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REGULAR ARTICLE

Juvenile downstream migration patterns of an anadromous fish, allis shad (*Alosa alosa*), before and after the population collapse in the Gironde system, France

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Abstract

Diadromous fish have exhibited a dramatic decline since the end of the 20th century. The allis shad (*Alosa alosa*) population in the Gironde-Garonne-Dordogne (GGD) system, once considered as a reference in Europe, remains low despite a fishing ban in 2008. One hypothesis to explain this decline is that the downstream migration and growth dynamics of young stages have changed due to environmental modifications in the rivers and estuary. We retrospectively analysed juvenile growth and migration patterns using otoliths from adults caught in the GGD system 30 years apart during their spawning migration, in 1987 and 2016. We coupled otolith daily growth increments and laser ablation inductively-coupled plasma mass spectrometry measurements of Sr:Ca, Ba:Ca, and Mn:Ca ratios along the longest growth axis from hatching to an age of 100 days (i.e., during the juvenile stage). A back-calculation allowed us to estimate the size of juveniles at the entrance into the brackish estuary. Based on the geochemistry data, we distinguished four different zones that juveniles encountered during their downstream migration: freshwater, fluvial estuary, brackish estuary, and lower estuary. We identified three migration patterns during the first 100 days of their life: (a) Individuals that reached the lower estuary zone, (b) individuals that reached the brackish estuary zone, and (c) individuals that reached the fluvial estuary zone. On average, juveniles from the 1987 subsample stayed slightly longer in freshwater than juveniles from the 2016 subsample. In addition, juveniles from the 2016 subsample entered the brackish estuary at a smaller size. This result suggests that juveniles from the 2016 subsample might have encountered more difficult conditions during their downstream migration, which we attribute to a longer exposure to the turbid maximum zone. This assumption is supported by the microchemical analyses of the otoliths, which suggests based on wider Mn:Ca peaks that juveniles in 2010s experienced a longer period of physiological stress during their downstream migration than juveniles in 1980s. Finally, juveniles from the 2016 subsample took longer than 100 days to exit the lower estuary than we would have expected from previous studies. Adding a new marker (i.e., Ba:Ca) helped us refine the interpretation of the downstream migration for each individual.

KEYWORDS
hypoxia, life history, migration patterns, migratory fish, otolith microchemistry, turbidity maximum zone

1 | INTRODUCTION

Over the past decades, a substantial loss of aquatic biodiversity has been observed (Ceballos et al., 2015; Hooper et al., 2012; Worm et al., 2006). However, linking causes and effects can be challenging. Aquatic biodiversity responds strongly to anthropogenic pressures. The Gironde-Garonne-Dordogne (GGD) system, which encompasses the largest southwestern European estuary (Romaña, 1994) and two main rivers, the Garonne and Dordogne rivers, has also experienced major changes over the past three decades (Chevillot et al., 2016). Since early 1980, a gradual increase in temperature (Lobry & Castelnaud, 2015) and salinity (Lanoux et al., 2013) has been observed. In recent years, a marinization effect has modified zooplankton (Chaalali et al., 2013; David et al., 2007) and estuarine fish communities (Chevillot et al., 2016). The Garonne River has suffered most from anthropogenic impacts as urban populations alongside this river have increased by 1 million people between 1980 and 2010, representing a 28.1% increase in population size since 1980 (INSEE, 2017), especially around the cities of Toulouse and Bordeaux.

Anadromous fish reproduce in freshwater and migrate to the sea to grow until maturation (McDowall, 2008). Over the past decades, the abundance of anadromous fish has dramatically declined (Limburg & Waldman, 2009) due to cumulative threats at sea and in river ecosystems (Lin et al., 2018). For example, dams (Rolls, 2011) and changes in river flows (Milner et al., 2012) have disrupted the longitudinal connectivity of anadromous fish migration pathways during the river phase. Thus, the early life stages of anadromous fish are particularly vulnerable during their downstream migration to the estuarine and marine habitats (McDowall, 2008).

Allis shad, *Alosa alosa* (von Linnaeus, 1758), is an European clupeid anadromous species spawning in freshwater after a growth phase of 3 to 8 years at sea (Baglinière & Elie, 2000; McDowall, 2008; Sabatié et al., 2009). Historically present along the Atlantic east coast from Norway to Morocco and in the western part of the Mediterranean coast (Cassou-Leins & Cassou-Leins, 1981), the distribution range of allis shad populations has contracted since the end of the 20th century, and in parallel, the size of most populations has declined (Truslé & Quignard, 2013; Lassalle et al., 2008; Limburg & Waldman, 2009; Rougier et al., 2012). The population in the GGD system used to be the most abundant in Europe (Martin Vandembulcke, 1999). Yet, this population collapsed at the end of the 20th century, and numbers have remained low despite a fishing moratorium established in 2008 (Rougier et al., 2012). In the 1980s, between 583 and more than 1000 t of allis shad spawners were caught annually in total in both rivers (Baglinière et al., 2003). However, in 2019, only 1700 spawners (2.4 t) were recorded in the Garonne and Dordogne fishways (MIGADO, 2019), which represents a decrease of more than 99.5% when compared to the 1980s.

Rougier et al. (2012) hypothesized that the population collapse might be due to a higher mortality rate of juvenile allis shad during their downstream migration. Many watersheds suffer from hypoxia, a decrease in dissolved oxygen caused by human activities (Diaz & Rosenberg, 2008). Hypoxia zones commonly occur around major cities due to the input of organic matter and nutrients from wastewater discharges (Liu et al., 2015), and mainly from summer to early autumn (Schmidt et al., 2019). Spatial extension of an hypoxic zone is unfavorable for diadromous species (Hrycik et al., 2017; Schmidt et al., 2019). Therefore, more episodes of persistent turbidity associated with subsequent hypoxia (González-Ortegón et al., 2010) mainly in the estuarine zone have deteriorated environmental conditions for juveniles migrating downstream. In the Gironde system, hypoxic zones, mainly found in the Turbidity Maximum Zone (TMZ) and predominantly located in the fluvial estuary, are influenced by several environmental variables such as temperature, flow regime, particulate load, tidal cycle, and urban input. To substantiate a casual linkage between an extension of the turbidity zone and the population decline, it is important to investigate whether the downstream migration patterns including the passage of this area differ before and after the collapse.

The analysis of otoliths daily increments (calcified structures present in the inner ear of fish) with chemical analysis is a suitable method to retrospectively investigate juvenile migration patterns through zones with different water chemistry (Gillanders, 2005;

Limburg et al., 2001). For example, the ratios of barium and strontium (Ba:Ca and Sr:Ca, respectively) are commonly used to track fish migration, especially along salinity gradients. Manganese to calcium ratio (Mn:Ca) can be used to detect low oxygen availability for the fish, as the solubility of Mn in water mostly depends on oxygen concentration (Limburg et al., 2015; Limburg & Casini, 2018). An increase in dissolved Mn and Ba may occur due to active oxidation–reduction reactions in hypoxic zones (Abril et al., 2000; Audry et al., 2007). Historical otolith collections are important and can reveal information about the past conditions (see Nachón et al., 2020 for more details). Here, the downstream migration patterns of allis shad in the GGD system before (1980s) and after (2010s) the population collapse were compared by analysing otolith microstructure and microchemistry. Accordingly, the following questions were addressed: (a) Do the downstream migration patterns of allis shad juvenile differ before and after the population collapse? (b) Are there indications that juveniles were exposed to a longer period and higher levels of oxygen shortage after the collapse? (c) Did the body condition when reaching the brackish estuary zone change? Finally, (d) did returning spawners differ in terms of body size and age before and after the collapse?

2 | MATERIALS AND METHODS

2.1 | Study area

Both the Garonne and Dordogne rivers, with a total length of 647 and 483 km, respectively, join to form the largest (70 km long, up to 12 km wide) macro-tidal estuary in South-West Europe: the Gironde estuary (Figure 1). The average combined river discharge from the Dordogne and Garonne rivers is 760 $m^3 \cdot s^{-1}$ but, it varies from 200 $m^3 \cdot s^{-1}$ during the dry season to above 2000 $m^3 \cdot s^{-1}$ during the wet season (Jalón-Rojas et al., 2015). The upstream limit of the dynamic tidal wave is modulated by river flow and can reach a maximum distance of 170 km upstream from the mouth in the Garonne River and around 160 km in the Dordogne River (Castaing & Allen, 1981), before being dissipated by bed and lateral friction (Jalón-Rojas et al., 2015). In the convergent estuarine zone of the GGD system, the tidal range increases toward upstream, and the maximum tidal range reaches more than 6.0 m at 130 km from the mouth; therefore, tidal currents are strongest in the freshwater portions of the estuary (Allen et al., 1980). Due to the asymmetry between shorter but more intense flood currents and longer but less intense ebb currents, the tide traps fine suspended sediments leading to a TMZ in both the Garonne and Dordogne rivers (Allen et al., 1980; Castaing & Allen, 1981; Doxaran et al., 2009; Jalón-Rojas et al., 2015; Sottolichio et al., 2001; Sottolichio & Castaing, 1999). The TMZ has gradually become more concentrated in suspended sediments matter and has expanded over the past decades (Jalón-Rojas et al., 2015).

At high river flow, the TMZ is restricted to the lower part of the brackish estuary, approximately between KP 80 to KP 0 (Sottolichio & Castaing, 1999). At low river flow, which usually occurs from July to September, when juvenile allis shad migrate downstream, the TMZ is shifted upstream by the tidal pumping and expands to near the freshwater tidal limit, approximately between KP 0 and KP -70 (Figure 1) in the Garonne River, and for similar distances in the Dordogne River (Doxaran et al., 2009; Jalón-Rojas et al., 2015). Additionally, the long-term monitoring of the mean river flow during the low discharge (summer) period (as defined by Jalón-Rojas et al., 2015) has been performed over the past 55 years, showing a clear drop of the mean flow, especially after the 1980s (Figure 2).

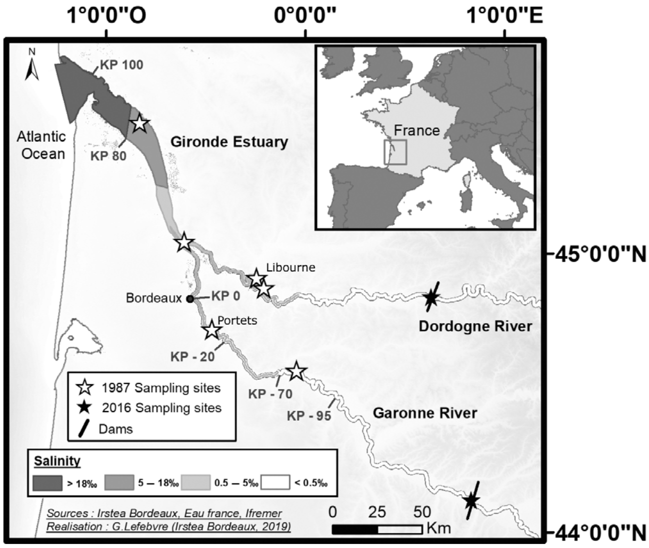

FIGURE 1 Map of the study area, the Gironde estuary with the Dordogne and Garonne rivers. Open and filled stars represent sampling sites from 1987 and 2016, respectively. Gray shades indicate different salinity zones. Kilometric points (KP) correspond to the kilometer from the city of Bordeaux (KP 0) to the open ocean (positive values) and to the riverheads (negative values).

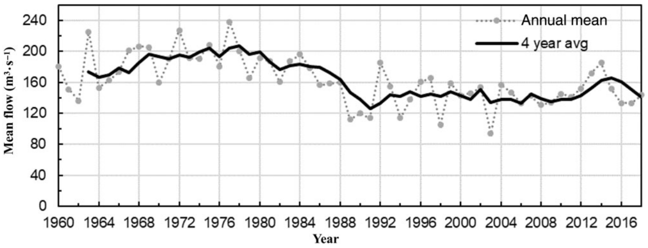

FIGURE 2 Mean of Garonne river flow during the "low discharge" (LD) annual period, from 1960 to 2018, and 4-year average (see text for explanation). Data from Banque Hydro public data.

2.2 | Fish sampling

Mature allis shad were collected at several sites in the Gironde system (Figure 1) in 1987 ($n = 76$) and 2016 ($n = 57$). All samples were taken during the spawning season, between April and June, without any restrictions for site, time, size, or sex. Fish from 1987 were sampled by professional fishermen using a trammel net composed of one central layer (110 mm mesh size) and two lateral layers (700 mm mesh size), whereas fish from 2016 were trapped in fish passes in both the Garonne and Dordogne rivers. For each fish, total length (TL in cm), total weight (TW in g; no weight could be assessed for five individuals), and sex were recorded.

A subsample of these fish was used for microchemistry analyses ($n = 30$ in 1987 and $n = 32$ in 2016). For these fish, scales were collected, and age (in years) was estimated by several readers recording winter rings (Baglinière et al., 2001; Wright et al., 2002). This information was used to determine the year when these individuals migrated downstream as juveniles. The sex ratio in this subsample was equally distributed (17 females and 13 males in 1987, 17 females to 15 males in 2016). We assumed that these fish originated from the Dordogne and Garonne rivers based on the strong homing behavior of allis shad (Martin et al., 2015; Randon et al., 2018).

2.3 | Ethics statement

No live animals were experimented during this study. All fish and otoliths from the 1987 samples were obtained from the collection at INRAE (National Institute for Agriculture and Environment) research institute of Bordeaux. The 2016 samples came from the MIGADO Association, a group working on migratory fish in the Garonne, Dordogne, Charente, and Seudre rivers.

2.4 | Otolith preparation and analysis

Sagittal otoliths for both sampling periods were analysed in this study. The two sagittal otoliths were extracted shortly after adult sampling and stored in a desiccation chamber at the research institute of INRAE Bordeaux until the present study. Otoliths were extracted, cleaned with ultrapure water, dried, and stored until preparation. To estimate the daily age and investigate the juvenile migration pathway, one otolith was embedded in epoxy resin, sectioned along the transversal plane, and polished gradually until the primordium was reached. We studied the first 100 days of life, as described in Lochet et al. (2008). The number of daily growth increments and distance every 5 days (dist-5 days in μm) were recorded from hatching to 100 days with the NIS-Elements software version D2.30. Successive use of the river and estuarine zones during juvenile migration was determined by measuring concentrations of ^{43}Ca, ^{88}Sr, ^{138}Ba, and ^{55}Mn from the core to the edge along the otolith growth axis using femtosecond-laser ablation inductively-coupled plasma mass spectrometry (see analytic details in Tabouret et al. [2011]). Based on the daily age distances (μm), each element:Ca ratio value, measured every 3.45 μm, was averaged to obtain a mean value for 5 days.

Data from juveniles sampled in the Garonne and Dordogne rivers between 2001 and 2015 (Randon et al., 2018) were used to estimate the freshwater threshold values of Sr:Ca and Ba:Ca ratios. The Sr:Ca and Ba:Ca threshold values of the lower estuary part (salt concentration >18‰) were estimated by averaging the values of Sr:Ca and Ba:Ca ratios corresponding to the marine life (otolith edge) from fish caught from the 1987 and 2016 sampling years.

During their downstream migration, juvenile allis shad cross four consecutive habitat zones with different hydrodynamic and physicochemical conditions. To identify these zones on the juvenile portion of the otoliths of spawners, we used the variations in Sr:Ca and Ba:Ca ratios in the water, as otolith Sr:Ca and Ba:Ca ratios usually reflect the water composition (Daverat et al., 2005). Therefore, we used the observed (Daverat et al., 2012; Martin et al., 2015) and expected—conservative mixing in the saline gradient (Walther & Limburg, 2012)—variations in dissolved Sr:Ca and Ba:Ca in the four zones.

The upstream freshwater zone exhibits invariably low Sr:Ca and high Ba:Ca ratios. The fluvial estuary zone can reasonably be characterized by invariably low Sr:Ca and an increase followed by a decrease in Ba:Ca ratio (Figure S1). The decrease in Ba:Ca ratio might be related to active exchanges of elements in the TMZ area (Colbert & McManus, 2005). The brackish estuary zone exhibits an exponential increase in Sr:Ca ratio and a continuous decrease in Ba:Ca ratio. Finally, the lower estuary zone is expected to display high Sr:Ca and low Ba:Ca ratios (Figure S1). These trends helped us interpret the elemental profiles of the juvenile portion of allis shad otoliths (Figure 3).

Otolith profiles were interpreted as follows: high otolith Ba:Ca ratio (> 13.9) was interpreted as the stay in freshwater. An increase in otolith Ba:Ca ratio marked the entry into the fluvial estuary zone. When the Sr:Ca ratio started to increase (>0.57), fish were considered to have moved on to the brackish estuary. The lower estuary was reached when the Ba:Ca ratio stabilized at low levels (<1.2) while the Sr:Ca ratio was high (Sr:Ca >2.24) and constant. For each individual, the duration of stay in each of the four zones was estimated by counting daily increments (Figure 3).

The mean duration of stay and the elemental ratios in each zone were compared between fish from the 1987 and 2016 subsamples using non-parametric Wilcoxon tests, as data were not normally distributed. Based on the otolith profiles, we distinguished three different patterns of downstream migration within the first 100 days of life: (a) individuals that reached at least the lower estuary (high and constant Sr:Ca and low Ba:Ca ratios around age 100 days; pattern A); (b) individuals that reached at least the brackish estuary (Sr:Ca ratios around age 100 days still increasing while Ba:Ca ratios still decreasing; pattern B); and (c) individuals that reached only the fluvial estuary (Sr:Ca ratios under the freshwater threshold value throughout first 100 days; pattern C).

To back-calculate the TL of juveniles when they reached the brackish estuary zone, we used the formula of Francis (1990). We used the TL of both fish and otoliths at catch together with cumulated daily ring distance of the otolith at the time when fish reached the brackish estuary. In total, 18 individuals out of the 30 for the 1987 subsample and 18 out of the 32 individuals from the 2016 subsample reached the brackish estuary. However, two individuals from the 1987 subsample had missing data and were not included in TL comparison between both subsamples.

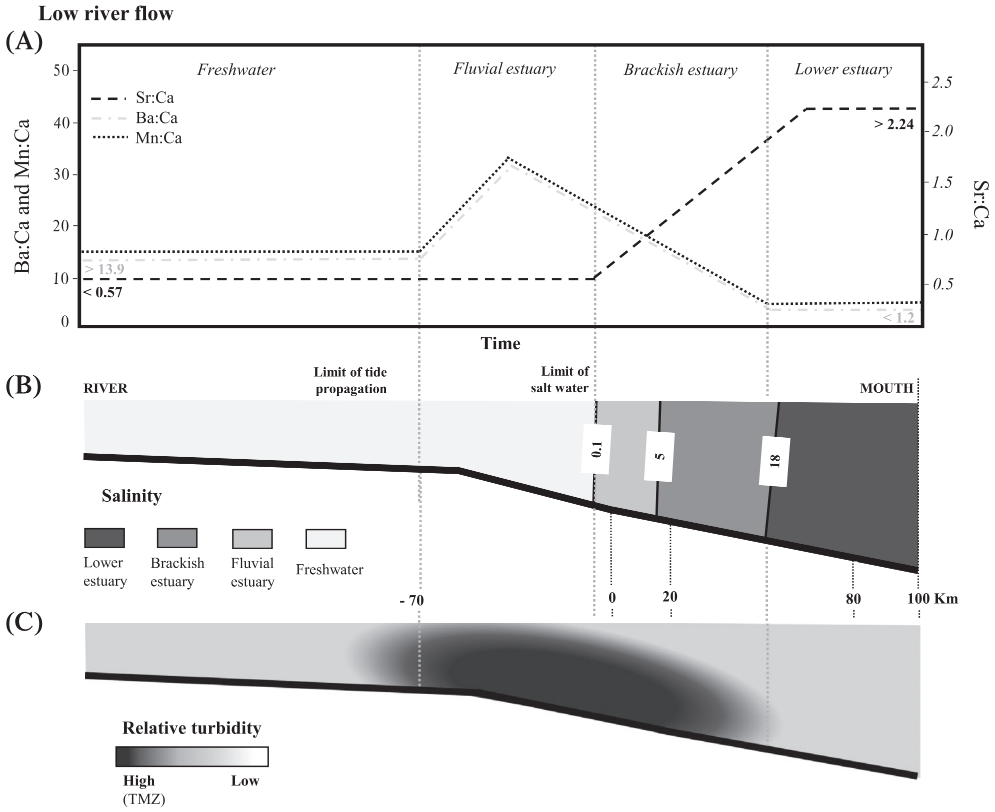

FIGURE 3 (a) Expected variations in otoliths of Sr:Ca, Ba:Ca and Mn:Ca ratios along the Gironde estuary continuum. (b) Salinity gradient and (c) location of the Turbidity Maximum Zone (TMZ) during low river flow conditions, which is common from July to September, during allis shad (*Alosa alosa*) downstream migration. The kilometric points (KP) corresponds to the distance from Bordeaux (KP 0) to the open sea (positive values) and to the river heads (negative values).

All datasets were checked for normal distribution and homoscedasticity. For univariate analyses on normally distributed and homoscedastic data, *t*-tests and ANOVA were used. Data violating these criteria were analysed using Wilcoxon- and χ^2 tests. All statistical analyses were performed using R software version 3.3.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Downstream migration patterns of juvenile allis shad

The fluctuations in otolith Ba:Ca and Sr:Ca ratios indicated that some of the individuals sampled reached the lower estuary zone (Figure 4a; migration pattern A) during their first 100 days after hatching, some individuals reached the brackish estuary zone (Figure 4b; migration pattern B), whereas some individuals reached only the freshwater zone (Figure 4c; migration pattern C). Furthermore, synchronic variations in Ba:Ca and Mn:Ca ratios were found in a large majority of allis shad otoliths (Figure 4a–c). Most individuals exhibiting pattern A were from the 1987 subsample (80%), whereas the remaining 20% were represented by individuals from the 2016 subsample. The two subsamples contributed equally to patterns B and C (i.e., 45% [1987] and 55% [2016] for pattern B and 48% [1987] and 52% [2016] for pattern C).

The time spent in different zones varied greatly among individuals. In the freshwater zone, it ranged from 10 to 55 days for the 1987 subsample and from 5 to 65 days for the 2016 subsample with a median value at 30 and 15 days, respectively (Figure 5d). In the fluvial estuary zone, it ranged from 30 to 80 days for the 1987 subsample and 30 to 90 days for the 2016 subsample with a median observed at 58 and 65 days, respectively. Time spent in the fluvial estuary zone was longest in fish following migration pattern C (Figure 5c). Regardless of the subsample, these fish stayed at least 72 days in the fluvial estuary zone and did not reach the brackish estuary zone within the 100 days of otolith reading. Time spent in the fluvial estuary zone was shortest in migration pattern A (Figure 5a), with intermediate durations of stay in pattern B (Figure 5b). Finally, individuals spent from 5 to 35 days for the 1987 subsample and from 5 to 55 days for the 2016 subsample in the brackish estuary zone with a median value of 18 and 20 days, respectively (Figure 5d).

When considering the three migration patterns all together (Figure 5d), juvenile allis shad from the 1987 subsample stayed in the freshwater zone significantly longer than those from the 2016 subsample (Wilcoxon test: $W = 632$, $p = 0.015$). Interestingly, the duration of stay in freshwater for pattern B only showed a significant difference between the two subsamples, with juveniles from the 1987 subsample staying significantly longer in the freshwater zone than those from the 2016 subsample (Wilcoxon test: $W = 191$, $p = 0.004$, Figure 5b). Despite the small number of individuals for pattern A ($n = 5$), no significant differences were found in the duration of stay in freshwater for patterns A and C ($n = 25$) (Wilcoxon tests: all $p > 0.05$). When considering the three migration patterns all together (Figure 5d), the duration of stay in the fluvial estuary did not significantly differ between the 1987 and 2016 subsamples (Wilcoxon tests: $p > 0.05$). The duration of stay in the brackish estuary did not

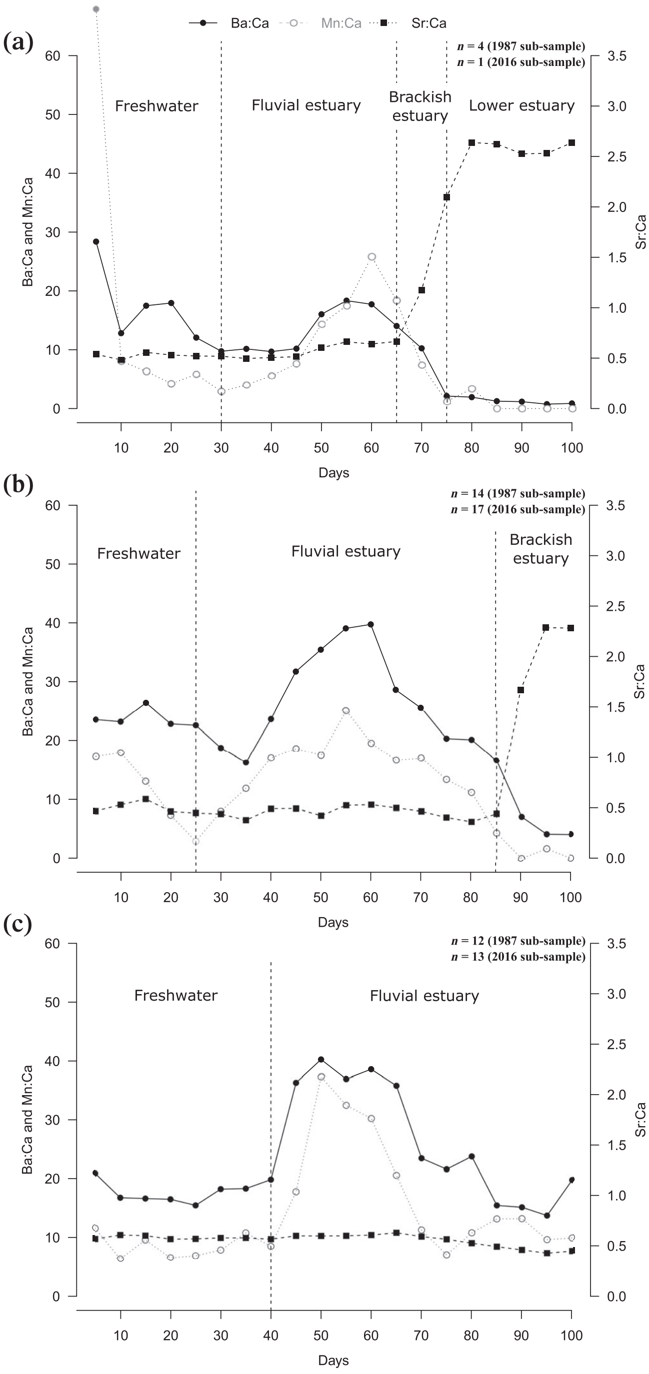

FIGURE 4 Examples of otolith elemental ratio time series of allis shad juvenile (*Alosa alosa*). These series include individuals from both the 1987 and 2016 subsamples. Three different patterns of downstream migration were observed during the first 100 days after hatching: (a) individual that has reached the lower estuary zone, (b) individual that has reached the brackish estuary zone, and (c) individual that has reached the fluvial estuary zone.

significantly differ either (Wilcoxon tests, all $p > 0.05$). When the three migration patterns were analysed separately, the duration of stay in the fluvial and brackish estuary zones (Figure 5a, 4b,c) did not significantly differ between the 1987 and 2016 subsamples (Wilcoxon tests, all $p > 0.05$).

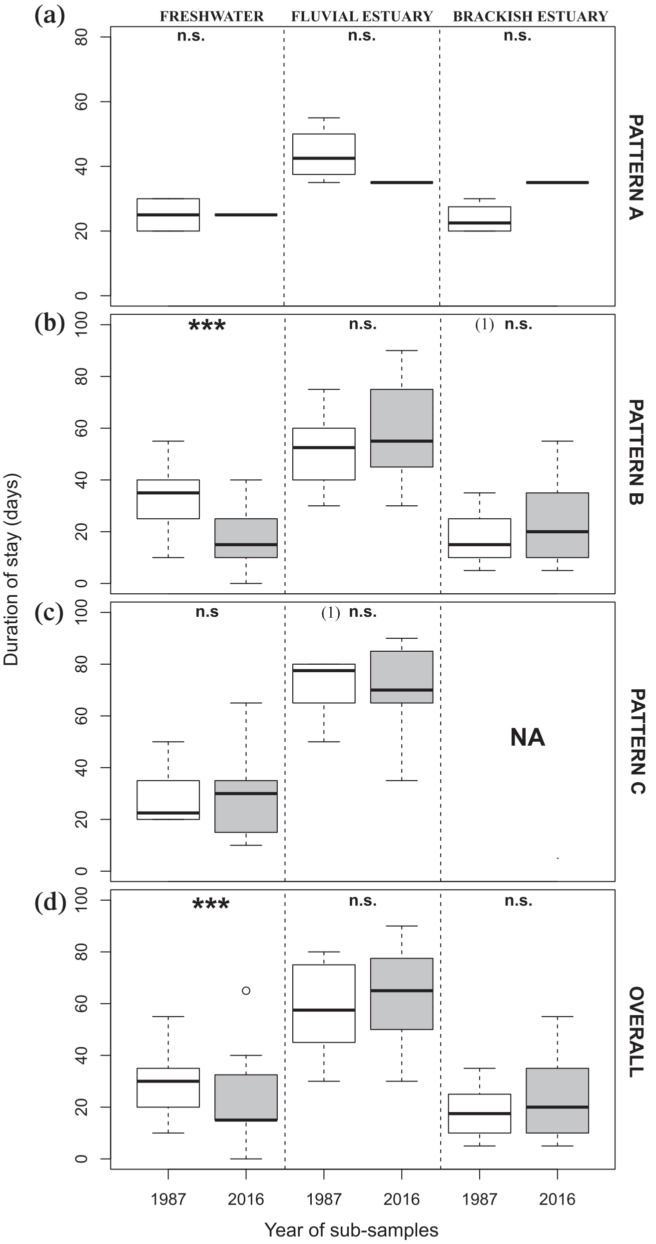

FIGURE 5 Duration of stay of allis shad juvenile (*Alosa alosa*) in different zones during their downstream migration in the Gironde-Garonne-Dordogne system for individuals from the 1987 and 2016 subsamples. (a, b, and c) represent different patterns of migration, whereas (d) represents all patterns together. The asterisks indicate a significant difference ($p < 0.05$) between subsampling years. (1) represents the duration of stay for both subsamples in either fluvial estuary (pattern c) or brackish estuary (pattern b) from their first entry up to 100 days only. The boxes represent medians, first and third quartiles. Values greater than 1.5 times the interquartile range away from the median are represented by an empty circle.

3.2 | Indirect measurement of changes in oxygen levels in the estuarine zones

A highest Mn mean value was observed for pattern C of the 2016 subsamples (40.37 ± 24.76), whereas pattern B of the 1987 subsamples had a

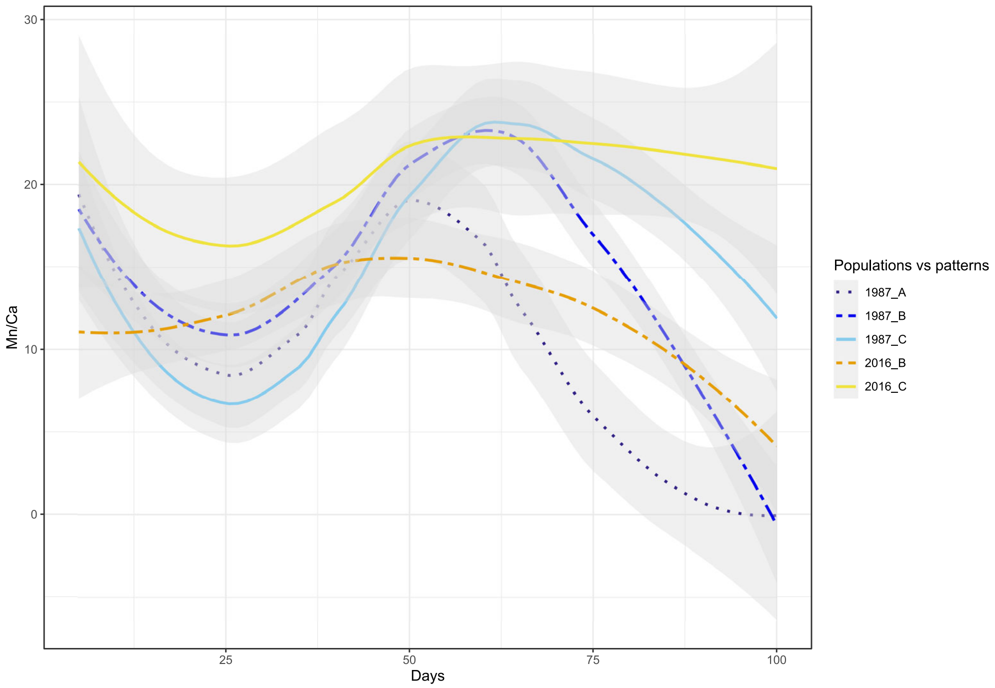

FIGURE 6 Dynamics of Mn:Ca ratios (Loess regression) during the first 100 days after hatching of allis shad (*Alosa alosa*) from the 1987 and 2016 subsamples. For each subsample, individuals were grouped based on migration patterns (a–c) (see Figure 3; Table 1). Pattern A of the 2016 subsample is not shown due to small sample size ($n = 1$). Gray bands represent the 95% C.I.

highest mean value of 37.74 ± 10.86 (Table S1). Otolith Mn:Ca ratios in the fluvial estuary peaked at 33.3 ± 12.0 and 33.4 ± 20.4 for juveniles from the 1987 and 2016 subsamples, respectively, and did not significantly differ (Wilcoxon-test: $W = 544$, $p > 0.05$). These Mn:Ca ratio peaks were reached at a similar age for individuals from the 1987 (62 ± 13 days) and 2016 (55 ± 20 days) subsamples (Wilcoxon-test: $W = 598$, $p > 0.05$). For all three migration patterns, variations in otolith Mn:Ca ratios during the first 100 days after hatching revealed that, with the longer duration of stay in the fluvial estuary where the TMZ is located, Mn:Ca peaks became higher, wider, and they were reached at an older age (Figure 6). The 1987 subsamples exhibiting pattern B showed a higher peak of Mn:Ca than the 2016 subsamples. For pattern C, the peak of Mn:Ca was similar between both subsamples; however, the 1987 subsample peak of Mn:Ca decreased faster, whereas it stayed high at least until 100 days for the 2016 subsample.

Otolith Ba:Ca ratios peaked at 32.2 ± 12.1 and 28.4 ± 9.7 in fish from the 1987 and 2016 subsamples, respectively (Wilcoxon-test: $W = 551$, $p > 0.05$). The peak was reached at age 57 ± 16 days and 51 ± 21 days for fish from the 1987 and 2016 subsamples, respectively (Wilcoxon-test: $W = 562.5$, $p > 0.05$).

In the lower estuary zone, Sr:Ca and Ba:Ca ratios differed slightly between fish from the 1987 and 2016 subsamples. Sr:Ca ratios increased from 2.24 ± 0.40 to 2.33 ± 0.42 (Wilcoxon-test: $W = 157{,}930$, $p < 0.001$). In contrast, average Ba:Ca ratios decreased significantly from 1.27 ± 0.59 to 1.22 ± 0.69 (Wilcoxon-test: $W = 199{,}510$, $p = 0.0054$).

3.3 | Body condition of juveniles at the entrance of the brackish estuary

The TL of allis shad at the time of their arrival in the brackish estuary zone varied greatly, from 1.9 to 14.4 cm (Figure 7). The TL of the 1987 subsample varied from 4.3 to 14.4 cm with a median equal to 7.7 cm, whereas the TL of the 2016 subsample varied from 1.9 to 11.8 cm with a median equal to 6.7 cm. On average, juvenile allis shad from the 2016 subsamples were slightly but, not significantly, smaller than individuals from the 1987 subsample (T-test: $t = -1.458$, $df = 30.96$, $p = 0.155$).

3.4 | Age, length, and weight of returning spawners

The age of returning spawners in the 1987 and 2016 subsamples was comparable, ranging from 4 to 7 years (Table 1). Most individuals in both subsamples were 5 years old (73% and 47% for both 1987 and 2016 subsamples, respectively). The proportion of older individuals in the 2016 subsample increased slightly, but not significantly due to the low number of spawners ($n = 2$ for 1987 and $n = 3$ for 2016 subsamples) in this group (χ^2 test: $\chi = 4.75$, $df = 3$, $p = 0.190$).

On average, female spawners from the 1987 subsample returned with a TL of 54.3 ± 3.2 cm and a TW of 1676.8 ± 340.8 g, whereas the 2016 subsample female spawners had a TL of 59.1 ± 3.4 cm and a TW of 1725.1 ± 592.0 g. Males were significantly smaller than females (Wilcoxon-test: $W = 197.5$, $p < 0.001$; Figure S2). The 1987 subsample male spawners had a TL of 50.3 ± 3.0 cm and a TW of 1283.4 ± 243.7 g, whereas the males from the 2016 subsample measured on average 52.0 ± 4.5 cm and weighed 1105.2 ± 37.2 g (Figure S2). A significant interaction of the factors year and sex in the ANOVA on TL indicated that this increase in body size was greater in females than males (Table 2).

4 | DISCUSSION

The present study reported allis shad juvenile downstream migration from the otolith microchemistry analysis of spawners. This retrospective

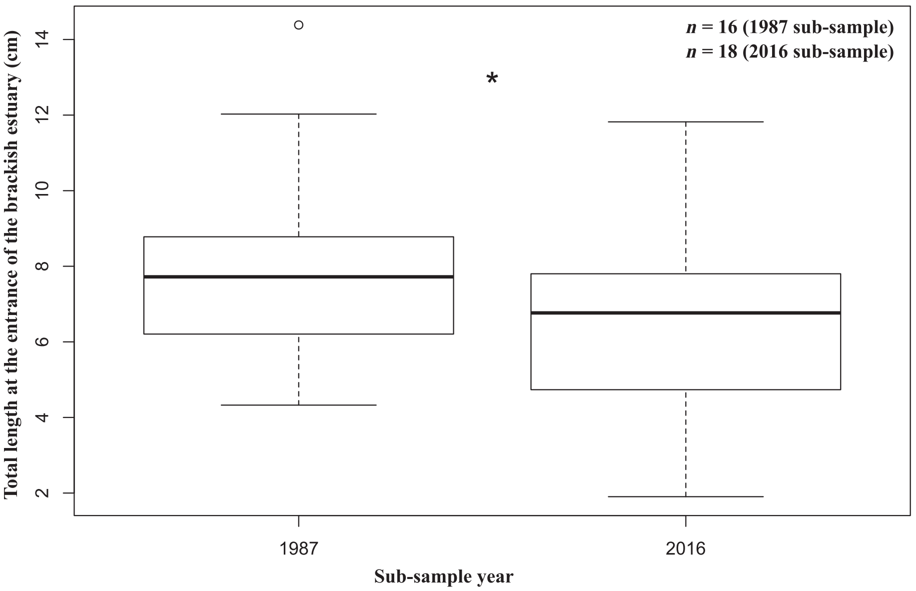

FIGURE 7 Total length of allis shad (*Alosa alosa*) juveniles from the 1987 and 2016 subsamples when entering the brackish estuary of the Gironde-Garonne-Dordogne system. The asterisk indicates a significant difference between subsamples ($p < 0.05$). The boxes represent medians, first and third quartiles. Values greater than 1.5 times the interquartile range away from the median are represented by an empty circle.

TABLE 1 Age of returning spawners from the 1987 and 2016 subsamplings.

	Year of birth			
Age of fish (years)	1987 cohorts	2016 cohorts	1987 subsample (*N*)	2016 subsample (*N*)
4	1983	2012	2 (7%)	2 (6%)
5	1982	2011	21 (73%)	15 (47%)
6	1981	2010	5 (17%)	12 (38%)
7	1980	2009	2 (3%)	3 (9%)

TABLE 2 Results from ANOVA analyses on changes in (a) total length and (b) total weight of returning adult allis shad in the Gironde-Garonne-Dordogne system before (1987) and after (2016) the population collapse.

	Factor	*df*	Sum-of-squares (SS)	*F*	*p*
(a) Total length	Year	1	33253	27.0	**<0.001**
	Sex	1	96503	78.2	**<0.001**
	Year:Sex	1	7104	5.8	**0.02**
	Residuals	129	159153		
(b) Total weight	Year	1	146177	0.9	0.34
	Sex	1	7803941	49.2	**<0.001**
	Year:Sex	1	407001	2.6	0.11
	Residuals	124	19683429		

Note: Bold values represent a significant difference ($p < 0.05$).

analysis revealed the downstream migration patterns of individuals that successfully completed their downstream migration, survived to the adult phase, and returned to freshwater to reproduce. Thus, the downstream migration of these individuals occurred under abiotic conditions sufficiently favorable for them to survive. Our study provides novel insights on the allis shad life history in the GGD system over 30 years.

4.1 | Downstream migration patterns of juvenile allis shad

Water chemistry data for Sr, Ba, Mn in the GGD estuary continuum are rare, especially during the period from summer to early fall, when juvenile allis shad are expected to migrate downstream. However, the fluctuations in otolith microchemistry we observed follow a pattern similar to the water chemistry data available. Sr:Ca ratios in the water remain invariably low and constant across freshwater and fluvial estuary (Daverat et al., 2005). As Sr and Ca generally mix conservatively across estuarine gradients (Walther & Limburg, 2012), the Sr:Ca ratio in the Gironde is expected to exponentially increase as salinity goes from 0 to 15 ‰ and increase more linearly in the marine environment. The Sr:Ca ratio in the otoliths of allis shad followed a similar pattern: first, we measured low and constant Sr:Ca values, then a rapid increase, and finally, high and constant Sr:Ca values. These results suggest that the otolith Sr:Ca ratio can be used to infer movements from the non-saline zone (freshwater and fluvial estuary) to a salty gradient (brackish estuary), to the lower estuary. Ba:Ca ratios in the water are high in freshwater and then drop in the estuarine zones of both the Garonne and Dordogne rivers, around the cities of Portets and Libourne, respectively (Figure S1). The area around these cities coincides with the upstream limit of the TMZ during the period of low water flow in summer and early fall (Etcheber et al., 2011). Thus, the variability in Ba:Ca ratios in the otoliths of allis shad seemed in agreement with the variability observed in the water.

Our results showed three patterns in the juvenile downstream migration of allis shad in the GGD system and revealed important characteristics. First, for both periods of sampling (1987 and 2016), about half of the juveniles did not reach the lower estuary in the first 100 days of their life as they were still in the fluvial or brackish estuary. These findings differ from those of Lochet et al. (2009) who showed that juvenile allis shad exited to the sea at the age of 99 days. This discrepancy might reflect the plasticity of the species as they adapt to temporal variations in environmental conditions. The juveniles in our study migrated during the years 1980 to 1983 and 2009 to 2012, whereas juveniles in Lochet et al. (2008, 2009) migrated downstream in 1997, 1998, or 1999. This discrepancy might also result from a different methodology. Lochet et al. (2008, 2009) investigated downstream migration of returning spawners using otolith Sr:Ca ratios only, whereas our study also included Ba:Ca, allowing us to do a more refined analysis of the migration patterns. Indeed, Macdonald and Crook (2010) observed that the addition of other markers, such as Ba:Ca, improves resolution at finer scales. Second, only 3% of the fish from the 2016 subsample had entered the lower estuary within the first 100 days compared to 13% of the 1987 subsample. The fact that individuals from the 2016 subsample took longer to reach the lower estuary suggests that it might not be favorable for these fish to enter the lower estuary too young/small, possibly because of higher costs of osmoregulation and higher risk of mortality (Zydlewski & Wilkie, 2012). Leguen et al. (2007) exposed juvenile allis shad to moderate salinity (25 ‰) and high salinity (30 ‰) over time, which highlighted a strongest salinity tolerance (low mortality) for older juveniles (> 74 days old). Juveniles from the 2016 subsample in our study might have delayed their entry in a higher salinity area to increase their chance of survival. Finally, we observed a higher proportion of fish reaching only the brackish estuary (pattern B) in recent years (47% and 55% for 1987 and 2016, respectively). This observation might be explained by a marinization of the estuary, as described in Chaalali et al. (2013), with greater values of Sr:Ca and lower values of Ba:Ca in the most upstream part of the estuary during the recent decades. Yet, despite the extension of the salinity front reported in dry years such as 2011 (Schmidt, 2020), quantifying the exact salinity entry distance is difficult due to the several variables to take into account (flow regime, extreme event, year, and migration speed). Juveniles from the 2016 subsample would have reached the salinity front at an earlier age than the ones from the 2000 samples of Lochet et al. (2009) and our 1987 subsample. This assumes that all juveniles started their downstream migration from a similar location, which is probably the case as dams were created in the 1980s (Félix & Félix, 1993), restricting spawning locations to few downstream spawning grounds since then. The downstream migration of juveniles in the 1980s was limited to the period 1980–1983, coinciding with the year of birth of the adults caught in 1987, aged 4 to 7 years old. At that time, fish lifters were not yet built. Consequently, reproduction was mainly restricted to the areas downstream of the dams. The downstream migration period of the 2010 samples was estimated to have occurred between 2009 and 2012. During this time frame, three decades later, a significant decline was observed in the population. The population was estimated by counting individuals on the spawning grounds and those using the fish lifters, showing that the majority of individuals spawned mainly downstream of the dams and that only a tiny percentage went upstream of the dams. For example, all active spawning grounds monitored in 2016 were located downstream of Golfech (MIGADO, 2017). Thus, based on the majority of individuals spawning in the usual downstream spawning areas, it is reasonable to deduce that spawning locations during the period studied (years 1980–2010) were similar.

4.2 | Indirect measurement of changes in oxygen levels in the estuarine zones

Interpreting the fluctuations in otolith Mn:Ca ratios can be complex as this ratio can vary with growth or exposure to hypoxic conditions (Limburg et al., 2015). In a previous study, Atlantic croaker (*Micropogonias undulates*) exposed to constant hypoxic conditions during a controlled laboratory experiment showed an increase in otolith Mn:Ca ratio that did not seem related to endogenous hypoxia stress (Mohan et al., 2014). More recently, Limburg et al. (2015) reported high otolith Mn:Ca concentrations in Baltic Sea cod (*Gadus morhua*) in hypoxic zones, whereas these concentrations tended to decline as the water became more oxygenated. These studies strongly suggest that high concentrations of dissolved Mn in hypoxic zones are incorporated into otoliths and can be used as a tracer for migration in hypoxic zones. Our results suggest that high concentration of Mn:Ca in the otoliths reflects the high dissolved Mn in the TMZ of the GGD system. Juveniles that spent their first 100 days in the fluvial estuary, where most hypoxic conditions of the TMZ occur, showed earlier and wider Mn:Ca peaks in the otoliths and indirectly illustrate the longer and hardest conditions in the TMZ for the 2016 subsample. The lower Mn:Ca peak observed in fish from the 2016 subsample that only reached the brackish estuary might be interpreted as a short stay of the individuals in the highest zone of the TMZ. In contrast, the fish from the 1987 subsample that also remained in the brackish estuary in their first 100 days might have stayed long enough in this high hypoxic zone to incorporate a lot of dissolved Mn but reached a normal oxygen zone more quickly. The duration of stay in the freshwater zone significantly differed between the fish from the 1987 and 2016 subsamples. Fish from the 2016 subsample that reached the brackish estuary in their first 100 days spent less time (18 days on average) in the freshwater zone than fish from the 1987 subsample (32 days on average). From a spatial point of view, the young shad from both subsamples followed the same pattern. However, young shads from the

2016 subsample also encountered the TMZ at a younger age, as early peaks of Ba:Ca and Mn:Ca in the otoliths were observed. Regardless of the pattern of migration, the wider peaks of Mn:Ca in the otoliths of fish from the 2016 subsample strongly suggest that these individuals stayed longer in the TMZ.

Those results align with the expansion and the persistence of the TMZ in the estuarine zones this last decade, as shown by physical and hydrological data (Jalón-Rojas et al., 2015; Lajaunie-Salla et al., 2017). By comparing recent turbidity records with fluvial regime, Jalón-Rojas et al. (2015) defined a "low discharge" (LD) period when the river discharge is <260 $m^3 \cdot s^{-1}$, which is the favorable period for the TMZ installation in the tidal part of the GGD system. The mean discharge for every annual LD from 1960 shows a clear drop of about 24% by the end of the 1980s (Figure 2). Due to the longer and more intense droughts, the TMZ has persisted longer after the 1980s and cannot be flushed as well as 30 years ago (Jalón-Rojas et al., 2015). The lower flow in the Garonne River triggered a feedback loop, based on the increase in mud on the river bed and the amplification of the tidal wave in the tidal river (Jalón-Rojas et al., 2018). This mechanism has led to more intense mud trapping and higher persistence of the TMZ over the past decades (Jalón-Rojas et al., 2021). The modification of the river bed reduced the bottom hydraulic drag, which helps the amplification of the tidal wave, and closed the morphodynamic feedback loop, as reported by Winterwerp et al. (2013) in other European estuaries. Additionally, the rapid expansion of the human population alongside major rivers such as the Garonne River in recent decades has led to an increase in wastewater, which exacerbates the phenomenon of eutrophication, and an extension of turbidity and hypoxia zones (Howarth et al., 2011). Under these conditions, juvenile allis shad from the 2016 subsample experienced harsher conditions than shad from the 1987 subsample.

4.3 | Body condition of juveniles at the entrance of the brackish estuary

We expected a decrease in growth of juveniles before they reached the brackish estuary because of the upstream extension and intensification of the TMZ. Our results partly meet our expectation, as juveniles from the 2016 subsample were slightly smaller than juveniles from the 1987 subsample. In the case of Baltic Sea cod, the intensification of hypoxic zones was predicted to reduce the growth of fish spending longer time in this hypoxic condition (Orio et al., 2022). Recent studies showed slower growth rate and higher mortality of young clown (*Amphiprion percula*) and orange-spotted grouper (*Epinephelus coioides*) exposed to a high concentration of suspended matter (Hess et al., 2015; Wong et al., 2013). In addition to a reduced growth, allis shad could suffer from an increased mortality in the TMZ after the regime shift in the 1980s. Extended periods in turbid water also led to structural changes in the gills (Cumming & Herbert, 2016). Intensive bacterial activity and oxydo-reduction processes associated with turbidity resulted in hypoxia events that decreased fish metabolism. Moreover, productivity is very low in freshwater tidal zones (Whitfield et al., 2012) and in the lowest salinity estuary zones where the turbidity is high (Schmidt et al., 2019). With a spatial and intensity increase of the tidal zone, juvenile shad in recent years would have had to cope with less food available leading to a smaller size than their 1987 subsample. Furthermore, an experimental study by Baumann et al. (2021) showed that exposure to low oxygen and increased temperature decreased the survival rate of allis shad juvenile. However, this hypothesis would need to be addressed with a different approach than examining the otoliths of individuals that survived to adult age.

4.4 | Age, length, and weight of returning spawners

Similar to previous studies, the spawners sampled in 1987 and 2016 were mostly 5 and 6 years old, with females bigger and heavier than males (Aprahamian et al., 2003; Baglinière et al., 2003). Interestingly, the size of spawners differed between the two samplings. Adults caught in 2016 were longer than those in 1987. Despite a longer migration performed by the 2016 subsample before their catch, females were similar in weight in both subsamples, whereas males caught in 2016 were slightly lighter than the ones in 1987. It remains open whether these changes in adult size result from changes in juvenile growth or from altered conditions encountered during their growth phase in the ocean or could partly also reflect a change in age structure of the returning shads. The decrease observed in fitness resulting from lower or similar weight with a greater body length might lower the reproductive success and decrease the quantity and quality of the offspring through parental effects (Audzijonyte et al., 2013; Hixon et al., 2014; Lorenzen, 2016), which may also contribute to the poor performance of the population.

5 | CONCLUSION

This study shed light on the downstream migration patterns of allis shad spawners returning to the GGD system. Our results suggest that spawners collected in 1987 and 2016 used similar tactics while migrating downstream as juveniles. However, juveniles from 2016 subsample took longer than 100 days to exit the lower estuary than expected. In fact, individuals from the 2016 subsample tended to encounter harsher environmental conditions during their downstream migration. The longer time spent in the TMZ and the marinization phenomenon of the fluvio-estuary area between the early 1980s and 2010s might be one of the reasons for the lower growth of juveniles in the 2016 subsample. The impact of the TMZ could become more severe without any action to regulate the fluvial hydrology during dry season. The comparison of migratory patterns before and after the collapse of allis shad, an economically important species now classified as endangered, brings more awareness of the negative impacts of anthropogenic pressures on aquatic ecosystems. Finally, our study confirms that variations in Mn:Ca ratio in otoliths seem to be a good tracer of oxygen deficits (from normoxic to hypoxic zones) in high eutrophic zones, such as estuaries, which are important habitats for migratory fish communities. Long-term monitoring of allis shad migration patterns by collecting data regularly over several years, to identify new trends and strategies, should be implemented, especially in the context of continuous anthropogenic pressures and environmental changes (longer hypoxic and turbid conditions). Additionally, given the ecological context, habitat restoration programmes, especially in the estuarine area that appears to represent a crucial habitat, appear to be a fundamental effort to improve the quality of the habitat improving the well-being of shads and other migratory species.

AUTHOR CONTRIBUTIONS

Supervision: F. Daverat. Conceptualization: E. Boussinet, S. Stoll and F. Daverat. Methodology: E. Boussinet, D. J. Nachón, S. Stoll and G. Bareille. Software & analyses: E. Boussinet, A. Sottolichio, H. Tabouret, C. Pécheyran and S. Stoll. Resources: G. Bareille, A. Sottolichio and D. J. Nachón. Writing - Review & Editing: E. Boussinet, D. J. Nachón, A. Sottolichio, A. Lochet, S. Stoll. G. Bareille, H. Tabouret, C. Pécheyran, M-L. Acolas and F. Daverat.

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