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Zooplankton community responses to regional-scale weather variability: a synoptic climatology approach

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ABSTRACT: Estuarine and coastal ecosystems are strongly affected by variations in climate through alterations in freshwater input, which result in changes in water temperature and salinity. Predicting the response of estuarine systems to future scenarios of climate change requires knowledge of the present relationships between estuarine and coastal communities and variations in local weather patterns. Synoptic climatology is a method that identifies recurrent weather patterns at a regional scale (1000s of km) and is valuable for predicting estuarine ecosystem responses to environmental variability. This method was applied for a region of southwest Europe, and the effects of weather patterns on the zooplankton community of the Mondego Estuary (Portugal) were investigated. We identified 9 weather patterns for the region during the last 61 yr. A regression analysis related these weather patterns with freshwater flow in the estuary during the winter, and subsequently years between 2003 and 2011 were classified as average, dry or wet by a percentile approach. The abundance and spatial distribution of the zooplankton community responded to weather pattern variability during the winter. For example, years that featured lower precipitation, freshwater flow and higher salinity were characterized by marine planktonic groups. Salinity appeared to be the main factor related to zooplankton community changes. This study shows that the synoptic climatology approach is effective at capturing regional-scale dynamics of estuaries and at providing baseline climate relationships with estuarine zooplankton communities, which can be used to predict future response to climate change.

KEY WORDS: Plankton communities · Synoptic climatology · Mondego Estuary · Climate variability

1. INTRODUCTION

Climate variability affects abundance, structure and biodiversity of marine ecosystems (Beaugrand et al. 2008, Cloern et al. 2010, Doney et al. 2012). Estuaries are particularly vulnerable to short- and long-term climate fluctuations, as they are dynamic environments that integrate the effects of the sea and the surrounding watershed. Worldwide, estuarine ecosystems have been affected by climate change, mainly through alterations in freshwater input, increasing air and water temperature, shifts in connectivity to the sea and increased intrusion of marine waters (e.g. Goberville et al. 2010, Chaalali et al. 2013). Estuaries constitute important habitats, including nursery and refuge areas, for a multitude of commercially important species; therefore, a better knowledge of their sensitivity to both human intervention and climate variability is warranted (Costanza et al. 1997, Beck et al. 2001, Seitz et al. 2013).

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Large-scale climate patterns such as the NAO and ENSO influence ecological processes such as community composition and species abundance, showing effectiveness as measures of climate change impacts on biological communities (Attrill & Power 2002, Hays et al. 2005, Robinson & Graham 2013). However, in some areas, the link between large-scale indices and local climate is weak and/or non-linear; thus, these relationship may be difficult to reveal (Stenseth et al. 2003). The 'synoptic climatology' approach (cf. Yarnal 1993) summarizes regional atmospheric processes and is a useful tool for classifying local climate variability, in order to describe the interannual variability in estuarine systems and the effects of climate forcing on biological communities (Kimmel et al. 2006, 2009, Miller et al. 2006, Wood & Austin 2009).

The response of the Mondego Estuary (Portugal) biological communities to environmental fluctuation has been studied over recent years. Impacts of extreme events on estuarine communities included variations in macrofauna abundance and secondary production (Dolbeth et al. 2008, Grilo et al. 2011), species growth rates (Bordalo et al. 2011), and changes in fish community composition (Baptista et al. 2010, Nyitrai et al. 2012) or in zooplankton spatial distributions (Marques et al. 2007, Primo et al. 2011). The relationship between the NAO and local estuarine communities was also examined for juvenile fish and jellyfish in the Mondego Estuary. Results showed that this large-scale atmospheric pattern failed in capturing species response to climate variability and was not directly related to local precipitation and river flow, which appear to be the important drivers in the communities (Martinho et al. 2009, Primo et al. 2012). Nevertheless, the NAO was related to interannual abundance patterns of the common goby *Pomatoschistus microps* (Nyitrai et al. 2013).

Zooplankton organisms are critical components of pelagic food webs and respond strongly to environmental changes, being particularly good indicators of climate change and food-web interactions (Hays et al. 2005, Molinero et al. 2008). Due to their fundamental role in linking primary productivity and higher trophic levels, investigating zooplankton relationships with regional climate variability will provide an insight on how the interconnectivity between trophic levels might change in the future. The present study analyzes zooplankton time-series data between 2003 and 2011, and tests the applicability of the synoptic climatology approach to planktonic communities in the Mondego Estuary. This study aims: (1) to characterize recent interannual climate variability by regional weather patterns and (2) to evaluate their effects in the main zooplanktonic species/groups.

2. MATERIALS AND METHODS

Regional-scale climate variability was quantified using synoptic climatology classification, described in Yarnal (1993) and Miller et al. (2006). Sea-level pressure (SLP) data from 1950–2011 was obtained from the National Center for Atmospheric Research, USA (NCAR; http://ncar.ucar.edu). Of all the large-scale predictors, SLP is the most frequently used, being particularly valuable due to its long record, which aids model development, and shows a relatively stable relationship with the surface environment (Yarnal 1993, Yarnal et al. 2001). Usually just one level is used as an input, since multiple levels can show high levels of dependence, and bring little extra information to the model (Huth et al. 2008). Daily data were acquired for a 5° × 5° latitude–longitude grid, in order to create a 5 × 9 point grid of SLP covering the area from 30–50° N latitude and 25° W–15° E longitude (Fig. 1). Predominant weather patterns in that period were identified by reducing variability using a principal component analysis (PCA) and hierarchical clustering (*k*-means). The first 6 principal components (PCs) explained 92% of the variance observed, and the model chosen by the Bayesian information criterion (BIC) identified 9 predominant weather patterns (clusters). Finally, average SLP maps were produced for each of the 9 clusters by taking the mean value for each grid point within the daily maps. These clusters represent the main atmospheric circulation patterns experienced in the region.

Long-term environmental data for the Mondego Estuary basin were used to classify local weather patterns. Mean daily precipitation (Stns 13G/02UG and 13F/01G in the Mondego watershed, upstream of the sampled stations; period 1950–2011), and mean monthly freshwater flow (Stns 12G/04H and 12G/01AE; period 1955–2011) were obtained from the Portuguese Water Institute (INAG; http://snirh.pt/). Mean daily air temperature was also acquired from the Portuguese Water Institute for Stns 12G/05C and 13H/04C, and also from Ogimet (www.ogimet.com) for Stns 085490 and 085480, to complete the period of 1969–2011.

Correlation analysis was performed on annual data (1955–2011) between the total number of days of each weather pattern and river flow. Analysis was performed using all the data and only for the winter

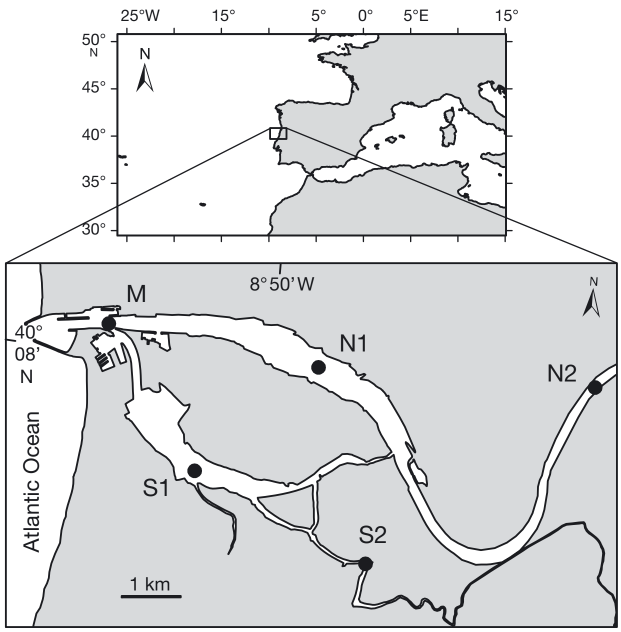

Fig. 1. Map of synoptic climate region with inset of the Mondego Estuary. Black dots: stations sampled for plankton data

period (December–February), and the best cluster predictors were identified by stepwise regression. A robust, least trimmed squares regression model was then used to determine outliers from freshwater flow data. The outliers (1955, 1976, 1990 and 2008) were then removed and a second regression model was performed on the modified data set. The analysis indicated a stronger correlation using only winter period (December–February), so subsequent analysis was restricted to this period.

Plankton data (2003–2011) were collected during monthly surveys at 5 stations (Fig. 1). Detailed descriptions of the collection procedure and sample handling can be found in Marques et al. (2006) and Primo et al. (2011). Sampled years were classified as dry, average and wet according to the freshwater river flow, using a percentile approach: freshwater river flow data was summarized from 1955–2011, calculating minimum, 25th percentile, median, 75th percentile, and maximum. From the 2003–2011 period, years that had flows below the 25th percentile were considered dry years (2004, 2005, 2007, 2008, 2011) and those with values above the 75th percentile were considered wet years (2003, 2010), while the remaining years were considered as average (2006, 2009). Mean winter anomalies were calculated by subtracting the cumulative winter daily frequencies and precipitation, and the average winter daily air temperature and monthly river flow from the corresponding long-term average. Anomalies were calculated for each weather pattern and averaged for the representative years of dry, average and wet conditions.

Main species and groups were chosen to represent the zooplanktonic component of the Mondego system and the final data matrix contained data on Copepoda, Cladocera, Hydromedusae, Siphonophora, Decapoda, *Acartia tonsa*, *A. clausi*, *Copidodiaptomus numidicus*, *Daphnia* spp., and *Penilia avirostris*.

Synoptic climatology analyses were performed with R software (R Development Core Team 2009) using the mclust package (Fraley & Raftery 2012). Sampled years were grouped into conditions (dry, average and wet) and differences tested for the environmental factors (precipitation, air temperature and river flow) by 1-way ANOVA in Sigmaplot® software. Due to the lack of normality, an $\ln(x + 1)$ transformation was applied to river flow data. Whenever there were differences between conditions, *a posteriori* Tukey pairwise comparisons were performed. Biological data was analyzed using a univariate permutational analysis of variance (PERMANOVA; PRIMER v. 6 and PERMANOVA+ v. 1, PRIMER-E) since they violated the ANOVA assumptions, even after transformation. The PERMANOVA is an analysis of variance test that can be applied to one or more factors in a great variety of designs (unbalanced, asymmetric, lacking replication) using permutation methods on the basis of a resemblance matrix (Anderson 2001). This analysis was performed on square root-transformed data, based on Euclidean distances between samples and considering all the factors as fixed. Biological data were tested for differences between conditions (dry, average and wet) and sampling stations (M, S1, S2, N1, N2). The software also calculated *t*-statistic tests as pairwise comparisons, whenever a significant difference ($p < 0.05$) was found.

3. RESULTS

We classified each day during 1950–2011 into 1 of 9 weather patterns (Fig. 2). Each weather pattern, or cluster, represented a spatial map of SLP associated with characteristic surface conditions. A day classified into a particular cluster will have surface conditions that show particular deviations from the long-term average condition in precipitation, air temperature and river flow (Table 1). Also, certain clusters were more prevalent in distinct seasons and varied in terms of total number of occurrences. For example, Clusters 1 and 4 occurred mainly during winter and were associated with positive precipitation anomalies and increased rived flow. In contrast,

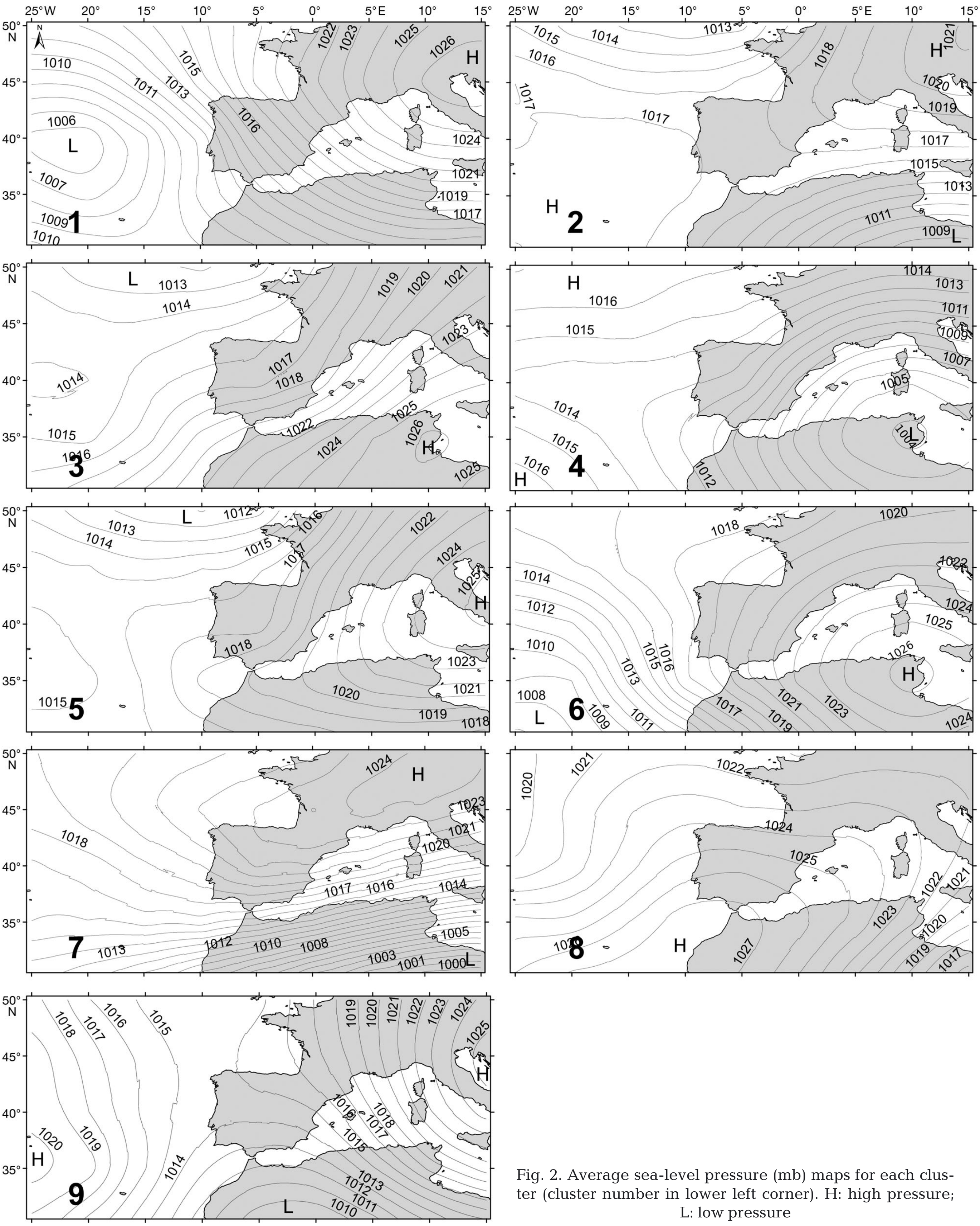

Fig. 2. Average sea-level pressure (mb) maps for each cluster (cluster number in lower left corner). H: high pressure; L: low pressure

Table 1. Meteorological characteristics for each weather pattern (winter period). Seasonality represents seasons in which the pattern occurs

Cluster	Days of occurrence	Winter days (%)	Precipitation anomaly (mm)	Air temperature anomaly (°C)	River flow anomaly (×10^3 m^3)	Seasonality
1	879	15.5	1.8 ± 8.3	−1.0 ± 2.8	25 992	Winter
2	60	1.1	−2.2 ± 3.4	−0.4 ± 2.83	−252 567	Spring/summer/fall
3	129	2.3	−2.4 ± 3.3	−2.6 ± 3.1	−162 274	Spring/summer/fall
4	1049	18.5	3.6 ± 10.4	0.5 ± 3.2	31 575	Winter
5	22	0.4	−2.9 ± 1.5	−1.0 ± 2.1	−333 358	Summer
6	533	9.4	−2.8 ± 2.7	−0.3 ± 2.7	−48 114	Fall/winter/spring
7	850	15.0	0.3 ± 7.7	1.1 ± 2.6	−4 626	Winter
8	1542	27.2	−3.1 ± 2.8	0.1 ± 2.8	−19 713	Winter
9	579	10.2	2.0 ± 9.2	−0.5 ± 2.7	17 637	Fall/winter/spring

Clusters 2 and 5 occurred infrequently, but were associated with negative precipitation anomalies and river flow values far below the winter long-term average for the Mondego Estuary.

A stepwise regression model that related river flow with frequency of weather pattern occurrence identified Clusters 1 and 4 as the best predictors of river flow, once the outliers were removed (Fig. 3A). The final model (adjusted $R^2 = 0.44$, $p < 0.0001$) included 51 years, and these 2 weather patterns explained 44 % of the freshwater flow during winter (Fig. 3B). This significant relationship reinforced the classification of sampled years by river flow variation. Additionally, due to the strong relation of river flow and estuarine communities it is possible to study the indirect influence of weather patterns and precipitation on biological communities.

During dry conditions, weather patterns 1 and 4 occur with less frequency, whereas weather patterns 6, 7 and 8 occur with greater frequency, compared to the long-term average (Fig. 4). The direct opposite pattern was observed when surface conditions were wet, with an increased occurrence of weather pattern 4 and a decreased occurrence of weather patterns 7, 8 and 9 (Fig. 4). Compared with the long-term mean, sampled periods of average conditions showed high frequency of weather patterns 3, 8 and 9 and low frequency of weather patterns 6 and 7 (Fig. 4).

Winter precipitation during wet conditions was slightly higher compared to the long-term mean, and both average and dry conditions showed negative anomalies (Table 2). Winter air temperatures showed a positive anomaly during all conditions; however, the anomaly was highest during years dominated by dry environmental conditions. River flow during wet years was higher than the long-term average and lower during dry years (Table 2). One-way ANOVA showed significant differences between wet and dry conditions for winter precipitation ($F = 7.15$; post hoc Tukey test: $q = 3.61$, $p < 0.05$) and river flow discharges ($F = 9.27$; post hoc Tukey test: $q = 4.24$, $p < 0.05$).

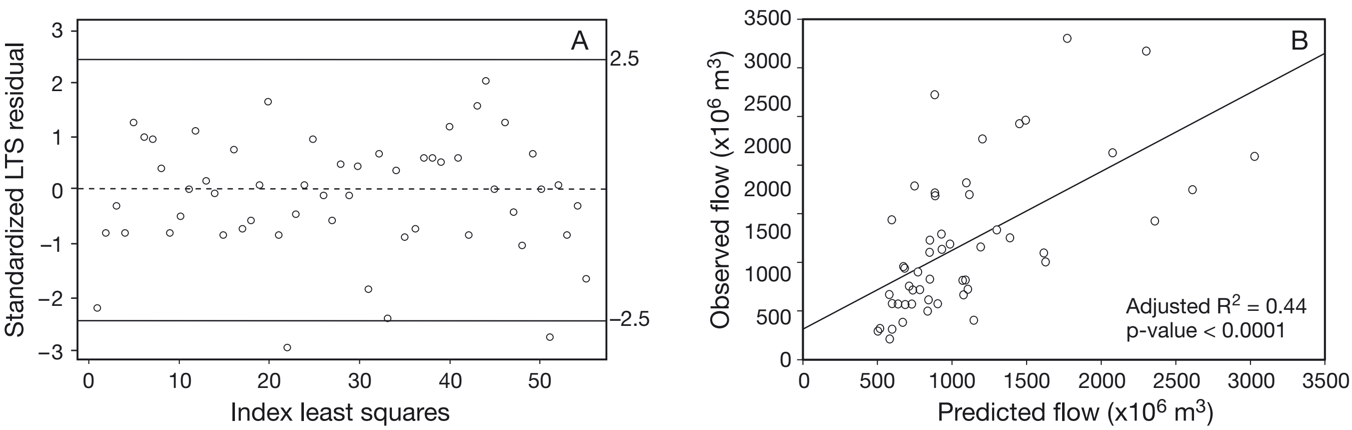

Fig. 3. Multiple linear regression model of the frequency of occurrence of weather patterns and river flow. (A) Plot of residuals by year, identifying outliers removed; (B) comparison of predicted versus observed results from the final model. LTS: Least Trimmed Squares; solid horizontal lines represent reference lines of 2.5 times the standard deviation beyond which residuals can be considered as outliers

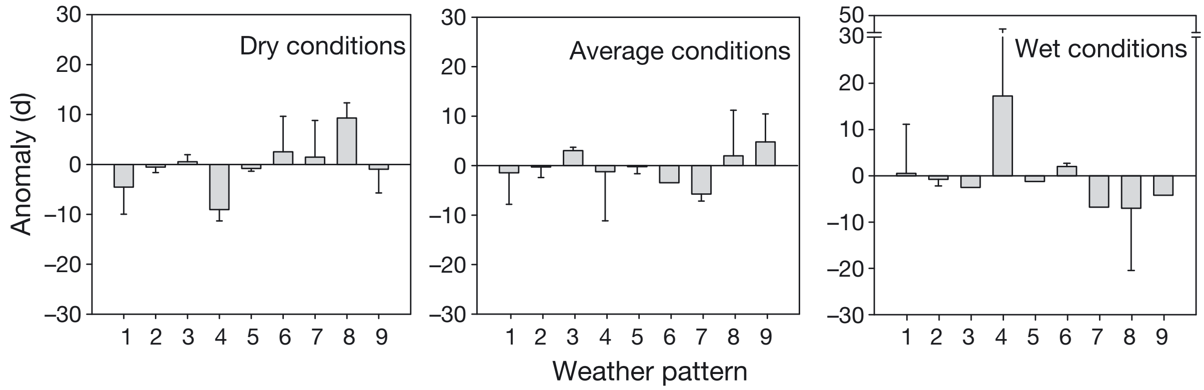

Fig. 4. Winter weather pattern deviations from long-term average frequency-of-occurrence (number of days) for years dominated by dry, average and wet conditions. Error bars: standard deviation

The contrasting freshwater flow conditions and associated weather patterns have also influenced zooplanktonic communities in the estuary. Copepod densities were generally higher at upstream sampling stations (pseudo-F = 7.34, p(perm) < 0.05), peaking at Stn S2 during the 2 wet years, but not significantly different between all the conditions. A similar pattern was seen in the dominant species *Acartia tonsa* (Fig. 5; pseudo-F = 13.90, p(perm) < 0.05). The freshwater copepod *Copidodiaptomus numidicus* reached higher densities at Stn N2 (pseudo-F = 11.53, p(perm) < 0.05), with no distinction between the years with wet and with dry conditions, while *A. clausi* was mainly present at the downstream stations (pseudo-F = 8.27, p(perm) < 0.05) and with increased density during the dry years (pseudo-F = 3.41, p(perm) < 0.05) (Fig. 5).

Cladocera spatial distribution varied according with the weather conditions (pseudo-F = 2.42, p(perm) < 0.05), being more abundant at the upstream stations during the 2 wet years. The dominant cladoceran species was *Daphnia* spp. with higher densities at Stn N2 (pseudo-F = 3.85, p(perm) < 0.05) during the 2 wet and 2 average years (pseudo-F = 7.54, p(perm) < 0.05) (Fig. 5). The marine cladoceran, *Penilia avirostris*, had higher abundances, though not significantly different, at downstream locations and during dry periods (Fig. 5).

Both Siphonophora (pseudo-F = 5.56, p(perm) < 0.05) and Decapoda (pseudo-F = 5.16, p(perm) < 0.05) density increased during dry conditions, and decapods also showed increases in abundance at Stn S1 (pseudo-F = 5.60, p(perm) < 0.05) (Fig. 5). Hydromedusae showed a similar pattern; however, their density increased during dry conditions and in 2 years with wet conditions (pseudo-F = 3.73, p(perm) < 0.05) (Fig. 5).

5. DISCUSSION

The synoptic climatology approach resulted in a classification of regional weather variability and was strongly associated with changes in environmental conditions relevant to estuarine dynamics. After the removal of outliers, the frequency of Clusters 1 and 4 explained 44 % of the variability in freshwater input to the Mondego Estuary (Fig. 3). The removal of outliers was important, since the model is better suited to forecast typical inter-annual variations in flow that still have significant impact on communities, rather than infrequent events that may lead to significant changes in the estuary (Miller et al. 2006). The amount of unexplained variation still present in the model can be due to the exclusion of extreme precipitation values that have immediate effects on the flow. Flow depends primarily on precipitation, evapotranspiration and the ability of the ground to store water (Bates et al. 2008), so in the remaining period, other factors such as evapotranspiration can have a higher effect on this relationship. Thus, the model is better suited for the winter period, probably because

Table 2. Winter precipitation, air temperature and river flow anomalies (±SD) during wet, average and dry conditions

	Precipitation anomaly (mm)	Air temperature anomaly (°C)	River flow anomaly ($\times10^6$ m^3)
Wet conditions	14.80 (±44.69)	0.56 (±0.46)	87.94 (±36.88)
Regular conditions	−58.85 (±64.76)	0.29 (±1.13)	1.65 (±18.89)
Dry conditions	−161.14 (±47.34)	0.81 (±0.84)	−68.60 (±20.56)

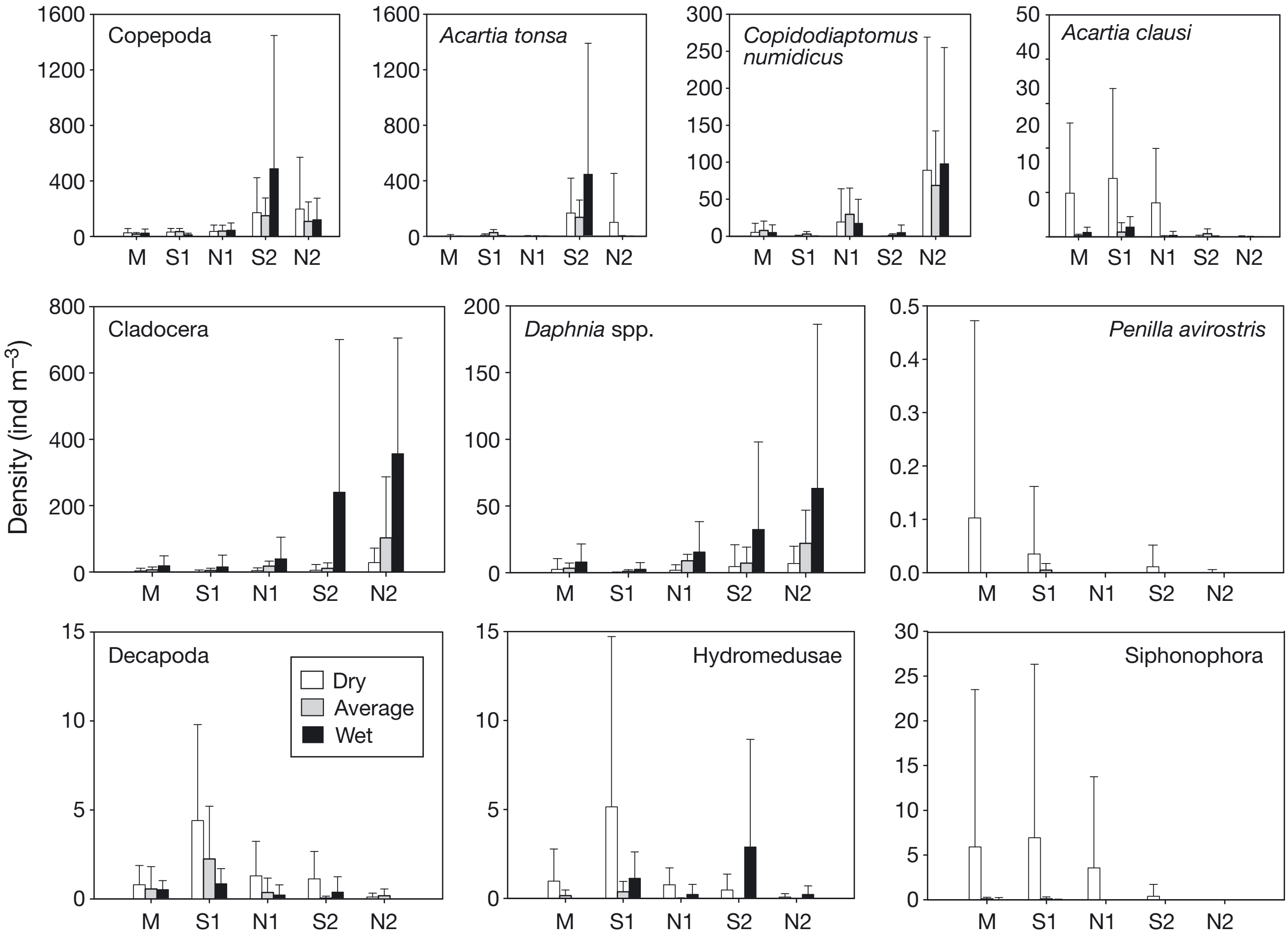

Fig. 5. Response of main zooplanktonic groups and species (density, mean ± SD) at the 5 sampling stations of Mondego Estuary (see Fig. 1) during dry, average and wet conditions

the weather pattern–precipitation–flow relationship is the strongest. Synoptic climatology related the regional climate patterns with Mondego river flow. The advantage of synoptic climatology over using flow data alone is that synoptic climatology allows some measure of prediction of future estuarine conditions (Fig. 3). Our classification based on flow allowed us to interpret our planktonic data with respect to 2 years with wet conditions, 2 years with average conditions and 5 years with dry conditions. The plankton data record is not long enough to include more 'replicate' years with dry and wet conditions.

Zooplankton communities in the Mondego Estuary are dominated by Copepoda species, mainly *Acartia tonsa* (Marques et al. 2006). In the present study, both total Copepoda and *A. tonsa* showed increased abundances during the 2 wet years at Stn S2, and during dry conditions at Stn N2. However, these differences were not significant, presumably due to the highly patchy and variable nature of zooplankton populations within this estuary. Previous studies have reported an increase of *A. tonsa* during dry periods, mainly at the north arm of the estuary (Marques et al. 2007, Primo et al. 2009). Freshwater copepod species like *Copidodiaptomus numidicus* were more abundant upstream, but with no clear distinction between conditions. Other freshwater groups showed significantly higher densities during the 2 wet years, as in the case of the dominant Cladoceran, *Daphnia* spp. The lower salinities allowed the establishment of a freshwater community in the estuary, more evident at the upstream areas. On the contrary, marine taxa like the copepod *A. clausi*, Siphonophora, Decapoda and Hydromedusae mainly present at the downstream areas showed increased abundances during dry conditions. Most of these taxa showed low abundance during the winter; however, dry conditions and associated low freshwater inflow allowed a higher intrusion of marine species in the estuary. Salinity variability in estuaries is associated with the advective properties of freshwater discharge and plays a critical role in communities, affecting species' temporal and spatial variability (Licandro & Ibanez 2000, Fernández-Delgado et al. 2007).

The synoptic climatology approach was previously applied to planktonic communities at Chesapeake Bay, USA (Kimmel et al. 2006, 2009, Miller et al. 2006). As a small estuary, the Mondego responds to river flow variability in different ways than larger estuarine North Atlantic habitats at similar latitudes, such as this. In that area, winter weather patterns are related with spring discharge, showing a time lag between precipitation and river flow (Najjar 1999). In contrast, the effect of weather patterns in the Mondego Estuary was more immediate, possibly related with differences in drainage area, snowpack storage, evapotranspiration and water residence time. For instance, the Mondego River basin has a drainage area of 7000 km^2, contrasting with the Susquehanna River basin (71 000 km^2), with a spring discharge strongly related with the precipitation stored as snow and ice (Miller et al. 2006). Also, residence time in the Mondego Estuary is 1–2 d during winter and is strongly related with freshwater inflow (Kenov et al. 2012).

In Chesapeake Bay, the abundance of copepods seems to decline during dry conditions, while in the Mondego Estuary, significant differences were detected for *A. clausi*, a marine copepod species that seems to increase in abundance during dry periods in the estuary. This was also observed for other marine groups such as Hydromedusae and Siphonophora. Considering higher trophic levels, anadromous fish in Chesapeake Bay linked to tidal freshwater areas suffered a decline during dry conditions (Kimmel et al. 2009). A similar pattern has been described for the Mondego Estuary, the fish assemblages of which suffer depletion in freshwater species and a reduction in abundance and production of resident fish and commercially important nursery species (Dolbeth et al. 2008, Martinho et al. 2009, Baptista et al. 2010). The Chesapeake Bay community response to different weather conditions is related to trophic interactions (Kimmel et al. 2009); however, in the present study at the Mondego Estuary, this is not evident, since changes in species of different trophic levels seemed not to be related. The stronger short-term response of the system to freshwater input results in the transport of estuarine communities, as opposed to creating spatial overlap between predators and prey, as may occur in larger estuaries with longer residence times. It could be argued that increases in some predators (Decapoda and Hydromedusae; Fig. 5) may impact zooplankton populations, but we had no direct evidence that this was the case. Changes in feeding mode and mean trophic level of fish may occur during dry and flood events (e.g. Livingston 1997, Nyitrai et al. 2012, Peer et al. 2013). In the Mondego Estuary, alternative consumers and estuarine production can balance the increase of new marine species during dry conditions.

Salinity variability was therefore the major factor driving the zooplankton community, affecting differences between weather conditions and spatial variability inside the estuary. Salinity gradient has been regarded as one of the best predictors for estuarine species abundance and spatio-temporal community structure (Tackx et al. 2004, Morais et al. 2009, Selleslagh et al. 2009). In the Mondego Estuary, river flow variations and associated changes in the salinity gradient had strong impact on seasonal and spatial distribution of zooplankton species. While these species seem to be strongly influenced due to advection (Marques et al. 2006, Primo et al. 2009, 2011), for pelagic organisms such as fish, river flow seems essential for their egg and larval development, larval migration and recruitment of marine juveniles into the estuary (Martinho et al. 2009, Dolbeth et al. 2010). Accordingly, it is expected that years with higher (lower) winter frequency of weather patterns 1 and 4 will present higher (lower) precipitation and river flow values and increased abundance of freshwater (marine) species in the Mondego Estuary.

The main findings of this study result from the synoptic climatology approach, and confirm previous studies in the Mondego Estuary zooplankton community, reinforcing the value of synoptic climatology to identify, quantify and evaluate the effects of climate variability on coastal ecosystems. Results also show that air temperature rose in the region during the last few years (2003–2011), with increased winter values during dry conditions. Changes in temperature can also influence distribution, growth, mortality and phenology of planktonic species (e.g. Hirst & Kiørboe 2002, Leandro et al. 2006, Edwards & Richardson 2004). This rising temperature scenario reinforces the importance of studying and predicting ecosystem responses to changing climate; thus, synoptic climatology can be a powerful predictive tool to assess the effect of climate variability on biological communities.

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