

Evidence for Changes in Estuarine Zooplankton Fostered by Increased Climate Variance

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ABSTRACT

Estuaries are among the most valuable aquatic systems in terms of their services to human welfare. They offer an ideal framework to assess multiscale processes linking climate and food web dynamics through the hydrological cycle. Resolving food web responses to climate change is fundamental to resilience management of these threatened ecosystems under global change scenarios. Here, we examined the temporal variability of the plankton food web in the Mondego Estuary, central Iberian Peninsula, over the period 2003 to 2012. The results pointed out a cascading effect from climate to plankton communities that follow a non-stationary behavior shaped by the climate variance envelope. Concurrent changes in hydrographic processes at the regional, that is, upwelling intensity, and local, that is, estuarine hydrology, scales were driven by climatic forcing promoted by the North Atlantic Oscillation; the influence of

which permeated the physical environment in the estuary affecting both autotrophic and heterotrophic communities. The most conspicuous change arose around 2008 and consisted of an obvious decrease in freshwater taxa along with a noticeable increase in marine organisms, mainly driven by gelatinous zooplankton. The observed increase in small-sized cosmopolitan copepods, that is, *Clausocalanus arcuicornis*, *Oithona plumifera*, thermophilic species, that is, *Penilia avirostris*, and gelatinous zooplankton suggests a structural change in the Mondego plankton community. These results provide empirical support to the expectation that expanding climate variance changes plankton structure and functioning, likely fostering trophic interactions in pelagic food webs.

Key words: Iberian coast plankton; North Atlantic climate; North Atlantic Oscillation; non-stationary; climate variance; Mondego Estuary—Portugal.

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Author's contributions SCM and JCM conceived, designed and performed the research; JCM analyzed the data; SCM, UA, MAP contributed to reagents/materials/analysis tools; SCM, MAP, FM, JF, ALP, UA contributed to field campaigns/laboratory procedure; SCM and JCM wrote the paper.

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INTRODUCTION

Estuaries encompass vast socioeconomic resources, that is, food production, recreation and nutrient recycling and are among the most valuable aquatic systems in terms of their services to human welfare

(Constanza and others 1997). Estuaries face immediate effects of climate forcing that foster modifications in the structure and function, thereby threatening ecosystem assets (IPCC 2007; Cloern and others 2016). In addition, their direct exposure to anthropogenic influences, that is, land-use, pollution and overfishing (Kennish and Elliott 2011), warns of synergistic interactions of climate and anthropogenic forces that could magnify climate effects (Wiedenmann and others 2012). Long-term field surveys and the adequate data mining are therefore plainly warranted to understand the response of marine populations to the above synergies. The success in this challenging endeavor will help to anticipate ecological responses to growing climate and human stress, eventually shedding light on the long-term sustainable use of coastal resources.

Climate variations profoundly impact marine ecosystems through changes in the physical environment and subsequent effects on plankton communities (Hays and others 2005). These organisms form the base of food webs, and therefore any substantial changes in their structure or biomass may permeate the entire network, ultimately affecting trophic cycling and fish recruitment (Taylor and others 2002; Beaugrand and Reid 2003). Hence, the pivotal role plankton play in trophic dynamics and food web stability makes these organisms fundamental indicators in environmental assessment programs. In the western Iberian coast, former studies showed that hydrographic modifications covary with the secular trend of both sea surface temperatures and the North Atlantic Oscillation (NAO) (Pérez and others 2010). The NAO is characterized by a north–south dipole structure with simultaneous atmospheric pressure anomalies between temperate (that is, near the Azores Islands) and high latitudes (that is, near Iceland), and drives the main pattern of atmospheric circulation in the North Atlantic and surrounding seas (Hurrell and others 2003). In the central area of the western Iberian coast is located the Mondego Estuary, a highly productive system, where a consistent ecological survey started a decade ago on a monthly basis. Earlier analyses of these data showed conspicuous changes in zooplankton assemblages, including an increase in abundance, which have been ascribed to changes in freshwater flow regimes (Marques and others 2007; Primo and others 2009; Primo and others 2011). However, underlying mechanisms and their potential link with Atlantic Ocean–atmospheric processes remain elusive.

Here we examined the Mondego Estuary plankton data over the period 2003–2012 in regard to

climate forcing and test the hypothesis that the strength of the relationship between environmental variability and plankton increases along with changes in the climate variance envelope, that is, the amplitude of the climatic signal (Molinero and others 2013). Quantifying such varying relationships is fundamental to depict potential scenarios of a predominant role of climate versus ecological processes as drivers of temporal patterns of plankton. To tackle these questions, we assessed the non-stationary signals of climate, hydrology and plankton and their relationship with the North Atlantic climate. We aim at quantifying the strength of links in the climate–plankton network under varying climate forcing. Our approach unveils cascading interactions from climate variability to plankton structure, which allow identifying factors shaping plankton dynamics in the central Iberian coast.

MATERIALS AND METHODS

Biological and Physical Data

Plankton samples were collected monthly at high tide from January 2003 to December 2012 in the Mondego Estuary (40°08'N, 8°50'W) located on the west coast of Portugal (Figure 1). This ecosystem experiences a Mediterranean temperate climate and is exposed to the influence of the North Atlantic Ocean climate mainly driven by the NAO variability.

Hydrological variability ascribed to salinity and temperature was recorded using WTW Cond 3310 sensors simultaneously with plankton samples. Water samples were also collected for chlorophyll *a* concentration (Chl *a*, mg m⁻³), as a measure of total phytoplankton biomass. In turn, zooplankton samples were collected monthly from January 2003 to December 2012 at the mouth of the estuary, which corresponds to the station more exposed to the ocean–climate influence. Samples were taken by subsurface horizontal hauls, using a 335-mm mesh plankton net with a 0.5-m opening, equipped with a Hydro-bios flowmeter (Marques and others 2006). Immediately after collection samples were fixed and stored with buffered formaldehyde (5%). In the laboratory, samples were sub-sampled by means of a Folsom splitter and organisms were counted under a dissecting microscope. Although the mesh size used underestimates accurate abundances of small zooplankton, the consistency of the sample treatment throughout the whole period makes samples comparable among them. These data are therefore useful to provide a reasonable

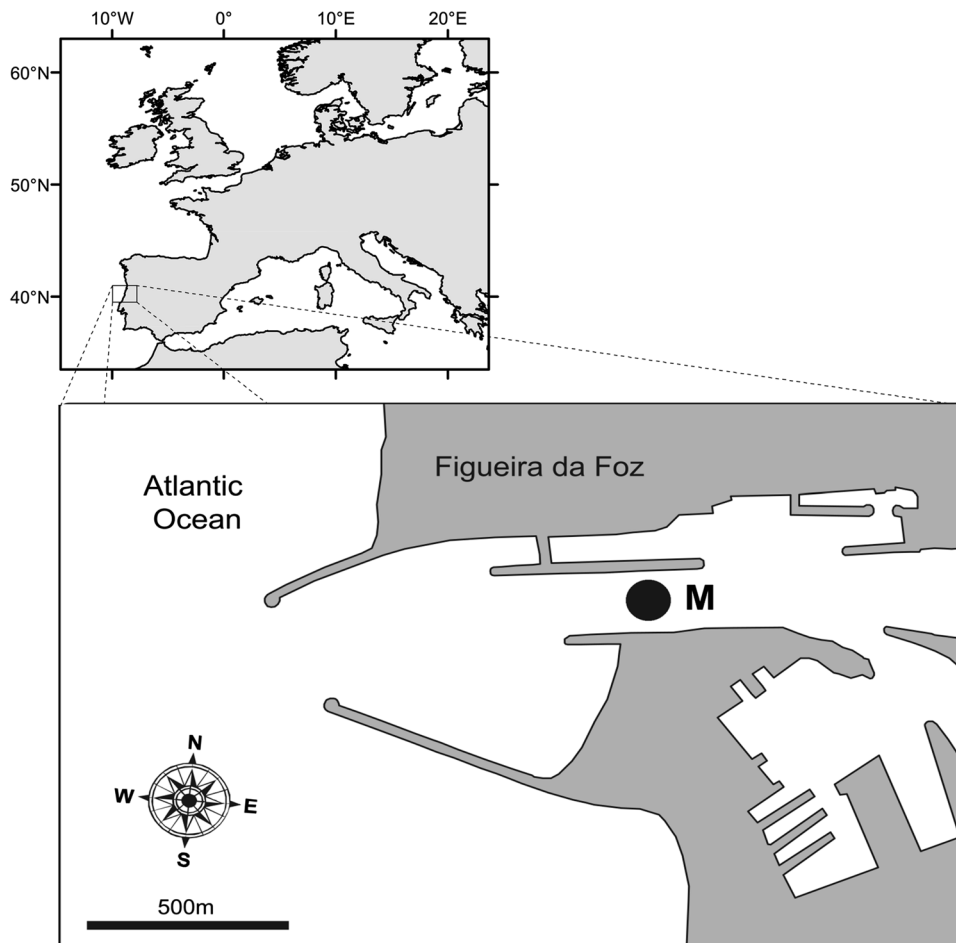


Figure 1. Map of the study area. The sampling location in the mouth of the Mondego Estuary is indicated.

assessment of the plankton decadal variations in the Mondego Estuary and its potential relationship with climate variability.

For the purposes of our analyses, we used the main species composing each group (Figure 2; Table 1); appendicularia encompassed the species *Oikopleura dioica*, chaetognata was characterized by *Sagitta friederici*, cladocera included the freshwater species *Bosmina longirostris*, *Daphnia* spp., *Ceriodaphnia* sp. and *Chydorus sphaericus*, and the marine species *Penilia avirostris*, *Evadne nordmani*, *Podon polyphemoides*, *Podon intermedius*. Likewise, copepods included freshwater (*Copidodiaptomus numidicus*, *Acanthocyclops trajani*), estuarine (*Acartia tonsa*) and marine species (*Acartia clausi*, *Temora longicornis*, *Paracalanus parvus*, *Clausocalanus arcuicornis*, *Oithona plumifera*, *Centropages chierchae*, *Corycaeus anglicus*), whereas gelatinous carnivores include *Muggiaea atlantica*, *Obelia* sp., *Sarsia* sp., *Lizzia blondina* and *Liriope tetraphylla*.

Climate variability in the Mondego Estuary area was assessed by using monthly anomaly fields of atmospheric parameters, that is, air temperature, sea surface temperature (SST), sea level pressure,

300 hPa geopotential height, precipitation and ongoing longwave radiation (olr), at the nearest grid point (40°N, 8.5°W) over the period 2003–2013 from the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalney and others 1996). Local precipitation records were acquired from INAG (Portuguese Water Institute, also available at the Web site www.snirh.inag.pt) station Source 13F/01G.

As large-scale forcing acting upon the Mondego Estuary, monthly records of the North Atlantic Oscillation (NAO) were used, and monthly upwelling index data (UI) provided by the Instituto Español de Oceanografía. This index corresponds to the offshore area relative to the Mondego Estuary (Figueira da Foz region) and was computed by the Meteogalicia WRF atmospheric model.

Statistical Analysis

Statistical analysis was performed through a seven-step procedure that allowed assessing climate forcing effects on the local environment, and ultimately on interannual changes of the zooplankton

Figure 2. Z-scores (zero mean, unit variance) of inter-annual abundance variability of the main zooplankton taxa in the Mondego Estuary.

community. First, time series were standardized to zero mean and unit variance, and linear regressions were performed to remove temporal trends. For subsequent analyses, residual values were used.

Second, we identified dominant patterns of regional climate variability in the region relative to the Mondego Estuary. To do so, principal component analysis (PCA) was applied on a matrix Z , composed by the ensemble of regional atmospheric variables (sea surface temperature, atmospheric pressure, precipitation and air temperature). PCA allows integrating in few variables the mutually independent principal components (PCs), which encompass the main signals relative to the regional atmospheric forcing (Molinero and others 2005). Here PC1 (45% of the total variance) was used as a proxy of regional climate variability. Likewise, this procedure was used to identify the dominant hydrological signal in the Mondego Estuary ascribed to the variability of monthly records of temperature and salinity.

Third, structural changes in NAO, regional climate forcing and local environmental variables (hydrology) were addressed using cumulative sum of ordinary least square residuals (CUSUM-OLS) (Zeileis and others 2003). The method is an extension of the classical CUSUM analysis using ordinary least squares (OLS) residuals. OLS residuals were obtained from fitting the PC1 scores to a linear regression with time as a covariate, and CUSUM-OLS was used to calculate the empirical fluctuations. To identify significant changes in the temporal structure, a boundary limit was calculated using a generalized fluctuation test, establishing as the model null hypothesis that the fluctuations remained constant with a 0.95 confidence limit.

Fourth, the influence of NAO on local hydrological conditions and zooplankton interannual changes was assessed on a monthly scale by means of wavelet analysis (continuous wavelet transform, CWT, Morlet function). This technique is widely used for the decomposition of the variance over a time/frequency diagram and has been shown robust to assess geophysical and ecological time series (Grinsted and others 2004; Cazelles and others 2008). This way allowed computing the wavelet coherence to quantify their correlation in the time frequency space. The 5% statistical significance level was determined by using bootstrap simula-

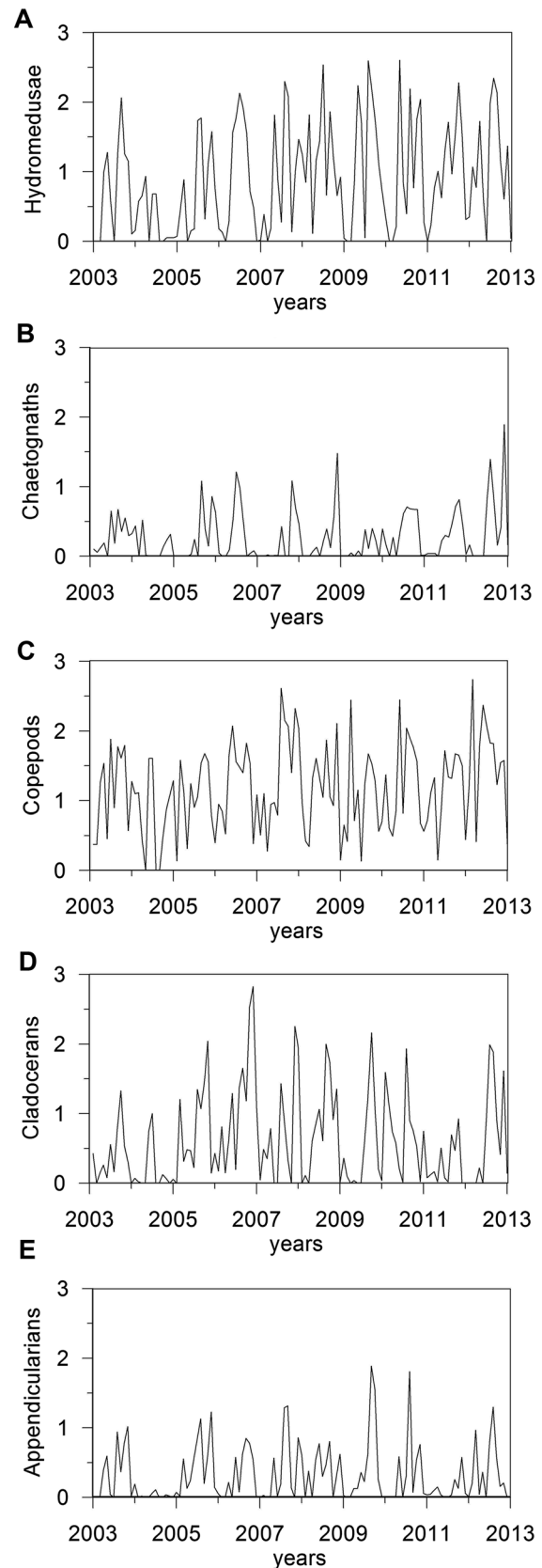


Table 1. List of Mesozooplankton Species in Mondego Estuary

Group	Taxon	Habitat	Average	SD	
Appendicularia	<i>Oikopleura dioica</i>	Marine	3.01	7.95	
	<i>Fritillaria borealis</i>	Marine	0.54	4.47	
Chaetognatha	<i>Sagitta friederici</i>	Marine	2.47	8.34	
Cladocera	<i>Penilia avirostris</i>	Marine	15.62	125.25	
	<i>Evadne nordmani</i>	Marine	11.07	40.73	
	<i>Podon intermedius</i>	Marine	3.10	18.61	
	<i>Podon leuckarti</i>	Marine	2.87	7.88	
	<i>Podon polyphemoides</i>	Marine	2.15	9.05	
	<i>Daphnia</i> spp.	Fresh	0.89	4.04	
	<i>Ceriodaphnia</i> spp.	Fresh	0.39	2.70	
	<i>Bosmina</i> spp.	Fresh	0.22	1.06	
	<i>Simocephalus vetulus</i>	Fresh	0.11	0.97	
	<i>Chydorus sphaericus</i>	Fresh	0.11	0.69	
	Copepoda	<i>Acanthocyclops trajani</i>	Fresh	0.82	4.12
		<i>Acartia clausi</i>	Marine	63.37	127.09
		<i>Acartia</i> spp. (copepodite)	Mixed	2.32	18.68
		<i>Acartia tonsa</i>	Brackish	6.52	39.45
		<i>Calanus helgolandicus</i>	Marine	0.57	2.46
<i>Calanus helgolandicus</i> (copepodite)		Marine	0.58	2.58	
<i>Centropages chierchiae</i>		Marine	2.99	14.45	
<i>Centropages</i> sp.		Marine	0.19	1.23	
<i>Centropages</i> sp. (copepodite)		Marine	0.25	1.07	
<i>Clausocalanus arcuicornis</i>		Marine	11.74	48.31	
<i>Copidodiaptomus numidicus</i>		Fresh	1.44	5.88	
<i>Corycaeus anglicus</i>		Marine	0.98	2.89	
<i>Oithona plumifera</i>		Marine	3.12	8.20	
<i>Oithona</i> spp. (copepodite)		Mixed	0.35	3.48	
<i>Paracalanus parvus</i>		Marine	12.08	76.57	
<i>Pseudocalanus elongatus</i>		Marine	0.34	1.20	
<i>Temora longicornis</i>		Marine	19.45	68.34	
<i>Temora</i> sp. (copepodite)	Marine	0.22	1.25		
Hydromedusae	<i>Clytia hemisphaerica</i>	Marine	0.30	1.00	
	<i>Liriope tetraphylla</i>	Marine	0.75	3.55	
	<i>Lizzia blondina</i>	Marine	1.66	5.15	
	<i>Obelia</i> spp.	Marine	2.04	5.87	
	<i>Podocorynoides minima</i>	Marine	0.25	1.36	
	<i>Solmaris corona</i>	Marine	0.16	0.81	
	Unidentified hydromedusae	Marine	0.13	0.67	
Siphonophora	<i>Muggiaea atlantica</i>	Marine	22.03	65.30	
Thaliacea	<i>Doliolum</i> spp.	Marine	3.23	16.76	

Groups and taxa are arranged alphabetically within the table.

For each taxon, there is information on its habitat, abundance (ind m^{-3}) average and standard deviation (SD).

*Species showing an abundance larger than 0.1%.

tions (1000 times) considering a first-order autoregressive process with lag-1 autocorrelation. The statistical significance was assessed relative to the null hypotheses that the signal is generated by a stationary process, that is, mean and variance of the time series do not vary with time (Grinsted and others 2004). Then, from the CWT the wavelet coherence was computed to identify areas with high common power and significant links in the

time frequency space between NAO, hydrology and zooplankton. The temporal relationship was graphically displayed. Only data within the cone of influence were considered for the interpretation.

Fifth, the influence of regional scale environmental variations was assessed by means of the monthly upwelling index (UI) time series. Heat maps were used to display seasonal changes in UI over the period investigated. To do so, data were

standardized to zero mean and unit variance, and the range of values was quantile divided. To each quantile a specific color was assigned from white (quantile 0.10) to black (quantile 0.90), representing low and high values, respectively. Subsequently, to identify significant changes in UI interannual variability the cumulative sum of standardized annual values was computed. Dominance of positive (negative) UI values corresponds to a dominance of upwelling (downwelling) offshore of the Mondego Estuary.

Sixth, changes in the structure of zooplankton community were computed by means of principal component analysis applied on the matrix composed by monthly records of zooplankton taxa (copepods, cladocerans, chaetognaths, gelatinous zooplankton, cirripedia and decapod larvae). In addition, potential changes in the zooplankton structure linked to the relative contribution of marine and freshwater taxa, as well as the predominance of gelatinous zooplankton, were assessed by computing temporal trends of each group. Zooplankton seasonal variability was displayed by means of heat maps, whereas interannual trends were depicted by generalized additive models (GAMs) with years as covariates. Cubic splines with maximal 3, 4 and 5 degrees of freedom (4, 5 and 6 knots) were used for each species to obtain the best compromise between model complexity and fit to the observed data. Model selection was used through generalized cross-validation score minimization. GAMs were performed using the *mgcv* library in R.

Seventh, the quantitative assessment of the links in the climate–plankton network and the identification of predominant factors shaping the abundance and structure of zooplankton were achieved by structural equation modeling. The a priori structure of the path model is based on the hypothesis that large-scale climate cascades influencing regional and local hydroclimate conditions, both jointly drive the physical environment relative to plankton, thereby shaping the structure and functioning of plankton communities; however, in concomitance with changes in climate variance, we may expect a varying strength in the pathways connecting climate–plankton. The choice was based on the taxonomic resolution and data availability, as we only have the bulk of phytoplankton biomass, but not the main groups, we therefore opted to apply a top-down approach. For each scenario of climate variance, specific effects of climate and environmental variables and their covariations with plankton structure were assessed using variance partitioning and further explored

through path analysis (Alsterberg and others 2013). The strength of the links and the quantification of the overall model were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1000 replicates), whereas the Bayesian information criterion (BIC) and chi-square values were used to assess the robustness of models (Peres-Neto and others 2006). The individual path coefficients (that is, partial regression coefficients) that indicate the strength of the relation between causal and response variables and the fit of the overall path model were evaluated using the R library *sem*.

RESULTS AND DISCUSSION

Climate and the Physical Environment in the Mondego Estuary

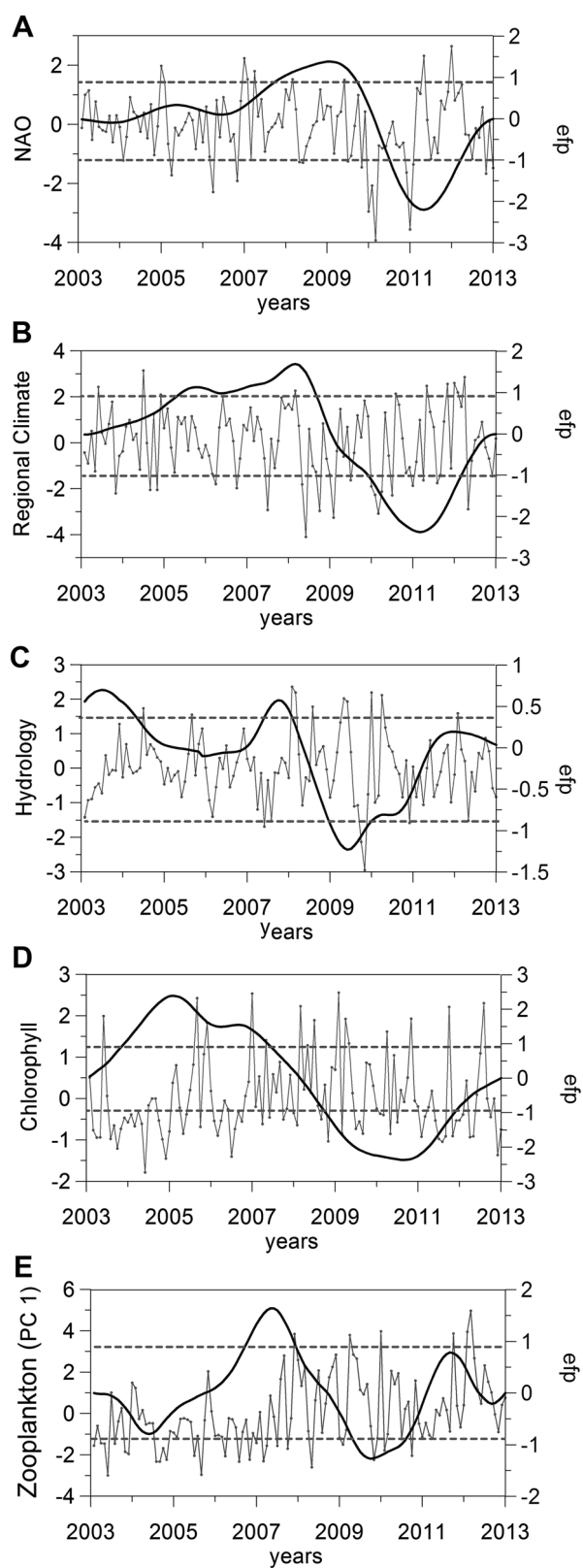
The multiscale climate forcing ascribed to the NAO and regional hydroclimate conditions displayed a conspicuous variability at monthly and interannual scales (Figure 3A, B). The interannual changes of the NAO showed enhanced variance, twofold higher, after 2008 that encompassed a dramatic drop in the NAO during 2010–2011, followed by a marked reversal change of the signal. In turn, the physical environment in the Mondego Estuary showed prominent monthly variations of hydrological conditions (Figure 3C) that exhibited as well larger variance around 2007–2010 followed by a slight decrease. Likewise, the magnitude in their variance change was 2.5-fold higher. The governing pattern of the temporal structure of climatic and hydrological signals showed concurrent changes around 2008–2012. The NAO and the main pattern of variability of regional climate (PC1) exhibited prominent changes in 2008–2009 and 2010–2012, respectively (CUSUM test $p < 0.05$), whereas the structure of the hydrological signal showed significant changes around 2008–2010 (CUSUM test $p < 0.05$). The emergent patterns appeared related to enhanced variance in regional wind and precipitation, which are shaped by the NAO. This suggests a close connection between the Mondego Estuary and the NAO through the influence of this climate phenomenon on regional atmospheric variables in the Northeast Atlantic coast, that is, temperature, atmospheric pressure, wind, precipitation, the variability of which permeated the environmental conditions in the estuary, as suggested by the temporal patterns of autotrophic and heterotrophic communities (Figure 3D, E). Indeed, phytoplankton and zooplankton plankton compartments showed signifi-

Figure 3. Interannual variability of hydroclimate forcing acting upon the Mondego Estuary and local hydrological conditions over the period 2003–2013. Temporal structure of **A** the North Atlantic Oscillation, **B** regional climate, **C** local hydrology, **D** chlorophyll and **E** zooplankton (PC1 54%). Structural changes are shown by the cumulative sum of ordinary least square residuals (OLS-based CUSUM process) denoted by the *thick line*. Confidence intervals ($p < 0.05$) are indicated by horizontal *dashed lines*.

cant changes after 2008 concurrently with the modifications in the hydroclimate forcing. The observed pattern of the phytoplankton interannual variability, as indexed by chlorophyll concentration, and zooplankton (PC1 54% of variability) displayed major changes around 2008 and 2009–2011 (CUSUM test $p < 0.05$).

Varying Responses to Discontinuous Climate Forcing

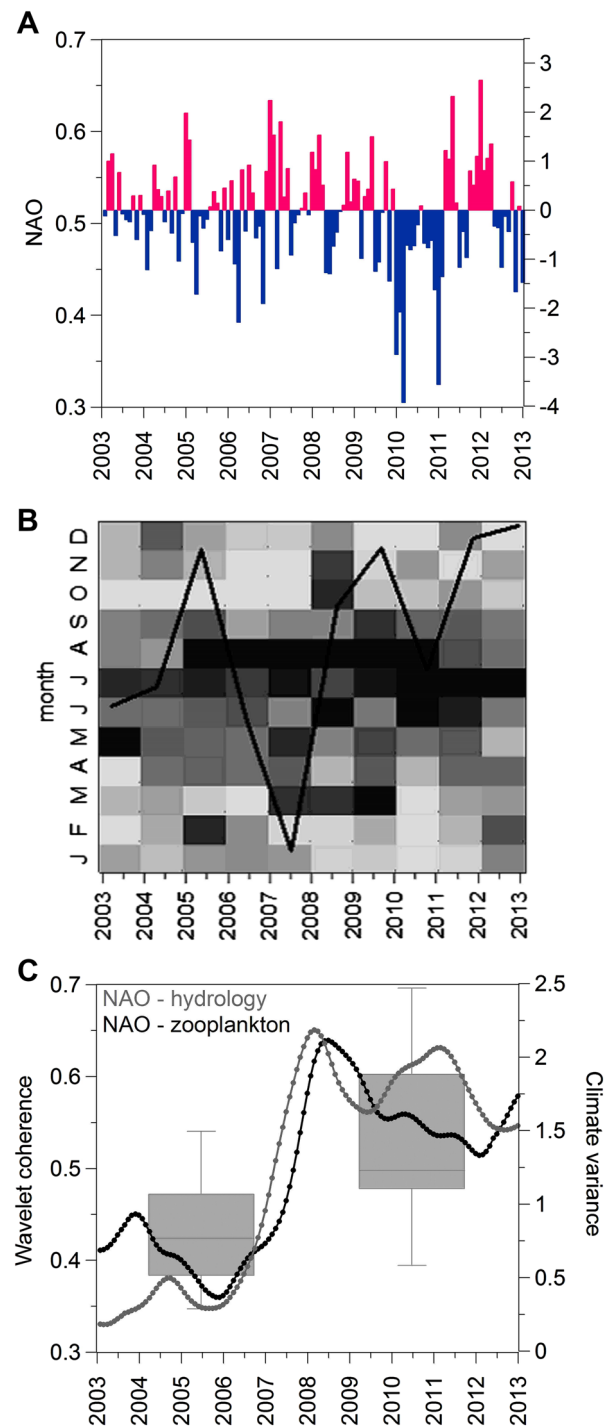
The North Atlantic climate variance (Figure 4A) and the upwelling index (UI) offshore the Mondego Estuary (Figure 4B) portrayed the hydroclimate forcing on the Mondego Estuary. The seasonal variability of the upwelling signal showed a peak in summer, whereas interannual changes rose after 2007 and reached a maximum in 2008 (Figure 4B). Likewise, the NAO displayed a larger variance after 2008 reaching a maximum around 2010–2012. The strength of such hydroclimate influence on the local environmental conditions and the zooplankton community was depicted by the wavelet coherence between both couples NAO hydrology and NAO zooplankton (Figure 4C). Results showed a parallel change in the relationship between NAO and both hydrology and zooplankton. In the two cases, a significant increase in the wavelet coherence evolved around 2008 reaching maximum coherence in 2009. The strength of the link between these signals slightly decreases after 2009, although it remained threefold higher than the values observed prior 2008 (Figure 4C). The western coast of the Iberian Peninsula is one of the four major upwelling regions in the world. This seasonal phenomenon mainly occurs during spring–summer and is driven by along-coast wind forcing, which responds to both large-scale changes in the global circulation (Miranda and others 2012). In particular, the positive phase of the NAO alters the hydroclimatic environment over the northeast European coast enhancing anticyclonic activity of NW Iberia and yielding conspicuous changes in the UI (Santos and others 2011). The



process fosters primary production as nutrient inputs from deep waters increase, thereby improving environmental conditions for zooplankton growth.

Figure 4. **A** Monthly and interannual variability of the North Atlantic Oscillation. The temporal pattern displays a variance after 2008. **B** Seasonal and interannual variability of the upwelling index (UI) in the area relative to the Mondego Estuary depicted by heat maps of the monthly UI. The colour scale, from *white* to *black*, denotes the lowest and highest values, respectively. The pattern of change is further displayed as cumulative annual deviations of the overall mean during the period 2003–2012 (*thick line*). The inflexion point in UI appears concurrent with the enhanced coherence in NAO hydrology and NAO zooplankton patterns. **C** Cross-wavelet coherence between NAO and local hydrology, and NAO and zooplankton. The relationship exhibits a time-varying link that markedly increased, in both hydrology and zooplankton, circa 2008 concurrently with the enhanced North Atlantic climate variance. *Box-and-whisker plot* showed the changes in climate variance between the periods 2003–2007 and 2008–2012. Significant differences were depicted by bootstrapped *t* test ($p < 0.05$).

The above climate-mediated changes in the Mondego Estuary promoted a reorganization of the zooplankton community after 2007, which was driven by a decrease in freshwater taxa along with an increase in marine neritic species (Figure 5A, B). It is worth noticing that the taxa responsible for the observed major changes in the structure of the zooplankton compartment were mainly gelatinous groups, for example, microfilter-feeders (thaliaceans) and carnivores (hydromedusae and siphonophores). The abundance variability of these groups increased after 2008 showing higher abundance and larger bloom events (Figure 5C, D). The species driving these changes were the thaliaceans *Doliolum* spp. and *Oikopleura dioica*, and the gelatinous carnivores *Muggiaea atlantica*, *Sagitta friederici*, *Clytia hemisphaerica*, *Liriope tetraphylla* and *Obelia* spp. The observed higher abundances in all these species after 2007 stressed not only a larger marine influence, promoted by enhanced UI, but also an increase in small cosmopolitan copepods, that is, *C. arcuicornis*, *O. plumifera* and *P. parvus*, and thermophilic species, that is, *P. avirostris*. The latter have also showed an increasing abundance and prevalence in northern Europe that parallel rising temperatures in the last decade (Johns and others 2005). Likewise, our results stress the mounting abundance of gelatinous zooplankton, filter-feeders and carnivores, which agrees with recent findings in the Northeast Atlantic coast showing a close relationship between climate variations and gelatinous zooplankton abundance changes (Lynam and others 2011; Reygondeau and others 2015). Overall, the observed structural change in



the zooplankton community lies in the direction of pervasive structural changes in coastal ecosystems of the Northeast Atlantic. Indeed, increased abundances of copepod cosmopolitan species and gelatinous zooplankton in the western English Channel have been shown linked with hydroclimate changes playing out in the North Atlantic Ocean (Reygondeau and others 2015). These changes warn of the potential negative effect on

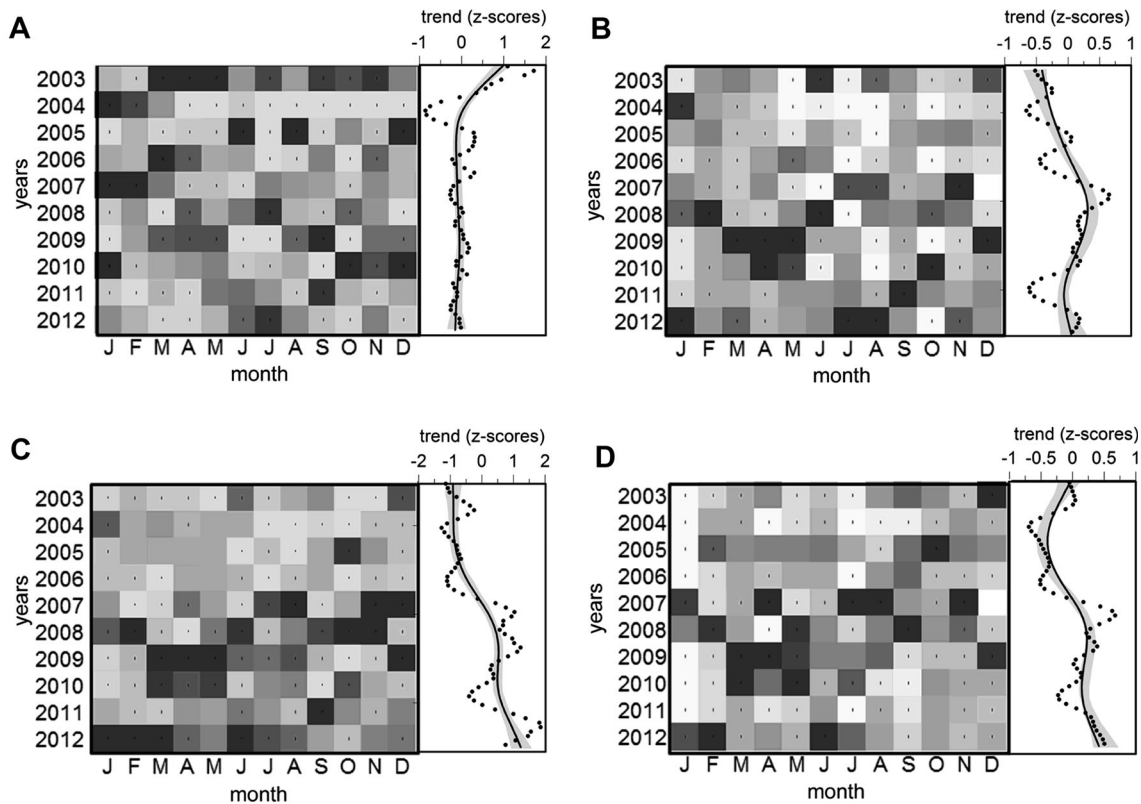


Figure 5. Heat maps and temporal trends of zooplankton illustrate the seasonal and interannual variability. **A** Freshwater zooplankton, **B** marine zooplankton, **C** appendicularians, **D** jellyfish.

ichthyoplankton as the increase in gelatinous zooplankton may substantially reduce the main food for fish larvae, for example, crustacean zooplankton, either through competition (filter-feeders) or predation (carnivores). Hence, our results point toward direct and indirect climate effects on the plankton system of Mondego Estuary. The former through their influence on metabolism, growth and/or reproduction, whereas the latter acting via ecosystem interactions, such as competition or enhanced predation.

Climate-Related Structural Changes in Estuarine Plankton

The results described here portray a close connection between the structure of zooplankton communities in the Mondego Estuary and climate phenomena acting on the North Atlantic Ocean. The link can be tracked by the influence of the NAO on the regional coupling ocean–atmosphere and the subsequent effects on precipitation, regional wind and eventually UI. The consequences of these processes altered the water mass dynamics in the estuary and shaped the zooplankton structure. A positive phase in the NAO promotes a

higher frequency and strength of winter storms crossing the Atlantic Ocean, while yielding drier than normal winters in the south of Europe (Hurrell and others 2003). The influence further affects river flow regimes, which tend to be lower (higher) when the NAO is in its positive (negative) phase (Trigo and others 2004; de Castro and others 2006). Also, during the positive phase of NAO an increase of anticyclonic activity off NW Iberia favors the upwelling strength, while it is weakened during the negative phase of NAO (Pérez and others 2010).

Results of the structural equation model allowed assessing the strength of pathways linking climate and plankton, and further revealed that such pathways varied under different scenarios of climate variance (Figure 6). The scenario prior 2008 showed a positive relationship between the NAO and water temperature and salinity (path coefficients: 0.21 and 0.25, respectively) and the UI (path coefficient: 0.25), which in turn is related to the estuarine temperature and salinity (path coefficients: -0.25 and 0.28 , respectively). During this period temperature was influenced the variability of chaetognaths, cladocerans and phytoplankton (path coefficients: 0.35 in all cases), whereas no

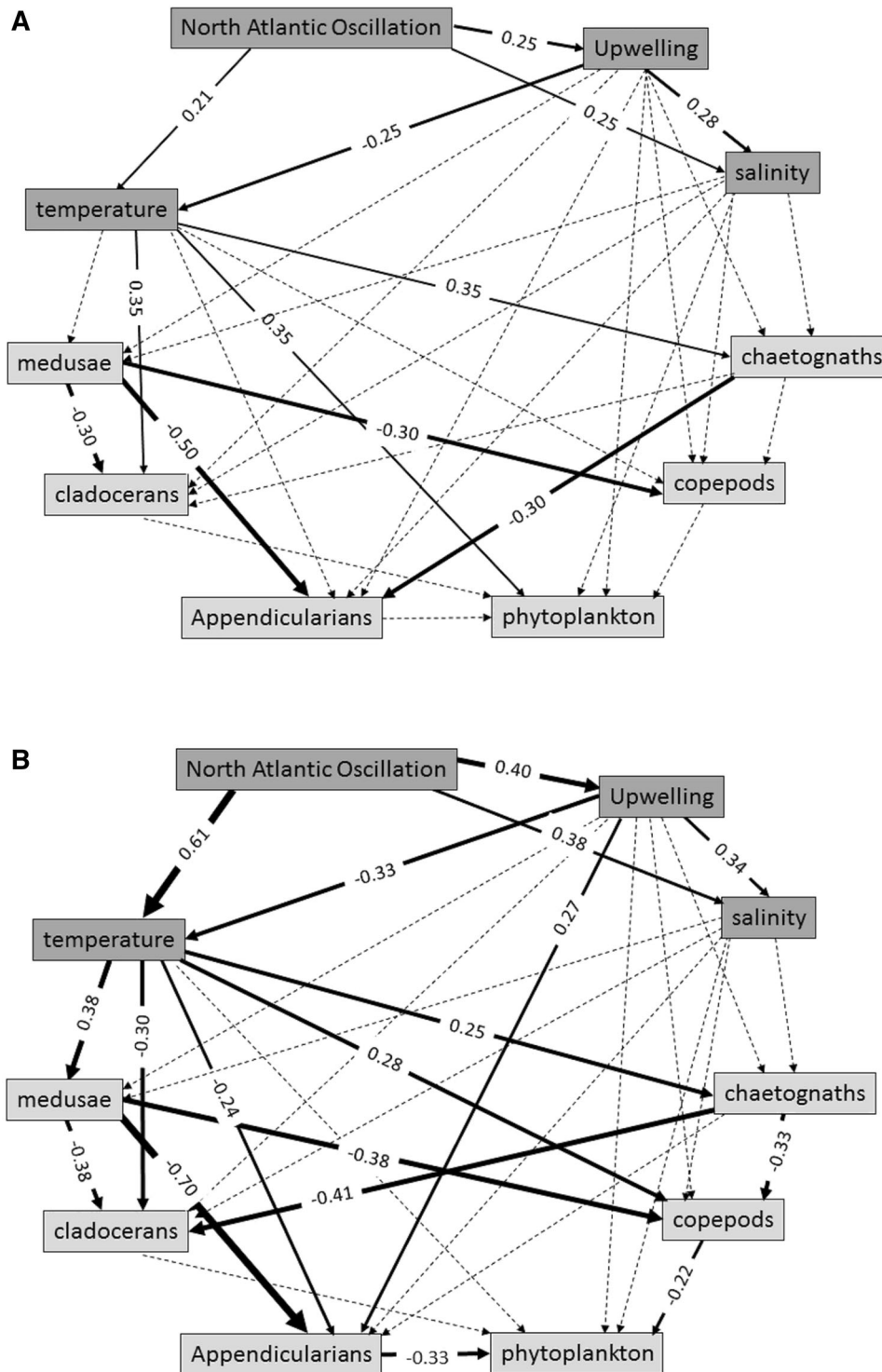


Figure 6. Path diagrams displaying the strength of interactions in the climate–plankton network. Solid paths are statistically significant ($p < 0.05$), whereas dashed lines are not. At each significant path the standardized coefficients are displayed. The models correspond to two scenarios of contrasting climate variance, 2003–2007 (**A**) and 2008–2012 (**B**). Notice the significant change in the strength of links after 2007. The variance explained by the model is also indicated.

significant relationships were detected with the other groups. Moreover, the model pointed out a predation pressure of medusa on cladocerans, copepods and appendicularians (path coefficients: -0.30 , -0.30 , -0.50 , respectively), and chaetognaths on appendicularians (path coefficient: -0.30), whereas none of the groups appeared re-

lated with phytoplankton (Figure 6A). In clear contrast, the scenario after 2008 showed a conspicuous increase in climate influence, as indexed by the NAO, on regional hydrographic features (UI; path coefficient: 0.40) and temperature and salinity conditions, (path coefficients: 0.51 and 0.38 , respectively). Subsequently, the relationship

between UI and estuarine hydrological conditions displayed a larger interaction (path coefficient: -0.33 and 0.34 , respectively for temperature and salinity). The novel configuration shows a prominent positive influence of water temperature on medusa, copepods and chaetognaths, (path coefficients: 0.38 , 0.28 , 0.25 , respectively), whereas a negative influence on cladocerans and appendicularians was identified (path coefficient: -0.30). The stronger negative influence of medusa on cladocerans, copepods and appendicularians (path coefficients: -0.38 , -0.38 , -0.70 , respectively), as well as that of chaetognaths on cladocerans (path coefficient: -0.41), emphasizes a stronger predation pressure. Likewise, the observed higher abundances of copepods and appendicularians appear to have a larger impact on phytoplankton (path coefficient: -0.22 , -0.33 , respectively) (Figure 6B). These results pointed out cascading effects from climate to plankton communities and highlight that the strength of the relationships within the climate–plankton network appears closely related with the magnitude of climate forcing and its non-stationary behavior.

The influence of the NAO in the Iberian coast has wide implications on precipitation scenarios (Zhang and others 1997). Indeed, this region has experienced important hydroclimate changes in the last years, including a shift in the regime of precipitation (Marques and others 2014), that foster drought conditions and gave rise to prolonged periods of reduced freshwater inflow. These environmental modifications substantially affected estuarine communities, that is, decline in secondary production of the intertidal benthic invertebrate and fish communities (Dolbeth and others 2007, 2008), displacement of fish assemblages to upstream areas (Martinho and others 2007), and reduce abundance and recruitment levels of several marine–estuarine-dependent taxa (Dolbeth and others 2008; Martinho and others 2009). Although former studies have focused exclusively on the impact of local environment conditions, these results point out that these changes are closely related with the atmospheric phenomena governing the North Atlantic sector.

These findings emphasize that a multiscale approach to account for multiple processes operating at different temporal and spatial scales is necessary to fully comprehend how climate variability influences environmental and ecological processes (Molinero and others 2005; Reygondeau and others 2015). Failure to incorporate a multiscale approach impairs identifying mediator factors linking climate phenomena and ecological processes and

their intrinsic non-stationary temporal variability. Ultimately this may create a misleading picture of marine network responses to climate changes, which compromise long-term sustainable management of ecosystem assets. In the Mondego estuarine system, the non-stationary link between the NAO and plankton dynamics is modulated by interacting factors operating at intermediate scales, such as regional wind and upwelling processes, which shape the physical environment relative to plankton communities.

Overall, these results provide empirical support to the expectation that expanding climate variance changes plankton structure and functioning likely enhancing bottom-up controls in pelagic food webs (Molinero and others 2013). Future work will aim to integrate impacts across trophic levels from ongoing environmental changes and growing anthropogenic pressures. The synergies of which have the potential to magnify climate effects (Hidalgo and others 2011) thereby altering plankton structure and likely promoting the proliferation of potentially harmful populations, that is, gelatinous zooplankton.

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