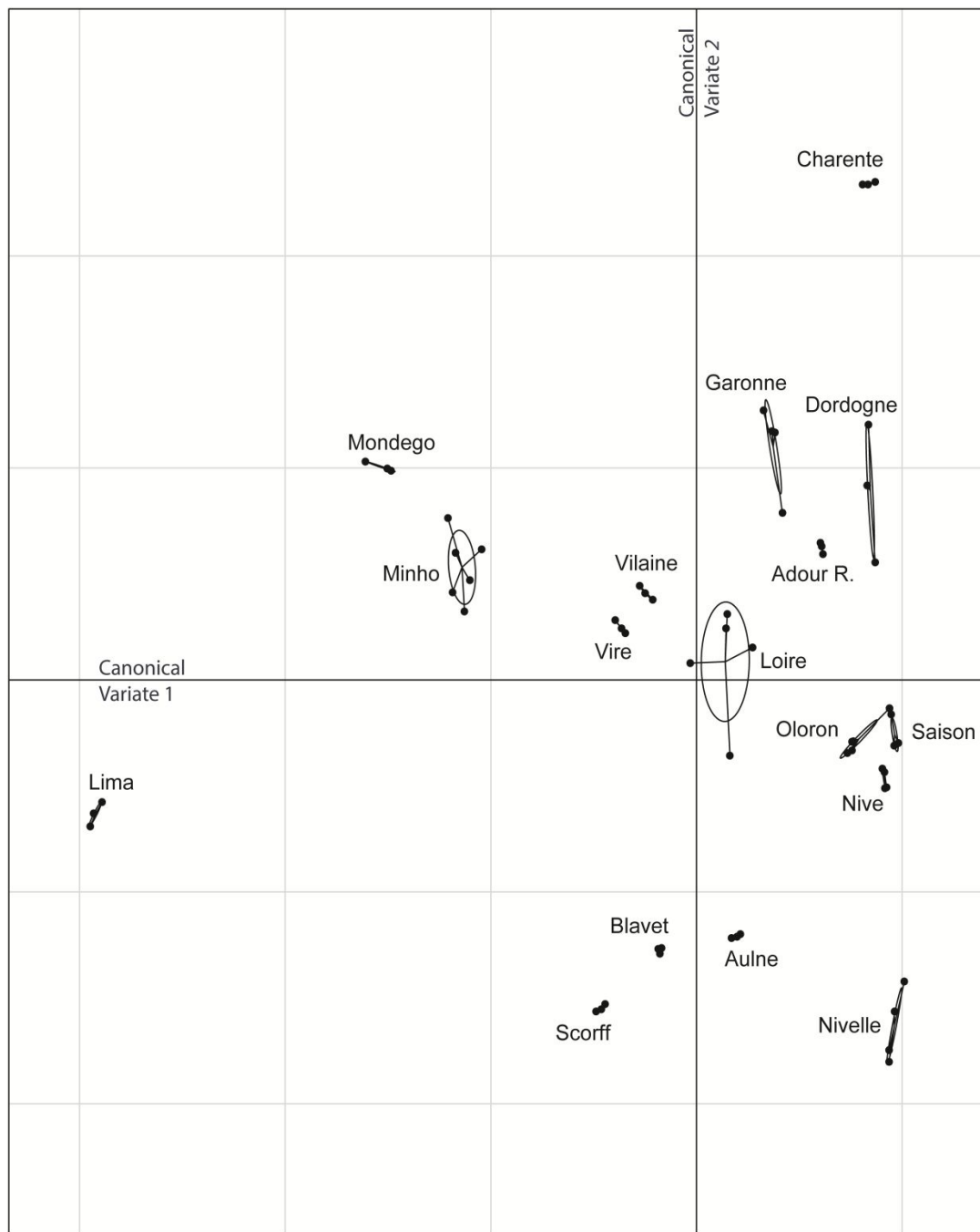


Fig. 6. Canonical discriminant plot of isotope ($^{87}\text{Sr}:^{86}\text{Sr}$) and elemental ($\text{Sr}:\text{Ca}$ and $\text{Ba}:\text{Ca}$) signatures from water samples collected from 17 rivers in 2013. Symbols represent water samples, and ellipses are 95% confidence intervals around each group.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

Table 1. Total canocical 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 Sr: ⁸⁶ Sr	-0.88	0.362
Sr:Ca	0.151	-0.518
Ba:Ca	0.034	-0.205

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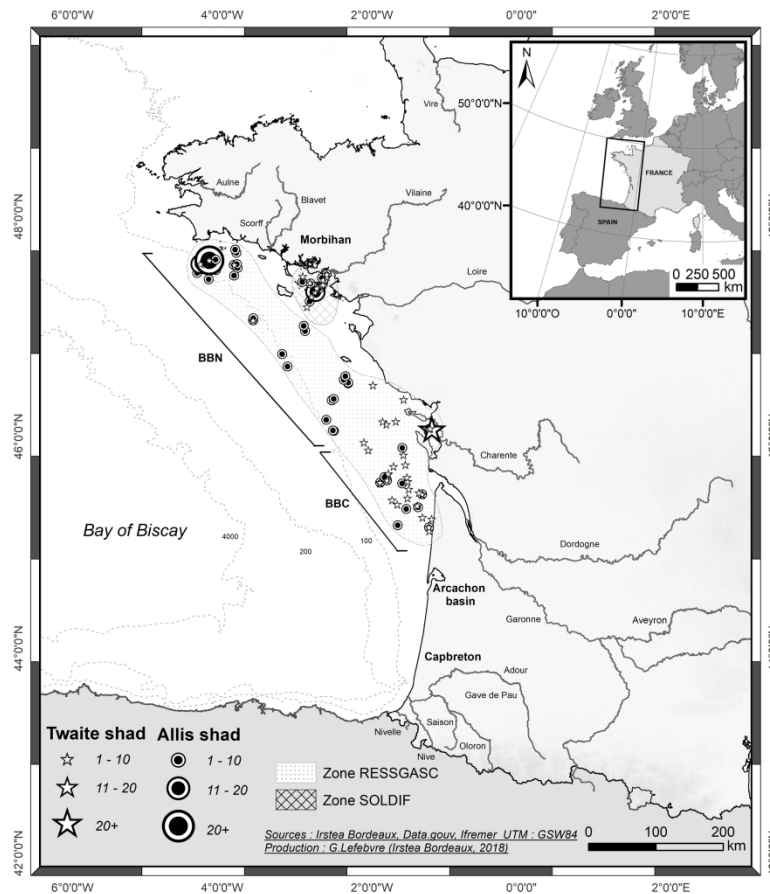
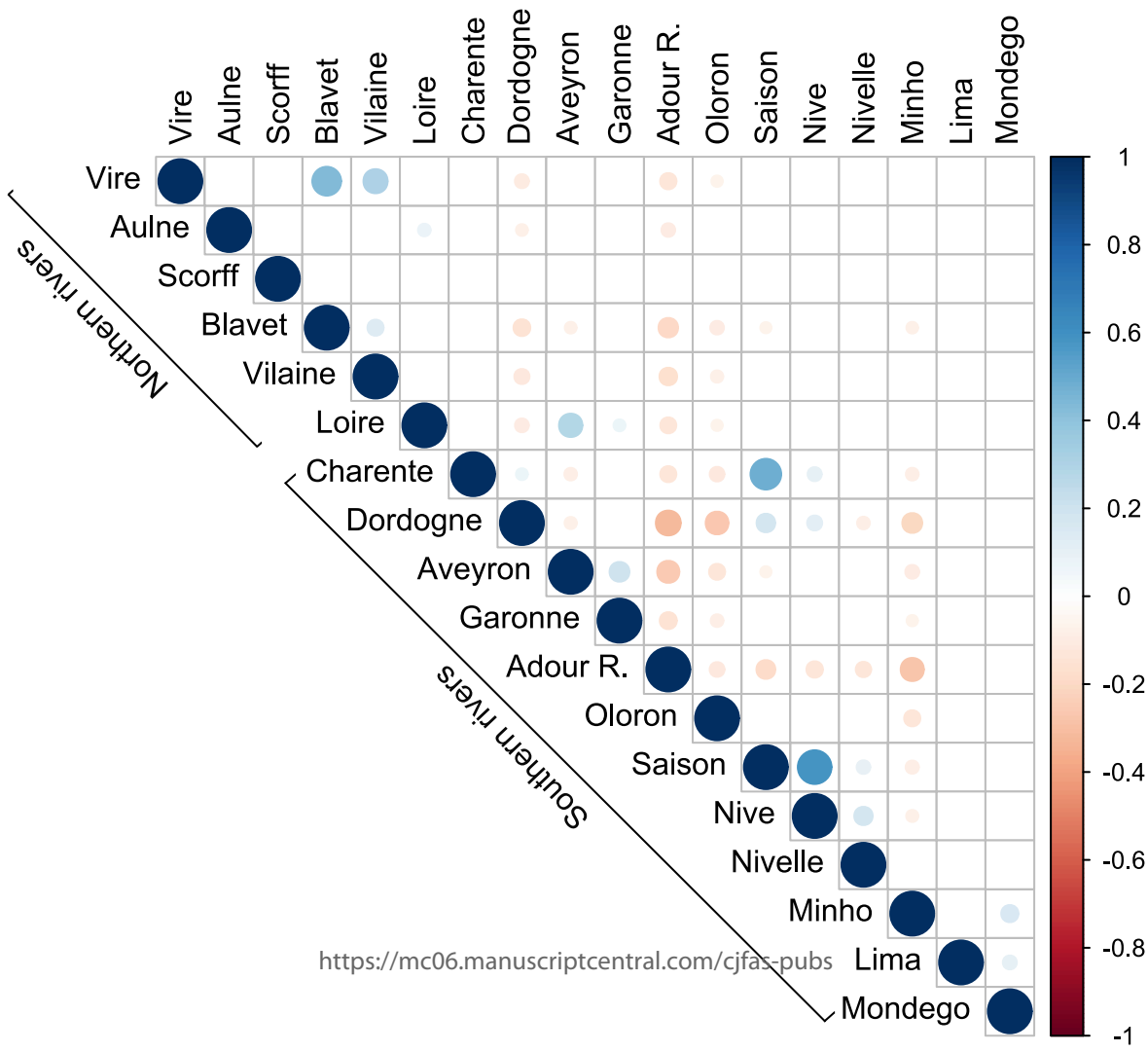
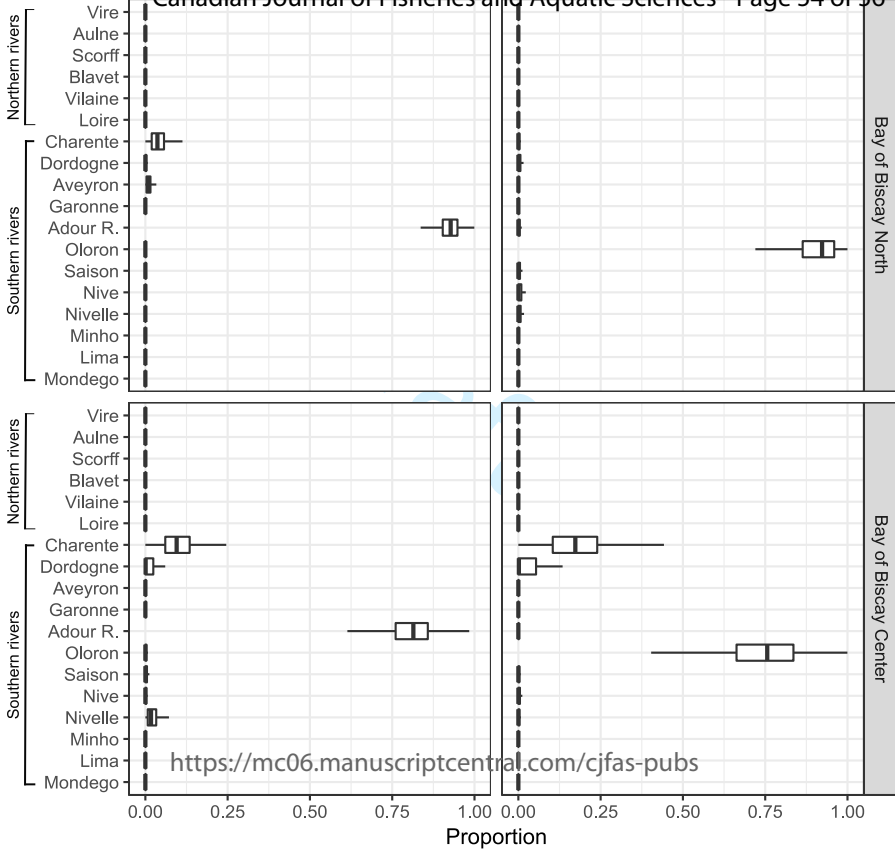


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210x297mm (300 x 300 DPI)



Natal origin



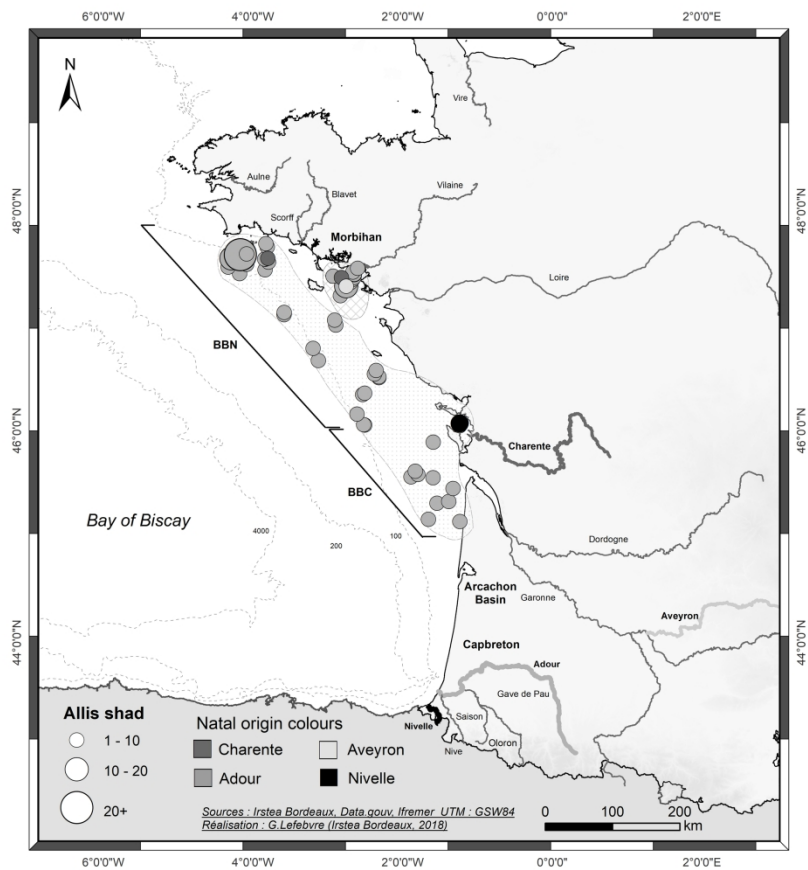


Fig. 4. Most probable natal river assignments for Allis shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Allis shad are color-coded for the identification of the natal origin of individuals.

210x297mm (300 x 300 DPI)

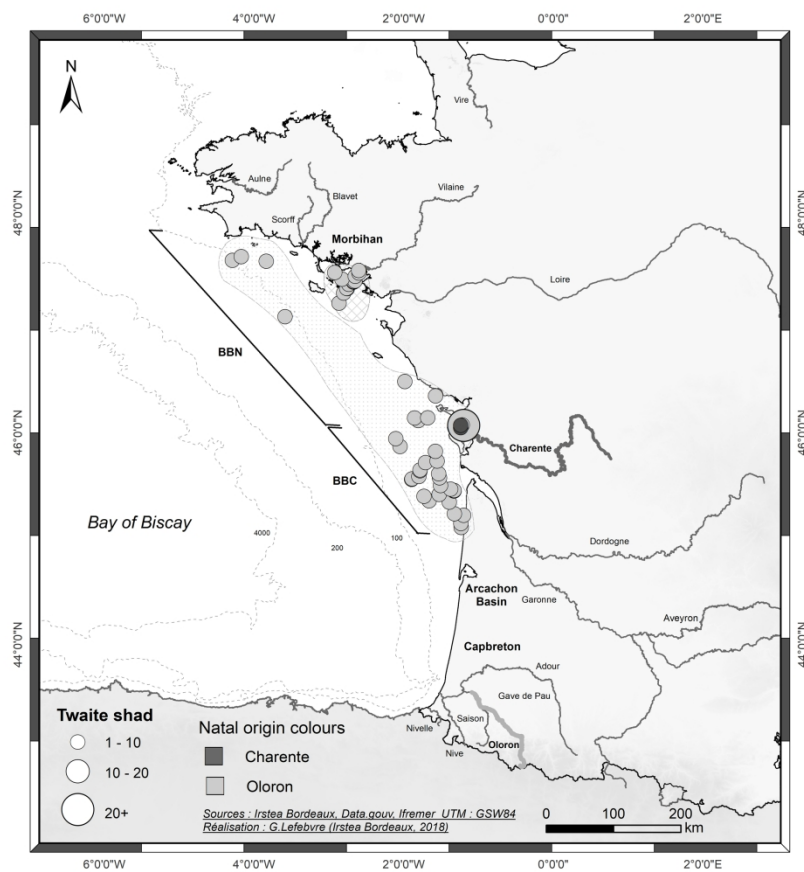


Fig. 5. Most probable natal river assignments for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.

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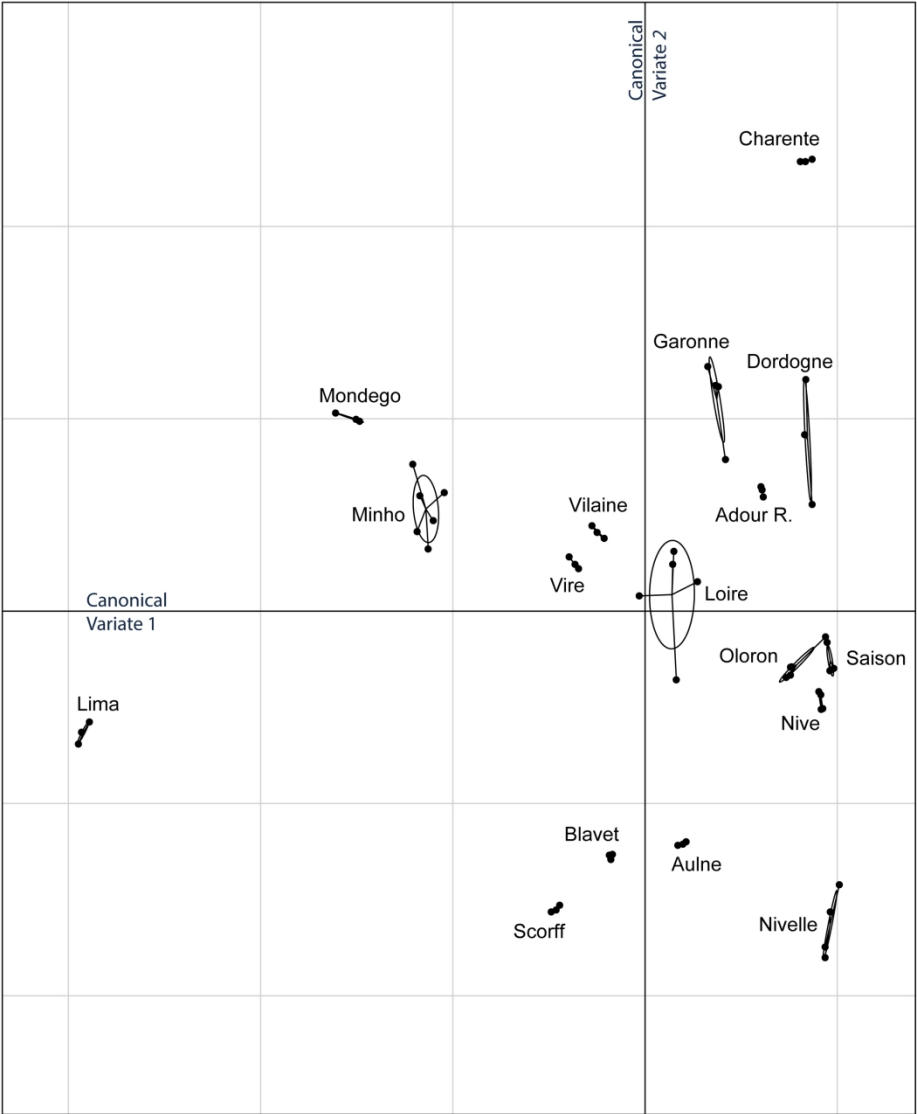


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214x239mm (300 x 300 DPI)