HAL
open science

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

David José Nachón, Gilles Bareille, Hilaire Drouineau, Hélène Tabouret, Catherine Taverny, Catherine Boisneau, Sylvain Bérail, Christophe Pécheyran, Fanny Claverie, Françoise Daverat

To cite this version:

David José Nachón, Gilles Bareille, Hilaire Drouineau, Hélène Tabouret, Catherine Taverny, et al.. 80's population-specific compositions of two related anadromous shad species during the oceanic phase determined by microchemistry of archived otoliths. Canadian Journal of Fisheries and Aquatic Sciences, 2020, 77 (1), pp.164-176. 10.1139/cjfas-2018-0444 . hal-02175519

HAL Id: hal-02175519

https://hal.science/hal-02175519

Submitted on 10 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Canadian Science Publishing | Canadian Journal of Fisheries and Aquatic Sciences

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

Journal:	*Canadian Journal of Fisheries and Aquatic Sciences*
Manuscript ID	cjfas-2018-0444.R1
Manuscript Type:	Article
Date Submitted by the Author:	05-Mar-2019
Complete List of Authors:	Nachón, David; IRSTEA EABX, Aquatic Ecosystems and Global Changes research unit, 50 avenue de Verdun 33612 ; Estación de Hidrobioloxía 'Encoro do Con', Universidade de Santiago de Compostela, Castroagudín, s/n 36617 Bareille, Gilles; CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA*, UMR 5254, 64000, Drouineau, Hilaire; IRSTEA EABX, Aquatic Ecosystems and Global Changes research unit, 50 avenue de Verdun 33612 Tabouret, Hélène; CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA*, UMR 5254, 64000, Taverny, Catherine; F.D.A.A.P.P.M.A. 33, 10 ZA du Lapin – 33750 Boisneau, Catherine; UMR CNRS CITERES 7324, Université de Tours, 33 Allée F de Lesseps, 37200 Berail, Sylvain; CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA*, UMR 5254, 64000, Pécheyran, Christophe; CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA*, UMR 5254, 64000, Claverie, Fanny; CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA*, UMR 5254, 64000, Daverat, Françoise; IRSTEA EABX, Aquatic Ecosystems and Global Changes research unit, 50 avenue de Verdun 33612
Keyword:	MARINE < Environment/Habitat, BIOCHEMISTRY < General, ECOLOGY < General, DISPERSAL < General, DIADROMOUS SPECIES < Organisms
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

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

David José Nachón[1], Gilles Bareille, Hilaire Drouineau, Hélène Tabouret, Catherine Taverny, Catherine Boisneau, Sylvain Berail, Christophe Pécheyran, Fanny Claverie and Françoise Daverat[2]

IRSTEA EABX, Aquatic Ecosystems and Global Changes research unit, 50 avenue de Verdun 33612 Cestas France.
david-jose.nachon-garcia@irstea.fr, hilaire.drouineau@irstea.fr, francoise.daverat@irstea.fr

CNRS/ Univ Pau & Pays Adour/ e2s UPPA, Institut des Sciences Analytiques et de Physicochimie pour l'Environnement et les Materiaux – MIRA, UMR 5254, 64000, Pau, France.
gilles.bareille@univ-pau.fr, helene.tabouret@univ-pau.fr, sylvain.berail@univ-pau.fr, christophe.pecheyran@univ-pau.fr, fanny.claverie@univ-pau.fr

F.D.A.A.P.P.M.A. 33, 10 ZA du Lapin – 33750 Beychac-et-Caillau, France.
catherine.taverny@peche33.com

UMR CNRS CITERES 7324, Université de Tours, 33 Allée F de Lesseps, 37200 Tours, France.
catherine.boisneau@univ-tours.fr

[1]David José Nachón, Estación de Hidrobioloxía 'Encoro do Con', Universidade de Santiago de Compostela, Castroagudín, s/n 36617 Vilagarcía de Arousa, España. davidjose.nachon@usc.es

[2]Corresponding author: Françoise Daverat. IRSTEA EABX, Aquatic Ecosystems and Global Changes research unit, 50 avenue de Verdun 33612 Cestas France, tel: + 33 (0)5 57 89 27 07. Fax: + 33 (0) 5 57 89 08 01. françoise.daverat@irstea.fr.

Abstract

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

Introduction

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

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

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. 2000*a*; 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. 2003*a*, 2003*b*; 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. 2000*b*; 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. 2000*b*; Aprahamian et al. 2003*a*). 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°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 S1[3]).

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).

[3]Supplementary 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}Sr:^{86}Sr, Sr:Ca and
242 Ba:Ca ratios), from water samples and juvenile otoliths of Allis shad, as well as both adults
243 collected in 18 rivers throughout its 2000s distribution range (Randon et al. 2018). Since no
244 model of microchemical data was available for Twaite shad, the same Allis shad model was
245 also used for this species. This was justified by the fact that there was no ^{87}Sr:^{86}Sr biological
246 fractionation (Kennedy et al. 2000; Walther and Thorrold 2008; Pouilly et al. 2014). In
247 consequence, the otoliths of both shad species from a given system would share the same
248 ^{87}Sr:^{86}Sr ratios. In addition, Strontium incorporation rate was found to be the same for both
249 species (Lochet 2006). Because of the close phylogenetic relationship of both species, we can
250 assume that it would be similar for Ba (Bentzen et al. 1993; Alexandrino et al. 2006; Chang
251 and Geffen 2013). According to the available literature, both species occupied to a large
252 extent the same rivers in the 1980s as in the 2000s (Taverny 1991; Baglinière 2000; Bruslé
253 and Quignard 2013). Thus we can assume that our model includes all natal river populations
254 that could most likely be found in the marine stock mix during the 1980s.

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

included all individuals caught between 46–48º 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 {θc,p} denoting the probabilities that a given fish captured in a river (c) during each period (p) was born in each of the kb 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 Ff vector containing the kb 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

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

of rivers (Martin et al. 2015; Willmes et al. 2018). While Northern granitic French rivers have high ^{87}Sr:^{86}Sr ratios between 0.71160 ± 1.00E-04 and 0.71429 ± 1.01E-04, Southern sedimentary French rivers have low Sr values between 0.70823 ± 5.70E-05 and 0.71037 ± 1.22E-04 (Martin et al. 2015). Our Bayesian model of natal origin was mainly driven by ^{87}Sr:^{86}Sr ratios, while Sr:Ca and Ba:Ca ratios complemented the discrimination (Martin et al. 2015). ^{87}Sr:^{86}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 S2[3]). 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 slights 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

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

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

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

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

552 populations dispersing from areas close to the native river to areas hundreds of kilometres
553 away. Stock specific composition at sea is important for management and may be useful to
554 prioritize protection of main population sources of shads.

555 Acknowledgements

556 This study was co-funded by Agence de l'Eau Adour Garonne and Nouvelle Aquitaine
557 Region within the SHAD'EAU FAUNA projects. Thanks to the biostatistics engineer
558 Sebastien Boutry from IRSTEA Center of Bordeaux for his help in producing the graphics.
559 Special thanks go to the technician Guillaume Lefebvre, also from IRSTEA Center of
560 Bordeaux, for his help in drawing the maps. We are also grateful to Eric Rochard, Patrick
561 Lambert, Alexis Paumier and Mélanie Gaillard from IRSTEA Center of Bordeaux for fruitful
562 discussions. Finally, we are grateful to the Associate Editor and reviewers for their relevant
563 remarks and advice that largely improved the quality of this work.

565 **References**

566 Albiges, C., Rochard, E., and Castelnaud, G. 1985. Etude de suivi halieutique de l'estuaire de
567 la Gironde 1985. Groupement de Bordeaux, Equipe Estuaires – Division A. L. A.,
568 Bordeaux.

569 Alexandrino, P., Faria, R., Linhares, D., Castro, F., Le Corre, M., Sabatié, R., Baglinière,
570 J.L., and Weiss, S. 2006. Interspecific differentiation and intraspecific substructure in
571 two closely related clupeids with extensive hybridization, *Alosa alosa* and *Alosa*
572 *fallax*. J. Fish. Biol. **69**: 242–259. doi:doi.org/10.1111/j.1095-8649.2006.01289.x.

573 Andrée, K.B., López, M.A., Alexandrino, P., Faria, R., and Gisbert, E. 2011. A preliminary
574 genetic analysis of a recently rediscovered population of the Twaite shad (*Alosa*
575 *fallax*) in the Ebro river, Spain (Western Mediterranean). J. Appl. Ichthyol. **27**: 21–23.
576 doi:10.1111/j.1439-0426.2011.01847.x.

577 Aprahamian, M.W., Aprahamian, C.D., Baglinière, J.L., Sabatié, R., and Alexandrino, P.
578 2003*a*. *Alosa alosa* and *Alosa fallax* spp.: literature review and bibliography. R&D
579 Technical Report W1-014/TR, Environment Agency, Warrington.

580 Aprahamian, M.W., Baglinière, J.L., Sabatié, R., Alexandrino, P., Thiel, R., and Aprahamian,
581 C.D. 2003*b*. Biology, Status, and Conservation of the Anadromous Atlantic Twaite
582 shad *Alosa fallax fallax*. *In* Biodiversity, status and conservation of world's shads.
583 *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society Symposium
584 35, Bethesda. pp. 103–124.

585 Ayata, S.D., Lazure, P., and Thiébaut, É. 2010. How does the connectivity between
586 populations mediate range limits of marine invertebrates? A case study of larval

587 dispersal between the Bay of Biscay and the English Channel (North-East Atlantic).
588 Prog. Oceanogr. **87**(1–4): 18–36. doi:10.1016/j.pocean.2010.09.022.

589 Baglinière, J.L. 2000. Le genre *Alosa* sp. *In* Les aloses (*Alosa alosa* et *Alosa fallax* spp.).
590 Écobiologie et variabilité des populations. *Edited by* J.L. Baglinière and P. Elie.
591 CEMAGREF-INRA Editions, Paris. pp. 3–30.

592 Baglinière, J.L., Sabatié, M.R., Aprahamian, M.W., Alexandrino, P., Aprahamian, C.D.,
593 Assis, C.A., Cassou–Leins, J.J., Le Corre, M., Mennesson–Boisneau, C., Martin–
594 Vandembulcke, D., Rochard, E., and Teixeira, C. 2001. Guide pour l´interpretation
595 des écailles et l´estimation de l´âge chez les aloses (*Alosa* spp.) de la Façade
596 Atlantique-est et de la Méditerranée-ouest. Bull. Fr. Pêche Piscic. **357/360**: 485–527.
597 doi:10.1051/kmae:2001001.

598 Baglinière, J.L., Sabatié, M.R., Rochard, E., Alexandrino, P., and Aprahamian, M.W. 2003.
599 The allis shad *Alosa alosa*: biology, ecology, range, and status of populations. *In*
600 Biodiversity, status and conservation of world's shads. *Edited by* K.E. Limburg and
601 J.R. Waldman. American Fisheries Society Symposium 35, Bethesda. pp. 85–102.

602 Bandoh, H., Kida, I., and Ueda, H. 2011. Olfactory responses to natal stream water in
603 sockeye salmon by BOLD fMRI. PLoS ONE, **6**(1): e16051.
604 doi:10.1371/journal.pone.0016051.

605 Belaud, A., Carette, A., Cassou–Leins, F., and Cassou–Leins, J.J. 2001. Choix des sites de
606 fraie par la grande alose (*Alosa alosa* L.) en moyenne Garonne. Bull. Fr. Pêche Piscic.
607 **362/363**: 869–880. doi:10.1051/kmae:2001024.

608 Belliard, J., Marchal, J., Ditche, J.M., Tales, E., Sabatié, R., and Baglinière, J.L. 2009. Return
609 of adult anadromous allis shad (*Alosa alosa* L.) in the river Seine, France: a sign of
610 river recovery?. River. Res. Appl. **25**(6): 788–794. doi:10.1002/rra.1221.

611 Bentzen, P., Leggett, W.C., and Brown, G.G. 1993. Genetic relationships among the shads
612 (*Alosa*) revealed by mitochondrial DNA analysis. J. Fish. Biol. **43**: 909–917.
613 doi:10.1111/j.1095-8649.1993.tb01165.x.

614 Berdahl, A., Westley, P.A., Levin, S.A., Couzin, I.D., and Quinn, T.P. 2016. A collective
615 navigation hypothesis for homeward migration in anadromous salmonids. Fish. Fish.
616 **17**(2): 525–542. doi:10.1111/faf.12084.

617 Bertin, X., Bruneau, N., Breilh, J.F., Fortunato, A.B., and Karpytchev, M. 2012. Importance
618 of wave age and resonance in storm surges: The case Xynthia, Bay of Biscay. Ocean.
619 Model. **42**: 16–30. doi:10.1016/j.ocemod.2011.11.001.

620 Brennan, S.R., Torgersen, C.E., Hollenbeck, J.P., Fernandez, D.P., Jensen, C.K., and
621 Schindler, D.E. 2016. Dendritic network models: Improving isoscapes and
622 quantifying influence of landscape and in-stream processes on strontium isotopes in
623 rivers. Geophys. Res. Lett. **43**(10): 5043–5051. doi:10.1002/2016GL068904.

624 Bruslé, J., and Quignard, J.P. 2013. Biologie des poissons d'eau douce européens. Lavoisier,
625 Paris.

626 Campana, S.E., and Thorrold, S.R. 2001. Otoliths, increments, and elements: keys to
627 comprehensive understanding of fish populations?. Can. J. Fish. Aquat. Sci. **58**(1):
628 30–38. doi:10.1139/f00-177.

Cassou–Leins, F., and Cassou–Leins, J.J. 1981. Recherches sur la biologie et l´halieutique des migrateurs de la Garonne et principalement de l´Alose, *Alosa alosa* L. M.Sc. thesis, Institut National Polytechnique, Toulouse.

Cassou–Leins, J.J., Cassou–Leins, F., Boisneau, P., and Baglinière, J.L. 2000. La reproduction. *In* Les aloses (*Alosa alosa* et *Alosa fallax* spp.). Écobiologie et variabilité des populations. *Edited by* J.L. Baglinière and P. Elie. INRA-CEMAGREF, Paris. pp. 73–92.

Castelnaud, G., Rochard, E., and Le Gat, Y. 2001. Analyse de la tendance de l'abondance de l'alose *Alosa alosa* en Gironde à partir de l'estimation d'indicateurs halieutiques sur la période 1977-1998. Bull. Fr. Pêche Piscic. **362/363**: 989–1015. doi:10.1051/kmae:2001032.

Cellule Migrateurs Charente Seudre. 2017. Rapport des actions. EPTB Charente, Groupement des fédérations de pêche du Poitou-Charentes, CREAA. Programme d'actions 2016-2020 pour la sauvegarde et la restauration des poissons migrateurs amphihalins sur les bassins Charente et Seudre [online]. Available from http://oai.eau-adour-garonne.fr/oai-documents/61719/GED_00000000.pdf [accessed 6 November 2018].

Chang, M.Y., and Geffen, A.J. 2013. Taxonomic and geographic influences on fish otolith microchemistry. Fish. Fish. **14**(4): 458–492. doi:10.1111/j.1467-2979.2012.00482.x.

Costoya, X., Fernández–Nóvoa, D., and Gómez–Gesteira, M. 2017. Loire and Gironde turbid plumes: Characterization and influence on thermohaline properties. J. Sea. Res. **130**: 7–16. doi:10.1016/j.seares.2017.04.003.

650 Daverat, F., Martin, J., Fablet, R., and Pécheyran, C. 2011. Colonisation tactics of three
651 temperate catadromous species, eel *Anguilla anguilla*, mullet *Liza ramada* and
652 flounder *Plathychtys flesus*, revealed by Bayesian multielemental otolith
653 microchemistry approach. Ecol. Freshw. Fish. **20**: 42–51. doi:10.1111/j.1600-
654 0633.2010.00454.x.

655 De Groot, S.J. 2002. A review of the past and present status of anadromous fish species in the
656 Netherlands: is restocking the Rhine feasible?. Hydrobiologia, **478**: 205–218.
657 doi:10.1023/A:1021038916271.

658 Denwood, M. 2013. runjags: an R package providing interface utilities, distributed computing
659 methods and additional distributions for MCMC models in JAGS. J. Stat. Softw.
660 **71**(9): 1–25. doi:10.18637/jss.v071.i09.

661 Elie, P., Taverny, C., Mennesson-Boisneau, C., and Sabatié, M.R. 2000. L'exploitation
662 halieutique. *In* Les aloses (*Alosa alosa* et *Alosa fallax* spp.). Écobiologie et variabilité
663 des populations. *Edited by* J.L. Baglinière and P. Elie. CEMAGREF-INRA Editions,
664 Paris. pp. 199–226.

665 Gao, Y., and Beamish, R.J. 2003. Stable isotope variations in otoliths of Pacific halibut
666 (*Hippoglossus stenolepis*) and indications of the possible 1990 regime shift. Fish. Res.
667 **60**(2–3): 393–404. doi:10.1016/S0165-7836(02)00134-0.

668 Hamann, E.J., and Kennedy, B.P. 2012. Juvenile dispersal affects straying behaviors of adults
669 in a migratory population. Ecology, **93**(4): 733–740. doi:10.1890/11-1009.1.

670 Hasselman, D.J., Anderson, E.C., Argo, E.E., Bethoney, N.D., Gephard, S.R., Post, D.M.,
671 Schondelmeier, B.P., Schultz, T.F., Willis, T.V., and Palkovacs, E.P. 2015. Genetic

stock composition of marine bycatch reveals disproportional impacts on depleted river herring genetic stocks. Can. J. Fish. Aquat. Sci. **73**(6): 951–963. doi:10.1139/cjfas-2015-0402.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia, **120**(3): 314–326. doi:10.1007/s004420050865.

Hobson, K.A., Barnett-Johnson, R., and Cerling, T. 2010. Using isoscapes to track animal migration. *In* Isoscapes. Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. *Edited by* J.B. West, G.J. Bowen, T.E. Dawson and K.P. Tu. Springer, Dordrecht, pp. 273–298.

Huntsman, B.M., Falke, J.A., Savereide, J.W., and Bennett, K.E. 2017. The role of density-dependent and–independent processes in spawning habitat selection by salmon in an Arctic riverscape. PloS ONE, **12**(5): e0177467. doi:doi.org/10.1371/journal.pone.0177467.

ICES. 2015. Report of the Workshop on Lampreys and Shads (WKLS), 27–29 November 2014, Lisbon, Portugal. ICES CM 2014/SSGEF:13 [online]. Available from http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGEPD/2015/01%20WKLS%20%20Report%20of%20the%20Workshop%20on%20Lampreys%20and%20Shads.pdf [accessed 6 November 2018].

Irigoien, X., Fernandes, J.A., Grosjean, P., Denis, K., Albaina, A., and Santos, M. 2008. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. J. Plankton. Res. **31**(1): 1–17. doi:10.1093/plankt/fbn096.

693 Jalón–Rojas, I., Schmidt, S., and Sottolichio, A. 2015. Turbidity in the fluvial Gironde
694 Estuary (southwest France) based on 10-year continuous monitoring: sensitivity to
695 hydrological conditions. Hydrol. Earth. Syst. Sc. **19**(6): 2805–2819. doi:10.5194/hess-
696 19-2805-2015.

697 Johnson, R.C., Garza, J.C., MacFarlane, R.B., Grimes, C.B., Phillis, C.C., Koch, P.L., Weber,
698 P.K., and Carr, M.H. 2016. Isotopes and genes reveal freshwater origins of Chinook
699 salmon *Oncorhynchus tshawytscha* aggregations in California's coastal ocean. Mar.
700 Ecol. Prog. Ser. **548**: 181–196. doi:10.3354/meps11623.

701 Jolly, M.T., Aprahamian, M.W., Hawkins, S.J., Henderson, P.A., Hillman, R.,
702 O'Maoiléidigh, N., Maitland, P.S., Piper, R., and Genner, M.J. 2012. Population
703 genetic structure of protected allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*).
704 Mar. Biol. **159**(3): 675–687. doi:10.1007/s00227-011-1845-x.

705 Keefer, M.L., and Caudill, C.C. 2014. Homing and straying by anadromous salmonids:
706 Areview of mechanisms and rates. Rev. Fish. Biol. Fisher. **24**(1): 333–368.
707 doi:10.1007/s11160-013-9334-6.

708 Kennedy, B.P., Blum, J.D., Folt, C.L., and Nislow, K.H. 2000. Using natural strontium
709 isotopic signatures as fish markers: methodology and application. Can. J. Fish. Aquat.
710 Sci. **57**(11): 2280–2292. doi:10.1139/f00-206.

711 Koutsikopoulos, C., and Le Cann, B. **1996**. Physical processes and hydrological structures
712 related to the Bay of Biscay anchovy. Sci. Mar. **60**(2): 9–19.

Laiz, I., Ferrer, L., Plomaritis, T.A., and Charria, G. 2014. Effect of river runoff on sea levelfrom in-situ measurements and numerical models in the Bay of Biscay. Deep-Sea. Res. Pt. II. **106**: 49–67. doi:10.1016/j.dsr2.2013.12.013.

Lambert, P., Pronier, O., Rochard, E., and Martin–Vandembulcke, D. 1997. Analyse des données issues du suivi de la faune circulante aux abords de la centrale de Braud et Saint-Louis. Cas des juvéniles d'aloses (*Alosa alosa*), des crevettes blanches (*Palaemon longirostris*) et des civelles d'anguilles (*Anguilla anguilla*). Etude 28, Departement gestion des milieux aquatiques, Unité Ressources aquatiques continentales, Bordeaux.

La Mesa, G., Annunziatellis, A., Filidei Jr. E., and Fortuna, C.M. 2015. Modeling environmental, temporal and spatial effects on Twaite Shad (*Alosa fallax*) bycatches in the central Mediterranean Sea. Fish. Oceanogr. **24**(2): 107–117. doi:10.1111/fog.12093.

Lassalle, G., Trancart, T., Lambert, P., and Rochard, E. 2008. Latitudinal variations in age and size at maturity among allis shad *Alosa alosa* populations. J. Fish Biol. **73**(7): 1799–1809. doi:10.1111/j.1095-8649.2008.02036.x.

Legrand, M., and Besse, T. 2018. Paroles de migrateurs. Retour sur l'année 2017. Rapport n°16 [online]. Available from http://www.migrateurs-loire.fr/telechargement/documentation/paroles-de-migrateurs/Paroles-de-Migrateurs-N16.pdf [accessed 6 November 2018].

Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., and Désaunay, Y. 2003. Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France) and the contribution of different habitats to

736 the adult population. J. Sea. Res. **50**(2–3): 139–149. doi:10.1016/S1385-
737 1101(03)00059-5.

738 Limburg, K.E., and Waldman, J.R. 2009. Dramatic Declines in North Atlantic Diadromous
739 Fishes. BioScience, **59**(11): 955–965. doi:10.1525/bio.2009.59.11.7.

740 Lochet, A. 2006. Dévalaison des juveniles et tactiques gagnantes chez la grande Alose *Alosa*
741 *alosa* et l´Alose feinte *Alosa fallax*: Apports de la microchimie et de la microstructure
742 des otolithes. M.Sc. thesis, Université Bordeaux I, Bordeaux.

743 Loewen, T.N., Reist, J.D., Yang, P., Koleszar, A., Babaluk, J.A., Mochnacz, N., and Halden,
744 N.M. 2015. Discrimination of northern form Dolly Varden Char (*Salvelinus malma*
745 *malma*) stocks of the North Slope, Yukon and Northwest Territories, Canada via
746 otolith trace elements and $^{87}Sr/^{86}Sr$ isotopes. Fish. Res. **170**: 116–124.
747 doi:10.1016/j.fishres.2015.05.025.

748 Lohmann, K.J., Putman, N.F., and Lohmann, C.M.F. 2008. Geomagnetic imprinting: a
749 unifying hypothesis of long-distance and natal homing in salmon and sea turtles. P.
750 Natl. Acad. Sci. USA. **105**: 19096–19101. doi:10.1073/pnas.0801859105.

751 Martin, J., Bareille, G., Berail, S., Pécheyran, C., Gueraud, F., Lange, F., Daverat, F., Bru, N.,
752 Beall, E., Barracou, D., and Donard, O. 2013. Persistence of a southern Atlantic
753 salmon population: Diversity of natal origins from otolith elemental and Sr isotopic
754 signatures. Can. J. Fish. Aquat. Sci. **70**(2): 182–197. doi:10.1139/cjfas-2012-0284.

755 Martin, J., Rougemont, Q., Drouineau, H., Launey, S., Jatteau, P., Bareille, G., Berail, S.,
756 Pécheyran, C., Feunteun, E., Roques, S., Clavé, D., Nachón, D.J., Antunes, C., Mota,
757 M., Réveillac, E., and Daverat, F. 2015. Dispersal capacities of anadromous Allis shad

population inferred from a coupled genetic and otolith approach. Can. J. Fish. Aquat. Sci. **72**(7): 991–1003. doi:10.1139/cjfas-2014-0510.

Martin–Vandembulcke, D. 1999. Dynamique de population de la grande alose (*Alosa alosa*, L. 1758) dans le bassin versant Gironde–Garonne–Dordogne (France): analyse et prévision par modélisation. M.Sc. thesis, Toulouse: Ecole Nationale Polytechnique, Toulouse.

Mennesson–Boisneau, C. 1990. Migration, répartition, reproduction et caractéristiques biologiques des aloses (*Alosa* sp.) dans le bassin de la Loire. M.Sc. thesis, Universités de Rennes et de Paris Val de Marne, Paris.

Morais, P., and Daverat, F. 2016. An Introduction to Fish Migration. CRC Press, New York.

Motos, L., Uriarte, A., and Valencia, V. **1996**. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). Sci. Mar. **60**(2): 237–255.

Munro, A.R., McMahon, T.E., and Ruzycki, J.R. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Can. J. Fish. Aquat. Sci. **62**(1): 79–87. doi:10.1139/f04-174.

Nachón, D.J. 2017. Dinámica poblacional y microquímica de los otolitos de las poblaciones de saboga, *Alosa fallax* (Lacépède, 1803), de los ríos Ulla y Miño. M.Sc. thesis, Universidade de Santiago de Compostela, Santiago de Compostela.

Nachón, D.J., Mota, M., Antunes, C., Servia, M.J., and Cobo, F. 2016. Marine and continental distribution and dynamic of the early spawning migration of twaite shad (*Alosa fallax* (Lacépède, 1803)) and allis shad (*Alosa alosa* (Linnaeus, 1758)) in the

780 north-west of the Iberian Peninsula. Mar. Freshwater. Res. **67**(8): 1229–1240.
781 doi:10.1071/MF14243.

782 Perrier, C., Evanno, G., Belliard, J., Guyomard, R., and Baglinière, J.L. 2009. Natural
783 recolonization of the Seine River by Atlantic salmon (*Salmo salar*) of multiple
784 origins. Can. J. Fish. Aquat. Sci. **67**(1): 1–4. doi:10.1139/F09-190.

785 Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs
786 sampling. *In* Proceedings of the 3rd International Workshop on Distributed Statistical
787 Computing (DSC 2003), Vienna , 20–22 March 2003. Kurt Hornik, Friedrich Leisch
788 and Achim Zeileis. pp. 1–10.

789 Pouilly, M., Point, D., Sondag, F., Henry, M., and Santos, R.V. 2014. Geographical origin of
790 Amazonian freshwater fishes fingerprinted by $^{87}Sr/^{86}Sr$ ratios on fish otoliths and
791 scales. Environ. Sci. Technol. **48**(16): 8980–8987. doi:10.1021/es500071w.

792 Prouzet, P., Martinet, J.P., and Badia, J. 1994. Caractérisation biologique et variation des
793 captures de la grande alose (*Alosa alosa*) par unité d'effort sur le fleuve Adour
794 (Pyrénées Atlantiques, France). Aquat. Living. Resour. **7**(1): 1–10.
795 doi:10.1051/alr:1994001.

796 Putman, N.F., Lohmann, K.J., Putman, E.M., Quinn, T.P., Klimley, A.P., and Noakes, D.L.
797 2013. Evidence for geomagnetic imprinting as a homing mechanism in Pacific
798 salmon. Curr. Biol. **23**(4): 312–316. doi:10.1016/j.cub.2012.12.041.

799 Randon, M., Daverat, F., Bareille, G., Jatteau, P., Martin, J., Pécheyran, C., and Drouineau,
800 H. 2018. Quantifying exchanges of Allis shads between river catchments by

combining otolith microchemistry and abundance indices in a Bayesian model. ICES. J. Mar. Sci. **75:** 9–21. doi:10.1093/icesjms/fsx148.

Rougier, T., Drouineau, H., Dumoulin, N., Faure, T., Deffuant, G., Rochard, E., and Lambert, P. 2014. The GR3D model, a tool to explore the Global Repositioning Dynamics of Diadromous fish Distribution. Ecol. Model. **283**: 31–44. doi:10.1016/j.ecolmodel.2014.03.019.

Rougier, T., Lambert, P., Drouineau, H., Girardin, M., Castelnaud, G., Carry, L., Aprahamian, M.W., Rivot, E., and Rochard, E. 2012. Collapse of allis shad, *Alosa alosa*, in the Gironde system (southwest France): environmental change, fishing mortality, or Allee effect?. ICES. J. Mar. Sci. **69**(10): 1802–1811. doi:10.1093/icesjms/fss149.

Sabatié, M.R. 1993. Recherches sur l´écologie et la biologie des aloses au Maroc (*Alosa alosa* Linné, 1758 et *Alosa fallax* Lacépède, 1803): exploitation et taxonomie des populations atlantiques, bioécologie des aloses de l´oued Sebou. M.Sc. thesis, Université de Bregtane Occidentale, Brest.

Schmidt, S., Etcheber, H., Sottolichio, A., and Castaing, P. 2016. Le réseau MAGEST: bilan de 10 ans de suivi haute-fréquence de la qualité des eaux de l'estuaire de la Gironde [online]. Available from http://www.magest.u-bordeaux1.fr/files/docs/PublicationHFMAREL2014-SchmidtS.pdf [accessed 27 February 2019].

Taverny, C. 1991. Contribution à la connaissance de la dynamique des populations d´aloses (*Alosa alosa* L. et *Alosa fallax* Lacépède), dans le système fluvio-estuarien de la

Gironde: pêche, biologie et écologie. Étude particulière de la dévalaison et de l´impact des activités humaines. M.Sc. thesis, Université de Bordeaux 1, Bordeaux.

Taverny, C., and Elie, P. 2001. Répartition spatio-temporelle de la grande alose *Alosa alosa* (Linné, 1766) et de l´alose feinte *Alosa fallax* (Lacépède, 1803) dans le Golfe de Gascogne. Bull. Fr. Pêche. Piscic. **362/363**: 803–821. doi:10.1051/kmae:2001020.

Taverny, C., Belaud, A., Elie, P., and Sabatié, M.R. 2000*b*. Influence des activités humaines. *In* Les aloses (*Alosa alosa* et *Alosa fallax* spp.). Écobiologie et variabilité des populations. *Edited by* J.L. Baglinière and P. Elie. INRA-CEMAGREF, Paris. pp. 227–248.

Taverny, C., Cassou–Leins, J.J., Cassou–Leins, F., and Elie, P. 2000*a*. De l´oeuf à l´adulte en mer. *In* Les aloses (*Alosa alosa* et *Alosa fallax* spp.). Écobiologie et variabilité des populations. *Edited by* J.L. Baglinière and P. Elie. INRA-CEMAGREF, Paris. pp. 93–124.

Trancart, T., Rochette, S., Acou, A., Lasne, E., and Feunteun, E. **2014**. Modeling marine shad distribution using data from French bycatch fishery surveys. Mar. Ecol. Prog. Ser. **511**: 181–192. doi:10.3354/meps10907.

Turner, S.M., Limburg, K.E., and Palkovacs, E.P. 2015. Can different combinations of natural tags identify river herring natal origin at different levels of stock structure?. Can. J. Fish. Aquat. Sci. **72**(6): 845–854. doi:10.1139/cjfas-2014-0403.

Walther, B.D., and Limburg, K.E. 2012. The use of otolith chemistry to characterize diadromous migrations. J. Fish. Biol. **81**(2): 796–825. doi:10.1111/j.1095-8649.2012.03371.x.

Walther, B.D., and Thorrold, S.R. 2006. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Mar. Ecol. Prog. Ser. **311**: 125–130. doi:10.3354/meps311125.

Walther, B.D., and Thorrold, S.R. 2008. Continental-scale variation in otolith geochemistry of juvenile American shad (*Alosa sapidissima*). Can. J. Fish. Aquat. Sci. **65**: 2623–2635. doi:10.1139/F08-164.

Walther, B.D., and Thorrold, S.R. 2010. Limited diversity in natal origins of immature anadromous fish during ocean residency. Can. J. Fish. Aquat. Sci. **67**(10): 1699–1707. doi:10.1139/F10-086.

Walther, B.D., Thorrold, S.R., and Olney, J.E. 2008. Geochemical signatures in otoliths record natal origins of American Shad. Trans. Am. Fish. Soc. **137**: 57–69. doi:10.1577/T07-029.1.

Willmes, M., Bataille, C.P., James, H.F., Moffat, I., McMorrow, L., Kinsley, L., Amstrong, R.A., Eggins, S., and Grün, R. 2018. Mapping of bioavailable strontium isotope ratios in France for archaeological provenance studies. Appl. Geochem. **90**: 75–86. doi:10.1016/j.apgeochem.2017.12.025.

Zimmerman, C.E., Swanson, H.K., Volk, E.C., and Kent, A.J. 2013. Species and life history affect the utility of otolith chemical composition for determining natal stream of origin for Pacific salmon. Trans. Am. Fish. Soc. **142**(5): 1370–1380. doi:10.1080/00028487.2013.811102.

Table captions

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).

Figure captions

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

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

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

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

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

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

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}Sr:^{86}Sr	-0.880	0.362
Sr:Ca	0.151	-0.518
Ba:Ca	0.034	-0.205

Figures

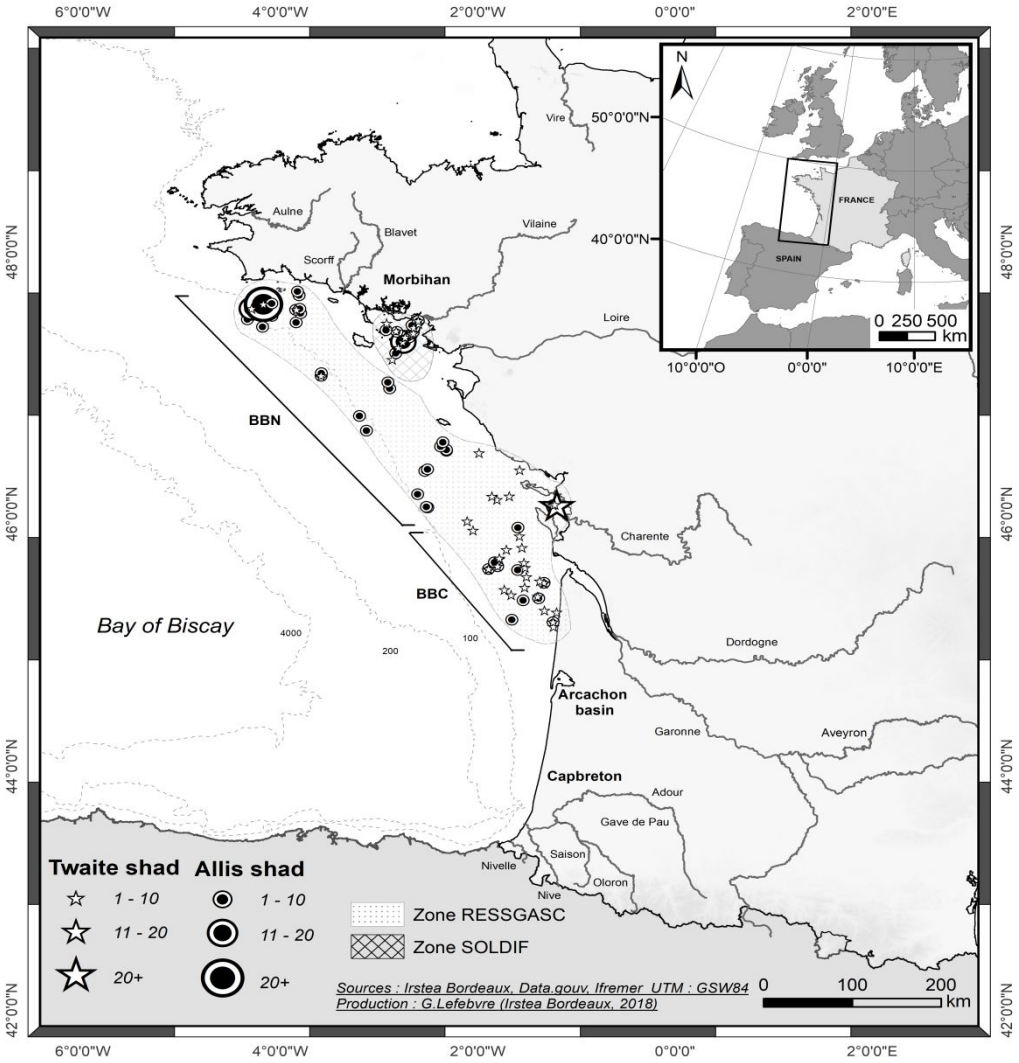


Fig.1. Sampling surveys campaigns and collection locations of the Allis shad and Twaite shad subadults retained for this study. Marine catches were grouped into two marine regions, Bay of Biscay North (BBN) and Bay of Biscay Center (BBC). The French rivers where water and Allis shad otoliths samples 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.

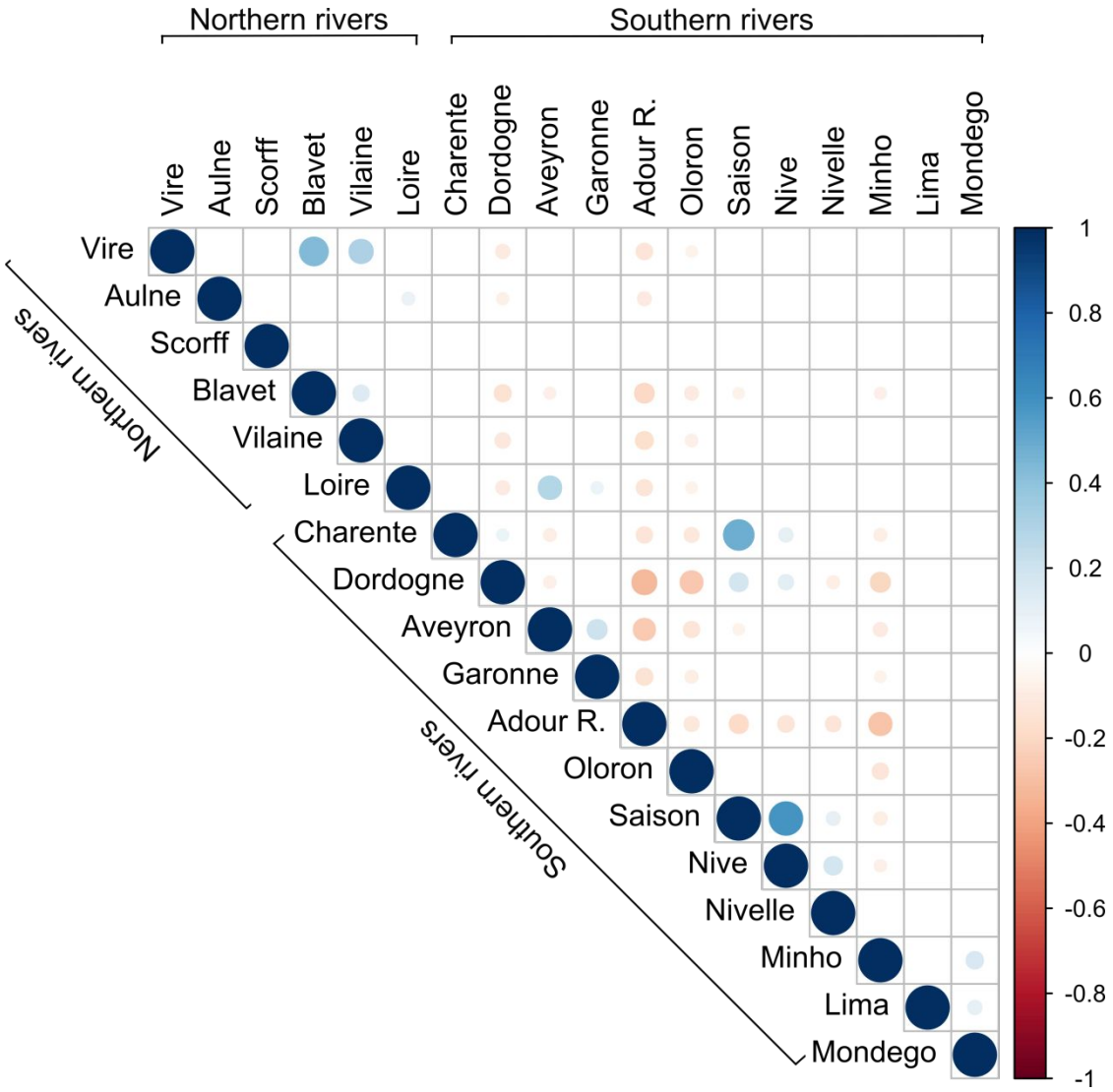


Fig.2. Confusion matrix of reallocation between rivers. Rivers were ordered from north to south. If the correlation is positive there is confusion while if the correlation is negative it means that there is a good discrimination between rivers. Colours (or shades of grey) as well as the size of the circles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

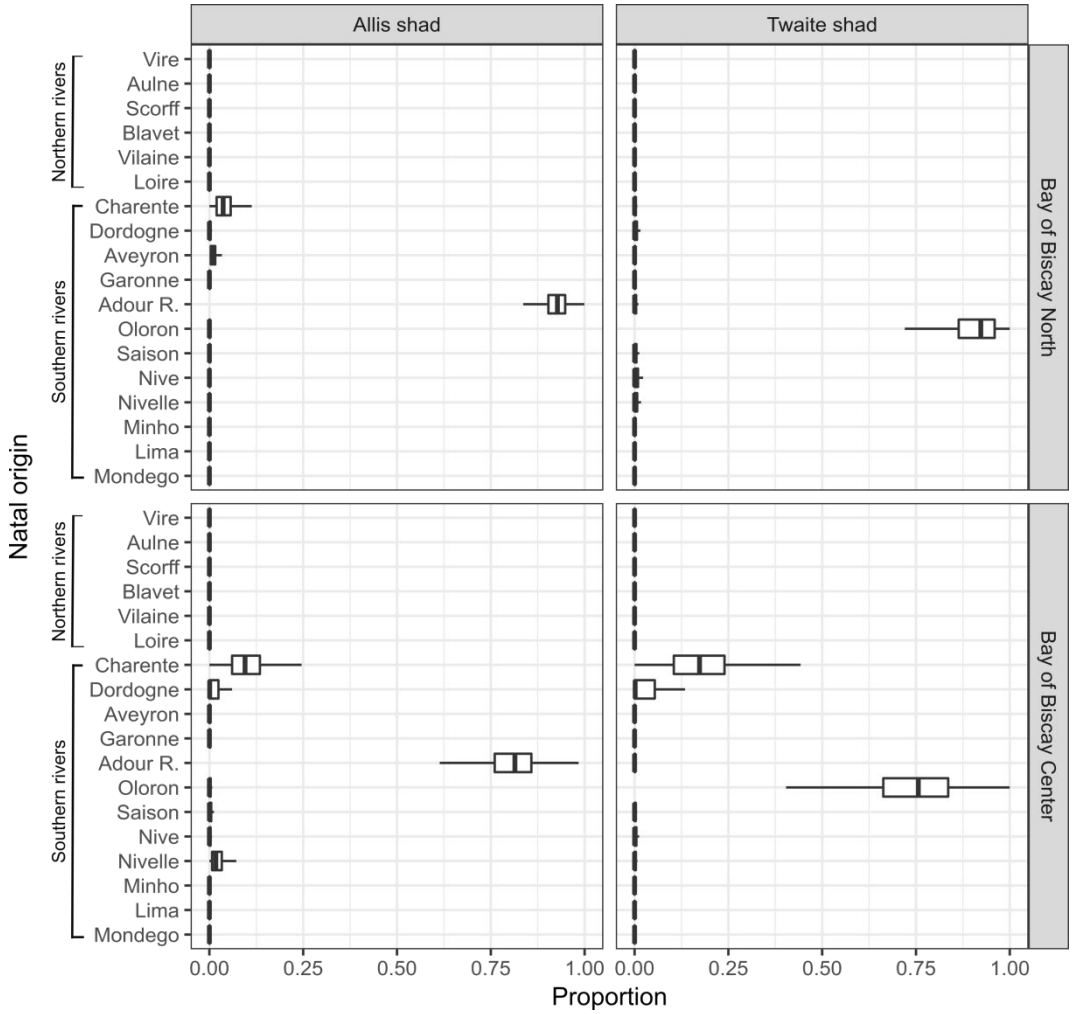


Fig.3. Summary of all reallocation probabilities for each river separated by species and marine region. Rivers were ordered from north to south. Each boxplot represent the first quantile (25%), the median (50%) and the last quantile (75%) of the distribution. The segments are the 95% credibility intervals.

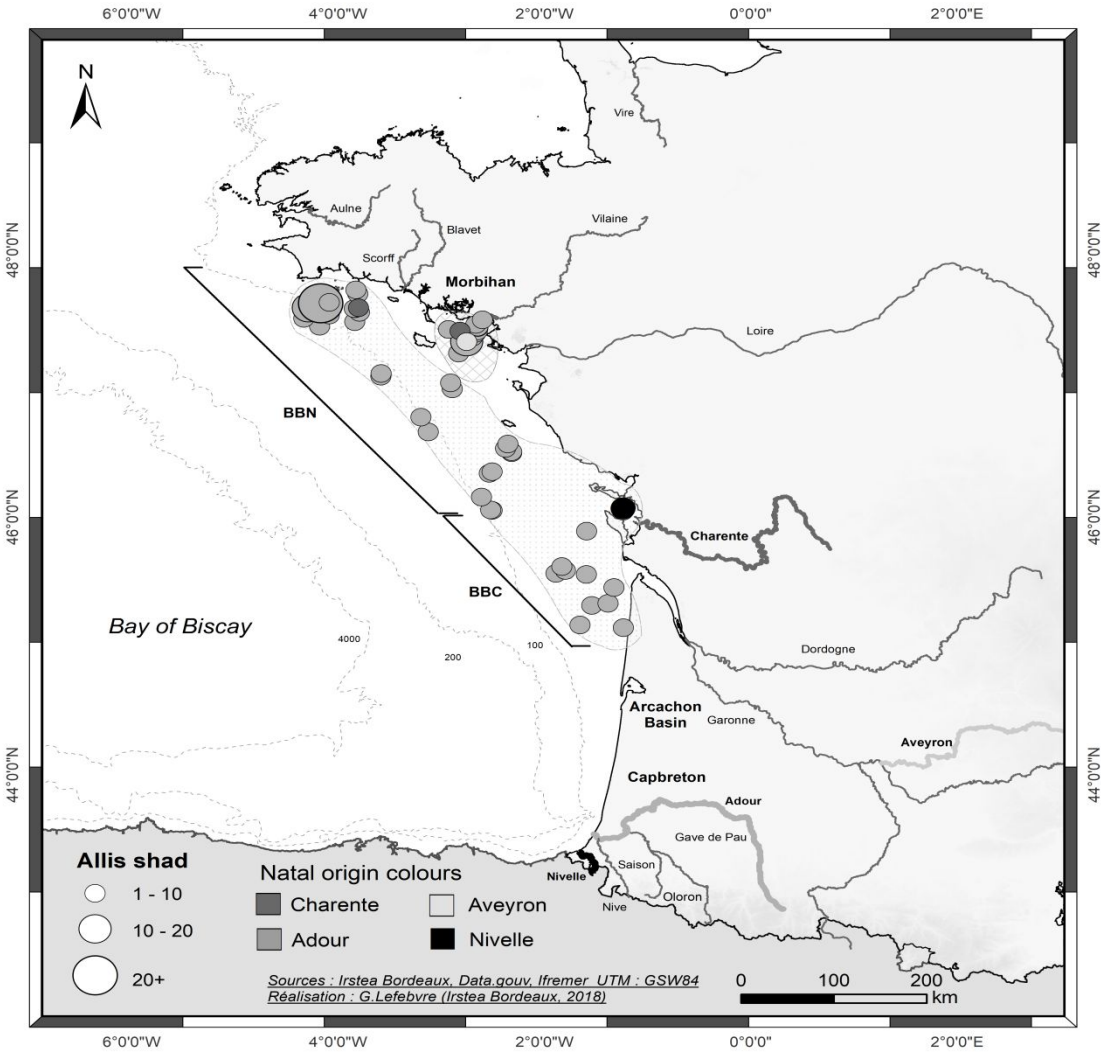


Fig.4. Most probable natal river assignations for Allis shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Allis shad are color-coded for the identification of the natal origin of individuals.

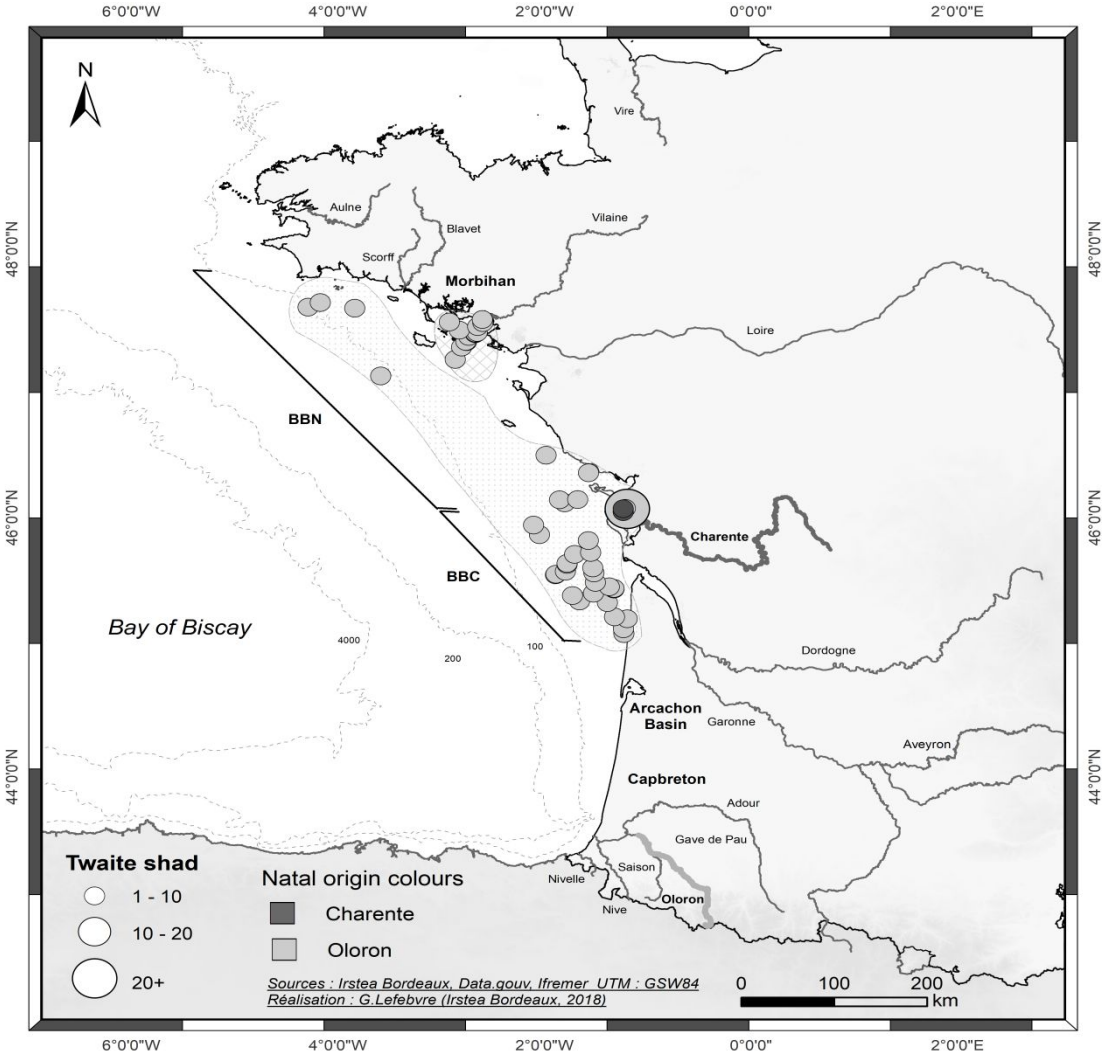


Fig.5. Most probable natal river assignations for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.

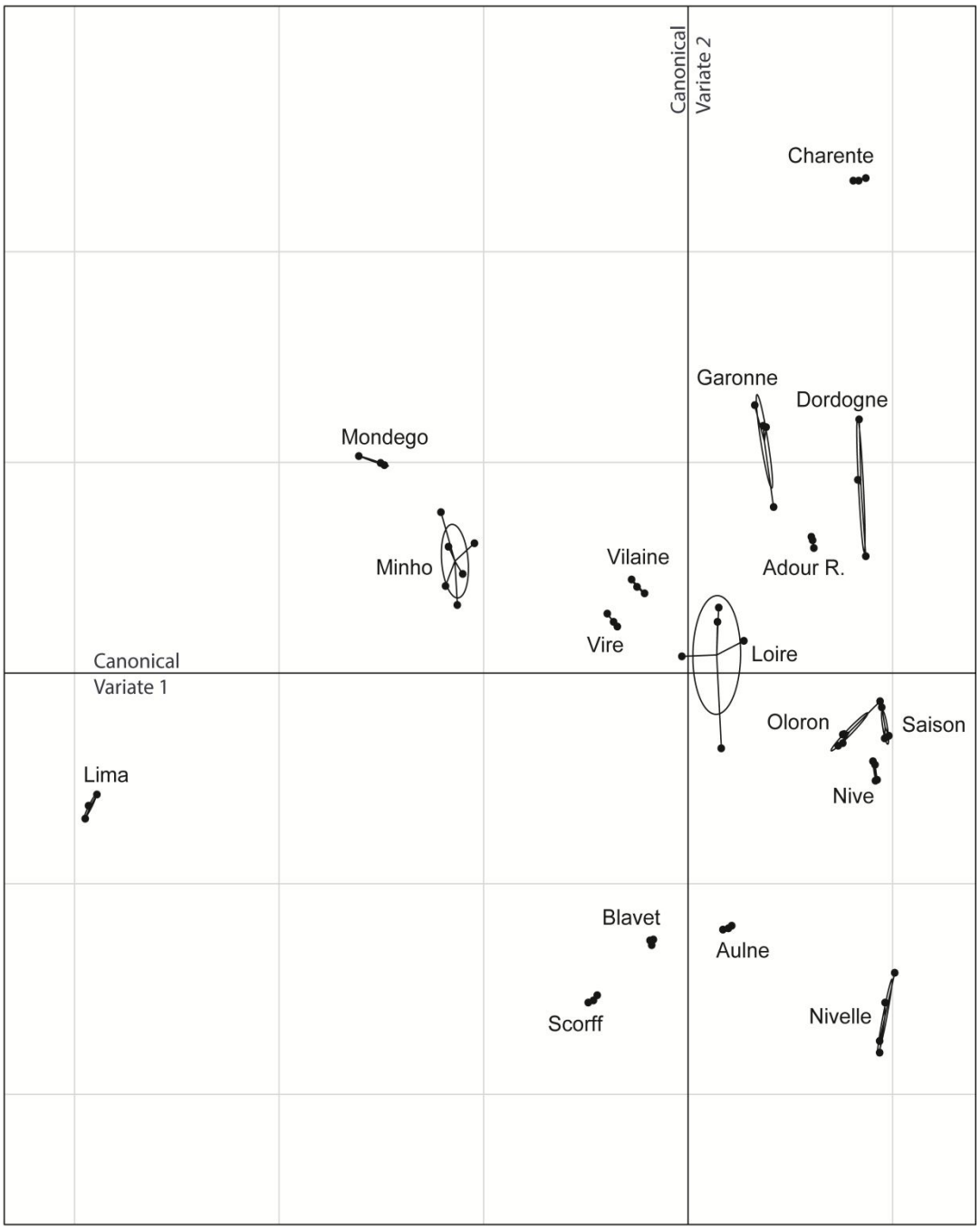


Fig. 6. Canonical discriminant plot of isotope (^{87}Sr:^{86}Sr) and elemental (Sr:Ca and Ba:Ca) signatures from water samples collected from 17 rivers in 2013. Symbols represent water samples, and ellipses are 95% confidence intervals around each group. Grid scale is given (*d* = 1). Taken from Martin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

Draft

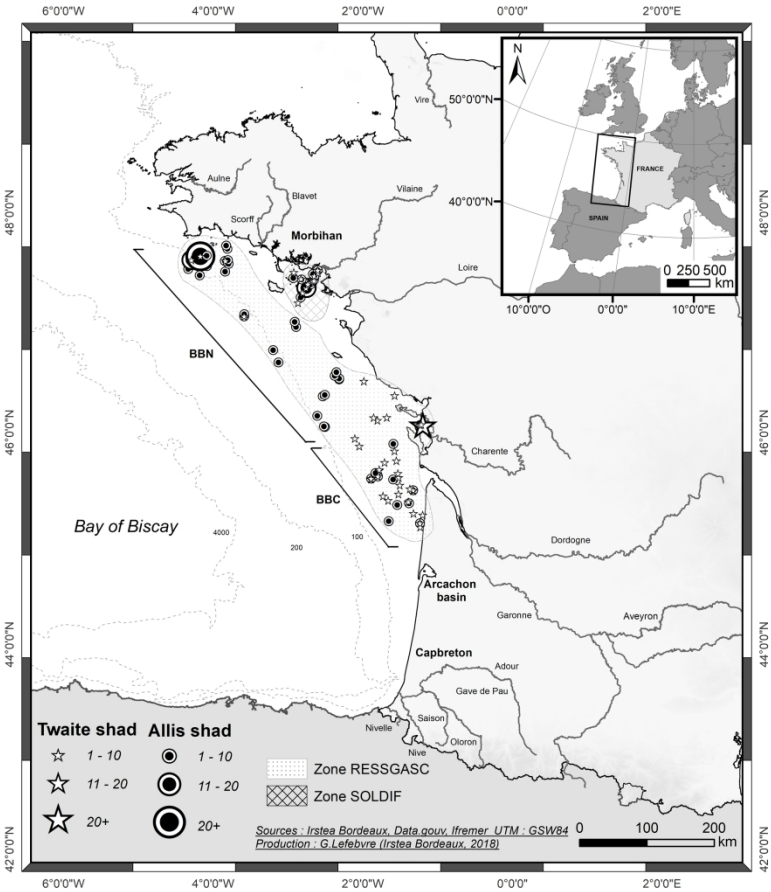
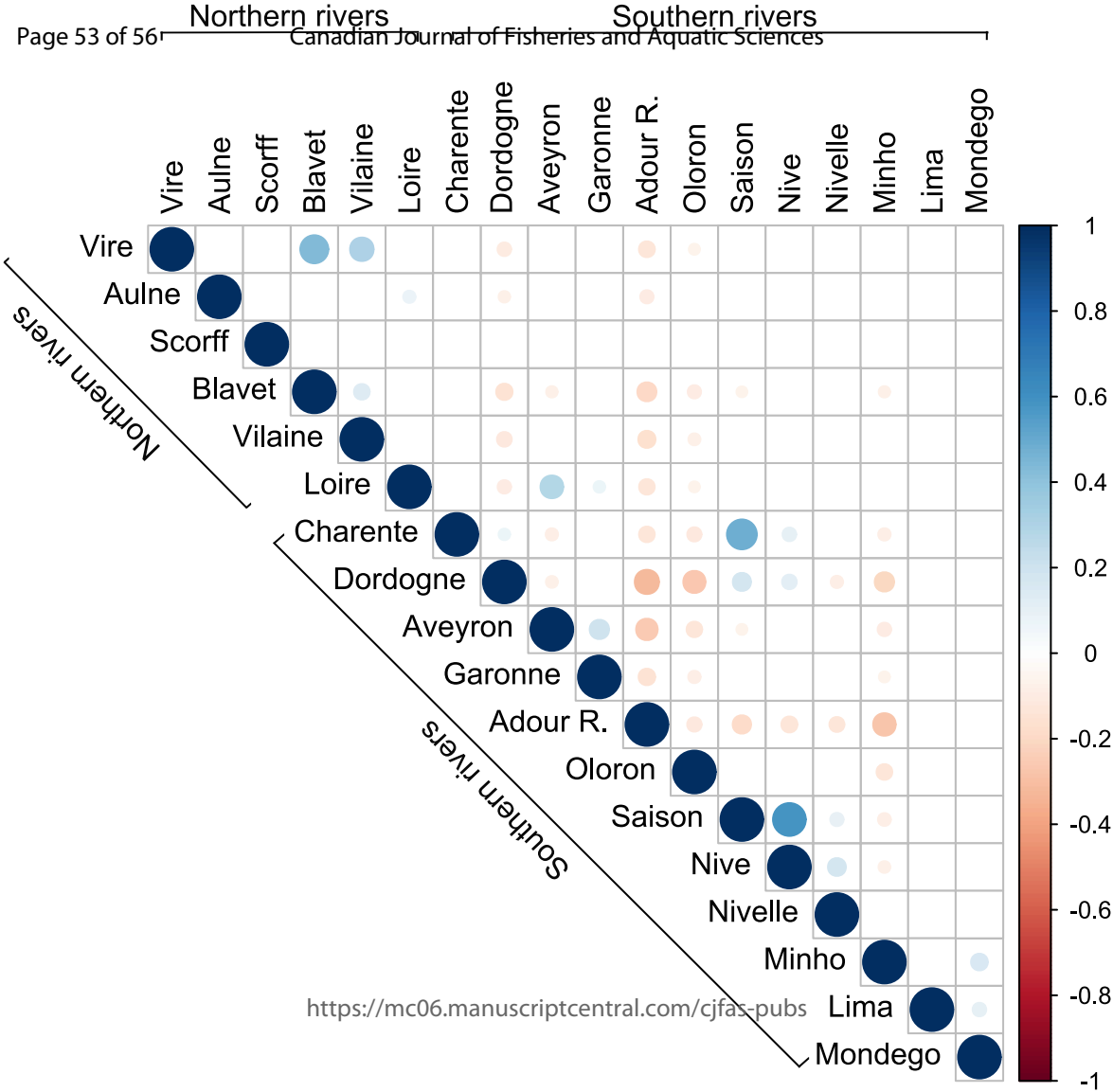
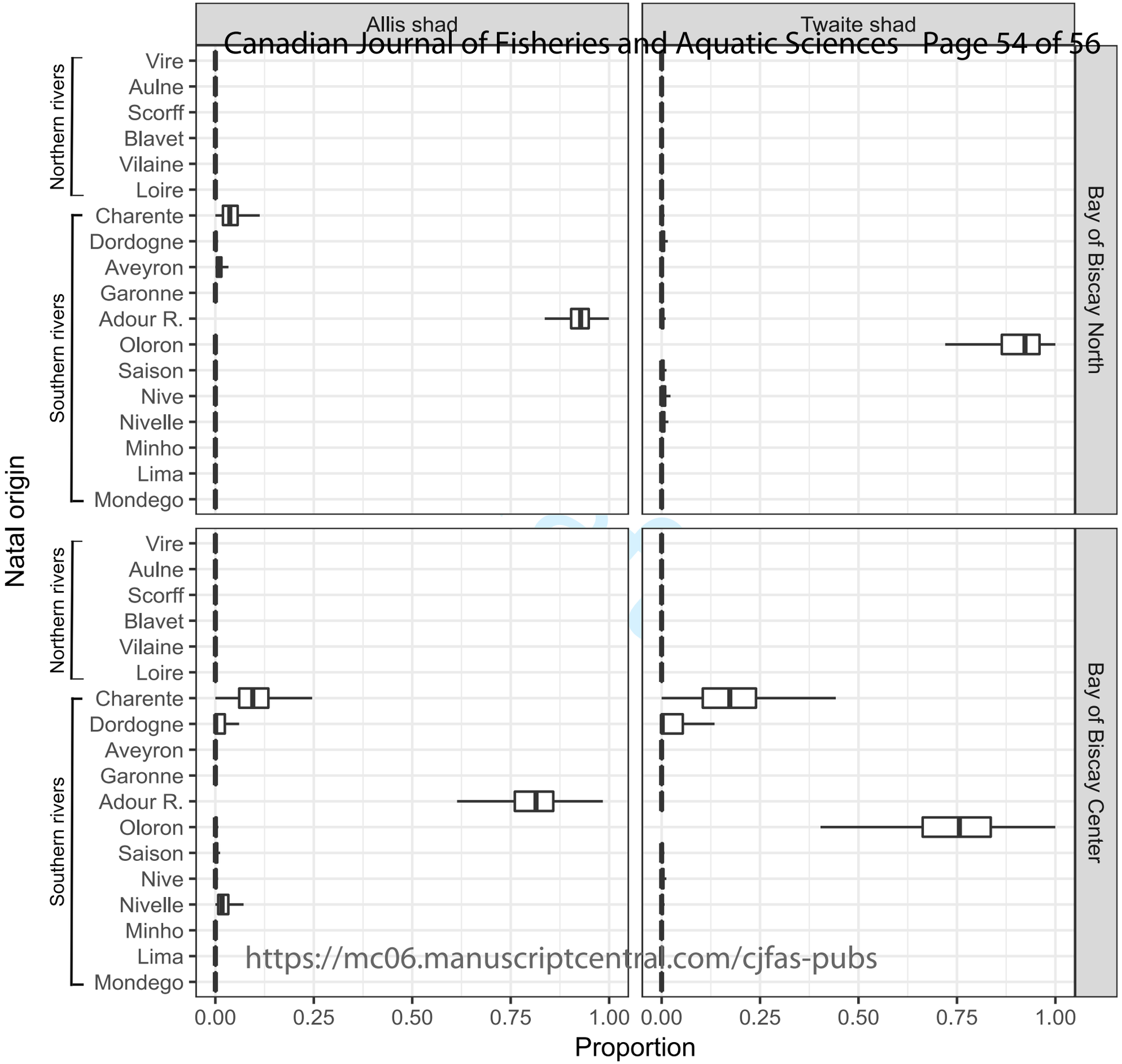


Fig. 1. Sampling surveys campaigns and collection locations of the Allis shad and Twaite shad subadults retained for this study. Marine catches were grouped into two marine regions, Bay of Biscay North (BBN) and Bay of Biscay Center (BBC). The French rivers where water and Allis shad otoliths samples 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.

210x297mm (300 x 300 DPI)


Northern rivers
Southern rivers
Vire
Aulne
Scorff
Blavet
Vilaine
Loire
Charente
Dordogne
Aveyron
Garonne
Adour R.
Oloron
Saison
Nive
Nivelle
Minho
Lima
Mondego
Northern rivers
Southern rivers
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1



https://mc06.manuscriptcentral.com/cjfas-pubs

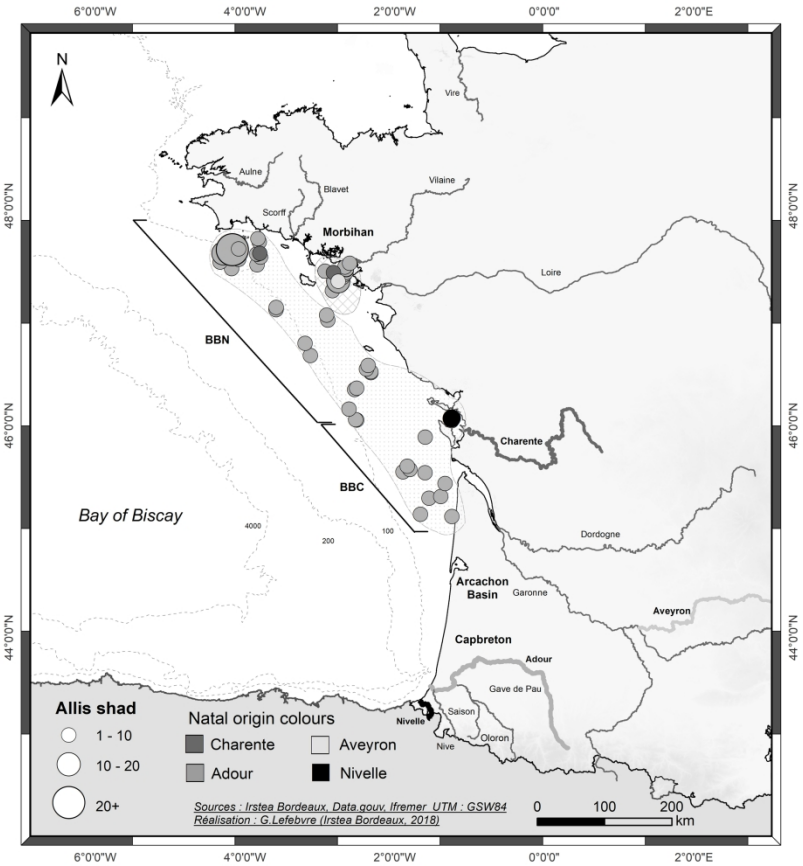


Fig. 4. Most probable natal river assignations for Allis shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Allis shad are color-coded for the identification of the natal origin of individuals.

210x297mm (300 x 300 DPI)

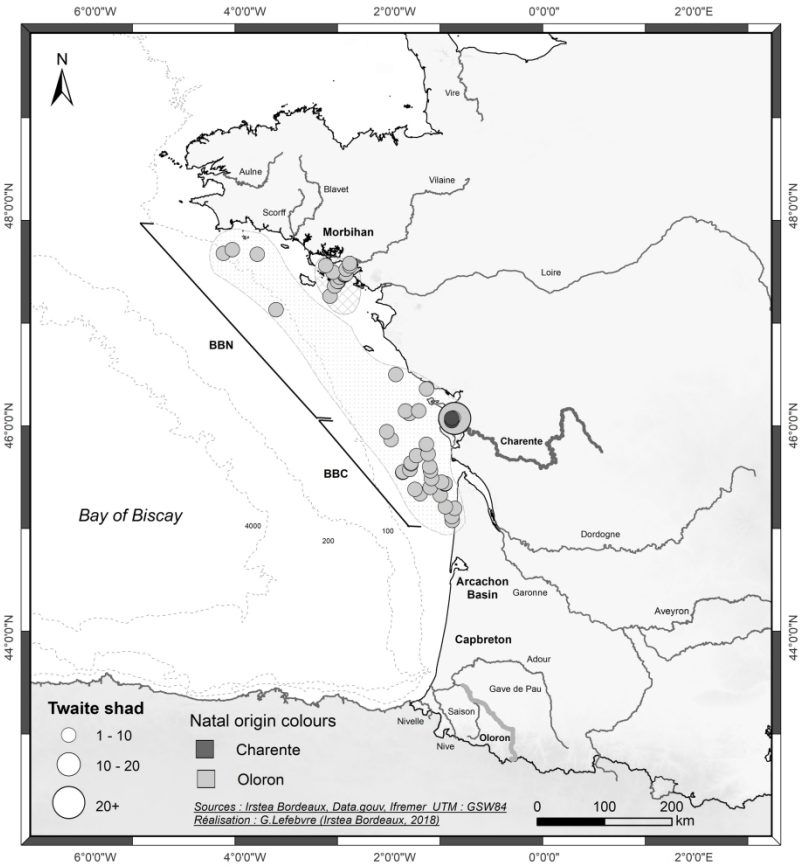


Fig. 5. Most probable natal river assignations for Twaite shad subadults. The map shows all potential sources and those that have contributed individuals to mixtures of subadults Twaite shad are color-coded for the identification of the natal origin of individuals.

210x297mm (300 x 300 DPI)

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