

Shifts in estuarine zooplankton variability following extreme climate events: a comparison between drought and regular years

Sónia Cotrim Marques^{1,*}, Ana Lígia Primo¹, Filipe Martinho¹,
Ulisses Miranda Azeiteiro^{1,2}, Miguel Ângelo Pardal¹

¹CFE — Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, PO Box 3046, 3001-401 Coimbra, Portugal

²University Aberta, Department of Science and Technology, 4200-055 Porto, Portugal

ABSTRACT: Climate change will likely lead to an increase in temperature and an occurrence of extreme droughts and floods in the 21st century. In particular, coastal and estuarine systems are highly sensitive to climate extremes and changing precipitation patterns, and thus offer invaluable scenarios for the evaluation of climate variability. Zooplankton assemblages and hydroclimate variables were monitored for 8 yr. The main objective was to assess the impact of climate variability, particularly of the 2 most recent drought events in the Mondego estuary (Portugal, southern Europe), which occurred in 2004–2005 and 2007–2008, on the zooplankton population dynamics, with emphasis on how stochastic extrinsic perturbation might influence these populations. Principal component analysis revealed dramatic environmental changes during drought periods, which were reflected in the seasonal and inter-annual patterns in the zooplankton, indicating that hydroclimate forcing is critical in defining zooplankton dynamics. Lower precipitation and higher salinities were the main drivers for the observed patterns, i.e. a major penetration of seawater led to a higher prevalence of marine species. Results also revealed a conspicuous increase in warm water taxa since 2006, which was significantly related to pronounced changes in water temperature. This synchronous variability between water temperature and zooplankton abundance, which had not been evaluated and discriminated in previous studies, suggests the potential impact of warming on zooplankton assemblages. Hence, this study demonstrates the crucial role of zooplankton as valuable indicators of hydrological changes associated with climate factors in estuarine ecosystems.

KEY WORDS: Mondego estuary · Time-series analysis · Climate variability · Drought events · Zooplankton–climate interactions · Observational monitoring

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INTRODUCTION

Coastal ecosystems are strongly affected by natural variations in climate. In addition, the cumulative effects of human-induced climatic changes can have a further effect on the ecosystem structure and trophic dynamics in many estuaries (Hoffmeyer 2004, Kimmel et al. 2006). The projected effects of climate change in estuaries include sea level rise and increases in water temperatures and in the variability of precipitation events, which may lead to weather

extremes (IPCC 2007). As is already well known, the specific vulnerability of any single estuary will depend on its physical properties (e.g. flushing time, depth and size), geomorphology and species composition (e.g. Attrill & Power 2000, Scavia et al. 2002, Marques et al. 2007). Despite this, estuaries are expected to be vulnerable to environmental change to a high degree. Thus, weather extremes, which are increasing in magnitude and frequency worldwide, will influence the health of our coastlines, including the species that inhabit them.

Impacts of changes in mean climate values (which we term 'trend effects') should be separated from those produced by changes in the magnitude or frequency of extreme events ('event effects') (Jentsch et al. 2007). Although species have dealt with climate variability throughout their evolutionary history, a challenge for the functioning of species and ecosystems is the rapid rate of change currently being observed (Root et al. 2003, Scheffer & Carpenter 2003). The main question arising in this context is therefore: how will such a rate of change affect species' life histories, ecological interactions and, ultimately, ecosystem functioning. During the past years the answer has been elusive and a matter of ongoing debate (Hays et al. 2005 and references therein). In line with this, growing recognition of the importance of climate extremes as one of the most important facets of climate change has stimulated a number of recent studies that have focused on the ecosystem impacts of periods of climatic extremity (e.g. Easterling et al. 2000, Smith 2011, Diez et al. 2012).

European ecosystems are vulnerable to major climate change impacts and extreme events such as river floods, droughts, or coastal flooding (EEA 2012, Goberville et al. 2010). In particular, major droughts have been observed in recent decades in Europe, such as the one that occurred during 2005 on the Iberian Peninsula (Marques et al. 2007, Martinho et al. 2007). Additionally, Lehner et al. (2006) found that under 2 climate model projections, a general, significant increase in the severity and frequency of droughts across southern Europe is to be expected. A few reports provide some indications as to how climate variability will be manifested in coastal areas (e.g. Vincent et al. 2002), such as in the Mondego estuary (Portugal), where intense precipitation and drought episodes during recent years led to significant changes in the structure and functioning of biological communities (e.g. Dolbeth et al. 2007, Marques et al. 2007, Martinho et al. 2007, Cardoso et al. 2008). Nevertheless, the forcing mechanisms controlling the variability are still far from properly understood, mainly due to the limited length of the records.

Because there are many processes connecting climate patterns with higher trophic levels, a retrospective study of lower trophic levels should elucidate the mechanisms linking variations in climate, hydrographic environment and ecosystems. In fact, recent evidence suggests that zooplankters are more sensitive indicators of change than environmental variables (Taylor et al. 2002, Hays et al. 2005). Besides being an important food resource in pelagic ecosystems, zooplankton further acts as an integrator of hydroclimatic

forcing, providing an accurate diagnosis of the ecosystem state (Beaugrand 2005). One of the major challenges for marine scientists is to understand and predict the response of aquatic biota to global change (Dam 2013). The phenotypic plasticity of some species and the tolerance to hydrological variability will determine the zooplanktonic structure characteristic of highly unstable ecosystems, such as estuaries. Hence, with growing interest on the impacts of climate change on coastal ecosystems, the need to understand the dynamics of zooplankton in estuaries continues to increase. Furthermore, research on the sensitivity of zooplankton to extreme climate events, such as extreme droughts, is important, as the influences of climate may disrupt ecological interactions between trophic levels, following the logic of the match–mismatch hypothesis (Cushing 1990).

Efforts to detect changes in plankton communities are confounded by sparse available information in some coastal areas. Nonetheless, relevant inter-annual variability observed in the weather conditions over the Iberian Peninsula attest to the decreasing trend in annual precipitation in Portugal (Rodrigo & Trigo 2007, Santos et al. 2010). Although the influence of freshwater inflows on estuarine zooplankton has previously been documented (Marques et al. 2007, Primo et al. 2009), we believe that further research is necessary to assess the relationship between such biological and environmental variations. This paper describes the results of 8 yr of monitoring hydroclimate variables and zooplankton assemblages with the main objectives being (1) to analyze the response of zooplankton communities to stochastic extrinsic perturbations, manifested through changes in environmental conditions and (2) to highlight patterns related to specific local hydrodynamics. Identification of biological changes in relation to time-series variations in coastal marine systems is a strategy used to monitor the influence of climate variability on marine communities, and a way to find important groups or species that act as indicators of the health or stable state of ecosystems (Colebrook 1985).

MATERIALS AND METHODS

The studied ecosystem was the Mondego estuary, situated on the west coast of Portugal (40° 08' N, 8° 50' W). This estuary experiences a Mediterranean temperate climate. About 7 km from the sea, the river branches into 2 arms (northern and southern), which converge again near the mouth. The biological characteristics of the ecosystem are mostly controlled by

meteorology, hydrodynamics and by river run-off (Marques et al. 2007, Nyitrai et al. 2012). In addition, water exchanges with the Atlantic have a strong influence on the composition and dynamics of pelagic communities.

Zooplankton data

Zooplankton samples covered an 8 yr period (2003 to 2010). Sampling was performed monthly, at 5 sampling stations distributed throughout both arms (Marques et al. 2006). Samples were collected by subsurface horizontal hauls, using a 335 μm mesh bongo net with a 0.5 m opening. Subsequently, all organisms collected were fixed and stored with buffered formaldehyde (5%).

All organisms present in the samples were identified to the lowest possible taxonomic level, and abundance was expressed as the number of organisms per cubic meter (ind. m^{-3}). Data on certain groups such as early life stages and smaller organisms were removed, since we considered them to be

underestimated by the sampling method. Rare species were pooled into higher taxonomic levels.

To obtain a proxy for zooplankton abundance, we arranged our data based on (1) plankton functional types (i.e. groups are based on similar taxonomic groups), (2) seasonality (Fig. 1) and (3) representativeness for each sampling site (parameters previously defined by Marques et al. 2008, see Table 2). This arrangement resulted in a matrix of 21 variables, representing the zooplankton components of the Mondego system (Table 1). The quarterly mean was estimated by averaging monthly data as follows: winter (January, February and March), spring (April, May and June), summer (July, August and September) and autumn (October, November and December).

Hydroclimate parameters

The abiotic environment is represented by the hydrologic variables (Table 2). Surface salinity and temperature were recorded *in situ* simultaneously with each zooplankton sampling. Water samples

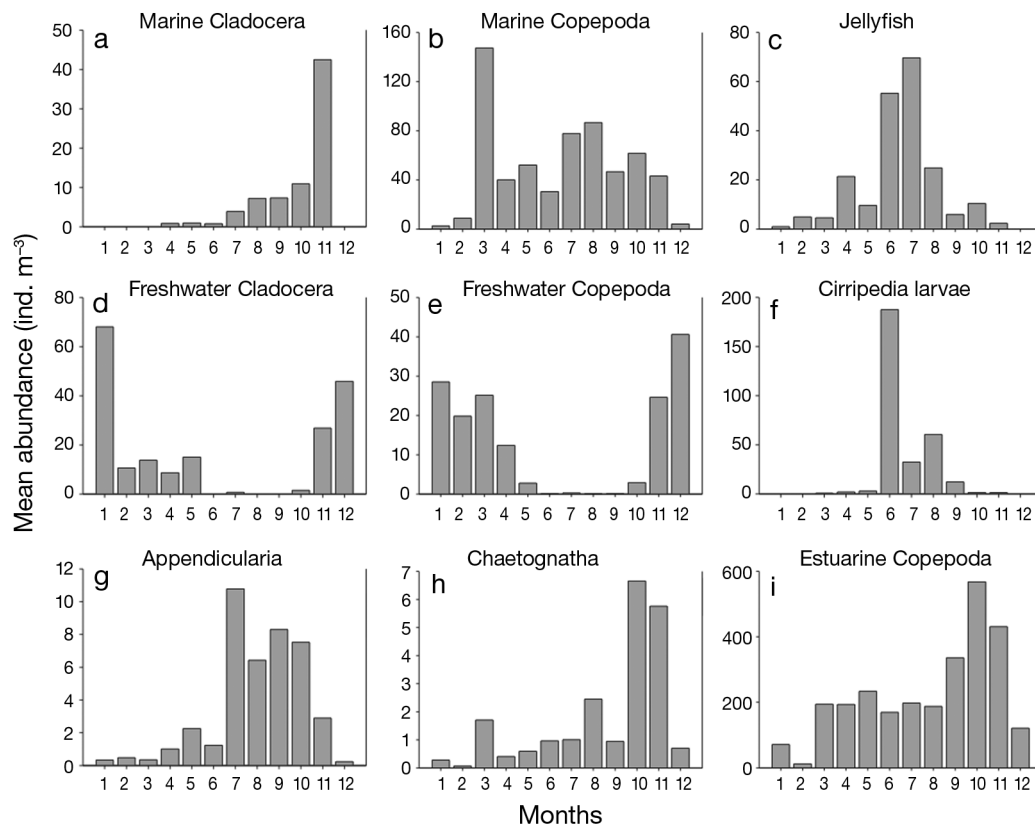


Fig. 1. Main patterns of the seasonal cycle (by month, estimated average of the 5 sites) of (a) marine Cladocera, (b) marine Copepoda, (c) jellyfish, (d) freshwater Cladocera, (e) freshwater Copepoda, (f) Cirripedia larvae, (g) Appendicularia, (h) Chaetognatha and (i) estuarine Copepoda sampled in Mondego estuary from 2003 to 2010

Table 1. Principal component analysis of zooplankton abundance for the period 2003 to 2010. Zooplankton variables and contribution to first 2 principal components (PC1, PC2). The highest contributions to each principal component are in **bold**

Variable Bio Matrix (ind. m ⁻³)	Abbreviation	Season	PC1	PC2
Appendicularia	App_sum	Summer	-0.29	-0.14
Chaetognatha	Chae_aut	Autumn	-0.87	1.61
Cirripedia larvae	Cirr_spr	Spring	-0.80	1.74
	Cirr_sum	Summer	1.56	1.31
Marine	M_Cld_sum	Summer	0.43	1.43
Cladocera	M_Cld_aut	Autumn	0.61	-0.60
Freshwater	FW_cld_win	Winter	1.83	0.63
Cladocera	FW_cld_spr	Spring	-0.20	-0.03
	FW_cld_aut	Autumn	1.89	0.50
Freshwater	FW_cop_win	Winter	1.61	-0.33
Copepoda	FW_cop_spr	Spring	-0.03	-0.28
	FW_cop_aut	Autumn	1.04	-0.77
Estuarine	E_cop_win	Winter	-0.75	0.11
Copepoda	E_cop_spr	Spring	-0.13	1.27
	E_cop_sum	Summer	0.96	1.83
	E_cop_aut	Autumn	-0.15	0.92
Marine	M_cop_spr	Spring	1.75	0.10
Copepoda	M_cop_sum	Summer	-0.35	-0.08
	M_cop_aut	Autumn	-1.06	1.73
Jellyfish	Jelly_spr	Spring	-0.16	0.96
	Jelly_sum	Summer	-0.24	-0.26

Table 2. Principal component analysis of hydroclimate parameters for the period 2003 to 2010. Hydroclimatic variables and contribution to the first 2 principal components (PC1, PC2). The highest contributions to each principal component are in **bold**

Variable Env Matrix	Abbreviation	Season	PC1	PC2
Water temperature (°C)	WT_win	Winter	-1.24	-0.12
	WT_spr	Spring	1.12	0.73
	WT_sum	Summer	0.57	-0.97
	WT_aut	Autumn	0.04	1.80
Salinity	Sal_win	Winter	-1.29	-1.11
	Sal_spr	Spring	-1.35	-0.46
	Sal_sum	Summer	-0.94	1.33
	Sal_aut	Autumn	-1.66	-0.68
Precipitation (mm)	P_win	Winter	1.05	1.29
	P_spr	Spring	-0.97	0.17
	P_sum	Summer	0.97	-0.71
	P_aut	Autumn	1.02	1.29
Suspended particulate matter (mg m ⁻³)	SPM_win	Winter	0.45	-1.13
	SPM_spr	Spring	-0.56	1.13
	SPM_sum	Summer	0.93	-0.65
	SPM_aut	Autumn	-0.11	-1.47
Chlorophyll <i>a</i> (mg m ⁻³)	Chla_win	Winter	-1.65	0.52
	Chla_sum	Spring	-0.99	1.44
	Chla_spr	Summer	-0.33	0.35
	Chla_aut	Autumn	0.74	-0.36

were also collected for determination of total suspended solids and chlorophyll *a* concentration as a measure of total phytoplankton biomass. See Marques et al. (2006) for further methodological details and for processing of samples.

In order to study the effects of extreme events (droughts) on the estuarine hydrologic environment we used precipitation data, which were measured at the Soure 13F/01G station and acquired from INAG (Portuguese Water Institute, also available at www.snirh.pt).

Numerical analysis

First, zooplankton abundance was log transformed in order to approach a normal distribution and to minimize the dominant effect of exceptional catches (Legendre & Legendre 1998). Missing values in the data sets were interpolated, using averages of the previous and following months.

Standardized principal component analysis.

To condense these data and to avoid non-orthogonality, the zooplankton variables were summarized as 2 major axes of a standardized principal component analysis (PCA) (Krzyszowski 1988). This approach was applied to extract the main inter-annual and seasonal patterns from the zooplankton time-series (see Table 1 for the complete listing of all PCA variables) and performed with CANOCO software (ter Braak & Šmilauer 1998). Since PCA axes are, by definition, orthogonal and so independent of one another, this procedure creates composite independent zooplankton variables and avoids the chance of multicollinearity (for a detailed description see Sirabella et al. 2001, references therein). All further analyses therefore were carried out using the combined and condensed zooplankton information represented by the inter-annual fluctuations of these 2 axes. A similar procedure was applied to analyze the variations in the hydroclimate parameters. In addition, the equilibrium contribution corresponding to each descriptor (see Legendre & Legendre 1998) was represented in the scatterplot of eigenvectors. It is therefore possible to judge whether the contribution of each descriptor to the reduced space is greater or smaller than expected, under the hypothesis

of an equal contribution to all principal axes, by comparing the lengths of their projections to an equilibrium circle with radius (r) defined as:

$$r = \sqrt{(d/p)}$$

where d is the number of dimensions and p the number of variables used in the analysis; d was equal to 2 in both PCAs. The circle of equilibrium contribution is drawn at $\sqrt{2/21}$ for biotic indicators and $\sqrt{2/20}$ for environmental variables. Therefore, for any given pair of axes, the variables that have vectors longer than this radius make a higher contribution than average and can be interpreted with confidence.

CUSUM. In order to detect change points in both zooplankton and hydro-climate parameters, the cumulative sum (CUSUM) of the deviations from the mean of the reference period 2003 to 2010 were computed. The interpretation was based on the sign and steepness of the slopes which reflect the deviation of a period from the time-series mean value (Ibañez et al. 1993).

Correlation analysis. Finally, in order to identify the multiple drivers responsible for zooplankton variability and to understand the main processes that

may have triggered the observed changes, correlation analyses were carried out between the first and second principal components of the biological samples, which constitute the main mode of temporal variability, and the hydroclimatic parameters.

RESULTS

Environmental and zooplankton community variability

The inter-annual changes of zooplankton using the first 2 eigenvectors are shown in Fig. 2a, which together explain 44% of the total variability in zooplankton. The trajectory of the first PC1 sample scores (explaining ~23% of total variance) highlights 2 periods with slight decreases (2004–2005 and 2007–2008) and a period with a sharp increase in 2010. The trajectory of PC2 (explaining ~21% of total variance) was characterized by a rapid shift, from negative to positive values, during 2007 and 2008. Afterwards, values of PC2 decrease to negative values. The pattern again showed a sharp increase in 2010.

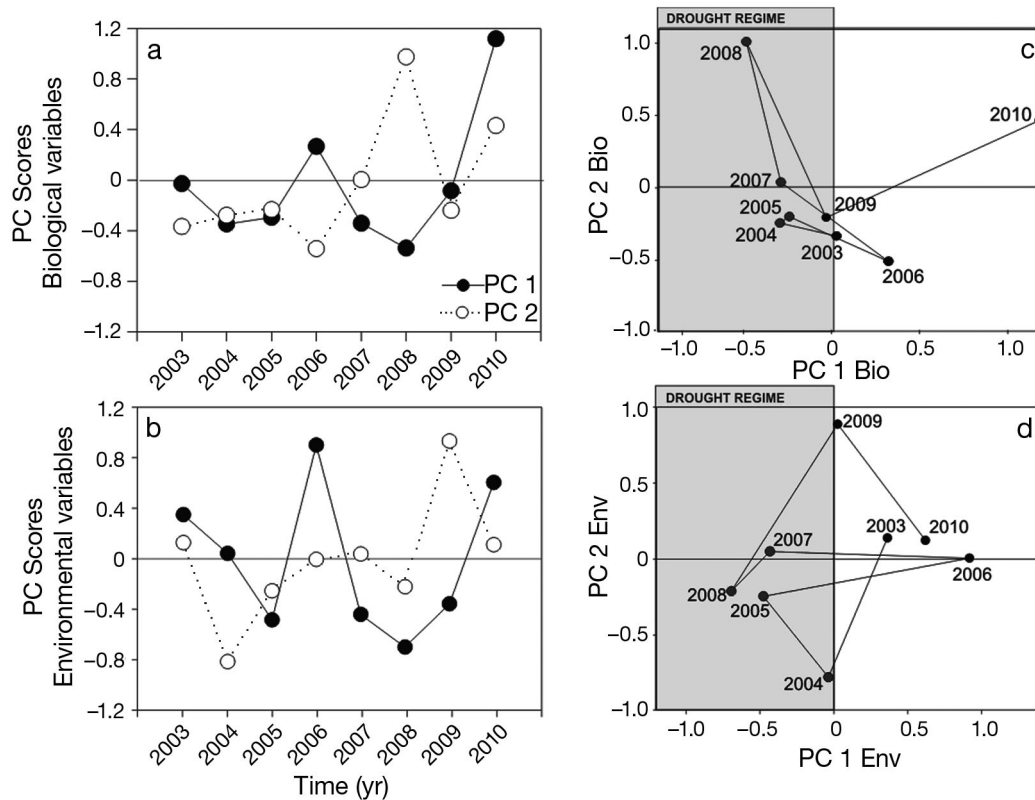


Fig. 2. Inter-annual variability (2003 to 2010) as shown by results of the first 2 principal components (PC1 and PC2) and the time-trajectory for (a,c) zooplankton and (b,d) hydroclimate variables. ●: PC1; ○: PC2; grey shading: the 2 yr periods 2004–2005 and 2007–2008 characterized by drought regimes

The analyzed period also underwent anomalous change in the hydrographic regime (Fig. 2b). The first 2 environmental principal components explained 29 and 22% of the total variance, respectively. The pattern observed in PC1 revealed similar inter-annual changes compared with those derived from biotic variables. Accordingly, the Pearson correlation coefficient indicates positive significant correlation between both abiotic and biological components ($r_p = 0.74$, $p = 0.04$). However, the change to negative PC1 scores was more abrupt. Furthermore, a positive upturn was evident in 2006 and again in 2010. PC2 showed different variations compared with those of zooplankton. A decrease in PC2 values was identified in 2004. Besides this, the pattern showed an increase to positive values in 2009, followed by a decrease in 2010.

The time-trajectory of PC1 versus PC2 scores detected during the study period was related to recognizable meteorological and hydrographic processes that are expected to influence zooplankton dynamics. It is possible to distinguish the periods where drought regimes prevailed (2004–2005 and 2007–2008) (Fig. 2c,d). Furthermore, the pattern of scores resulting from the PCA of biological variables also highlights 2008 from among the years under the drought conditions, while environmental scores distinguished 2004. Concerning the years in which regular regimes occurred, different conditions were attributed to 2009 (environmental PCs; Fig. 2d) and 2010 (zooplankton PCs; Fig. 2c).

Key zooplankton and environmental drivers

The scores plot with the first 2 principal components allowed identification of the inter-annual and seasonal changes in the zooplankton community and environmental conditions of the estuarine system (Fig. 3, Tables 1 & 2). The dispersion diagram reflects the clear separation between the drought and regular conditions. Further, it was possible to recognize the main key drivers that characterize the different regimes observed.

The main zooplankton drivers are highlighted in Fig. 3a and Table 1. The year 2003 was characterized by PC1 scores scattered in the middle of the plot, presenting the zooplankton variables an equal contribution. During this year we observed higher abundances of freshwater copepods and a lower abundance of estuarine copepods and jellyfish, during the spring. The first drought period of 2004–2005 was characterized by higher abundances of estuarine copepods in the winter than in the warm seasons. Interestingly,

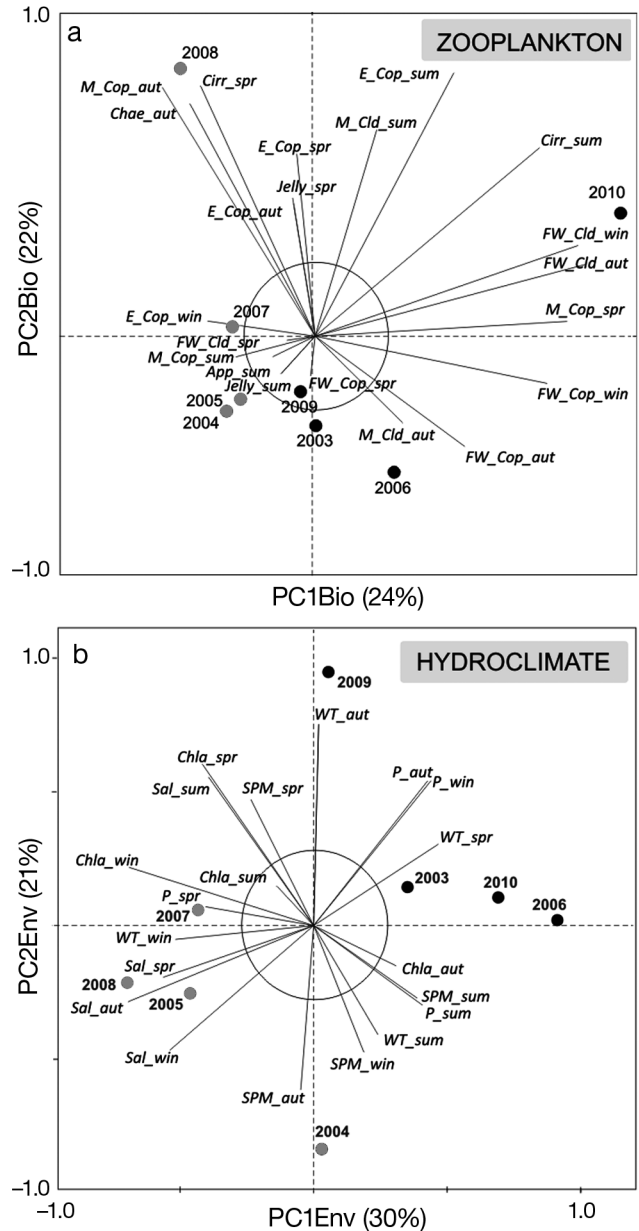


Fig. 3. PCA scores plots of the first 2 principal components (PC1 and PC2) from analysis performed on the matrix of selected (a) zooplankton and (b) hydro-climate parameters (8 yr \times variables). Two distinct conditions are represented — ●: drought regime periods, 2004–2005 and 2007–2008; ●: years of regular hydrologic conditions. See Tables 1 & 2 for abbreviations

in the autumn of 2006, increases in the abundance of marine cladocerans and freshwater copepods coincided. In 2007 the most important drivers were the highest abundance of estuarine copepods during winter, as well as marine copepods during summer, which both declined during regular hydrologic conditions. The year 2008 was marked by abundance peaks of cirripedia larvae during spring and ma-

rine copepods and chaetognaths during summer. The zooplankton scores found in 2009 indicated recovery of the system to a state similar to that in 2003, while 2010 was characterized by the highest PC1 scores, which were mainly driven by higher abundances of freshwater copepods and cladocerans in autumn/ winter.

Concerning the scores plot of the hydroclimate PCA (Fig. 3b, Table 2), it is important to note that the dominant signal during the 2 yr drought periods of 2004–2005 and 2007–2008 was the higher salinity. Characteristic features of 2004 include lower temperatures and high suspended particulate matter during autumn. In addition, the period 2007–2008 was also characterized by higher winter water temperature, and 2007 by high spring precipitation and winter chlorophyll *a* values. Key drivers representative of 2009 were the higher water temperatures in autumn and the high precipitation values during autumn and winter, with the last characteristic being typical of regular years. As regards 2003, 2006 and 2010, the increase in temperature in spring and decrease in winter were highlighted, as well as both low chlorophyll *a* concentrations in winter and precipitation during spring.

CUSUM analysis of time-series

Considering the cumulative sums performed on both zooplankton and environmental time-series, different patterns appeared according to the timing of potential change (Fig. 4). A

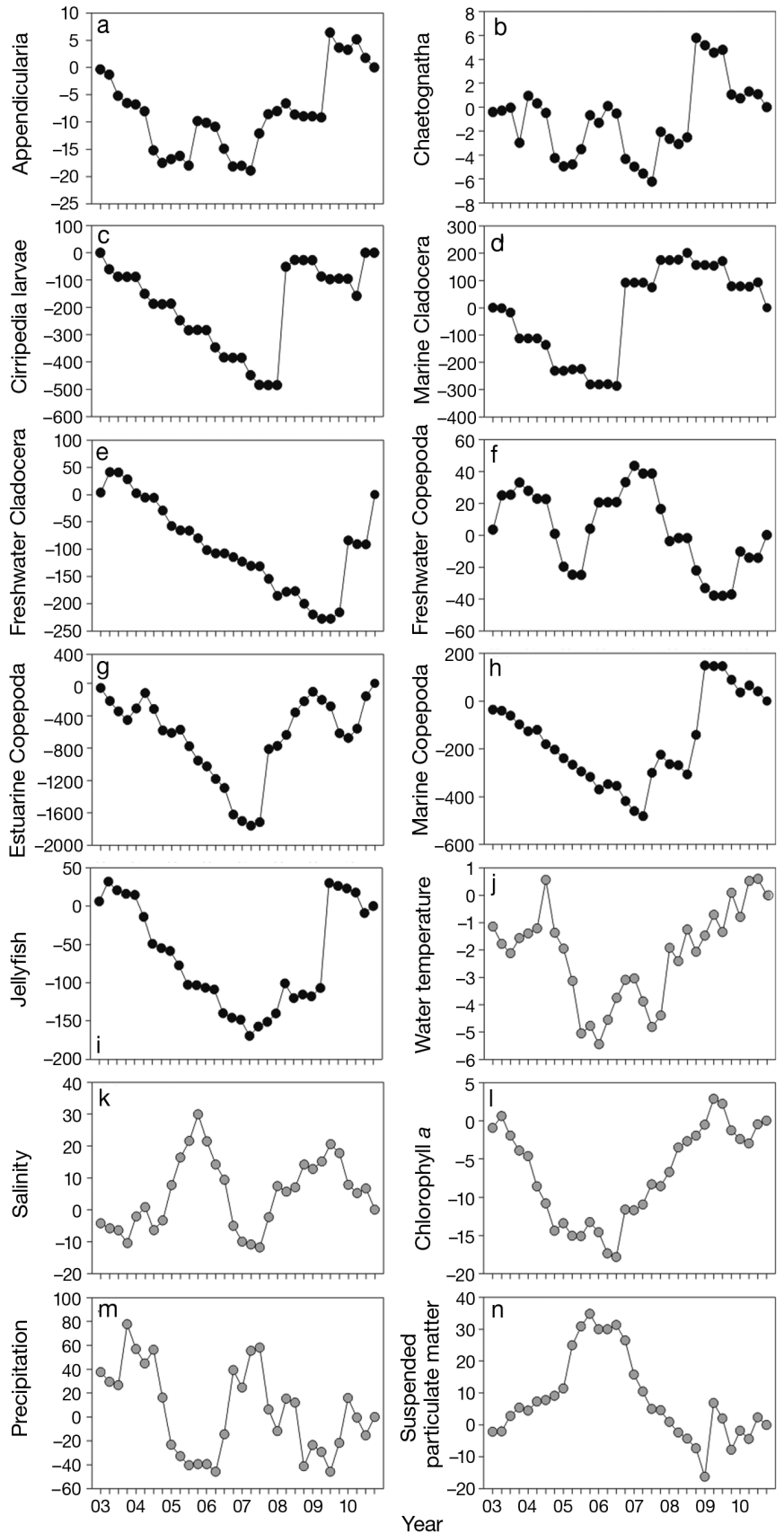


Fig. 4. Cumulative sums of normal standard deviates of the zooplankton time-series (●): (a) Appendicularia, (b) Chaetognatha, (c) Cirripedia larvae, (d) marine Cladocera, (e) freshwater Cladocera, (f) freshwater Copepoda, (g) estuarine Copepoda, (h) marine Copepoda and (i) jellyfish; and environmental parameters (○): (j) water temperature, (k) salinity, (l) chlorophyll *a*, (m) precipitation and (n) suspended particulate matter; 2003 to 2010 (winter, spring, summer and autumn, 3 mo averages)

positive slope in the CUSUM of each time-series indicates the period in which the variable was higher than the time-series average, and a negative slope indicates when the variable was lower. For instance, abundance of estuarine copepods showed a strong decline relative to the time-series mean until the autumn of 2007, when their abundance started to increase. For this group, a slight decrease was observed later in 2009, and then a rise again in 2010 (Fig. 4g). The CUSUM abundance time-series for cirriped larvae exhibited a strong break point in the spring of 2008, and for jellyfish, during the summer of 2009, whereas changes occurred in the autumn of 2006 for the marine cladocerans (Fig. 4c,d). Generally, the abundance of marine taxonomic groups (Appendicularia, Chaetognatha, jellyfish and marine copepods) exhibited a rise in the period from 2007 until 2010, when they started to decrease once more (Fig. 4).

Regarding environmental variability, the cumulative sums of water temperature showed 2 main periods delimited by one major change. The first period, before 2006, was characterized by a downward change with the exception of 2004 (summer). Afterwards, an upward change was observed, though including a minor decrease during 2007 (Fig. 4j). The CUSUM time-series of salinity revealed a clearly inverse relationship with the freshwater assemblages (Table 3). Thus, 2 main periods of positive slope, 2004–2005 and 2007–2009 (summer), were highlighted by the cumulative sums (Fig. 4k). Chlorophyll *a* presented a clear shift in the downward change during the autumn of 2006 (Fig. 4l), while suspended particulate matter generally showed the opposite pattern (Fig. 4n). CUSUM analysis of precipitation

values showed a higher variability, increasing after 2006, decreasing in 2008 and rising again in the latter part of 2009 (Fig. 4m).

Overall, despite the variability in the CUSUM analysis, we observed a significant positive correlation between water temperature and the abundance of the majority of the groups analyzed, with the exception of freshwater copepods, which showed a negative correlation (Table 3). The correlation between temperature and chlorophyll *a* was particularly strong ($r = 0.53$, $p < 0.001$), and may have also played a role in influencing the changes in abundance of those zooplankton groups, since a positive correlation was also detected between them and chlorophyll *a* concentration. Chlorophyll *a* and suspended particulate matter also showed significant correlations with most groups, generally being positive for chlorophyll *a*. Precipitation and salinity presented significant correlations with freshwater communities (Table 3).

DISCUSSION

As in other southern European regions, Portugal is characterized by a mild Mediterranean climate, with a dominant seasonal signal marked by a warm and dry summer period, more pronounced in the southern regions, but with well-known vulnerability to climate variability (de Lima et al. 2013). As a general trend, it is expected that this region will suffer from higher temperatures in the future. However, with respect to the patterns of precipitation, it is not clearly evident whether this is really changing in a systematic manner (EEA 2012). Regional climate models estimate slightly lower precipitation decreases for southern Europe by the end of

the 21st century (Miranda et al. 2006, PCC 2007), including the Iberian Peninsula, an area that is currently vulnerable to droughts (Lehner et al. 2006). In fact, during recent years an irregular distribution of precipitation and high inter-annual variability has been observed in Portugal. As a result, these changes appear to have altered the hydrological regime of the Mondego estuary in particular, given that drought conditions gave rise to prolonged periods of reduced freshwater inflow.

The present study provides supporting evidence in the relationships between reported changes in climate

Table 3. Pearson correlations (r) between the cumulative sums of the main zooplankton groups, expressed as ind. m^{-3} , and the environmental parameters temperature ($^{\circ}C$), salinity, chlorophyll *a* ($mg\ m^{-3}$), precipitation (mm) and suspended particulate matter ($mg\ m^{-3}$). Significant p-values are in bold; * $0.1 > p > 0.05$; ** $0.05 > p > 0.01$; *** $0.01 > p > 0.001$

	Water temperature	Salinity	Chlorophyll <i>a</i>	Precipitation	Suspended particulate matter
Appendicularia	0.57***	0.15	0.77***	-0.09	-0.59***
Chaetognatha	0.45**	0.43*	0.61***	-0.40*	-0.42*
Cirripedia larvae	0.70***	0.12	0.70***	-0.04	-0.57**
Marine Cladocera	0.37*	-0.22	0.72***	0.14	-0.73***
Freshwater Cladocera	0.10	-0.46**	-0.16	0.51**	0.18
Freshwater Copepoda	-0.37*	-0.70***	-0.37*	0.70***	0.30
Estuarine Copepoda	0.68***	0.17	0.64***	-0.12	-0.56**
Marine Copepoda	0.73***	0.16	0.80***	-0.13	-0.67***
Jellyfish	0.66***	-0.05	0.53**	0.15	-0.40*

factors, such as river run-off, and the biological effects. Analysis of the current time-series revealed that a chronological series of ecological events occurred in the ecosystem during the 8 yr study. The most prominent feature shown by the PCA results was the shift from a zooplankton community composed of marine, estuarine and freshwater populations (as described by Marques et al. 2006) to one characterized by a conspicuous absence of freshwater species, during atypical dry years. As shown by the output of PC1 scores on environmental variables, the lower precipitation and higher salinities (indicative of reduced river flow) may have played a role in influencing the patterns observed for zooplankton in the system, corroborated by the strong correlation between the first principal component of the biological and environmental variables. Such a pattern was strongly evident during winter, autumn and spring conditions, since >75 to 90% of the annual precipitation occurs from October to May (Vicente Serrano 2006).

This can certainly be explained by the fact that the Mondego estuary has undergone dramatic environmental changes in the period encompassed by this study, including at least 2 drought periods (2004–2005 and 2007–2008). Although the effect of dry conditions in the estuary has previously been reported (e.g. Marques et al. 2007), the dataset provided in the present paper offered a unique opportunity to investigate changes, during 2 drought events, in the abundance and composition of zooplankton in relation to environmental variability. We used a natural record of environmental variability (drought-induced estuarine salinity increase) and our knowledge of the susceptibility of zooplankton population dynamics relative to the frequency of events of increased salinity. The present study revealed that the years 2008 and 2010 stood out from those remaining, presenting distinct community compositions. While 2008 seems to represent an aggravation of the drought conditions, 2010 seems to define a period of intense freshwater influence. For instance, in 2008, a higher abundance of estuarine copepods and marine cladocerans was observed in summer; marine copepods and chaetognaths, in autumn; and cirripeds, in spring. This evidence indicates that the patterns of distribution can be more or less affected in their amplitude, duration, or in the shift of seasonal development. It is argued that species differ in their physiological tolerances, life-history strategies and colonization, and in their dispersal abilities. Species traits underlie the high variability in strength of climate response across species, even among those subjected to similar cli-

matic trends (Parmesan & Yohe 2003). On the other hand, 2010 was characterized by a marked freshwater community, with higher abundances of copepods and cladocerans in autumn and winter, due to an increase in run-off into the estuary. It is well known that the hydrology and ecology of shallow estuaries (such as the Mondego estuary) are strongly influenced by river flow. Not surprisingly, salinity in the estuary was highly variable and increased during the dry periods, a pattern also confirmed by the negative significant correlation between salinity and climate-driven freshwater run-off in previous studies (e.g. Marques et al. 2007, Martinho et al. 2007). For aquatic populations, the advective properties of freshwater discharge play a critical role in their distribution patterns and richness, as well as on their temporal variability (Licandro & Ibanez 2000, Leandro et al. in press). As highlighted by our results, the variability in advective transport had implications for zooplankton structure. Advective transport allowed stabilization of the environmental estuarine conditions, mainly in the winter, and the recolonization of important species such as *Acartia tonsa* (Marques et al. 2007), a broadcaster spawner that lays its eggs freely in the water column, consequently making it more susceptible to advective transport (Kimmel et al. 2006). However, this situation also led to a major penetration of seawater into the system and, consequently, influenced the overall marine community composition. These important changes in the structure of zooplankton communities were in accordance with observations of estuarine pelagic and benthic communities after similar ecological events (e.g. Marques et al. 2007, Martinho et al. 2007, Grilo et al. 2011, Primo et al. 2011, Nyitrai et al. 2012). It is reasonable to assume that the zooplankton change reported in the present study will affect the temporal and spatial association between species interacting at different trophic levels (Edwards & Richardson 2004) and may help to explain the recently reported ecological changes. For instance, Nyitrai et al. (2012) noticed that planktivorous and invertebrate feeders occurred in higher abundances in dry years, while the opposite was verified for omnivorous species.

The CUSUM analysis allowed the detection of critical points during the study period. Most of the marine species showed a shift in the summer/autumn of 2007, after which their mean abundance increased. This indicates an increased marine influence in the estuary, creating a suitable habitat that allowed the entrance of these species. Most of these groups also showed a decline in 2010. In contrast, freshwater species followed an upward change in 2010, which

was probably related to an increase in precipitation and, consequently, lower salinity. This relationship was even clearer for freshwater copepods, for which the correlation was stronger.

However, some groups presented more pronounced change than others. For instance, the spring of 2008 was detected to be an important changing point for Cirripedia larvae. These barnacle larvae usually have a very short planktonic life, although they can represent a large proportion of the zooplankton on a seasonal time-scale. In general, few data are available on cirriped larvae. We determined the spring of 2008 to be one of the warmer periods during our study and found a high prevalence of *Sacculina carcini*, a cirriped that parasitizes the ubiquitous green crab *Carcinus maenas* (Costa et al. 2013). Cirriped larvae are an important group; since they were very abundant at Mondego estuary during the spring and summer, their increasing abundance may have had an impact on the community by increasing the competition for food, as well as the grazing pressure on the phytoplankton stock. The cumulative sums pattern of marine cladocerans indicated the autumn of 2006 to be a critical point for this group. In fact, Primo et al. (2009) refer to a later intensity peak than that previously recorded, driven by the dominant species *Penilia avirostris*. It is therefore reasonable to consider that the observed changes may also have been affected by bottom-up processes. Edwards et al. (2001) noted that the shift in a phytoplankton community towards the dominance of dinoflagellates and naked flagellates may benefit *P. avirostris*, the main food source of which is nanoplankton, e.g. flagellates. Thus, a possible explanation is that both the rising temperature during the autumn and the dominance of small phytoplankton affected the population growth of marine cladocerans.

Regarding jellyfish, besides the previously mentioned change in 2007, the upward change was stronger during the summer of 2009. This peak has already been mentioned for the studied area and may be driven by temperature (Primo et al. 2012). In fact, medusae are likely to be sensitive to local environmental factors such as temperature (Molinero et al. 2009, Gibbons & Richardson 2009), since increasing temperatures can enhance their survival and growth (Brodeur et al. 1999). The influence of estuarine water temperature on jellyfish communities was particularly clear in our results, as indicated by the strong correlation between both time-series.

Coastal waters have warmed during the last century, leading to profound consequences for the dynamic regime of coastal ecosystems (Scavia et al. 2002,

Goberville et al. 2010). Accordingly, our results, using CUSUM analysis, indicate a causal link between temperature and changes in zooplankton groups. In fact, water temperature presented a positive correlation with all of the main marine groups—groups that were not evaluated and discriminated in previous studies (Marques et al. 2007, Primo et al. 2009). Subsequently, it is plausible to conclude that water temperature exerted a relevant influence in the Mondego zooplankton dynamics. Indeed, all time-series showed breaking points after 2006 for marine cladocerans, after 2007 for marine and estuarine copepods and after 2008 for cirriped and jellyfish abundance. This difference in timing was explained by Walther (2001), given that species show individualistic responses to temperature and other environmental variables, depending upon the particular threshold values of the physiological processes of their life history.

A number of studies have determined that change in temperature alone is also an important environmental factor, strongly affecting vital physiological rates such as respiration and excretion (Roddie et al. 1984, Gaudy et al. 2000). Furthermore, it can modify the life-history traits of zooplanktonic organisms such as copepods, through its influence on egg production, growth, development and mortality rates (e.g. Halsband-Lenk et al. 2002, Hirst & Kiørboe 2002, Leandro et al. 2006), as well as on the phenology and dormancy cycles of certain planktonic species (Edwards & Richardson 2004).

Considering this, local variability of freshwater flow was the dominant signal in the present time-series, and would explain the observed variability in species groups/populations at shorter temporal scales. However, this effect could be masked by larger time-scale phenomena occurring simultaneously, such as a rise in temperature, leading to a higher abundance of warm-water taxa. In brief, more than one mechanism was probably operating simultaneously, thus establishing the complex nonlinear relationships between climate variability and zooplankton dynamics (Hays et al. 2005), an issue that needs to be assessed based on longer observation periods.

Although the time-series we examined was not long enough to capture large-scale climate regime shifts, it synthesizes the results of pioneering research on the vulnerability and reorganization of zooplankton communities in response to climate variability, specifically in association with 2 consecutive drought events. This study has contributed substantially to our further knowledge of the response of the zooplankton community to weather events. This in-

formation will help develop baseline data, guidelines for drought climatology and referencing levels for shallow estuarine ecosystems and contribute to the accurate evaluation of the effects of environmental perturbations and the forecasting of expected recovery times. Besides emphasizing the complexity of the system, these findings stress the need for further research into the potential impacts of environmental and climate changes on these key estuarine systems.

Acknowledgements. The present work was supported by FCT (Portuguese Foundation for Science and Technology) through the COMPARE Project (PTDC/MAR/121788/2010) financed by POPH (Portuguese Operational Human Potential Program), QREN Portugal (Portuguese National Strategic Reference Framework) and MCTES (Portuguese Ministry of Science, Technology, and Higher Education). S.C.M. (SFRH/BPD/65541/2009), F.M. (SFRH/BPD/63527/2009) and A.L.P. (SFRH/BPD/91030/2012) are postdoctoral fellows of the FCT. Special thanks to Joana Falcão for her invaluable assistance and dedication with the identification of samples, and to all colleagues who helped during the fieldwork. Four anonymous reviewers provided invaluable comments and suggestions for the manuscript.

LITERATURE CITED

- Atrill MJ, Power M (2000) Effects on invertebrate populations of drought-induced changes in estuarine water quality. *Mar Ecol Prog Ser* 203:133–143
- Beaugrand G (2005) Monitoring pelagic ecosystems from plankton indicators. *ICES J Mar Sci* 62:333–338
- Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish Oceanogr* 8:296–306
- Cardoso PG, Raffaelli D, Lillebø AI, Verdelhos T, Pardal MA (2008) The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. *Estuar Coast Shelf Sci* 76:553–565
- Colebrook JM (1985) Sea surface temperature and zooplankton, North Sea, 1948–1983. *J Cons Int Explor Mer* 42:179–185
- Costa S, Bessa F, Pardal MA (2013) The parasite *Sacculina carcini* Thompson, 1836 (Cirripedia, Rhizocephala) in the crab *Carcinus maenas* (Linnaeus, 1758) (Decapoda, Portunidae): influence of environmental conditions, colour morphotype and sex. *Crustaceana* 86:34–47
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Dam HG (2013) Evolutionary adaptation of marine zooplankton to global change. *Ann Rev Mar Sci* 5:349–370
- de Lima MIP, Espírito Santo F, Ramos AM, de Lima JLMP (2013) Recent changes in daily precipitation and surface air temperature extremes in mainland Portugal, in the period 1941–2007. *Atmos Res* 127:195–209
- Diez JM, D'Antonio CM, Dukes JS, Grosholz ED and others (2012) Will extreme climatic events facilitate biological invasions? *Front Ecol Environ* 10:249–257
- Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. *Estuar Coast Shelf Sci* 74:263–273
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Edwards M, Reid P, Planque B (2001) Long-term and regional variability of phytoplankton biomass in the North-east Atlantic (1960–1995). *ICES J Mar Sci* 58:39–49
- EEA (European Environment Agency) (2012) Climate change, impacts and vulnerability in Europe 2012: an indicator-based report. EEA, Copenhagen
- Gaudy R, Cervetto G, Pagano M (2000) Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. *J Exp Mar Biol Ecol* 247:51–65
- Gibbons MJ, Richardson AJ (2009) Patterns of jellyfish abundance in the North Atlantic. *Hydrobiologia* 616: 51–65
- Goberville E, Beaugrand G, Sautour B, Treguer P (2010) Climate-driven changes in coastal marine systems of western Europe. *Mar Ecol Prog Ser* 408:129–159
- Grilo TF, Cardoso PG, Dolbeth M, Bordalo MD, Pardal MA (2011) Effects of extreme climate events on the macrobenthic communities' structure and functioning of a temperate estuary. *Mar Pollut Bull* 62:303–311
- Halsband-Lenk C, Hirche HJ, Carlotti F (2002) Temperature impact on reproduction and development of congener copepod populations. *J Exp Mar Biol Ecol* 271:121–153
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecol Evol* 20: 337–344
- Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195–209
- Hoffmeyer MS (2004) Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. *J Plankton Res* 26:181–189
- Ibañez F, Fromentin JM, Caste J (1993) Application de la methode des sommes cumulees a l'analyse des series chronologiques en oceanographie. *C R Acad Sci Paris Sci Vie Life Sci* 316:745–748
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z and others (eds) Contribution of Working Group I to the 4th assessment report of the IPCC. Cambridge University Press, Cambridge
- Jentsch A, Kreyling J, Beierkuhnlein C, Jenuch A (2007) A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* 5:365–374
- Kimmel DG, Mille WD, Roman MR (2006) Regional scale climatic forcing of Chesapeake Bay zooplankton dynamics. *Estuaries Coasts* 29:375–387
- Krzanowski WJ (1988) Principles of multivariate analysis. Clarendon Press, Oxford
- Leandro SM, Queiroga H, Rodriguez L, Tiselius P (2006) Temperature dependent development and somatic growth in two allopatric populations of *Acartia clausi* (Copepoda: Calanoida). *Mar Ecol Prog Ser* 322:189–197
- Leandro SM, Tiselius P, Queiroga H (in press) Spatial and temporal scales of environmental forcing of *Acartia* pop-

- ulations (Copepoda: Calanoida) in the Canal de Mira (Ria de Aveiro, Portugal). ICES J Mar Sci
- Legendre P, Legendre L (1998) Numerical ecology, 2nd English edn. Elsevier, Amsterdam
- Lehner B, Döll P, Alcamo J, Henrichs T, Kaspar F (2006) Estimating the impact of global change on flood and drought risks in Europe: a continental, integrated analysis. *Clim Change* 75:273–299
- Licandro P, Ibanez F (2000) Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. *J Plankton Res* 22:2225–2253
- Marques SC, Azeiteiro UM, Marques JC, Neto JM, Pardal MA (2006) Zooplankton and ichthyoplankton communities in a temperate estuary: spatial and temporal patterns. *J Plankton Res* 28:297–312
- Marques SC, Azeiteiro UM, Martinho F, Pardal MA (2007) Climate variability and planktonic communities: the effect of an extreme event (severe drought) in a southern European estuary. *Estuar Coast Shelf Sci* 73:725–734
- Marques SC, Azeiteiro UM, Leandro SM, Queiroga H and others (2008) Predicting zooplankton response to environmental changes in a temperate estuarine system. *Mar Biol* 155:531–541
- Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. *Estuar Coast Shelf Sci* 75: 537–546
- Miranda PMA, Valente MA, Tomé AR, Trigo R, Coelho F, Aguiar A, Azevedo EB (2006) O clima de Portugal nos séculos XX e XXI. In: Santos FD, Miranda P (eds) Alterações climáticas em Portugal: Cenários, impactos e medidas de adaptação—Projecto SIAM II. Gradiva, Lisbon, p 169–209
- Molinero JC, Buecher E, Lucic D, Malej A, Miloslavic, M (2009) Climate and Mediterranean jellyfish: assessing the effect of temperature regimes on jellyfish outbreak dynamics. *Annales: series historia naturalis* 19:11–18
- Nyitrai D, Martinho F, Dolbeth M, Baptista J, Pardal MA (2012) Trends in estuarine fish assemblages facing different environmental conditions: combining diversity with functional attributes. *Aquat Ecol* 46:201–214
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Primo AL, Azeiteiro UM, Marques SC, Martinho F, Pardal MA (2009) Changes in zooplankton diversity and distribution pattern under varying precipitation regimes in a southern temperate estuary. *Estuar Coast Shelf Sci* 82: 341–347
- Primo AL, Azeiteiro UM, Marques SC, Pardal MA (2011) Impact of climate variability on ichthyoplankton communities: an example of a small temperate estuary. *Estuar Coast Shelf Sci* 91:484–491
- Primo AL, Marques SC, Falcão J, Crespo D, Pardal MA, Azeiteiro UM (2012) Environmental forcing on jellyfish communities in a small temperate estuary. *Mar Environ Res* 79:152–159
- Roddie BD, Leakey RJG, Berry AJ (1984) Salinity–temperature tolerance and osmoregulation in *Eurytemora affinis* (Poppe) (Copepoda: Calanoida) in relation to its distribution in the zooplankton of the upper reaches of the Forth estuary. *J Exp Mar Biol Ecol* 79:191–211
- Rodrigo FS, Trigo RM (2007) Trends in daily rainfall in the Iberian Peninsula from 1951 to 2002. *Int J Climatol* 27: 513–529
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on animals and plants. *Nature* 421:57–60
- Santos JF, Pulido Calvo I, Portela MM (2010) Spatial and temporal variability of droughts in Portugal. *Water Resour Res* 46:W03503, doi:10.1029/2009WR008071
- Scavia D, Field JC, Boesch DF, Budde Meier RW and others (2002) Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25:149–164
- Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18:648–656
- Sirabella P, Giuliani A, Colosimo A, Dipnner J (2001) Breaking down the climatic effects on cod recruitment by principal component analysis and canonical correlation. *Mar Ecol Prog Ser* 216:213–222
- Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J Ecol* 99:656–663
- Taylor AH, Allen JI, Clark PA (2002) Extraction of a weak climatic signal by an ecosystem. *Nature* 416:629–632
- ter Braak CJ, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (Version 4). Microcomputer Power, Ithaca, NY
- Vincent D, Luczak C, Sautour B (2002) Effects of a brief climatic event on zooplankton community structure and distribution in Arcachon Bay (France). *J Mar Biol Assoc UK* 82:21–30
- Walther GR (2001) Adapted behaviour and shifting ranges of species—a result of recent climate warming. In: Walther GR, Burga CA, Edwards PJ (eds) 'Fingerprints' of climate change. Adapted behaviour and shifting species ranges. Kluwer Academic/Plenum Publishers, New York, NY, p 329

Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA

Submitted: May 16, 2013; Accepted: October 31, 2013
Proofs received from author(s): February 3, 2014