



HAL
open science

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

Julien Richirt, Eric Goberville, Vania Ruiz-Gonzalez, Benoit Sautour

► **To cite this version:**

Julien Richirt, Eric Goberville, Vania Ruiz-Gonzalez, Benoit Sautour. Local changes in copepod composition and diversity in two coastal systems of Western Europe. *Estuarine, Coastal and Shelf Science*, 2019, 227, pp.106304. 10.1016/j.ecss.2019.106304 . hal-02303415

HAL Id: hal-02303415

<https://hal.sorbonne-universite.fr/hal-02303415>

Submitted on 29 Oct 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

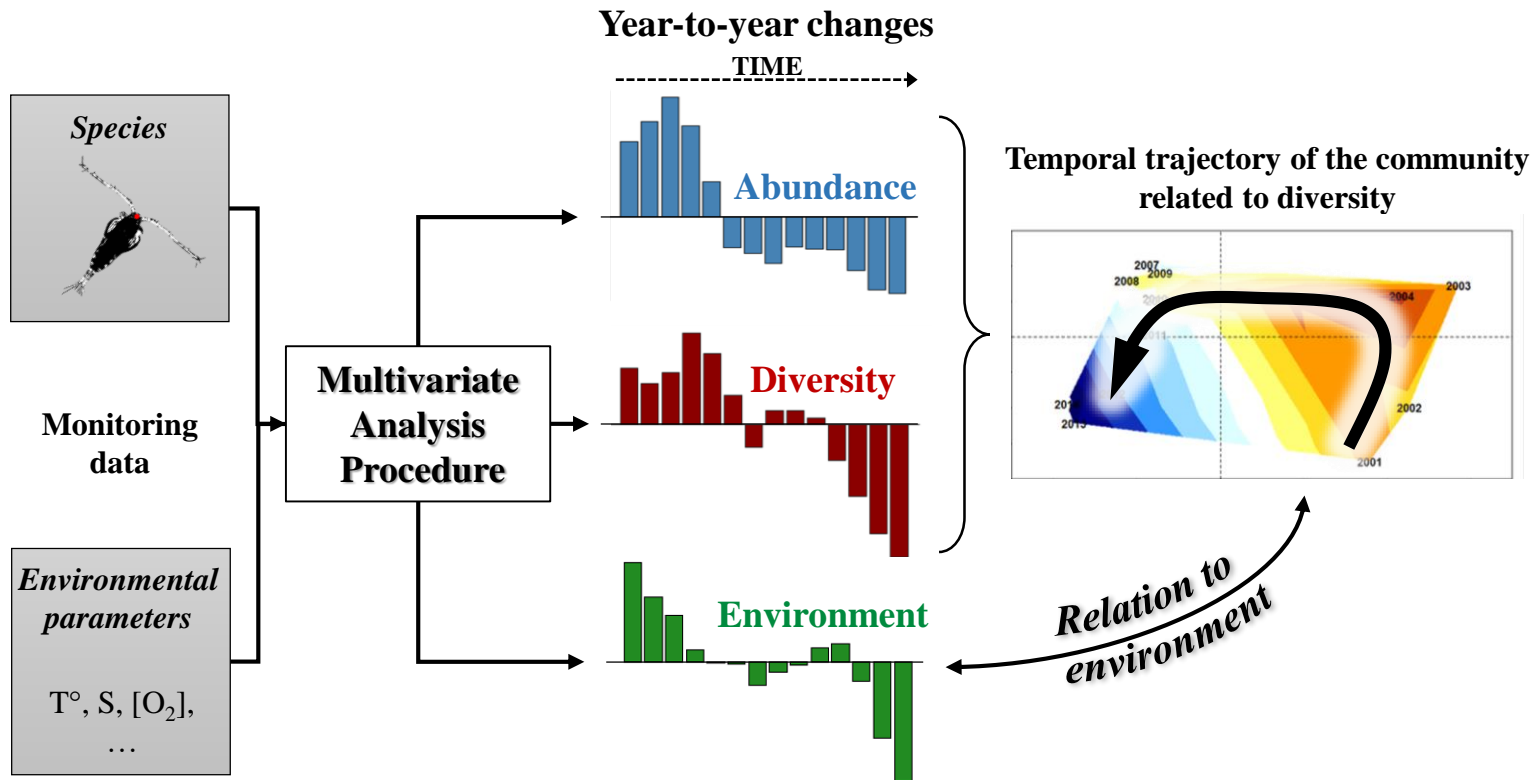
¹Université de Bordeaux, UMR CNRS 5805 EPOC Environnements et Paléo-environnements Océaniques et Continentaux, Rue Geoffroy Saint Hilaire, 33600 Pessac, France.

²Université d'Angers, LPG-BIAF, UMR CNRS 6112, 49045 Angers cedex, France

³Unité Biologie des organismes et écosystèmes aquatiques (BOREA), Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles, CNRS, IRD, CP53, 61, Rue Buffon, 75005, Paris, France

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)



1
2
3
4 1 Local changes in copepod composition and diversity in two coastal
5 2 systems of Western Europe
6
7 3
8
9 4
10 5
11 6

12 6 Julien Richirt^{1,2*}, Eric Goberville^{3*}, Vania Ruiz-Gonzalez¹ and Benoît Sautour¹
13
14 7
15 8
16

17 9 ¹Université de Bordeaux, UMR CNRS 5805 EPOC Environnements et Paléo-environnements
18 10 Océaniques et Continentaux, Rue Geoffroy Saint Hilaire, 33600 Pessac, France.

19 11 ²Université d'Angers, LPG-BIAF, UMR CNRS 6112, 49045 Angers cedex, France

20 12 ³Unité Biologie des organismes et écosystèmes aquatiques (BOREA), Muséum National
21 13 d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des
22 14 Antilles, CNRS, IRD, CP53, 61, Rue Buffon, 75005, Paris, France
23
24
25
26
27
28
29
30

31 17 * Both authors contributed equally

32 18 E-mail: richirt.julien@gmail.com / eric.goberville@upmc.fr
33
34
35
36
37
38
39
40

41 24 Abstract: 282 words

42 25 Main text: 6425 words

43 26 References: 97

44 27 Figures: 6

45 28 Tables: 3

46 29 Supplementary Figures: 4

47 30 Supplementary Tables: 3
48
49
50
51
52
53
54
55
56
57
58
59

33 *submitted to Estuarine, Coastal and Shelf Science*
34

60
61
62 **ABSTRACT**
63

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

119
120
121 **59 1. Introduction**
122
123
124

125 60 Coastal marine systems, which are among the most ecologically and economically important
126
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
130
131 63 forcing is not restricted to a particular biological component but extends to all ecological units, affecting
132
133 64 marine biodiversity from phytoplankton to top predators (Frederiksen et al., 2006; Chaalali et al.,
134
135 65 2013a), leading to alterations in the structure and functioning of coastal systems (Chevillot et al., 2018),
136
137 66 with possible ramifications for the terrestrial realm (Luczak et al., 2013). For example, three decades of
138
139 67 observation have revealed synchronous climate, environmental and biological community shifts in the
140
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
144
145 70 induced concomitant changes in hydrological and biological conditions, including abrupt modifications
146
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
150
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
156
157 76 measure the status of ecological conditions (Duffy et al., 2013; Elahi et al., 2015). Long-term
158
159 77 observations are essential to disentangle natural variations from unusual or extreme events (Lovett et
160
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
164
165 80 affect ecosystems (Goberville et al., 2010). To compile monitoring data across large numbers of species
166
167 81 and ecosystems, scientists and policymakers often rely on diversity indices (Pereira et al., 2013), easy-
168
169 82 to-implement measures of biodiversity for which the effort in calculation and computation is much less
170
171 83 cumbersome than multivariate approaches. These indices are also known to be appropriate tools for a
172
173 84 rapid and efficient communication between the scientific community, government agencies, funding
174
175
176
177

178
179
180 85 institutions and the general public (*e.g.* Lovett et al., 2007). However, many metrics exist and none
181
182 86 emerges as the best overall (Bandeira et al., 2013) nor combines all different facets of diversity (Salas
183
184 87 et al., 2006; Rombouts et al., 2013). Using a range of complementary indices enables to better evaluate
185
186 88 both the strengths and weaknesses of the different metrics in detecting changes over time (Rombouts et
187
188 89 al., 2013; Loiseau and Gaertner, 2015) or in assessing ecosystem status, when combined with relevant
189
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).
195
196 93 Major consumers of primary production, detrital organic matter or bacterial production according to
197
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
203
204 97 and on the sinking flux of particulate organic carbon, they significantly contribute to the biological
205
206 98 carbon pump (Beaugrand et al., 2010). Highly sensitive to changes in environmental conditions,
207
208 99 copepods also rapidly integrate environmental signals over generation time and transfer potential
209
210 100 changes to the next generation (Goberville et al., 2014).

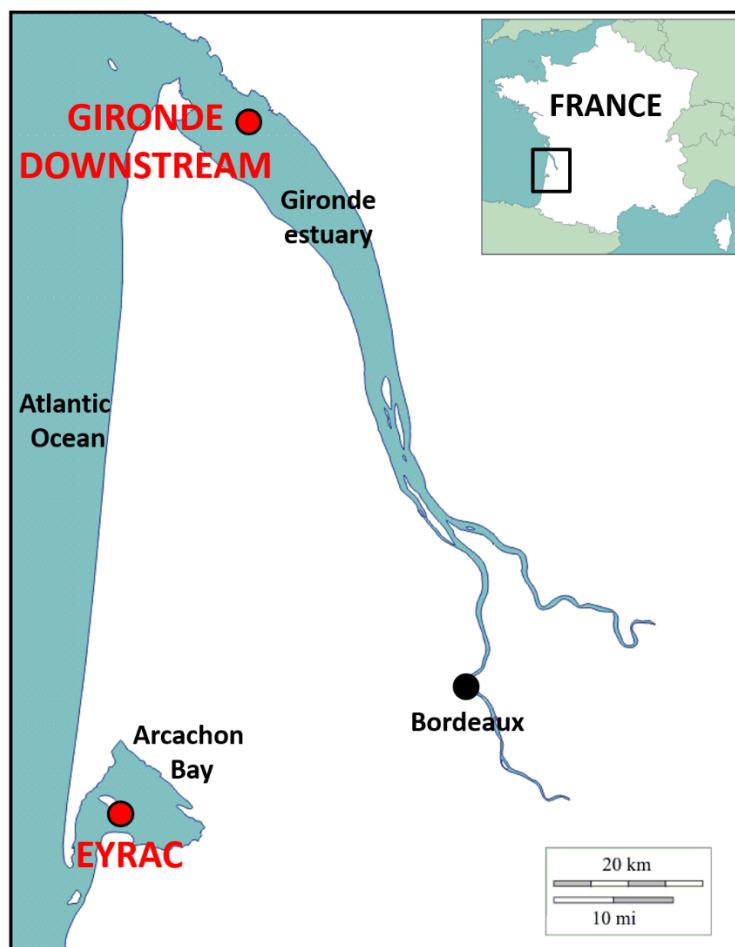
211
212
213 101 Changes in copepod abundances, diversity and community structure can have rapid and major
214
215 102 consequences on higher trophic level species. For example, previous studies have paralleled changes in
216
217 103 the abundance of *Calanus finmarchicus* or *Pseudocalanus* spp and alterations 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
228
229 109 the effects of anthropogenic impacts (Bandeira et al., 2013; Serranito et al., 2016). This list, far from
230
231 110 being exhaustive, sheds light on copepods as ideal candidates for tracking ecosystem changes
232
233 111 (Richardson, 2008).

237
238
239 112 Here, by using data from zooplankton surveys from 1998 to 2014, we examine year-to-year
240
241 113 changes in copepod communities (species abundances and taxonomic diversity) in two nearby littoral
242
243 114 areas of Western Europe (*i.e.* the Arcachon Bay and the Gironde estuary) that share similar climate
244
245 115 conditions but contrasting physical, chemical and hydrological environments. The following questions
246
247 116 are addressed: Do copepod communities differ between the two sites and change over time? Are trends
248
249 117 in taxonomic diversity apparent and linked to environmental changes? To study changes in species
250
251 118 abundances and diversity that took place in the Arcachon Bay and the Gironde estuary over the last two
252
253 119 decades, we combine a principal component analyses based-approach and commonly used taxonomic
254
255 120 diversity indices that account for the number of species (*e.g.* species richness), the evenness of
256
257 121 abundance distribution among species (*e.g.* Pielou index) and the variability in communities among
258
259 122 years (*e.g.* Jaccard index). We then investigate divergences between these two adjacent sites and explore
260
261 123 the possible mechanisms that explain diversity trends and species responses to environmental changes.
262

263 264 124 **2. Materials and methods**

265 266 267 268 125 *2.1. Sampling sites*

269
270
271 126 We selected two coastal systems located in the southeast of the Bay of Biscay along the French
272
273 127 coast (Fig. 1) to examine year-to-year changes in copepod abundances and diversity.
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295



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
367
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
373
374 149 s⁻¹ and 342 m³ s⁻¹, respectively) act on the growth of estuarine species in oligo- and mesohaline water
375
376 150 masses. In this naturally stressed environment (Dauvin et al., 2009), an increasing gradient of
377
378 151 zooplankton diversity is observed from the upstream to the downstream areas (Sautour and Castel, 1995;
379
380 152 Chaalali et al., 2013a).

381 382 153 *2.2. Biological datasets*

383
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
388
389 156 at high tide = 8.2m) and from 2001 to 2014 by the SOARC survey ('Service d'Observation du bassin
390
391 157 d'ARCachon') at the Eyrac site (average depth at high tide = 8m). A standardised protocol has been
392
393 158 established before conducting the surveys, so that sampling is carried out at a monthly scale in both
394
395 159 sites, at high tide and in the top first two meters below the surface using horizontal tow and a standard
396
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.

400
401 162 In the laboratory, samples were sorted and copepods were counted and identified to the species
402
403 163 level as far as possible. Identification was carried out with a stereomicroscope Zeiss Axiovert (200 and
404
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).

414
415
416 166 Because rare species may reflect stochastic sampling effects (Poos and Jackson, 2012) and
417
418 167 decrease the signal-to-noise ratio (Borcard et al., 2011) only species with a presence >5% over the period
419
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,
438
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
478
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
482
483 195 Eyrac site and the first three PCs for the Gironde downstream site were thus examined (Fig. 2).
484

485
486 196 A possible influence of the moving average process was tested by applying a Procrustes procedure
487
488 197 (with 999 permutations; Legendre and Legendre, 2012): by comparing two matrices that describe the
489
490 198 same entity (here copepod abundances), the Procrustes test statistically evaluate whether the two
491
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
495
496 201 dependency on meteorological conditions during sampling (*e.g.* intense winds), the number of samples
497
498 202 per year may vary over time (Fig. S3), potentially leading to bias in the temporal comparison of annual
499
500 203 abundances (Beaugrand and Edwards, 2001). To examine how sampling effort may influence the
501
502 204 characterisation of changes in coastal copepods, we considered a decreasing number of months to
503
504 205 calculate annual means (from 10 months - *i.e.* the maximum of samples available for the more well-
505
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
509
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
517
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)

524
525

526 215 Changes in alpha (α ; Whittaker, 1972) and beta (β ; Anderson et al., 2006) diversity of coastal
527
528 216 copepods were assessed by using 13 easily interpretable diversity indices - among the most commonly
529
530
531

532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590

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

591
592
593 243 (Eyrac site, Fig. 5a) and 1998-2014 (Gironde downstream site, Fig. 5b-c), the value of changes in
594
595 244 taxonomic diversity (*i.e.* results from the PCA performed on indices) was assigned and represented by
596
597 245 a colour scale; the blue (red) gradient corresponds to high negative (positive) values. By characterising
598
599 246 each year by reference to changes in copepod diversity, this representation showed time series of
600
601 247 responses of each site, *i.e.* changes in copepod communities over the time period.
602

603
604 248 To characterise the main year-to-year changes that took place in physical, chemical and
605
606 249 hydrological conditions at each site, we followed the same procedure than that applied to identify
607
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

630
631
632 260 Year-to-year changes in PC1 of the PCA performed on copepod abundances at the Eyrac site
633
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
643
644 266 negatively related to changes in the first PC, showing an increase in their abundance from 2006 to 2014.
645
646 267 The second principal component (19% of the total variability) exhibited periods of negative (2001-2002
647
648
649

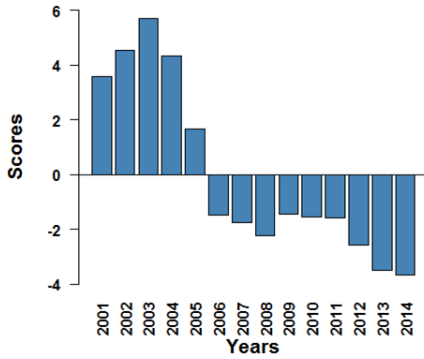
650
651
652 268 and 2012-2014) and positive (2003-2011) anomalies (Fig. 2b). The study of the second eigenvector
653
654 269 revealed that an increase in the abundance of *Acartia discaudata* and *Parapontella brevicornis*, and to
655
656 270 a lesser extent *Centropages typicus*, occurred between 2003 and 2011, while a reduction in the
657
658 271 abundance of *Calanus helgolandicus* and *Oncaea* spp. was observed.
659
660

661 272 3.1.2. The Gironde downstream site

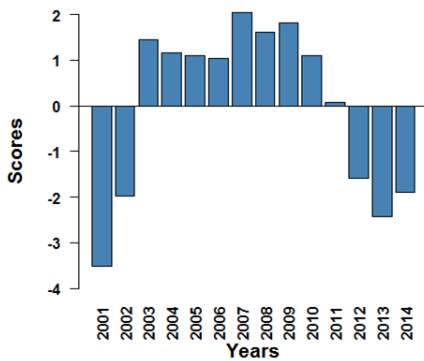
662
663 273 The first PC of the PCA performed on copepods at the Gironde downstream site (28.6% of the
664
665 274 total variability) showed periods of positive (1998-2003 and 2012-2014) and negative (2003-2011)
666
667 275 anomalies (Fig. 2c). Inspection of the first eigenvector indicated that *Oncaea* spp., *C. helgolandicus* and,
668
669 276 to a lesser extent, *Pseudodiaptomus marinus* and *Eurytemora affinis* were positively related to PC1,
670
671 277 corresponding to a reduction in their abundance between 2003 and 2011 (Table 1, Fig. S4b). In contrast,
672
673 278 the abundance of *Temora stylifera*, *Centropages hamatus*, *Pseudocalanus elongatus* and *Acartia clausi*
674
675 279 increased. After a period of strong negative anomalies (1998-2003), year-to-year changes in PC2 (25.9%
676
677 280 of the total variability) mainly expressed positive anomalies from 2003 (Fig. 2d). *Acartia tonsa* was the
678
679 281 only species strongly negatively correlated with this change, revealing a constant decline. Species such
680
681 282 as *Oithona* spp., *E. acutifrons* or *C. typicus* were positively related to PC2, corresponding to an increase
682
683 283 in abundance over the last decade. Year-to-year changes in the third PC (19.6% of the total variability)
684
685 284 displayed pronounced positive values from 2001 to 2005, at the time the component showed negative
686
687 285 anomalies (2006-2013). *A. discaudata* and *Acartia bifilosa* were positively related to PC3, denoting
688
689 286 decreasing abundances from the mid-2000s, while *D. anglicus* increased. For the period 2001-2014, this
690
691 287 third PC revealed strong similarities with the PC1 observed at the Eyrac site (Fig. 2a versus Fig. 2e).
692
693
694
695
696
697
698
699
700
701
702
703
704
705
706
707
708

EYRAC

a) PC1 : 57.7%



b) PC2 : 19%

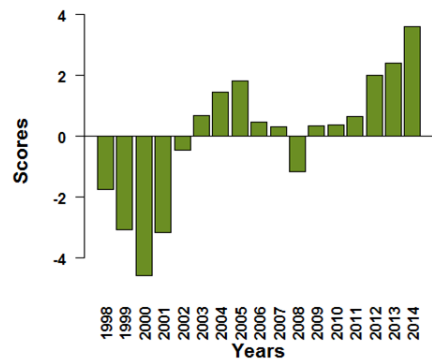


GIRONDE DOWNSTREAM

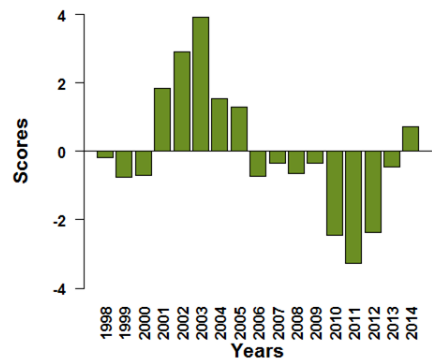
c) PC1 : 28.6%



d) PC2 : 25.9%



e) PC3 : 19.6%



288

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.

294

768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808
809
810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826

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

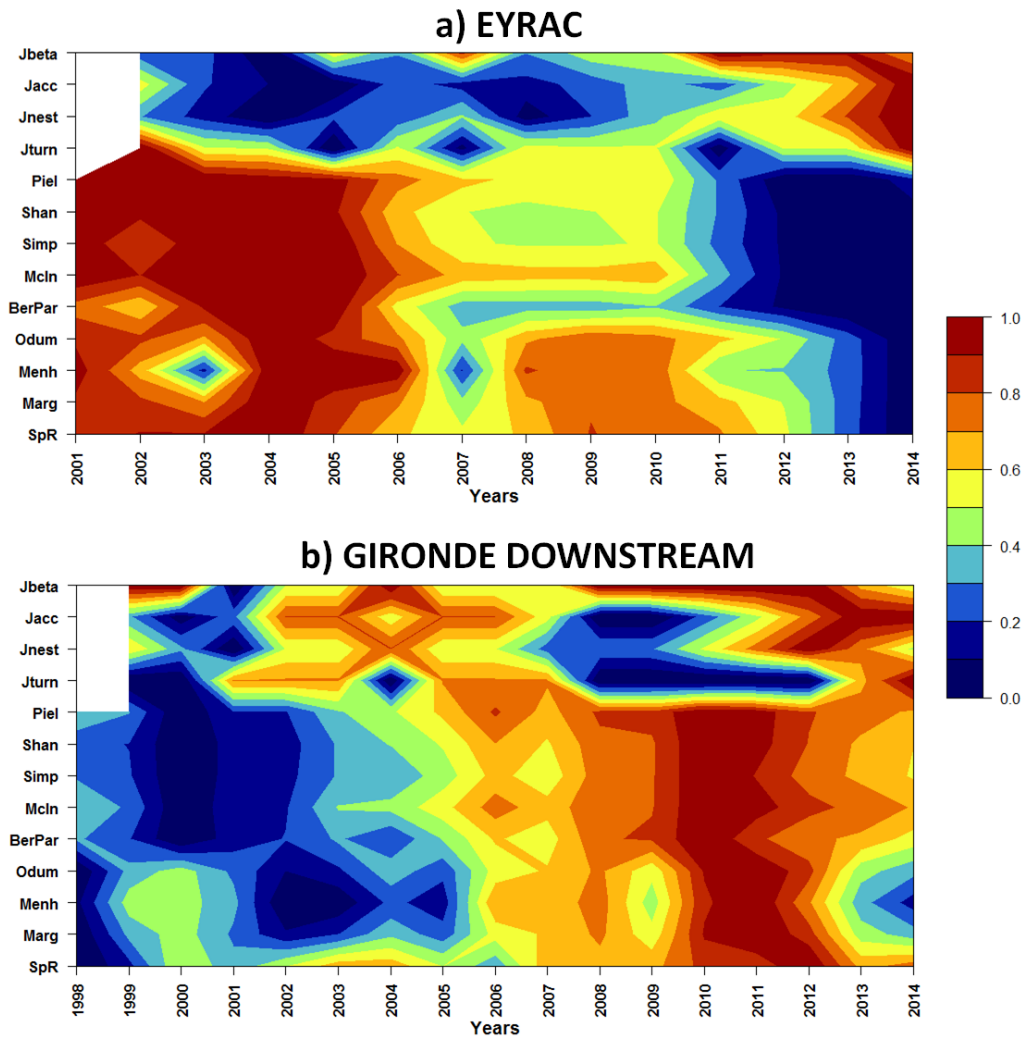
295 **Table 1.** Results from the standardised PCAs performed on copepod abundances. The first two
 296 eigenvectors (for Eyrac) and the first three eigenvectors (for Gironde downstream) are included and
 297 show the contribution of each species to the principal components. Values in bold were superior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

827
828
829
830
831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863
864
865
866
867
868
869
870
871
872
873
874
875
876
877
878
879
880
881
882
883
884
885

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.

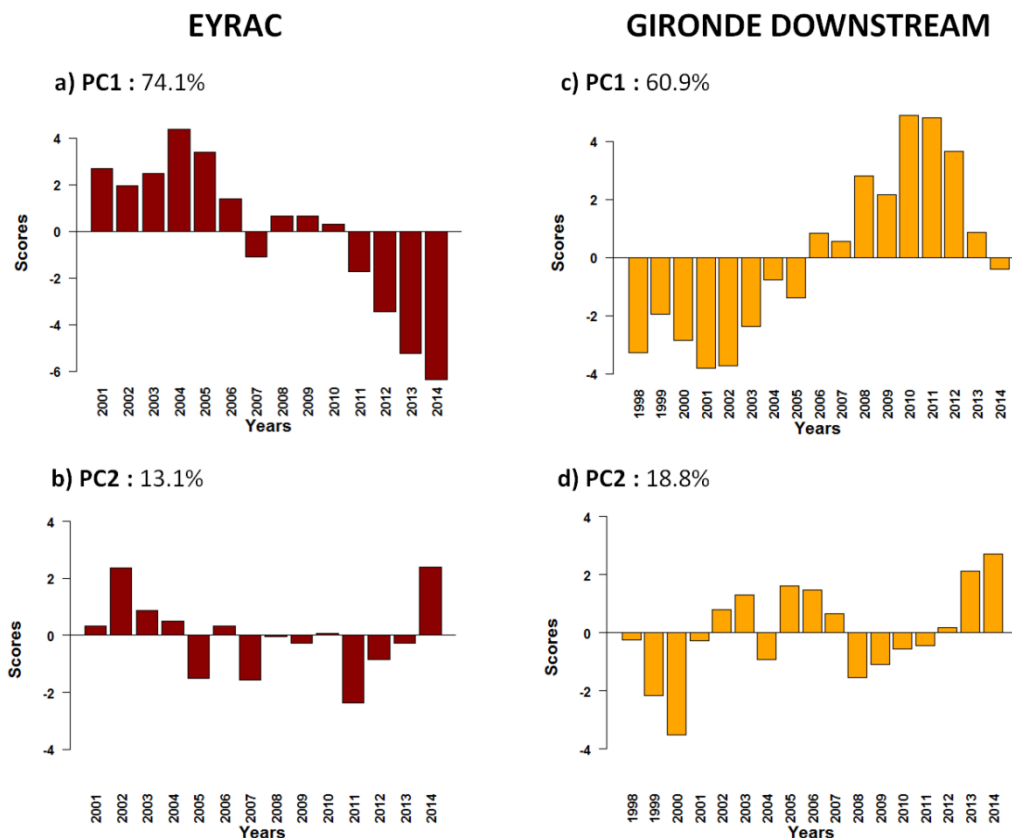
312 3.2.1. The Eyrac site

886
887
888 313 The general patterns of copepod diversity at the Eyrac site (Fig. 3a) and results from the PCA
889
890 314 based on indices (Fig. 4a-b, Table 2 and Fig. S4c) revealed a clear contrast between α and β -diversity
891
892 315 measures, leading to two groups. The first group encompassed α -diversity indices that mostly
893
894 316 contributed to the PC1 (74.1% of the total variability; Fig. 4a, Table 2). The highest values of the
895
896 317 component (2001-2006), were followed by a period of low values until 2011. Only a slight difference
897
898 318 in the timing of changes was observed between indices based on the number of species (*e.g.* species
899
900 319 richness) and evenness and heterogeneous indices such as Pielou and Simpson indices (Fig. 3a). Low α -
901
902 320 diversity, detected from 2011, corresponded to a loss of species, probably related to a decrease in typical
903
904 321 coastal species such as *I. clavipes* and *C. helgolandicus*; copepod assemblages became dominated by
905
906 322 three taxa: *E. acutifrons*, *Oithona* spp. and *Oncaea* spp. (Fig. S2). The second group, which gathered
907
908 323 together β -diversity indices (*i.e.* the Jaccard's dissimilarity index and its components), showed low
909
910 324 values until 2011-2012 that suggested weak alterations in species assemblages during this period. From
911
912 325 2011, the marked increase in β -diversity trend revealed a high variability in assemblages in relation to a
913
914 326 loss of species, probably because a perturbation in community structure took place at the Eyrac site (Ives
915
916 327 & Carpenter, 2007). Year-to-year changes in the PC2 (13.1% of the total variability; Fig. 4b) were
917
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
924
925 331 α and β -diversities (Fig. 3b), a result supported by results from the PCA (Fig. 4c-d, Table 2 and Fig.
926
927 332 S4d). Alpha-diversity measures, which were related to the first PC of the PCA on indices (60.9% of the
928
929 333 total variability; Fig. 4c), exhibited inverse patterns of variation when compared to Eyrac: low values
930
931 334 were observed until the mid-2000s, followed by a strong increase until 2011 and a progressive decrease
932
933 335 from 2012. This reduction in α -diversity is especially visible for metrics based on the number of species
934
935 336 (*e.g.* Menhinick indice). Year-to-year changes in β -diversity indices were mainly associated to the
936
937 337 second principal component (18.8% of the total variability; Fig. 4d) and showed an increase in β -
938
939 338 diversity during the periods 2001-2007 and 2011-2014. In contrast to 2007-2010, a higher variability in
940
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|.

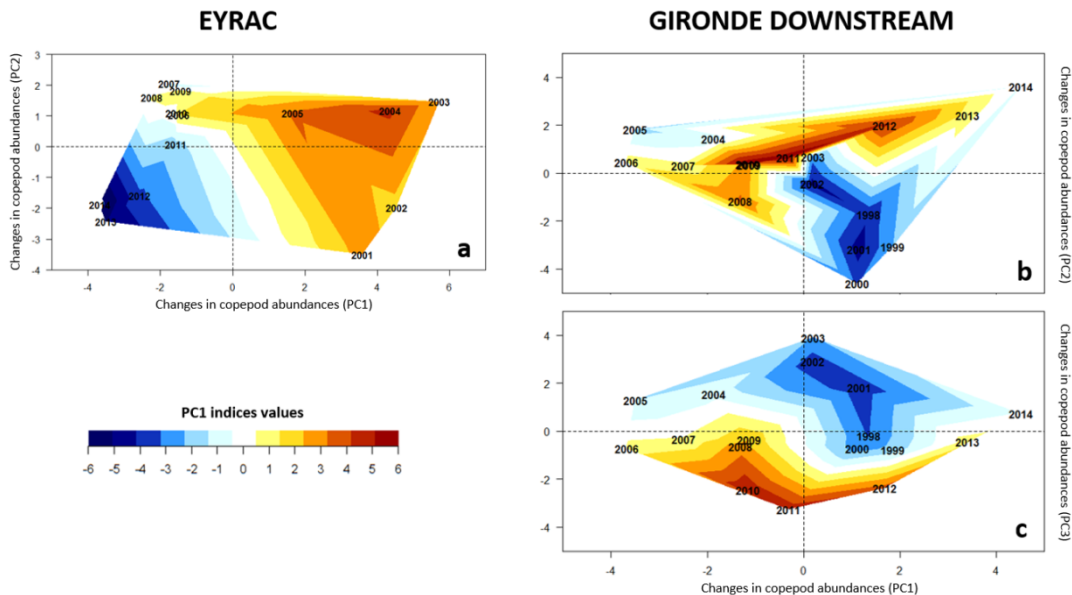
3.3. Relationships between changes in copepod abundances, taxonomic diversity and environmental conditions

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

1063
1064
1065
1066
1067
1068
1069
1070
1071
1072
1073
1074
1075
1076
1077
1078
1079
1080
1081
1082
1083
1084
1085
1086
1087
1088
1089
1090
1091
1092
1093
1094
1095
1096
1097
1098
1099
1100
1101
1102
1103
1104
1105
1106
1107
1108
1109
1110
1111
1112
1113
1114
1115
1116
1117
1118
1119
1120
1121

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.

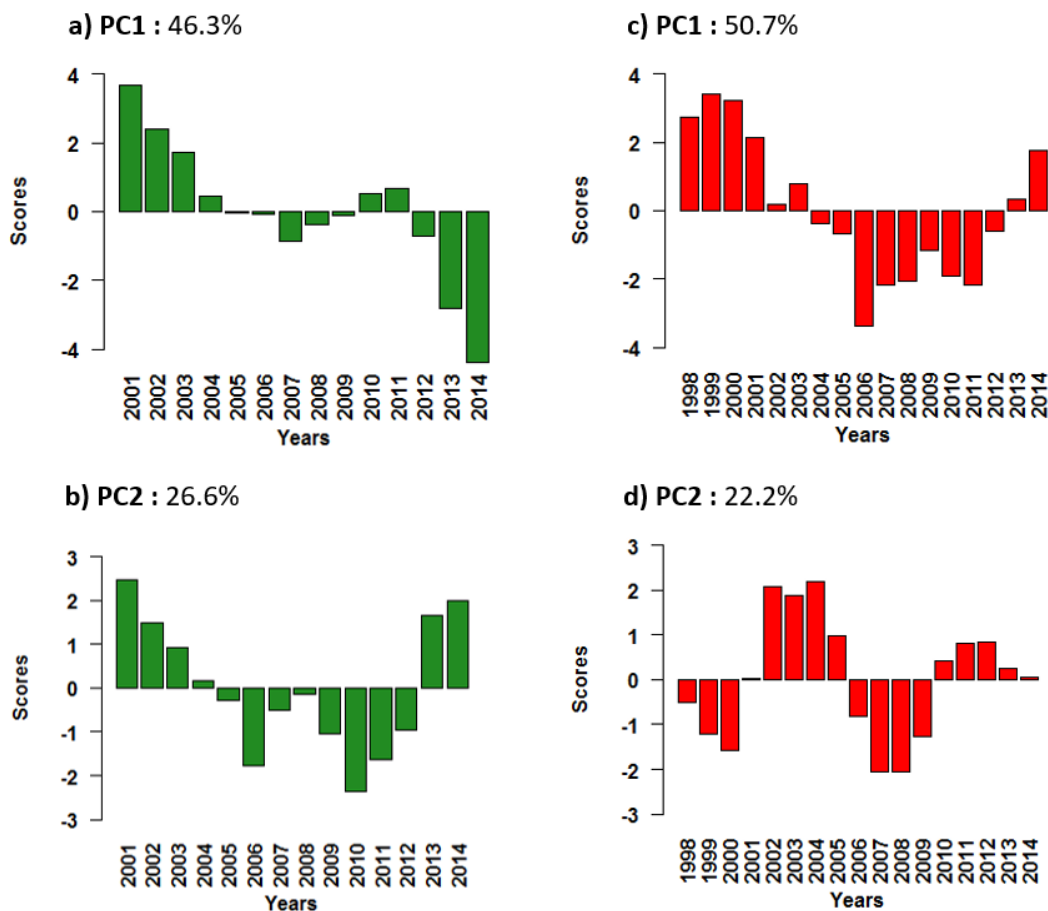


368
369 **Figure 5.** Relationships between changes in coastal copepod diversity and changes in coastal
370 copepod abundances for the Eyrac site (left panel) and the Gironde downstream site (right panels) (a)
371 Relationships between changes in diversity (first PC of the PCA performed on taxonomic 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

1122
1123
1124
1125
1126
1127
1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160
1161
1162
1163
1164
1165
1166
1167
1168
1169
1170
1171
1172
1173
1174
1175
1176
1177
1178
1179
1180

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.



394

1181
1182
1183
1184
1185
1186
1187
1188
1189
1190
1191
1192
1193
1194
1195
1196
1197
1198
1199
1200
1201
1202
1203
1204
1205
1206
1207
1208
1209
1210
1211
1212
1213
1214
1215
1216
1217
1218
1219
1220
1221
1222
1223
1224
1225
1226
1227
1228
1229
1230
1231
1232
1233
1234
1235
1236
1237
1238
1239

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, $r=0.563$, $p=0.06$

1240
1241
1242
1243
1244
1245
1246
1247
1248
1249
1250
1251
1252
1253
1254
1255
1256
1257
1258
1259
1260
1261
1262
1263
1264
1265
1266
1267
1268
1269
1270
1271
1272
1273
1274
1275
1276
1277
1278
1279
1280
1281
1282
1283
1284
1285
1286
1287
1288
1289
1290
1291
1292
1293
1294
1295
1296
1297
1298

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

1299
1300
1301
1302
1303
1304
1305
1306
1307
1308
1309
1310
1311
1312
1313
1314
1315
1316
1317
1318
1319
1320
1321
1322
1323
1324
1325
1326
1327
1328
1329
1330
1331
1332
1333
1334
1335
1336
1337
1338
1339
1340
1341
1342
1343
1344
1345
1346
1347
1348
1349
1350
1351
1352
1353
1354
1355
1356
1357

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

1358
1359
1360
1361
1362
1363
1364
1365
1366
1367
1368
1369
1370
1371
1372
1373
1374
1375
1376
1377
1378
1379
1380
1381
1382
1383
1384
1385
1386
1387
1388
1389
1390
1391
1392
1393
1394
1395
1396
1397
1398
1399
1400
1401
1402
1403
1404
1405
1406
1407
1408
1409
1410
1411
1412
1413
1414
1415
1416

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.*

1417
1418
1419 490 *acutifrons*, neritic eurytopic species increasingly encountered in the polyhaline area of the estuary and
1420
1421 491 typically observed in the estuarine plume (Sautour et al., 2000) and *E. affinis* and *A. tonsa*, found in
1422
1423 492 great abundance in the oligo-mesohaline area of the estuary (David et al., 2005). Changes in physical,
1424
1425 493 chemical and hydrological conditions might have been responsible for variations in environmental
1426
1427 494 gradients in the downstream part of the Gironde estuary, with a stronger presence - at the sampling site
1428
1429 495 - of neritic waters which benefit marine species such as *C. helgolandicus*. While the increase in *P. parvus*
1430
1431 496 and *E. acutifrons* was probably induced by enhanced coastal water intrusions, as described upstream in
1432
1433 497 relation to the large mouth of the estuary and importance of the tidal prism (Jouanneau and Latouche,
1434
1435 498 1981; Chaalali et al., 2013b), the rise in *E. affinis* and *A. bifilosa* may have been favoured by punctual
1436
1437 499 inputs of freshwater (David et al., 2007). A warming of the estuary was associated to increasing
1438
1439 500 abundance of *A. tonsa* (Chaalali et al., 2013b; see their Fig. 5), but also to the establishment of the
1440
1441 501 Asiatic copepod, *P. marinus* (Brylinski et al., 2012). Increasing α -diversity in this site is consistent with
1442
1443 502 the rise in richness reported for a large number of coastal ecosystems worldwide (Elahi et al., 2015). In
1444
1445 503 the southeastern Bay of Biscay, in response to water quality improvement, changes in environmental
1446
1447 504 conditions and the arrival of new species, a zooplankton recolonisation of the inner estuary of Bilbao
1448
1449 505 took place between 1998 and 2011, with an increase in neritic copepod species and - to a lesser extent -
1450
1451 506 in the abundances of appendicularians, meroplanktonic bivalves and gastropods, (Uriarte et al., 2016).
1452
1453 507 Farther north, a long-term increase in copepod species richness was noticed in the Western Channel over
1454
1455 508 1988-2007 (Eloire et al., 2010). Contrasting individual trends in species abundances were observed
1456
1457 509 between this study and ours, however. While we also showed a rise in *Oncaea* spp. and *C. helgolandicus*
1458
1459 510 - that implies basin scale changes in species abundances (Eloire et al., 2010) - our conclusions on *P.*
1460
1461 511 *elongatus*, *Temora longicornis* and *A. clausi* diverge, suggesting (i) site-specific species responses,
1462
1463 512 probably induced by the local ecological context, and/or (ii) a consequence of the delineation of species'
1464
1465 513 distributional limits (see distribution maps in Castellani and Edwards, 2017).

1466
1467 514 By allowing quantitative assessments, diversity indices are welcomed by decision makers to
1468
1469 515 define policy guidelines, to determine suitable targets or to evaluate the effectiveness of management
1470
1471 516 actions (Gubbay, 2004; Laurila-Pant et al., 2015). Selecting one metric rather than another can influence

1476
1477
1478 517 the assessment of trends in diversity, however (Morris et al., 2014; Loiseau and Gaertner, 2015),
1479
1480 518 especially in littoral areas where strong environmental gradients and high variability of physico-
1481
1482 519 chemical parameters take place (Dauvin et al., 2009; Bouchet et al., 2018). Here, the use of a wide range
1483
1484 520 of indices strengthened our confidence in the characterisation of sudden changes in biodiversity as well
1485
1486 521 as the quantification of long-term trends; although we conceded that both functional and phylogenetic
1487
1488 522 diversity were not scrutinised due to data availability (Loiseau et al., 2016). In each site, diversity indices
1489
1490 523 performed similarly over the study period, not only because of the mathematical convergence between
1491
1492 524 some indices (Bandeira et al., 2013; Morris et al., 2014), but also because of the significance of changes
1493
1494 525 in copepod species. This was supported by the multivariate approach performed on species abundances.
1495
1496 526 While diversity indices are straightforward to effectively summarise and communicate diversity trends,
1497
1498 527 our results highlighted that combination with multivariate approaches provide useful insights into
1499
1500 528 community changes (*e.g.* distinguishing ‘winners’ and ‘losers’ species; see McGill et al., 2015).
1501
1502 529 Information of why diversity fluctuates is essential for proper interpretation of changes but it is also
1503
1504 530 essential to recall that long-term biodiversity time-series only inform on species abundances and variety
1505
1506 531 at a given location and at a number of points in time (Magurran et al., 2010). This was well summarised
1507
1508 532 by Magurran et al. (2010) who wrote: “*researchers cannot necessarily assume that responses to change*
1509
1510 533 *documented in long-term datasets will be universal, even where the same types of organisms are*
1511
1512 534 *involved*”.

1513
1514 535 Over the last few decades, many countries have mandated assessment of coastal water bodies
1515
1516 536 and classical diversity indices have been intensively used to characterise diversity patterns (Beaugrand
1517
1518 537 and Edwards, 2001; Magurran, 2013), to detect anthropogenic pressures (Serranito et al., 2016) or to
1519
1520 538 investigate ecosystem level consequences of diversity changes (Gagic et al., 2015). In the minds of
1521
1522 539 many, the unprecedented pace of global changes necessarily induced negative diversity trends, at any
1523
1524 540 spatial scale. This led policymakers to put emphasis on the need to mitigate diversity loss from local to
1525
1526 541 global levels (McGill et al., 2015) while disregarding possible positive diversity trends (Sax and Gaines,
1527
1528 542 2003). However, we showed here that opposite signals may emerge between nearby sites owing to local
1529
1530 543 ecological conditions (*e.g.* anthropogenic impacts, initial richness, species dominance; Elahi et al.,
1531
1532
1533
1534

1535
1536
1537 544 2015), environmental peculiarities of each system (McGill et al., 2015) or stochastic processes (Stegen
1538
1539 545 et al., 2013). Our findings provide evidence that more local studies need to be initiated in order to (1)
1540
1541 546 define site-specific ‘reference conditions’ and (2) better evaluate diversity trajectories at very fine scales
1542
1543 547 at which ecologists often work (Elahi et al., 2015). The degree of perturbation of an ecosystem should
1544
1545 548 be compared with a site in which only natural conditions are a source of variability (Davies and Jackson,
1546
1547 549 2006); but such references rarely exist (Goberville et al., 2011a). In addition, and because plankton
1548
1549 550 species of confined ecosystems (*e.g.* estuarine, lagoons, coastal basins...) can be present only a very
1550
1551 551 short period of time in the water column - with consequences on both their recording and biodiversity
1552
1553 552 assessment (Belmonte et al., 2013) - qualitative changes in communities in these areas must rely on
1554
1555 553 standardised long-term monitoring (Belmonte et al., 2013). In that sense, the inception of a long-term
1556
1557 554 survey of both near-shore and off-shore waters of the Bay of Biscay must be encouraged within the
1558
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.

1564 557 **Acknowledgements**

1565
1566
1567 558 We thank the National Institute for the Science of the Universe (CNRS) and the colleagues
1568
1569 559 associated to SOGIR-SOARC-SOMLIT – technicians, researchers, captains and crews – who have
1570
1571 560 contributed to the collection of the zooplankton samples. This work was part of the regional research
1572
1573 561 project INDICOP 2014-10464 (Région Nord – Pas-de-Calais).

1576 562 **References**

- 1577
1578
1579 563 Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta
1580 564 diversity. *Ecology Letters* 9, 683-693.
- 1581 565 Bachelet, G., Leconte, M., 2015. Macrofaune benthique. In: Quintin J.Y. et al.: Surveillance écologique
1582 566 du site du Blayais, année 2014. Rapp. IFREMER RST ODE/DYNECO/AG/15-01, pp. 199-228.
- 1583 567 Bandeira, B., Jamet, J-L., Jamet, D., Ginoux. J-M., 2013. Mathematical convergences of biodiversity
1584 568 indices. *Ecological Indicators* 29, 522-528.
- 1585 569 Baselga, A., Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. *Methods in*
1586 570 *Ecology and Evolution* 3, 808-812.
- 1587 571 Basu, B.K., Pick, F.R., 1996. Factors regulating phytoplankton and zooplankton biomass in temperate
1588 572 rivers. *Limnology and Oceanography* 41, 1572-1577.
- 1589
1590
1591
1592
1593

1594
1595
1596 573 Beaugrand, G., 2012. Unanticipated biological changes and global warming. *Marine Ecology Progress Series* 445, 293-301.
1597 574
1598 575 Beaugrand, G., Edwards, M., 2001. Differences in performance among four indices used to evaluate
1599 576 diversity in planktonic ecosystems. *Oceanologica Acta* 24, 467-477.
1600 577 Beaugrand, G., Edwards, M., Legendre, L., 2010. Marine biodiversity, ecosystem functioning, and
1601 578 carbon cycles. *Proceedings of the National. Academy of Sciences of the United States of America*
1602 579 107, 10120-10124.
1603 580 Beaugrand, G., Harlay, X., Edwards, M., 2014. Detecting plankton shifts in the North Sea: a new abrupt
1604 581 ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series* 502, 85-104.
1605 582 Beaugrand, G., Kirby, R.R., 2016. Quasi-deterministic responses of marine species to climate change.
1606 583 *Climate Research*. 69, 117-128.
1607 584 Beaugrand, G., Reid, P.C., 2012. Relationships between North Atlantic salmon, plankton, and
1608 585 hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science* 69, 1549-1562.
1609 586 Belmonte, G., Vaglio, I., Rubino, F., Alabiso, G., 2013. Zooplankton composition along the confinement
1610 587 gradient of the Taranto Sea System (Ionian Sea, south-eastern Italy). *Journal of Marine Systems*,
1611 588 128, 222-238.
1612 589 Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology with R*. New York: Springer Verlag,
1613 590 306p.
1614 591 Bouchet, V.M.P., Goberville, E., Frontalini, F., 2018. Benthic foraminifera to assess Ecological Quality
1615 592 Statuses in Italian transitional waters. *Ecological Indicators* 84, 130-139.
1616 593 Box, G.E.P., Jenkins, G.W., 1976. *Time series analysis: forecasting and control*. Holden-Day, San
1617 594 Francisco, 575 p.
1618 595 Brylinski, J-M., Antajan, E., Raud, T., Vincent, D., 2012. First record of the Asian copepod
1619 596 *Pseudodiaptomus marinus* Sato, 1913 (Copepoda: Calanoida: Pseudodiaptomidae) in the
1620 597 southern bight of the North Sea along the coast of France. *Aquatic Invasions* 7, 577-584.
1621 598 Castel, J., Courties, C., 1982. Composition and differential distribution of zooplankton in Arcachon Bay.
1622 599 *Journal of Plankton Research* 4, 417-433.
1623 600 Castellani, C., Edwards, M., 2017. *Marine Plankton: A Practical Guide to Ecology, Methodology, and*
1624 601 *Taxonomy*. Oxford University Press, 704p.
1625 602 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated
1626 603 modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* 1,
1627 604 e1400253.
1628 605 Chaalali, A., Beaugrand, G., Boët, P., Sautour, B., 2013a. Climate-caused abrupt shifts in a European
1629 606 macrotidal estuary. *Estuaries and Coasts* 36, 1193-1205.
1630 607 Chaalali, A., Chevillot, X., Beaugrand, G., David, V., Luczak, C., Boët, P., Sottolichio, A., Sautour, B.,
1631 608 2013b. Changes in the distribution of copepods in the Gironde estuary: A warming and
1632 609 marinisation consequence? *Estuarine, Coastal and Shelf Science* 134, 150-161.
1633 610 Chao, A., Shen, T-J., 2003. Nonparametric estimation of Shannon's index of diversity when there are
1634 611 unseen species in sample. *Environmental and Ecological Statistics* 10, 429-443.
1635 612 Chelton, D.B., 1984. Commentary: short-term climatic variability in the northeast Pacific Ocean, in:
1636 613 Percy, W. (Ed.), *The influence of ocean conditions on the production of salmonids in the North*
1637 614 *Pacific*. Oregon State University Press, Corvallis, pp. 87-99.
1638 615 Chevillot, X., Pierre, M., Rigaud, A., Drouineau, H., Chaalali, A., Sautour, B., Lobry, J., 2016. Abrupt
1639 616 shifts in the Gironde fish community: an indicator of ecological changes in an estuarine
1640 617 ecosystem. *Marine Ecology Progress Series* 549, 137-151.
1641 618 Chevillot, X., Tecchio, S., Chaalali, A., Lassalle, G., Selleslagh, J., Castelnaud, G., David, V., Bachelet,
1642 619 G., Niquil, N., Sautour, B., Lobry, J., 2018. Global changes jeopardize the trophic carrying
1643 620 capacity and functioning of estuarine ecosystems. *Ecosystems*, pp. 1-23.
1644 621 Cloern, J.E., Hieb, K.A., Jacobson, T., Sansó, B., Di Lorenzo, E., Stacey, M.T., Largier, J.L., Meiring,
1645 622 W., Peterson, W.T., Powell, T.M., 2010. Biological communities in San Francisco Bay track
1646 623 large-scale climate forcing over the North Pacific. *Geophysical Research Letters* 37, L21602.

1653
1654
1655
1656
1657
1658
1659
1660
1661
1662
1663
1664
1665
1666
1667
1668
1669
1670
1671
1672
1673
1674
1675
1676
1677
1678
1679
1680
1681
1682
1683
1684
1685
1686
1687
1688
1689
1690
1691
1692
1693
1694
1695
1696
1697
1698
1699
1700
1701
1702
1703
1704
1705
1706
1707
1708
1709
1710
1711

- 624 Cushing, D.H., 1984. The gadoid outburst in the North Sea. ICES Journal of Marine Science 41, 159-
625 166.
- 626 Dauvin, J.-C., Bachelet, G., Barillé, A.-L., Blanchet, H., De Montaudouin, X., Lavesque, N., Ruellet,
627 T., 2009. Benthic indicators and index approaches in the three main estuaries along the French
628 Atlantic coast (Seine, Loire and Gironde). Marine Ecology 30, 228-240.
- 629 David, V., Sautour, B., Chardy, P., 2007. Successful colonization of the calanoid copepod *Acartia tonsa*
630 in the oligo-mesohaline area of the Gironde estuary (SW France) - Natural or anthropogenic
631 forcing? Estuarine, Coastal and Shelf Science 71, 429-442.
- 632 David, V., Sautour, B., Chardy, P., Leconte, M., 2005. Long-term changes of the zooplankton variability
633 in a turbid environment: The Gironde estuary (France). Estuarine, Coastal and Shelf Science 64,
634 171-184.
- 635 Davies, S.P., Jackson, S.K., 2006. The biological condition gradient: a descriptive model for interpreting
636 change in aquatic ecosystems. Ecological Applications 16, 1251-1266.
- 637 Davison, A.C., Hinkley, D.V., 1997. Bootstrap methods and their application. Cambridge University
638 Press, United States of America, 592pp.
- 639 de Montaudouin, X., Lucia, M., Binias, C., Lassudrie, M., Baudrimont, M., Legeay, A., Raymond, N.,
640 et al., 2016. Why is Asari (=Manila) clam *Ruditapes philippinarum* fitness poor in Arcachon Bay:
641 A meta-analysis to answer? Estuarine, Coastal and Shelf Science 179, 226-235.
- 642 Duffy, J.E., Amaral-Zettler, L.A., Fautin, D.G., Paulay, G., Rynearson, T.A., Sosik, H.M., Stachowicz,
643 J.J., 2013. Envisioning a marine biodiversity observation network. BioScience 63, 350-361.
- 644 Elahi, R., O'Connor, Mary I., Byrnes, Jarrett E.K., Dunic, J., Eriksson, Britas K., et al., 2015. Recent
645 trends in local-scale marine biodiversity reflect community structure and human impacts. Current
646 Biology 25, 1938-1943.
- 647 Eloire, D., Somerfield, P.J., Conway, D.V.P., Halsband-Lenk, C., Harris, R., Bonnet, D., 2010.
648 Temporal variability and community composition of zooplankton at station L4 in the Western
649 Channel: 20 years of sampling. Journal of Plankton Research 32, 657-679.
- 650 Fraser, J., 1968. Standardization of zooplankton sampling methods at sea. Monographs on
651 oceanographic methodology 2, 1-174.
- 652 Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to
653 top predators: bottom-up control of a marine food web across four trophic levels. Journal of
654 Animal Ecology 75, 1259-1268.
- 655 Frontier, S., 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes
656 principales: Comparaison avec le modèle du bâton brisé. Journal of Experimental Marine Biology
657 and Ecology 25, 67-75.
- 658 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., et al., 2015.
659 Functional identity and diversity of animals predict ecosystem functioning better than species-
660 based indices. Proceedings of the Royal Society B: Biological Sciences 282.
- 661 Goberville, E., Beaugrand, G., Edwards, M., 2014. Synchronous response of marine plankton
662 ecosystems to climate in the Northeast Atlantic and the North Sea. Journal of Marine Systems
663 129, 189-202.
- 664 Goberville, E., Beaugrand, G., Sautour, B., Tréguer, P., 2010. Climate-driven changes in coastal marine
665 systems of Western Europe. Marine Ecology Progress Series 408, 129-147.
- 666 Goberville, E., Beaugrand, G., Sautour, B., Tréguer, P., 2011. Evaluation of coastal perturbations: a new
667 mathematical procedure to detect changes in the reference state of coastal systems. Ecological
668 Indicators 11, 1290-1300.
- 669 Gubbay, S., 2004. A review of marine environmental indicators reporting on biodiversity aspects of
670 ecosystem health. Royal Society for the Protection of Birds, Sandy, United Kingdom.
- 671 Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez,
672 L.F., et al., 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9,
673 228-241.
- 674 Heip, C.H., Herman, P.M., Soetaert, K., 1998. Indices of diversity and evenness. Océanis 24, 61-87.

1712
1713
1714 675 Horváth, Z., Vad, C. F., Tóth, A., Zsuga, K., Boros, E., Vörös, L., & Ptasnik, R., 2014. Opposing patterns
1715 676 of zooplankton diversity and functioning along a natural stress gradient: when the going gets
1716 677 tough, the tough get going. *Oikos* 123, 461-471.
1717 678 Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology* 22,
1718 679 415-427.
1719 680 Ibanez, F., Dauvin, J.-C., 1998. Shape analysis of temporal ecological processes: long-term changes in
1720 681 English Channel macrobenthic communities. *Coenoses* 13, 115-129.
1721 682 Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. *Science*, 317(5834), 58-62.
1722 683 Johnson, C., Pepin, P., Curtis, K.A., Lazin, G., Casault, B., Colbourne, E., Galbraith, P.S., Harvey, M.,
1723 684 Maillet, G., Starr, M., 2014. Indicators of pelagic habitat status in the northwest Atlantic.
1724 685 Canadian Science Advisory Secretariat Research Document 2014, 047.
1725 686 Jolliffe, I., 2002. Principal component analysis. Wiley Online Library, 487p.
1726 687 Jouanneau, J.M., Latouche, C., 1981. The Gironde Estuary. In *Contribution to Sedimentology*
1727 688 (Fürchtbauer, H., Lisitzyn, A.P., Millerman, J.D. & Seibold, E., eds). 10, Springer-Verlag,
1728 689 Stuttgart, pp. 1-115.
1729 690 King, J.R., Jackson, D.A., 1999. Variable selection in large environmental data sets using principal
1730 691 components analysis. *Environmetrics* 10, 67-77.
1731 692 Kujala, H., Burgman, M.A., Moilanen, A., 2013. Treatment of uncertainty in conservation under climate
1732 693 change. *Conservation Letters* 6, 73-85.
1733 694 Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J., Haughland, D.L., 2009.
1734 695 Indices for monitoring biodiversity change: Are some more effective than others? *Ecological*
1735 696 *Indicators* 9, 432-444.
1736 697 Laurila-Pant, M., Lehtikoinen, A., Uusitalo, L., Venesjärvi, R., 2015. How to value biodiversity in
1737 698 environmental management? *Ecological Indicators* 55, 1-11.
1738 699 Lefebvre, A., Guiselin, N., Barbet, F., Artigas, F.L., 2011. Long-term hydrological and phytoplankton
1739 700 monitoring (1992–2007) of three potentially eutrophic systems in the eastern English Channel
1740 701 and the Southern Bight of the North Sea. *ICES Journal of Marine Science* 68, 2029-2043.
1741 702 Legendre, P., Legendre, L., 2012. *Numerical Ecology*, Third Edition ed. Elsevier, 1006p.
1742 703 Lindenmayer, D., Pierson, J., Barton, P., Beger, M., Branquinho, C., Calhoun, A., Caro, T., et al., 2015.
1743 704 A new framework for selecting environmental surrogates. *Science of the Total Environment* 538,
1744 705 1029-1038.
1745 706 Loiseau, N., Gaertner, J.-C., 2015. Indices for assessing coral reef fish biodiversity: the need for a change
1746 707 in habits. *Ecology and Evolution* 5, 4018-4027.
1747 708 Loiseau, N., Gaertner, J.C., Kulbicki, M., Mérigot, B., Legras, G., Taquet, M., Gaertner-Mazouni, N.,
1748 709 2016. Assessing the multicomponent aspect of coral fish diversity: The impact of sampling unit
1749 710 dimensions. *Ecological Indicators* 60, 815-823.
1750 711 Lovett, G.M., Burns, D.A., Driscoll, C.T., Jenkins, J.C., Mitchell, M.J., Rustad, L., Shanley, J.B.,
1751 712 Likens, G.E., Haeuber, R., 2007. Who needs environmental monitoring? *Frontiers in Ecology and*
1752 713 *the Environment* 5, 253-260.
1753 714 Luczak, C., Beaugrand, G., Lindley, J.A., Dewarumez, J.-M., Dubois, P.J., Kirby, R.R., 2013.
1754 715 Population dynamics in lesser black-backed gulls in the Netherlands support a North Sea regime
1755 716 shift. *Biology Letters* 9, 20130127
1756 717 Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.McP., Elston, D.A., Scott, E.M., Smith, R.I.,
1757 718 Somerfield, P.J., Watt, A.D., 2010. Long-term datasets in biodiversity research and monitoring:
1758 719 assessing change in ecological communities through time. *Trends in Ecology & Evolution* 25:
1759 720 574-582.
1760 721 Magurran, A.E., 2013. *Measuring biological diversity*. John Wiley & Sons, 264p.
1761 722 McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in
1762 723 the Anthropocene. *Trends in Ecology & Evolution* 30, 104-113.
1763 724 Mérigot, B., Bertrand, J.A., Mazouni, N., Manté, C., Durbec, J.-P., Gaertner, J.-C., 2007. A multi-
1764 725 component analysis of species diversity of groundfish assemblages on the continental shelf of the

1771
1772
1773 726 Gulf of Lions (north-western Mediterranean Sea). *Estuarine, Coastal and Shelf Science* 73, 123-
1774 727 136.
1775 728 Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., et al., 2014.
1776 729 Choosing and using diversity indices: insights for ecological applications from the German
1777 730 Biodiversity Exploratories. *Ecology and Evolution* 4, 3514-3524.
1778 731 O'Brien, T.D., Li, W.K.W., Moran, X.A.G., 2012. ICES Phytoplankton and Microbial Plankton Status
1779 732 Report 2009/2010. ICES Cooperative Research Report. International Council for the Exploration
1780 733 of the Sea, Copenhagen, 197p.
1782 734 Pasquaud, S., Béguer, M., Larsen, M.H., Chaalali, A., Cabral, H., Lobry, J., 2012. Increase of marine
1783 735 juvenile fish abundances in the middle Gironde estuary related to warmer and more saline waters,
1784 736 due to global changes. *Estuarine, Coastal and Shelf Science* 104-105, 46-53.
1785 737 Peet, R.K., 1974. The Measurement of Species Diversity. *Annual Review of Ecology and Systematics*
1786 738 5, 285-307.
1787 739 Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., et
1788 740 al., 2013. Essential biodiversity variables. *Science* 339, 277-278.
1789 741 Peres-Neto, P.R., Jackson, D.A., 2001. How well do multivariate data sets match? The advantages of a
1790 742 Procrustean superimposition approach over the Mantel test. *Oecologia* 129, 169-178.
1791 743 Plus, M., Auby, I., Maurer, D., Trut, G., Del Amo, Y., Dumas, F., Thouvenin, B., 2015. Phytoplankton
1792 744 versus macrophyte contribution to primary production and biogeochemical cycles of a coastal
1793 745 mesotidal system. A modelling approach. *Estuarine, Coastal and Shelf Science* 165, 52-60.
1794 746 Plus, M., Dumas, F., Stanisière, J.Y., Maurer, D., 2009. Hydrodynamic characterization of the Arcachon
1795 747 Bay, using model-derived descriptors. *Continental Shelf Research* 29, 1008-1013.
1796 748 Poos, M.S., Jackson, D.A., 2012. Addressing the removal of rare species in multivariate bioassessments:
1797 749 The impact of methodological choices. *Ecological Indicators* 18, 82-90.
1798 750 Pyper, B.J., Peterman, R.M., 1998. Comparison of methods to account for autocorrelation analyses of
1799 751 fish data. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2127-2140.
1800 752 Razouls C., de Bovée F., Kouwenberg J. et Desreumaux N., 2005-2018. Diversity and Geographic
1801 753 Distribution of Marine Planktonic Copepods. Sorbonne Université, CNRS. Available at
1802 754 <http://copepodes.obs-banyuls.fr/en> [Accessed July 11, 2018].
1803 755 Richardson, A.J., 2008. In hot water: zooplankton and climate change. *ICES Journal of Marine Science*
1804 756 65, 279-295.
1806 757 Richardson, A.J., 2009. Plankton and Climate, in: John, H.S., Karl, K.T., Steve, A.T. (Eds.),
1807 758 *Encyclopedia of Ocean Sciences*. Academic Press, Oxford, pp. 455-464.
1808 759 Rombouts, I., Beaugrand, G., Artigas, L.F., Dauvin, J.C., Gevaert, F., Goberville, E., Kopp, D., et al.,
1809 760 2013. Evaluating marine ecosystem health: Case studies of indicators using direct observations
1810 761 and modelling methods. *Ecological Indicators* 24, 353-365.
1811 762 Rose, M., 1933. *Copépodes pélagiques*. Librairie de la faculté des sciences, Paris, 374p.
1812 763 Salas, F., Marcos, C., Neto, J.M., Patrício, J., Pérez-Ruzafa, A., Marques, J.C., 2006. User-friendly guide
1813 764 for using benthic ecological indicators in coastal and marine quality assessment. *Ocean & Coastal*
1814 765 *Management* 49, 308-331.
1815 766 Salas, F., Neto, J.M., Borja, A., Marques, J.C., 2004. Evaluation of the applicability of a marine biotic
1816 767 index to characterize the status of estuarine ecosystems: the case of Mondego estuary (Portugal).
1817 768 *Ecological Indicators* 4, 215-225.
1818 769 Sautour, B., Artigas, L.F., Delmas, D., Herbland, A., Laborde, P., 2000. Grazing impact of micro- and
1819 770 mesozooplankton during a spring situation in coastal waters off the Gironde estuary. *Journal of*
1820 771 *Plankton Research* 22, 531-552.
1822 772 Sautour, B., Castel, J., 1993. Distribution of zooplankton populations in Marennes-Oléron Bay (France),
1823 773 structure and grazing impact of copepod communities. *Oceanologica Acta*, 16: 279-290.
1824 774 Sautour, B., Castel, J., 1995. Comparative spring distribution of zooplankton in three macrotidal
1825 775 European estuaries. *Hydrobiologia* 311, 139-151.

1830
1831
1832
1833
1834
1835
1836
1837
1838
1839
1840
1841
1842
1843
1844
1845
1846
1847
1848
1849
1850
1851
1852
1853
1854
1855
1856
1857
1858
1859
1860
1861
1862
1863
1864
1865
1866
1867
1868
1869
1870
1871
1872
1873
1874
1875
1876
1877
1878
1879
1880
1881
1882
1883
1884
1885
1886
1887
1888

776 Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution* 18, 561-566.
777
778 Serranito, B., Aubert, A., Stemmann, L., Rossi, N., Jamet, J.L., 2016. Proposition of indicators of anthropogenic pressure in the Bay of Toulon (Mediterranean Sea) based on zooplankton time-series. *Continental Shelf Research* 121, 3-12.
779
780
781 Somavilla, R., González-Pola, C., Rodriguez, C., Josey, S.A., Sánchez, R.F., Lavín, A., 2009. Large changes in the hydrographic structure of the Bay of Biscay after the extreme mixing of winter 2005. *Journal of Geophysical Research: Oceans*. 114(C1).
782
783
784 Stegen, J.C., Freestone, A.L., Crist, T.O., Anderson, M.J., Chase, J.M., Comita, L.S., Cornell, H.V., et al., 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography* 22, 202-212.
785
786
787 Uriarte, I., Villate, F., Iriarte, A., 2016. Zooplankton recolonization of the inner estuary of Bilbao: influence of pollution abatement, climate and non-indigenous species. *Journal of Plankton Research* 38, 718-731.
788
789
790 Vincent, D., Luczak, C., Sautour, B., 2002. Effects of a brief climatic event on zooplankton community structure and distribution in Arcachon Bay (France). *Journal of the Marine Biological Association of the United Kingdom*. 82, 21-30.
791
792
793 Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon*, 213-251.
794
795
796 Willis, K., Cottier, F., Kwasniewski, S., Wold, A., Falk-Petersen, S., 2006. The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). *Journal of Marine Systems* 61, 39-54.
797
798 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., et al., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787-790.

The following supplement accompanies the article

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

¹Université de Bordeaux, UMR CNRS 5805 EPOC Environnements et Paléo-environnements Océaniques et Continentaux, Rue Geoffroy Saint Hilaire, 33600 Pessac, France.

²Université d'Angers, LPG-BIAF, UMR CNRS 6112, 49045 Angers cedex, France

³Unité Biologie des organismes et écosystèmes aquatiques (BOREA), Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles, CNRS, IRD, CP53, 61, Rue Buffon, 75005, Paris, France

* Both authors contributed equally

E-mail: richirt.julien@gmail.com / eric.goberville@upmc.fr

Supplement

submitted to Estuarine, Coastal and Shelf Science

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.

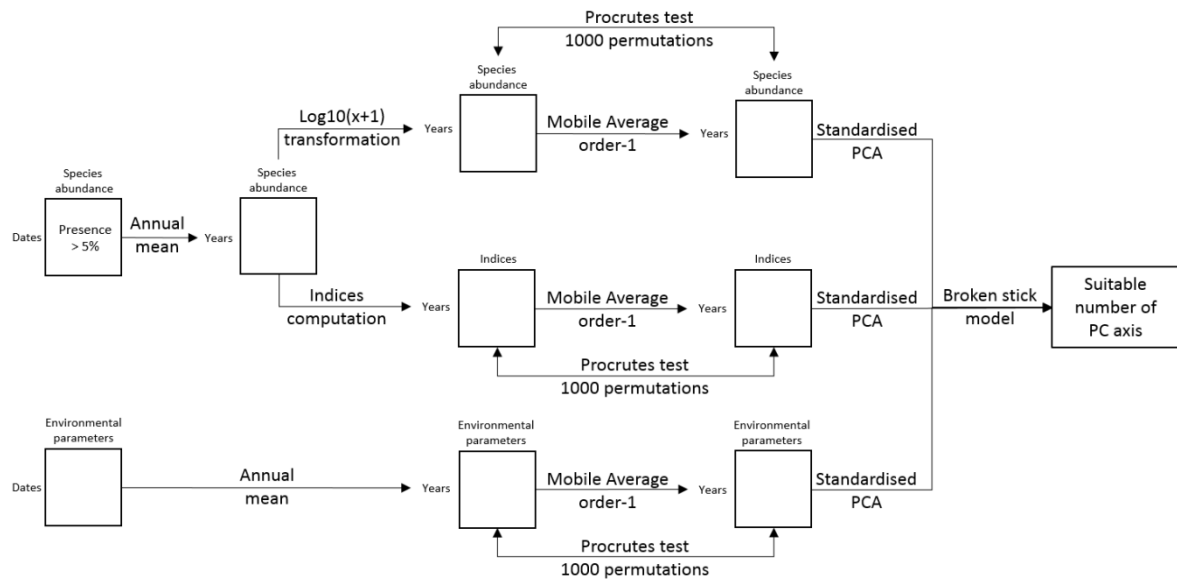
Supplementary Figure S3. Annual sampling effort (i.e. number of samples available per year) for Eyrac (dotted black line) and the Gironde downstream (red line).

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).

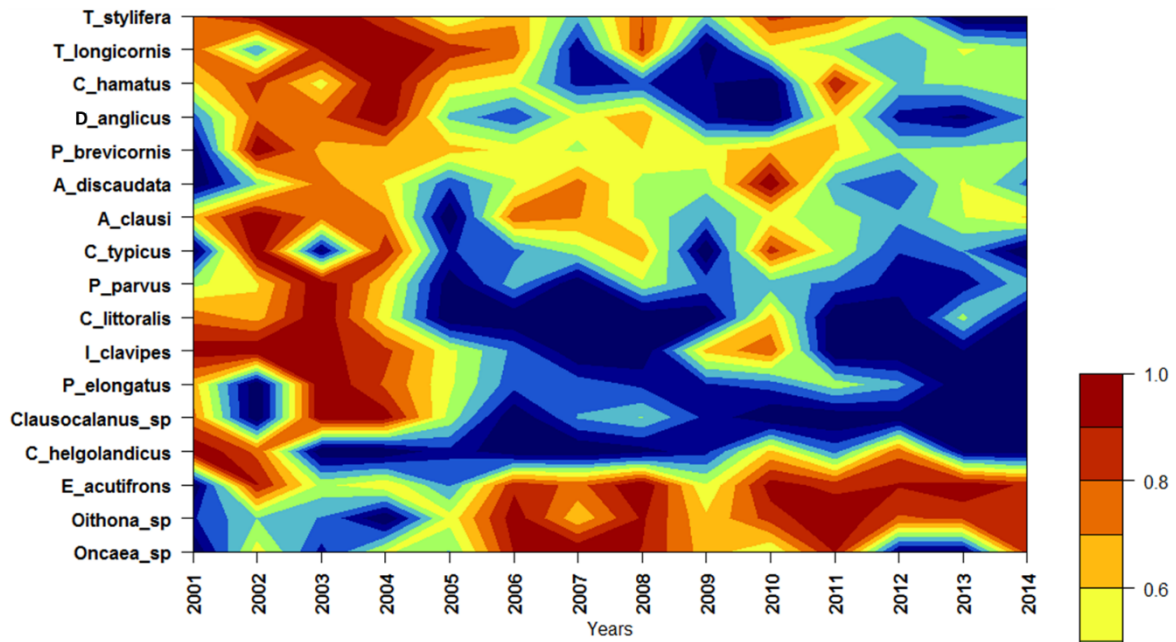
Supplementary Table S3. Results from the standardised PCAs performed on environmental parameters. The first two eigenvectors are included and show the contribution of each parameter to the principal components. Values in bold were superior to $|2.50|$.



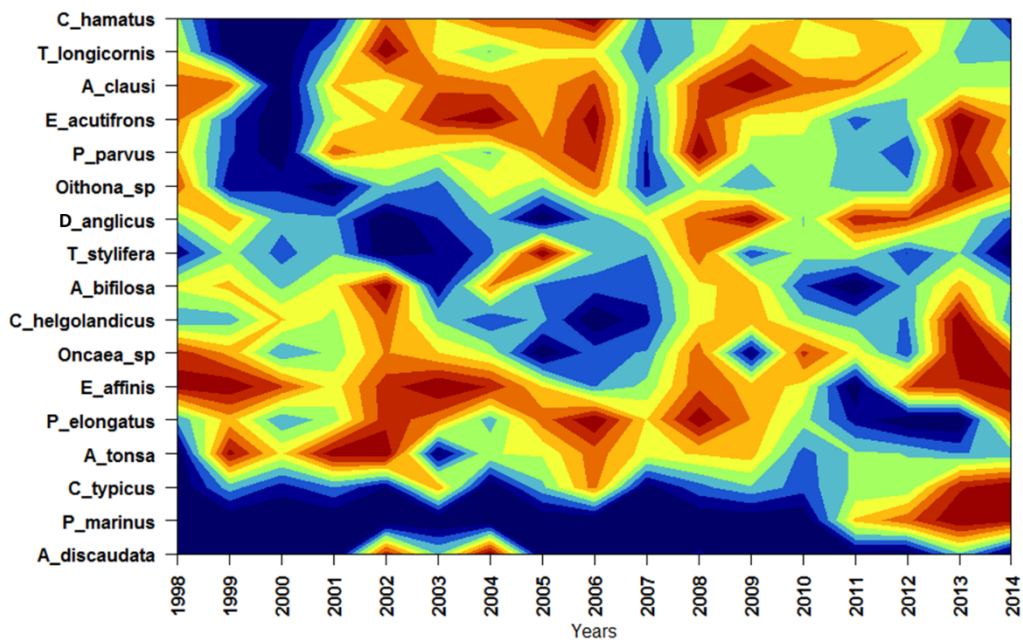
Supplementary Figure S1

Richirt et al.

a) EYRAC

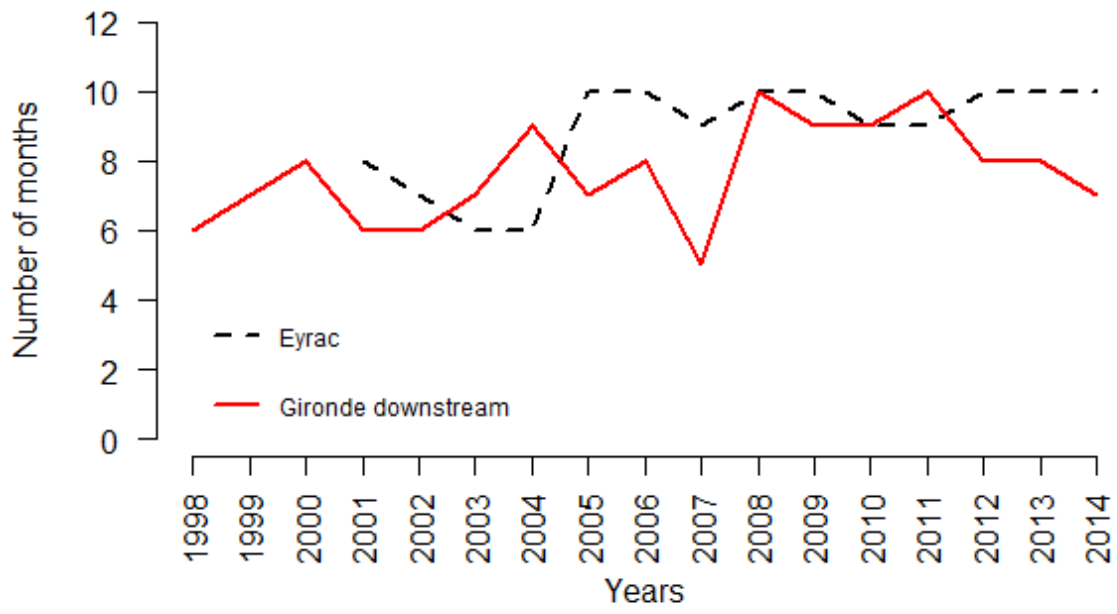


b) GIRONDE DOWNSTREAM



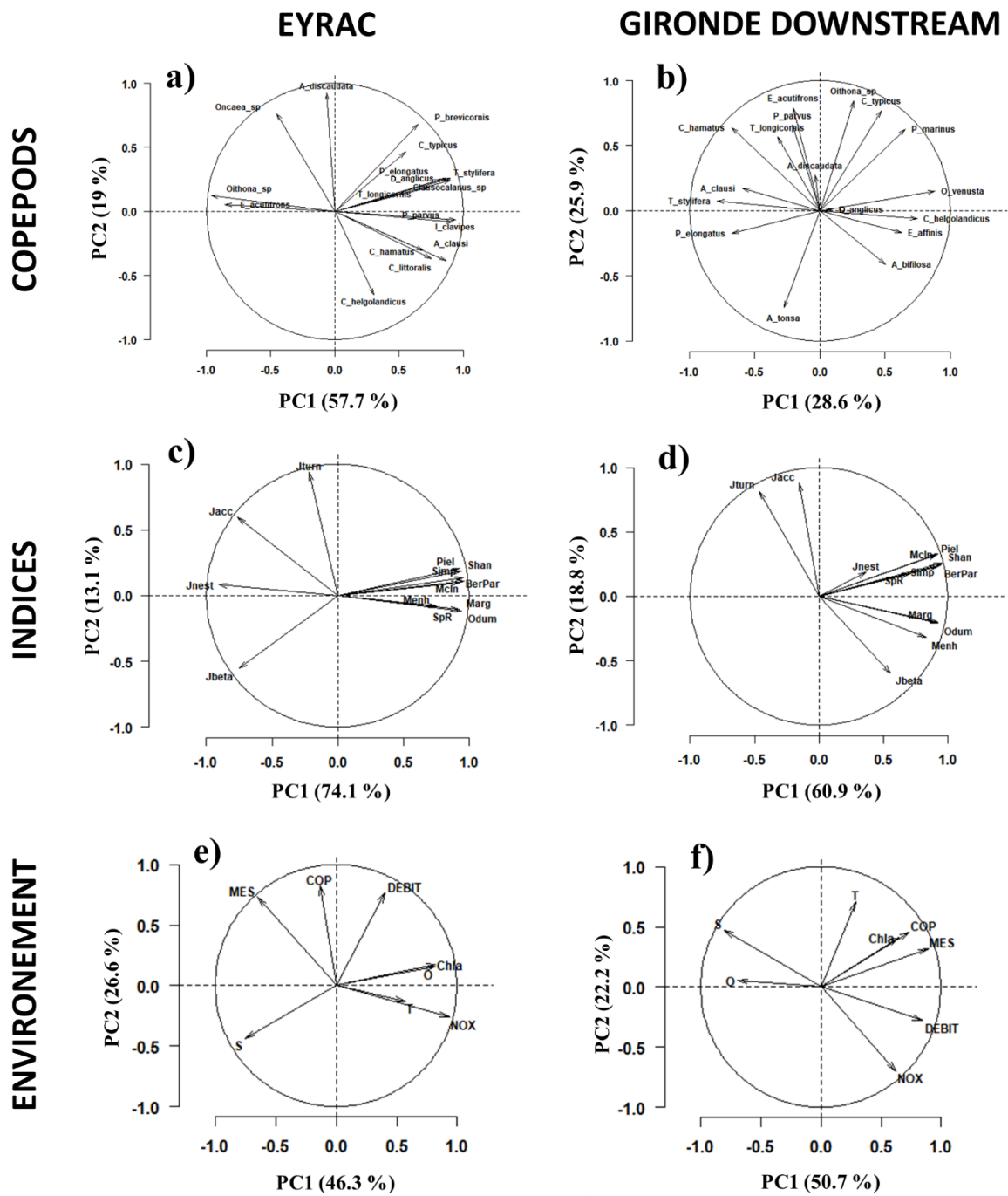
Supplementary Figure S2

Richirt et al.



Supplementary Figure S3

Richirt et al.



Supplementary Figure S4

Richirt et al.

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

Richirt et al.

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

Richirt et al.

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

Richirt et al.