



Interannual abundance changes of gelatinous carnivore zooplankton unveil climate-driven hydrographic variations in the Iberian Peninsula, Portugal



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ABSTRACT

The persistent massive blooms of gelatinous zooplankton recorded during recent decades may be indicative of marine ecosystem changes. In this study, we investigated the potential influence of the North Atlantic climate (NAO) variability on decadal abundance changes of gelatinous carnivore zooplankton in the Mondego estuary, Portugal, over the period 2003–2013. During the 11-year study, the community of gelatinous carnivores encompassed a larger diversity of hydromedusae than siphonophores; the former dominated by *Obelia* spp., *Lizzia blondina*, *Clythia hemisphaerica*, *Liriope tetraphylla* and *Solmaris corona*, while the latter dominated by *Muggiaea atlantica*. Gelatinous carnivore zooplankton displayed marked interannual variability and mounting species richness over the period examined. Their pattern of abundance shifted towards larger abundances ca. 2007 and significant phenological changes. The latter included a shift in the mean annual pattern (from unimodal to bimodal peak, prior and after 2007 respectively) and an earlier timing of the first annual peak concurrent with enhanced temperatures. These changes were concurrent with the climate-driven environmental variability mainly controlled by the NAO, which displayed larger variance after 2007 along with an enhanced upwelling activity. Structural equation modelling allowed depicting cascading effects derived from the NAO influence on regional climate and upwelling variability further shaping water temperature. Such cascading effect percolated the structure and dynamics of the community of gelatinous carnivore zooplankton in the Mondego estuary.

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1. Introduction

Marine ecosystems are sculpted by both the anthropogenic factors and interannual variations of large-scale climate patterns (Drinkwater et al., 2010; Roessig et al., 2005). The latter shaping environmental variability and nutrient dynamics, thereby playing a prominent influence on the structure and functioning of plankton (Molinero et al., 2013). Understanding how climate interacts with these communities is therefore fundamental to develop adequate policies for a sustained use of marine ecosystems assets (Chust

et al., 2013; Primo, 2012), as plankton constitute a major vector of energy transfer from primary productivity to fish.

Zooplankton communities have been useful to track climate-driven environmental changes (Hays et al., 2005). This is partly due to their pivotal role in marine food webs linking primary production with higher trophic levels, and to their non-linear responses face changing environmental conditions, which make them valuable sentinels of ecosystem changes (Hays et al., 2005; Taylor et al., 2002). In addition, these organisms are poikilothermic, and therefore not able to regulate internally environmental temperature. Hence, temperature changes in the marine environment directly affect their fundamental functional processes, such as ingestion, respiration and reproductive development

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(Mauchline, 1998).

Among zooplankton taxa, gelatinous carnivores species (e.g., medusa, ctenophores and siphonophores) have an important role in food web dynamics by shaping top-down and bottom-up controls (Hosia et al., 2014; West et al., 2009), through predation pressure and modifying nutrient cycles via excretion and organic matter decomposition (Condon et al., 2011; Pitt et al., 2007; Ruzicka et al., 2012). Gelatinous zooplankton organisms are provided with a suite of attributes that enable them surviving in disturbed marine ecosystems and recovering rapidly as conditions improve (Richardson, 2008). In recent years, extensive outbreaks of gelatinous plankton have been recorded in several estuarine and coastal waters raising concerns about potential changes in the entire pelagic ecosystem dynamics (Lucas et al., 2014). However, despite the increasing global interest on these events, knowledge gaps remain in regards to the underlying factors driving the abundance changes of these organisms (Condon et al., 2014). In this study, we assess interannual and seasonal changes of gelatinous carnivore zooplankton in the Mondego estuary over the period 2003 to 2013. The western coast of the Iberian Peninsula, where the study area is located, is one of the four major upwelling regions in the world. This seasonal phenomenon mainly occurs during the spring–summer season and is shaped by the anticyclonic activity (Alvarez et al., 2008; Pérez et al., 2010; Santos et al., 2011), promoted by the positive phase of the North Atlantic Oscillation (NAO) (Lynam et al., 2004; Santos et al., 2011).

Here we examine the potential cascading effects of large-scale atmospheric phenomena to local hydrography and to changes in abundance and structure of the gelatinous carnivore zooplankton in the Mondego estuary. We hypothesized that climate signals shape inter-annual abundance changes of these organisms through their influence on regional weather patterns and the upwelling activity, which in turn shape local hydrographic conditions, eventually promoting favorable conditions for gelatinous carnivore zooplankton. We quantified these relationships by using a structural modelling approach, and further assessed seasonal changes in gelatinous carnivores at the community and species levels.

2. Materials and methods

2.1. Study area

The Mondego Estuary (40°08'N, 8°50'W) is situated in a warm temperate region on the west coast of Portugal (Fig. 1), where the atmospheric variability is strongly influenced by NAO (Trigo et al., 2004). It is an intertidal and shallow system composed by two arms (north and south) divided by Murraceira Island and characterized by different hydrological characteristics. The northern arm is deeper (4–8 m deep at high tide), represents the principal navigation channel and directly connects with Mondego River. The southern arm is shallower (2–4 m deep at high tide), is more silted up than the northern arm, the navigation mainly depends on the tides and on the fresh flow inputs from a small tributary, the Pranto River, whose discharges are controlled by a sluice (Cardoso et al., 2004; Grilo et al., 2012). A full and complete description of the system can be found in Marques et al. (2005).

2.2. Biological data

The gelatinous carnivores organisms were collected monthly from January 2003 to December 2013 at three sampling stations in the Mondego Estuary (M – mouth; N1 – Northern Arm; S1 – Southern arm) (Fig. 1). Samples were taken by subsurface horizontal tows, using a plankton net (open diameter 0.5 m, mesh size 335 µm, tow speed: 2 knots, tow length: 3 min, 1 replicate plankton

tow per station). The volume of water filtered was estimated by a Hydro-Bios flow meter fixed in the opening of the net (the volume filtered averaged $39 \pm 22 \text{ m}^3$). Then, organisms were immediately fixed with 4% buffered formalin, transferred to 70% ethanol in the lab and separated under dissecting microscope. Gelatinous organisms were identified, whenever possible, to the lowest taxonomic level and abundance was expressed as number of organisms per cubic meter (ind.m^{-3}). Regarding siphonophores, only nectophores of *Muggiaea atlantica* and *Muggiaea kochi* were counted and used in data analysis.

2.3. Physical data

We used the North Atlantic Oscillation and regional atmospheric variability to assess the climate influence experienced by the Mondego estuary. The NAO is a pattern of atmospheric circulation characterized by cyclical oscillations of the difference in sea level pressure between Iceland and Azores, that influences the weather system over the North Atlantic, North Sea, and Europe (Hurrell, 1995). The NAO mixes up atmospheric mass between Arctic and subtropical Atlantic and affects the ocean through modifications in salinity, gyre circulation, and surface air temperature (Hurrell, 1995; Hurrell et al., 2003). In addition, we used Upwelling Index data (UI) provided by the Instituto Español de Oceanografía. Upwelling is an oceanographic phenomenon that involves wind-driven motion of cooler, nutrient-rich water toward the ocean surface, promoting higher primary production. Positive (negative) UI values mean upwelling (downwelling) conditions (Santos et al., 2011). This index corresponds to the upwelling activity in the offshore area relative to the Mondego Estuary (Figueira da Foz region) and was computed by the Meteogalicia WRF atmospheric model (<http://www.wrf-model.org>). At each sampling event the water temperature, salinity, pH and dissolved oxygen were measured with appropriate sensors (WTW). Data belong to the Mondego Estuary survey headed by the Centre of Functional Ecology, University of Coimbra.

2.4. Statistical analysis

To explore the potential effect of hydroclimate influence on the interannual variations of gelatinous organisms, a five-step procedure was used.

First, time series were standardized to zero mean and unit variance. Then, linear regressions were performed to remove temporal trends and residual values were retained for analysis.

Second, to describe dominant patterns of hydrographic variability in the Mondego estuary, it was applied a Principal Component Analysis (PCA) on a matrix, Z, composed by the hydrological records. This allows integrating in few variables the climate variability. The first principal component (PC1) accounted for 61% of the hydrological variance and was used as proxy of local environmental conditions.

Third, the relationship between the NAO and the abundance of gelatinous carnivores on a monthly scale was quantified. As climate signals are non-stationary wavelet analysis (Continuous Wavelet Transform, CWT) was used to assess the time-varying signal of each time series and then was also used the wavelet coherence method to quantify their correlation in the time frequency space (Grinsted et al., 2004). Continuous Wavelet Transform performs a local time-scale decomposition of time series quantifying its spectral characteristics as a function of time (Cazelles et al., 2008; Hidalgo et al., 2011). The Morlet wavelet function was used as it better describes time series with unknown frequencies and allows a better separation of the phase and the amplitude of the studied signal (Cazelles et al., 2008; Percival and Walden, 2000). The 5% statistical

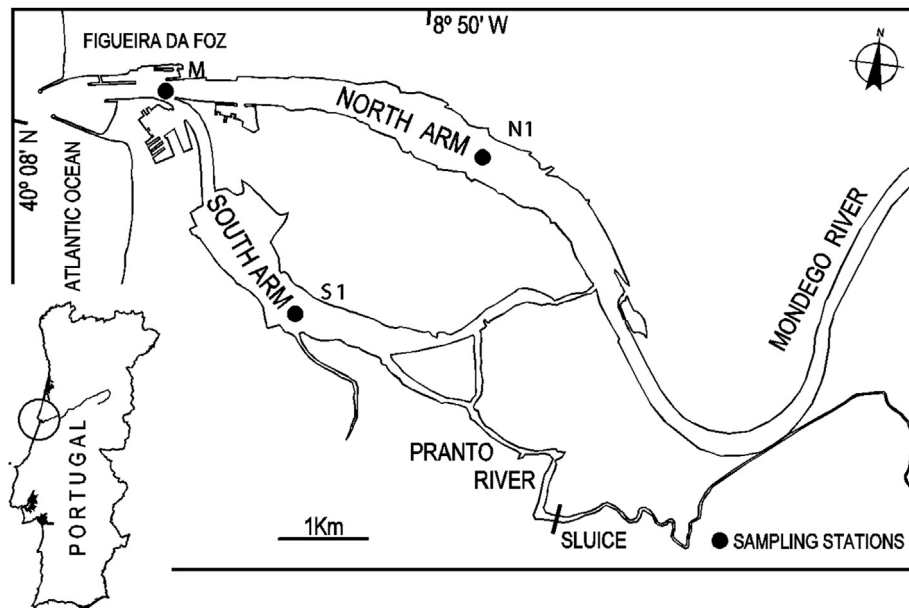


Fig. 1. Location of sampling stations (M: Mouth; S1: Southern arm; N1: Northern arm) in Mondego estuary.

significance level was determined by using bootstrap simulations (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, i.e. mean and variance of the time series do not vary with time (Percival and Walden, 2000). Then, from the CWT of each two climate phenomenon, the wavelet coherence method was performed, to identify areas with high common power and significant links in the time frequency space between the two phenomena. To graphically display the temporal relationship only data within the cone of influence was used.

Fourth, partitioning effects of external forces driving the overall variability of gelatinous carnivores were assessed and quantified using structural equation modelling (SEM), which allowed depicting direct and indirect effects, and their relative importance. The strength and sign of links and the quantification of the model structure were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1000 replicates), while the Bayesian Information Criterion (BIC) and Chi-square values were used to assess robustness and fit of the overall path model (Alsterberg et al., 2013). The individual path coefficients (i.e. partial regression coefficients) indicate the strength of the relationship between causal and response variables.

Fifth, heat diagrams were used to picture both seasonal and interannual abundance changes of gelatinous carnivore zooplankton. 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 colour was assigned from light grey (quantile 0.10) to dark grey (quantile 0.90), representing low and high values, respectively. In addition, abundance changes were detected using the cumulative sum of standardized ordinary least square residuals (OLS-based CUSUM test). This technique allows for computing the probability of significant modifications in a time-series, and is useful in detecting shifts in chronological records (Fernández De Puellés and Molinero, 2013). After identifying the main periods characterizing the interannual variability of the gelatinous carnivore community, we examined the seasonal changes by computing the mean annual cycle prior and after 2007. Statistical differences between mean annual cycles during each period were tested by

using a Kruskal-Wallis test. Furthermore, we assessed the inter-annual changes of the timing of seasonal peak; we centred Julian days to the median of the month in which the first annual peak was observed, i.e. abundance $>30 \text{ ind.m}^{-3}$. Thus, Julian days are centred to day 15 of each month (i.e. if the peak occurred in March the corresponding Julian day is March 15 = Julian day 74). The inter-annual variations of the timing of seasonal peak were regressed linearly against temperature to quantify their relationship.

Lastly, species-specific changes were computed. To do so, only species showing abundance larger than 0.1% in the whole community were used. A list of 28 species was selected and heat maps were built to show species year-to-year changes throughout the period examined.

3. Results

3.1. Gelatinous carnivore zooplankton abundance and composition

Predominant species of gelatinous carnivores in the Mondego estuary were mainly represented by hydromedusae and siphonophores, in particular by 20 taxa of hydromedusae and 2 taxa of siphonophores (Fig. 2 and Table 1).

During the 11-year time series, *Obelia* spp., *Lizzia blondina*, *Clythia hemisphaerica*, *Liriope tetraphylla* and *Solmaris corona* were the five dominant hydromedusae species, whereas *Muggiaea atlantica* was the dominant siphonophore species (Fig. 2 and Fig. 3). *M. atlantica* showed the higher abundances in July 2009, whereas lower abundances were found in December 2008 (Fig. 3). *Obelia* spp. and *Lizzia blondina* showed higher abundance values in 2003. In subsequent years, their presence in the Mondego estuary has been constant, with seasonal high abundance peaks (Figs. 2 and 3). *Liriope tetraphylla* presented maximum abundance in 2005, followed by a decrease until 2009, when its abundance increased again (Figs. 2 and 3). During the period investigated, *Clythia hemisphaerica* occurred every year, showing an increase of the seasonal abundance after 2008, reaching the maximum value in 2012 (Figs. 2 and 3). Lastly, *Solmaris corona* was observed every year although in very low abundances and it was completely absent during 2003 and 2010; the major peak of this species was observed in 2013

(Figs. 2 and 3). Beyond *M. atlantica*, which showed every year abundance $>10 \text{ ind.m}^{-3}$, notice that from years 2007–2008 most of species increased in abundance (Fig. 2).

3.2. Environmental variability

The NAO showed a marked variability at monthly and interannual scales (Fig. 4a). It was positive after 2008, although a dramatic drop occurred during the winters of 2010 and 2011, followed by a short, negative phase in 2013. Along with these changes, marked interannual variations were observed in the upwelling activity offshore the Mondego estuary, as indexed by the UI. The seasonal variability of the upwelling signal displayed a mean peak in summer, while interannual changes rose after 2007 and showed an absolute maximum late 2007 (Fig. 4b).

In turn, the aquatic environment in the Mondego Estuary displayed prominent monthly variations of hydrological conditions (Fig. 4c), that further exhibited larger variance around 2007–2010 (CUSUM test $p < 0.005$) followed by a slight decrease. Likewise, the magnitude in their variance change was 2.5-fold higher after 2007. The governing temporal pattern of climatic and hydrological signals displayed concomitant changes after 2007. The NAO and regional climate exhibited prominent changes after 2007–2009 and 2010–2012, respectively (CUSUM test $p < 0.05$).

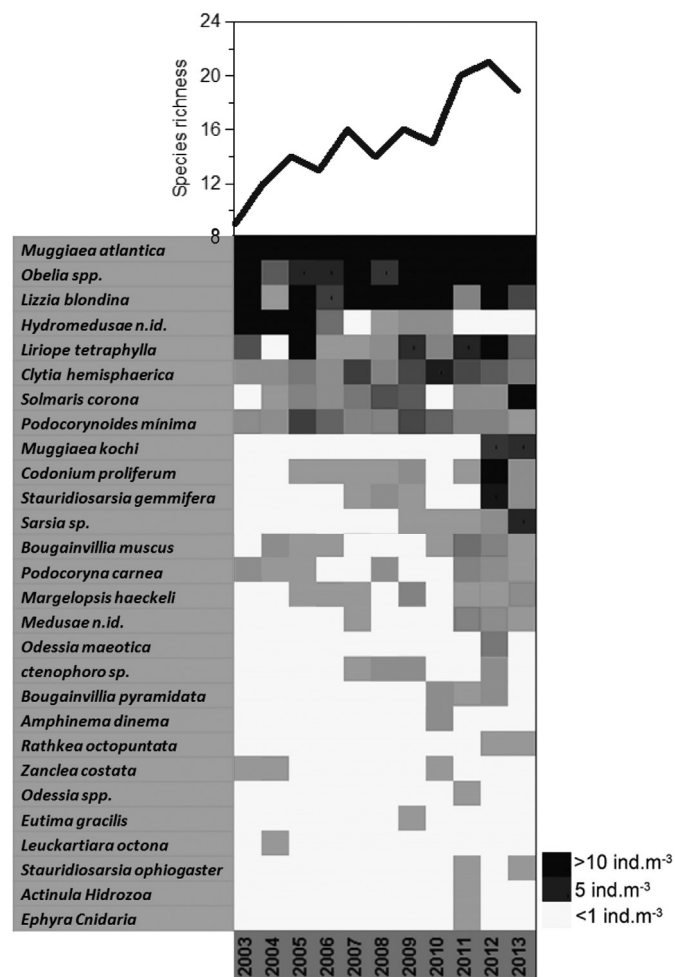


Fig. 2. Temporal variations and species richness of gelatinous carnivores' species throughout the period investigated. Notice that the years 2007–2008 rare species ($<1 \text{ ind.m}^{-3}$) increased in abundance.

Table 1

Species list and mean abundance (\pm standard deviation) throughout the period investigated.

Taxa	(2003–2007)		(2008–2013)	
	Mean	St. Dev.	Mean	St. Dev.
<i>Muggiaea atlantica</i>	9.0877	46.5256	21.2620	53.8679
<i>Lizzia blondina</i>	2.1398	9.5545	1.0166	2.9987
<i>Obelia</i> spp.	1.7595	7.4947	1.8448	5.3315
<i>Hydromedusae</i> n.id.	1.0224	3.7522	0.0159	0.1021
<i>Liriope tetraphylla</i>	0.4138	2.6960	0.4562	1.8436
<i>Podocorynoides minima</i>	0.1928	1.1374	0.1892	0.6317
<i>Clytia hemisphaerica</i>	0.1608	0.7514	0.3536	1.2538
<i>Solmaris corona</i>	0.0727	0.2737	0.2866	1.5116
<i>Codonium proliferum</i>	0.0449	0.2664	0.0676	0.3657
<i>Bougainvillia muscus</i>	0.0116	0.0592	0.0610	0.4084
<i>Podocoryna carnea</i>	0.0099	0.0968	0.0296	0.1683
<i>Margelopsis haeckeli</i>	0.0039	0.0379	0.0340	0.1927
<i>Zanclea costata</i>	0.0023	0.0187	0.0004	0.0059
<i>Medusae</i> n.id.	0.0010	0.0132	0.0355	0.1465
<i>Stauridiosarsia gemmifera</i>	0.0010	0.0102	0.1429	1.5503
<i>Ctenophoro</i> sp.	0.0008	0.0107	0.0175	0.1174
<i>Leuckartiara octona</i>	0.0007	0.0091	0.0000	0.0000
<i>Odessia</i> spp.	0.0000	0.0000	0.0011	0.0161
<i>Rathkea octopunctata</i>	0.0000	0.0000	0.0045	0.0307
<i>Odessia maeotica</i>	0.0000	0.0000	0.0318	0.3547
<i>Stauridiosarsia ophiogaster</i>	0.0000	0.0000	0.0005	0.0046
<i>Sarsia</i> sp.	0.0000	0.0000	0.1255	1.1239
<i>Muggiaea kochi</i>	0.0000	0.0000	0.2027	1.0027
<i>Eutima gracilis</i>	0.0000	0.0000	0.0008	0.0119
<i>Ephyra Cnidaria</i>	0.0000	0.0000	0.0002	0.0022
<i>Bougainvillia pyramidata</i>	0.0000	0.0000	0.0125	0.0941
<i>Amphinema dinema</i>	0.0000	0.0000	0.0097	0.1316
<i>Actinula Hidrozoa</i>	0.0000	0.0000	0.0002	0.0029

3.3. Couplings between NAO, regional climate and gelatinous carnivore organisms' variability

The potential connection between the above climate changes, as indexed by the NAO and the variability of gelatinous carnivore zooplankton was assessed by means of wavelet analysis (Fig. 4d). Results showed a discontinuous interaction between climate and gelatinous carnivores that is, prior 2007 the relationship was elusive, while a significant increase arose afterwards, as pointed out by their wavelet coherence. It is worth noticing that the maximum coherence came along with the largest hydroclimate forcing, i.e. larger variance of climate and hydrology, which translated into a larger marine influence into the Mondego estuary system. The partitioning effects through the SEM unveiled cascading influences from NAO and UI on local hydrology, ultimately influencing the overall temporal pattern of gelatinous carnivore zooplankton in the Mondego estuary (Fig. 5). The atmospheric forcing promoted by the NAO was closely linked with regional climate variability (path coefficient = 0.68), as well as with interannual changes in UI (path coefficient = 0.33). These changes permeated local hydrological conditions affecting salinity (path coefficients = 0.25 and 0.28, UI and regional climate respectively), and temperature (path coefficients = -0.18 and 0.22 , UI and regional climate respectively). In turn, temperature showed closely linked with changes in gelatinous carnivore zooplankton (path coefficient = 0.54) acting as a mediator factor between large, i.e. NAO, and regional, i.e. UI, scale forcing processes with estuarine ecological changes.

3.4. Interannual and seasonal changes of gelatinous carnivore zooplankton in the Mondego estuary

In the light of the above climate-related environmental changes, we portrayed the interannual and seasonal patterns of gelatinous carnivore variability (Fig. 6a and b). Superposed to the marked year-

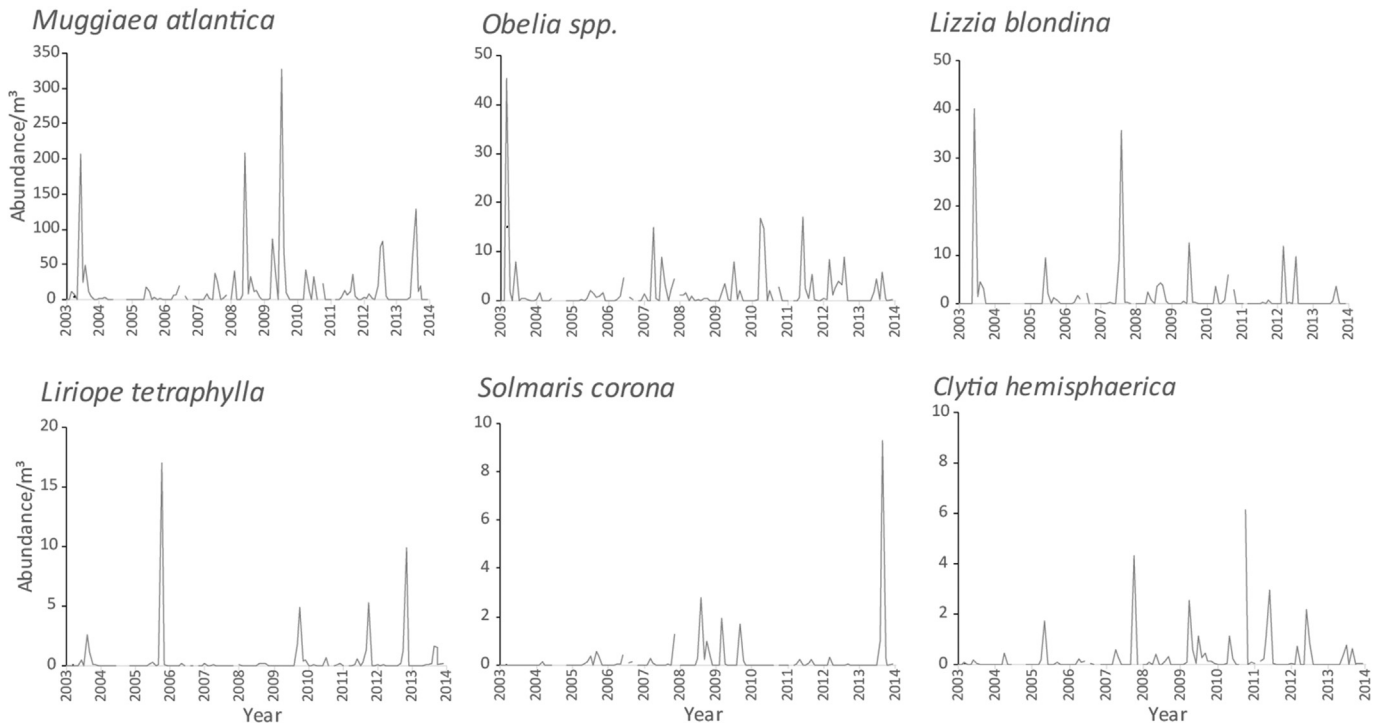


Fig. 3. Mean monthly abundance of the most abundant species of gelatinous carnivores' organisms in the Mondego estuary during the period investigated.

to-year changes, we found a major change late 2007 (CUSUM test $p < 0.05$) (Fig. 6a), which corresponded to a conspicuous abundance increase of mean annual values. At the shorter time scale, noticeable changes occurred in the phenology of the group. For instance, we found an earlier timing of the seasonal peak after 2007, as well as a conspicuous increase in the species richness (Fig. 6b). These changes depicted modifications in the annual pattern prior and after 2007. During the period 2003–2007, the annual pattern showed a unimodal peak, in summer, as the main feature in the seasonal abundance changes. Afterwards, during the period 2008–2013, the mean seasonal abundance changes displayed a bimodal pattern, with major abundance in spring and summer. The former peak corresponding to the earlier phenology likely driven by enhanced spring temperatures (Fig. 6c). Indeed, the timing of the seasonal peak of gelatinous carnivores shifted earlier during high winter spring temperatures, while lower temperatures during the same period delayed the seasonal peak. The shift in the seasonal timing was ca. 122 days; that is, under high temperatures gelatinous carnivores peaked as earlier as March, while under low temperatures the peak occurred in July (Fig. 6d). Furthermore, during the years 2008–2013, we assisted an increase in the abundance of the most occurring species and further observed the insurgence of new species (Table 1).

4. Discussion

4.1. Climate variability and gelatinous carnivore zooplankton

Presently, evidence has been shown on the relationship between the abundance and distribution of gelatinous carnivore zooplankton and climate variability (Lynam et al., 2005; Molinero et al., 2008). The results presented here, however, pointed out that such a relationship displays a discontinuous interaction due to the non-stationary character of climate forcing (Fernández De

Puelles and Molinero, 2013; Hidalgo et al., 2011; Molinero et al., 2013). The relation increases after 2007, along with higher variation of the upwelling activity and local hydrological conditions, which promoted the increasing trend in the abundance of gelatinous carnivores and species richness found over the period investigated. The observed changes of the NAO enhanced the variance in regional wind and precipitation, and the increase of the upwelling activity. A number of recent studies have pointed out the influence of upwelling events in the distribution pattern of gelatinous zooplankton (Miglietta et al., 2008; Pavez et al., 2010; Sanvicente-Añorve et al., 2009). In addition, temperature has been also identified as one of the most important factors influencing temporal and spatial distribution patterns of gelatinous carnivore zooplankton (Blackett et al., 2014; Lucas et al., 2014; Pavez et al., 2010; Sanvicente-Añorve et al., 2009). Indeed, warm temperatures promote an increase of asexual reproduction in hydrozoans and, consecutively, an upsurge in the abundance of Hydromedusae species (Purcell, 2005), which may explain the earlier appearance of hydromedusae in the Mondego estuary during the second period, 2008–2013.

An additional explanation as possible driver of the observed changes in these organisms is the variation in freshwater flow. Recent studies pointed out the close connection between river discharge (river plume advection) and the increased presence of marine species in the Mondego estuary (e. g. Baptista et al., 2010; Marques et al., 2014; Primo et al., 2015, 2011). In concurrence with the observed changes, the same authors pointed out marked drought events in the Mondego estuary over the period 2003–2013. The increased prevalence of marine conditions in the estuary promote the entrance of marine species, including gelatinous carnivore zooplankton, which can alter the structure and dynamics of the estuarine community.

Current understanding of upwelling events influence on biological communities structure points out the enhancement of

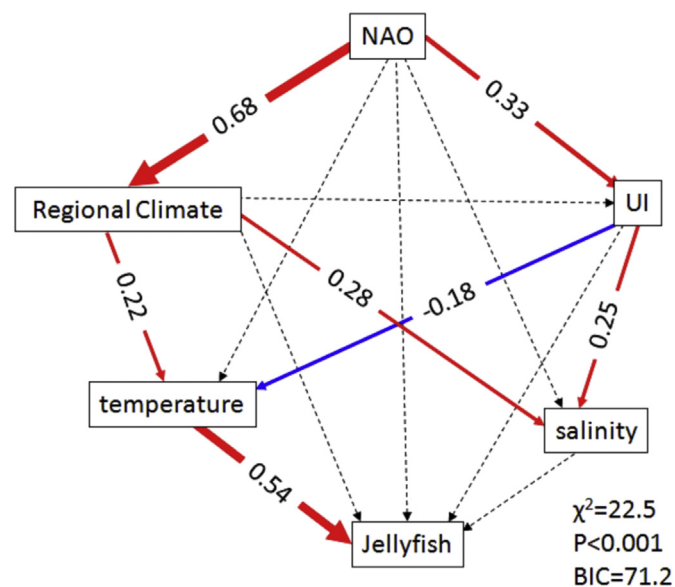
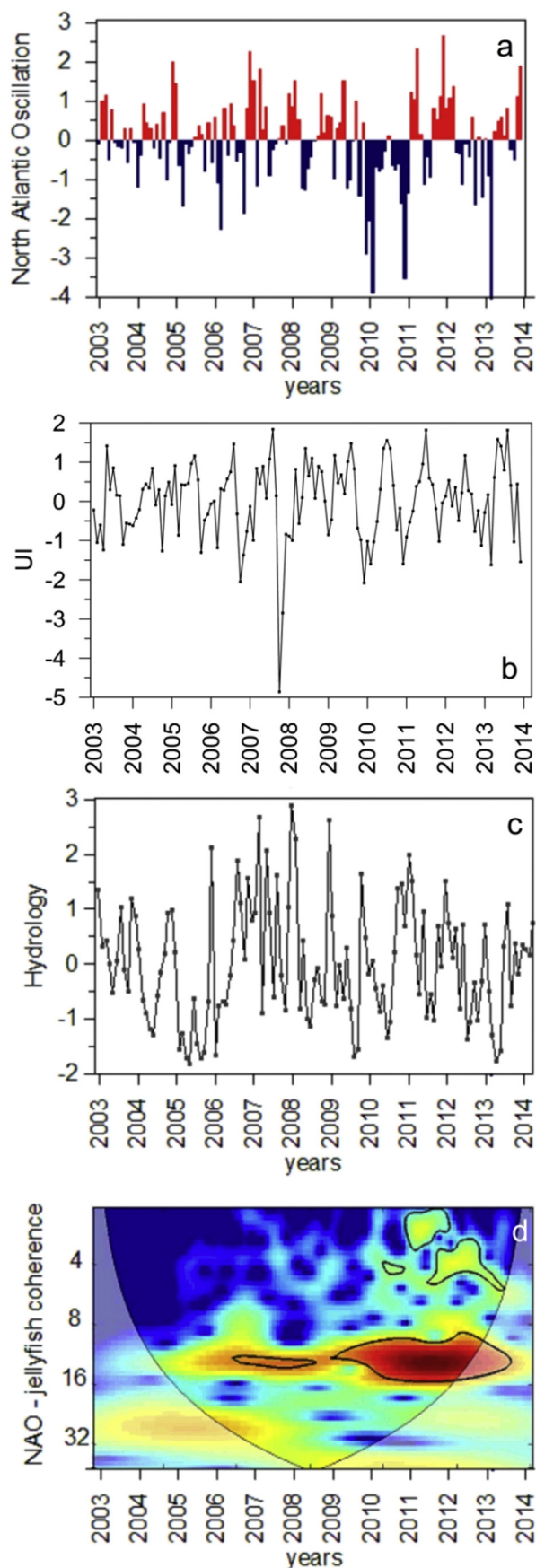


Fig. 5. Path diagram showing direct and indirect effects of climate-related forcing on the temporal variations of gelatinous carnivores' organisms. Red paths are statistically significant ($p < 0.001$), whereas dashed lines are not. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

primary production, as nutrients inputs from deep waters increase. Therefore, we also hypothesized that the mechanism linking NAO and gelatinous carnivore plankton in the Mondego estuary, includes changes in the primary production and reproduction of prey ultimately leading to local gelatinous zooplankton blooms (Drinkwater et al., 2010; Lynam et al., 2005).

4.2. Gelatinous carnivore zooplankton community in Mondego estuary

The calyccophoran siphonophore *Muggiaea atlantica*, a typical boreal Atlantic species, constitute the bulk of the gelatinous carnivore community in the Mondego estuary, accounting for the annual maxima of the population. This species is widespread in inshore temperate waters, while a spring-summer peak appears as a common pattern in several inshore temperate waters (Blackett et al., 2015). Siphonophores, particularly *M. atlantica*, are known as voracious planktivorous predators, and their growth rate tend to increase with increasing prey density, e.g. copepods (Purcell, 1982), the major constituent of zooplankton community. In this study, the temporal pattern of gelatinous carnivore zooplankton was consistent with the copepods and marine cladocera abundance as described by Marques et al. (2014). This jellyfish-copepod link was previously reported by Primo (2012), which revealed significant relationship between summer gelatinous carnivore zooplankton community in Mondego estuary and the copepod *Acartia clausi*, the major constituent of the mesozooplankton community in Mondego ecosystem.

It is worth noting that the structure led by the species contribution to the total abundance is similar in the two identified periods, with *M. atlantica* as the dominant species throughout the

Fig. 4. a: North Atlantic Oscillation. b: Upwelling Index in Figueira da Foz; c: Hydrological variability in the Mondego Estuary; d: Wavelet coherence between the North Atlantic Oscillation and the gelatinous carnivores monthly changes.

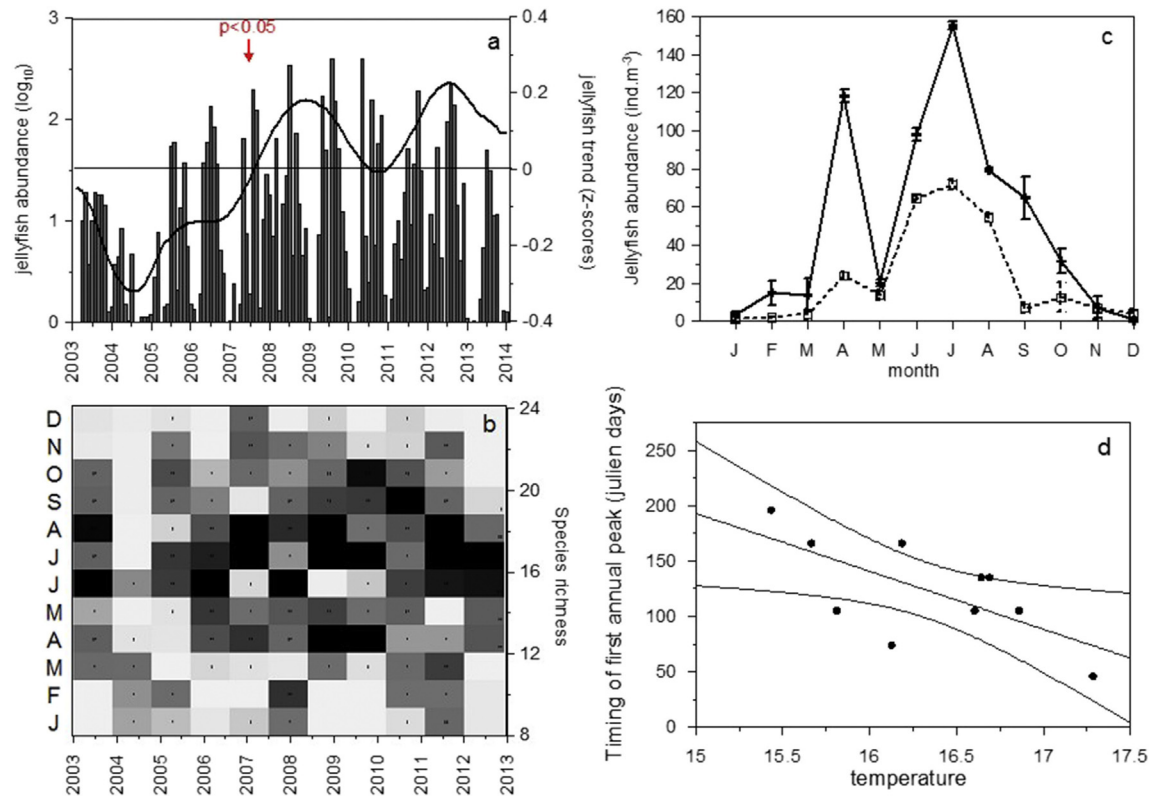


Fig. 6. a: Interannual and b: seasonal changes of gelatinous carnivores abundance in the Mondego estuary; c: changes noticed in the mean annual cycle during the years 2003–2007 (dashed line) and 2008–2013 (continuous line); d: relation between the timing of seasonal peak of gelatinous carnivores expresses in julyen days versus spring temperature.

study. The progressive expansion of the distribution of this species into some regions (Batistić et al., 2013; Blackett et al., 2014) suggests that this species is able to exploit favorable environmental conditions more efficiently than other siphonophores.

As observed here, the relationship of gelatinous carnivore abundance with temperature evolves according to the strength of the hydroclimate forcing, with higher abundances concurrent with higher temperatures. It is worth noticing that the gelatinous carnivore zooplankton community changed, not only in terms of abundance or structure (i.e. diversity), but they also showed conspicuous phenological changes with the main seasonal peak appearing earlier in high winter-spring temperatures and shifting the annual pattern from unimodal (summer peak) to bimodal (spring and summer peaks). These phenological changes are in agreement with former studies showing that at small spatial scales, such as small estuarine systems, spring temperature is a main driver of gelatinous carnivore zooplankton blooms (Mills, 2001; Purcell et al., 2012; Robinson and Graham, 2014).

The results obtained in this study showed a close connection between the atmospheric field playing out in the North Atlantic region and the hydrographic patterns around the Mondego estuary. This is the first study in the Iberian Peninsula, Portugal, identifying the effects of mounting winter-spring temperatures on the structure (species richness) and dynamics (phenology) of gelatinous carnivore zooplankton. These results provide baseline information for comparison with other temperate estuarine systems while elucidates major factors shaping plankton communities in the Iberian Peninsula.

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