Marine Environmental Research 120 (2016) 103–110

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

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

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A R T I C L E I N F O

Article history:
Received 5 January 2016
Received in revised form
15 July 2016
Accepted 25 July 2016
Available online 28 July 2016

Keywords:
Gelatinous carnivore zooplankton
North Atlantic climate
NAO
Upwelling
Mondego estuary

A B S T R A C T

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.

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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http://dx.doi.org/10.1016/j.marenvres.2016.07.012

(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 cost 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 ± 22 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 Artic 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