Local changes in copepod composition and diversity in two coastal systems of Western Europe

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ABSTRACT

While long-term monitoring is essential to improve our knowledge of marine ecosystems health, it remains challenging to summarise complex ecological data in order to characterise and understand biodiversity trends. To compile monitoring data across large numbers of species, scientists and policymakers mainly rely on diversity and species richness indices. This task may prove complicated however, as many indices exist and no individual metric undoubtedly emerges as the best overall. Here, using data from zooplankton surveys from 1998 to 2014, we examined year-to-year changes in copepod communities in two littoral ecosystems of Western Europe - the Arcachon Bay and the Gironde estuary - that share similar climate, but with different local ecological processes, especially hydrological conditions. We tested the ability of commonly used α and β-diversity metrics, such as species richness, Pielou's evenness or Jaccard's index, to mirror year-to-year changes in species abundances and we detected a synchronous change in both copepod abundances and α-diversity that took place *circa* 2005 in the two sites. In response to changes in environmental conditions such as nutrients, salinity, river discharge or particulate matter, two opposite biodiversity trends were observed, with a decrease in copepod diversity in the Arcachon Bay but an increase in the downstream part of the Gironde estuary. Although diversity metrics allowed us to well detect trends, the use of multivariate approaches such as principal component analysis provided important information on how and why diversity fluctuates. Our study provides evidence that long-term monitoring programmes must be encouraged for optimising management and conservation actions such as the Marine Strategy Framework Directive and that more local comparative studies need to be initiated for better characterising diversity trajectories at very fine scales at which ecologists often work.

1. Introduction

Coastal marine systems, which are among the most ecologically and economically important ecosystems on the planet (Harley et al., 2006), are known to be highly sensitive to climate fluctuations and direct anthropogenic pressures (Harley et al., 2006; Goberville et al., 2011). The impact of these forcing is not restricted to a particular biological component but extends to all ecological units, affecting marine biodiversity from phytoplankton to top predators (Frederiksen et al., 2006; Chaalali et al., 2013a), leading to alterations in the structure and functioning of coastal systems (Chevillot et al., 2018), with possible ramifications for the terrestrial realm (Luczak et al., 2013). For example, three decades of observation have revealed synchronous climate, environmental and biological community shifts in the San Francisco Bay (Cloern et al., 2010). In the Gironde estuary, large (*e.g.* the Atlantic Multidecadal Oscillation) and regional (*e.g.* annual sea surface temperature and winds) climate-driven processes have induced concomitant changes in hydrological and biological conditions, including abrupt modifications in the composition and structure of pelagic communities (Chaalali et al., 2013a; Chevillot et al., 2016). Concurrently, habitat loss, overexploitation and pollution are major human threats that affect coastal diversity (Duffy et al., 2013; Elahi et al., 2015).

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Global alteration of coastal ecosystems in recent decades has led policymakers to encourage monitoring programs worldwide and estimating biodiversity appears as the most relevant way to measure the status of ecological conditions (Duffy et al., 2013; Elahi et al., 2015). Long-term observations are essential to disentangle natural variations from unusual or extreme events (Lovett et al., 2007), to better capture the inherent variability and stochasticity associated to surveys and ecosystems (Kujala et al., 2013; Beaugrand and Kirby, 2016) and to identify the main forcing that can affect ecosystems (Goberville et al., 2010). To compile monitoring data across large numbers of species and ecosystems, scientists and policymakers often rely on diversity indices (Pereira et al., 2013), easy-to-implement measures of biodiversity for which the effort in calculation and computation is much less cumbersome than multivariate approaches. These indices are also known to be appropriate tools for a rapid and efficient communication between the scientific community, government agencies, funding institutions and the general public (*e.g.* Lovett et al., 2007). However, many metrics exist and none emerges as the best overall (Bandeira et al., 2013) nor combines all different facets of diversity (Salas et al., 2006; Rombouts et al., 2013). Using a range of complementary indices enables to better evaluate both the strengths and weaknesses of the different metrics in detecting changes over time (Rombouts et al., 2013; Loiseau and Gaertner, 2015) or in assessing ecosystem status, when combined with relevant indicator species (Lindenmayer et al., 2015).

Copepods are ubiquitous and play pivotal roles in the functioning of marine systems and in biogeochemical cycles (*e.g.* Richardson, 2008) even in low-diversity ecosystems (Horváth et al., 2014). Major consumers of primary production, detrital organic matter or bacterial production according to environmental conditions, copepods are an intermediate link within the pelagic food web and provide the main pathway for energy from lower to higher trophic levels (*e.g.* fish, marine mammals; Richardson, 2008). By acting on the mean residence time of particulate organic matter in surface waters and on the sinking flux of particulate organic carbon, they significantly contribute to the biological carbon pump (Beaugrand et al., 2010). Highly sensitive to changes in environmental conditions, copepods also rapidly integrate environmental signals over generation time and transfer potential changes to the next generation (Goberville et al., 2014).

Changes in copepod abundances, diversity and community structure can have rapid and major consequences on higher trophic level species. For example, previous studies have paralleled changes in the abundance of *Calanus finmarchicus* or *Pseudocalanus* spp and alterations in commercially exploited fish stocks such as Atlantic cod *Gadus morhua*, Atlantic salmon *Salmo salar* and Atlantic herring *Clupea harengus* (Cushing, 1984; Beaugrand and Reid, 2012; Johnson et al., 2014). Biogeographical shifts in calanoid copepods in the northeast Atlantic have been related to changes in water masses and atmospheric forcing (Beaugrand, 2012). In a Mediterranean coastal bay, taxonomic diversity indices (*e.g.* Simpson's index, Pielou's evenness) have been computed from zooplankton species to determine the effects of anthropogenic impacts (Bandeira et al., 2013; Serranito et al., 2016). This list, far from being exhaustive, sheds light on copepods as ideal candidates for tracking ecosystem changes (Richardson, 2008).

Here, by using data from zooplankton surveys from 1998 to 2014, we examine year-to-year changes in copepod communities (species abundances and taxonomic diversity) in two nearby littoral areas of Western Europe (*i.e.* the Arcachon Bay and the Gironde estuary) that share similar climate conditions but contrasting physical, chemical and hydrological environments. The following questions are addressed: Do copepod communities differ between the two sites and change over time? Are trends in taxonomic diversity apparent and linked to environmental changes? To study changes in species abundances and diversity that took place in the Arcachon Bay and the Gironde estuary over the last two decades, we combine a principal component analyses based-approach and commonly used taxonomic diversity indices that account for the number of species (*e.g.* species richness), the evenness of
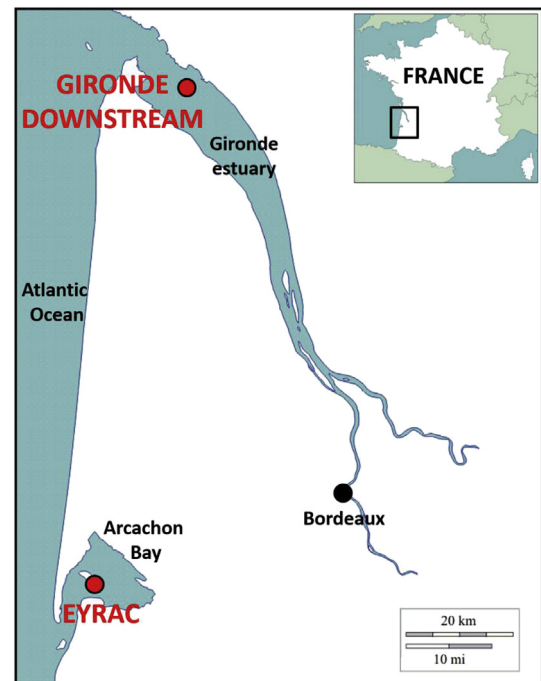

Fig. 1. Map of the Gironde Estuary and Arcachon Bay showing the two studied sites: the Eyrac site and the Gironde downstream site.

abundance distribution among species (*e.g.* Pielou index) and the variability in communities among years (*e.g.* Jaccard index). We then investigate divergences between these two adjacent sites and explore the possible mechanisms that explain diversity trends and species responses to environmental changes.

2. Materials and methods

2.1. Sampling sites

We selected two coastal systems located in the southeast of the Bay of Biscay along the French coast (Fig. 1) to examine year-to-year changes in copepod abundances and diversity.

The Eyrac site (44°40′N, 1°10′W; Fig. 1) is situated in the median neritic waters (salinity: 26.8–33.2; Vincent et al., 2002) of the Arcachon Bay, a temperate mesotidal ecosystem highly influenced by tides and winds (Plus et al., 2009). The Arcachon Bay is open to the Bay of Biscay through two narrow channels (4–5 m depth) separated by several sandbanks. This distinctive narrow entrance has important effects on the water mass exchange between the Bay and the Atlantic Ocean: the tidal prism is equal to 384 million of cubic meters, 64% of the lagoon total volume being flushed in and out at each tidal cycle (Plus et al., 2009). Neritic water masses within the Bay are influenced mainly by freshwater inputs from the Leyre river ($20\,m^3\,s^{-1}$). The Arcachon Bay is therefore quite confined and water residence time is approximately 20 days (Plus et al., 2009). The zooplankton community is described as diverse (Sautour and Castel, 1993), with eurytopic continental and neritic, and autochthonous species, associated to polyhaline water masses (due to low freshwater inputs, typical estuarine species are confined to the inner eastern part of the Bay; Vincent et al., 2002).

The Gironde downstream site (45°31′N, 0°57′W; Fig. 1) is representative of the polyhaline zone of the Gironde estuary (salinity > 30; Chaalali et al., 2013b), which is one of the most turbid and largest macrotidal estuary of Europe. Its large mouth allows important exchanges with the Bay of Biscay (tidal prism: 1.1 to 2.0 billion cubic metres; Jouanneau and Latouche, 1981) and no autochthonous zooplankton species can develop in polyhaline water masses (excepting

meroplankton organisms whose adults inhabit the estuary). Important freshwater inputs from the Garonne and Dordogne rivers (647 $m^3 s^{-1}$ and 342 $m^3 s^{-1}$, respectively) act on the growth of estuarine species in oligo- and mesohaline water masses. In this naturally stressed environment (Dauvin et al., 2009), an increasing gradient of zooplankton diversity is observed from the upstream to the downstream areas (Sautour and Castel, 1995; Chaalali et al., 2013a).

2.2. Biological datasets

Species samples were collected at the two fixed sampling sites (Fig. 1), from 1998 to 2014 by the SOGIR survey ('Service d'Observation de la GIRonde') at the Gironde downstream site (average depth at high tide = 8.2 m) and from 2001 to 2014 by the SOARC survey ('Service d'Observation du bassin d'ARCachon') at the Eyrac site (average depth at high tide = 8 m). A standardised protocol has been established before conducting the surveys, so that sampling is carried out at a monthly scale in both sites, at high tide and in the top first 2 m below the surface using horizontal tow and a standard 200 μm WP2 net (Fraser, 1968). The volume of water filtered through the net was recorded with a Hydrobios digital flowmeter and samples were fixed in 5% seawater/buffered formalin.

In the laboratory, samples were sorted and copepods were counted and identified to the species level as far as possible. Identification was carried out with a stereomicroscope Zeiss Axiovert (200 and 400) and following Rose (1933), the World Register of Marine Species database (WoRMS; www.marinespecies.org) and the taxonomic classification provided by Razouls et al. (2005–2018).

Because rare species may reflect stochastic sampling effects (Poos and Jackson, 2012) and decrease the signal-to-noise ratio (Borcard et al., 2011) only species with a presence > 5% over the period 1998–2014 were retained (Table S1). This procedure, similar to the approach applied in Ibanez and Dauvin (1998), allowed the selection of 17 species in each site, with 13 species being common to both ecosystems (Table 1 and Table S1). For each site, copepod abundances were averaged per year to remove the effect of seasonality prior to further analysis.

2.3. Environmental parameters

Changes in physico-chemical properties of coastal waters at the Eyrac and the Gironde downstream sites were estimated using data from the 'Service d'Observation en Milieu LITtoral' (SOMLIT; somlit. epoc.u-bordeaux1. fr) collected on a bi-monthly basis at sub-surface and high tide (see Goberville et al., 2010 for further details). Here, we focused on seven parameters: temperature, salinity, oxygen, total nitrogen (TN) concentration (computed by summing nitrate, nitrite and ammonium concentrations), particulate organic carbon (POC), suspended particulate matter (SPM) and chlorophyll a. Note that species samples (from the SOGIR and SOARC surveys) and environmental parameters (from the SOMLIT programme) were sampled simultaneously. In addition, we included data on mean river discharges recorded (i) near the Leyre River mouth for the Eyrac site and (ii) in the downstream part of the Gironde estuary (http://www.hydro.eaufrance. fr/, Ministère de l'Ecologie et du Développement Durable).

2.4. Analysis 1: year-to-year changes in coastal copepod abundances (see Fig. S1)

Since species abundance data exhibited skewed distributions, data were transformed using the log10 (x + 1) function (Fig. S2; Jolliffe, 2002). A simple moving average of order-1 was applied to reduce the noise inherent to these data; we therefore highlighted long-term variability while minimising the influence of short-term fluctuations (Legendre and Legendre, 2012).
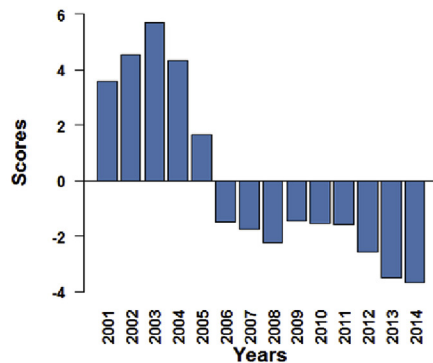
To characterise year-to-year changes in coastal copepod abundances, standardised Principal Component Analyses (PCAs) were performed separately on correlation matrices during the period 2001–2014 for the Eyrac site and 1998–2014 for the Gironde downstream site. For each PCA, we then applied a broken-stick model (Frontier, 1976) to assess the number of principal components (PCs) to retain for interpretation, i.e. the number of PCs with eigenvalues exceeding the expected value generated by a random distribution (King and Jackson, 1999; Legendre and Legendre, 2012). The first two PCs for the Eyrac site and the first three PCs for the Gironde downstream site were thus examined (Fig. 2).

A possible influence of the moving average process was tested by applying a Procrustes procedure (with 999 permutations; Legendre and Legendre, 2012): by comparing two matrices that describe the same entity (here copepod abundances), the Procrustes test statistically evaluate whether the two multivariate datasets (i.e. before and after application of the moving average procedure) can be interchanged in the analysis (Peres-Neto and Jackson, 2001; Legendre and Legendre, 2012). Because of dependency on meteorological conditions during sampling (e.g. intense winds), the number of samples per year may vary over time (Fig. S3), potentially leading to bias in the temporal comparison of annual abundances (Beaugrand and Edwards, 2001). To examine how sampling effort may influence the characterisation of changes in coastal copepods, we considered a decreasing number of months to calculate annual means (from 10 months - i.e. the maximum of samples available for the more well-documented years; Fig. S3 - to 6 months, following a bootstrap procedure with 999 permutations; Davison and Hinkley, 1997) and we re-performed standardised PCAs on each re-computed dataset. We then calculated Spearman correlation coefficients between the first two (for the Eyrac site) and three PCs (for the Gironde downstream site) (Table S2).
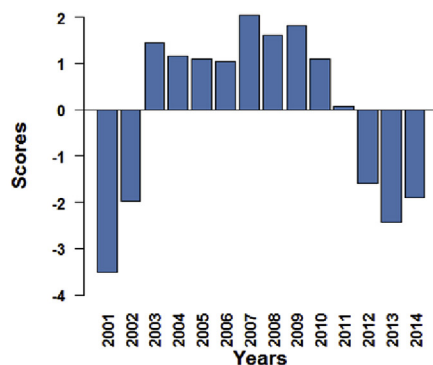
Results from these two sensitivity analyses confirmed that our conclusions were neither highly affected by sampling effort (all years were therefore retained for analysis) nor the moving average procedure (Procrustes correlation = 0.821, p ≤ 0.001 for the Eyrac site; Procrustes correlation = 0.808, p ≤ 0.001 for the Gironde downstream site).

Table 1
Results from the standardised PCAs performed on copepod abundances. The first two eigenvectors (for Eyrac) and the first three eigenvectors (for Gironde downstream) are included and show the contribution of each species to the principal components. Values in bold were superior to |5.88|.

Species	Eyrac		Gironde downstream		
	PC1	PC2	PC1	PC2	PC3
Acartia bifilosa	–	–	5.22	−3.81	**13.15**
Acartia clausi	4.85	−2.87	**−7.25**	0.68	−0.11
Acartia discaudata	−0.04	**26.49**	−0.03	1.7	**20.96**
Acartia tonsa	–	–	−1.55	**−12.56**	2.91
Calanus helgolandicus	0.94	**−13.07**	**11.49**	−0.08	0.27
Centropages hamatus	5.76	−4.15	**−9.37**	**9.31**	0.75
Centropages typicus	3.12	**6.66**	4.58	**13.42**	−0.32
Clausocalanus sp	**8.27**	1.81	–	–	–
Cyclopinoïdes littoralis	**7.66**	−4.52	–	–	–
Ditrichocorycaeus anglicus	**8.27**	2.03	0.19	0	**−20.76**
Eurytemora affinis	–	–	**8.11**	−0.66	**10.36**
Euterpina acutifrons	**−7.47**	0.1	−0.85	**14.25**	**8.59**
Isias clavipes	**9.07**	−0.13	–	–	–
Oithona sp	**−9.42**	0.46	1.42	**16.15**	−0.1
Oncaea sp	−2.09	**−18.01**	**16**	0.51	0.01
Paracalanus parvus	**8.59**	−0.21	−0.92	**9.82**	4.46
Parapontella brevicornis	4.32	**14.4**	–	–	–
Pseudocalanus elongatus	**7.62**	2.04	**−9.31**	−0.68	**7.62**
Pseudodiaptomus marinus	–	–	**8.82**	**8.93**	−3.51
Temora longicornis	5.55	1.12	−2.17	**7.29**	0.6
Temora stylifera	**6.96**	1.92	**−12.73**	0.14	−5.51

EYRAC

a) PC1 : 57.7%
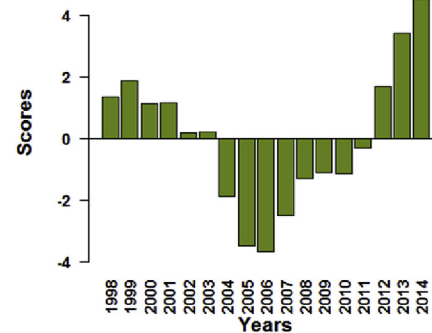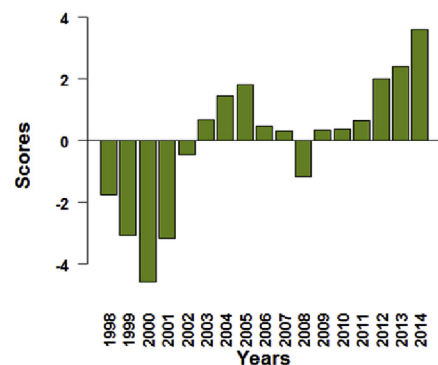

b) PC2 : 19%

GIRONDE DOWNSTREAM

c) PC1 : 28.6%

d) PC2 : 25.9%
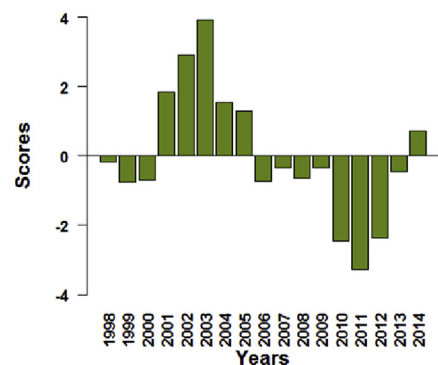

e) PC3 : 19.6%

Fig. 2. Year-to-year changes in pelagic copepod abundances in the two coastal systems calculated from a standardised principal component analysis (PCA). (**a-b**) First two principal components (PCs) calculated from the standardised PCA performed on copepod abundances in Eyrac. (**c-e**) First three principal components (PCs) computed from the standardised PCA applied on copepod abundances in the Gironde downstream site.

2.5. Analysis 2: year-to-year changes in taxonomic diversity of coastal copepods (see Fig. S1)

Changes in alpha (α; Whittaker, 1972) and beta (ß; Anderson et al., 2006) diversity of coastal copepods were assessed by using 13 easily interpretable diversity indices - among the most commonly used in the literature - and known to be pertinent to a wide range of biological compartments and ecosystems (Lamb et al., 2009; Bandeira et al., 2013; Magurran, 2013). Because β-diversity indices allow to take into account the identities of all species, they are regarded as complementary to α-diversity metrics which ignore species identity (e.g. species richness; Baselga and Orme, 2012).

To compute α-diversity, 4 indices (i.e. species richness, Odum,

Margalef and Menhinick indices) were used as measures of the number of species in a community, 2 indices (reciprocal Berger-Parker and Pielou's evenness indices) as a measure of the evenness (i.e. indices of the community structure; Peet, 1974; Legendre and Legendre, 2012; Bandeira et al., 2013) and 3 heterogeneous indices (reciprocal of un-biased Simpson, McIntosh and corrected Shannon-Wiener indices; Heip et al., 1998; Chao and Shen, 2003) that combined the number of species and evenness (Mérigot et al., 2007). Beta diversity, i.e. the variability in species assemblages among years in a given area (Anderson et al., 2006), was calculated using the Jaccard's dissimilarity index and the partitioning approach (Baselga and Orme, 2012) to evaluate the nest-edness (i.e. changes in assemblages' composition caused by the gain/loss of species between t and t+1) and turnover components (i.e.
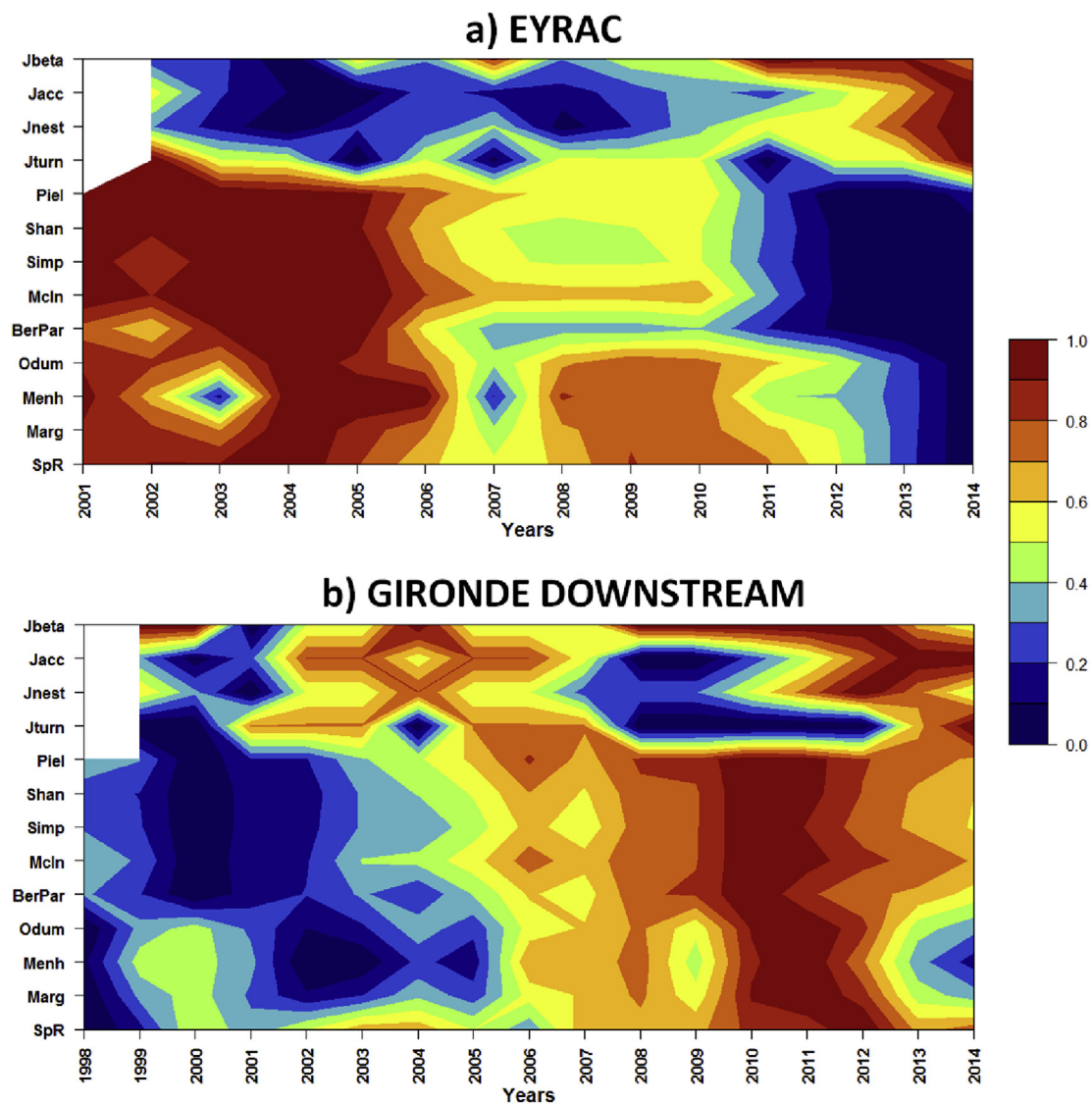
Fig. 3. Diversity indices calculated for pelagic copepod species in (**a**) Eyrac (2001–2014) and (**b**) Gironde downstream (1998–2014). SpR: Species Richness, Marg: Margalef indice, Menh: Menhinick indice, Odum: Odum indice, BerPer: Berger-Parker indice, McIn: McIntosh indice, Simp: Simpson indice, Shan: Shannon indice, Piel: Pielou's eveness derived from Shannon indice, Jturn: turnover component of Jaccard indice, Jnest: nestedness component of Jaccard indice, Jacc: Jaccard indice, Jbeta: beta ratio. For visual comparison indices were normalised between 0 and 1. White areas correspond to missing values.

changes in assemblages' composition caused by species replacement processes between t and t + 1). The β-ratio estimated the contribution of each component (*i.e.* species replacement *vs.* nestedness; Baselga and Orme, 2012).

Diversity indices were calculated for each site, at an annual scale and on non-logged abundances. For visual comparison, taxonomic diversity indices were normalised between 0 and 1 (Fig. 3). The major changes in diversity (Fig. 4) were then extracted by performing the same methodology than that applied on copepod abundances (see '*Analysis 1: Year-to-year changes in coastal copepod abundances*').

2.6. Analysis 3: relationships between changes in copepod abundances, taxonomic diversity and environmental conditions (see Fig. S1)

Relationships between changes in copepod abundances and in taxonomic diversity were investigated using a bi-plot approach which displays associations graphically (Fig. 5; Goberville et al., 2014). For each site, the PCs retained from the PCAs performed on species abundances were represented in a plane to display similarities/dissimilarities among years. For each year of the period 2001–2014 (Eyrac

site, Fig. 5a) and 1998–2014 (Gironde downstream site, Fig. 5b–c), the value of changes in taxonomic diversity (*i.e.* results from the PCA performed on indices) was assigned and represented by a colour scale; the blue (red) gradient corresponds to high negative (positive) values. By characterising each year by reference to changes in copepod diversity, this representation showed time series of responses of each site, *i.e.* changes in copepod communities over the time period.

To characterise the main year-to-year changes that took place in physical, chemical and hydrological conditions at each site, we followed the same procedure than that applied to identify changes in copepod abundances and diversity (see 2.4 and 2.5): (1) a one-year moving average on annual means, (2) a Procrustes test and (3) a PCA performed on logged data. Pearson correlation analyses (Table 3) were then performed between the first PCs obtained from Analysis 1 and 2 and the first two PCs calculated from the PCA applied on environmental parameters at each site. Following the procedure recommended by Pyper and Peterman (1998), probabilities were computed and corrected to account for temporal autocorrelation: Box and Jenkins (1976) autocorrelation function modified by Chatfield was calculated and applied to adjust the degree of freedom using Chelton (1984) formula.
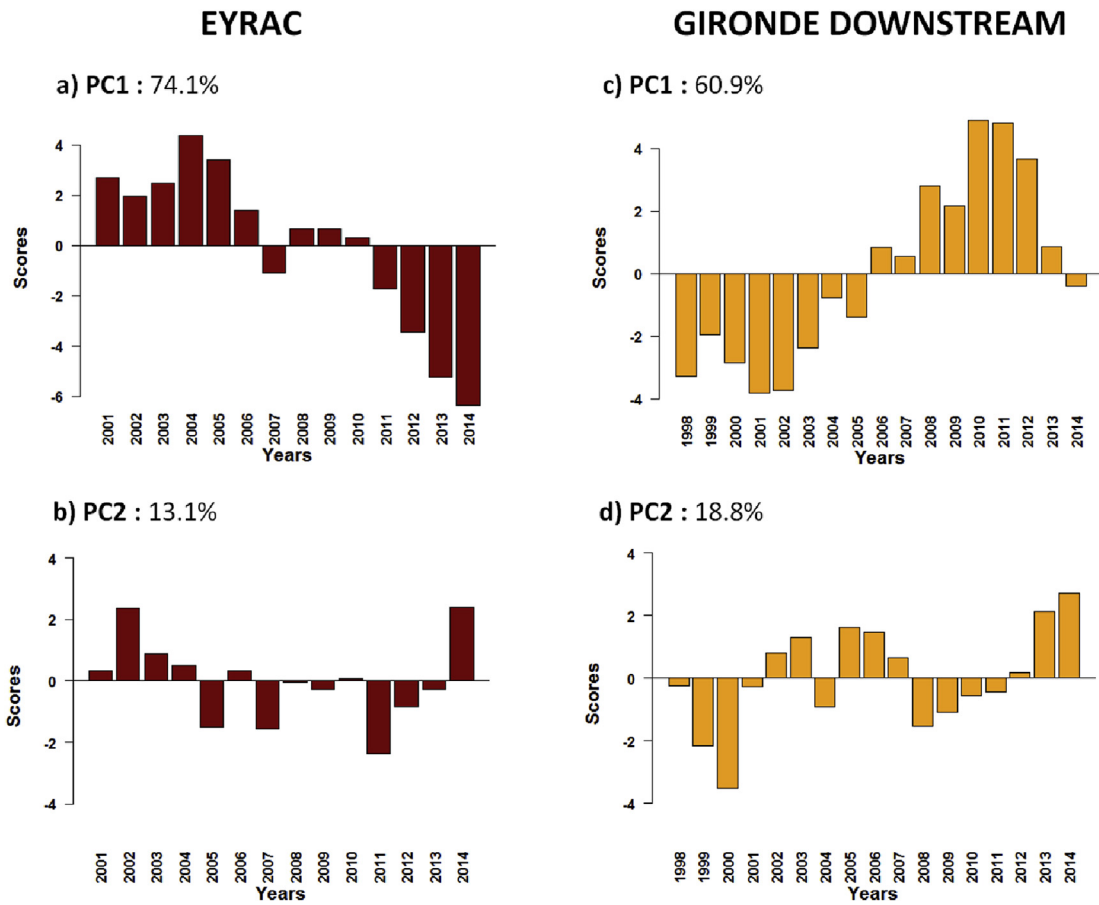
Fig. 4. Year-to-year changes in coastal copepod taxonomic diversity in the two coastal systems. (**a**) First and (**b**) second principal components (PCs) calculated from the standardised PCA performed on diversity indices in Eyrac. (**c**) First and (**d**) second principal components (PCs) calculated from the standardised PCA performed on diversity indices in the Gironde downstream site.
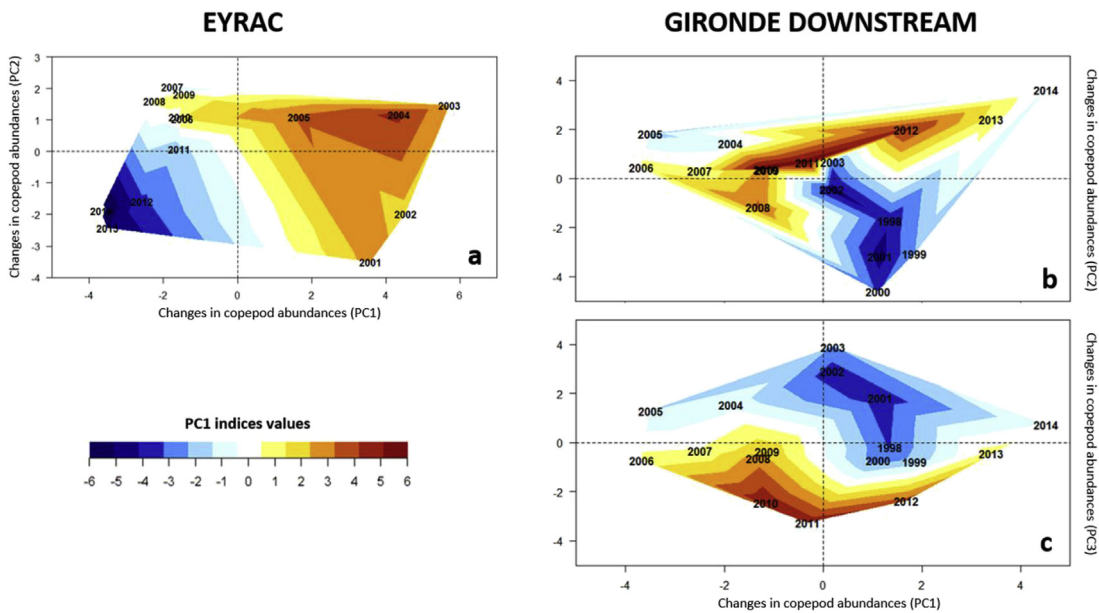

Fig. 5. Relationships between changes in coastal copepod diversity and changes in coastal copepod abundances for the Eyrac site (left panel) and the Gironde downstream site (right panels) (a) Relationships between changes in diversity (first PC of the PCA performed on taxonomic diversity indices) and the first two PCs of the PCA performed on coastal copepod abundances at the Eyrac site. (b–c) Relationships between changes in diversity and the first and (b) second or (c) third PC from the PCA performed on coastal copepod abundances at the Gironde downstream site. The values of changes in measures of diversity were interpolated and represented by the colour scale (see Analysis 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Results from the standardised PCAs performed on taxonomic diversity for each site. The first two eigenvectors show the contribution of each index to the principal components. Values in bold were superior to |7.69|.

Indices	Eyrac		Gironde downstream	
	PC1	PC2	PC1	PC2
Species richness	**8.8**	−0.65	6.31	1.28
Margalef	**9.22**	−0.8	**10.81**	−1.62
Menhinick	5.83	−0.37	**8.72**	−4.21
Odum	**9.19**	−0.81	**10.77**	−1.78
Berger-Parker	**8.85**	0.56	**10.73**	2.27
McIntosh	**9.59**	0.72	**10.78**	4.48
Simpson	**9.42**	1.06	**11.31**	2.42
Shannon	**9.27**	2.03	**11.46**	2.72
Piélou's eveness	**9.01**	2.51	**10.56**	4.23
Beta ratio	−5.83	**−17.89**	3.87	**−14.56**
Jaccard's dissimilarity index	−6.03	**20.7**	−0.29	**31.63**
Turnover	−0.49	**51.5**	−2.71	**27.41**
(component of Jaccard's dissimilarity index)				
Nestedness	**−8.46**	0.39	1.69	1.4
(component of Jaccard's dissimilarity index)				

3. Results

3.1. Year-to-year changes in coastal copepod abundances

3.1.1. The Eyrac site

Year-to-year changes in PC1 of the PCA performed on copepod abundances at the Eyrac site (57.7% of the total variability) showed high values of the component from 2001 to 2005, followed by a decrease in the trend and negative values from 2006 onwards (Fig. 2a). Examination of the first eigenvector indicated that species such as *Isias clavipes*, *Paracalanus parvus* and *Ditrichocorycaeus anglicus* were positively correlated with the component, corresponding to a decrease in their abundance from the mid-2000s onwards (Table 1, Fig. S4a). *Oithona* spp. and *Euterpina acutifrons* were strongly negatively related to changes in the first PC, showing an increase in their abundance from 2006 to 2014. The second principal component (19% of the total variability) exhibited periods of negative (2001–2002 and 2012–2014) and positive (2003–2011) anomalies (Fig. 2b). The study of the second eigenvector revealed that an increase in the abundance of *Acartia discaudata* and *Parapontella brevicornis*, and to a lesser extent *Centropages typicus*, occurred between 2003 and 2011, while a reduction in the abundance of *Calanus helgolandicus* and *Oncaea* spp. was observed.

3.1.2. The Gironde downstream site

The first PC of the PCA performed on copepods at the Gironde

downstream site (28.6% of the total variability) showed periods of positive (1998–2003 and 2012–2014) and negative (2003–2011) anomalies (Fig. 2c). Inspection of the first eigenvector indicated that *Oncaea* spp., *C. helgolandicus* and, to a lesser extent, *Pseudodiaptomus marinus* and *Eurytemora affinis* were positively related to PC1, corresponding to a reduction in their abundance between 2003 and 2011 (Table 1, Fig. S4b). In contrast, the abundance of *Temora stylifera*, *Centropages hamatus*, *Pseudocalanus elongatus* and *Acartia clausi* increased. After a period of strong negative anomalies (1998–2003), year-to-year changes in PC2 (25.9% of the total variability) mainly expressed positive anomalies from 2003 (Fig. 2d). *Acartia tonsa* was the only species strongly negatively correlated with this change, revealing a constant decline. Species such as *Oithona* spp., *E. acutifrons* or *C. typicus* were positively related to PC2, corresponding to an increase in abundance over the last decade. Year-to-year changes in the third PC (19.6% of the total variability) displayed pronounced positive values from 2001 to 2005, at the time the component showed negative anomalies (2006–2013). *A. discaudata* and *Acartia bifilosa* were positively related to PC3, denoting decreasing abundances from the mid-2000s, while *D. anglicus* increased. For the period 2001–2014, this third PC revealed strong similarities with the PC1 observed at the Eyrac site (Fig. 2a *versus* Fig. 2e).

3.2. Year-to-year changes in taxonomic diversity of coastal copepods

The 13 diversity indices were calculated and represented by a contour diagram, their trends being ordered to emphasise common patterns of variability in α and β-diversity (Fig. 3). For each site, a standardised PCA was performed on indices to (1) determine groups of diversity measures (Loiseau et al., 2016) and (2) characterise year-to-year changes in taxonomic diversity (Fig. 4, Table 2 and Figs. S4c–d).

3.2.1. The Eyrac site

The general patterns of copepod diversity at the Eyrac site (Fig. 3a) and results from the PCA based on indices (Fig. 4a–b, Table 2 and Fig. S4c) revealed a clear contrast between α and β-diversity measures, leading to two groups. The first group encompassed α-diversity indices that mostly contributed to the PC1 (74.1% of the total variability; Fig. 4a, Table 2). The highest values of the component (2001–2006), were followed by a period of low values until 2011. Only a slight difference in the timing of changes was observed between indices based on the number of species (*e.g.* species richness) and evenness, and heterogeneous indices such as Pielou and Simpson indices (Fig. 3a). Low α-diversity, detected from 2011, corresponded to a loss of species, probably related to a decrease in typical coastal species such as *I. clavipes* and *C. helgolandicus*; copepod assemblages became dominated by three taxa: *E. acutifrons*, *Oithona* spp. and *Oncaea* spp. (Fig. S2). The second group, which gathered together β-diversity indices (*i.e.* the Jaccard's

Table 3
Correlations between the first two principal components (PCs) of the principal component analyses (PCAs) performed on environmental parameters and the first PCs of the PCA performed on copepod abundances and taxonomic diversity. Probability were corrected to account for temporal autocorrelation with the method recommended by Pyper and Peterman (1998). Significant correlations (r > |0.5|) are in bold.

		Environment							
		Eyrac				Gironde downstream			
		PC1		PC2		PC1		PC2	
		r	p	r	p	r	p	r	P
Species abundances (Fig. 2)	PC1	**0.761**	**0.080**	0.346	0.501	**0.691**	**0.128**	0.053	0.900
	PC2	−0.010	0.981	−0.666	0.071	−0.479	0.337	0.444	0.270
	PC3	–	–	–	–	0.321	0.535	0.425	0.294
Taxonomic diversity (Fig. 4)	PC1	**0.781**	**0.038**	−0.111	0.812	**−0.719**	**0.172**	−0.125	0.789
	PC2	−0.018	0.955	**0.563**	**0.057**	−0.260	0.468	0.402	0.250

dissimilarity index and its components), showed low values until 2011–2012 that suggested weak alterations in species assemblages during this period. From 2011, the marked increase in β-diversity trend revealed a high variability in assemblages in relation to a loss of species, probably because a perturbation in community structure took place at the Eyrac site (Ives and Carpenter, 2007). Year-to-year changes in the PC2 (13.1% of the total variability; Fig. 4b) were mainly explained by β-diversity indices (Table 2).

3.2.2. The Gironde downstream site

At the Gironde downstream, the patterns of diversity also showed differences between trends in α and β-diversities (Fig. 3b), a result supported by results from the PCA (Fig. 4c–d, Table 2 and Fig. S4d). Alpha-diversity measures, which were related to the first PC of the PCA on indices (60.9% of the total variability; Fig. 4c), exhibited inverse patterns of variation when compared to Eyrac: low values were observed until the mid-2000s, followed by a strong increase until 2011 and a progressive decrease from 2012. This reduction in α-diversity is especially visible for metrics based on the number of species (*e.g.* Menhinick indice). Year-to-year changes in β-diversity indices were mainly associated to the second principal component (18.8% of the total variability; Fig. 4d) and showed an increase in β-diversity during the periods 2001–2007 and 2011–2014. In contrast to 2007–2010, a higher variability in species assemblages was observed during this period. While the trend in β-diversity from 2001 to 2007 coincided with a rise in α-diversity - and therefore species gain (*e.g. T. stylifera, D. anglicus*) - increasing β-diversity from 2011 was related to a decrease in α-diversity (*i.e.* species loss).

3.3. Relationships between changes in copepod abundances, taxonomic diversity and environmental conditions

For each site, the principal components that derived from the PCAs performed on copepod abundances were represented in a plane (Fig. 5). For each observation (*i.e.* annual changes in abundances; *Analysis 1*), we attributed the value corresponding to the first PC of the PCAs performed on diversity indices (*Analysis 2*). Given the high percentage of explained variance, we only considered the PC1 of the PCA on diversity indices (74.1% and 60.9% of the total variability; see Fig. 4a, c). After interpolation in the plane, these values were represented by a colour scale to graphically represent the relationships between changes in copepod abundances and taxonomic diversity.

At the Eyrac site, the highest anomalies in abundances observed prior 2006 coincided with positive values of changes in diversity (Fig. 5a). After a period of relative stability between 2006 and 2010 (*i.e.* no high anomaly was detected), negative anomalies in the first two PCs were related to strong negative changes in diversity (Fig. 5a). At the Gironde downstream site, the negative anomalies of the PC2 (1998–2002) were mainly linked to high negative values of changes in diversity (with the exception of 2008; Fig. 5b), and *vice versa*. The same contrasting - but more pronounced - pattern emerged with the positive values of the PC3: the period prior 2005 was mainly related to negative changes in diversity (Fig. 5c). A clear modification in copepod communities (for both species abundances and diversity) took place in the mid-2000s in the two sites.

To estimate a possible influence of changes in environmental conditions, we first performed a PCA on physical, chemical and hydrological variables, for each site (Fig. 6 and Table 3). Year-to-year changes in PC1 at the Eyrac site (46.3% of the total variability; Fig. 6a) showed high values of the component from 2001 to 2003, which then plateaued and shifted down from 2012. The second PC (26.6% of the total variability; Fig. 6b) exhibited a marked decrease from 2001 to the mid-2000s, followed by negative pseudo-cyclical values and two years of positive anomalies in recent years. The examination of the first two eigenvectors (Table S3) indicated a rise in oxygen, chlorophyll *a* and total nitrogen that paralleled a reduction in river discharge, particulate

matter (SPM and POC) that took place from 2001 to the mid-2000s. When considering the two first PCs (Fig. S4e), a clear opposite pattern of changes was detected between salinity and river discharge, indicating that the decrease in freshwater from the Leyre River mainly correlated with an increase in salinity. The first PC of the PCA performed at the Gironde downstream site (50.7% of the total variability; Fig. 6c) exhibited a strong decrease from 1998 to the mid-2000s, followed by a period of negative (2004–2012) and positive (2013–2014) anomalies. The largest contributions to this change revealed that the reduction in freshwater inputs at the Gironde estuary coincided with an increase in salinity and a decline in particulate matter (Table S3). Year-to-year changes in PC2 (22.2% of the total variability; Fig. 6d) showed a pseudo-cyclical variability of ~4 years with temperature and total nitrogen that predominantly contributed to the component.

Results from correlation analysis highlighted patent relationships between modifications in the water column properties (as inferred from the PCAs performed on environmental parameters) and changes in copepod abundances and taxonomic diversity (Table 3). Considering interpretations of the PCAs (Figs. 2, 4 and 6 and Fig. S4), we revealed that the increase in salinity, total nitrogen, chlorophyll *a* and oxygen at the Eyrac site, as well as the decrease in river discharge and particulate matter, were positively related to a decline in α and β-diversity (r = 0.781, p = 0.04 between PCs1, r = 0.563, p = 0.06 between PCs2; Table 3). This decline in diversity metric was consecutive to a shift towards dominance of *E. acutifrons*, *Oithona* spp. and *Oncaea* spp., and a reduction in the abundance of most other species as showed by the high correlations we calculated with the PCs of the PCA performed on copepod abundances (r = 0.761, p = 0.08 between PCs1, r = −0.666, p = 0.07 between PCs2). At the Gironde downstream site, the relations we found involve only the first PCs obtained from the different PCAs (Table 3). The decrease in both river discharge and particulate matter, and the concomitant rise in salinity were highly positively related (r = 0.691, p = 0.13) to the increasing abundance of species such as *T. stylifera* and *A. clausi*. This coincided with an increase in α-diversity, as displayed by the correlation between the environment and diversity (r = −0.719, p = 0.17).

4. Discussion

Because zooplankton species are highly sensitive to environmental changes, rapidly reproducing organisms with wide dispersal ability according to hydrodynamic processes, and as they integrate and transfer environmental signals over generation time, species assemblages are known to mirror ecosystems conditions (Richardson, 2009; Goberville et al., 2014). Drifters by definition, zooplankton species are associated to different water masses (Richardson, 2009) and changes in assemblages in an area are often linked to advective processes, such as water exchanges between neighbouring regions (Willis et al., 2006). Monitoring zooplankton as indicators of changes offers therefore undeniable advantages and estimating species diversity is relevant to examine how climate variability, hydrographic conditions and/or anthropogenic activities influence ecosystem status (*e.g.* Beaugrand and Edwards, 2001; Serranito et al., 2016). However, the way in which species diversity is measured can sometimes lead to contradictory results (McGill et al., 2015), especially when analyses ignore ecological context (Elahi et al., 2015). In addition, the selection of the appropriate diversity indices remains challenging in littoral ecosystems because of the naturally high variability in zooplankton community composition, assemblages being the result of a continuous mixing between continental, neritic and autochthonous species, when water masses residence time is long enough (Sautour and Castel, 1993). Each species having its own sensitivity to environmental conditions (Hutchinson, 1957), species within a community are likely to not react in the same way to environmental changes (Beaugrand et al., 2014).

By investigating copepod assemblages in median neritic waters of Arcachon Bay and in the polyhaline zone of the estuary, 20 and 23
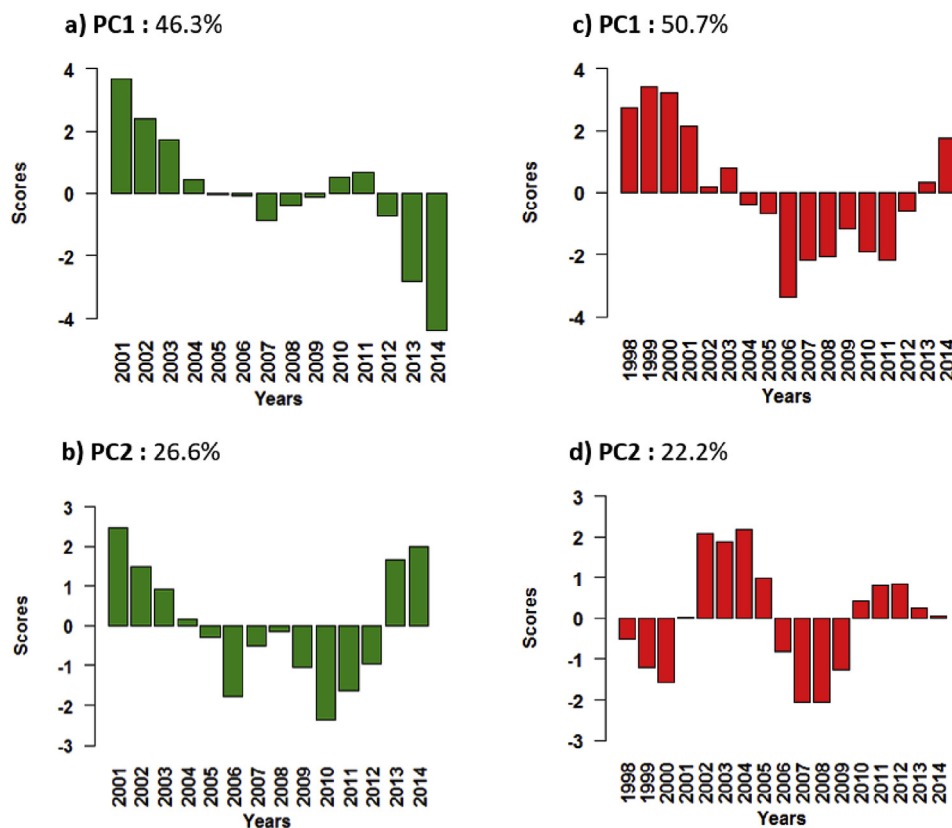
Fig. 6. Year-to-year changes in environmental conditions in the two coastal systems. (**a**) First and (**b**) second principal components (PCs) calculated from the standardised PCA performed on environmental parameters in Eyrac. (**c**) First and (**d**) second principal components (PCs) calculated from the standardised PCA performed on environmental parameters in the Gironde downstream site (see Table S3).

species have been reported, respectively (Table S1), a level of diversity equivalent to studies previously performed in each region (*e.g.* in the Arcachon Bay, Castel and Courties, 1982; in the polyhaline zone of the estuary, Sautour and Castel, 1995). Due to their geographical proximity and comparable large-scale and regional climate influences (Plus et al., 2009; Goberville et al., 2010), most of the species were common to both ecosystems: a mixing of typical coastal neritic species originating from the Bay of Biscay (*e.g. T. stylifera*, *A. clausi*, *C. helgolandicus*; Castel and Courties, 1982; Sautour et al., 2000) and euryhaline species adapted to polyhaline areas (*e.g. E. acutifrons*, *A. discaudata;* Vincent et al., 2002; David et al., 2005). Species such as *C. helgolandicus* or *I. clavipes* in Arcachon Bay and *A. discaudata* or *C. typicus* in the Gironde downstream site are typical coastal neritic species that only appeared sporadically at the sampling station over the study period and whose trends and abundances have been mostly related to water masses and their residence time (Castel and Courties, 1982).

Our analyses revealed strong links between changes in environmental conditions and modifications in species abundances and taxonomic diversity. This result is in line with other works that documented synchronisms between plankton assemblages/species, water column properties and climate at different scales of influence (*e.g.* Goberville et al., 2010, 2014; Harley et al., 2006). River discharge, salinity and particulate matter - local manifestations of changes in hydrological conditions - appeared as the main parameters governing year-to-year variability in littoral copepods. Changes in copepod abundances and diversity in the mid-2000s are paralleled by alterations in other biological compartments, supporting that environmental changes may have had a large and significant impact on both ecosystems. While a sudden decrease in the abundance of subtidal benthic macrofauna was reported in 2005 in the lower part of the Gironde estuary (Bachelet and Leconte, 2015), a synchronous increase in both the occurrence and abundance of marine fish juveniles was noticed in relation to salinity changes in its lower (Pasquaud et al., 2012) and middle parts (Chevillot et al., 2016). In the Arcachon Bay, a severe seagrass decline, concomitant with an

increase in phytoplankton and macroalgae production, was observed between 2005 and 2007 (Plus et al., 2015). For the first time in 2005, Brown Muscle Disease emerged in the Arcachon Bay, leading to a steady decline of Asari clam stocks in the years that followed (de Montaudouin et al., 2016). This mid-2000s event also coincides with what have been found in other littoral zones of Western Europe (O'Brien et al., 2012; Lefebvre et al., 2011) and is likely to have been triggered by the extremely cold and dry winter of 2005 in southwestern Europe and its consequences on the upper ocean hydrographic structure of the Bay of Biscay (Somavilla et al., 2009). We caution however that not all species reacted at the same time and with the same magnitude in both sites. Such a situation has been already depicted in the North Sea where only 40% of plankton species exhibited an abrupt shift in the late 1980s (Beaugrand et al., 2014), this fraction being mainly characterised by species located at the edge of their distributional range, and therefore more sensitive to subtle environmental changes (Beaugrand, 2012).

In a context of global spasm of biodiversity loss, an overall decrease in α-diversity is expected in almost all ecosystems (*e.g.* Worm et al., 2006; Ceballos et al., 2015). However, our results substantiated that trends in diversity are more intricate at finer spatial scales, and that they may be strongly influenced by local ecological context (Sax and Gaines, 2003; Elahi et al., 2015; McGill et al., 2015). At the Eyrac site, and despite slight variations between indices, a patent reduction in α-diversity was observed since the mid-2000s: typical autochthonous and neritic species (*P. brevicornis* and *D. anglicus*, respectively) decreased in abundance while *E. acutifrons* and *Oithona* spp. became strongly dominant. Because of the close relationships between plankton community structure and hydrological processes, the development of these polyhaline eurytopic species could have been supported by a decrease in freshwater inputs - as suggested by the reduction in river discharges - and an increase in water residence time (Basu and Pick, 1996). The steady rise in *E. acutifrons*, *Oithona* spp., *Oncaea* spp. and *C. helgolandicus* - although to a lesser extent - reinforced the imbalance in the community structure and intensified the reduction in α-diversity (*e.g.*

Salas et al., 2004).

In the Gironde downstream site, a patent increase in α-diversity - associated to a relative equitability among five taxa - was detected since the mid-2000s: *P. parvus, Oithona* spp. and *E. acutifrons*, neritic eurytopic species increasingly encountered in the polyhaline area of the estuary and typically observed in the estuarine plume (Sautour et al., 2000) and *E. affinis* and *A. tonsa*, found in great abundance in the oligo-mesohaline area of the estuary (David et al., 2005). Changes in physical, chemical and hydrological conditions might have been responsible for variations in environmental gradients in the downstream part of the Gironde estuary, with a stronger presence - at the sampling site - of neritic waters which benefit marine species such as *C. helgolandicus*. While the increase in *P. parvus* and *E. acutifrons* was probably induced by enhanced coastal water intrusions, as described upstream in relation to the large mouth of the estuary and importance of the tidal prism (Jouanneau and Latouche, 1981; Chaalali et al., 2013b), the rise in *E. affinis* and *A. bifilosa* may have been favoured by punctual inputs of freshwater (David et al., 2007). A warming of the estuary was associated to increasing abundance of *A. tonsa* (Chaalali et al., 2013b; see their Fig. 5), but also to the establishment of the Asiatic copepod, *P. marinus* (Brylinski et al., 2012). Increasing α-diversity in this site is consistent with the rise in richness reported for a large number of coastal ecosystems worldwide (Elahi et al., 2015). In the southeastern Bay of Biscay, in response to water quality improvement, changes in environmental conditions and the arrival of new species, a zooplankton recolonisation of the inner estuary of Bilbao took place between 1998 and 2011, with an increase in neritic copepod species and - to a lesser extent - in the abundances of appendicularians, meroplanktonic bivalves and gastropods, (Uriarte et al., 2016). Farther north, a long-term increase in copepod species richness was noticed in the Western Channel over 1988–2007 (Eloire et al., 2010). Contrasting individual trends in species abundances were observed between this study and ours, however. While we also showed a rise in *Oncaea* spp. and *C. helgolandicus* - that implies basin scale changes in species abundances (Eloire et al., 2010) - our conclusions on *P. elongatus*, *Temora longicornis* and *A. clausi* diverge, suggesting (*i*) site-specific species responses, probably induced by the local ecological context, and/or (*ii*) a consequence of the delineation of species' distributional limits (see distribution maps in Castellani and Edwards, 2017).

By allowing quantitative assessments, diversity indices are welcomed by decision makers to define policy guidelines, to determine suitable targets or to evaluate the effectiveness of management actions (Gubbay, 2004; Laurila-Pant et al., 2015). Selecting one metric rather than another can influence the assessment of trends in diversity, however (Morris et al., 2014; Loiseau and Gaertner, 2015), especially in littoral areas where strong environmental gradients and high variability of physico-chemical parameters take place (Dauvin et al., 2009; Bouchet et al., 2018). Here, the use of a wide range of indices strengthened our confidence in the characterisation of sudden changes in biodiversity as well as the quantification of long-term trends; although we conceded that both functional and phylogenetic diversity were not scrutinised due to data availability (Loiseau et al., 2016). In each site, diversity indices performed similarly over the study period, not only because of the mathematical convergence between some indices (Bandeira et al., 2013; Morris et al., 2014), but also because of the significance of changes in copepod species. This was supported by the multivariate approach performed on species abundances. While diversity indices are straightforward to effectively summarise and communicate diversity trends, our results highlighted that combination with multivariate approaches provide useful insights into community changes (*e.g.* distinguishing 'winners' and 'losers' species; see McGill et al., 2015). Information of why diversity fluctuates is essential for proper interpretation of changes but it is also essential to recall that long-term biodiversity time-series only inform on species abundances and variety at a given location and at a number of points in time (Magurran et al., 2010). This was well summarised by Magurran et al.

(2010) who wrote: "*researchers cannot necessarily assume that responses to change documented in long-term datasets will be universal, even where the same types of organisms are involved*".

Over the last few decades, many countries have mandated assessment of coastal water bodies and classical diversity indices have been intensively used to characterise diversity patterns (Beaugrand and Edwards, 2001; Magurran, 2013), to detect anthropogenic pressures (Serranito et al., 2016) or to investigate ecosystem level consequences of diversity changes (Gagic et al., 2015). In the minds of many, the unprecedented pace of global changes necessarily induced negative diversity trends, at any spatial scale. This led policymakers to put emphasis on the need to mitigate diversity loss from local to global levels (McGill et al., 2015) while disregarding possible positive diversity trends (Sax and Gaines, 2003). However, we showed here that opposite signals may emerge between nearby sites owing to local ecological conditions (*e.g.* anthropogenic impacts, initial richness, species dominance; Elahi et al., 2015), environmental peculiarities of each system (McGill et al., 2015) or stochastic processes (Stegen et al., 2013). Our findings provide evidence that more local studies need to be initiated in order to (1) define site-specific 'reference conditions' and (2) better evaluate diversity trajectories at very fine scales at which ecologists often work (Elahi et al., 2015). The degree of perturbation of an ecosystem should be compared with a site in which only natural conditions are a source of variability (Davies and Jackson, 2006); but such references rarely exist (Goberville et al., 2011). In addition, and because plankton species of confined ecosystems (*e.g.* estuarine, lagoons, coastal basins …) can be present only a very short period of time in the water column - with consequences on both their recording and biodiversity assessment (Belmonte et al., 2013) - qualitative changes in communities in these areas must rely on standardised long-term monitoring (Belmonte et al., 2013). In that sense, the inception of a long-term survey of both near-shore and off-shore waters of the Bay of Biscay must be encouraged within the Marine Strategy Framework Directive. We strongly believe that a better characterisation of diversity changes at local scale will reinforce our comprehension of global diversity trends.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106304.

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