

1 Interannual variations in neritic copepods of the Basque coast 2 (Southeastern Bay of Biscay): has there been a community shift in the 3 2010s decade?

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15 Abstract

16 The interannual variations in absolute and relative densities of copepods from the
17 neritic waters of the southeastern Bay of Biscay and their relationship to climate
18 teleconnections and local environmental factors were assessed using time series for the
19 1998-2015 period. Multivariate analysis revealed opposite patterns of variation between
20 relevant spring vs. summer/autumn species, both in absolute densities (the spring
21 species *Acartia clausi* and *Centropages typicus* vs. mainly the summer/autumn *Oncaea*
22 *media*, but also *Ditrichocorycaeus anglicus*, *Oithona nana*, *Temora stylifera* and
23 *Oithona plumifera*) and more strongly (58.2% of variance) in relative densities (spring
24 *Acartia clausi* vs. summer *Paracalanus parvus*). All seasons North Atlantic Oscillation
25 (NAO), winter and spring East Atlantic (EA) pattern together with summer water
26 temperature and chlorophyll *a* showed positive correlations with these copepod density
27 patterns, whereas the summer EA pattern and NAO and the spring and summer AMO,
28 together with the upwelling index of all seasons showed negative correlations. In these
29 patterns of copepod variations two step changes were detected, one in 2006-2008
30 towards an increase in the spring species and the other one in 2013-2014 towards an
31 increase of summer species. This latter change is in agreement with the abrupt
32 community shifts predicted in the literature for 2014.

33 **Keywords:** zooplankton, copepod, Bay of Biscay, shift, time series, climate

34 Introduction

1 Current global change has brought about a growing consensus on the urgent need to
2 detect changes in the abiotic and biotic components and processes of ecosystems,
3 understand their causes and be able to predict future changes (Philippart et al., 2011). In
4 the marine environment zooplankton play key roles in food webs and biogeochemical
5 cycles and are particularly sensitive to environmental changes, being able to give a fast
6 response at the ecologically relevant population and community levels (Richardson,
7 2008; Dam, 2013). There is increasing evidence that zooplankton can track changes in
8 environmental conditions that occur at interannual to multidecadal scales (Taylor and
9 Stephens, 1980; Beaugrand et al., 2002; Beaugrand, 2003; Reygondeau et al., 2015;
10 Morse et al., 2017; Molinero et al., 2018; Ivory et al., 2019; Bode et al., 2020, Villarino
11 et al. 2020) and can therefore be used as indicators of marine environmental change
12 (Bedford et al., 2020).

13 Zooplankton do not respond individually to external factors, but their response is
14 rather to a combination of multiple climate, hydrographic and other environmental
15 factors, both large-scale and local ones (Kimmel and Duffy-Anderson, 2020). Marine
16 ecologists are using more and more large-scale climate teleconnection patterns because
17 they synthesize an array of climatic factors and can affect water circulation patterns and
18 other hydrographic features too (Ottersen et al., 2004) and they seem to better predict
19 ecological processes than local weather (Hallet et al., 2004). In agreement, long-term
20 zooplankton abundance and community structure variations have frequently been found
21 to be linked to changes in large-scale atmospheric forcing, e.g. the NAO (North Atlantic
22 Oscillation) (Alheit et al., 2005; Piontkovski et al., 2006) and the Atlantic Multidecadal
23 Oscillation (AMO) (Ivory et al., 2019) in the North Atlantic, the ENSO (El Niño-
24 Southern Oscillation), the PDO, (Pacific Decadal Oscillation) or the East Asian Winter
25 Monsoon (EAWM) in the North Pacific (Rebstock, 2002; Molinero et al., 2018).
26 Climate teleconnection patterns, though, usually exhibit regional differences in their
27 relationships with local climate variables and, therefore, their association with
28 ecological processes in both terrestrial and aquatic environments may also show cross
29 regional differences (Gordo et al., 2011; Gouveia et al., 2008; Uriarte et al., 2021). In
30 the Northeast Atlantic, these associations have been more intensely studied in areas like
31 the North Sea, but they are still poorly understood in other regions, as for example the
32 Basque coast (southeastern Bay of Biscay, Cantabrian Sea) which is located in a
33 transitional zone between north and south Europe. Furthermore, the response of

1 zooplankton to SST (sea surface temperature) changes can also vary among different
2 Northeast Atlantic regions (MacGinty et al., 2011). Previous studies comparing
3 interannual dynamics of zooplankton and copepod communities found no coherence
4 between those of the southeastern Bay of Biscay and those of western English Channel,
5 northern North Sea, the Kattegat or the eastern Mediterranean (Fanjul et al., 2017;
6 Villarino et al. 2020). Therefore, we are still far from achieving a comprehensive
7 knowledge of how zooplankton respond to environmental change across regions of the
8 Northeast Atlantic (Beaugrand et al., 2019).

9 Also, when analyzing long-term variations it is increasingly evident that regime
10 shifts or abrupt community shifts have occurred. An abrupt community shift has been
11 defined as a stepwise shift in community structure (Beaugrand et al., 2019). One of the
12 most studied ones in the Northeast Atlantic was detected in the North Sea in the late
13 1980s and was characterized mainly by a shift in the relative abundances of the calanoid
14 copepods *C. finmarchicus* and *C. helgolandicus* brought about by a shift from a
15 negative to a positive phase of the NAO, manifested as a shift to a warmer environment,
16 and which also affected other biological components of the ecosystem including fish
17 (Beaugrand, 2004; Alheit et al., 2005; Weijerman et al., 2005). We now know that
18 regime shifts in the late 1980s occurred rather synchronously in other areas too and that
19 several other regime shifts have occurred since the 20th century within the Northeast
20 Atlantic (Beaugrand et al., 2015). In fact, a noticeable change was also reported in the
21 late 1980s in the shelf copepod community of the Basque coast, in the Bay of Biscay,
22 with the occurrence and increase in abundance of the previously unrecorded warm-
23 affinity species *Temora stylifera* throughout the 1988-1990 period (Villate et al., 1997).
24 After 2000 the NAO lost its persistent positive phase and predictor potential (Dippner et
25 al., 2014), but in the early 2010s the NAO and the EA pattern showed a change to a
26 positive phase (see NOAA data at <https://www.ncdc.noaa.gov/teleconnections/>) which
27 may have induced abrupt community shifts in marine biological communities. In fact,
28 Beaugrand et al. (2019) predicted and unprecedented large-scale abrupt community shift
29 in 2014, as a result of a strong El Niño event and major shifts in northern hemisphere
30 climate.

31 The aim of the present study was to describe the changes in the absolute and
32 relative densities of the copepod community from the neritic waters of the Basque coast
33 (southeastern Bay of Biscay) during the 1998-2015 period and assess their relationship

1 to the major teleconnection patterns with effects in the North Atlantic (NAO, EA pattern
2 and AMO) and local environmental factors, primarily to analyze the changes that may
3 have occurred as a consequence of the early 2010s shifts in large-scale atmospheric
4 forcing.

5 **Material and methods**

6 **Study area**

7 Two nearby sampling sites of the Basque coast (43° 20.9' N - 3° 1.6' W and 43° 24.2' N
8 - 2° 41.7' W) were jointly analysed to obtain an overall view of this zone of the
9 southeastern Bay of Biscay (Figure 1). Both sites are nearshore (< 1 km offshore),
10 located in the mouths of sea-dominated shallow (mean water depth of < 13 m) estuaries.
11 The water column is partially mixed/well mixed and mean salinity is around 34.8
12 (ranging between 30.3 and 35.6), whilst mean water temperature is around 16.1 °C
13 (ranging between 10.8 and 24.9). Other abiotic and biotic features have been
14 summarized in Fanjul et al. (2019).

15 **Data set acquisition and data pretreatment**

16 Monthly samplings were carried out in both sites on consecutive days from 1998 to
17 2015. Water column measurements (every 0.5 m) for salinity (Sal) and water
18 temperature (WT) were recorded *in situ* by portable multiparameter meters.
19 Concurrently, water was collected using a Niskin-type bottle, filtered (Whatman GF/C),
20 and chlorophyll *a* concentration (Chl *a*) was determined spectrophotometrically
21 according to the monochromatic method with acidification (Lorenzen, 1967). Data used
22 in this work correspond to measurements carried out mostly between 2 and 5 m depth.
23 Likewise, the salinity stratification index (Str) was calculated as the maximum
24 difference in salinity between consecutive depths (Villate et al. 2013).

25 Zooplankton samples were taken by horizontal trawling of a 200- μ m mesh size net,
26 with a built-in Mechanical Flow Meter, for 3-5 min at the ~~aforementioned~~ depth.
27 Samples were preserved in 4 % buffered formalin until identification and counting in
28 the laboratory. Results were expressed in density units (ind. m⁻³). For the purpose of this
29 study, 12 copepod taxa (mostly species) were selected, whose abundance represented >
30 90% of the total copepod community during the study period. The selected copepod
31 species (occasionally genus or genera assemblage) were 6 calanoid copepods: *Acartia*
32 *clausi* (Acla), *Centropages typicus* (Ctyp), *Temora longicornis* (Tlon), *T. stylifera*

1 (Tsty), the genus *Calanus* (Cala), mostly represented by *C. helgolandicus* and the
2 copepod assemblage PCPC-calanus, which includes the genera *Paracalanus* (basically
3 *P. parvus*), *Clausocalanus*, these two genera accounting for circa. 75% and circa 25%
4 of this genera assemblage, respectively, and the occasionally occurring *Pseudocalanus*
5 (mostly *P. elongatus*) and *Ctenocalanus* (*C. vanus*); 5 cyclopoid copepods: *Oithona*
6 *plumifera* (Oplu), *O. nana* (Onan), *O. similis* (Osim), *Oncaea media* (Omed),
7 *Ditrichocorycaeus anglicus* (Dang); and 1 harpacticoid copepod *Euterpina acutifrons*
8 (Eacu).

9 For each species absolute densities were log-transformed ($\log x+1$) and relative
10 densities (%) were also calculated.

11 Several sources were used for obtaining the monthly hydro-meteorological data.
12 The river flow (Flow) data were provided by the Provincial Council of Bizkaia, the
13 upwelling index (Upw) data were downloaded from the webpage of the Spanish
14 Institute of Oceanography (<http://www.indicedeafloramiento.ieo.es/interactivo.html>),
15 whilst the teleconnection indices used, i.e. NAO
16 (<http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.c>
17 urrent.ascii), EA (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/ea_index.tim) and
18 AMO (<https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>), were obtained from the
19 NOAA (National Oceanic and Atmospheric Administration).

20 In addition, seasonal averages were calculated from the monthly values. Winter (w)
21 values were obtained from the January, February and March values, spring (sp) values
22 from those of April, May and June, summer (s) values from those of July, August and
23 September and autumn (a) ones from those of October, November and December.
24 Likewise, and only in the case of the NAO index, an additional pooling was done for
25 the winter season (w*) averaging values from December, January, February and March.
26 It should be noted that although both NAO winter indices were highly correlated ($r =$
27 0.94, $p < 0.001$), we used both indices for comparative purposes since both ways of
28 pooling the winter months have been used in the literature (e.g. Jing et al., 2019). Both
29 monthly data and seasonally averaged data were used for the local environmental
30 variables (Sal, WT, Chl a, Str, Upw and Flow) and teleconnection indices (NAO, EA
31 and AMO), which were used as explanatory variables of the year-to-year variations in
32 the copepod community.

1 Occasional missing values (fewer than 5%) in the monthly data sets were filled in
2 by interpolation using the values of the previous and following months.

3 **Data treatment**

4 In order to extract the interannual variability of the copepod community Principal
5 Component Analyses (PCA) of the absolute ($\log x+1$) and relative (%) densities of the
6 studied copepod species were carried out using Canoco v. 4.55. Each of these PCAs
7 were performed jointly for the two sampling sites and using month as a covariable. Only
8 the first two principal components (PCs) were depicted.

9 For the purpose of our study, we extracted the trend component of the first two PCs
10 of the PCA of the absolute ($\log x+1$) and relative (%) densities of the copepod
11 community as well as of the individual species by the additive decomposition of the
12 time series using R software (R Core Team, 2020).

13 In order to analyze the relationship between the explanatory variables and the
14 trends of the two main modes of variability (PC1 and PC2) obtained from the PCA of
15 the absolute ($\log x+1$) and relative (%) densities of the copepod species, Spearman rank
16 correlation analyses were performed. Only the significant ($p < 0.05$) results are shown.
17 This correlation analysis is suitable when exploring potential deterministic shifts since,
18 in this cases, parameters of a process such as its mean, variance or trend change (Reiss,
19 2007). Correlation tests were carried out by means of SPSS Statistics for Windows,
20 Version 25.0 (IBM Corp., Armonk, NY).

21 **Results**

22 The interannual variations represented by the PC 1 of the PCA of the absolute densities
23 of copepod species accounted for 26.1% of the variability (Figure 2) and revealed a
24 progression in time with marked fluctuations, the strongest one being in 2012. All
25 species appeared aligned on the same side of this PC, but the taxa that contributed most
26 to this mode of variation were *Euterpina acutifrons*, *Oithona similis*, the assemblage
27 PCPC-calanus and *Oithona nana* (Figures 2 and 3). The teleconnection index that best
28 correlated with the trend of the copepod taxa densities PC 1 was winter NAO, although
29 other climate indices such as spring and autumn AMO (positive) and winter and spring
30 EA pattern (negative) also showed significant ($p < 0.05$) relationships (Table 1).
31 Amongst the local environmental factors, the upwelling and salinity stratification
32 indices showed the strongest positive correlations and summer and autumn river flow

1 and winter and autumn chlorophyll *a* the highest negative correlations (Table 1).
2 Chlorophyll *a* for the whole year and each season also correlated negatively with the
3 trend of the main mode of variation of copepod taxa densities.

4 The interannual variations represented by the PC 2 of the PCA of copepod taxa
5 absolute densities accounted for 13.3% of the variability (Figure 2). This second main
6 mode of variation was mainly represented by the interannual changes in density of
7 summer/autumn species, chiefly of *Oncaea media*, but also of *Ditrichocorycaeus*
8 *anglicus*, *Oithona nana*, *Temora stylifera* and *Oithona plumifera* in opposition to those
9 of the spring species *Acartia clausi* and *Centropages typicus* (Figures 2 and 4). The
10 interannual trend of the PC 2 scores showed relatively high values during the period
11 1999-2006, a marked decline from 2006 to 2008, remaining in lower values than the
12 rest of the series until 2013, showing a marked increase from 2013 to 2015. Spring
13 species showed highest densities in the second period and decreased drastically in the
14 last two years, while summer-autumn species showed highest densities in the first
15 period and increased again in the last two years (Figure 4). The trend of the mode of
16 variation depicted by the PC 2 was positively related mainly to the spring EA pattern,
17 winter and spring NAO, spring, summer and autumn chlorophyll *a*, and winter
18 stratification and river flow and negatively related to summer EA pattern, winter and
19 spring water temperature, spring and autumn river flow and stratification and upwelling
20 index of all seasons (Table 2).

21 The interannual variations represented by the PC 1 of the PCA of copepod species
22 relative densities accounted for 58.2% of the variability (Figure 5). This main mode of
23 variability reflected the alternation in de dominance of the PCPC-calanus assemblage,
24 dominated by the summer species *P. parvus*, and the spring species *A. clausi*. In the
25 interannual trends of the relative densities of these two species we can also distinguish 3
26 periods: a) the 1998-2005 period with similar contributions of the two species; the
27 2006-2013 period dominated by *A. clausi* and 2014-2015 dominated by *P. parvus*
28 (Figure 6). Similar to results for the PC 2 of the absolute densities, all seasons NAO and
29 winter and spring EA pattern were positively related to the trend of the scores of the PC
30 1 of the relative density of copepods, whereas summer EA and winter and spring AMO
31 were negatively correlated (Table 3). Regarding local environmental factors, we can
32 highlight that the winter and spring water temperatures, winter chlorophyll *a* and the
33 upwelling index and salinity of all seasons were negatively correlated to this PC 1,

1 whereas summer and autumn water temperatures and summer chlorophyll *a* and river
2 flow were positively correlated (Table 3).

3 The interannual variations represented by the PC 2 of the PCA of copepod taxa
4 relative densities accounted for a much lower percentage of the variability than the PC
5 1, i.e. 18.5% (Figure 5). The main feature of the PC 2 trend was the occurrence of
6 cycles of 3-5 yr. periodicity with a marked peak in the third cycle in the middle of the
7 series (in 2006) and the taxa that contributed most to this mode of variability were the
8 cyclopoids *O. media*, *O. similis* and *O. nana* in opposition to the calanoids PCPC-
9 calanus and *A. clausi* (Figure 7). The variables that best correlated with the PC 2 trend
10 were autumn river flow and salinity stratification, which showed a negative correlation,
11 together with spring NAO index and summer salinity stratification (Table 4).

12 Discussion

13 The main mode of variability (PC 1) of the absolute densities of the neritic copepods
14 under study illustrated a mode of variation common to all species that reflected mainly
15 the interannual dynamics of the most fluctuating species, primarily that of *Euterpina*
16 *acutifrons* followed by those of *O. similis*, the PCPC-calanus assemblage and *O. nana*.
17 Therefore, the highest percentage of copepod density variability was accounted for
18 species that showed short-term interannual periodicity. Cycles of 1.5 to 3 year have
19 been observed for species like *Euterpina acutifrons*, *O. similis* and *O. nana* in coastal
20 zooplankton time series close to the Bay of Biscay (Buttay et al. 2017). The strong peak
21 of 2012 is associated to an event of unusual high density of several copepod species that
22 was also observed for other non-copepod components of the zooplankton community
23 (Fanjul et al. 2017). A more interesting feature that emerged from the interannual
24 variations of the copepod community was the opposite patterns between relevant spring
25 and summer/autumn species, both when changes in absolute, but more strongly in
26 relative densities were analyzed from 2006 to 2015. Variations in the relative densities
27 involved mainly changes from the dominance at the annual scale of the spring peaking
28 *A. clausi* to that of the summer peaking PCPC assemblage (dominated by *Paracalanus*
29 *parvus*). Absolute density variations (PC 2) showed opposite patterns of
30 summer/autumn species, mainly of *Oncaea media*, but also of *Ditrichocorycaeus*
31 *anglicus*, *Oithona nana*, *Temora stylifera* and *Oithona plumifera* on the one hand and
32 the spring species *Acartia clausi* and *Centropages typicus* on the other. Opposite
33 winter/spring and summer/autumn zooplankton responses to climate variations have

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3 1 been found mainly in phenological patterns (Edwards and Richardson, 2004; Mackas et
4 al., 2012), however opposite patterns of interannual variation in abundance between
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6 3 winter/spring and summer/autumn copepods have also been reported elsewhere, e.g. the
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8 4 Adriatic Sea (Bernardi Aubry et al., 2012). Furthermore, differences in the timing of
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10 5 abrupt community shifts for spring and autumn zooplankton communities have also
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12 6 been reported (Morse et al., 2017). In addition, we found that the pattern in relative
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14 7 densities accounted for a much higher percent of the variance (58.2%) than the one of
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16 8 absolute densities (PC 2; 13.3% of the variance), which shows that the relative
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18 9 dominance is more affected than the total abundance of copepods by
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20 10 climate/hydrographical change, a feature documented at least for specific groups of
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22 11 copepods in other studies too (Bedford et al., 2020; Bode et al., 2020; Klais et al. 2017).

23 12 The main features of a further pattern stemming from the relative densities were the
24
25 13 recurrent cycles and the peak in the middle of the series (year 2006) which segregated
26
27 14 the highest contributing calanoid copepods *A. clausi* and PCPC-calanus from low
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29 15 contributing cyclopoids such as *O. media*, *O. nana* and *O. similis*. In agreement with
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31 16 this, in the 2006 to 2008 period the PC2 of the absolute densities showed a marked
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33 17 decline. This mode of variation had a much lower weight in the variance of the relative
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35 18 densities of copepods, likely due to the low contribution of the small cyclopoid species
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37 19 largely responsible for this mode of variation in the mesozooplankton fraction
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39 20 abundance. However, it has already been shown for the study area that when the
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41 21 microzooplankton fraction is also quantified *O. media*, *O. nana* and *O. similis* can reach
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43 22 values of relative abundance in the range of those observed for *A. clausi* and *P. parvus*,
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45 23 and sometimes become dominant in the annual cycle (Villate 1991, Villate et al. 2004).

46 24 As regards the drivers of these opposite changes in density/dominance of relevant
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48 25 spring and summer/autumn copepods, it appears that higher summer and autumn
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50 26 temperatures and summer chlorophyll *a* levels and river flows, together with stronger
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52 27 downwelling and lower autumn flows were the most favourable conditions for the
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54 28 summer/autumn copepods, whereas higher winter and spring water temperatures and
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56 29 weaker downwelling, higher winter chlorophyll *a* concentrations (only in the case of
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58 30 relative abundances), and higher river flow and stratification in spring were the most
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60 31 favourable ones for the spring ones. Temperature can enhance zooplankton production
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33 32 and hatching of dormant eggs (Ambler et al. 1985) and has often been found to be a
major factor driving long-term zooplankton density and community structure variations

1 (Beaugrand 2003; Alvarez-Fernandez et al., 2012; Harris et al., 2014; Morse et al.,
2 2017; Molinero et al., 2018; Ivory et al., 2019, Kimmel and Duffy-Anderson, 2020).
3 Previous studies on the zooplankton of the neritic waters of the southeastern Bay of
4 Biscay, using shorter time series, showed no significant correlations of water
5 temperature with the main mode of zooplankton community interannual variability
6 (1998-2005 yr. period) (Villate et al., 2017), or showed a low yet negative correlation
7 between temperature and copepod community composition variability (1999-2013 yr.
8 period) (Villarino et al., 2020). However, in those two studies correlations were not
9 tested with season-specific explanatory variables, and as we can see from the present
10 results, winter and spring water temperatures can have opposite sign correlations in this
11 area. This reinforces the suitability of analyzing the effects of season-specific
12 explanatory variables, as pointed out also by Uriarte et al. (2021) in a study of
13 zooplankton phenological changes. Regarding the correlation with chlorophyll *a* levels,
14 phytoplankton biomass is an important food source for grazer and omnivore copepods
15 and relationships of zooplankton dynamics with phytoplankton have been reported in
16 the Bay of Biscay (Stenseth et al., 2006) and elsewhere too (Kim et al., 2017). In
17 addition, hydrographic features, such as water column stratification (Ivory et al., 2019),
18 intrusion of fresher water (Kane, 2007) or upwelling processes (Bode et al., 2009;
19 González-Gil et al., 2015) can also play important roles in interannual zooplankton
20 variations. Upwelling enhances primary production and can thus promote zooplankton
21 abundance increases (González-Gil et al., 2015; Buttay et al., 2016), but weaker wind-
22 driven Ekman transport offshore (upwelling) or stronger transport onshore
23 (downwelling) has also been claimed to promote higher retention of zooplankton (Bode
24 et al., 2009; Buttay et al., 2016), including meroplankton (Queiroga et al., 2007), near
25 the coast in Iberian shelf waters. In the southeastern Bay of Biscay, upwelling events are
26 much weaker than on the northwestern Iberian coast (Valencia et al., 2004) and the
27 upwelling index mostly indicates the occurrence of weaker or stronger downwelling.
28 Our data shows a positive relationship of downwelling with summer copepods and this
29 could be due to a higher retention of zooplankton near the coast when there is a stronger
30 Ekman transport onshore. However, the mechanistic link between variations in the
31 downwelling and zooplankton dynamics at BU should be better studied.

32 Superimposed to local drivers, climate teleconnection patterns have often been
33 found to be linked to long-term patterns of variation in zooplankton. In the Northeast

1 Atlantic correlations have been found mostly with the NAO, but also with the AMO,
2 concomitant to sea warming (Alheit et al., 2005; Piontkovski et al., 2006; Edwards et al.
3 2013). Our results showed that in the neritic waters of the southeastern Bay of Biscay
4 all seasons NAO indices and the spring EA pattern (also the winter EA pattern in the
5 case of absolute densities) were positively correlated with the opposite pattern of
6 density and relative density of winter/spring species vs summer/autumn species,
7 whereas the summer EA pattern and most seasons AMO indices, the latter more weakly,
8 were negatively correlated with the aforementioned interannual changes in
9 density/dominance of relevant spring and summer/autumn copepods. As in our case,
10 opposite interannual changes of abundance have been reported for *C. typicus* and *T.*
11 *styliifera* in a Mediterranean area by Molinero et al (2005), but they found that low NAO
12 years lead to high abundance of *T. styliifera* and low abundance of *C. typicus* while our
13 results reveal an opposite response of these species to NAO values. This might be the
14 result of a differentiated effect of the NAO on local climatic and oceanographic drivers of
15 copepod dynamics in each area. The mechanistic links between teleconnection patterns
16 and plankton can be complex and therefore more difficult to unravel, because the former
17 synthesize an array of climatic factors and can affect water circulation patterns and
18 other hydrographic features too (Ottersen et al., 2004). Regarding the relationships of
19 the climate teleconnections with local climate and hydrographic variables at BU, the
20 clearest one was the negative/positive relationship of the NAO and EA pattern with
21 upwelling/downwelling. In agreement, the EA pattern was found to be positively linked
22 to southwesterly winds and downwelling in the Bay of Biscay (Borja et al., 2008). The
23 EA pattern has also been found to be correlated with holozooplankton phenology
24 changes at BU (Uriarte et al., 2021). Furthermore, in those phenological variations at
25 BU different time periods were identified which were similar to those defined by the
26 variations in absolute and relative densities of spring vs. summer-autumn copepods
27 observed in the present study.

28 In both the absolute and relative density patterns of spring versus summer/autumn
29 copepods in the southeastern Bay of Biscay stepwise changes were detected. Step
30 changes in long-term copepod density variations are quite common and have
31 increasingly been detected in recent decades. One of the best studied ones was the
32 aforementioned *C. finmarchicus*/*C. helgolandicus* change in the North Sea in the 1980s
33 which was identified as a regime shift towards a warm dynamic regime with effects at

1 the ecosystem level, including impacts on fish and fisheries (Beaugrand et al., 2002;
2 Beaugrand and Ibanez, 2004; Alheit et al., 2005; Weijerman et al., 2005). Other well
3 documented regime shifts in the North Sea are the cold event in the late 1970s (Edwards
4 et al. 2002) and a step-change that occurred in the late 1990s-beginning of 2000s
5 (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014), the latter one being detected
6 roughly at a similar time in northwestern Iberian shelf waters (Bode et al., 2020)
7 amongst other areas. In general, regime shifts have been detected in many ocean regions
8 and seas and some of them have occurred quasi-synchronously in different areas
9 (Beaugrand et al., 2015). Our time series from BU began in the late 1990s, so we have
10 no data to test if zooplankton shifts occurred in the late 1980s and late 1990s, but there
11 is evidence of a regime shift that occurred before the 2000s in the Bay of Biscay which
12 affected different components (birds, fish, cetaceans) of the food web (Hemery et al.,
13 2008). In our study at BU, 3 periods were distinguished in the relative density of
14 copepod community time series: the 1998-2007, the 2008-2013 and the 2014-2015.
15 That is to say, step changes in copepods circa 2006-2008 (towards an increase in spring
16 species) and circa 2013-2015 (towards an increase in summer species) were observed.
17 In the western English Channel (Station L4), Reygondeau et al. (2015) also
18 distinguished two step changes at roughly similar times, i.e. (2007-2008) and (2013-
19 2014), and they observed opposite directions of change in the densities of *Acartia* spp.
20 (mostly *Acartia clausi*) and *Paracalanus parvus*, but changes also affected other
21 copepods and, unlike in our study, the direction of change for each species was
22 maintained throughout both periods. Beaugrand et al. (2019) have recently predicted
23 unprecedented abrupt community shifts for many marine regions in 2014 linked to a
24 strong El Niño event and major shifts in northern hemisphere climate. For instance, both
25 the NAO and the EA pattern have changed into a positive phase in the early 2010s
26 (NOAA) and our 2013-2015 shift in zooplankton fully agrees with the timing of
27 Beugrand et al.'s prediction. Although our zooplankton monitoring has not stopped, the
28 data of copepod densities currently available reaches only the year 2015 due to the
29 paucity in the analysis of zooplankton samples. Future research should aim to assess the
30 persistence of the zooplankton step change we detected in 2013-2015 and possible
31 effects in other zooplankton too.

32 **Conclusions**

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3 1 This study has shown that winter/spring vs summer/autumn copepod dichotomical
4 response to long-term hydro-climatic variations can go beyond the classical opposite
5 2 phenological responses to include opposite responses in the long-term variations in
6 3 absolute and relative densities, and that this response evidences correlations with large-
7 4 scale atmospheric teleconnections, such as the NAO and particularly the EA pattern.
8 5 Results have further shown that copepod density changes occurred in a stepwise manner
9 6 and the timing of the abrupt change in 2013-2015 agrees well with the prediction of
10 7 Beaugrand et al. (2019) of an unprecedented abrupt community shift during these years.
11 8

12 9 Our results therefore confirm that zooplankton respond rapidly to atmospheric
13 10 forcing (Richardson, 2008), which highlights the usefulness of zooplankton as indicator
14 11 of climate/environmental change and reinforces the need for maintaining existing
15 12 zooplankton time series around the world updated and to extend the monitoring efforts
16 13 to additional regions to obtain a clearer picture of the long-term zooplankton dynamics
17 14 and their drivers across regions.

15 **Data availability statement**

16 Data are available on reasonable request to the authors.

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Table 1. Coefficients of Spearman rank correlations of the trends of the teleconnection indices (NAO, EA pattern and AMO) and the local environmental variables (Sal: salinity; WT: water temperature; DOS: dissolved oxygen saturation; Chla: concentration of chlorophyll *a*; Str: salinity stratification; RF: river flow; Pre: precipitation; Upw: upwelling index) with the main mode of variability (PC 1) of the copepod densities (log x+1) for the whole year (Y) and for each season (W/W*: winter (January-February-March) / winter* (December-January-February-March); Sp: spring (April-May-June); S: summer (July-August-September); A: autumn (October-November-December)). Only significant positive (light grey) and negative (dark grey) correlations are shown with the significance level represented by asterisks (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; ns stands for not significant.

| PC1 (Absolute Density) | | | | | | | | | | | |
|------------------------|------------------------|---------------|--------------|-------------------------|---------------|-----|---------------|--------------|---------------|-----|--------------|
| | Teleconnection indices | | | Environmental variables | | | | | | | |
| | NAO | EA | AMO | Sal | WT | DOS | Chla | Str | RF | Pre | Upw |
| Y | 0.146 ** | -0.218 *** | 0.111 * | ns | ns | ns | -0.211 *** | 0.295 *** | ns | ns | 0.382 *** |
| W | 0.124 * | -0.248 *** | 0.102 * | 0.152 ** | ns | ns | -0.211 *** | 0.266 *** | 0.135 ** | ns | 0.347 *** |
| W* | 0.338 *** | | | | | | | | | | |
| Sp | 0.198 *** | -0.209 *** | 0.227 *** | ns | ns | ns | -0.106 * | 0.262 *** | 0.134 ** | ns | 0.353 *** |
| S | -0.285 *** | ns | 0.138 ** | 0.174 *** | -0.224 *** | ns | -0.127 * | 0.268 *** | -0.335 *** | ns | 0.121 * |
| A | ns | ns | 0.159 ** | 0.101 * | 0.142 ** | ns | -0.244 *** | 0.199 *** | -0.291 *** | ns | 0.428 *** |

Table 2. Coefficients of Spearman rank correlations of the trends of the teleconnection indices (NAO, EA pattern and AMO) and the local environmental variables (salinity, water temperature, dissolved oxygen saturation, concentration of chlorophyll *a*, salinity stratification, river flow, precipitation and upwelling index) with the PC 2 of the copepod densities (log $x+1$), for the whole year (Y) and for each season. Abbreviations, shading and asterisks as in Table 1.

| PC 2 (Absolute Density) | | | | | | | | | | | |
|-------------------------|--------------|---------------|---------------|-------------------------|---------------|-----|--------------|---------------|---------------|-----|---------------|
| Teleconnection indices | | | | Environmental variables | | | | | | | |
| | NAO | EA | AMO | Sal | WT | DOS | Chla | Str | RF | Pre | Upw |
| Y | 0.463 *** | 0.183 *** | ns | -0.436 *** | 0.292 *** | ns | 0.235 *** | -0.241 *** | -0.221 *** | ns | -0.389 *** |
| W | 0.361 *** | ns | -0.127 * | -0.414 *** | -0.178 *** | ns | ns | 0.202 *** | 0.143 ** | ns | -0.442 *** |
| W* | 0.332 *** | | | | | | | | | | |
| Sp | 0.430 *** | 0.538 *** | -0.286 *** | -0.259 *** | -0.332 *** | ns | 0.278 *** | -0.518 *** | -0.456 *** | ns | -0.199 *** |
| S | 0.119 * | -0.424 *** | -0.119 * | -0.544 *** | 0.265 *** | ns | 0.557 *** | ns | 0.110 * | ns | -0.477 *** |
| A | 0.319 *** | 0.101 * | 0.240 *** | ns | 0.311 *** | ns | 0.108 * | -0.625 *** | -0.613 *** | ns | -0.226 *** |

Table 3. Coefficients of Spearman rank correlations of the trends of the teleconnection indices (NAO, EA pattern and AMO) and the local environmental variables (salinity, water temperature, dissolved oxygen saturation, concentration of chlorophyll a, salinity stratification, river flow, precipitation and upwelling index) with the PC 1 of the relative abundance of copepods (%), for the whole year and for each season. Abbreviations, shadings and asterisks as in Table 1.

| PC 1 (Relative abundance) | | | | | | | | | | | |
|---------------------------|--------------|--------------|--------------|-------------------------|--------------|-----|-----------|------------|-------------|-----|---------------|
| Teleconnection indices | | | | Environmental variables | | | | | | | |
| | NAO | EA | AMO | Sal | WT | DOS | Chla | Str | RF | Pre | Upw |
| Y | 0.444 *** | 0.336 *** | -0.130 ** | -0.602 *** | 0.239 *** | ns | ns | ns | 0.146 ** | ns | -0.579 *** |
| W | 0.252 *** | 0.269 *** | -0.209 *** | -0.638 *** | -0.172 *** | ns | -0.171 ** | 0.273 *** | 0.405 *** | ns | -0.612 *** |
| W* | 0.320 *** | 0.401 *** | -0.399 *** | -0.432 *** | -0.462 *** | ns | ns | -0.306 *** | -0.282 *** | ns | -0.463 *** |
| Sp | 0.135 ** | 0.401 *** | -0.399 *** | -0.432 *** | -0.462 *** | ns | ns | -0.306 *** | -0.282 *** | ns | -0.463 *** |
| S | 0.357 *** | -0.341 *** | ns | -0.621 *** | 0.221 *** | ns | 0.378 *** | -0.204 *** | 0.196 *** | ns | -0.451 *** |
| A | 0.452 *** | 0.144 ** | 0.162 ** | -0.345 *** | 0.383 *** | ns | ns | -0.295 *** | -0.257 *** | ns | -0.288 *** |

Table 4. Coefficients of Spearman rank correlations of the trends of the teleconnection indices (NAO, EA pattern and AMO) and the local environmental variables (salinity, water temperature, dissolved oxygen saturation, concentration of chlorophyll a, salinity stratification, river flow, precipitation and upwelling index) with the PC 2 of the relative abundance of copepods (%), for the whole year and for each season. Abbreviations, shadings and asterisks as in Table 1.

| PC 2 (Relative abundance) | | | | | | | | | | | |
|---------------------------|------------------------|---------------|--------------|-------------------------|--------------|-----|---------------|---------------|---------------|-----|--------------|
| Y | Teleconnection indices | | | Environmental variables | | | | | | | |
| | NAO | EA | AMO | Sal | WT | DOS | Chla | Str | RF | Pre | Upw |
| Y | ns | ns | ns | -0.130 ** | 0.273 *** | ns | ns | -0.155 ** | -0.521 *** | ns | 0.105 * |
| W | ns | -0.168 ** | ns | ns | 0.104 * | ns | -0.273 *** | 0.123 * | -0.207 *** | ns | 0.183 *** |
| Sp | 0.310 *** | ns | 0.169 ** | -0.179 *** | ns | ns | ns | ns | -0.127 * | ns | 0.166 ** |
| S | -0.189 *** | -0.181 *** | -0.163 ** | -0.150 ** | 0.153 ** | ns | 0.224 *** | 0.241 *** | ns | ns | ns |
| A | ns | -0.144 ** | ns | ns | ns | ns | 0.131 ** | -0.308 *** | -0.565 *** | ns | 0.167 ** |

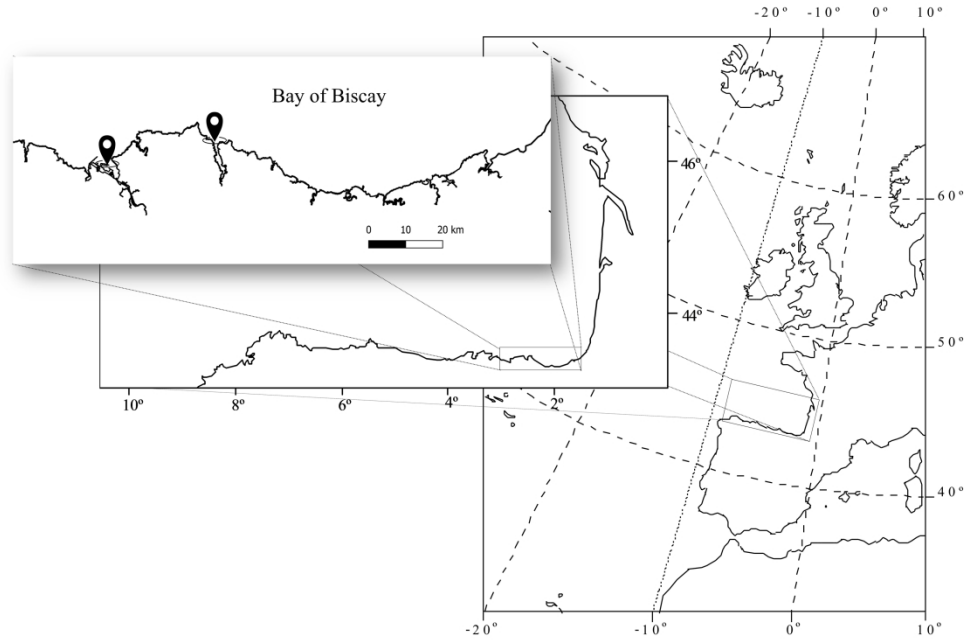


Figure 1. Study area and location of sampling sites.

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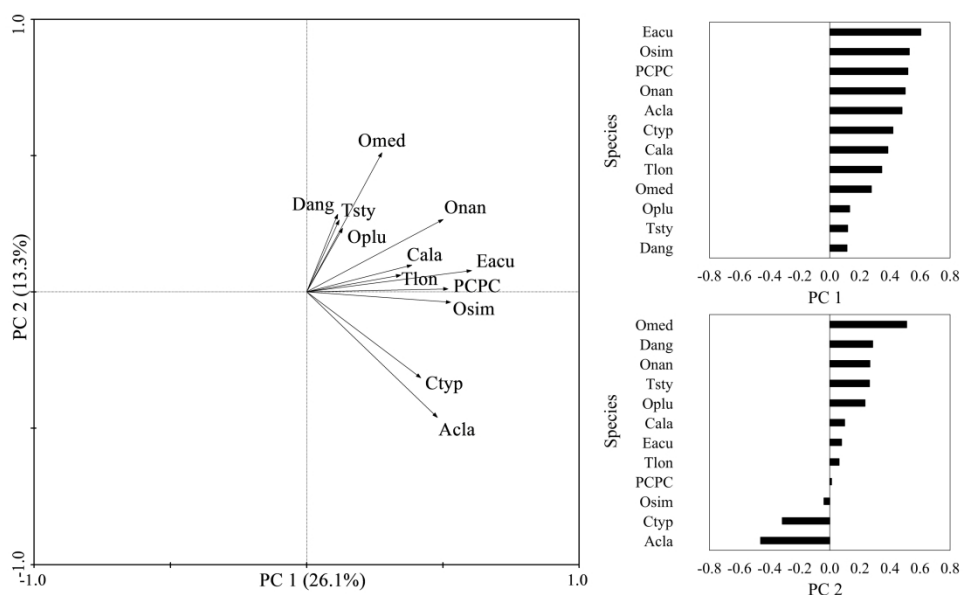


Figure 2. Left panel: PCA biplot of the density (log x+1) of the studied copepod species. Percentage variability explained by each PC in parenthesis. Right panel: Plots of species scores on the main mode of variability (PC 1; top panel) and on the second main mode of variability (PC 2; bottom panel) obtained from the copepod density (log (x + 1) PCA analysis. Species abbreviations: Acla: *Acartia clausi*, Cala: *Calanus helgolandicus*, Ctyp: *Centropages typicus*, Dang: *Ditrichocorycaeus anglicus*, Eacu: *Euterpina acutifrons*, Onan: *Oithona nana*, Oplu: *Oithona plumifera*, Osim: *Oithona similis*, Omed: *Oncaea media*, PCPC: *PCPC-calanus*, Tlon: *Temora longicornis*, Tsty: *Temora stylifera*.

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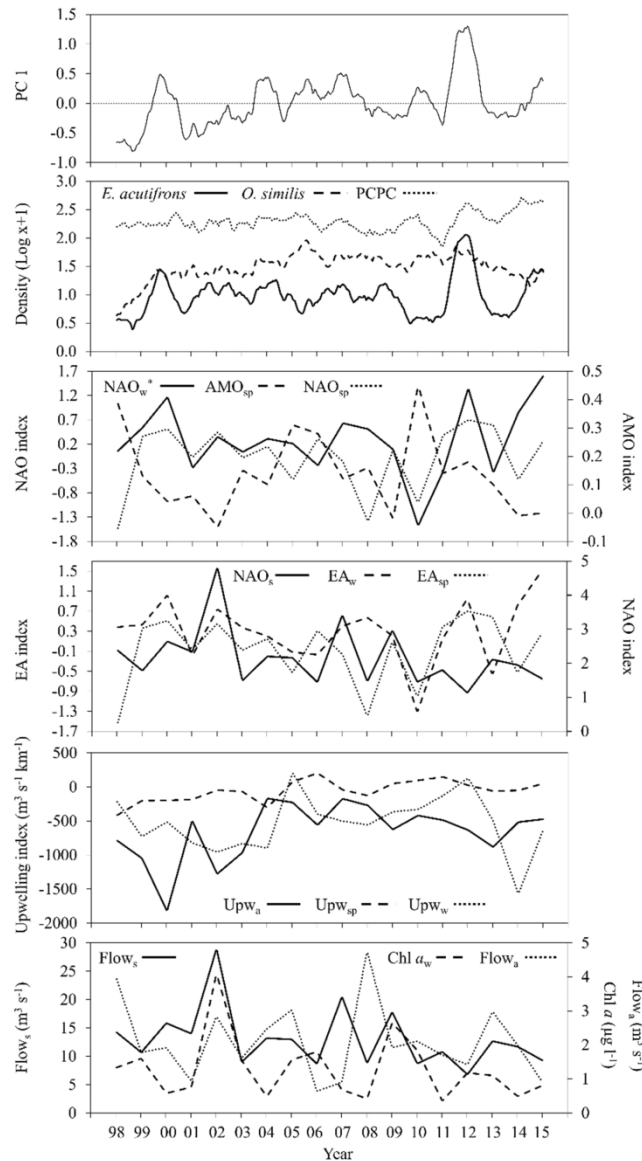


Figure 3. Interannual trend of the main mode of variability (PC 1) of the density (log $x+1$) of the copepod species (top panel) and of the best-correlated explanatory variables (rest of panels). Species abbreviations as in Figure 2. Explanatory variable abbreviations: NAO: North Atlantic Oscillation index, EA: East Atlantic index, AMO: Atlantic Multi-Decadal Oscillation, Upw: upwelling index, Flow: river flow, Sal: salinity, WT: Water temperature, Str: stratification index, Chl a: concentration of chlorophyll a. Season-specific explanatory variables are represented by additional subscript abbreviations (w: winter JFM, w*: winter DJFM sp: spring, s: summer, a: autumn). The horizontal line separates positive and negative values.

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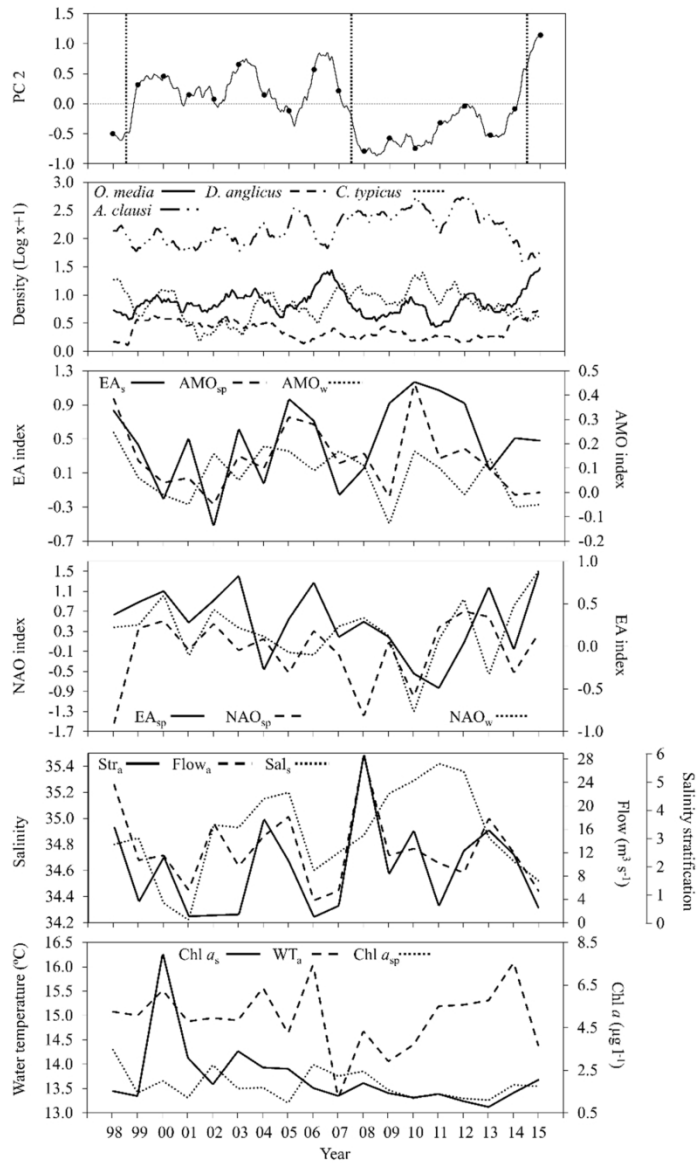


Figure 4. Interannual trend of the second main mode of variability (PC 2) of the density (log x+1) of the copepod species (top panel) and of the best-correlated explanatory variables (rest of panels). Species abbreviations as in Figure 2. Explanatory variable abbreviations as in Figure 3. The horizontal line separates positive and negative values and the vertical ones the timing of step changes.

139x219mm (300 x 300 DPI)

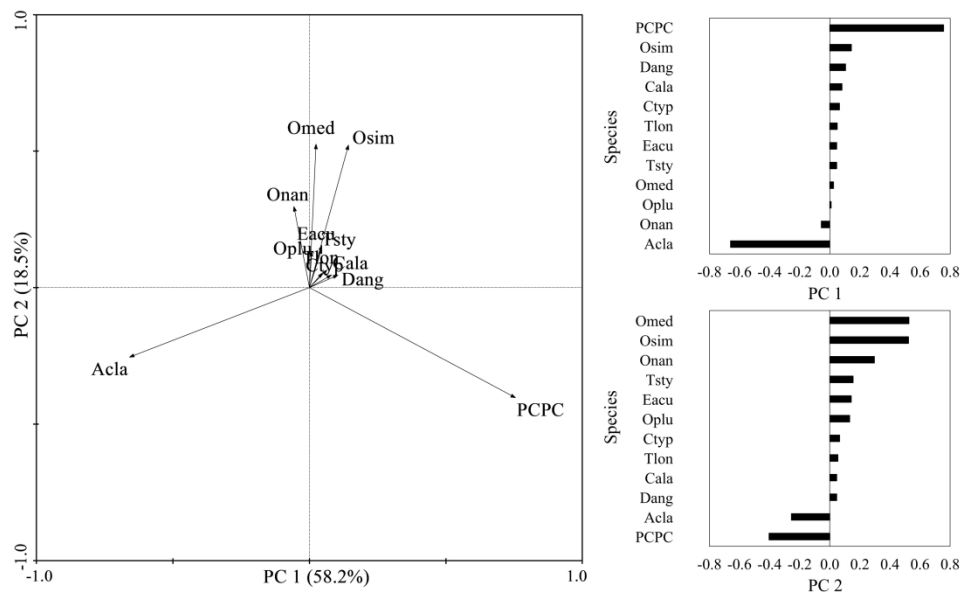


Figure 5. Left panel: PCA biplot of the relative density (percentage) of the studied copepod species. Percentage variability explained by each PC in parenthesis. Right panel: Plots of species scores on main mode of variability (PC 1; top panel) and of the second main mode of variability (PC 2; bottom panel) obtained from the copepod relative density PCA analysis. Species abbreviations as in Figure 2.

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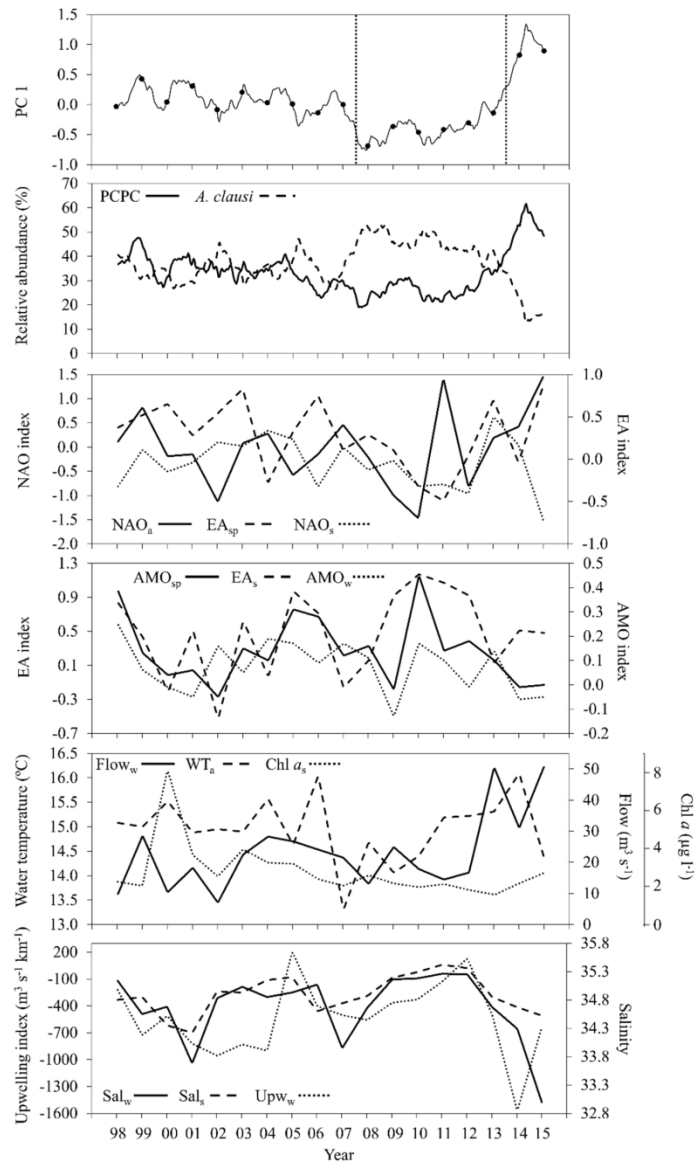


Figure 6. Interannual trend of the main mode of variability (PC 1) of the relative density (percentage) of the copepod species (top panel) and of the best correlated explanatory variables (rest of panels). Species abbreviations as in Figure 2. Explanatory variable abbreviations as in Figure 3. The horizontal line separates positive and negative values and the vertical ones the timing of step changes.

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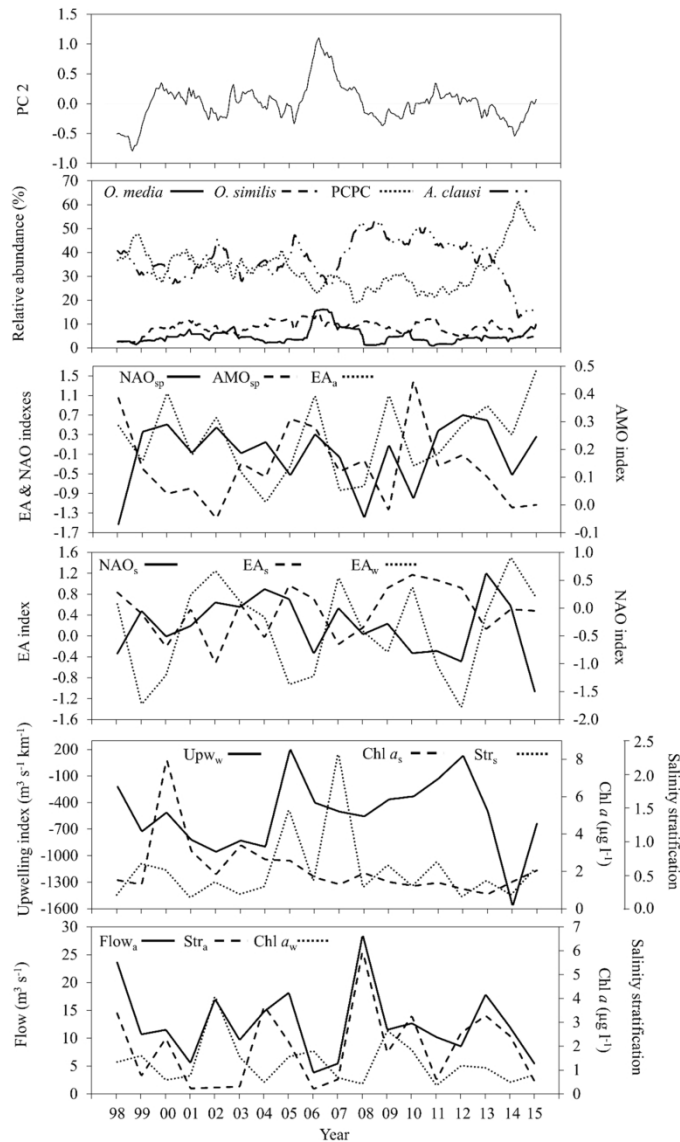


Figure 7. Interannual trend of the second main mode of variability (PC 2) of the relative density (percentage) of the copepod species (top panel) and of the best correlated explanatory variables (rest of panels). Species abbreviations as in Figure 2. Explanatory variable abbreviations as in Figure 3. The horizontal line separates positive and negative values.

150x249mm (300 x 300 DPI)