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Thibault Rougier, Patrick Lambert, Hilaire Drouineau, Michel Girardin, Gérard Castelnaud, et al.. Collapse of allis shad, *Alosa alosa*, in the Gironde system (southwest France): environmental change, fishing mortality, or Allee effect?. ICES Journal of Marine Science, 2012, 69 (69), pp.1802-1811. 10.1093/icesjms/fss149 . hal-00841115

HAL Id: hal-00841115

<https://institut-agro-rennes-angers.hal.science/hal-00841115>

Submitted on 15 May 2020

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Collapse of allis shad, *Alosa alosa*, in the Gironde system (southwest France): environmental change, fishing mortality, or Allee effect?

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Rougier, T., Lambert, P., Drouineau, H., Girardin, M., Castelnaud, G., Carry, L., Aprahamian, M., 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 Journal of Marine Science, 69: 1802–1811.

Received 21 March 2012; accepted 26 July 2012.

At the end of the 20th century the allis shad population in the Gironde was the largest in Europe. During the first decade of the 21st century, catches declined dramatically by two orders of magnitude, and a fishery moratorium was implemented in 2008. This deterioration in the status of the stock was confirmed by three independent assessments (abundance of juveniles and of potential and effective spawners). Three hypotheses on the cause of the collapse were examined: (i) an environmental change in freshwater and/or in the estuary; (ii) an increase in marine and/or estuarine mortality; and (iii) the presence of an Allee effect. Changes in flow, temperature, and water quality over the period were inconclusive, but remain a possible causative factor. The instantaneous rate of marine (mean: 0.7 year⁻¹, s.e. 0.1 year⁻¹) and estuarine (mean: 2.6 year⁻¹, s.e. 0.1 year⁻¹) mortalities showed no trend between 1991 and 2003. Nevertheless, the past high estuarine (fishing) mortalities combined with a demographic Allee effect in the reproduction dynamics could explain the population collapse and hamper the stock recovery under the moratorium. This conclusion is, however, tentative as it was not possible to prove the presence of the density-dependent mechanism associated with the demographic Allee effect.

Keywords: Allee effect, allis shad, depensation, Gironde estuary, mortality, population dynamics, spawner–recruitment relationship.

Introduction

Allis shad (*Alosa alosa* L.) is an anadromous clupeid spawning in the higher middle watercourse of rivers. Fish migrate to sea during their first year, where they grow and return to freshwater to spawn at between 3 and 6 years for males and approximately a year later for females (Baglinière *et al.*, 2003).

Allis shad is included in appendix III of the Bern Convention (Ministère des affaires étrangères, 1990) and in Appendix II and V of the European Community Habitats Fauna and Flora Directive (CEE, 1992). Allis shad is classified as ‘least concern’ on the red list of the International Union for the Conservation of Nature (Freyhof and Kottelat, 2008), but was classified as

‘vulnerable’ by the French committee of the IUCN in 2010 (IUCN-France, MNHM, SFI, and ONEMA, 2010). Despite these protective measures, it appears to have been in serious decline for a number of years (Limburg and Waldman, 2009). Its distribution area (originally along the Atlantic coast from Norway to Morocco) has decreased considerably since the middle of the 20th century (Figure 1a) because of overfishing, dam construction, water quality degradation, and deterioration in spawning grounds (Baglinière, 2000; De Groot, 2002; Limburg and Waldman, 2009). Currently, populations of *A. alosa* exist along the northeastern Atlantic coasts in some large rivers of France (Loire, Gironde–Garonne–Dordogne, and Adour) and Portugal (Minho and Lima).

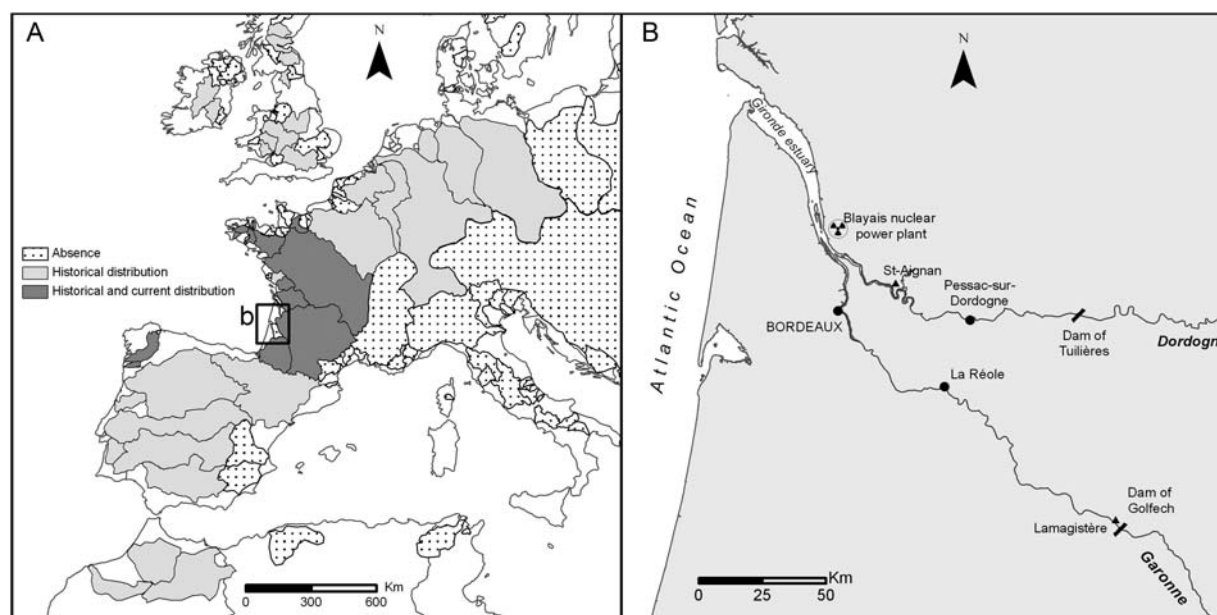


Figure 1. (a) Historical and current distribution of self-sustaining allis shad populations (G. Lassalle, database established by Irstea for the European Environment Agency). The rectangle represents the study area developed in b. (b) Downstream part of the Gironde basin.

Throughout its geographical range, allis shad is harvested by commercial and recreational fisheries in the estuaries and lower sections of rivers during the reproduction migration from marine feeding areas to freshwater spawning grounds (Baglinière *et al.*, 2003). In France, between 1989 and 1997, allis shad landings represented 33.1% of the total diadromous fish production, with an average annual value of €1.3 million (Castelnaud *et al.*, 2001). In 1997, ~20% of the commercial fishers were recorded as fishing for allis shad (Castelnaud *et al.*, 2001), but by 2003 Baglinière *et al.* (2003) indicated that the economic value of allis shad had seriously declined as a result of the elimination or decline of stocks. Today, this species has only local economic importance.

The biology and ecology of allis shad populations have received a great deal of attention in the last 30 years (Mennesson-Boisneau and Boisneau, 1990; Prouzet *et al.*, 1994; Cassou-Leins *et al.*, 2000; Taverny *et al.*, 2000; Véron *et al.*, 2001; Aprahamian *et al.*, 2002; Acolas *et al.*, 2004, 2006; Lochet *et al.*, 2009). Nevertheless few studies have dealt with the population dynamics of this species (Martin Vandembulcke, 1999; Lambert *et al.*, 2001).

Until the end of the 20th century, the Gironde population was the largest allis shad population in Europe (Baglinière, 2000) and was still considered as a reference population (Martin Vandembulcke, 1999). A dramatic drop in landings led to the Gironde Basin's diadromous fish management committee implementing a total moratorium in 2008. This rapid decline in shad populations is not an isolated case and has been observed previously in other river basins (Table 1). The moratorium in the Gironde provides the opportunity for the stock to recover, but there is a need to examine the cause(s) of the population collapse and the formulation of a recovery plan.

In this study, we explore the relationship between stock and recruitment of the Gironde allis shad population. This kind of relationship has been the subject of many studies and controversies but still remains critical for setting biological or management

reference points, especially for semelparous species such as many salmonids (Chaput *et al.*, 1998; Schnute *et al.*, 2000) or allis shad. In the last decades, several authors have dealt with various sources of uncertainty and statistical pitfalls that exist in the estimation of the stock–recruitment model parameters (Walters, 1985; Hilborn and Walters, 1992). Research has been notably hampered by temporal autocorrelation in stock–recruitment data series (Walters, 1990; Korman *et al.*, 1995; Megrey *et al.*, 2005), measurement errors in both stock and recruitment data (Ludwig and Walters, 1981; Walters and Ludwig, 1981), or high variability in spawner–recruit data (Hinrichsen, 2001).

In a stock–recruitment relationship, the Allee effect (Allee, 1931), also known in the fishery literature as the depensation in fish stock productivity (Hilborn and Walters, 1992; Myers *et al.*, 1995; Gascoigne and Lipcius, 2004), can seriously accelerate population decline and drive a population to extinction, or at least heavily hamper its recovery (Walters and Kitchell, 2001). The Allee effect corresponds to a positive relationship between fitness and population size or density (Stephens and Sutherland, 1999), leading to a drop in the productivity when the stock size decreases. It has been recognized as a key pattern in population dynamics that may lead to a rapid decline in population abundance (Courchamp *et al.*, 1999; Stephens and Sutherland, 1999; Walters and Kitchell, 2001; Chen *et al.*, 2002; Gregory *et al.*, 2010).

In this study, we explore three possible, non-exclusive causes for the collapse in the Gironde allis shad population: (i) an environmental change which could affect the reproduction success or the survival of allis shad juveniles; (ii) an increase in mortality during either the juvenile marine phase or the estuarine adult phase; or (iii) the presence of an Allee effect in the population dynamics. To test our assumptions, we (i) analysed environmental datasets to detect whether there had been a regime shift; (ii) used juvenile and spawner abundance estimates to determine any trend in mortality rates; and (iii) used the same abundance estimates to study stock–recruitment relationships.

Table 1. Three examples of shad population decline.

Species	Location	Causes of decline mentioned	Management plan	Current situation	Reference(s)
<i>Alosa alosa</i>	Morocco	Aquatic pollution Hydroelectric impoundments Industrial installations	No	Disappearance	Sabatié and Baglinière (2001)
<i>Alosa alosa</i>	Rhine river	Overfishing Destruction of spawning habitat	No	Disappearance	De Groot (2002)
<i>Alosa sapidissima</i>	Atlantic coast of both the USA and Canada	Overfishing Excessive predation Biotic and abiotic environmental changes Loss of spawning and nursery habitat (water quality degradation, dams, and other impediments)	Multiple management plans since the 1980s including a moratorium (Maryland waters in 1980; Virginia's rivers and the Virginia portion of Chesapeake Bay in 1994)	Absence of recovery or slow recovery (depending on the basin)	Olney and Hoening (2001), ASMFC (2007, 2010)

Material and methods
Study area

The data used in our study were collected in the Gironde estuary and in the lower part of the Garonne and Dordogne rivers (Figure 1b). The Gironde estuary is located in the southwest of France, it is 75 km in length measured from the sea to the confluence of the Garonne and the Dordogne rivers, its width varies from 2 km at the confluence of the Garonne and Dordogne to 11 km at its widest point, and it has a total surface area of 625 km² (measured at high tide). On the Garonne and on the Dordogne, the first barrier is at 270 km (Golfech dam) and at 200 km (Tuilières dam), from the sea, respectively (Figure 1b). In 1987, fish passes together with video counting equipment were installed at these two dams (Travade et al., 1998).

Environmental data

Daily estimates of estuarine water temperature (°C) close to the Blayais nuclear power plant and flow (m³ s⁻¹) of the Garonne (La Réole) and Dordogne (Pessac-sur-Dordogne) (Figure 1b) were provided by EDF (Electricité De France) and the Port of Bordeaux, respectively, between 1991 and 2009. Three statistics were calculated for temperature and flow: (i) the annual mean; (ii) the summer–autumn mean (between July and December) as it corresponds to the period of outmigration of the juveniles; and (iii) the spring mean (between April and June) when the adults are migrating upriver for spawning. Annual estimates of water quality [normalized global biological index (IBGN) AFNOR (1992)] between 1989 and 2007 were provided by the Adour-Garonne water agency for two allis shad spawning areas on the Garonne (Lamagistère) and on the Dordogne (Saint Aignan) (Figure 1b). IBGN is the French standard method used in applied ecology to determine the biological quality of rivers. The index ranges between 0 and 20, with a high index value indicating good water quality. The index is based on the presence or absence of some pollution-sensitive macroinvertebrate taxa. IBGN was used as a proxy for the status and composition of the benthic macroinvertebrate community.

Ordinary least squares-based CUSUM tests (Ploberger and Krämer, 1992) were used to detect the existence of a structural change in the time-series and *F* statistics (Andrews, 1993; Andrews and Ploberger, 1994) to identify the breakpoints in the time period. The analysis was undertaken using R software (R Development Core Team, 2011) and functions ‘efp’, ‘Fstats’, and ‘breakpoints’ of the ‘strucchange’ package (Zeileis et al., 2002, 2003).

Stock–recruitment data

Juvenile abundance estimate (recruitment)

The size of the juvenile population was estimated from trawl surveys carried out between 1991 and 2008 (Pronier and Rochard, 1998; Girardin and Castelnaud, 2010). The survey consisted of four transects in the upper and middle estuary. Each transect consisted of three stations sampled on a monthly basis, one station close to each bank and one in the median axis of the estuary. At each station, one sample was taken at the surface and one on the bed of the estuary. Surface hauls were carried out using two 4.0 × 1.0 m rectangular frame subconical nets, fitted on both sides of the boat. The subconical nets had a stretched mesh of 18 mm in the main section and 1 mm in the terminal section. A dragnet with a 2.0 × 1.2 m frame was used for the

benthic haul. The frame was kept 0.2 m off the bed by runners. The net meshes were identical to those used at the surface. Fish caught were preserved in buffered formalin before being identified and counted in the laboratory (Pronier and Rochard, 1998).

Juvenile density at each station was estimated monthly from the filtered volume calculated using a flowmeter placed at the entrance of each net. The estimate of the size of the juvenile population in the whole estuary was calculated according to Lambert *et al.* (2001), for each month. The first juveniles enter the estuary in July, stay no more than 2 weeks, and no juveniles remain more than 1 year in freshwater (Lochet *et al.*, 2008). Hence for each cohort y (e.g. recruited in year y), the estimate of abundance, $R(y)$, was calculated as the sum of the abundance data between July of year y and June of year $y + 1$.

Adult abundance estimates (stock)

Annual estimate of potential spawners $N_p(y)$, corresponding to the total number of allis shad that enter in the estuary for a reproduction migration (natural mortality is assumed to be insignificant compared with fishing mortality during the migration), was calculated as

$$N_p(y) = N_{(y)} + C(y) \quad (1)$$

where $C(y)$ is an estimate of the number of adult allis shad caught and $N_e(y)$ an estimate of the number of effective spawners.

The catch $C(y)$ was estimated by annual surveys of the fishery undertaken by the French National Research Institute of Science and Technology for Environment and Agriculture (Irstea) until the implementation of the moratorium in 2008 (Chanseau *et al.*, 2005; Beaulaton, 2008). $N_e(y)$ was estimated from video counts of fish migrating through Golfech and Tuileries fish passes, and counts on spawning areas located downstream of these obstacles which were provided by the MIGADO association (Chanseau *et al.*, 2005).

Population dynamics

Simplified age structure

We developed a three-stage model based on the abundance estimates of shad juveniles in the estuary, of potential spawners, and of effective spawners, Δt_{cat} , Δt_{mar} and Δt_{ana} , representing the duration of the juvenile catadromous migration, the duration of the shads' marine phase, and the duration of the anadromous migration of the adults, respectively.

Since Lambert *et al.* (2001) showed that >75% of adult allis shad found in the Gironde estuary were 5 years old [confirming the results of previous studies (Douchement, 1981; Taverny, 1991)], a single age at reproduction of 5 years was adopted. Following Lochet *et al.* (2008), we assumed an average age of juveniles in the estuary (at the end of the catadromous migration) of 4 months ($\Delta t_{cat} = 0.33$ year). The reproduction anadromous migration (from the estuary to the spawning areas) lasts on average 4 months (Lochet, 2006). Hence, we fixed Δt_{ana} to 0.33 year. The average marine phase was thus 4 years and 4 months ($\Delta t_{mar} = 4.33$ years) to be consistent with a 5-year lifespan.

Mortality

The annual mortality $Z_{mar}(y)$ affecting a cohort born in year y during the marine phase (and assumed to be constant throughout this phase) was calculated from the abundance of juveniles $R(y)$ and of potential spawners $N_p(y + \Delta t_{mar})$ (corresponding to the

potential spawners issued from the cohort recruited in year y):

$$Z_{mar}(y) = -\ln[N_p(y + \Delta t_{mar})/R(y)]/\Delta t_{mar} \quad (2)$$

The estuarine mortality $Z_{est}(y)$ for a cohort born in year y corresponds to the mortality during the estuarine anadromous migration. It was calculated using the abundance of potential spawners $N_p(y + \Delta t_{mar})$ and effective spawners $N_e(y + \Delta t_{mar} + \Delta t_{ana})$:

$$Z_{est}(y) = -\ln[N_e(y + \Delta t_{mar} + \Delta t_{ana})/N_p(y + \Delta t_{mar})]/\Delta t_{ana} \quad (3)$$

$Z_{mar}(y)$ and $Z_{est}(y)$ were calculated for each cohort from 1991 to 2003. Average values \bar{Z}_{mar} and \bar{Z}_{est} were then used to calculate the theoretical number of potential ($\bar{N}_p(y + \Delta t_{mar})$) and effective spawners ($\bar{N}_e(y + \Delta t_{mar} + \Delta t_{ana})$) produced by a given number of juveniles (replacement lines of potential and effective spawners; Equation (4) and Equation (5), respectively):

$$\bar{N}_p(y + \Delta t_{mar}) = R(y)e^{-\Delta t_{mar}\bar{Z}_{mar}}, \quad (4)$$

$$\bar{N}_e(y + \Delta t_{mar} + \Delta t_{ana}) = R(y)e^{-\Delta t_{mar}\bar{Z}_{mar} - \Delta t_{ana}\bar{Z}_{est}}. \quad (5)$$

The replacement line of effective spawner corresponds to the situation before the moratorium was implemented, while the replacement line of potential spawner corresponds to the no-harvested situation.

Reproduction

Three spawner–recruit curves in abundance were tested:

a Ricker model (Ricker, 1954)

$$R_{pred,1}(y) = \alpha_1 N_e(y) e^{-\beta_1 N_e(y)}, \quad (6)$$

a Beverton–Holt model (Beverton and Holt, 1957)

$$R_{pred,2}(y) = \frac{\alpha_2 N_e(y)}{\beta_2 + N_e(y)}, \quad (7)$$

and a modified Beverton–Holt model allowing for an Allee effect (Myers *et al.*, 1995; Liermann and Hilborn, 1997)

$$R_{pred,3}(y) = \frac{\alpha_3 N_e(y)^d}{\beta_3^d + N_e(y)^d}. \quad (8)$$

In the Ricker expression [Equation (6)], the parameter α_1 is the slope at the origin, while $1/\beta_1$ represents the maximum recruitment level. In the two Beverton–Holt models [Equations (7) and (8)], the parameters α_2 and α_3 are the asymptote that recruitment approaches at high spawner levels, and the parameters β_2 and β_3 are the level of spawners that produce half of the asymptotic recruitments. In the modified Beverton–Holt model [Equation (8)], d is the Allee effect parameter. For $d = 1$, the model displays the normal Beverton–Holt spawner–recruit relationship. A reduced rate of recruitment at low spawner levels, or demographic Allee effect, occurs for $d > 1$. This depensation parameter d has no straightforward biological interpretation and is not a particularly good measure of the intensity of depensation (Liermann and Hilborn, 1997).

The parameters for the stock recruitment relationship were estimated using the maximum likelihood assuming a lognormal

distribution of recruitment around the mean $R_{pred,k}$ (the recruitment predictions for the corresponding model). When assuming a lognormal distribution of recruitment, maximizing the log-likelihood function is equivalent to minimizing:

$$L_k(\theta_k) = \sum_y [\ln(R_{pred,k}(y) + \lambda) - \ln(R(y))]^2, \quad (9)$$

with L_k the function to be minimized for the model k , θ_k the unknown parameters of model k ($k = 1, 2$, and 3 for Ricker, Beverton–Holt, and modified Beverton–Holt models, respectively), and λ , a constant that was required to avoid convergence problems, fixed to 2.9×10^4 (around half of the observed minimum recruitment value). The minimization was carried out using the ‘optim’ function provided by R software (R Development Core Team, 2011).

The lognormality of process errors has been justified on theoretical grounds (Peterman, 1981; Hilborn and Walters, 1992; Shelton, 1992) and has been shown to be consistent with observed data for salmonids (Bradford, 1995). We deliberately ignored interannual dependence in random noise to simplify the problem formulation (graphical analysis of the model residuals and the first-order autocorrelation coefficient estimation were carried out to check this assumption). The correlation between model residuals and environmental dataserries was checked using Spearman correlation tests.

Standard errors and subsequent confidence intervals were estimated by inverting the Hessian matrix at the optimum.

To compare the model performances, we used the Akaike Information Criterion with small sample bias adjustment (AIC_c) (Burnham and Anderson, 2002) which is more appropriate for small datasets than the traditional Akaike Information Criterion (Akaike, 1981).

Results

Environmental data

Despite interannual fluctuations, flow and temperature between 1991 and 2009 did not show any significant regime shift during the period either for the annual statistic (Figure 2a and b, Table 2) or for the spring and summer–autumn statistics (Table 2). In contrast, ordinary least squares-based CUSUM tests were significant for the IBGN at the two spawning sites, with a structural change in 1995 and 1998 for Lamagistère and Saint Aignan, respectively (Table 2), showing an improvement of water quality for the two sites until 1995 and 1998 and then stabilization (Figure 2c).

Abundance estimates

There was a strong decline in juvenile abundance during the period analysed, with particularly low levels of recruitment (R) from 2003 onward (Figure 3, Table 3). Estimates of both potential spawners (N_p) and effective spawners (N_e) showed a similar decline of $>98\%$ when compared with the middle of the 1990s (Figure 3, Table 3).

Mortality

Estimated marine and estuarine mortality rates [mean values: \bar{Z}_{mar} , 0.7 year^{-1} (s.e. 0.1) and \bar{Z}_{est} , 2.6 year^{-1} (s.e. 0.1)] (Figure 4, Table 4) have shown interannual fluctuations, but no trend was detected during the period analysed (cohort 1991–2003). These average values were used to provide an indicative

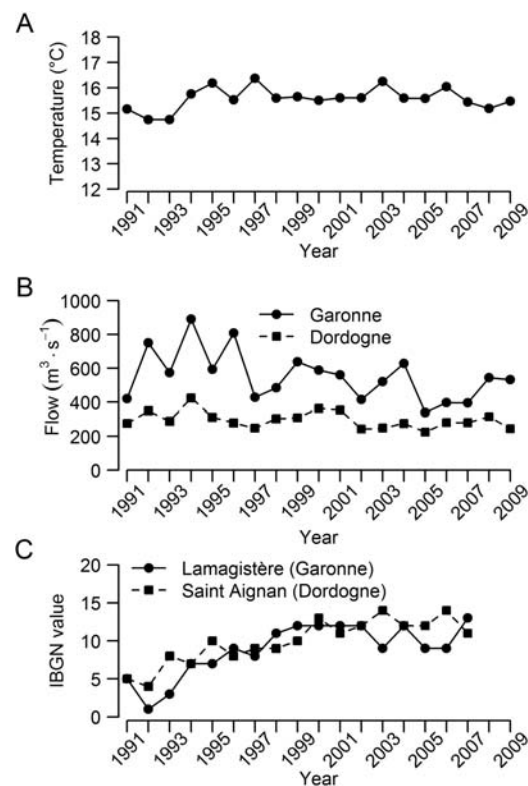


Figure 2. (a) Trend in the mean annual estuarine temperature, 1991–2009. (b) Trend in the mean annual flow in the Garonne and Dordogne, 1991–2009. (c) Trend in the IBGN index (normalized global biological index) at Lamagistère (Garonne) and Saint Aignan (Dordogne) spawning areas, 1991–2007.

Table 2. P -values of ordinary least squares-based CUSUM tests for environmental data for the period between 1991 and 2009.

	Annual mean (January– December)	Spring mean (April– June)	Summer– autumn mean (July–December)
Temperature	0.184	0.197	0.633
Garonne Flow	0.165	0.901	0.115
Dordogne Flow	0.135	0.768	0.0830
IBGN Lamagistère	0.00438* (1995)	–	–
IBGN Saint Aignan	0.00410* (1998)	–	–

Significance ($\alpha = 0.05$) is denoted by an asterisk, and the regime shift is denoted by the year in parentheses.

estimate for the \bar{N}_p (no-harvested situation) and \bar{N}_e (before moratorium implementation) replacement line in the stock–recruitment relationship (Figure 5).

Stock–recruitment

According to the AIC_c values, the Ricker model [Equation (6); $AIC_c = 194.1$], the classic Beverton–Holt model [Equation (7); $AIC_c = 194.1$], and the modified Beverton–Holt model [Equation (8); $AIC_c = 194.5$] have a very similar performance (Table 5). However, the classic Beverton–Holt and the Ricker model were not reliable because of an unlikely high estimate of

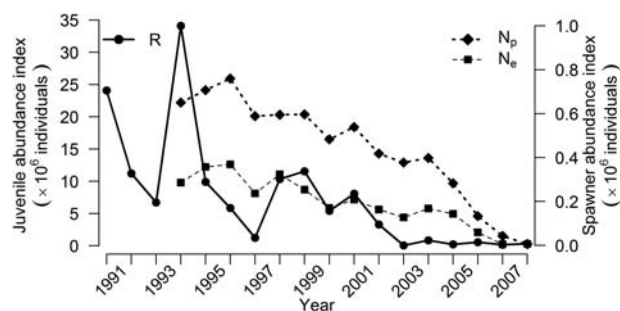


Figure 3. Abundance estimates of juveniles (left y-axis; R) and of potential and effective spawners (right y-axis; N_p and N_e respectively), 1991–2008.

Table 3. Abundance estimates for juveniles (R), and effective (N_e) and potential (N_p) spawners.

Year	R (individuals)	N_e (individuals)	N_p (individuals)
1991	24 073 958	NA	NA
1992	11 217 243	NA	NA
1993	6 728 047	NA	NA
1994	34 120 025	285 918	650 610
1995	9 900 524	357 441	707 070
1996	5 849 145	369 053	759 858
1997	1 235 357	236 733	588 586
1998	10 345 208	323 647	594 676
1999	11 559 592	254 022	596 496
2000	5 400 373	170 777	483 092
2001	8 069 673	208 840	539 305
2002	3 294 436	163 593	418 306
2003	51 297	127 175	377 461
2004	842 125	168 051	398 406
2005	208 224	143 742	282 969
2006	564 378	59 054	133 578
2007	169 394	5619	42 862
2008	308 280	6429	6429

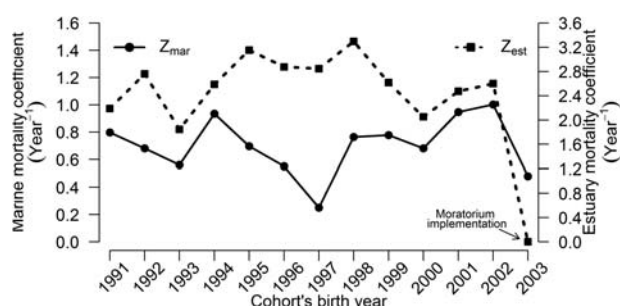


Figure 4. Trend in marine (Z_{mar} , left y-axis) and estuarine mortality rates (Z_{est} , right y-axis), cohorts 1991–2003.

asymptotic recruitment (Table 5) and a poor fit to the data, leaving the modified Beverton–Holt model as the one that best described the population dynamics. Time-series of model residuals do not exhibit a specific pattern, and first-order autocorrelation of model residuals were not significant (Pearson $r = 0.40$, $p = 0.17$). Moreover, no correlations between model residuals and environmental data series were observed (Spearman $\rho < 0.43$, $p > 0.12$ for all series).

Table 4. Estimated instantaneous marine (Z_{mar}) and estuarine (Z_{est}) mortality rates.

Cohort's birth year	Z_{mar} (year ⁻¹)	Z_{est} (year ⁻¹)
1991	0.80	2.21
1992	0.68	2.78
1993	0.56	1.86
1994	0.93	2.62
1995	0.70	3.17
1996	0.55	2.89
1997	0.25	2.85
1998	0.76	3.32
1999	0.78	2.64
2000	0.68	2.07
2001	0.94	2.50
2002	1.00	2.60
2003	0.48	0

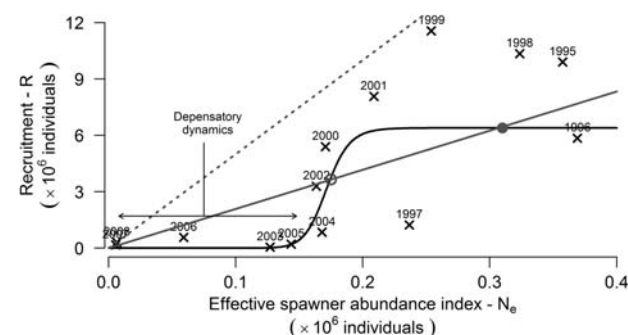


Figure 5. Selected stock–recruitment relationship for Gironde allis shad. The crosses correspond to the observations between 1995 and 2008. The solid curve is the fitted modified Beverton–Holt model [Equation (8)]. The solid grey line is the replacement line for the potential spawners (N_p) stock, and the broken grey line is the replacement line for the effective spawners (N_e) stock. In the no-harvest situation, a stable equilibrium is obtained at an effective spawners level of 0.31 million individuals (filled circle) and an unstable equilibrium at 0.17 million individuals (open circle), while no positive equilibrium point existed when the stock was harvested between 1995 and 2008.

The asymptotic recruitment (α_3) was estimated to be 6.40 [95% confidence interval (CI), 2.27–18.1] millions of individuals. Half the asymptotic recruitments occurs with a spawner abundance (β_3) of 0.172 (95% CI, 0.145–0.203) million individuals. The depensation parameter d was estimated at 19.2 (95% CI, 6.77–54.7); as the lower 95% CI was > 1 , this suggests the presence of a demographic Allee effect in the reproduction process (Figure 5).

The spawner–recruit curve and the two stock replacement lines (N_e and N_p) (Figure 5) show that when the stock was harvested in the estuary, there was no positive equilibrium point. This indicates that the initial phase of the population decline could be the result of overexploitation. In the no-harvest situation, a stable equilibrium is obtained at an effective spawners level of 0.31 million individuals and an unstable equilibrium at 0.17 million individuals. This theoretical approach indicates that in the no-harvest situation, the viability of the stock is threatened when the effective number of spawners is < 0.17 million.

Table 5. Results of model parameter estimates and AIC_c values for the three tested models.

	α		β		d		AIC _c
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	
Modified Beverton–Holt model	6.40×10^6	$[2.27 - 18.1] \times 10^6$	0.172×10^6	$[0.145 - 0.203] \times 10^6$	19.2	6.77–54.7	194.5
Beverton–Holt model	8.73×10^6	X	6.80×10^5	X	–	–	194.1
Ricker model	1.28	0.62–2.63	2.74×10^{-9}	X	–	–	194.1

Parameter estimates cannot be directly compared between models since they do not have the same meanings. Note that the α estimate for the Beverton model and the $1/\beta$ estimate for the Ricker model which correspond to the asymptotic recruitment in millions of individuals are unrealistically elevated. X, the CI could not be estimated because of convergence problems; –, parameter not relevant in the corresponding model.

Discussion

The collapse of the allis shad population in the Gironde basin appears to be the consequence of high estuarine mortalities (due to the fishery) in an initial phase, combined with a depensation effect in the population dynamics that hampers stock recovery. At the current level of abundance, a self-sustaining population may not exist for much longer.

The fitting of a stock–recruitment relationship was not straightforward because of correlations between parameters which may explain the unreliable results generated using classic Beverton–Holt and Ricker models. The addition of a fixed λ in Equation (9) was needed to avoid the strong influence of years with low recruitments on the estimates (since the lognormal error distribution implies low standard deviations for small predicted values). Moreover, the juvenile abundance estimate is less reliable when the population is small, according to scientific experts (M. Girardin, pers. comm.). Moreover, estimating λ as a free parameter gives very similar results (not presented here). Without λ , no Allee effect was detected. However, the fits were graphically very poor (providing a biologically unrealistic high level of asymptotic recruitment), and the algorithm converged poorly (Table 5).

Despite difficulties with estimating the stock–recruitment relationship, ignoring a plausible Allee effect in the stock–recruitment process would be inconsistent with the precautionary approach to manage the Gironde basin allis shad. Consequently, awaiting further studies, the estimated threshold of 0.17 million effective spawners could be considered as a prerequisite before reopening the fishery. Nevertheless, given the uncertainty estimations in replacement line and in the stock–recruitment relationship, this threshold should be used with caution.

The collapse in the population was unlikely to have been caused by a change in marine or estuarine mortalities alone (which were stable from 1995 to 2008); rather, our results suggest a combination of a constant high level of mortalities and a depensation effect as the causes. In the absence of evidence of any anthropogenic mortality at sea, Z_{mar} can be compared with the natural mortality rates available for other shad species. Brown (1972) estimated an instantaneous rate of natural mortality of 0.5 year^{-1} for a freshwater alewife (*Alosa pseudoharengus*) population in Lake Michigan. For eight anadromous populations of the same species in eastern North America, Gibson and Myers (2003) used a low value of 0.4 year^{-1} in their age-structure model for immature alewife while at sea, which was simply derived from Hoenig's (1983) empirical relationship between natural mortality and longevity. For *Alosa fallax*, Aprahamian et al. (2010) estimated sea mortality as 0.67 year^{-1} . In spite of clear ecological and biometrical differences between the species, our value of 0.7 year^{-1} is consistent and close to these values. In contrast, Martin Vandembulcke (1999) used a value of 0.35 year^{-1} in her model

of the Gironde allis shad population. The difference resulted from an underestimation of the size of the juvenile population due to an incorrect assumption about the duration of residency of the juveniles in the estuary. Our method was adjusted following the study of Locket et al. (2009) which demonstrated that allis shad juveniles stay on average only 2 weeks in the estuary, as opposed to 3–6 months assumed by Martin Vandembulcke (1999).

Estuarine natural mortality during the reproduction run is assumed to be negligible compared with fishing mortality. Z_{est} averaging 2.6 year^{-1} is therefore equivalent to an average exploitation rate of 58%. This value is close to those values reported for the same population by Martin Vandembulcke (1999) (67% between 1989 and 1996) and Chanseau et al. (2005) (61% between 1987 and 2001). These values are clearly associated with an overexploitation of the stock.

Modelling the population dynamics suggested evidence of a demographic Allee effect. This effect is associated with an underlying density-dependent process (Stephens et al., 1999). Among many hypotheses proposed in the literature (Berec et al., 2007), we suggest three possible explanations for such a density-dependent effect for the Gironde allis shad population. According to the low level of the population, a first density-dependent mechanism could be mate limitation (Gascoigne et al., 2009) when spawners have difficulties in finding a mate. A second explanation can be found in the spawning behaviour of this species. Allis shad spawn at night in a succession of characteristic behavioural sequences (rapid circular swimming near the surface) with the emission of a splashing known as the bull phenomenon (Cassou-Leins et al., 2000; Acolas et al., 2004). The second density-dependent mechanism could therefore be reproductive facilitation problems when individuals are less likely to reproduce if they do not perceive others reproducing. Finally, considering the schooling behaviour of juveniles and the resulting potential for cooperative antipredator behaviour during their seaward migration, a third possible density-dependent mechanism could also occur if juvenile mortality increases with decreasing stock size. It was not possible to prioritize one of these three mechanisms and we cannot exclude that they act simultaneously, as suggested by Berec et al. (2007).

Sakuramoto (2005) pointed to the importance of environmental factors in the explanation of density-dependent mechanisms commonly associated with stock–recruitment relationships. Our original hypotheses were that (i) a temperature or flow change, or a modification of the composition in the benthic macroinvertebrate community, might have resulted in a decrease in the survival of allis shad juveniles as the diet of the juveniles consists mainly of benthic macroinvertebrates such as worms, chironomids, or molluscs (Cassou-Leins, 1981; C. Buard, unpublished data); or (ii) a change in the flow or temperature of the Garonne or Dordogne could have impacted on the spawning migration. In relation to

temperature, laboratory experiments have shown that critical temperatures for juvenile allis shad are occasionally encountered in the Gironde basin but do not last long enough to have a significant impact (P. Jatteau, pers. comm.). Moreover, our analysis of river flow and estuarine temperature did not show any structural change that might be causing an increase in juvenile mortality, since 2000. Even if the year 2003 was marked by an exceptionally hot and dry summer, the normal climatic conditions in the following years could not simply explain the trend observed since 2003. The detected structural change in IBGN at the two spawning areas seems to reflect an increase in both indices before stabilizing in 1995 (for Lamagistère) and in 1998 (for Saint Aignan). However, it is unlikely that these shifts might be causing an increase in juvenile mortality as they indicate an improvement in water quality and an increase in the species richness of the macro-invertebrate community.

Despite our analysis of environmental data, it is not possible to exclude a population collapse due to environmental change. This is because our environmental data may not be representative of the entire Gironde basin, and local perturbations may have a significant impact on the stock. Also other environmental factors could explain the population decrease [hypoxia or high and persistent turbidity events in the estuary (González-Ortegón *et al.*, 2010)]. A recent study suggests a functional shift in the estuarine ecosystem of the Gironde, with a dramatic increase in the presence of certain marine fish species (notably the meagre *Argyrosomus regius*) in the lower estuary (Pasquaud *et al.*, 2012) which could result in an increase in predation of the shad juveniles. Predation might also be a factor in freshwater as Syväranta *et al.* (2009) have shown that anadromous fish (mainly *A. alosa* and the thin-lipped mullet *Liza ramada*) contributed >50% of the summer diet of European catfish (*Silurus glanis*) in the Gironde.

Currently it is not possible to reject the hypothesis that environmental or ecosystem change is the main factor responsible for the depensation observed in the reproduction dynamics. The precautionary approach leads us to consider the existence of a demographic Allee effect in the population dynamics of the Gironde allis shad, possibly in synergy with an environmental change. The Allee effect implies that the population is doomed, given its current abundance, unless the environment changes in a favourable way. Artificial restocking at a high (and probably unfeasible) level might be a way to support recovery of this stock. Allis shads from neighbouring watersheds (Adour or Charente) may also contribute to the recovery of the stock by colonizing the Gironde basin (natural restocking).

As there was no positive equilibrium point in the population dynamics until the implementation of the moratorium, we conclude that the high estuarine mortality together with a demographic Allee effect caused the Gironde allis shad population to collapse. However, this population has existed for centuries and has been harvested at high exploitation levels since the middle of the 20th century. Considering the population dynamics over the last 15 years, the Gironde allis shad population should never have existed. A regime shift therefore should have occurred at the beginning of the 1990s which probably affected the reproduction process as recruitment levels seem to be higher before that time (Table 3). This putative regime shift could have resulted in a decrease in the allis shad fecundity or a decrease of the basin's carrying capacity due to a functional change in the ecosystem. We cannot exclude the possibility that the establishment of fish passes on the Garonne and Dordogne dams at the end of the

1980s had influenced the dynamics through a stronger Allee effect. More precisely, establishment of fish passes at the end of the 1980s may have increased the surface of available spawning grounds. The density of allis shad may consequently have decreased in each spawning area ('dilution' of mature fish), and thus decreased the mating probabilities.

Currently, population levels are still very low, and the implementation of the moratorium in 2008 was essential to reduce anthropogenic mortality. A critical size of ~0.17 million effective spawners should be a prerequisite before reopening the fishery. An age-structure model could give more reliable estimates of thresholds, as would incorporating environmental data in the model (Arahamian *et al.*, 2010). However, despite the uncertainties around the estimated threshold, it would be unwise to ignore it (Brook *et al.*, 2011). If a demographic Allee effect conclusion is correct, the Gironde allis shad population is in critical danger of extinction, and management measures may not be sufficient (Walters and Kitchell, 2001).

Under the current circumstances, the allis shad population must be supported to ensure the return of the stock to acceptable levels. Extrapolating from the case for the American shad in Chesapeake Bay, the recovery of the populations may take decades. The essential decision to introduce a fishing moratorium should be only the first step in the management of the population. The moratorium should be maintained for at least one generation (4–6 years), with ongoing research to confirm precisely the reasons for the collapse of the allis shad population in the Gironde. According to the tenuous population dynamics at low abundance highlighted in this work and to the documented range contraction of this species (Baglinière *et al.*, 2003), the 'least concern' status (Freyhof and Kottelat, 2008) for allis shad should be reevaluated.

Acknowledgements

We thank the fishers and all the persons who took part in the sampling surveys. We thank Anais Just for her help in map drawing. We thank EDF (Electricité De France), the MIGADO association, the Adour-Garonne water agency, and the 'Grand Port Maritime de Bordeaux' for contributing to the data collection. This study was supported by the 'Région Aquitaine', the European fund for Regional Development (FEDER), the Adour-Garonne water agency and the French National Research Institute of Science and Technology for Environment and Agriculture (Irstea).

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