Climate-driven shifts in decapod larvae assemblages in a temperate estuary

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ABSTRACT

The study examines the complex impact of climatic patterns, driven by the North Atlantic Oscillation (NAO), on regional climate, hydrology, and sea surface temperatures. Focused on the period from 2003 to 2012, the research specifically investigates the influence of thermal variability on decapod larval communities. Monthly zooplanktonic sampling conducted at the Mondego Estuary, Portugal, entrance over a decade revealed the prevalence of *Carcinus maenas*, *Diogenes pugilator,* and *Pachigrapsus marmoratus* larvae. These assemblages displayed notable interannual and seasonal fluctuations, often corresponding with changes in sea surface temperatures. Significant system shifts around 2007, instigated by the large-scale NAO, led to subsequent modifications in sea surface temperature and decapod larvae communities' dynamics. Post-2007, there was an upward trajectory in both species' abundance and richness. Phenologically during the former period, the community exhibited two abundance peaks, with the earlier peak occurring sooner, attributed to heightened temperatures instead of the unique peak exhibited before 2007. The research further elucidated the occurrences of Marine Heatwaves (MHW) in the region, delving into their temporal progression influenced by the NAO. Although water temperature emerged as a crucial factor influencing decapod larvae communities annually and seasonally, the study did not observe discernible impacts of MHW events on these communities. These communities represent essential trophic links and are crucial for the survival success of adult decapods. Given the rapid pace of climate change and increasing temperatures, it is imperative to assess whether these environmental shifts, particularly in thermal conditions, affect these meroplanktonic communities.

1. Introduction

Decapod species, spanning diverse habitats from marine to freshwater environments, hold a pivotal role in both benthic and pelagic ecosystems. They serve as vital prey for fish and bird species, forming essential trophic links. Additionally, these species, particularly adult benthic ones, act as significant predators, regulating herbivory and space competition through top-down mechanisms (Boudreau and Worm, 2012). Additionally, certain decapod species hold substantial economic importance in fishing sectors, as highlighted in the review by

Bondad-Reantaso et al. (2012). Decapod crustaceans undergo an early planktonic life stage, a vital phase for population persistence, dispersal, colonization of new habitats, and recruitment (Wale et al., 2021). During this initial part of their lifecycle, larvae are particularly vulnerable to predation (Harrington and Hamlin, 2019), and environmental changes (Wacker and Harzsch, 2021). Understanding the bio-ecology of these early larval stages is essential for improved assessment and prediction of fishing stocks, as well as for gaining insights into the health of the ecosystems (Queiroga et al., 2007).

Estuarine ecosystems exhibit several key characteristics that make

them ideal nursery grounds for numerous fish and invertebrate species, including decapods. These systems are highly productive, offering abundant food resources, calm and shallow waters, and a variety of shelters from predators (Guerreiro et al., 2021). However, estuaries are also dynamic environments, influenced by oceanic tides and river runoff, leading to variations in environmental parameters such as salinity and water temperature. In addition to these short-term environmental dynamics, estuaries are vulnerable to the impacts of climate change. Global observations since the 1970s have revealed a widespread warming trend in oceans, leading to acidification, increased stratification, and reduced nutrient levels (Kennedy et al., 2019; Moltó et al., 2021; Peng et al., 2022; Montie et al., 2023). These changes affect ecosystem interactions as well as primary and secondary production (Fu et al., 2016; Bindoff et al., 2019; Kim and Kim, 2021).

This study focuses on the Mondego Estuary, a highly productive system located along the western Iberian coast, Portugal. Extensive research has been conducted on this system, encompassing a broad spectrum of trophic levels. Studies have delved into the adult and juvenile fish communities (e.g.: Dolbeth et al., 2007; Martinho et al., 2007; Baptista et al., 2010; Nyitrai et al., 2012; Lourenço et al., 2023; Vaz et al., 2023), ichthyoplankton (e.g.: Marques et al., 2006; Primo et al., 2012a, 2012b; Monteiro et al., 2020), general planktonic assemblages (Vieira et al., 2003; Azeiteiro et al., 2005; Marques et al., 2007, 2018; Primo et al., 2023), and even more specific groups such as gelatinous plankton (D'Ambrosio et al., 2016; Dolgner et al., 2021). However, meroplanktonic decapod assemblages have only been briefly addressed by Gonçalves et al. (2003), who investigated larval emission patterns of a restricted set of species, *Carcinus maenas* (Linnaeus, 1758), *Crangon crangon* (Linnaeus, 1758), *Palaemon elegans* (Rathke, 1836), *Palaemon serratus* (Pennant, 1777), and *Palaemon adspersus* (Rathke, 1836), over different lunar and tidal conditions. Recently, Monteiro et al. (2021) conducted a study examining the impact of climate variability on the adult life stages of *C. maenas*. Their research delved into local factors such as water temperature, salinity, river flow, and large-scale climatic patterns, including the North Atlantic Oscillation (NAO) index and the East Atlantic mode (EA), to understand their influence on these communities. Large-scale climatic patterns have far-reaching effects on local and regional climates, extending their impact on communities' composition. Previous studies by D'Ambrosio et al. (2016) and Marques et al. (2018) demonstrated that shifts in the NAO index had cascading effects on the Mondego ecosystem. Around 2007 and subsequent years, there was an observed increase in the system's marinization state, leading to significant effects on species abundance and composition. These changes notably affected zooplanktonic communities, specifically appendicularians, chaetognaths, copepods, medusae, cladocerans, and phytoplankton (D'Ambrosio et al., 2016; Marques et al., 2018).

This study aimed to investigate the potential cascading impacts of large and regional-scale atmospheric and hydrological climate patterns on sea surface temperatures (SST), subsequently influencing the communities of decapod larvae in the outer Mondego Estuary from 2003 to 2012. The research explored the effects of SST on the abundance of decapod larvae assemblages, examining both long and short-term temporal scales, and considering its influence on phenology. Furthermore, the taxonomic characterization of the decapod larvae community composition was undertaken. The study additionally examined the occurrences of marine heatwaves (MHW) in the region, investigating their temporal progression, their association with the NAO index and potential influence on the decapod larvae communities. This level of investigation and characterization represents a novel approach for the decapod larvae communities at this specific study site.

2. Material and methods

2.1. Study site

The Mondego Estuary (40°08′N, 8°50′W) is a highly productive

mesotidal system with a characteristic Mediterranean temperate climate, located on the western Iberian coast, Portugal (Fig. 1). With an area of 8.6 km^2, the hydrological basin of the Mondego provides an average freshwater flow rate of 79 m^{3}s^{-1} (Dolbeth et al., 2010). The estuary is composed of two arms (north and south) with specific hydrological characteristics, separated by the Murraceira Island, converging again near the mouth, where the influence of both the river flow and neritic waters is strong, and the depth is around 6–13 m. For a fully detailed description of this estuarine system consult Marques et al. (2006). A considerable amount of knowledge on the conditions at Mondego Estuary is available in numerous publications covering the planktonic community (Marques et al., 2006, 2007, 2018; Monteiro et al., 2020; Primo et al., 2011, 2012a, 2018, 2023; Dolgner et al., 2021).

2.2. Biological data

Zooplankton samples were collected monthly between 2003 and 2012 during high tide, at the entrance of the estuary (Fig. 1), using surface horizontal tows or hauls with a ring plankton net with 335 μm mesh size, equipped with a Hydro-Bios flowmeter (volume filtered averaged 45 m^3). In the laboratory, plankton samples were transferred from 4% buffered formaldehyde to 80% ethanol and decapod larvae were separated from the rest of the sample, counted, and identified to the lowest taxonomic level through the stereoscopic microscope. The species abundance was expressed as individuals per 100 m^3 (ind.100 m^{-3}). The species taxonomic identification was performed using morphological descriptions and species key characteristics, following identification guides (e.g.,: Lebour, 1930; Pike, 1952; Pike and Williamson, 1959, 1964; Williamson and Rochanaburanonf, 1979; Barnich, 1996; dos Santos, 1999; Sakai, 1999; González-Gordillo et al., 2000; Yang et al., 2001; dos Santos and Paula, 2003; dos Santos and González-Gordillo, 2004; Pessani et al., 2004; Ortega et al., 2005; Bartilotti et al., 2008; Pohle and Santana, 2014; Buckland et al., 2017; Carreton et al., 2020; González-Gordillo and Cuesta, 2020).

The yearly community composition of decapod meroplankton in the study site was assessed using the Shannon-Wiener index (*H′*) (Shannon, 1948). The calculation for the index is as follows:

$$H^{'} = - \sum_{i=1}^{S} P_i \ln\left(P_i\right)$$

Here, *S* represents the total number of decapod species, and P_i denotes the proportion of individuals' abundance for a specific decapod species relative to the total abundance of individuals in the community. This methodology aimed to evaluate the ongoing status of decapod meroplankton within the outer Mondego Estuary.

2.3. Environmental data

Monthly environmental data including SST, air temperature and sea level pressure were extracted for a point (40°13′N, 8°90′W) near the entrance of the Mondego Estuary and acquired from the online database (http://dss.ucar.edu/pub/coads) of International Comprehensive Ocean Atmosphere Data Set (ICOADS). The upwelling index (UI) was extracted from online (http://www.indicedeafloramiento.ieo.es/interactivo.html) dataset of the Fleet Numerical Meteorology and Oceanography Center (FNMOC) for Figueira da Foz. Precipitation data was downloaded from National Water Resources Information System (SNIRH) and Portuguese Institute for Sea and Atmosphere (IPMA) (http://snirh.pt/, station 13F/01G and https://www.ipma.pt/, Cernache). To identify MHW, daily SST data was used. Finally, the North Altantic Oscillation index (NAO) index, downloaded from NOAA – National Centers for Environmental Information (https://www.ncei.noaa.gov/access/monitoring/nao/), was used as a large-scale environmental forcing.
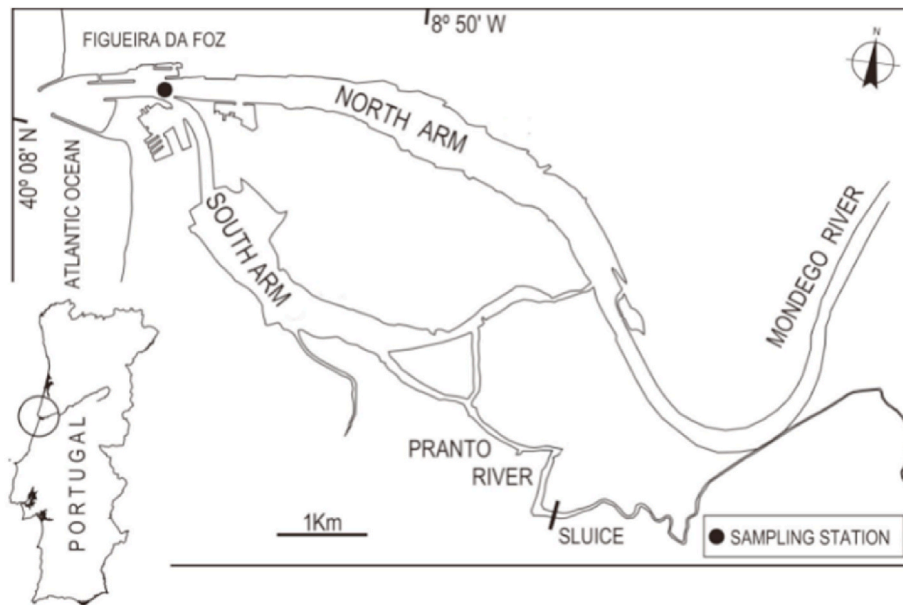
Fig. 1. Map of the study site, Mondego Estuary. The dot represents the sampling station at the entrance of the estuary.

2.4. Identification of marine heatwave events

To identify the MHW events, occurring in the entrance of the Mondego Estuary, the methodology proposed by Hobday et al. (2016) was implemented, using a set of daily SST. The gridded data was interpolated for a regular grid with 0.05° × 0.05° of spatial resolution. A specific point (40°13′N, 8°90′W) were chosen and the 30-year data set was extracted from the global grid. The methodology implemented by Hobday et al. (2016) consists of calculating a specific daily threshold defined as the SST's 90th percentile, for a 30-year period. The 90th percentile is calculated for the control point in the vicinity of the Mondego Estuary mouth within an 11-day window centered on the calendar day of interest for every year, and then the results are smoothed using a 31-day moving average for each day. An MHW event occurs when SST exceeds the 90th percentile value, which is considered the threshold, for at least 5 consecutive days with a maximum gap of less than 2 days to ensure that short-duration heat spikes are not considered. Once identified, MHW events are characterized regarding duration, mean intensity and cumulative frequency per year. Duration is defined as the period over which the temperature is larger than the seasonally varying threshold value, which represents the start and end dates. Mean intensity is the mean temperature anomaly relative to the threshold during the event. Cumulative frequency per year corresponds to the cumulative sum of MHW events during that year.

Additionally, the following generalized linear model (GLM) was implemented to verify if MHWs' mean intensity, cumulative frequency, and duration varied significantly over time:

$$Y^{'} = \alpha + t_i + \varepsilon_i$$

Where $Y^{'}$ represents the cumulative frequency, mean intensity, and duration of MHW events, α represents the intercept, t represents the explanatory variable time, and the error ε follows a Poisson distribution.

Furthermore, Spearman correlations were employed to assess the significance of relationships between the cumulative frequency, mean duration, and mean intensity of MHW in each year and the prevailing state of the NAO during that particular year.

2.5. Statistical data analyses

All data analysis was performed in the R programming environment

version 4.1.3. The significance level for all statistical tests used was P = 0.05.

First, data exploration was conducted following the protocol from Zuur et al. (2010). Due to the high variability of the biological data, and high number of zeros, decapod abundance data were log-transformed. Data were seasonally detrended, standardized to zero mean and unit variance, to remove the trend often associated with time series data.

Second, a principal component analysis was conducted, and the first principal component (PC1 23%) was extracted and used as a proxy for the whole community abundance. Likewise, the outcomes reflected variable regional climate patterns (PC1 41.6%) derived from regional climatic factors such as air temperature, sea level pressure, and precipitation.

Third, to identify the climatic relations, at different scales, (large, regional, and local) scale, as well as their influence on the decapod larvae community, a structural equation model (SEM). The model was performed for both time periods (2003–2007 and 2008–2012).

Fourth, the effects of SST on decapod larvae (PC1) abundance variability were quantified on a monthly scale by means of wavelet analysis (continuous wavelet transform, CWT, Morlet function) and moving variance (with Granger causality test).

Fifth, to evaluate if changes in the whole decapod larvae community (PC1) were significant along the time series, a cumulative sum of standardized ordinary least square residuals analysis (OLS-based CUSUM test) was used. This technique allows for computing the probability of significant modifications in a time-series and is useful in detecting shifts in time series records (Fernández de Puelles et al., 2014). Additionally, to visualize changes over time for each species abundance, the intrinsic trend was calculated using the Ensemble Empirical Mode Decomposition (EEMD) technique. This method decomposes a time series into amplitude-frequency modulated oscillatory components Cj ($j = 1,2, …, n$) and a residual trend Rn. The residual trend, Rn, is a curve that is either monotonic or contains only one extremum, beyond which no additional oscillatory components can be extracted.

$$x(t) = \sum_{j=0}^{n} C_j(t) + R_n(t)$$

The extracted Cj components represent various time-series modes across a range of timescales, from high to low frequencies, encompassing intra-annual variations, modulated annual cycles, inter-annual patterns,

decadal trends, and inter-decadal changes. Once these identifiable oscillatory components have been removed, the residual intrinsic trend ($Rn(t)$) does not conform to a predefined function and exhibits local temporal characteristics.

Sixth, after identifying the main periods characterizing the interannual variability of the decapod larvae community, we examined the seasonal changes by computing the mean annual cycle from 2003 to 2007 and from 2008 to 2012. These two periods were chosen taken in consideration important climatic changes which influenced the study site ecosystem, with cascading influence on planktonic communities, as supported by the previous work of D'Ambrosio et al. (2016) and Marques et al. (2018). Statistical differences between mean annual cycles, and species richness (Shannon-Wiener index) in each cycle, during each period were tested using a Kruskal-Wallis test. Furthermore, phenological changes were assessed based on seasonal peaks for the period of 2003–2007 and 2008–2012. Days of the year were centered in the median of the month in which the first annual peak was observed, (i.e., when log abundance suppressed 0.2 ind.100 m^{-3}). The interannual variations of the timing of seasonal peaks were linearly regressed against SST of the previous year's spring to quantify their relationship.

Additional details regarding the data analysis, specifically, SEM, CWT and moving variance are presented on the supplementary appendix.

3. Results

3.1. Decapod larvae community composition, abundance, and interannual variation

The composition of decapod larvae assemblages in the outer Mondego Estuary is comprised of a total of 17 identified taxa. Over the 10-year study period, there was a slight variability in species richness, with an apparent, but non-significant (Kruskall-Wallis *p-value* >0.05), increase in richness (Shannon-Wiener index) in more recent years, particularly since 2007 (Fig. 2). Three main species, namely *C. maenas, D. pugilator* and *P. marmoratus*, dominated the assemblages, while the other 14 taxa appeared in lower numbers (Table 1).

Larvae of the European green crab *C. maenas* was the most abundant species in the assemblages, constituting the majority and being consistently present in the communities, except for a temporary decline in 2006. However, its presence increased in subsequent years (Fig. 3). The anomuran hermit crab *D. pugilator*, the second most abundant species, made its appearance in the community from 2007 onward and remained present in the following years, peaking in late 2007 and exhibiting a noticeable increase in abundance (Fig. 3). The brachyuran marbled crab *P. marmoratus*, was the third most abundant species. It remained

Table 1

Mean larval density and standard deviation (s.d.) (ind.100 m^{-3}) of decapod taxa during the two time periods 2003–2007 and 2008–2012.

Family	Taxa	Mean density (mean ± s.d.)	
		2003–2007	2008–2012
Alpheidae	*Athanas nitescens*	0.1 ± 0.95	1.4 ± 10.61
Portunidae	*Carcinus maenas*	44.8 ± 90.69	110.1 ± 3.96
Crangonidae	*Crangon crangon*	9.1 ± 24.74	0.9 ± 3.96
Decapoda	Decapoda n.id.	1.9 ± 9.63	2.0 ± 6.13
Diogenidae	*Diogenes pugilator*	21.3 ± 165.75	43.4 ± 131.78
Grapsidae	*Pachigrapsus marmoratus*	14.2 ± 32.84	22.0 ± 60.11
Palaemonidae	*Palaemon elegans*	0.1 ± 0.49	1.9 ± 7.05
Palaemonidae	*Palaemon longirostris*	0.04 ± 0.35	0.8 ± 6.32
Palaemonidae	*Palaemon serratus*	0.0 ± 0.00	0.2 ± 1.33
Palaemonidae	*Palaemon* sp.	0.07 ± 0.48	2.9 ± 13.19
Palaemonidae	*Palaemon varians*	0.0 ± 0.00	2.0 ± 15.57
Pandalidae	*Pandalina brevirostris*	0.5 ± 3.02	0.8 ± 4.78
Crangonidae	*Philocheras* sp.	0.1 ± 0.99	0.0 ± 0.00
Porcellanidae	*Pisidia longicornis*	0.5 ± 2.68	3.6 ± 12.02
Porcellanidae	*Porcellana platycheles*	0.02 ± 0.13	0.45 ± 2.59
Processidae	*Processa* sp.	2.7 ± 9.03	3.4 ± 12.51
Panopeidae	*Rhitropanopeus harrisii*	10.0 ± 30.69	2.68 ± 15.83
Upogebiidae	*Upogebia* spp.	0.6 ± 3.10	2.0 ± 8.11

consistently present throughout the entire study period (Fig. 3), presenting slightly higher abundances, on average, in the period after 2007 (Table 1). The Harris mud crab *R. harrisii* (Gould, 1841) and the caridean shrimp *C. crangon*, experienced a decline on numbers on the period from 2008 to 2012, when compared to the previous period (Table 1). Notably, both species were absent from the community in specific years (2003, 2008, and 2011 for Harris mud crab; 2008, 2010, and 2011 for caridean shrimp) (Fig. 3). Conversely, Palaemonidae species and Porcellanidae, especially *Pisidia longicornis* (Linnaeus, 1767), exhibited an increase in abundance in the years after 2007. The remaining taxa, considered occasional species, became more numerous post-2007 as well (Fig. 3 and Table 1).

3.2. Environmental variability & climatic dynamics

The NAO's large-scale mode exhibits significant monthly and interannual variability (Fig. 4a). After 2008, it enters a positive phase, undergoes a notable negative period in the winters of 2010 and 2011, and briefly returns to a positive phase in the winter and spring of 2012. Concurrently, the Mondego Estuary's regional climate displays considerable variability across both years and months (Fig. 4b). Regional climate patterns (PC1 41.6%) revealed the primary contributor to PC1 was precipitation, accounting for 49.5% of the variance, followed by sea level pressure at 41.1%, and air temperature at 9.4%. A structural
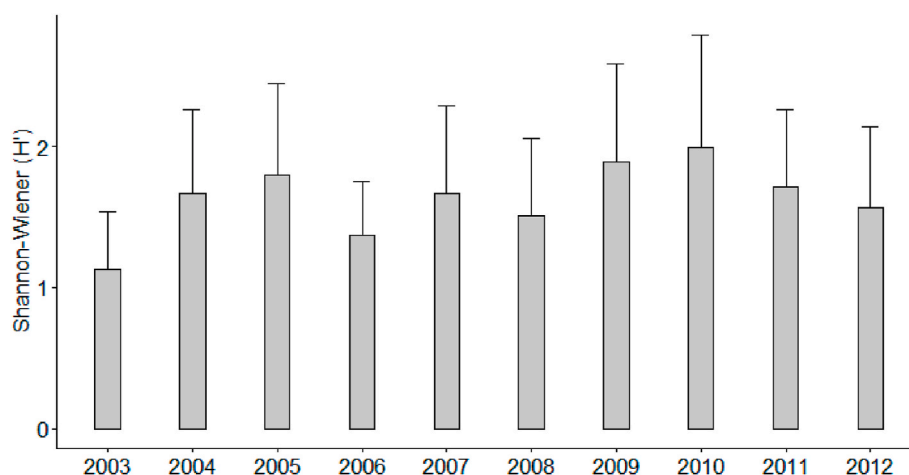

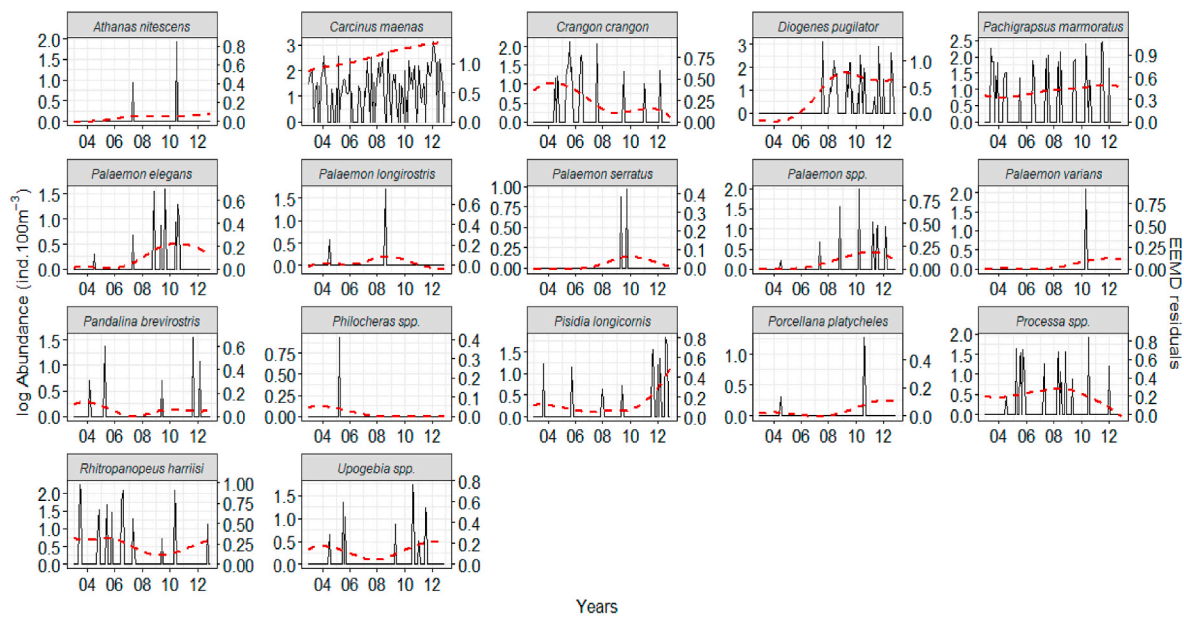**Fig. 2.** Species richness (Shannon-Weiner diversity index H′) along the years.

Fig. 3. Log mean abundance (ind.100 m^{-3}) variation of species along the time study (04–2004, 06–2006, 08–2008, 10–2010, 12–2012, and EEMD residuals in the right y axis, the dashed red line represents the respective trend over time.
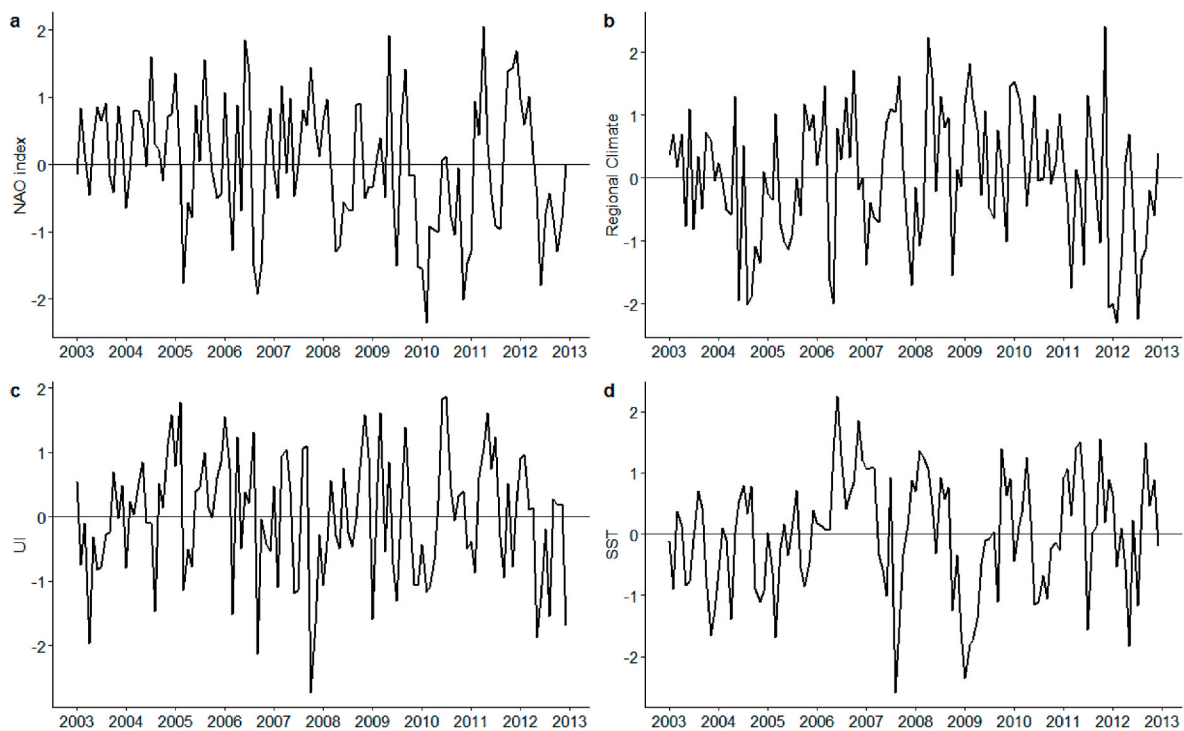

Fig. 4. Yearly variation of a) North Atlantic Oscillation (NAO); b) Regional climate, c) Upwelling Index (UI); d) Sea Surface Temperatures (SST) (z-scores).

equation model reveals a negative correlation (path coefficient = −0.332) between the NAO and the regional climate during the 2008–2012 period (Fig. 5). Negative NAO states tend to coincide with positive peaks in the regional climate (Fig. 4).

The UI measured offshore of the Mondego Estuary exhibits annual variations over the time series (Fig. 4c). Seasonal variability in the up-welling signal indicates a mean peak in summer, with interannual changes escalating after 2007 and reaching an absolute maximum in late 2007 (Fig. 4c). NAO dynamics significantly influence upwelling recirculation in the region throughout the entire decade, with increased force

during the 2008–2012 period (path coefficient = 0.332). However, no effect of the regional climate on upwelling dynamics is detected (Fig. 5).

The SST also undergoes changes across the years and months. The SST time series reflects a negative maximum peak during mid-2007 and a subsequent occurrence in 2009 (Fig. 4d). Changes in the NAO index indirectly influences SST through the regional climate for the period of 2008–2012 (path coefficient = - 0.274) (Fig. 5). However, no direct influence of the NAO on SST is observed during both time periods (Fig. 5). Negative peaks in the regional climate are often associated with positive SST peaks during the second half of the decade (Fig. 4). This
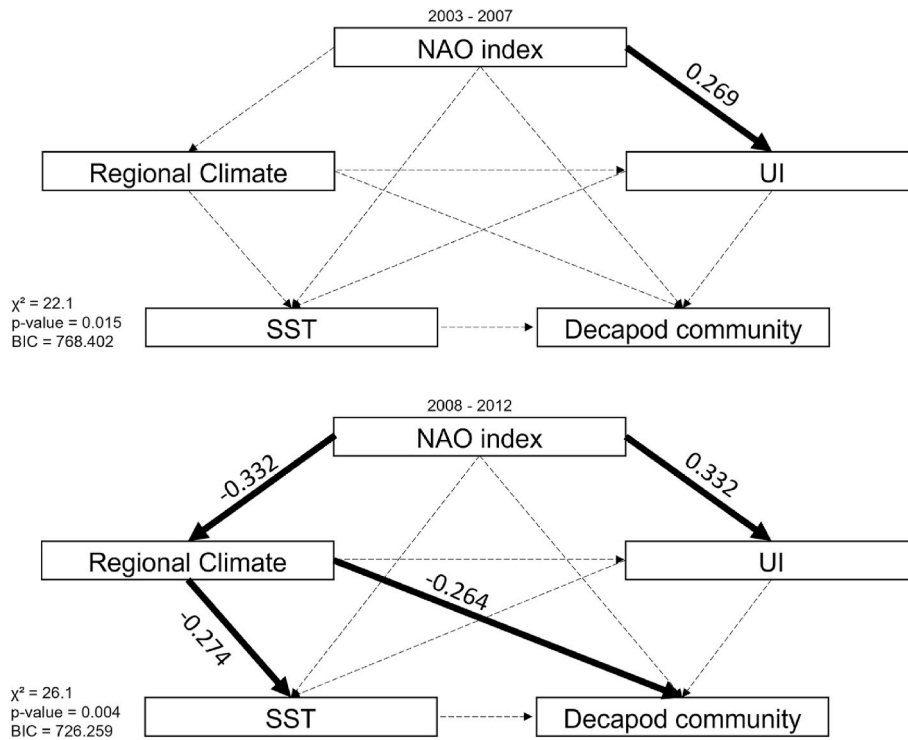
Fig. 5. Path diagram showing direct and indirect effects of climate-related forcing at large, regional, and local scales with the decapod larvae community at the Mondego Estuary, in both time periods (2003–2007 and 2008–2012). Bold arrows represent statistically significant correlation paths (p < 0.05), while dashed lines represent non-significant paths.

suggests that the NAO's influence on SST may be mediated by the regional climate.

A more pronounced climatic forcing is evident during the period of 2008–2012 compared to 2003–2007, with a substantial impact on the decapod community (PC1 23%) directly influenced by the regional climate (path coefficient = −0.264) (Fig. 5). The taxa leading this PC1 were *C. maenas* (56.2% contribution to PC1), *Diogenes pugilator* (Roux, 1829) (17.1%), *Pachygrapsus marmoratus* (Fabricius, 1787) (16.0%), *Rhitropanopeus harriisi* (Gould, 1841) (3.1%), *C. crangon* (2.9%), and *Processa* spp. (2.7%), by respective contribution to the PC1. The remaining taxa individually contributed less than 2.5% to the PC1.

3.3. Interactions between sea surface temperatures and decapod larvae variability

The potential connection between SST and the variability of decapod larvae was assessed using wavelet analysis (Fig. 6a) and moving variance (Fig. 6b). Results revealed a discontinuous interaction between water temperature and decapod larvae, indicating that the relationship was elusive before 2007. However, a significant increase emerged during late 2007 and early 2008, continuing through 2009, 2010 and 2011, as evidenced by wavelet coherence (Fig. 6a). Moving variance of both decapod larvae (PC) and SST followed a similar pattern, exhibiting a corresponding peak during 2007. The Granger causality test between the two variables was significant, (p < 0.001), suggesting that SST values can be used to predict future values of decapod larvae abundance (Fig. 6b).

Considering the above climate-related environmental changes, we portrayed the interannual and seasonal patterns of decapod larvae variability (Fig. 7a and b). At the end of 2006 and early 2007, an abrupt decrease in organisms in the community occurred (CUSUM test p < 0.05), with no larvae present in the assemblages. Furthermore, there was an observed increase in subsequent years, corresponding to a noticeable rise in mean annual values. The community displayed phenological changes, with a unimodal peak in summer from 2003 to 2007. However,

from 2008 to 2012, a bimodal pattern emerged, characterized by higher abundance in spring and summer (Fig. 7b). Notably, the timing of the seasonal peak of decapod larvae shifted in response to the previous year's warmer spring temperatures. With increasing temperatures, the peak occurred 151 days earlier, still during wintertime, whereas under lower temperatures, the first peak occurred only in June (Fig. 7c). These earlier peaks were particularly prominent during 2008–2012.

3.4. Marine heatwave events on the outer Mondego Estuary

From 1990 to 2012, a total of 43 MHW events have been detected for the region, with 20 of those occurring from 2003 to 2012 (Table 1S – Supplementary appendix). The mean duration of the events over this period (1990–2012) was 13 days, with a mean intensity of 1.9 °C above the 90th percentile threshold (Fig. 8).

Between 1990 and 1997, there were a total of 5 MHW events, making these years the years with most MHWs. The longest MHW occurred in 2006 and lasted 48 days, while the second longest event occurred in 1997 and lasted 45 days. These prolonged events exhibited relatively high intensity, with mean temperature increases of 2.4 °C and 2.0 °C above the threshold, respectively.

The highest intensity, 2.7 °C above the climatology, was observed in three separate events: one in 2009, another in 2010, and the last in 2011. These events lasted 16, 10, and 8 days respectively, emphasizing the inverse relationship between MHW intensity and duration in these significant occurrences.

Based on the GLM results, it was found that frequency of MHW events, as well as their intensity and duration, did not show significant changes from 1990 to 2012 in the Mondego Estuary (p > 0.05) (Fig. 8).

In the examination of variations in the frequency, mean duration, and mean intensity of MHWs per year based on the predominant NAO state for that year, no significant correlations were observed (p > 0.05).
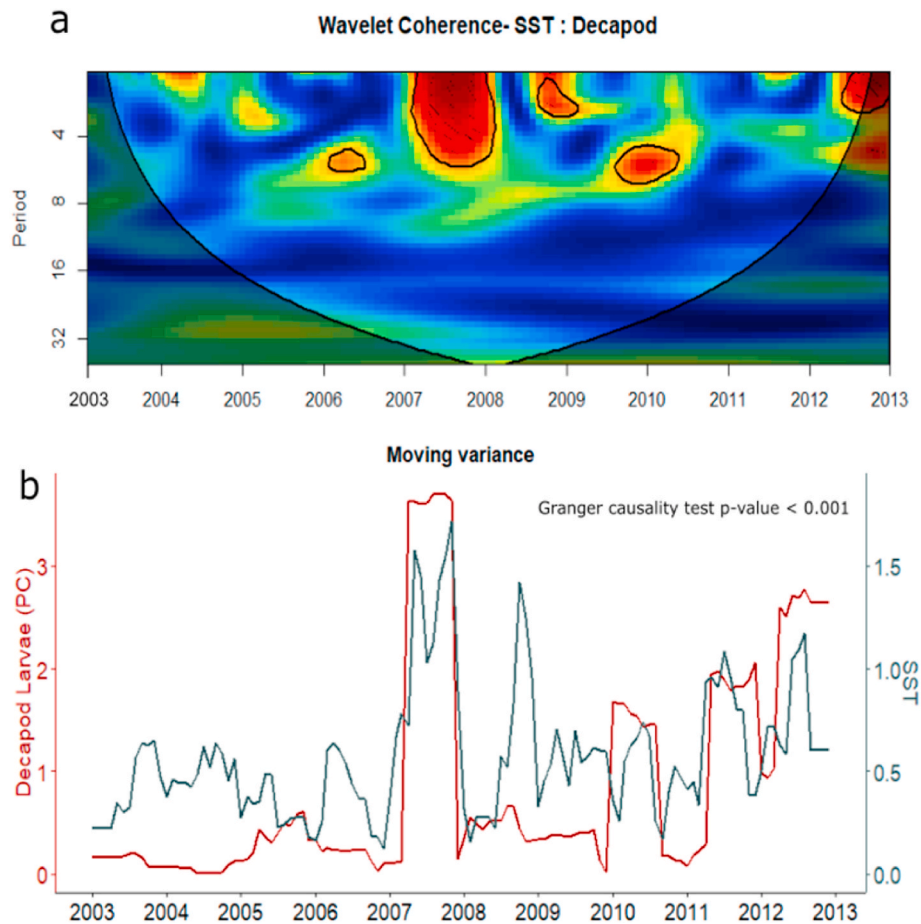
Fig. 6. a) SST: Decapod (PC1) wavelet coherence; b) Decapod larvae (PC) and SST moving variance. Granger causality test p < 0.001.

4. Discussion

The decapod larvae community found on the mouth of the Mondego Estuary from 2003 to 2012 exhibited a taxonomic composition similar to that observed in other Portuguese estuaries and coastal waters (dos Santos, 1999; dos Santos and Paula, 2003; dos Santos and González-Gordillo, 2004; dos Santos et al., 2008; Bartilotti et al., 2014; Pochelon et al., 2017). A previous study by Gonçalves et al. (2003) in the Mondego Estuary identified *Carcinus maenas* and *Crangon crangon* to be some of the most abundant species in the estuary, in line with the current study findings. The European green crab (*C. maenas*) is one of the typical species of coastal Portuguese waters (Pereira et al., 2000; Almeida et al., 2008; Monteiro et al., 2021; Portela et al., 2023) and constitutes a significant portion of the decapod larvae assemblages in the Mondego Estuary. Its thermal and euryhaline tolerance accounts for its great adaptability to estuarine systems (Young and Elliott, 2020), nonetheless being vulnerable to climatic shifts (Quinn, 2018; Monteiro et al., 2021).

The anomuran hermit crab (*D. pugilator*), and the brachyuran marbled crab (*P. marmoratus*), typical southern European species, have been increasing their range northernward due to warmer conditions in their native habitats (Mcgrath and Costello, 2000; Türkay, 2014). In the present study, their numbers increased considerably after 2007. Conversely, *C. crangon* and *R. harrisii* both experienced a decline in numbers post-2007, likely attributed to their different ecological strategies. *C. crangon* larvae are known to migrate between deeper and shallower waters to avoid low temperatures and salinity (Bilgin et al., 2008), and thus may have evaded from being captured in this study. The Harris mud crab, originally native to North America, has been identified as an exotic species in European waters. In 1995, its larvae were first observed in the Mondego Estuary (Gonçalves et al., 1995).

The remaining taxa were considered as occasional rare species, many of which were absent from the community before 2007. These taxa, particularly palaemonid shrimp and porcelanidae crab species, made their first appearance in subsequent years, mirroring a pattern observed in other zooplanktonic groups in the Mondego Estuary. The findings of D'Ambrosio et al. (2016) and Marques et al. (2018) both have revealed an increase in species richness and abundance of gelatinous zooplanktonic species in the estuarine waters of Mondego after 2007, with rare species becoming more abundant in the assemblages.

The above-mentioned alterations were caused by a climatic shift after 2007 with subsequent influence on the upcoming years. D'Ambrosio et al. (2016) and Marques et al. (2018) have identified a cascading link between the large-scale climatic mode NAO and the regional and local climate, with further influence onto the gelatinous zooplanktonic community, similarly observed in the present study for the decapod meroplankton.

The large-scale climatic mode NAO has a positive influence on the upwelling index regime at the Mondego, in line with previous findings for the region (deCastro et al., 2008). The Northwestern Iberian upwelling regime, prevalent from May to October, is characterized by intense upwelling hydrology caused by strong coastal northernly wind conditions during that same period, enhancing the system's productivity by bringing cold, nutrient-rich water to the surface (Santos et al., 2011). Furthermore, the large-scale climatic mode NAO influences regional climate and sea surface temperatures. Positive NAO phases in southern Europe are typically associated with mild wind conditions, reduced precipitation, and lower temperatures (Wallace and Gutzler, 1980). After 2007, the climatic forcing of NAO on the hydrological and environmental conditions increased, promoting higher variation of the upwelling activity, regional climate and SST, which promoted the
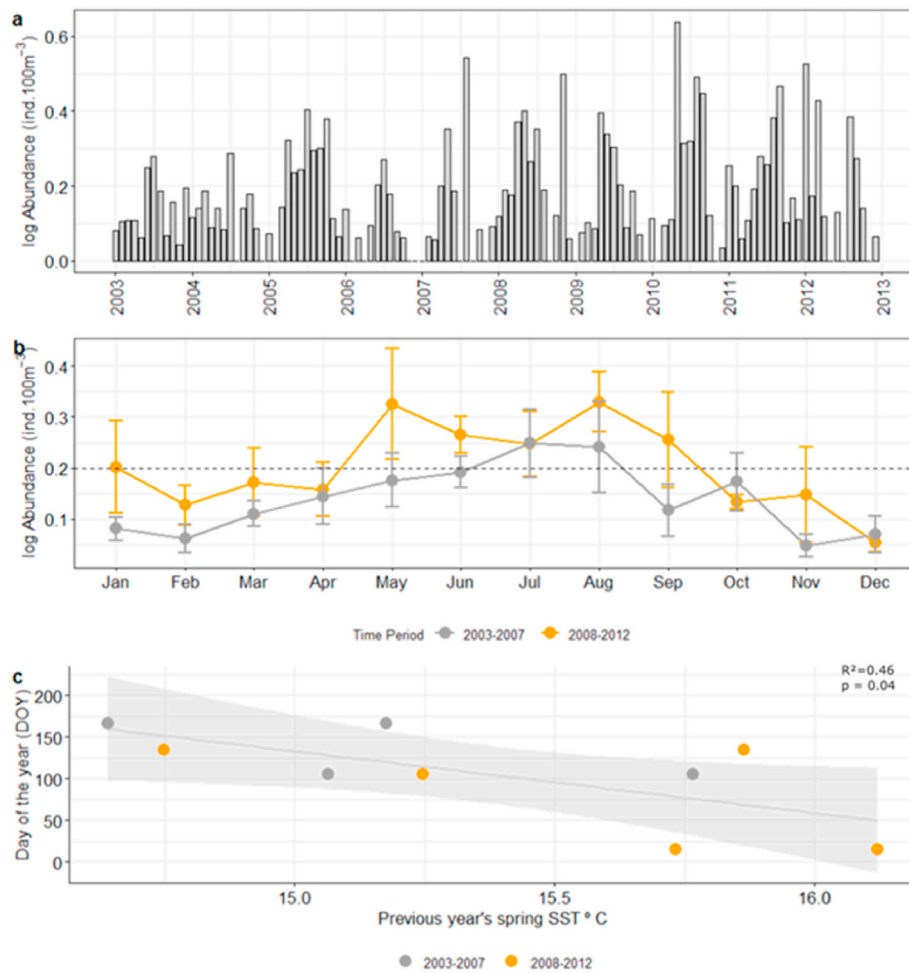
Fig. 7. a) Yearly variation of log abundance (ind.100 m⁻³); b) Seasonal variation of decapod larvae community abundances (ind.100 m⁻³) according to different time periods (2003–2007) and (2008–2013), dashed horizontal line at 0.2 ind.100 m⁻³ represents the threshold above which was considered as peak abundance (Kruskal Wallis Chi-square = 5.7, p = 0.017); c) Previous year's spring SST °C regressed against the first peak date of decapod larvae (in day of the year), for both periods (2003–2007 and 2008–2012).

increasing trend in the abundance of decapod larvae and changed the community taxonomic composition over the period investigated. The heightened upwelling activity may have contributed to an increased productivity in the area, thereby enhancing the availability of food in the environment (D'Ambrosio et al., 2016).

Apart from the studies by (D'Ambrosio et al., 2016) and Marques et al. (2018), which provide clear evidence of the influence of NAO on species richness and abundance of zooplanktonic assemblages, other studies conducted on the Mondego Estuary have also pointed to an indirect effect of NAO on the aquatic assemblages, including in adult, juvenile and larvae life forms of fish species (Bento et al., 2016; Monteiro et al., 2020), and recently on the adult life stages of *C. maenas* (Monteiro et al., 2021). The climatic shift on the Mondego led to an increased marinization of the system, resulting in a higher occurrence of marine zooplanktonic species in the assemblages (Marques et al., 2018). While Marques et al. (2018) previously hypothesized that the increased number of gelatinous marine zooplankton could lead to a decrease in decapod larvae numbers, due to competition and predation, the current findings contradict this hypothesis. Since 2007, there has been an upward trend in the abundance of the decapod larvae community. Although many gelatinous zooplankters are known to prey on decapod larvae (Morgan, 1992) smaller marine zooplankton, such as marine copepods, which are known to serve as food items for planktonic decapod stages, have also increased in the system (Marques et al., 2018), possibly decreasing natural mortality and leading in the observed

increase in decapod larvae numbers (Fusté and Gili, 1991; González-Gordillo and Rodríguez, 2003). Further, several authors have described an association between decapod and jellyfish assemblages, as jellyfish may not only serve as prey for adult decapod species, but also enhance protection and mobility of decapod crustaceans (Wassenberg and Hill, 1989; Gonçalves et al., 2016; Ates, 2017; Carman et al., 2017; Duarte et al., 2022).

Additionally, the effect of SST was notorious for influencing the number of decapod larvae in the community, on a seasonal and interannual basis. A robust correlation is evident between fluctuations in SST and the abundance of decapod larvae assemblages. This connection was notably pronounced in 2007, marked by an absolute maximum peak in SSTs during the summer months. The genesis of this peak is attributed to alterations in sea level pressure, stemming from reduced sea ice formation over the Arctic (Giorgi and Coppola, 2007; Orsolini et al., 2012). This, in turn, impacted the climate across Northern Europe and extended to lower latitudes, encompassing the Iberian Peninsula. The summer of 2007 in these regions stood out for its notable dry and warm conditions (Giorgi and Coppola, 2007; Orsolini et al., 2012). Within this timeframe, diverse taxa in the community, specifically *C. maenas, C. crangon, D. pugilator, R. harrisii, P. marmoratus,* and Processidae species, exhibited increased abundances. The substantial variation in SST observed in 2007 may have allowed species with different life strategies and affinity to different thermal regimes to thrive during the same period. Previous studies have associated warmer winter temperatures with higher
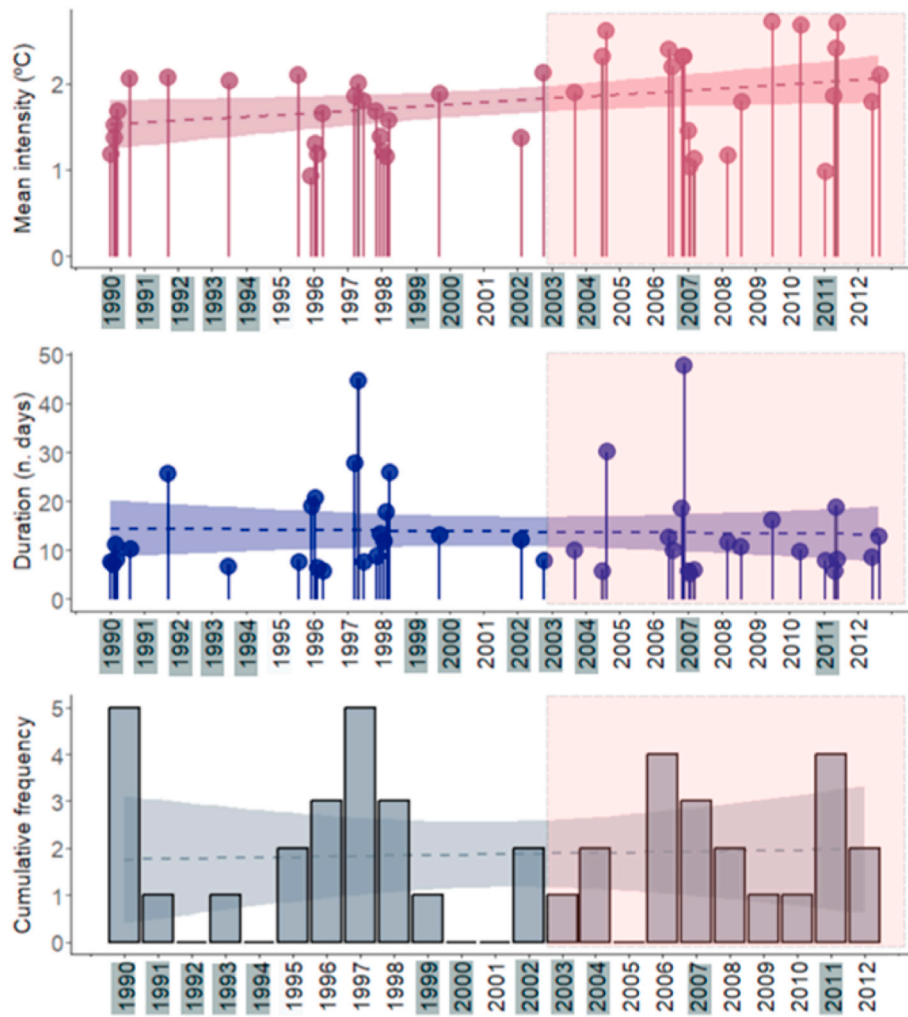
Fig. 8. Marine heatwaves in the outer Mondego Estuary, from 1990 to 2012. a) Mean intensity of each event (°C), b) duration (number of days), and c) cumulative frequency of events per year. The background shaded area indicates the 95% confidence limits of the GLM estimate. Red rectangular areas highlight the years of the present study (2003–2012). On the x axis, years with a grey rectangular areas represent years with a predominantly positive NAO state, while years without it represent years with a predominantly negative NAO state.

numbers of *C. maenas* larvae in the subsequent year assemblages (Berrill, 1982; MacDonald et al., 2018). Many species reproduce when environmental conditions are most favorable for offspring survival. Warmer temperatures often lead to earlier phytoplanktonic blooms, resulting in high productivity and food availability for zoeal survival (Beaugrand et al., 2000; Reid et al., 2001). Consequently, higher temperatures can advance phenological peaks, subsequently increasing larvae abundance (Durant et al., 2019) as observed in the present study for the period of 2008–2012. Temperature not only influences the reproductive population of parents but also affects larvae life stages, influencing their development and survival. Evidence suggests that the thermal capacity of decapod larvae is lower than that of adult life stages (deRivera et al., 2007). Warmer conditions often lead to shorter development times for these early life stages, expediting the recruitment process (Richardson, 2008; Jackson et al., 2014). This accelerated development may result in smaller body sizes at the time of settlement, further jeopardizing survival in juvenile and adult stages, as evidenced by Jackson et al. (2014), Giménez et al. (2021) and Landeira et al. (2017). Despite limited information on the maximum thermal capacity and optimal temperatures for most decapod crustacean species, mesocosm trials have revealed relatively high thermal capacities for adult life stages in two community-associated decapod species. Specifically, *C. maenas* exhibits a thermal range of 29.7–38.3 °C (Cuculescu et al., 1998; Jørgensen et al., 2017), while *C. crangon* shows a thermal range around 25 °C (Reiser

et al., 2014) - well below temperatures observed in the study site. Optimal temperatures for both species are reported to be 18 °C (Dawirs et al., 1989; Costa et al., 2019).

Additionally, extreme warm events like MHWs, which are becoming more intense, frequent, and longer lasting, portray negative consequences for decapod populations, as evidenced in the review by Monteiro et al. (2023). Interestingly, the evolution of these events in the Mondego estuary appears relatively stable and moderate when compared to global trends. Over the years, the intensity, frequency, and duration of MHWs in this ecosystem have not shown significant changes, possibly due to the intense upwelling in the region, which may help to mitigate water warming, as noticed by Suursaar (2020) and Izquierdo et al. (2022) in other upwelling systems around the world. It is clear that temperature influences early decapod planktonic life stages. However, the impact of more extreme events is not perceived for the analyzed time series. This lack of perception can be attributed to the temporal constraints of both time series, planktonic sampling campaigns, conducted once a month, and the duration of marine heatwave events (13 days, on average) makes it difficult to perceive smaller-scale changes. Additionally, these events exhibit mild duration (13 days on average) and intensity (1.8 °C above average) in comparison to other MHW events around the world (e.g.: Olita et al., 2006; Michaud et al., 2021; Holser et al., 2022). Moreover, despite the NAO index being recognized as a predominant climatic mode in the North Atlantic, no correlations were

identified between the NAO state and metrics related to MHWs, in line with the findings of Holbrook et al. (2019) for the Iberian region.

5. Conclusions

The current study delved into the assemblages of decapod larvae in the outer Mondego Estuary spanning over a decade, revealing notable shifts in taxonomic composition and abundance, particularly post-2007. Key species, such as the European green crab (*C. maenas*), exhibited prominent abundance patterns, while others like *D. pugilator* and *P. marmoratus* experienced increased abundances. This study establishes a correlation between climate factors and the dynamics of decapod larvae, underscoring the influence of the large-scale climatic mode NAO and its impact on SST in shaping the community post-2007. The hypothesis linking climate factors to observed alterations is supported by robust correlations, particularly the significant influence of SST on abundance. Future research directions are proposed, emphasizing the intriguing interplay between NAO and decapod larvae communities, as well as the global repercussions of MHWs. It is recommended that zooplanktonic data be collected at a higher frequency scale (days or weeks) to better capture the potential influence of extreme climatic events, which was not apparent at a broader temporal scale (months and years). Ultimately, this research contributes to a comprehensive understanding of how climate factors impact the decapod larvae community in the outer Mondego Estuary, providing valuable insights into the intricate relationships between NAO, SST, and MHWs. These findings not only advance our comprehension of this specific ecosystem but also lay the groundwork for comparative analyses with other temperate estuarine ecosystems, contributing to a broader understanding of the factors influencing decapod larvae dynamics.

CRediT authorship contribution statement

Marta Monteiro: Writing – original draft, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Miguel Ângelo Pardal:** Writing – review & editing, Resources, Project administration. **Ulisses Miranda Azeiteiro:** Writing – review & editing, Supervision. **Susana Cardoso Pereira:** Writing – review & editing, Formal analysis, Data curation. **Nuno Vaz:** Writing – review & editing, Formal analysis, Data curation. **Ana Lígia Primo:** Writing – review & editing, Resources, Project administration. **Eduardo Ramirez-Romero:** Validation, Methodology, Formal analysis, Conceptualization. **Juan-Carlos Molinero:** Validation, Methodology, Formal analysis, Conceptualization. **Sónia Cotrim Marques:** Writing – review & editing, Supervision, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106526.

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