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X. Chevillot, M. Pierre, A. Rigaud, Hilaire Drouineau, A. Chaalali, et al.. Abrupt shifts in the Gironde fish community: an indicator of ecological changes in an estuarine ecosystem. *Marine Ecology Progress Series*, 2016, 549, pp.137-151. 10.3354/meps11681 . hal-01411213

HAL Id: hal-01411213

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Submitted on 7 Dec 2016

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Abrupt shifts in the Gironde fish community: an indicator of ecological changes in an estuarine ecosystem

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ABSTRACT: For decades, global climate change has directly and indirectly affected the structure and function of ecosystems. Abrupt changes in biodiversity have been observed in response to linear or sudden modifications to the environment. These abrupt shifts can cause long-term reorganizations within ecosystems, with communities exhibiting new functional responses to environmental factors. Over the last 3 decades, the Gironde estuary in southwest France has experienced 2 abrupt shifts in both the physical and chemical environments and the pelagic community. Rather than describing these shifts and their origins, we focused on the 3 inter-shift periods, describing the structure of the fish community and its relationship with the environment during these periods. We described fish biodiversity using a limited set of descriptors, taking into account both species composition and relative species abundances. Inter-shift ecosystem states were defined based on the relationship between this description and the hydro-physico-chemical variables and climatic indices defining the main features of the environment. This relationship was described using generalized linear mixed models on the entire time series and for each inter-shift period. Our results indicate that (1) the fish community structure has been significantly modified, (2) environmental drivers influencing fish diversity have changed during these 3 periods, and (3) the fish–environment relationships have been modified over time. From this, we conclude a regime shift has occurred in the Gironde estuary. We also highlight that anthropogenic influences have increased, which re-emphasizes the importance of local management in maintaining fish diversity and associated goods and services within the context of climate change.

KEY WORDS: Ecosystem state · Fish diversity · Estuary · Generalised linear mixed models · GLMM · Time series · Shift · Inter-shift periods

INTRODUCTION

The structure and function of many of the world's ecosystems have undergone significant environmental and anthropogenic changes (Loreau et al. 2001, Beaugrand et al. 2008, Cloern et al. 2010). Such changes can reduce species diversity, modify predator–prey

interactions, and ultimately erode the resilience of the ecosystem as a whole (Holling 1973, Barnosky et al. 2012). Thus, sudden, non-linear, substantial and temporally persistent changes in ecosystem states (Scheffer et al. 2001, Goberville et al. 2014), also known as abrupt ecosystem shifts (AES; Beaugrand et al. 2014), can be observed. Understanding these

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changes and identifying their causes is particularly important for managing coastal and estuarine zones (Harley et al. 2006), as they provide goods (food, raw materials) and services (support of commercial and leisure activities; Costanza et al. 1997) for 75 % of the world's human population, which is concentrated around these areas (Goodland 1995). Due to this abundance of people and services (Hénocque & Denis 2001), coastal zones are vulnerable to global changes (Barnosky et al. 2012) including both climatic (Hoegh-Guldberg & Bruno 2010) and anthropogenic changes (e.g. climate change associated with anthropogenic modifications: pollution, erosion of biodiversity, land uses, fishing, dredging, chemical pollution, nutrient loading; Henocque 2001, Matthiessen & Law 2002). Estuarine ecosystems are associated with many of the important ecological functions of various taxa, particularly fish (nursery, migratory routes, trophic areas; Elliott & Hemingway 2002) and are also exposed to changing environmental conditions at various temporal and spatial scales (e.g. tidal and flood regimes, seasonal temperature variations; McLusky & Elliott 2004). Detecting, understanding, characterizing, and (if possible) predicting changes in the biodiversity and functioning of estuarine ecosystems in the face of these multiple threats remains both an ecological challenge and a necessity for estuary management.

Lobry et al. (2003) showed that the Gironde estuary, the largest estuarine area in southwest Europe and one of the principal nursery areas for commercially important fish species in the Bay of Biscay (Le Pape et al. 2003), has undergone significant changes in its biodiversity over the last 3 decades. The zooplankton community has been modified with the establishment of exotic species, and there have been significant changes in the number and abundance of species and the ecological niches of native species (Chaalali et al. 2013b). An invasion by an Asiatic shrimp species and extensive modifications to the dynamics of native species have also been detected (Béguier et al. 2012). An emblematic fish species, the smelt *Osmerus eperlanus*, has disappeared from the area (Pronier & Rochard 1998) while another species, the meagre *Argyrosomus regius*, is now frequent (Lobry et al. 2003). Several authors have suggested that the Gironde estuary, like many other estuarine ecosystems (Goberville et al. 2010), is going through a process of 'marinisation'. First termed by David et al. (2007) and later used in several papers (Pasquaud et al. 2012, Chaalali et al. 2013a), it describes the process whereby marine waters flow far upstream into the Gironde basin, and thus into the continent, due to

a drop in river discharge caused by the synergistic effect of reduced precipitation in the catchment area and increased water uptake for irrigated agriculture. The annual mean salinity has significantly increased in all sections of the estuary, though the trend is more perceptible in the downstream sections (Chaalali et al. 2013c). Consequently, this marination has led to a progressive increase in the number of marine fish species in the estuarine area (Pasquaud et al. 2012). Recently, Chaalali et al. (2013a) analysed an environmental and biological dataset encompassing the period between 1979 and 2009, and suggested that the Gironde estuarine ecosystem has experienced 2 climate-related AESs over the last 3 decades. The first was detected at the end of the 1980s (circa 1988) and the second at the beginning of the 21st century (circa 2002). The results of Chaalali et al. (2013a) showed that the principal biological components of the ecosystem (zooplankton and fish community) shifted at the same time as the large-scale hydro-climatic indices and local hydro-physical variables. These results would appear to suggest that the structure and function of ecological communities are subject to significant changes under the influence of local and large-scale hydro-climates. In line with the previous paper by Chaalali et al. (2013a), the purpose of the present study was to describe the structure and dynamics of the fish community of the Gironde estuary during the periods between ecological shifts (i.e. the inter-shift periods).

We describe the biodiversity of the fish community in the Gironde estuary through a multivariate analysis of a faunal dataset. This type of biological diversity analysis, which accounts for both species composition and relative species abundance, is a classical approach in numerical ecology and has been used in numerous studies (e.g. Hare & Mantua 2000, Weijerman et al. 2005). It allows all variables related to the fish community to be combined into a limited set of descriptors; the dynamics of changing biodiversity during the inter-shift periods can then be analyzed based on the relationship between these descriptors and the environment. Environmental data was described using climatic indices, hydrological variables and physico-chemical information. These relationships are defined as the 'state' or 'dynamic regime' of the ecosystem (Scheffer et al. 2001). In our approach, we assume that fish community structure is a good indicator of ecosystem health and function (Karr 1981, Hughes et al. 1998, Delpech et al. 2010). We also consider that the fish–environment relationship is an emergent property of underlying ecological processes shaping fish communities, based on the

theory of ‘environmental filters’ (Tonn et al. 1990, Keddy 1992). Modifications to these relationships may suggest that the ecosystem mechanisms themselves are undergoing changes. This assumption allows us to discuss (1) the occurrence of a regime shift in the ecosystem, (2) the homeostatic capacities of the estuarine fish community, and (3) implications for ecosystem and biodiversity management.

MATERIALS AND METHODS

Study site

The Gironde is a macro-tidal estuary in southwest France (45° 20' N, 0° 45' W; Fig. 1), extending 70 km from its mouth at Royan to the confluence of the

Garonne and Dordogne Rivers. The historical upstream salinity limit (where salinity = 0) used to be situated around the zone of confluence of the 2 rivers during low water periods, but has been moving upstream for the last few years as a result of the marination process (Chaalali et al. 2013c). The current salinity limit during summer is located near the city of Bordeaux, almost 25 km upstream along the Gironde River (authors' unpubl. data) (Fig. 1). The Gironde estuary is highly turbid, with concentrations of suspended particulate matter (SPM) often higher than 500 mg l⁻¹ (Allen et al. 1980, Abril 1999, Sottolichio & Castaing 1999, Sottolichio et al. 2011). Mean freshwater discharge is around 953 m³ s⁻¹ (1960 to 2004; Girardin et al. 2005).

Time series data

The main biological components (especially fish) and environmental parameters of the Gironde estuary have been surveyed regularly for several decades by various ecological monitoring programs (e.g. impact of the Blayais nuclear power plant, Service d'Observation en Milieu Littoral [SOMLIT]). We focused on the middle zone of the Gironde estuary for 2 reasons: it contains the greatest diversity and variations in biological communities including autochthonous, allochthonous and migratory species (Pasquaud et al. 2012, Chaalali et al. 2013b), and the surveys carried out in this area provide the most abundant and diverse range of data (Chaalali et al. 2013a).

Hydro-climatic data

We chose 4 climatic indices defined at the scale of the Northern Hemisphere to study the impact of general climate on fish community structure. The North Atlantic Oscillation (NAO) is the dominant source of variation in the Northern Hemisphere. It describes changes in the position of low atmospheric pressure around Iceland compared to the subtropical Atlantic high pressure center (Hurrell et al. 2001, Marshall et al. 2001). The NAO influences wind intensity and direction, thus regulating quantities of precipitation over the North Atlantic (Hurrell 1995). The East Atlantic Pattern

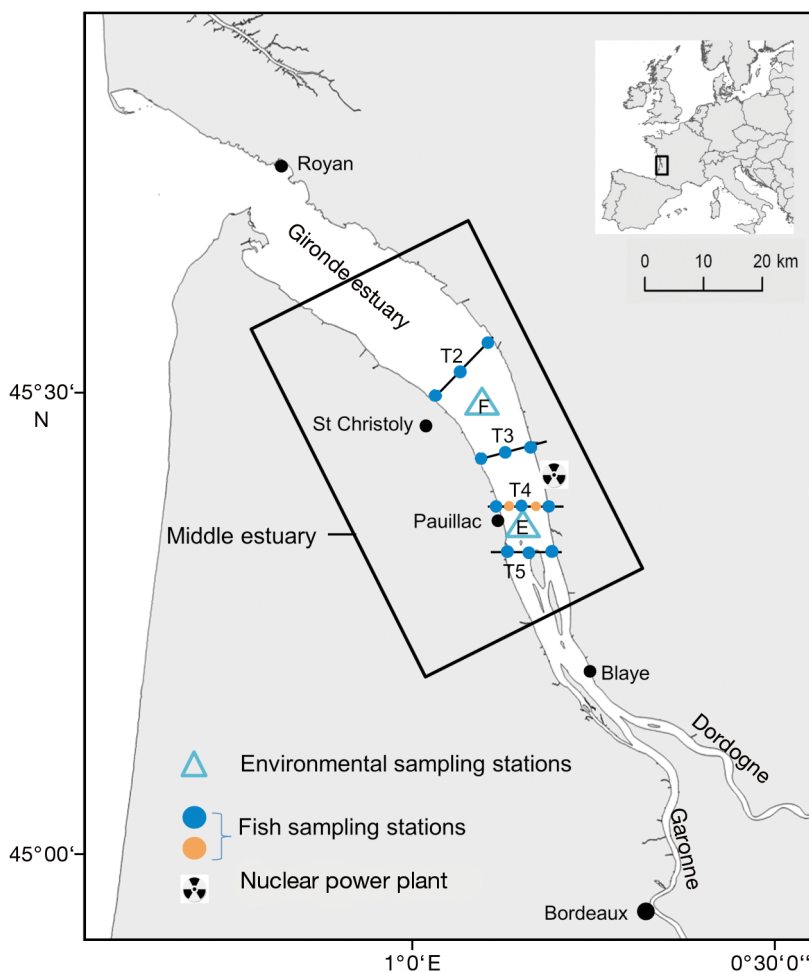


Fig. 1. Study area in the Gironde estuary, southwest France. Blue triangles: sampling stations for environmental parameters; blue and orange circles on transects T2–T5: fish hauls. Orange points are additional stations sampled up to 1989

(EAP) index is similar to the NAO but relates to the subtropical area (Barnston & Livezey 1987, deCastro et al. 2006). This index is an important element to consider because of its strong influence on the environment of western Europe and the French coast (Msadek & Frankignoul 2009). The Atlantic Multidecadal Oscillation (AMO) index describes an oscillation between warm and cold temperature phases of the North Atlantic (Knight et al. 2005). This oscillation has a strong impact on sea surface temperature (SST) at a large scale and a strong influence on the European summer climate (Kerr 2000). The Northern Hemisphere Temperature index (NHT) is a combination of land and SST anomalies over the Northern Hemisphere. Monthly standardized values from 1985 to 2014 (Table 1) were provided for the above data indices by the United States National Oceanic and Atmospheric Administration's (NOAA) Climate Prediction Center (www.cpc.ncep.noaa.gov).

Five variables were used to describe the meteorological influence. Estuary water discharge (flow) data were provided by the Bordeaux Port Authority (Bordeaux Port Atlantique). This variable represents the combined effects of both natural (precipitation and snow melt) and anthropogenic (water use and regulation) influences at the catchment scale. Air temperature (T_{air}) and precipitation (precip) data were provided by Météo France Mérignac (data collected at the Pauillac meteorological station; see Fig. 1). Precipitation data were used as a proxy for precipitation on the catchment area. The difference in trends between local precipitation and river discharge may thus be interpreted, at least partially, as the effect of anthropogenic activity. Local T_{air} com-

bines the effects of large-scale processes and local variations, which can then be compared to the NHT. Wind force (Wind_F) and direction (Wind_D) data were measured at the mouth of the estuary (Royan; Fig. 1) to account for local ocean influence, which can affect marine water mass input and fish larva transport (Huret et al. 2010, Petitgas et al. 2013).

Wind_F, flow, T_{air} and precip data were de-seasonalised by a moving average (order = 13, weight of 0.5 given to the bound values) to account for within-year variability. Wind_D data were transformed into a code that indicates the number of months (per year) for which the northwestern wind (the prevailing wind for the Gironde estuary) was dominant. All data were normalized to scale the units, between 1985 and 2014.

Physico-chemical data

The physico-chemical data used in this study were obtained from ecological monitoring programs for estuarine water bodies, performed both for the Blayais nuclear power plant ecological survey and the SOMLIT monitoring program (INSU-CNRS, <http://somlit.epoc.u-bordeaux1.fr>; Goberville et al. 2010, Savoye et al. 2012). We included the variables water temperature (T_{water}), salinity (S), and SPM; parameters that were assumed to have a direct impact on fish species composition and community structure (Selleslagh & Amara 2008, Pasquaud et al. 2012). Samples were collected monthly from March to November (1 m below the water surface and 1 m above the bottom, at 3 h intervals during the tidal

Table 1. Metadata of variables used in this study. NAO: North Atlantic Oscillation; AMO: Atlantic Multidecadal Oscillation; NHT: Northern Hemisphere Temperature index; EAP: East Atlantic Pattern index. Flow: estuary water discharge; Wind_D: wind direction; Wind_F: wind force; T_{air} : air temperature; Precip: precipitation; S: salinity; SPM: suspended particulate matter

Data	Temporal range	Spatial range	Units	Source
NAO	1985–2014	North Atlantic Ocean	–	United States National Oceanic and Atmospheric Administration's Climate Prediction Center
AMO	1985–2014	Atlantic Ocean	–	
NHT	1985–2014	Northern Hemisphere	°C	
EAP	1985–2014	Atlantic Ocean	–	
Flow	1985–2014	Gironde estuary	$\text{m}^{-3} \text{s}^{-1}$	Bordeaux Port Atlantique
Wind_D	1985–2014	Gironde estuary	No. of mo yr^{-1}	Météo France (Mérignac station)
Wind_F	1985–2014	Gironde estuary	km h^{-1}	
T_{air}	1985–2014	Gironde estuary	°C	
Precip	1985–2014	Gironde estuary	mm m^{-2}	
Water	1985–2014	Middle of Gironde estuary	°C	SOMLIT program
S	1985–2014		–	
SPM	1985–2014		g l^{-1}	

cycle). Two sampling stations (Stns E and F; Fig. 1) were located in our study area.

Data provided from Stns E and F were averaged monthly to integrate tidal and vertical variability. Monthly means of physico-chemical data between

1985 and 2014 were regularized using linear methods to fill in missing data, and de-seasonalised using the above described method (Table 1). All environmental variables are shown in a multi-panel plot (Fig. 2).

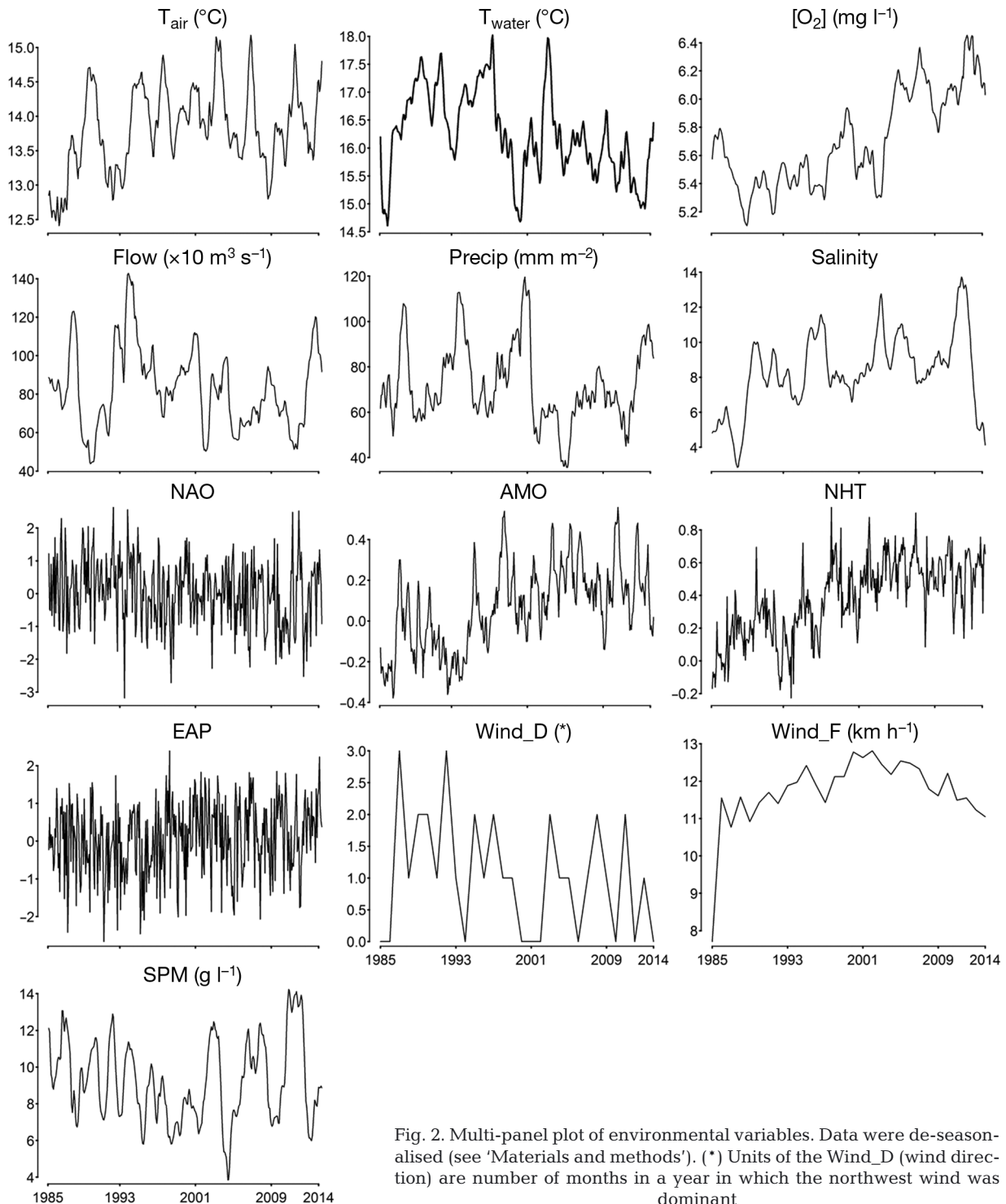


Fig. 2. Multi-panel plot of environmental variables. Data were de-seasonalised (see 'Materials and methods'). (*) Units of the Wind_D (wind direction) are number of months in a year in which the northwest wind was dominant

Fish sampling data

Fish data were collected during surveys conducted by the French Institute for Research in Environmental Science and Technology (Irstea). Irstea has been carrying out these surveys since 1979, with the aim of monitoring small/juvenile fish and shrimps around the Blayais nuclear power plant. The surveys are ongoing (see Lobry et al. 2006, Selleslagh et al. 2012b), and are undertaken at least once each month. The sampling protocol has been slightly modified over time, but without affecting the abundance indices estimates, and has remained unchanged since 1991 (Pronier & Rochard 1998).

Our sampling sites were located along 4 transects (numbered from 1 to 4 downstream to upstream; Fig. 1). Each transect consisted of 3 sites, one close to each bank and one on the middle axis of the estuary. Single samples were taken simultaneously from each site, one from near the surface using two 4 × 1 m rectangular frame nets and another from near the bottom using a dragnet (maintained at 0.2 m above the bed) with a 2.0 × 1.2 m frame. Sampling lasted 5 to 7 min and was performed in the daytime, in the mid-way stage of the flood tide and high tide slack, with the gear being towed against the current (for details see Pronier & Rochard 1998, Lobry et al. 2006, Selleslagh et al. 2012a).

We used data collected between 1985 and 2014. Prior to 1985, too many data points were missing for meaningful analysis of the data. Fish densities at each sampling station, expressed as no. ind. 1000 m⁻³, were averaged monthly from bottom and surface

Table 2. Fish species considered in the present study examining biodiversity in the Gironde estuary. 'Frequency' corresponds to the frequency of appearance in the sampling data (Lobry et al. 2003) between 1985 and 2014

Species	Common name	Species code	Frequency (%)
<i>Alosa alosa</i>	Allis shad	ASH	9.5
<i>Alosa fallax</i>	Twaite shad	TSH	27.0
<i>Anguilla anguilla</i>	Eel	EEL	25.3
<i>Argyrosomus regius</i>	Meagre	MEG	3.0
<i>Dicentrarchus labrax</i>	Seabass	SBS	27.5
<i>Engraulis encrasicolus</i>	Anchovy	ANC	34.8
<i>Gasterosteus aculeatus</i>	Stickleback	STK	21.2
<i>Liza ramada</i>	Mullet	MUL	45.5
<i>Osmerus eperlanus</i>	European smelt	SME	13.44
<i>Platichthys flesus</i>	Flounder	FLO	4.4
<i>Pomatoschistus</i> sp.	Goby	GOB	73.5
<i>Solea</i> sp.	Sole	SOL	3.3
<i>Sprattus sprattus</i>	Sprat	SPT	19.9
<i>Syngnathus rostellatus</i>	Pipefish	PIP	39.8

samples to obtain a single mean value per month and per year (Table 2). Only fish species with a frequency >2% (i.e. number of appearances of that species in samples / total number of samples) (Lobry et al. 2003) were used in this study in order to remain consistent with the previous study by Chaalali et al. (2013a) (Table 2). A total of 17 mo of data were missing over the time period we analyzed, which represents 5% of total fish data. Therefore, data were linearly regularized on a monthly basis to fill in missing data. The data were then de-seasonalised using the methods described above. Data were normalized to reduce the variation in abundance between species.

Data analysis

Fish community structure: standardized principal component analysis

A standardized principal component analysis (PCA; see details in Beaugrand et al. 2002, Chaalali et al. 2013a) was carried out on a fish community matrix (360 months × 14 fish species). This PCA provided an overview of the structure and composition of the fish community through time. A new matrix was created (Fish_PC) from the results of this PCA. This matrix gathered monthly loadings for the first 3 principal components from the PCA (360 months × 3 variables: Fish_PC1; Fish_PC2, and Fish_PC3).

Study of ecosystem states: statistical models

A fish community time series was constructed using Fish_PC1, Fish_PC2, and Fish_PC3. This chronological dataset was analyzed using Chronoclust (Legendre & Legendre 1998) and STARS (Rodionov 2004) in order to detect shifts in the series (see the Supplement at www.int-res.com/articles/suppl/m549p137_supp.pdf). The dates of these shifts were compared with the ones obtained by Chaalali et al. (2013a).

Generalized linear mixed models (GLMMs) were used to describe the relationship between fish community structure (as described by the PCA results) and environmental variables at both local and regional scales. A GLMM was an appropriate tool with which to investigate these relationships because it can account for between-year variability without explicitly examining it (Bolker et al. 2009).

Models were implemented at 2 different scales to address the 2 main goals of this study. The first goal

was to determine if the relationship between environmental and community structure (defined by the 3 principal components of the fish PCA) has remained constant over the last 3 decades. To address this question, a GLMM model was built for each component of the fish community structure (i.e. for each Fish_PCx). A similar approach was implemented at the individual species scale (see the Supplement). All 12 environmental variables (Table 1) were treated as fixed effects. A period factor variable defining inter-shift periods (1985–1988, 1989–2002 or 2003–2014) was also treated as a fixed effect. The same applied to all interactions between the environmental and period variables. A random effect variable (year) was added to account for variability in between-year fish abundance. A forward stepwise strategy was then used to select the best models based on Akaike's Information Criterion (AIC) (Akaike 1973). Models were selected when their AIC score was 2 points lower than the previous model. All possible models were computed; those with the smallest AIC value were selected for each fish-PC.

The models were constructed as follows:

$$y = \alpha + \beta x + p + \beta x \cdot p + u + \varepsilon \quad (1)$$

where y is the Fish_PCx (i.e. the loadings of fish principal component 'x'), βx is the environmental variable, p is the period variable, u is the year random effect and ε is the statistical error. When the interaction between variable and periods was significant, Tukey's HSD test (Tukey 1949) was performed to compare the 3 different inter-shift periods.

The second question involved determining the main environmental drivers during each inter-shift period, and whether they remained consistent throughout the entire time series. In this second case, one GLMM model was built for each component of the fish community structure and for each period (3 Fish_PCx \times 3 periods = 9 models). All 12 environmental variables were included as fixed effects. A year random effect was also added to account for between-year fish abundance variability. The same forward stepwise method (described above) was used.

The models were constructed as follows:

$$y = \alpha + \beta x + u + \varepsilon \quad (2)$$

After preliminary tests, a Gaussian distribution was used with an identity link for each model of the study. The normality and homoscedasticity of the residuals were graphically verified. Two types of model R^2 were calculated using the method developed by Nakagawa & Schielzeth (2013). The first was the marginal R^2 (R^2_m); the second was the conditional R^2

(R^2_c). Both values considered the quality of the model adjustment with and without the random effect, respectively.

All analyses were conducted using the R package 'lme4' (Bates & Maechler 2009, R Development Core Team 2013).

RESULTS

Features and variations of the fish community structure

The structure of the fish community in the Gironde estuary was described using a standardized PCA (Fig. 3). We selected the first 3 principal components (PCs), which accounted for 65.87% of the total variance. The first PC (Fish_PC1) explained 35.86% of the total variance in community structure. It mainly opposed a positively correlated ($r > 0.5$) group of diadromous species (catadromous, C, and anadromous, A) composed of allis shad (ASH), twaite shad (TSH), eel (EEL), smelt (SME) and stickleback (STK), with a group of marine migrants (MMs) (e.g. anchovy, ANC) that were negatively correlated ($r = -0.87$). The second principal component (Fish_PC2) explained 18.11% of the total variance. It was associated with demersal and benthic MM species such as sole (SOL), meager (MEG), seabass (SBS), mullet (MUL), and flounder (FLO), which are catadromous species ($r > 0.4$). All were positively correlated with this component. The third PC (Fish_PC3) explained 11.92% of total variance, and was positively correlated with goby (GOB) and SOL ($r > 0.6$), and negatively correlated with MUL and sprat (SPT) ($r < -0.4$).

The dates of the shifts in analysis of the time series (~1988 and ~2003) were slightly different, but consistent with those previously obtained by Chaalali et al. (2013a) (~1987 and ~2001). We used the new dates in our study.

The panels on the right side of Fig. 3 show yearly loadings for the first 3 PCs. An ellipse surrounds each group of years, which corresponds to the 3 inter-shift periods defined by Chaalali et al. (2013a). We observed that for the 3 individual projection maps, the 3 groups of years were very distinct. The first inter-shift period observed prior to 1988 was characterized by a high proportion of diadromous species (ASH, TSH, EEL, SME, STK, C, and A; Table 2) and a low proportion of MMs, such as ANC. This period was also associated with a high proportion of SOL, FLO and MUL, and to a lesser extent, SBS and MEG. The

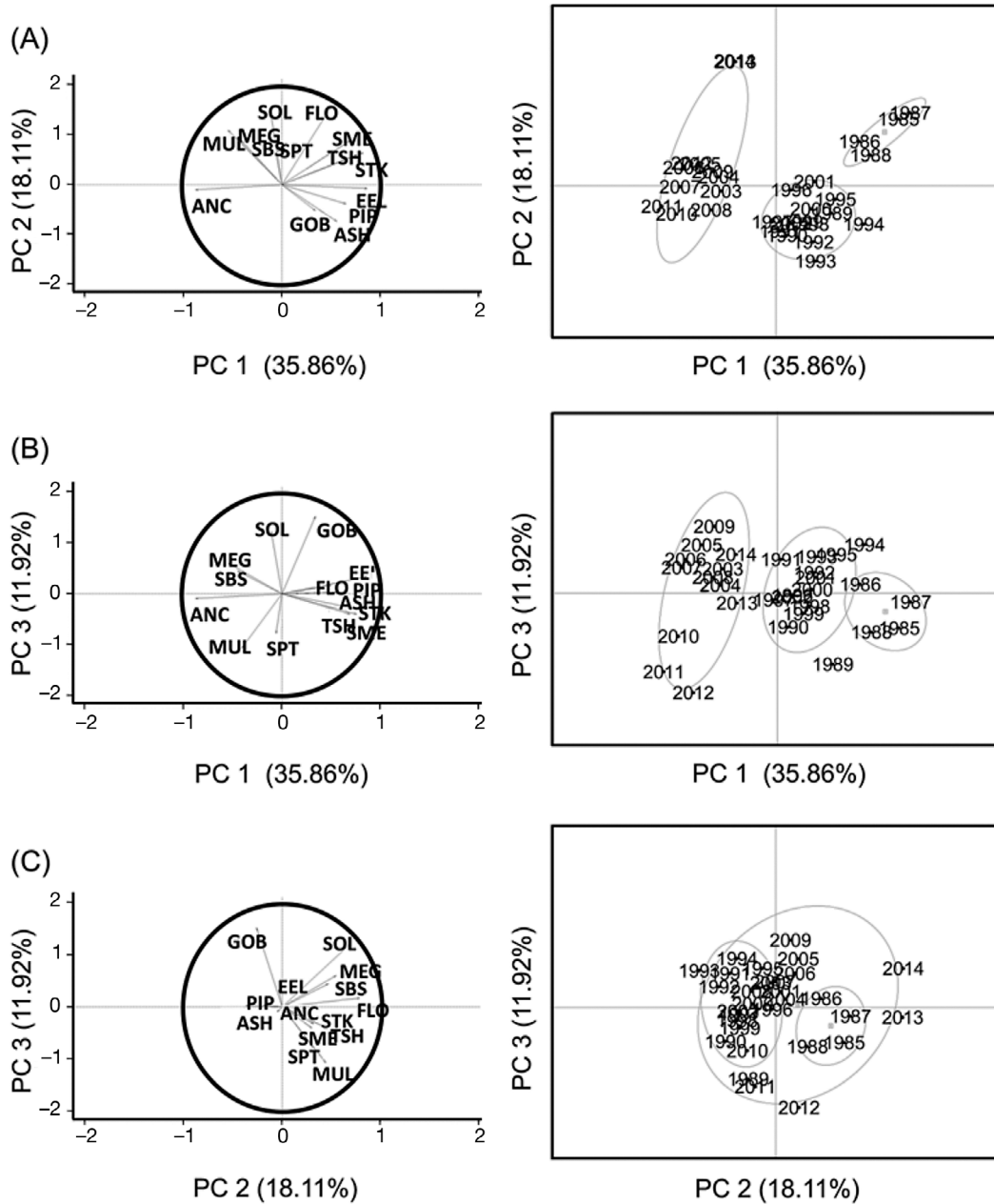


Fig. 3. Standardized principal components analysis on fish data showing (A–C) correlation circles of the first 3 principal components; the corresponding loadings maps are presented in the right panels. In brackets: percentage of explained variance for each principal component (PC) (relative eigenvalues). Species codes are provided in Table 1

third period, after 2002, had an opposite composition with a high proportion of ANC and a low proportion of diadromous species. In the middle period (between 1988 and 2002), the structure of the fish community was more mixed. During this period, the fish community composition was halfway between the initial situation (corresponding to an estuarine community with high proportion of diadromous species) and a MM community

Statistical modelling of the fish community–environment relationship

Constancy of fish–environment relationships

Table 3 shows the results of the 3 GLMM models, computed for each PC across the entire 30 yr time series. All significant variables ($p < 0.05$) are presented, and when the interaction is significant, the

Table 3. Generalized linear mixed model (GLMM) results for the inter-annual study of fish community and environmental drivers in the Gironde estuary. Sig. var.: significant variables (see Table 1 for variable abbreviations). Slope 1 to 3: slope of variable for each inter-shift period (slope 1: 1985–1988; slope 2: 1989–2002; slope 3: 2003–2014); (+) positive slope; (–) negative slope; Tukey's HSD: result of HSD test performed between periods (* $p < 0.05$; *** $p < 0.01$). R^2_c : conditional R^2 ; R^2_m : marginal R^2 (see Nakagawa & Schielzeth 2013). AIC: Akaike's Information Criterion

y	Sig. var.	Slope 1	Slope 2	Slope3	Tukey's HSD	R^2_m	R^2_c	AIC
Fish_PC1	Period	+	–	–	1985–1988 \neq 1989–2002* 2003–2014 \neq 1985–1988*** 2003–2014 \neq 1989–2002***	0.84	0.97	394.25
	Salinity		–					
	SPM \times Period	+	+	–				
	Wind_D \times Period	+	–	+				
	Precip \times Period	+	–	–				
	AMO \times Period	+	–	–				
Fish_PC2	Period	+	–	–	1985–1988 \neq 1989–2002* 2003–2014 = 1985–1988*** 2003–2014 = 1989–2002***	0.66	0.94	219.93
	SPM \times Period	+	–	–				
	Flow \times Period	+	–	–				
	Wind_F \times Period	–	+	–				
	T_{water}		+					
Fish_PC3	Wind_F		+		1985–1988 \neq 1989–2002* 2003–2014 \neq 1985–1988* 2003–2014 \neq 1989–2002*	0.16	0.92	394.53
	SPM \times Period	+	+	–				
	AMO \times Period	–	+	–				
	T_{air}		–					
	Precip		+					

sign of slope of the relationship with the environmental variable is also specified for each period. A total of 6 variables were selected to explain the variation in Fish_PC1 over the last 30 yr: period, S, SPM, Wind_D, precip, and AMO. Four variables explained the fish community structure with an inter-shift period interaction (SPM, Wind_D, precip and AMO). Their slopes changed for at least 2 periods. Tukey's HSD test showed that the interaction between community structure (Fish_PC1) and environmental drivers was significantly different between the 3 periods. A total of 5 variables were selected to explain the variation of the Fish_PC2 during the last 30 yr (period, SPM, flow, Wind_F and T_{water}); 3 variables explained the fish community structure with an inter-shift period interaction (SPM, flow, and Wind_F). Their slopes changed for at least 2 periods. Tukey's HSD indicated that the interaction between community structure (Fish_PC2) and environmental drivers differed significantly between the 2 first periods. Two variables explained the last part of the fish community structure (Fish_PC3) with an inter-shift period interaction (SPM and AMO). Tukey's HSD showed that the interaction between community structure (Fish_PC3) and environmental drivers was significantly different between the 3 periods.

Environmental drivers between shifts

Table 4 shows the results of the GLMMs for each PC during each inter-shift period. Variables that were significantly ($p < 0.05$) related to the composition/structure of the Gironde fish community are presented. Without describing all the models in detail, it can be noted here that environmental variables affecting fish community structure changed from one period to another for all 3 fish components. In some cases, the sign of the interaction changed for a given

Table 4. Generalized linear mixed model (GLMM) results for the inter-shift study of fish community and environmental drivers in the Gironde estuary. Sig. var.: significant variables (see Table 1 for variable abbreviations); R^2_c : conditional R^2 ; R^2_m : marginal R^2 (see Nakagawa & Schielzeth 2013); (+) positive slope; (–) negative slope

	1985–1988		1989–2003		2004–2014	
	Sig. var.	Slope	Sig. var.	Slope	Sig. var.	Slope
Fish_PC1	AMO	+	Precip	–	SPM	–
			Salinity	–		
			AMO	–		
			T_{water}	+		
		$R^2_m = 0.10$; $R^2_c = 0.83$		$R^2_m = 0.14$; $R^2_c = 0.88$		$R^2_m = 0.21$; $R^2_c = 0.87$
Fish_PC2	SPM	+	Flow	+	Wind_F	+
	Flow	+	Wind_F	+		
		$R^2_m = 0.66$; $R^2_c = 0.90$		$R^2_m = 0.23$; $R^2_c = 0.88$		$R^2_m = 0.07$; $R^2_c = 0.81$
Fish_PC3	NHT	+	SPM	+	Wind_F	+
			AMO	+	SPM	–
			Salinity	–	AMO	–
		$R^2_m = 0.07$; $R^2_c = 0.80$		$R^2_m = 0.03$; $R^2_c = 0.91$		$R^2_m = 0.27$; $R^2_c = 0.94$

variable between 2 periods (e.g. AMO for Fish_PC1). The influence of climate variables (AMO) on Fish_PC1 decreased over time in contrast to local hydro-physic-chemical ones (SPM). Fish_PC 2 showed an opposite trend. The results of Fish_PC3 were less clear, but we note that the model had low R^2_m values for the 2 first periods (0.07 and 0.03).

Variables selected in each model were the same as in previous models for the whole time series. The second period, defined as a halfway situation, seem to be more complex in terms of environmental relationships, with more drivers than the other periods. Note that this period was longer than the others.

DISCUSSION

Abrupt shifts in fish composition

Chaalali et al. (2013a) highlighted the occurrence of 2 AESs in the Gironde estuarine ecosystem between the late 1980s and the early 2010s. These authors focused on the co-occurrence of the shifts between climatic indices, environmental variables and several ecological communities, including fish. More specifically, they discussed the synchronicity of the shifts, assuming that the observed ecological changes could be directly linked to abrupt large- and small-scale climatic and physico-chemical changes. However, the aforementioned study did not characterize the changes experienced by the ecological communities, nor did it discuss their ecological significance as related to the use of the estuary by different species.

Our study focused on the fish community structure and composition in the Gironde during the 3 inter-shift periods that have occurred over the last 30 yr, as determined by Chaalali et al. (2013a). We first described changes in the structure of the fish community over those 3 periods, which allowed us to examine changes in use of the estuary by various fish species. By describing the ecological guilds of fish species present during each period, we provided a simple but instructive approach with which to assess changes in the use of the estuary by fish. As mentioned in previous studies (Beck et al. 2001, Gili 2002), estuaries are associated with important ecological functions such as primary and secondary production and nutrient cycling. They also act as essential feeding and nursery grounds for marine species, as well as providing a nursery area and corridor for diadromous fish. Our study shows how the importance of these different estuarine ecological roles has changed over recent decades.

Before 1989: the historical reference

At the beginning of the 1980s, before the first shift that happened around 1988, the fish community in the estuary was characterized by an abundance of diadromous species, such as allis and twaite shads, eel, stickleback, European smelt and flounder—but few marine species. At that time, the nursery function of the area was very important for diadromous fish and marine migrants, and the corridor function was important for diadromous species. Fish composition in the estuary has been defined by a number of authors (Mauvais & Guillaud 1994, Elliott & Dewailly 1995) as being a typical estuarine fish community. Assuming that both climate- and human-induced perturbations have increased since the late 1980s in the system, we hypothesize that this period looks the most like a reference period compared to the others.

Between 1989 and 2002: the marinisation period

The fish community structure associated with this particular period is not clear, evidenced by the central position of these years' loadings on each PCA map. This could be linked to very weak or (on the contrary) quite high variability in the community structure regarding both the ANC–diadromous opposition (on PC1) and MM abundance (PC2). The relative variance of the yearly loadings on the factorial map was significantly higher for this period (results not shown), leading us to assume that the variability in the fish community was fairly high. However, this result is partially biased by the number of years included in this period compared to the others. These results suggest that the same species occurred in the environment, but their abundances tended to oscillate. However, the main structural change in the fish community during this period probably concerned the global (although nonlinear) increase in marine fish species in the middle Gironde estuary. This is consistent with the results of Pasquaud et al. (2012), and other studies that described the 'marinisation' process during this period (e.g. Goberville et al. 2010). On the other hand, this result also corroborates the observations of other authors, who previously observed that diadromous species are sensitive to climate change and increases in temperature (see Lassalle et al. 2009 for a global study, Pronier & Rochard 1998 for smelt, and Cabral et al. 2001 and Hermant et al. 2010 for flounder in the Bay of Biscay and the Tagus). Despite this global trend for diadromous species, we observed a brief recovery of

allis shad abundance in the community during the beginning of this period, stressing that the driving factors are complex for this particular population (Rougier et al. 2012) and are probably specific to each diadromous fish population.

Post-2002 to present day

After 2002, the structure of the fish community appeared clearer. It contained a large proportion of MM species (ANC, SOL, and MEG) and a comparatively low relative abundance of diadromous species. It would appear that since 2002, the function of the Gironde estuary has become more of a nursery area for marine fish than a nursery or feeding grounds/corridor for diadromous fish. The first contribution of this study was to highlight that the fish community of the Gironde estuary has experienced extensive changes over the last 3 decades. The current fish community is clearly and significantly different from that of the past. The estuary has undergone a marination process which, rather than being progressive, continuous, and linear, was characterized by high variability in fish composition for all types of species.

Our approach was spatially constrained by available data and can, to some extent, be viewed as more of a geographical than a hydrological approach. We acknowledge that this approach is insufficient and needs to be addressed in the Gironde but also in other estuarine areas. However, this bias is widespread in the literature. Numerous papers describing estuarine fish biodiversity have been published using these types of dataset. At a European scale, some examples can be found in a non-exhaustive review by Elliott & Hemingway (2002). Focusing on the Gironde, several papers have been based on similar and/or on the same datasets as used here (i.e. Lobry et al. 2003, David et al. 2006) and provided topical results for the biodiversity of the Gironde estuarine. The spatial area on which we focused was the middle of the estuary, and encompasses the 3 main haline zones (from the polyhaline to the oligohaline zone, depending on the season). Considering that these zones are the most important in terms of both fish diversity and abundance in estuaries (Nicolas et al. 2010a,b), we assume that the observations we made at that scale are representative of the overall functioning of the water body. Furthermore, the influence of the sampling area encompasses between 190 and 250 km², which represents up to 60% of the total estuarine subtidal area (excluding intertidal mudflats; Lobry et al. 2006). And finally, the shift in the

salinity limit of the estuary of 25 km upstream in the lower part of the rivers resulted in an overall increase of estuarine area of less than 75 km², which would not significantly modify the spatial representativeness of the monitored area. Considering all these elements, we are confident that the data we used are representative of the fish biodiversity in the estuary.

Changes in fish–environment relationships

As suggested by Tonn et al. (1990) and Keddy (1992), ecological assemblages are the consequence of different environmental filters, which result in certain species being selected from among those present at a regional scale. The changes observed in the structure of the Gironde fish community lead us to question the link between fish community structure and the environment.

The observed fish community structure at a particular time, t , is related both to the environmental context at that time and at some prior time, e.g. during the spawning period or the critical larval phase. The environment was defined here as a combination of large-scale climate indices, local climate, and local hydrological and chemical variables. The results of our models indicate that the environmental factors at time t are significantly correlated with fish structure at the same time t , suggesting that environmental conditions can explain at least part of the variability in fish community structure. The lagged effects are likely embedded in the unexplained part of the models (i.e. the error). These lag effects could also partly explain the differences in the identified years of shifts between Chaalali et al. (2013a) and this study.

Our focus on the inter-shift periods is both relevant and innovative. Indeed, identifying drivers of change in animal communities is an important topic, and the way in which ecological changes—particularly in aquatic systems—are linked to observations and drivers of such changes at larger scales is still a topical issue. We specifically addressed 2 main questions: (1) has the fish–environment relationship, considered here as a proxy of ecosystem functioning, shifted during the last 3 decades in relation to previously defined AESs, and (2) did the driving environmental factors change between the 3 periods? To address the first question, we constructed a set of models calibrated for the entire dataset. The significant effects of the interactions between the environmental variables and period in the GLMM models we constructed indicate that the relationship between fish community structure and the environment is dif-

ferent among inter-shift periods. The slope sign of the relationship differed for at least 1 of the 3 periods for each of the variables selected. Both the intensity and direction of the fish–environment relationship varied from one period to another. The fitted models were particularly significant for PC1 and PC2. The R^2_m values were high (0.84 and 0.66, respectively) and quite close to those of R^2_c (0.97 and 0.94, respectively). As the difference between conditional and marginal R^2 (Nakagawa & Schielzeth 2013) can be viewed as a measure of the random effect (here, year), we can deduce that the fixed effects implemented in the model explain the variability in the fish community much better than inter-annual variability. Thus, it would appear that changes in fish community structure are very well explained by changes in the global, regional, and local environment, as examined in our study.

Our initial results were corroborated by a second set of models, fitted separately for each period. These models highlight that the main environmental drivers of the fish community are different and can act differently from one period to another, both in terms of intensity and direction. The environmental drivers selected in our models are similar to those highlighted in previous studies (Thiel et al. 1995, Beyst et al. 2001, McLusky & Elliott 2004, Selleslagh & Amara 2008)

Whatever the period, the environment acts at both large (i.e. AMO index) and local scales (hydro-physico-climatic variables such as wind direction and force, precipitation, river flow, and SPM). If we consider only PC1 (which explains more than one-third of community structure variability), the main structuring environmental factor during the first period was the large-scale climate-AMO index. During the second period, the state of the community shifted to a more variable transition phase, coinciding with marination. Both climate (AMO and precipitation) and local hydrology (salinity and water temperature) were related to variations in fish biodiversity during this period (1989 to 2002). In the final period (after 2002), the main driver was SPM, reflecting the importance of anthropogenic pressures. Indeed, SPM variations in the estuary are heavily dependent on river water input, and thus the balance between precipitation and water removal upstream (mainly for agriculture). SPM is also related to dredging in the estuary for navigation. Therefore considering this particular result, we can assume that during the third period, fish biodiversity was more sensitive to anthropogenic activity (through SPM and, to a lesser extent, through water flow). This assumption highlights the potential

importance of local management in maintaining fish biodiversity and associated goods and services (Vitousek et al. 1997, Pikitch et al. 2004).

Regime shifts versus environmental homeostasis

Our study was based upon an original association of PCA and inferential models. The PCA was performed in order to combine the numerous fish variables (describing fish densities through time) into a metric of fish biodiversity, and GLMMs were used to analyze this relationship with the environment. In contrast with multivariate methods that account for explanatory variables either by highlighting their correlations with fish variables (e.g. by including supplementary factors in a PCA) or by directly including them in the ordination process of the fish variables (e.g. redundancy analysis), GLMMs allow statistical tests to explore the significance and importance of explanatory variables. Furthermore, we included year as a random effect that accounted for between-year variability when exploring the fish–environment relationship with our models. And finally, by employing a forward stepwise process using AIC as a selection criterion, we selected the most parsimonious models. All of these factors and considerations led us to use a GLMM instead of multivariate methods alone.

By modelling the statistical relationship between fish PCA loadings and environmental factors, we revealed that the environmental factors that explain the variability in fish diversity varied through time. The underlying theoretical framework is that the environmental filters (as defined by Tonn et al. 1990, Keddy 1992) changed over time, resulting in the selection of different local species pools, which responded to different environmental drivers, and thus defined different 'regimes' or 'dynamics states'. Thus, our results support the regime-shift theory (Scheffer et al. 2001, Beaugrand et al. 2014). Indeed, if we consider that the state of the fish community is a good indicator of the state of the ecosystem (Karr 1981, Hughes et al. 1998, Delpech et al. 2010), the fact that fish–environment relationships varied from one period to another would appear to suggest the existence of contrasting ecological 'states', and thus the occurrence of true ecological AES (Beaugrand et al. 2014). This leads us to assume that this succession of homogeneous but contrasting periods is evidence that one or more 'regime shift(s)' (sensu Scheffer et al. 2001, deYoung et al. 2008) has occurred in the Gironde estuarine ecosystem.

This study was based on data similar to those used by Chaalali et al. (2013a). We considered the same breakpoints for the fish community as those authors evidenced for the whole ecosystem. However, our approach differed from that of the aforementioned authors in that we considered 5 yr of data. Also, the PCA computed for fish community data indicated that 2013 and 2014 were atypical compared to other years from the same period. These 2 years were particularly wet compared to the 2004 to 2012 period. Loadings for 2013 and 2014 appear in an intermediate position on PC1 and PC3, between the second and third period. It would be unreasonable to assume the occurrence of a new shift based only on these 2 new years of data. However, they do highlight a high environmental homeostasis within the fish community, which seems able — to a certain extent — to cope with rapid change in its hydrological surroundings. Finally, the rapid responses of fish assemblages to higher freshwater input during 2013–2014 when compared to the lower river inputs during 2004–2012 could suggest that estuary-associated species are well adapted to regime shifts, and are able to adapt accordingly. This particular observation is very interesting in terms of management because it indicates that in spite of the large-scale, deep-rooted impact of climate (via the marinisation process), some hydrologic measures (i.e. regulation of river flow) can also have significant effects on fish biodiversity. This questions perspectives on the evolution of biodiversity and ecosystem function in the estuary, whose dynamics remain very unpredictable despite a lack of concrete confirmation of any form of deep-rooted trend.

Estuarine ecosystems exhibit high environmental homeostasis capacities (Elliott & Quintino 2007). However in the Gironde, the intensity of the shifts and their frequency during the last few years (if the 2012 shift is confirmed) indicates that the dynamics of the system and its stability can be questioned. The fact that there have been so many fluctuations — or, at the very least, significant ecological changes — in such a small time frame (between the 2004–2012 and 2013–2014 periods) would appear to raise questions concerning the viability of the ecosystem.

The structure of the fish community is clearly not stable, and our results suggest that the ecosystem function is also unstable. However, the relationship between diversity and stability is still subject to debate (McCann 2000) and it would seem that identifying this relationship through empirical studies is far from easy (see Rooney & McCann 2012 for a review). This does not, however, allow us to conclude that there has been a true regime shift in the ecosys-

tem, even though its ecological functioning does seem to have shifted over the last 3 decades. A relevant dynamic, process-based model would be necessary in order to address this theoretical question. Despite the fact that the impact of environmental variables on fish communities has been widely addressed in the literature, there is still much work to do in order to account for the effects of possible changes in inter-specific relationships, and to address the synchronization and intensity of those relationships. A holistic modelling approach may be appropriate in developing this line of research.

Acknowledgements. Particular thanks are due to Patrick Lambert for his help and highly relevant comments. We also thank Arthur Rigaud for his participation and James Emery for his English correction. We thank all TRANSECT and SOMLIT team members, technicians, researchers, captains, and crews who have contributed to samplings since 1979. Data since 1997 can be downloaded at <http://somlit.epoc.u-bordeaux1.fr/fr>. These programs were supported by Electricité de France (EDF), the Institut Français de Recherche pour l'Exploitation des Mers (IFREMER) and the Centre National de la Recherche Scientifique (CNRS). This study is part of the TRAJEST project funded by the French Ministry in charge of Environment and the Regional Council of Aquitaine (CPER program).

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