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

Julien Richirt^{1,2*}, Eric Goberville^{3*}, Vania Ruiz-Gonzalez¹ and Benoît Sautour¹

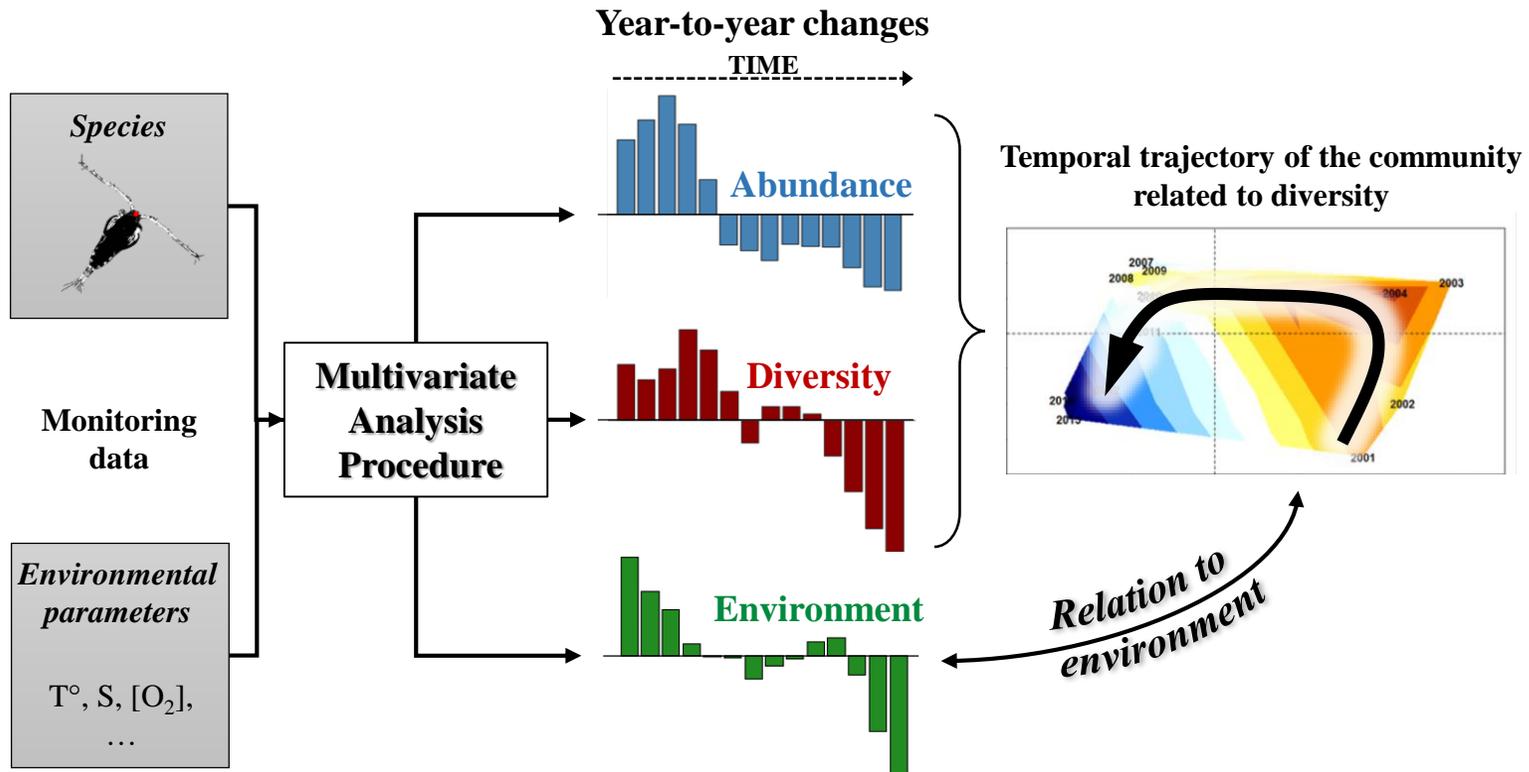
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Highlights

- Synchronous changes in copepod communities were detected in two littoral ecosystems (85)
- Opposite trends in diversity may emerge between nearby sites (62)
- Local-scale conditions and processes highly influence diversity trends (73)
- Multivariate analyses are important to understand how and why diversity fluctuates (84)



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12 6 Julien Richirt^{1,2*}, Eric Goberville^{3*}, Vania Ruiz-Gonzalez¹ and Benoît Sautour¹
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62 **ABSTRACT**
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36 While long-term monitoring is essential to improve our knowledge of marine ecosystems health,
37 it remains challenging to summarise complex ecological data in order to characterise and understand
38 biodiversity trends. To compile monitoring data across large numbers of species, scientists and
39 policymakers mainly rely on diversity and species richness indices. This task may prove complicated
40 however, as many indices exist and no individual metric undoubtedly emerges as the best overall. Here,
41 using data from zooplankton surveys from 1998 to 2014, we examined year-to-year changes in copepod
42 communities in two littoral ecosystems of Western Europe - the Arcachon Bay and the Gironde estuary
43 - that share similar climate, but with different local ecological processes, especially hydrological
44 conditions. We tested the ability of commonly used α and β -diversity metrics, such as species richness,
45 Pielou's evenness or Jaccard's index, to mirror year-to-year changes in species abundances and we
46 detected a synchronous change in both copepod abundances and α -diversity that took place *circa* 2005
47 in the two sites. In response to changes in environmental conditions such as nutrients, salinity, river
48 discharge or particulate matter, two opposite biodiversity trends were observed, with a decrease in
49 copepod diversity in the Arcachon Bay but an increase in the downstream part of the Gironde estuary.
50 Although diversity metrics allowed us to well detect trends, the use of multivariate approaches such as
51 principal component analysis provided important information on how and why diversity fluctuates. Our
52 study provides evidence that long-term monitoring programmes must be encouraged for optimising
53 management and conservation actions such as the Marine Strategy Framework Directive and that more
54 local comparative studies need to be initiated for better characterising diversity trajectories at very fine
55 scales at which ecologists often work.

56 **Keywords:** copepod communities, long-term changes, diversity indices, coastal systems, multivariate
57 analysis
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121 **1. Introduction**
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125 60 Coastal marine systems, which are among the most ecologically and economically important
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127 61 ecosystems on the planet (Harley et al., 2006), are known to be highly sensitive to climate fluctuations
128
129 62 and direct anthropogenic pressures (Harley et al., 2006; Goberville et al., 2011). The impact of these
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131 63 forcing is not restricted to a particular biological component but extends to all ecological units, affecting
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133 64 marine biodiversity from phytoplankton to top predators (Frederiksen et al., 2006; Chaalali et al.,
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135 65 2013a), leading to alterations in the structure and functioning of coastal systems (Chevillot et al., 2018),
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137 66 with possible ramifications for the terrestrial realm (Luczak et al., 2013). For example, three decades of
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139 67 observation have revealed synchronous climate, environmental and biological community shifts in the
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141 68 San Francisco Bay (Cloern et al., 2010). In the Gironde estuary, large (*e.g.* the Atlantic Multidecadal
142
143 69 Oscillation) and regional (*e.g.* annual sea surface temperature and winds) climate-driven processes have
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145 70 induced concomitant changes in hydrological and biological conditions, including abrupt modifications
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147 71 in the composition and structure of pelagic communities (Chaalali et al., 2013a; Chevillot et al., 2016).
148
149 72 Concurrently, habitat loss, overexploitation and pollution are major human threats that affect coastal
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151 73 diversity (Duffy et al., 2013; Elahi et al., 2015).

152
153 74 Global alteration of coastal ecosystems in recent decades has led policymakers to encourage
154
155 75 monitoring programs worldwide and estimating biodiversity appears as the most relevant way to
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157 76 measure the status of ecological conditions (Duffy et al., 2013; Elahi et al., 2015). Long-term
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159 77 observations are essential to disentangle natural variations from unusual or extreme events (Lovett et
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161 78 al., 2007), to better capture the inherent variability and stochasticity associated to surveys and
162
163 79 ecosystems (Kujala et al., 2013; Beaugrand and Kirby, 2016) and to identify the main forcing that can
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165 80 affect ecosystems (Goberville et al., 2010). To compile monitoring data across large numbers of species
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167 81 and ecosystems, scientists and policymakers often rely on diversity indices (Pereira et al., 2013), easy-
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169 82 to-implement measures of biodiversity for which the effort in calculation and computation is much less
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171 83 cumbersome than multivariate approaches. These indices are also known to be appropriate tools for a
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173 84 rapid and efficient communication between the scientific community, government agencies, funding
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180 85 institutions and the general public (*e.g.* Lovett et al., 2007). However, many metrics exist and none
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182 86 emerges as the best overall (Bandeira et al., 2013) nor combines all different facets of diversity (Salas
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184 87 et al., 2006; Rombouts et al., 2013). Using a range of complementary indices enables to better evaluate
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186 88 both the strengths and weaknesses of the different metrics in detecting changes over time (Rombouts et
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188 89 al., 2013; Loiseau and Gaertner, 2015) or in assessing ecosystem status, when combined with relevant
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190 90 indicator species (Lindenmayer et al., 2015).

191
192 91 Copepods are ubiquitous and play pivotal roles in the functioning of marine systems and in
193
194 92 biogeochemical cycles (*e.g.* Richardson, 2008) even in low-diversity ecosystems (Horváth et al., 2014).
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196 93 Major consumers of primary production, detrital organic matter or bacterial production according to
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198 94 environmental conditions, copepods are an intermediate link within the pelagic food web and provide
199
200 95 the main pathway for energy from lower to higher trophic levels (*e.g.* fish, marine mammals;
201
202 96 Richardson, 2008). By acting on the mean residence time of particulate organic matter in surface waters
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204 97 and on the sinking flux of particulate organic carbon, they significantly contribute to the biological
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206 98 carbon pump (Beaugrand et al., 2010). Highly sensitive to changes in environmental conditions,
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208 99 copepods also rapidly integrate environmental signals over generation time and transfer potential
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210 100 changes to the next generation (Goberville et al., 2014).

211
212
213 101 Changes in copepod abundances, diversity and community structure can have rapid and major
214
215 102 consequences on higher trophic level species. For example, previous studies have paralleled changes in
216
217 103 the abundance of *Calanus finmarchicus* or *Pseudocalanus* spp and alterations in commercially exploited
218
219 104 fish stocks such as Atlantic cod *Gadus morhua*, Atlantic salmon *Salmo salar* and Atlantic herring *Clupea*
220
221 105 *harengus* (Cushing, 1984; Beaugrand and Reid, 2012; Johnson et al., 2014). Biogeographical shifts in
222
223 106 calanoid copepods in the northeast Atlantic have been related to changes in water masses and
224
225 107 atmospheric forcing (Beaugrand, 2012). In a Mediterranean coastal bay, taxonomic diversity indices
226
227 108 (*e.g.* Simpson's index, Pielou's evenness) have been computed from zooplankton species to determine
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229 109 the effects of anthropogenic impacts (Bandeira et al., 2013; Serranito et al., 2016). This list, far from
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231 110 being exhaustive, sheds light on copepods as ideal candidates for tracking ecosystem changes
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233 111 (Richardson, 2008).

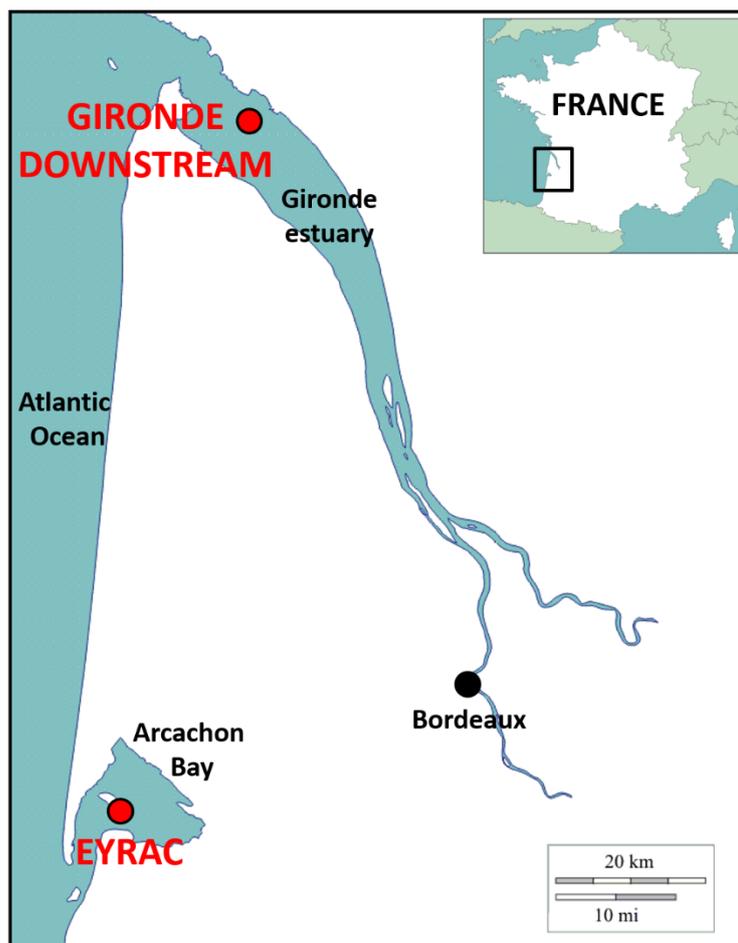
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112 Here, by using data from zooplankton surveys from 1998 to 2014, we examine year-to-year
113 changes in copepod communities (species abundances and taxonomic diversity) in two nearby littoral
114 areas of Western Europe (*i.e.* the Arcachon Bay and the Gironde estuary) that share similar climate
115 conditions but contrasting physical, chemical and hydrological environments. The following questions
116 are addressed: Do copepod communities differ between the two sites and change over time? Are trends
117 in taxonomic diversity apparent and linked to environmental changes? To study changes in species
118 abundances and diversity that took place in the Arcachon Bay and the Gironde estuary over the last two
119 decades, we combine a principal component analyses based-approach and commonly used taxonomic
120 diversity indices that account for the number of species (*e.g.* species richness), the evenness of
121 abundance distribution among species (*e.g.* Pielou index) and the variability in communities among
122 years (*e.g.* Jaccard index). We then investigate divergences between these two adjacent sites and explore
123 the possible mechanisms that explain diversity trends and species responses to environmental changes.

124 **2. Materials and methods**

125 *2.1. Sampling sites*

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



128

129 **Figure 1.** Map of the Gironde Estuary and Arcachon Bay showing the two studied sites: the Eyrac site
 130 and the Gironde downstream site.

131 The Eyrac site (44°40'N, 1°10'W; Fig. 1) is situated in the median neritic waters (salinity: 26.8-
 132 33.2; Vincent et al., 2002) of the Arcachon Bay, a temperate mesotidal ecosystem highly influenced by
 133 tides and winds (Plus et al., 2009). The Arcachon Bay is open to the Bay of Biscay through two narrow
 134 channels (4-5m depth) separated by several sandbanks. This distinctive narrow entrance has important
 135 effects on the water mass exchange between the Bay and the Atlantic Ocean: the tidal prism is equal to
 136 384 million of cubic meters, 64% of the lagoon total volume being flushed in and out at each tidal cycle
 137 (Plus et al., 2009). Neritic water masses within the Bay are influenced mainly by freshwater inputs from
 138 the Leyre river (20 m³ s⁻¹). The Arcachon Bay is therefore quite confined and water residence time is
 139 approximately 20 days (Plus et al., 2009). The zooplankton community is described as diverse (Sautour
 140 and Castel, 1993), with eurytopic continental and neritic, and autochthonous species, associated to

355
356
357 141 polyhaline water masses (due to low freshwater inputs, typical estuarine species are confined to the inner
358
359 142 eastern part of the Bay; Vincent et al., 2002).

361
362 143 The Gironde downstream site (45°31'N, 0°57'W; Fig. 1) is representative of the polyhaline zone
363
364 144 of the Gironde estuary (salinity > 30; Chaalali et al., 2013b), which is one of the most turbid and largest
365
366 145 macrotidal estuary of Europe. Its large mouth allows important exchanges with the Bay of Biscay (tidal
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368 146 prism: 1.1 to 2.0 billion cubic metres; Jouanneau and Latouche, 1981) and no autochthonous
369
370 147 zooplankton species can develop in polyhaline water masses (excepting meroplankton organisms whose
371
372 148 adults inhabit the estuary). Important freshwater inputs from the Garonne and Dordogne rivers (647 m³
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374 149 s⁻¹ and 342 m³ s⁻¹, respectively) act on the growth of estuarine species in oligo- and mesohaline water
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376 150 masses. In this naturally stressed environment (Dauvin et al., 2009), an increasing gradient of
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378 151 zooplankton diversity is observed from the upstream to the downstream areas (Sautour and Castel, 1995;
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380 152 Chaalali et al., 2013a).

381 382 153 *2.2. Biological datasets*

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384

385 154 Species samples were collected at the two fixed sampling sites (Fig. 1), from 1998 to 2014 by the
386
387 155 SOGIR survey ('Service d'Observation de la GIRONDE') at the Gironde downstream site (average depth
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389 156 at high tide = 8.2m) and from 2001 to 2014 by the SOARC survey ('Service d'Observation du bassin
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391 157 d'ARCachon') at the Eyrac site (average depth at high tide = 8m). A standardised protocol has been
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393 158 established before conducting the surveys, so that sampling is carried out at a monthly scale in both
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395 159 sites, at high tide and in the top first two meters below the surface using horizontal tow and a standard
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397 160 200µm WP2 net (Fraser, 1968). The volume of water filtered through the net was recorded with a
398
399 161 Hydrobios digital flowmeter and samples were fixed in 5% seawater/buffered formalin.

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401 162 In the laboratory, samples were sorted and copepods were counted and identified to the species
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403 163 level as far as possible. Identification was carried out with a stereomicroscope Zeiss Axiovert (200 and
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405 164 400) and following Rose (1933), the World Register of Marine Species database (WoRMS;
406
407 165 www.marinespecies.org) and the taxonomic classification provided by Razouls et al. (2005-2018).

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415
416 166 Because rare species may reflect stochastic sampling effects (Poos and Jackson, 2012) and
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418 167 decrease the signal-to-noise ratio (Borcard et al., 2011) only species with a presence >5% over the period
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420 168 1998-2014 were retained (Table S1). This procedure, similar to the approach applied in Ibanez and
421
422 169 Dauvin (1988), allowed the selection of 17 species in each site, with 13 species being common to both
423
424 170 ecosystems (Table 1 and Table S1). For each site, copepod abundances were averaged per year to
425
426 171 remove the effect of seasonality prior to further analysis.

428 172 *2.3. Environmental parameters*

431 173 Changes in physico-chemical properties of coastal waters at the Eyrac and the Gironde
432
433 174 downstream sites were estimated using data from the ‘Service d’Observation en Milieu LITtoral’
434
435 175 (SOMLIT; somlit.epoc.u-bordeaux1.fr) collected on a bi-monthly basis at sub-surface and high tide (see
436
437 176 Goberville et al., 2010 for further details). Here, we focused on seven parameters: temperature, salinity,
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439 177 oxygen, total nitrogen (TN) concentration (computed by summing nitrate, nitrite and ammonium
440
441 178 concentrations), particulate organic carbon (POC), suspended particulate matter (SPM) and chlorophyll
442
443 179 *a*. Note that species samples (from the SOGIR and SOARC surveys) and environmental parameters
444
445 180 (from the SOMLIT programme) were sampled simultaneously. In addition, we included data on mean
446
447 181 river discharges recorded (*i*) near the Leyre River mouth for the Eyrac site and (*ii*) in the downstream
448
449 182 part of the Gironde estuary (<http://www.hydro.eaufrance.fr/>, Ministère de l’Ecologie et du
450
451 183 Développement Durable).

454 184 *2.4. Analysis 1: Year-to-year changes in coastal copepod abundances (see Fig. S1)*

457 185 Since species abundance data exhibited skewed distributions, data were transformed using the
458
459 186 $\log_{10}(x + 1)$ function (Fig. S2; Jolliffe, 2002). A simple moving average of order-1 was applied to
460
461 187 reduce the noise inherent to these data; we therefore highlighted long-term variability while minimising
462
463 188 the influence of short-term fluctuations (Legendre and Legendre, 2012).

466 189 To characterise year-to-year changes in coastal copepod abundances, standardised Principal
467
468 190 Component Analyses (PCAs) were performed separately on correlation matrices during the period 2001-

473
474
475 191 2014 for the Eyrac site and 1998-2014 for the Gironde downstream site. For each PCA, we then applied
476
477 192 a broken-stick model (Frontier, 1976) to assess the number of principal components (PCs) to retain for
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479 193 interpretation, *i.e.* the number of PCs with eigenvalues exceeding the expected value generated by a
480
481 194 random distribution (King and Jackson, 1999; Legendre and Legendre, 2012). The first two PCs for the
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483 195 Eyrac site and the first three PCs for the Gironde downstream site were thus examined (Fig. 2).
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485
486 196 A possible influence of the moving average process was tested by applying a Procrustes procedure
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488 197 (with 999 permutations; Legendre and Legendre, 2012): by comparing two matrices that describe the
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490 198 same entity (here copepod abundances), the Procrustes test statistically evaluate whether the two
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492 199 multivariate datasets (*i.e.* before and after application of the moving average procedure) can be
493
494 200 interchanged in the analysis (Peres-Neto and Jackson, 2001; Legendre and Legendre, 2012). Because of
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496 201 dependency on meteorological conditions during sampling (*e.g.* intense winds), the number of samples
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498 202 per year may vary over time (Fig. S3), potentially leading to bias in the temporal comparison of annual
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500 203 abundances (Beaugrand and Edwards, 2001). To examine how sampling effort may influence the
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502 204 characterisation of changes in coastal copepods, we considered a decreasing number of months to
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504 205 calculate annual means (from 10 months - *i.e.* the maximum of samples available for the more well-
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506 206 documented years; Fig. S3 - to 6 months, following a bootstrap procedure with 999 permutations;
507
508 207 Davison and Hinkley, 1997) and we re-performed standardised PCAs on each re-computed dataset. We
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510 208 then calculated Spearman correlation coefficients between the first two (for the Eyrac site) and three
511
512 209 PCs (for the Gironde downstream site) (Table S2).
513

514 210 Results from these two sensitivity analyses confirmed that our conclusions were neither highly
515
516 211 affected by sampling effort (all years were therefore retained for analysis) nor the moving average
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518 212 procedure (Procrustes correlation=0.821, $p \leq 0.001$ for the Eyrac site; Procrustes correlation=0.808,
519
520 213 $p \leq 0.001$ for the Gironde downstream site).
521

523 214 2.5. Analysis 2: Year-to-year changes in taxonomic diversity of coastal copepods (see Fig. S1)

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526 215 Changes in alpha (α ; Whittaker, 1972) and beta (β ; Anderson et al., 2006) diversity of coastal
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528 216 copepods were assessed by using 13 easily interpretable diversity indices - among the most commonly
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217 used in the literature - and known to be pertinent to a wide range of biological compartments and
218 ecosystems (Lamb et al., 2009; Bandeira et al., 2013; Magurran, 2013). Because β -diversity indices
219 allow to take into account the identities of all species, they are regarded as complementary to α -diversity
220 metrics which ignore species identity (*e.g.* species richness; Baselga and Orme, 2012).

221 To compute α -diversity, 4 indices (*i.e.* species richness, Odum, Margalef and Menhinick indices)
222 were used as measures of the number of species in a community, 2 indices (reciprocal Berger-Parker
223 and Pielou's evenness indices) as a measure of the evenness (*i.e.* indices of the community structure;
224 Peet, 1974; Legendre and Legendre, 2012; Bandeira et al., 2013) and 3 heterogeneous indices (reciprocal
225 of unbiased Simpson, McIntosh and corrected Shannon-Wiener indices; Heip et al., 1998; Chao and
226 Shen, 2003) that combined the number of species and evenness (Mérigot et al., 2007). Beta diversity,
227 *i.e.* the variability in species assemblages among years in a given area (Anderson et al., 2006), was
228 calculated using the Jaccard's dissimilarity index and the partitioning approach (Baselga and Orme,
229 2012) to evaluate the nestedness (*i.e.* changes in assemblages' composition caused by the gain/loss of
230 species between t and t+1) and turnover components (*i.e.* changes in assemblages' composition caused
231 by species replacement processes between t and t+1). The β -ratio estimated the contribution of each
232 component (*i.e.* species replacement vs. nestedness; Baselga and Orme, 2012).

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

237 *2.6. Analysis 3: Relationships between changes in copepod abundances, taxonomic diversity*
238 *and environmental conditions (see Fig. S1)*

239 Relationships between changes in copepod abundances and in taxonomic diversity were
240 investigated using a bi-plot approach which displays associations graphically (Fig. 5; Goberville et al.,
241 2014). For each site, the PCs retained from the PCAs performed on species abundances were represented
242 in a plane to display similarities/dissimilarities among years. For each year of the period 2001-2014

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593 243 (Eyrac site, Fig. 5a) and 1998-2014 (Gironde downstream site, Fig. 5b-c), the value of changes in
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595 244 taxonomic diversity (*i.e.* results from the PCA performed on indices) was assigned and represented by
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597 245 a colour scale; the blue (red) gradient corresponds to high negative (positive) values. By characterising
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599 246 each year by reference to changes in copepod diversity, this representation showed time series of
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601 247 responses of each site, *i.e.* changes in copepod communities over the time period.
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603
604 248 To characterise the main year-to-year changes that took place in physical, chemical and
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606 249 hydrological conditions at each site, we followed the same procedure than that applied to identify
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608 250 changes in copepod abundances and diversity (see 2.4 and 2.5): (1) a one-year moving average on annual
609
610 251 means, (2) a Procrustes test and (3) a PCA performed on logged data. Pearson correlation analyses
611
612 252 (Table 3) were then performed between the first PCs obtained from Analysis 1 and 2 and the first two
613
614 253 PCs calculated from the PCA applied on environmental parameters at each site. Following the procedure
615
616 254 recommended by Pyper & Peterman (1998), probabilities were computed and corrected to account for
617
618 255 temporal autocorrelation: Box and Jenkins' (1976) autocorrelation function modified by Chatfield was
619
620 256 calculated and applied to adjust the degree of freedom using Chelton's (1984) formula.
621

622 623 257 **3. Results**

624 625 626 627 258 *3.1. Year-to-year changes in coastal copepod abundances*

628 629 259 3.1.1. The Eyrac site

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632 260 Year-to-year changes in PC1 of the PCA performed on copepod abundances at the Eyrac site
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634 261 (57.7% of the total variability) showed high values of the component from 2001 to 2005, followed by a
635
636 262 decrease in the trend and negative values from 2006 onwards (Fig. 2a). Examination of the first
637
638 263 eigenvector indicated that species such as *Isias clavipes*, *Paracalanus parvus* and *Ditrichocorycaeus*
639
640 264 *anglicus* were positively correlated with the component, corresponding to a decrease in their abundance
641
642 265 from the mid-2000s onwards (Table 1, Fig. S4a). *Oithona* spp. and *Euterpina acutifrons* were strongly
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644 266 negatively related to changes in the first PC, showing an increase in their abundance from 2006 to 2014.
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646 267 The second principal component (19% of the total variability) exhibited periods of negative (2001-2002
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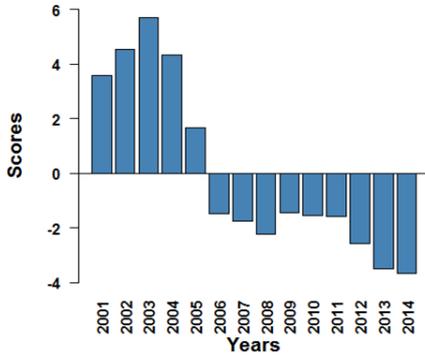
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268 and 2012-2014) and positive (2003-2011) anomalies (Fig. 2b). The study of the second eigenvector
653
269 revealed that an increase in the abundance of *Acartia discaudata* and *Parapontella brevicornis*, and to
654
655 a lesser extent *Centropages typicus*, occurred between 2003 and 2011, while a reduction in the
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657 abundance of *Calanus helgolandicus* and *Oncaea* spp. was observed.
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660 272 3.1.2. The Gironde downstream site

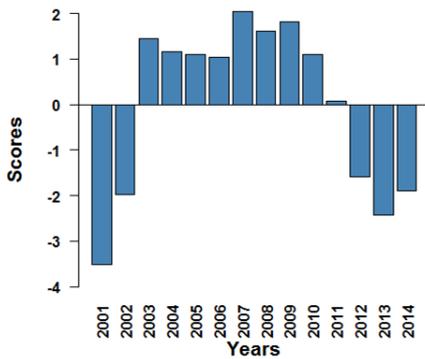
662
273 The first PC of the PCA performed on copepods at the Gironde downstream site (28.6% of the
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664 total variability) showed periods of positive (1998-2003 and 2012-2014) and negative (2003-2011)
665
666 anomalies (Fig. 2c). Inspection of the first eigenvector indicated that *Oncaea* spp., *C. helgolandicus* and,
667
668 to a lesser extent, *Pseudodiaptomus marinus* and *Eurytemora affinis* were positively related to PC1,
669
670 corresponding to a reduction in their abundance between 2003 and 2011 (Table 1, Fig. S4b). In contrast,
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672 the abundance of *Temora stylifera*, *Centropages hamatus*, *Pseudocalanus elongatus* and *Acartia clausi*
673
674 increased. After a period of strong negative anomalies (1998-2003), year-to-year changes in PC2 (25.9%
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676 of the total variability) mainly expressed positive anomalies from 2003 (Fig. 2d). *Acartia tonsa* was the
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678 only species strongly negatively correlated with this change, revealing a constant decline. Species such
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680 as *Oithona* spp., *E. acutifrons* or *C. typicus* were positively related to PC2, corresponding to an increase
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682 in abundance over the last decade. Year-to-year changes in the third PC (19.6% of the total variability)
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684 displayed pronounced positive values from 2001 to 2005, at the time the component showed negative
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686 anomalies (2006-2013). *A. discaudata* and *Acartia bifilosa* were positively related to PC3, denoting
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688 decreasing abundances from the mid-2000s, while *D. anglicus* increased. For the period 2001-2014, this
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690 third PC revealed strong similarities with the PC1 observed at the Eyrac site (Fig. 2a versus Fig. 2e).
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EYRAC

a) PC1 : 57.7%

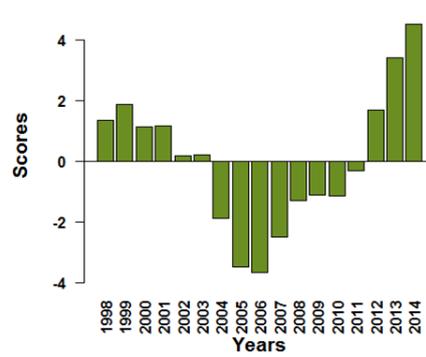


b) PC2 : 19%

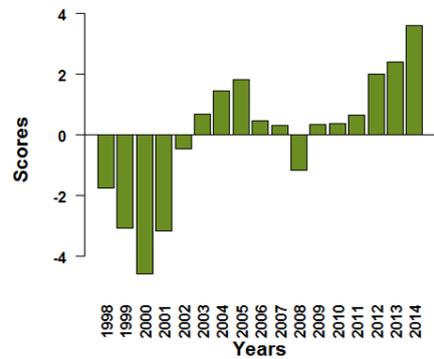


GIRONDE DOWNSTREAM

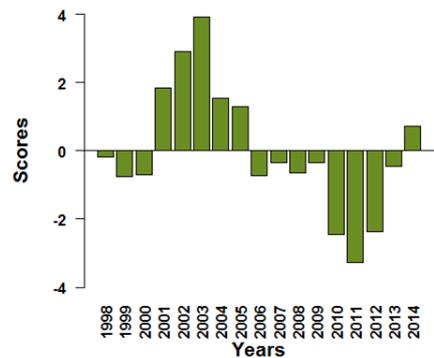
c) PC1 : 28.6%



d) PC2 : 25.9%



e) PC3 : 19.6%



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

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

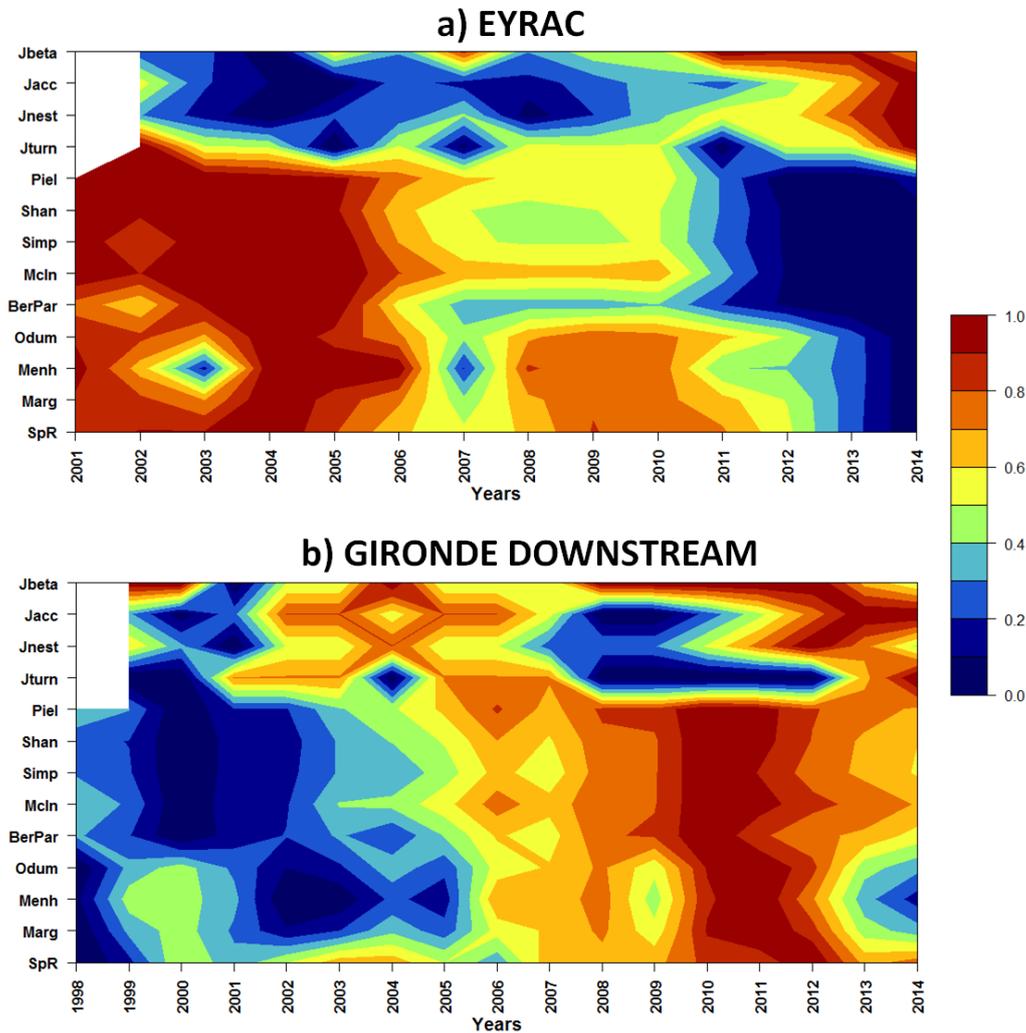
295 **Table 1.** Results from the standardised PCAs performed on copepod abundances. The first two
 296 eigenvectors (for Eyrac) and the first three eigenvectors (for Gironde downstream) are included and
 297 show the contribution of each species to the principal components. Values in bold were superior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

298 3.2. Year-to-year changes in taxonomic diversity of coastal copepods

299 The 13 diversity indices were calculated and represented by a contour diagram, their trends being
 300 ordered to emphasise common patterns of variability in α and β -diversity (Fig. 3). For each site, a
 301 standardised PCA was performed on indices to (1) determine groups of diversity measures (Loiseau *et*

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302 *al.*, 2016) and (2) characterise year-to-year changes in taxonomic diversity (Fig. 4, Table 2 and Fig.S4c-
303 d).



304
305 **Figure 3.** Diversity indices calculated for pelagic copepod species in (a) Eyrac (2001-2014) and (b)
306 Gironde downstream (1998-2014). SpR: Species Richness, Marg: Margalef indice, Menh: Menhinick
307 indice, Odum: Odum indice, BerPer: Berger-Parker indice, McIn: McIntosh indice, Simp: Simpson
308 indice, Shan: Shannon indice, Piel: Pielou's eveness derived from Shannon indice, Jturn: turnover
309 component of Jaccard indice, Jnest: nestedness component of Jaccard indice, Jacc: Jaccard indice, Jbeta:
310 beta ratio. For visual comparison indices were normalised between 0 and 1. White areas correspond to
311 missing values.

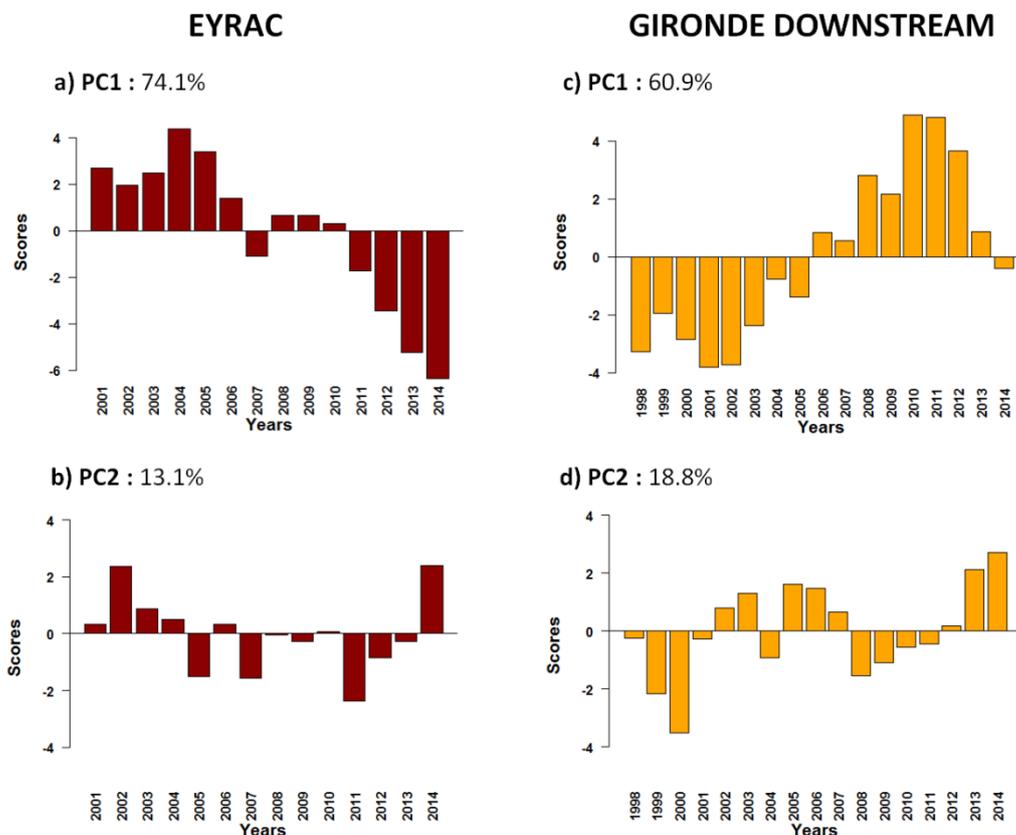
312 3.2.1. The Eyrac site

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888 313 The general patterns of copepod diversity at the Eyrac site (Fig. 3a) and results from the PCA
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890 314 based on indices (Fig. 4a-b, Table 2 and Fig. S4c) revealed a clear contrast between α and β -diversity
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892 315 measures, leading to two groups. The first group encompassed α -diversity indices that mostly
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894 316 contributed to the PC1 (74.1% of the total variability; Fig. 4a, Table 2). The highest values of the
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896 317 component (2001-2006), were followed by a period of low values until 2011. Only a slight difference
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898 318 in the timing of changes was observed between indices based on the number of species (*e.g.* species
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900 319 richness) and evenness and heterogeneous indices such as Pielou and Simpson indices (Fig. 3a). Low α -
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902 320 diversity, detected from 2011, corresponded to a loss of species, probably related to a decrease in typical
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904 321 coastal species such as *I. clavipes* and *C. helgolandicus*; copepod assemblages became dominated by
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906 322 three taxa: *E. acutifrons*, *Oithona* spp. and *Oncaea* spp. (Fig. S2). The second group, which gathered
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908 323 together β -diversity indices (*i.e.* the Jaccard's dissimilarity index and its components), showed low
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910 324 values until 2011-2012 that suggested weak alterations in species assemblages during this period. From
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912 325 2011, the marked increase in β -diversity trend revealed a high variability in assemblages in relation to a
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914 326 loss of species, probably because a perturbation in community structure took place at the Eyrac site (Ives
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916 327 & Carpenter, 2007). Year-to-year changes in the PC2 (13.1% of the total variability; Fig. 4b) were
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918 328 mainly explained by β -diversity indices (Table 2).

920 329 3.2.2. The Gironde downstream site

923 330 At the Gironde downstream, the patterns of diversity also showed differences between trends in
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925 331 α and β -diversities (Fig. 3b), a result supported by results from the PCA (Fig. 4c-d, Table 2 and Fig.
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927 332 S4d). Alpha-diversity measures, which were related to the first PC of the PCA on indices (60.9% of the
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929 333 total variability; Fig. 4c), exhibited inverse patterns of variation when compared to Eyrac: low values
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931 334 were observed until the mid-2000s, followed by a strong increase until 2011 and a progressive decrease
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933 335 from 2012. This reduction in α -diversity is especially visible for metrics based on the number of species
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935 336 (*e.g.* Menhinick indice). Year-to-year changes in β -diversity indices were mainly associated to the
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937 337 second principal component (18.8% of the total variability; Fig. 4d) and showed an increase in β -
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939 338 diversity during the periods 2001-2007 and 2011-2014. In contrast to 2007-2010, a higher variability in
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941 339 species assemblages was observed during this period. While the trend in β -diversity from 2001 to 2007

340 coincided with a rise in α -diversity - and therefore species gain (*e.g. T. stylifera, D. anglicus*) - increasing
 341 β -diversity from 2011 was related to a decrease in α -diversity (*i.e.* species loss).



342
 343 **Figure 4.** Year-to-year changes in coastal copepod taxonomic diversity in the two coastal systems. (a)
 344 First and (b) second principal components (PCs) calculated from the standardised PCA performed on
 345 diversity indices in Eyrac. (c) First and (d) second principal components (PCs) calculated from the
 346 standardised PCA performed on diversity indices in the Gironde downstream site.

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 evenness	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 (component of Jaccard's dissimilarity index)	-0.49	51.5	-2.71	27.41
Nestedness (component of Jaccard's dissimilarity index)	-8.46	0.39	1.69	1.4

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|.

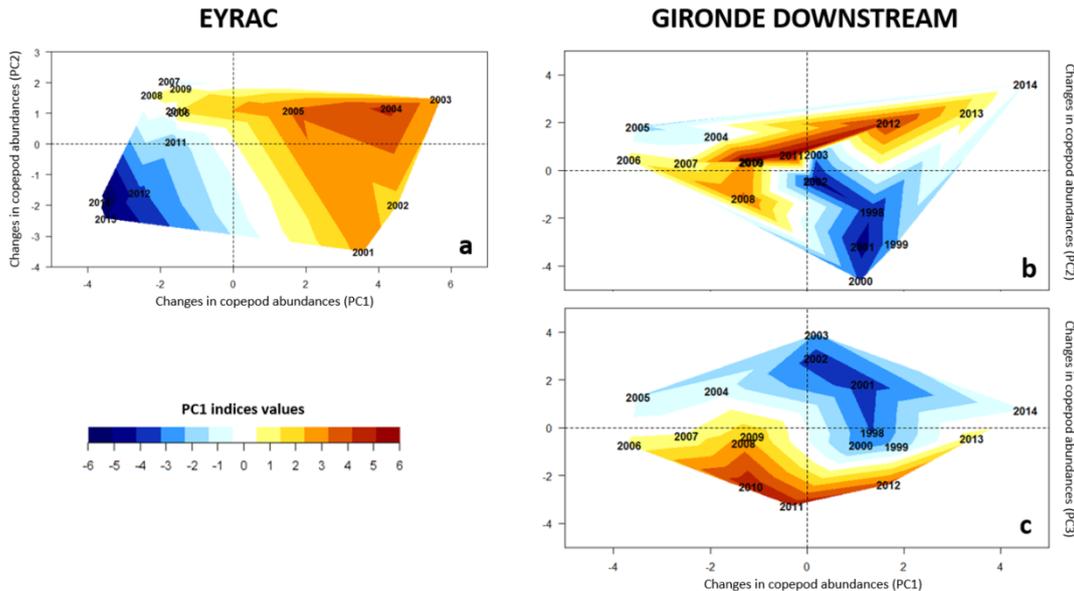
3.3. Relationships between changes in copepod abundances, taxonomic diversity and environmental conditions

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

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364 of 2008; Fig. 5b), and *vice versa*. The same contrasting - but more pronounced - pattern emerged with
365 the positive values of the PC3: the period prior 2005 was mainly related to negative changes in diversity
366 (Fig. 5c). A clear modification in copepod communities (for both species abundances and diversity) took
367 place in the mid-2000s in the two sites.

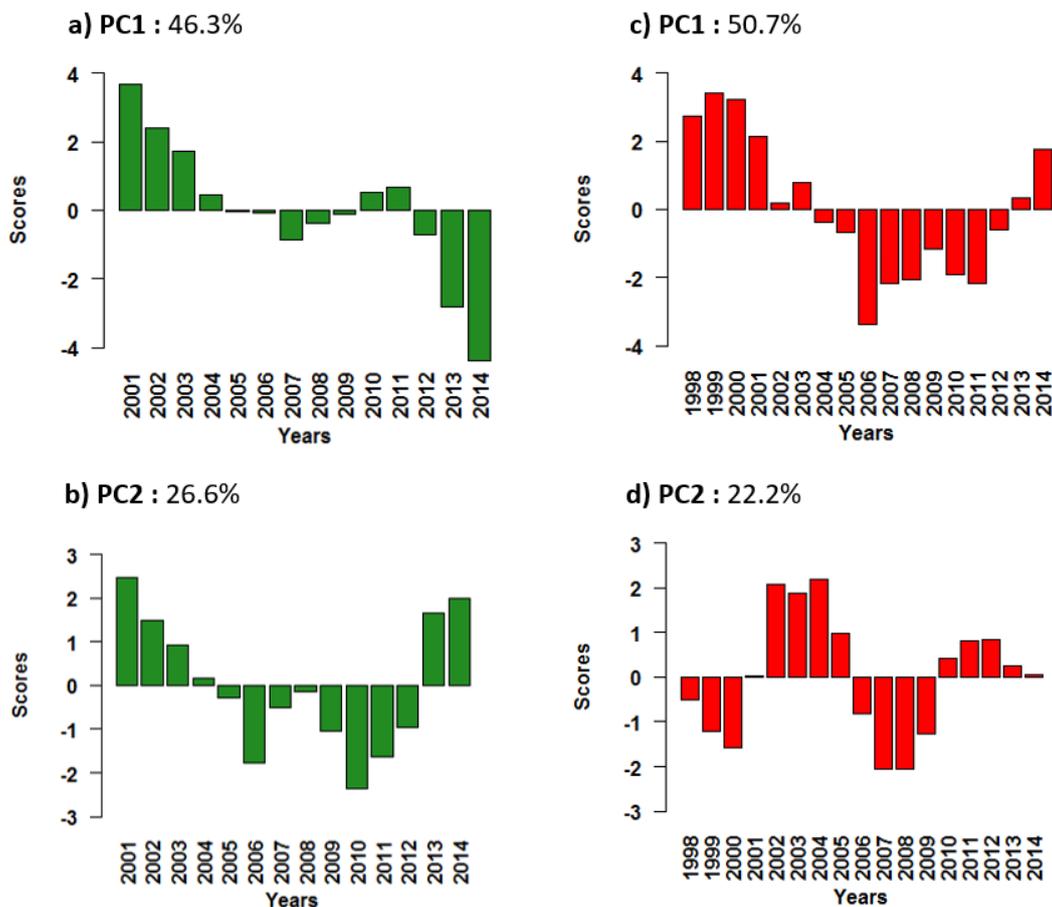


368
369 **Figure 5.** Relationships between changes in coastal copepod diversity and changes in coastal
370 copepod abundances for the Eyrac site (left panel) and the Gironde downstream site (right panels) (a)
371 Relationships between changes in diversity (first PC of the PCA performed on taxonomic diversity
372 indices) and the first two PCs of the PCA performed on coastal copepod abundances at the Eyrac site.
373 (b-c) Relationships between changes in diversity and the first and (b) second or (c) third PC from the
374 PCA performed on coastal copepod abundances at the Gironde downstream site. The values of changes
375 in measures of diversity were interpolated and represented by the colour scale (see Analysis 3).

376 To estimate a possible influence of changes in environmental conditions, we first performed a
377 PCA on physical, chemical and hydrological variables, for each site (Fig. 6 and Table 3). Year-to-year
378 changes in PC1 at the Eyrac site (46.3% of the total variability; Fig. 6a) showed high values of the
379 component from 2001 to 2003, which then plateaued and shifted down from 2012. The second PC
380 (26.6% of the total variability; Fig. 6b) exhibited a marked decrease from 2001 to the mid-2000s,
381 followed by negative pseudo-cyclical values and two years of positive anomalies in recent years. The

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382 examination of the first two eigenvectors (Table S3) indicated a rise in oxygen, chlorophyll *a* and total
383 nitrogen that paralleled a reduction in river discharge, particulate matter (SPM and POC) that took place
384 from 2001 to the mid-2000s. When considering the two first PCs (Fig S4e), a clear opposite pattern of
385 changes was detected between salinity and river discharge, indicating that the decrease in freshwater
386 from the Leyre River mainly correlated with an increase in salinity. The first PC of the PCA performed
387 at the Gironde downstream site (50.7% of the total variability; Fig. 6c) exhibited a strong decrease from
388 1998 to the mid-2000s, followed by a period of negative (2004-2012) and positive (2013-2014)
389 anomalies. The largest contributions to this change revealed that the reduction in freshwater inputs at
390 the Gironde estuary coincided with an increase in salinity and a decline in particulate matter (Table S3).
391 Year-to-year changes in PC2 (22.2% of the total variability; Fig. 6d) showed a pseudo-cyclical
392 variability of ~4 years with temperature and total nitrogen that predominantly contributed to the
393 component.



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395 **Figure 6.** Year-to-year changes in environmental conditions in the two coastal systems. **(a)** First
396 and **(b)** second principal components (PCs) calculated from the standardised PCA performed on
397 environmental parameters in Eyrac. **(c)** First and **(d)** second principal components (PCs) calculated from
398 the standardised PCA performed on environmental parameters in the Gironde downstream site (see
399 Table S3).

----- 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

400 **Table 3.** Correlations between the first two principal components (PCs) of the principal component
401 analyses (PCAs) performed on environmental parameters and the first PCs of the PCA performed on
402 copepod abundances and taxonomic diversity. Probability were corrected to account for temporal
403 autocorrelation with the method recommended by Pyper & Peterman (1998). Significant correlations (r
404 $> |0.5|$) are in bold.

405 Results from correlation analysis highlighted patent relationships between modifications in the
406 water column properties (as inferred from the PCAs performed on environmental parameters) and
407 changes in copepod abundances and taxonomic diversity (Table 3). Considering interpretations of the
408 PCAs (Figs. 2, 4, 6 and Fig S4), we revealed that the increase in salinity, total nitrogen, chlorophyll *a*
409 and oxygen at the Eyrac site, as well as the decrease in river discharge and particulate matter, were
410 positively related to a decline in α and β -diversity ($r=0.781$, $p=0.04$ between PCs1, $r=0.563$, $p=0.06$

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411 between PCs2; Table 3). This decline in diversity metric was consecutive to a shift towards dominance
412 of *E. acutifrons*, *Oithona* spp. and *Oncaea* spp., and a reduction in the abundance of most other species
413 as showed by the high correlations we calculated with the PCs of the PCA performed on copepod
414 abundances ($r=0.761$, $p=0.08$ between PCs1, $r=-0.666$, $p=0.07$ between PCs2). At the Gironde
415 downstream site, the relations we found involve only the first PCs obtained from the different PCAs
416 (Table 3). The decrease in both river discharge and particulate matter, and the concomitant rise in salinity
417 were highly positively related ($r=0.691$, $p=0.13$) to the increasing abundance of species such as *T.*
418 *styliifera* and *A. clausi*. This coincided with an increase in α -diversity, as displayed by the correlation
419 between the environment and diversity ($r=-0.719$, $p=0.17$).

420 **4. Discussion**

421 Because zooplankton species are highly sensitive to environmental changes, rapidly reproducing
422 organisms with wide dispersal ability according to hydrodynamic processes, and as they integrate and
423 transfer environmental signals over generation time, species assemblages are known to mirror
424 ecosystems conditions (Richardson, 2009; Goberville et al., 2014). Drifters by definition, zooplankton
425 species are associated to different water masses (Richardson, 2009) and changes in assemblages in an
426 area are often linked to advective processes, such as water exchanges between neighbouring regions
427 (Willis et al., 2006). Monitoring zooplankton as indicators of changes offers therefore undeniable
428 advantages and estimating species diversity is relevant to examine how climate variability, hydrographic
429 conditions and/or anthropogenic activities influence ecosystem status (e.g. Beaugrand and Edwards,
430 2001; Serranito et al., 2016). However, the way in which species diversity is measured can sometimes
431 lead to contradictory results (McGill et al., 2015), especially when analyses ignore ecological context
432 (Elahi et al., 2015). In addition, the selection of the appropriate diversity indices remains challenging in
433 littoral ecosystems because of the naturally high variability in zooplankton community composition,
434 assemblages being the result of a continuous mixing between continental, neritic and autochthonous
435 species, when water masses residence time is long enough (Sautour and Castel, 1993). Each species

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436 having its own sensitivity to environmental conditions (Hutchinson, 1957), species within a community
437 are likely to not react in the same way to environmental changes (Beaugrand et al., 2014).

438 By investigating copepod assemblages in median neritic waters of Arcachon Bay and in the
439 polyhaline zone of the estuary, 20 and 23 species have been reported, respectively (Table S1), a level of
440 diversity equivalent to studies previously performed in each region (e.g. in the Arcachon Bay, Castel
441 and Courties, 1982; in the polyhaline zone of the estuary, Sautour and Castel, 1995). Due to their
442 geographical proximity and comparable large-scale and regional climate influences (Plus et al., 2009;
443 Goberville et al., 2010), most of the species were common to both ecosystems: a mixing of typical
444 coastal neritic species originating from the Bay of Biscay (e.g. *T. stylifera*, *A. clausi*, *C. helgolandicus*;
445 Castel and Courties, 1982; Sautour et al., 2000) and euryhaline species adapted to polyhaline areas (e.g.
446 *E. acutifrons*, *A. discaudata*; Vincent et al., 2002; David et al., 2005). Species such as *C. helgolandicus*
447 or *I. clavipes* in Arcachon Bay and *A. discaudata* or *C. typicus* in the Gironde downstream site are typical
448 coastal neritic species that only appeared sporadically at the sampling station over the study period and
449 whose trends and abundances have been mostly related to water masses and their residence time (Castel
450 and Courties, 1982).

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

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

475 In a context of global spasm of biodiversity loss, an overall decrease in α -diversity is expected in
476 almost all ecosystems (e.g. Worm et al., 2006; Ceballos et al., 2015). However, our results substantiated
477 that trends in diversity are more intricate at finer spatial scales, and that they may be strongly influenced
478 by local ecological context (Sax and Gaines, 2003; Elahi et al., 2015; McGill et al., 2015). At the Eyrac
479 site, and despite slight variations between indices, a patent reduction in α -diversity was observed since
480 the mid-2000s: typical autochthonous and neritic species (*P. brevicornis* and *D. anglicus*, respectively)
481 decreased in abundance while *E. acutifrons* and *Oithona* spp. became strongly dominant. Because of the
482 close relationships between plankton community structure and hydrological processes, the development
483 of these polyhaline eurytopic species could have been supported by a decrease in freshwater inputs - as
484 suggested by the reduction in river discharges - and an increase in water residence time (Basu and Pick,
485 1996). The steady rise in *E. acutifrons*, *Oithona* spp., *Oncaea* spp. and *C. helgolandicus* - although to a
486 lesser extent - reinforced the imbalance in the community structure and intensified the reduction in α -
487 diversity (e.g. Salas et al., 2004).

488 In the Gironde downstream site, a patent increase in α -diversity - associated to a relative
489 equitability among five taxa - was detected since the mid-2000s: *P. parvus*, *Oithona* spp. and *E.*

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1418
1419 490 *acutifrons*, neritic eurytopic species increasingly encountered in the polyhaline area of the estuary and
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1421 491 typically observed in the estuarine plume (Sautour et al., 2000) and *E. affinis* and *A. tonsa*, found in
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1423 492 great abundance in the oligo-mesohaline area of the estuary (David et al., 2005). Changes in physical,
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1425 493 chemical and hydrological conditions might have been responsible for variations in environmental
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1427 494 gradients in the downstream part of the Gironde estuary, with a stronger presence - at the sampling site
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1429 495 - of neritic waters which benefit marine species such as *C. helgolandicus*. While the increase in *P. parvus*
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1431 496 and *E. acutifrons* was probably induced by enhanced coastal water intrusions, as described upstream in
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1433 497 relation to the large mouth of the estuary and importance of the tidal prism (Jouanneau and Latouche,
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1435 498 1981; Chaalali et al., 2013b), the rise in *E. affinis* and *A. bifilosa* may have been favoured by punctual
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1437 499 inputs of freshwater (David et al., 2007). A warming of the estuary was associated to increasing
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1439 500 abundance of *A. tonsa* (Chaalali et al., 2013b; see their Fig. 5), but also to the establishment of the
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1441 501 Asiatic copepod, *P. marinus* (Brylinski et al., 2012). Increasing α -diversity in this site is consistent with
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1443 502 the rise in richness reported for a large number of coastal ecosystems worldwide (Elahi et al., 2015). In
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1445 503 the southeastern Bay of Biscay, in response to water quality improvement, changes in environmental
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1447 504 conditions and the arrival of new species, a zooplankton recolonisation of the inner estuary of Bilbao
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1449 505 took place between 1998 and 2011, with an increase in neritic copepod species and - to a lesser extent -
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1451 506 in the abundances of appendicularians, meroplanktonic bivalves and gastropods, (Uriarte et al., 2016).
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1453 507 Farther north, a long-term increase in copepod species richness was noticed in the Western Channel over
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1455 508 1988-2007 (Eloire et al., 2010). Contrasting individual trends in species abundances were observed
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1457 509 between this study and ours, however. While we also showed a rise in *Oncaea* spp. and *C. helgolandicus*
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1459 510 - that implies basin scale changes in species abundances (Eloire et al., 2010) - our conclusions on *P.*
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1461 511 *elongatus*, *Temora longicornis* and *A. clausi* diverge, suggesting (i) site-specific species responses,
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1463 512 probably induced by the local ecological context, and/or (ii) a consequence of the delineation of species'
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1465 513 distributional limits (see distribution maps in Castellani and Edwards, 2017).

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1467 514 By allowing quantitative assessments, diversity indices are welcomed by decision makers to
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1469 515 define policy guidelines, to determine suitable targets or to evaluate the effectiveness of management
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1471 516 actions (Gubbay, 2004; Laurila-Pant et al., 2015). Selecting one metric rather than another can influence

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1478 517 the assessment of trends in diversity, however (Morris et al., 2014; Loiseau and Gaertner, 2015),
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1480 518 especially in littoral areas where strong environmental gradients and high variability of physico-
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1482 519 chemical parameters take place (Dauvin et al., 2009; Bouchet et al., 2018). Here, the use of a wide range
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1484 520 of indices strengthened our confidence in the characterisation of sudden changes in biodiversity as well
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1486 521 as the quantification of long-term trends; although we conceded that both functional and phylogenetic
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1488 522 diversity were not scrutinised due to data availability (Loiseau et al., 2016). In each site, diversity indices
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1490 523 performed similarly over the study period, not only because of the mathematical convergence between
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1492 524 some indices (Bandeira et al., 2013; Morris et al., 2014), but also because of the significance of changes
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1494 525 in copepod species. This was supported by the multivariate approach performed on species abundances.
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1496 526 While diversity indices are straightforward to effectively summarise and communicate diversity trends,
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1498 527 our results highlighted that combination with multivariate approaches provide useful insights into
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1500 528 community changes (*e.g.* distinguishing ‘winners’ and ‘losers’ species; see McGill et al., 2015).
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1502 529 Information of why diversity fluctuates is essential for proper interpretation of changes but it is also
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1504 530 essential to recall that long-term biodiversity time-series only inform on species abundances and variety
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1506 531 at a given location and at a number of points in time (Magurran et al., 2010). This was well summarised
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1508 532 by Magurran et al. (2010) who wrote: “*researchers cannot necessarily assume that responses to change*
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1510 533 *documented in long-term datasets will be universal, even where the same types of organisms are*
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1512 534 *involved*”.

1514 535 Over the last few decades, many countries have mandated assessment of coastal water bodies
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1516 536 and classical diversity indices have been intensively used to characterise diversity patterns (Beaugrand
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1518 537 and Edwards, 2001; Magurran, 2013), to detect anthropogenic pressures (Serranito et al., 2016) or to
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1520 538 investigate ecosystem level consequences of diversity changes (Gagic et al., 2015). In the minds of
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1522 539 many, the unprecedented pace of global changes necessarily induced negative diversity trends, at any
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1524 540 spatial scale. This led policymakers to put emphasis on the need to mitigate diversity loss from local to
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1526 541 global levels (McGill et al., 2015) while disregarding possible positive diversity trends (Sax and Gaines,
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1528 542 2003). However, we showed here that opposite signals may emerge between nearby sites owing to local
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1530 543 ecological conditions (*e.g.* anthropogenic impacts, initial richness, species dominance; Elahi et al.,
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1537 544 2015), environmental peculiarities of each system (McGill et al., 2015) or stochastic processes (Stegen
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1539 545 et al., 2013). Our findings provide evidence that more local studies need to be initiated in order to (1)
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1541 546 define site-specific ‘reference conditions’ and (2) better evaluate diversity trajectories at very fine scales
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1543 547 at which ecologists often work (Elahi et al., 2015). The degree of perturbation of an ecosystem should
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1545 548 be compared with a site in which only natural conditions are a source of variability (Davies and Jackson,
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1547 549 2006); but such references rarely exist (Goberville et al., 2011a). In addition, and because plankton
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1549 550 species of confined ecosystems (*e.g.* estuarine, lagoons, coastal basins...) can be present only a very
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1551 551 short period of time in the water column - with consequences on both their recording and biodiversity
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1553 552 assessment (Belmonte et al., 2013) - qualitative changes in communities in these areas must rely on
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1555 553 standardised long-term monitoring (Belmonte et al., 2013). In that sense, the inception of a long-term
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1557 554 survey of both near-shore and off-shore waters of the Bay of Biscay must be encouraged within the
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1559 555 Marine Strategy Framework Directive. We strongly believe that a better characterisation of diversity
1560
1561 556 changes at local scale will reinforce our comprehension of global diversity trends.

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The following supplement accompanies the article

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

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Supplement

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Figures and Tables Legends

Supplementary Figure S1. Statistical analyses applied in this study. PCA: standardised principal component analysis.

Supplementary Figure S2. Pelagic copepod abundances at **(a)** Eyrac (from 2001 to 2014) and **(b)** Gironde downstream (from 1998 to 2014). For visual comparison, abundances were $\log_{10}(x+1)$ transformed and normalised between 0 and 1.

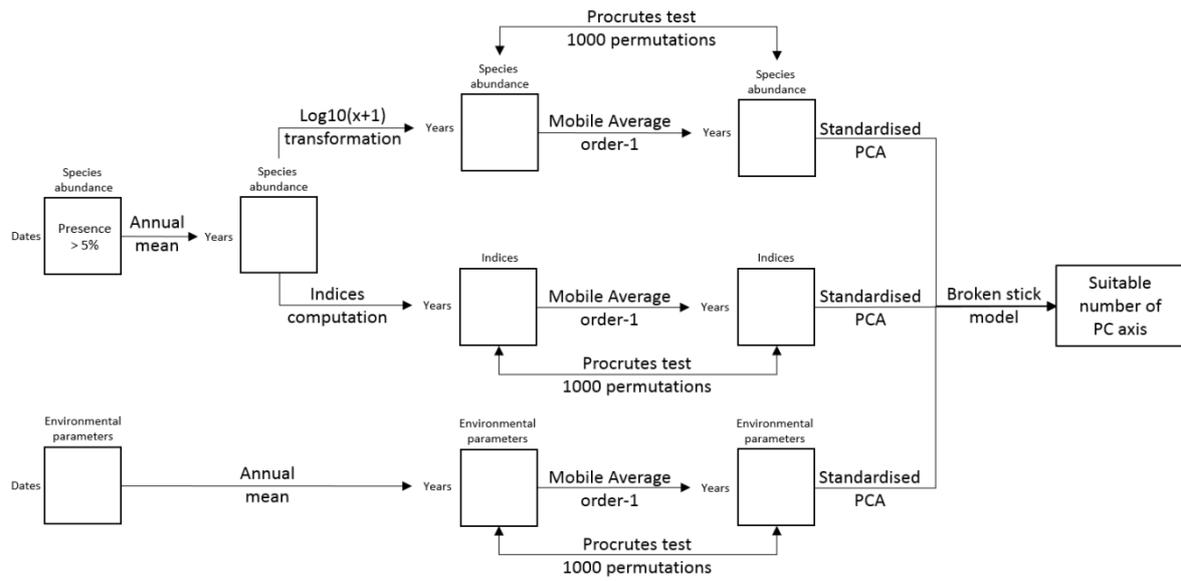
Supplementary Figure S3. Annual sampling effort (i.e. number of samples available per year) for Eyrac (dotted black line) and the Gironde downstream (red line).

Supplementary Figure S4. Projections of the variables onto the 1-2 factorial plans of the standardised PCA performed on **(a-b)** copepod abundances in **(a)** Eyrac (axis 1: 57.7%, axis 2: 19%) and **(b)** the Gironde downstream site (axis 1: 28.6%, axis 2: 25.9%); on **(c-d)** diversity indices in **(c)** Eyrac (axis 1: 71.1%, axis 2: 13.1%) and **(d)** the Gironde downstream site (axis 1: 60.9%, axis 2: 18.8%); on **(e-f)** environmental parameters in **(e)** Eyrac (axis 1: 46.3%, axis 2: 26.6%) and **(f)** the Gironde downstream site (axis 1: 50.7%, axis 2: 22.2%). See Figure 3 for the meaning of indices.

Supplementary Table S1. Total relative abundance and presence (in percentage) of copepod species sampled at the Eyrac (from 2001 to 2014) and the Gironde downstream sites (from 1998 to 2014). Species with percentages in bold have been retained for the PCA analyses (presence \square 5%).

Supplementary Table S2. Results from the sensitive analysis performed to account for changes in sampling effort. Spearman correlation coefficients between the first PCs (PC_x(tot.)) retained to characterise year-to-year changes in coastal copepod abundances in both study areas (see Figure 2) and the PCs obtained from the PCA analyses performed on re-estimated annual copepod abundances (PC_x(999 perm.)) with a decreasing number of months used in the calculation of annual means and following a bootstrap procedure (999 permutations). rho: Spearman correlation coefficient. PC(s): Principal Component(s).

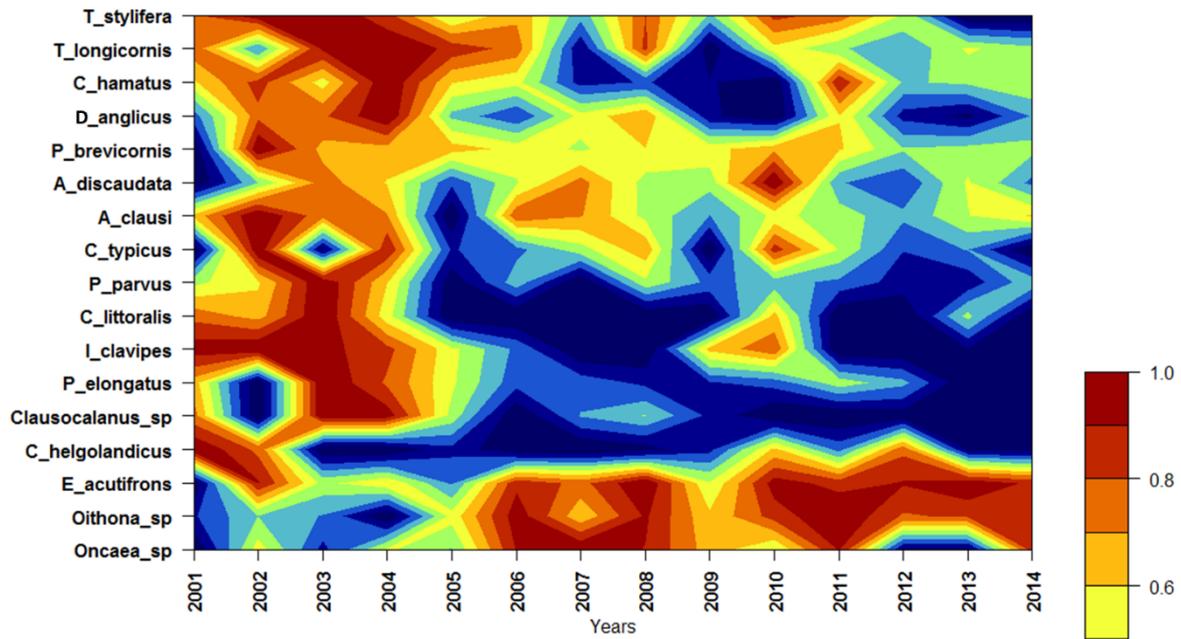
Supplementary Table S3. Results from the standardised PCAs performed on environmental parameters. The first two eigenvectors are included and show the contribution of each parameter to the principal components. Values in bold were superior to $|2.50|$.



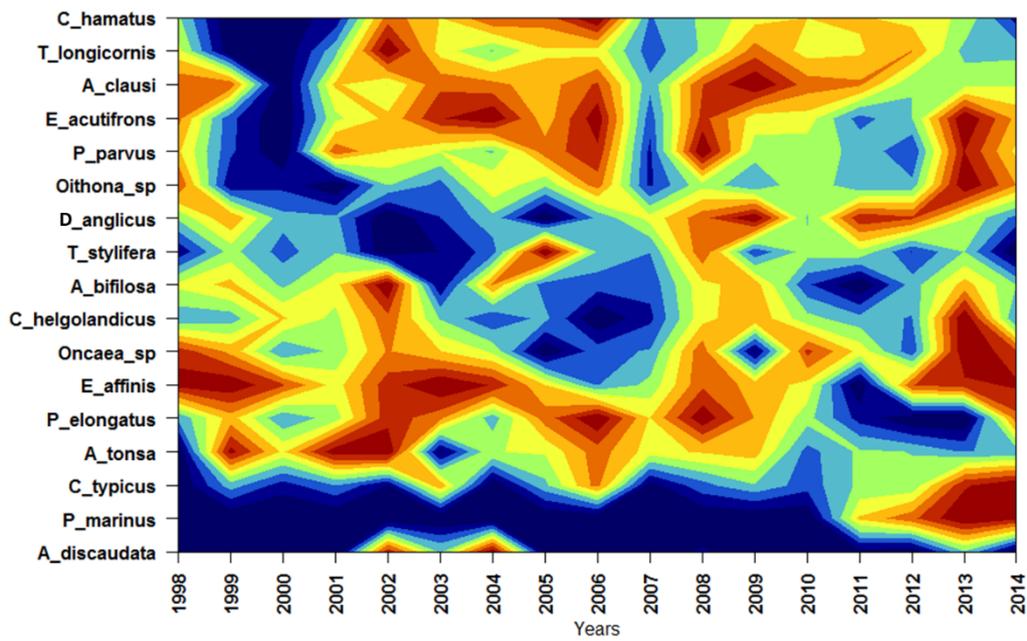
Supplementary Figure S1

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a) EYRAC

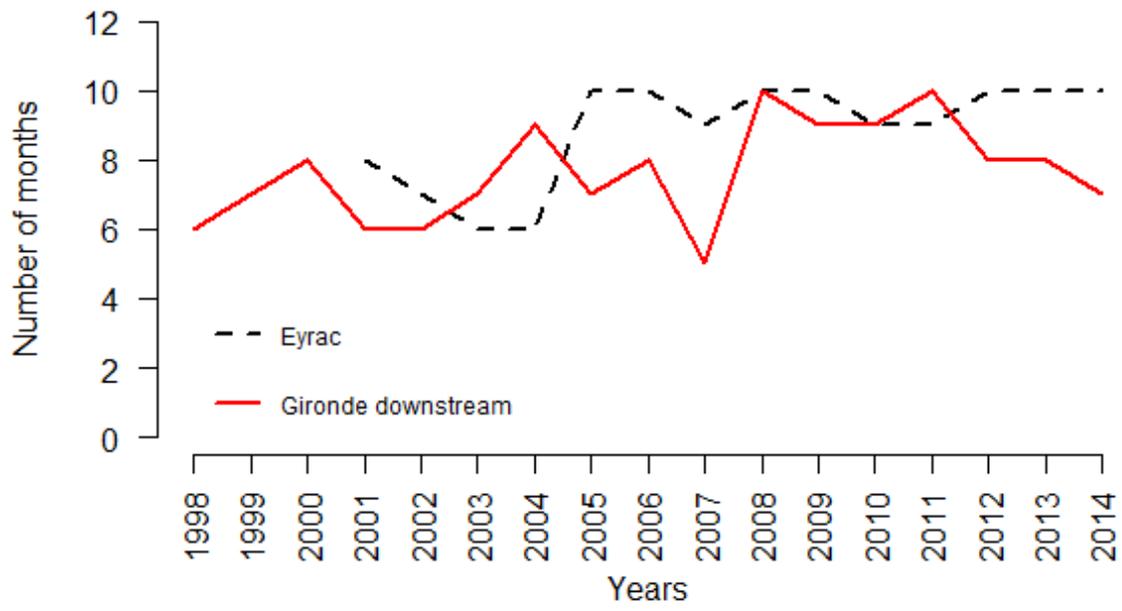


b) GIRONDE DOWNSTREAM



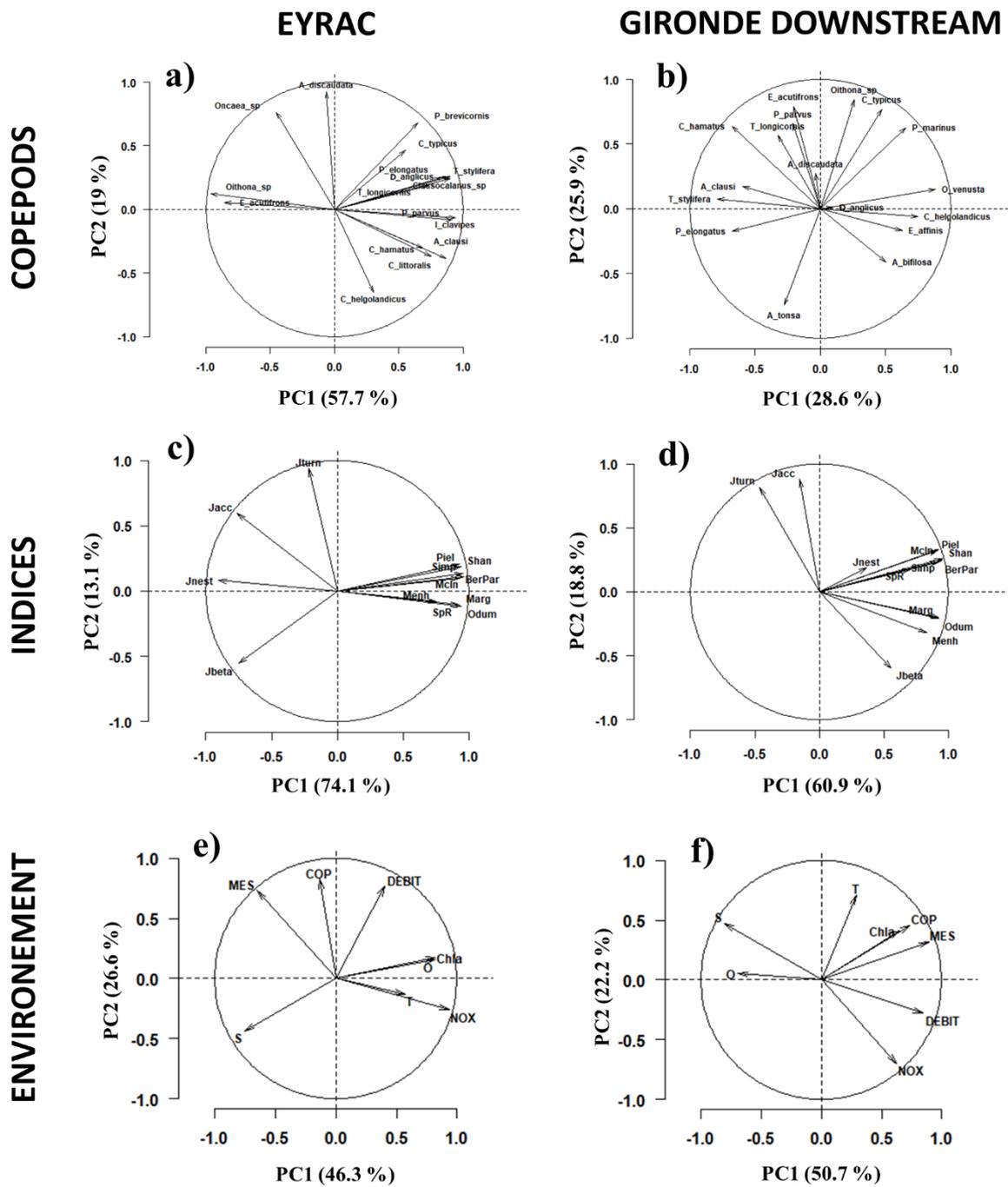
Supplementary Figure S2

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Supplementary Figure S3

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Supplementary Figure S4

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Species	Eyrac		Gironde downstream	
	Relative abundance (in %)	Presence (in %)	Relative abundance (in %)	Presence (in %)
<i>Acartia bifilosa</i>	--	--	11.63	65.4
<i>Acartia clausi</i>	5.26	43.5	2.81	46.2
<i>Acartia discaudata</i>	4.08	54	0.14	9.2
<i>Acartia tonsa</i>	--	--	14.73	35.4
<i>Alteutha interrupta</i>	--	--	0.01	2.3
<i>Calanus helgolandicus</i>	0.15	9.7	0.19	31.5
<i>Centropages hamatus</i>	0.55	37.9	4.75	49.2
<i>Centropages typicus</i>	0.39	15.3	0.25	20.8
<i>Clausocalanus sp</i>	0.49	19.4	--	--
<i>Cyclopinoïdes littoralis</i>	0.63	15.3	--	--
<i>Diaixis spp</i>	--	--	<0.01	1.5
<i>Ditrichocorycaeus anglicus</i>	0.56	43.5	0.19	40.8
<i>Pseudocalanus elongatus</i>	0.48	21	1.06	41.5
<i>Eurytemora affinis</i>	--	--	15.77	43.8
<i>Euterpina acutifrons</i>	41.53	98.4	17.67	83.8
<i>Goniopsyllus rostratus</i>	--	--	<0.01	1.5
<i>Isias clavipes</i>	0.67	17.7	--	--
<i>Labidocera wollastoni</i>	--	--	0.01	2.3
<i>Oithona spp</i>	10.07	92.7	1.11	41.5
<i>Oncaea spp</i>	4.66	69.4	0.51	45.4
<i>Paracalanus parvus</i>	17.03	95.2	18.96	93.1
<i>Paracartia grani</i>	0.14	4.8	--	--
<i>Parapontella brevicornis</i>	3.04	68.5	0.02	4.6
<i>Pseudodiaptomus marinus</i>	0.03	1.6	1.91	11.5
<i>Sapphirina spp</i>	0.03	3.2	0.03	4.6
<i>Temora longicornis</i>	7.74	62.9	7.80	48.5
<i>Temora stylifera</i>	2.46	33.1	0.46	25.4

Supplementary Table S1

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Number of months used to calculate annual means	Eyrac		Gironde downstream		
	PC1 (tot.)	PC2 (tot.)	PC1 (tot.)	PC2 (tot.)	PC3 (tot.)
	vs	vs	vs	vs	vs
	PCs1 (999 perm.)	PCs2 (999 perm.)	PCs1 (999 perm.)	PCs2 (999 perm.)	PCs3 (999 perm.)
	<i>rho</i>	<i>rho</i>	<i>rho</i>	<i>rho</i>	<i>rho</i>
10	1	1	1	1	1
9	0.973	0.893	0.750	0.665	0.836
8	0.958	0.818	0.639	0.529	0.733
7	0.939	0.756	0.592	0.482	0.644
6	0.917	0.676	0.551	0.426	0.542

Supplementary Table S2

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Environmental parameter	Eyrac		Gironde downstream	
	PC1	PC2	PC1	PC2
Temperature	-8.79	0.79	2.04	28.35
Salinity	-15.31	8.98	15.95	12.62
Oxygen	-18.04	1.11	11.83	0.15
Particulate Organic Carbon	-0.51	31.91	13.22	11.77
Suspended Particulate Matter	-11.38	25.11	19.55	5.72
Chlorophyll a	-18.14	1.44	10.24	9.50
Total Nitrogen	-23.48	3.20	9.64	27.56
River discharge	-4.34	27.45	17.53	4.33

Supplementary Table S3

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