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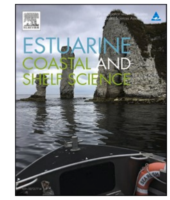

Characterization of marine heatwaves in the Cantabrian Sea, SW Bay of Biscay

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ABSTRACT

The trend towards an increased incidence of marine heatwaves (MHWs) due to climate change poses a serious threat to the health of coastal ecosystems. Here, we characterized MHWs based on daily *in situ* water temperature measurements collected from 1998 to 2019 in two intertidal coves, Oleiros and La Franca, located in the central Cantabrian Sea coast, N Spain. The two study locations cover the transition zone between cold- and warm-temperate benthic communities that characterizes the biogeography of intertidal assemblages along the SW Bay of Biscay. We examined the incidence, duration and magnitude of MHWs, and assessed the emergence of trends towards more frequent, prolonged and intense MHWs during the study period. We further assessed mechanistic links with modes of climate variability by examining the association between MHW occurrence and the East Atlantic pattern (EA). We detected 78 MHW events between Jan. 1998 and Mar. 2019 (40 in Oleiros, 38 in La Franca) and more than half were synchronous among study locations. The incidence, duration, and intensity of MHWs were higher during the positive phase of the EA, which is associated with air pressures above normal and southwesterly winds during summer. The recorded MHWs also coincided with documented shifts in the abundance and distribution of dominant macroalgae species that triggered abrupt changes in the structure of intertidal communities of the region. Our findings and the present scenario of climate change emphasize the need to enhance research around the trends in the occurrence of MHWs in the coast of northern Spain, and the NE Atlantic Ocean coast in general.

1. Introduction

Marine heatwaves (MHWs) are transient episodes of extreme ocean temperatures that can cause serious, long-lasting impacts on the structure and function of marine ecosystems (Hobday et al., 2016). These authors define MHWs as lasting for at least 5 days and being warmer than the 90th percentile of the climatological observations. Parallel to the general trend in global ocean warming, MHWs have become more intense and frequent in recent years under the influence of anthropogenic climate change (Fox-Kemper et al., 2021; Laufkötter et al., 2020). Extreme temperature events like MHWs often exert stronger impacts than gradual changes associated with ocean warming (Oliver et al., 2018), and often promote abrupt changes in the composition of marine ecosystems (Wernberg et al., 2016). These impacts entail changes in natural communities and considerable losses of the local ocean's goods and services, leading to serious socioeconomic issues (Smale et al., 2019). Analyzing trends and patterns in MHW occurrence has become a pressing issue, especially under their imminent increase in likelihood and severity around the world, according to future predictions (Frölicher et al., 2018; Collins et al., 2019).

In this global context, within the North-East Atlantic Ocean, the Cantabrian Sea is a narrow (~30 km) temperate coastal shelf sea that comprises the northern coast of Spain (southern Bay of Biscay). The Cantabrian coastal waters have experienced an unabated increase in sea surface temperature (SST) from the 1970s onwards by 0.22 °C decade^{-1} (deCastro et al., 2009; Chust et al., 2022), which exceeds the global trend [~0.15 °C decade^{-1}, Rhein et al. (2013)]. Increases in mean SSTs have been identified as one of the main reasons for the worldwide

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increase in MHW frequency and duration over the past century (Oliver et al., 2018). The occurrence of MHWs at a global scale has recently been addressed through multiproduct analyses relying on satellite data (Marin et al., 2021; Varela et al., 2021). However, the incidence of MHWs in northern Spain using field temperature data has only been recently assessed in Izquierdo et al., (2022). The projected increase in MHW severity (Oliver et al., 2019) and the ecological impacts witnessed by the scientific community (Smale et al., 2019) bring out the relevance of their study in the region.

The occurrence of MHWs has been linked to large-scale atmospheric circulation patterns (Holbrook et al., 2019). In the Bay of Biscay, the East Atlantic pattern (EA) is the dominant mode of climate variability (Borja et al., 2019). According to previous studies, it is among the most representative regional patterns of atmospheric variation in the Northern Hemisphere (Rodríguez-Puebla et al., 1998; Lorenzo et al., 2007). Modes of climate variability remotely modulate SSTs through the alteration of sea surface energy fluxes and oceanic advection currents (Holbrook et al., 2019). Their occurrence may hence prompt anomalous patterns in SST at a local-regional scale (Deser et al., 2010; deCastro et al., 2011). The occurrence of MHWs is attributed to the influence of different atmospheric and oceanic physical processes (Schlegel et al., 2021) that directly affect SST variations (Oliver et al., 2021). As a mode of large-scale atmospheric circulation pattern, the assessment of the EA's association with the incidence of MHWs in the Cantabrian coast is of considerable interest for quantifying trends and patterns of their occurrence in the region, as well as their impacts on different habitats.

Among these habitats, vegetated coasts form highly productive ecosystems that contribute important services (Barbier, 2017), including its role as a net carbon sink of anthropogenic emissions (Duarte, 2017). MHWs pose a serious risk to marine ecosystems dominated by macroalgae, altering the distribution and abundance of their populations and the associated community (Wernberg et al., 2016). Canopy-forming species (kelp, fucoids) play an essential role as habitat-forming species and primary producers of the coastal marine ecosystems of the Cantabrian Sea (Martínez et al., 2015). In the past few years, numerous authors have reported significant and progressive changes in the distribution of the main coastal seaweed species in northern Spain (Fernández and Anadón, 2008; Müller et al., 2009; Fernández, 2011, 2016; Viejo et al., 2011; Duarte et al., 2013; Voerman et al., 2013; Piñeiro-Corbeira et al., 2016; Casado-Amezúa et al., 2019; Des et al., 2020). These shifts have been mostly associated with the observed increase in SST in the region, among other factors (Gómez-Gesteira et al., 2008). The intensification of MHWs due to climate change compromises the endurance of these key organisms and that of the very ecosystem (Smale et al., 2019). Their disappearance entails a negative environmental impact for coastal communities and poses a threat to the maintenance of the highly valuable goods and services they provide.

Here, we analyzed the incidence and characteristics of MHWs over the period Jan. 1998–Mar. 2019 at two intertidal locations in central Cantabrian Sea, SW Bay of Biscay. To assess the influence of large-scale climatic anomalies on MHW incidence, we compared MHW records with the historical series of an atmospheric index capturing variability in the EA pattern. Finally, we screened the literature to identify potential impacts of MHWs on intertidal communities along the central Cantabrian coast. Our analyses bring to light the incidence and severity of MHWs on the Cantabrian coast while, in parallel, connect their occurrence to the influence of climate variability modes and address their impacts on local marine ecosystems.

2. Materials and methods

2.1. Study area

The study was conducted in the central Cantabrian Sea, SW Bay of Biscay (NE Atlantic). The Cantabrian coast is subjected to a marked thermal gradient from a cooler western area with an oceanic influence towards a warmer, more continental regime towards the inner Bay of Biscay (Lavín et al., 2006). Cape Peñas influences regional coastal circulation and alongshore upwelling patterns, which come ultimately defined by the prevailing seasonal winds (Valencia et al., 2004; Llope et al., 2006). Oleiros (6.200W 43.575N) and La Franca (4.575W 43.395N) constitute two coastal locations separated by ~100 km and by Cape Peñas, which represents an abrupt transition in average temperature in the westward warming trend of the Cantabrian Sea (Fig. 1). Altogether, the area represents a well-defined biogeographical transition zone between cold- and warm-temperate waters.

2.2. In situ temperature data

Daily *in situ* temperature measurements were collected from Jan. 1998 to Mar. 2019 (~21 years) at Oleiros and La Franca using TidbiT V2 water temperature dataloggers (ONSET Company). The data were retrieved with a reader HOBO Optic USB Base Station and converted to text files through the program HOBOWare Pro v.3.7.10 (ONSET Company). *In situ* water temperature dataloggers were fixed onto solid rock between 0.5 and 1m above minimum tidal level, ensuring that they will always stay submerged at high tide. Loggers were programmed to record water temperature twice per hour. We filtered the series to retain two daily records corresponding to the semidiurnal high tides, from which we took the average value as a measure of daily mean sea temperature.

The resulting time series misses daily temperature data during 6% of the study period in Oleiros and 18% in La Franca. In terms of length and temporal consistence the temperature series would be considered suboptimal according to Hobday et al. (2016) but remains nonetheless suitable for MHW research (Schlegel et al., 2019). The time series is framed within a warming period of the SSTs in the Cantabrian coast that began in the 1970s (deCastro et al., 2009). Ideally, the series should span its overall length to thoroughly assess MHW impacts upon natural communities within that period, as well as the evolution in their incidence (see Izquierdo et al., 2022). However, no *in situ* records prior to 1998 are available and although the series remains adequate for MHW characterization, the frequency, intensity and duration of the events detected in the present study might be underestimated.

Trends in sea temperature based on the *in situ* records were obtained from Gaussian regression coefficients based on Generalized Linear Models (GLM; Gelman and Hill, 2007) to assess the presence of warming or cooling trends in the respective study locations.

2.3. East Atlantic pattern (EA) historical series

The EA pattern, first described by Wallace and Gutzler (1981), is one of the most important modes of atmospheric variability in the north Atlantic/European sector. It consists of a north–south dipole in sea level pressure anomalies that spans the entire North Atlantic Ocean, with the centers located near 55°N, 20–35°W and 25–35°N, 0–10°W (Barnston and Livezey, 1987). Its structure resembles the North Atlantic Oscillation, although the EA pattern is associated with atmospheric circulation across the subtropical Atlantic that influence storm tracks and air mass transport towards southern Europe. The positive phase of the EA is associated with above-average SSTs and precipitation in the northeast Atlantic margin, including the Bay of Biscay (Rodríguez-Puebla et al., 1998; deCastro et al., 2008). The EA pattern has also been reported to have a notable impact over maximum atmospheric temperatures over the Iberian Peninsula (Frías et al., 2005). We extracted the monthly teleconnection index of the EA from the Climate Prediction Center of the NOAA's National Weather Service (NOAA National Weather Service, 2012) for the period 1998–2019. Northern Hemisphere teleconnection indices are calculated based on the Rotated Principal Component Analysis used by Barnston and Livezey (1987) applied to monthly mean standardized 500-mb height anomalies obtained from the Climate Data Assimilation System in the analysis region 20°N-90°N between Jan. 1950–Dec. 2000. The anomalies are standardized by the 1950–2000

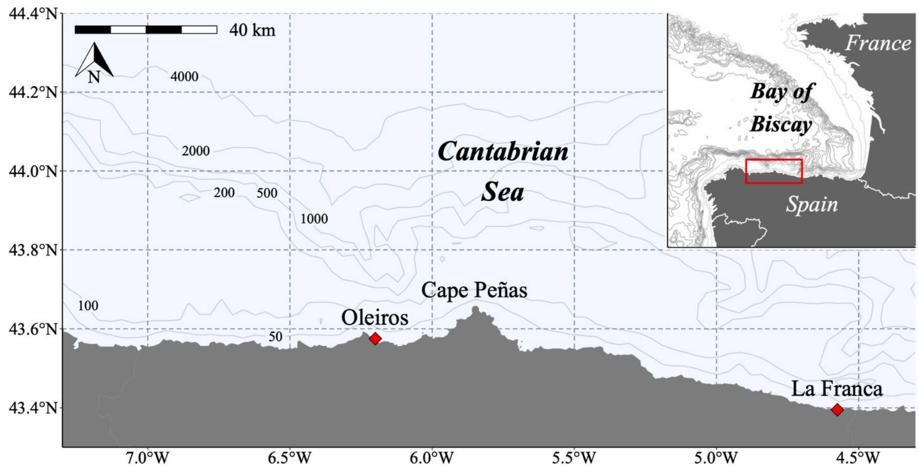

Fig. 1. Map showing the two study locations of Oleiros and La Franca, which are separated by Cape Peñas. Bathymetry data were extracted from the GEBCO Compilation Group (2021). Depth is expressed in meters.

base period monthly means and standard deviations. We examined the relationship between MHW incidence and the occurrence of either phase of the EA pattern through a Chi-squared test.

2.4. Characterization of marine heatwaves (MHWs)

We characterized MHWs following Hobday et al.'s (2016) criteria, which state that a MHW i) must last for at least 5 days ii) must be warmer than the 90th percentile of the climatological observations and iii) must be based, at least, on a 30-year historical baseline period. Although our time series is 21 years long, Schlegel et al. (2019) state that series as long as 10 years produce acceptable MHW metrics that may be used with some caution. We used *in situ* temperature data to create an annual climatological mean and a 90th percentile threshold, which allowed us to set up the framework to detect MHWs. We considered the total number of MHWs and MHW days to assess MHW incidence throughout time in both study locations. We also described and classified each MHW according to the following set of summary statistics: maximum intensity (highest temperature anomaly value during the MHW [i_{max}, °C]), mean intensity (mean temperature anomaly during the MHW [i_{mean}, °C]), cumulative intensity (sum of daily intensity anomalies [i_{cum}, °C days]) and duration (consecutive period of time [D, days]) (Table S1 in Supplementary File). The former temperature anomalies refer to the temperature that exceeds the annual climatological mean. Trends in MHW frequency, number of MHW days and MHW duration -discrete variables, *i.e.*, counts of events during some period of time- were estimated using Poisson GLMs (*e.g.*, Gelman and Hill, 2007). For this purpose, MHW duration and the number of MHW days were both fixed by the yearly possible number of MHW days in order to deal with missing data. MHW trends were examined both annually and seasonally for spring-summer [Mar–Aug] and autumn-winter months [Sep–Feb] (Table S2 in Supplementary File). We assessed model adequacy through standard residual checks and accounted for overdispersion of discrete data counts when necessary.

2.5. Technical implementation details

All analyses were implemented in R version 4.0.5 (RCore Team, 2021). MHW characterization and analysis were performed using the library *heatwaveR* (Schlegel and Smit, 2018), which applies the MHW definition from Hobday et al. (2016). We made extensive use of the libraries *tidyverse* (Wickham et al., 2019), *lubridate* (Grolemund and Wickham, 2011), *plyr* (Wickham, 2011) and *readxl* (Wickham and Bryan, 2019) to perform all calculations and regression analyses. We also used the R packages *cowplot* (Wilke, 2020), *rnaturalearth* (South, 2017a,b), *rnaturalearthdata* (South, 2017a,b), *ggspatial* (Dunnington, 2021), *mapSpain* (Hernangómez, 2021), *scales* (Wickham and Seidel, 2020), *metR* (Campitelli, 2021), *png* (Urbanek, 2013) and *extrafont* (Chang, 2014) for graphical design and the generation of the map of the study location.

3. Results

The analysis of sea temperature trends revealed a general, steady increase (slope = 0.009 °C year^{-1}; p-value = 0.012). Separately, Oleiros displayed an increasing trend (slope = 0.023 °C year^{-1}; p-value < 0.001); but no trend was detected in La Franca (slope = −0.004 °C year^{-1}; p-value = 0.456).

A total of 78 MHW events were detected between Jan. 1998 and Mar. 2019; 40 in Oleiros and 38 in La Franca, which comprised 557 and 498 MHW days respectively (~7% and ~6% of the total length of the series in days). Over half of the events registered were synchronous between study locations, with 22/40 MHWs for Oleiros and 21/38 MHWs for La Franca, which is ~55% for both cases (Table S1 in Supplementary File).

Both annual and seasonal MHW trend analyses failed to reveal an increase in any of the MHW features examined at both study locations (Table S2 in Supplementary File; p-value > 0.05 in every computation). Trends in MHW frequency presented estimates of increase, whereas those for the number of MHW days and MHW duration were mostly negative. Individually, no significant trends were found either (Table S2; Fig. 2). Annual estimates were of increase for all variables at both study locations, except for the number of MHW days and MHW duration at Oleiros. The occurrence of MHWs of great duration in 1998, together with the short length of the temperature series, are probably the cause for the annual decreasing estimates for most variables at Oleiros (and for the number of MHW days for both sites combined). The year 2006 had the highest number of MHWs (5 at Oleiros, 7 at La Franca) and some of most severe, long-lasting episodes at both locations (*i.e.*, $i_{max} \geq 3$ °C; $i_{mean} \geq 2$ °C; $i_{cum} \geq 100$ °C days; $D = 50$ days; see Table S1). Importantly, 25% and ~30% of the MHW days in Oleiros (140/557) and La Franca (149/498), respectively, took place during within this year (Fig. 2).

The EA pattern was predominately positive during the study period. The Chi-squared test revealed that the EA pattern influences the incidence of MHW episodes at Oleiros (X-squared = 128.73; df = 1; p-value < 0.001) and La Franca (X-squared = 46.791; df = 1; p-value < 0.001). The comparative analysis with the historical series of the EA revealed that ~88% and ~79% of the MHWs detected at Oleiros and La Franca respectively occurred during positive phases (95% confidence interval = [0.44, 0.80], Fig. 3). Furthermore, we found that >85% of the MHWs that were synchronous between Oleiros and La Franca took place during

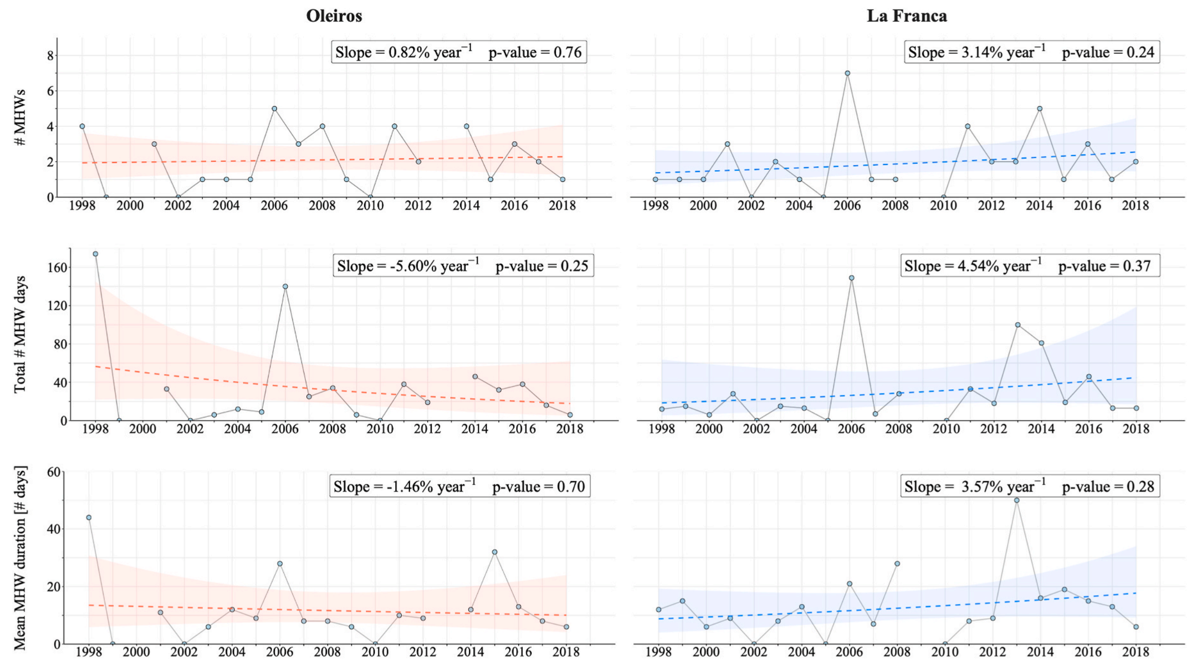

Fig. 2. Time series of marine heatwave frequency (1st row), total number of marine heatwave days (2nd row) and yearly averaged duration (3rd row) of marine heatwaves detected between 1998 and 2019 in Oleiros and La Franca. The slope and p-value of each trend are shown. Dashed lines represent the linear regression trend in Oleiros (red) and La Franca (blue). Shaded areas represent 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

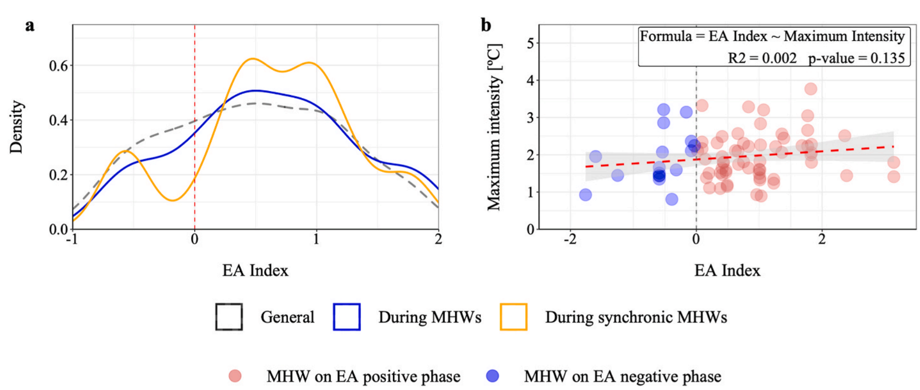

Fig. 3. (a) Statistical distribution of marine heatwaves according to current East Atlantic Index at their occurrence; **(b)** relationship between marine heatwave maximum intensity [i_{max}] and the East Atlantic pattern index.

positive phases too (19/22 MHWs at Oleiros; 18/21 MHWs at La Franca; 95% confidence interval = [0.53, 0.97] (Fig. 3). Most importantly, the warm phase of the EA entailed the occurrence of some of the most severe MHWs from both study locations, with episodes that registered $i_{max} \geq 3$ °C and $D \geq 1$ month (Fig. 4).

4. Discussion

Our analyses failed to acknowledge any significant trends in the incidence and duration of MHWs in two coastal locations located in the central Cantabrian Sea, SW Bay of Biscay, from Jan. 1998 to Mar. 2019. The incidence of MHWs in the region, on the other hand, seems to be related to the positive phase of the EA pattern, which involves above-average SSTs.

Since the late 20th century, the global upper ocean (0–700 m) has dramatically increased its warming rate, a fact that is mainly attributed to anthropogenic influences (Gulev et al., 2021). The surface temperatures over the coastal zone of northern Spain have experienced a noticeable rise during the last four decades, especially during spring-summer (Koutsikopoulos et al., 1998; Gómez-Gesteira et al., 2008; Voerman et al., 2013). Despite the amount of missing data and/or the limited extent of our temperature series -which does not span the overall length of the warming period undergone in the region-, the steady temperature increase revealed in this research for the two study locations combined supports the general warming trend in northern Spain. The former drawbacks, nonetheless, likely contributed to the discrepancies found in the significance of the temperature trends of each study location individually and the inconclusive trends observed in MHW frequency and duration (*i.e.*, see MHW trends in Izquierdo et al., 2022). Global-scale shifts in mean SST drive changes in MHW occurrence (Frölicher et al., 2018), and the current human-induced global warming scenario increases the probability for large and severe MHWs to take place (Laufkötter et al., 2020). Above average SST anomalies had been previously registered in the region for the years 1999, 2003 and 2006 (Duarte et al., 2013; Voerman et al., 2013). In our investigation, MHWs with $i_{max} \geq 3$ °C were detected in all 3 years at La Franca, and only in 2006 for Oleiros (Table S1 in Supplementary File). Besides the occurrence of the European heatwave in July 2006 (Chiriaco et al.,

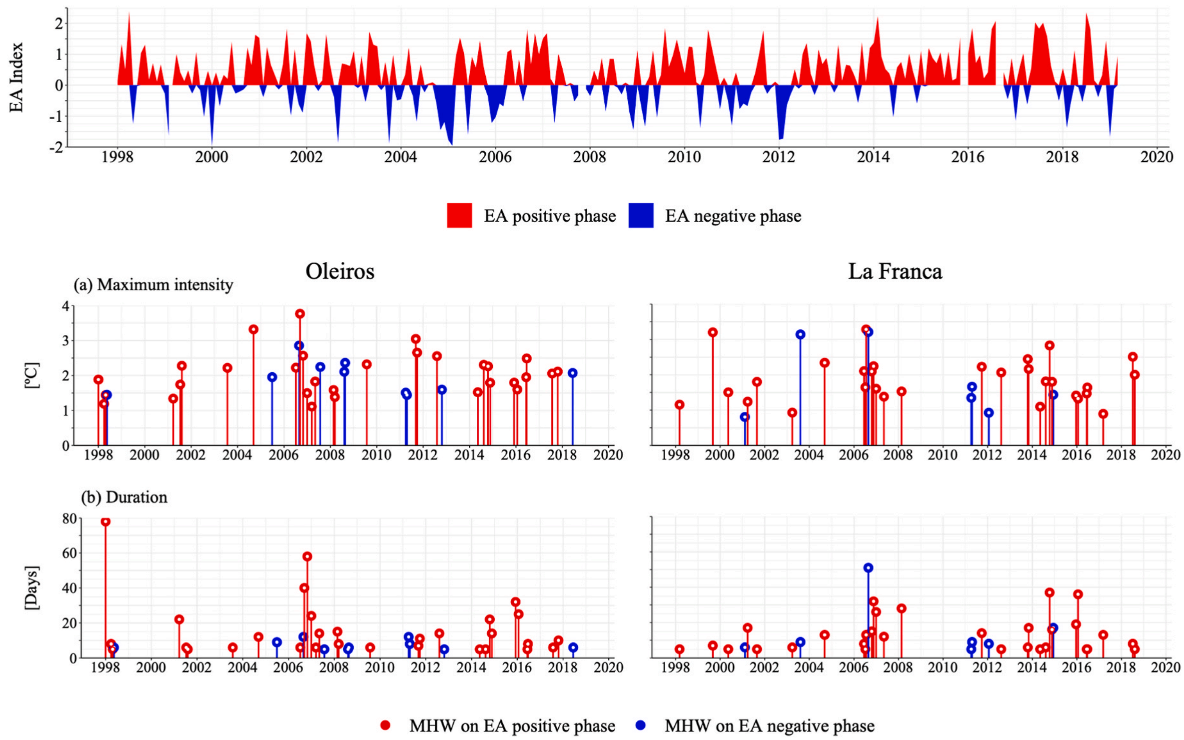

Fig. 4. First row: historical series of the East Atlantic pattern. Second row: (a) maximum intensity [i_{max}] and (b) duration [D] of the marine heatwaves detected in the time series from Oleiros and La Franca, classified according to their occurrence within the phases of the East Atlantic pattern. Results from marine heatwave mean [i_{mean}] and cumulative intensities [i_{cum}] are not shown here due to their big resemblance to marine heatwave maximum intensity and duration plots, respectively. Most of the detected marine heatwaves and, in general, the largest episodes of each metric took place within East Atlantic pattern positive phases at both locations.

2014), Le Cann and Serpette (2009) reported an unusually warm water inflow during autumn-winter in that year. Both events probably relate to the incidence of high-impact MHWs observed at both locations from summer through winter. This also contributes to explain the synchrony of the MHW episodes from both study locations in 2006 (5/5 [5/7] of the MHWs in Oleiros [La Franca] in that year were synchronous, Table S1).

The evidence provided in the present study shows that around three quarters-75% of the detected MHWs took place under the influence of the positive phase of the EA pattern. Climate variability modes such as the EA remotely modulate the inter-annual variation of a number of climate elements (*i.e.*, air temperatures, SSTs, precipitation, wind; Deser et al., 2010) and thus have a noticeable influence on important local atmospheric and/or oceanic processes. In general, these processes have a direct effect upon SST variations, which ultimately influences the likelihood of MHW occurrence. The EA pattern has been reported to be the most important variation explaining atmospheric temperature variability and around 25% of the SST variability in northern Spain (Sáenz et al., 2001; deCastro et al., 2011; Borja et al., 2019). Our observations reveal that most of the synchronous MHWs occurred during warm phases of the EA. Modes of climate variability act on a synoptic scale and its effect manifest after a few days on a large range of spatial and temporal scales (Holbrook et al., 2019) and are often responsible for abnormal weather patterns occurring simultaneously over seemingly vast distances (deCastro et al., 2008). This implies that, in essence, the observed synchrony in MHW incidence at Oleiros and La Franca is most likely due to the influence of the EA pattern acting over a range of ~100 km at least. Most likely, the positive phase of the EA affects SST variations through air-sea heat fluxes, which have proven to be a physical driver responsible for setting MHW properties in regions susceptible to atmospheric forcing (Oliver et al., 2021). Nonetheless, it would be desirable to consider new physical parameters (*i.e.*, wind or atmospheric pressure) in future investigations to look further into the possible mechanisms by which the EA pattern might be prompting the occurrence of MHWs in the region.

It has been recently predicted that the incidence and intensity of MHW will increase in the coming years, regardless of the global warming scenario, which further threatens global marine ecosystems and biodiversity (Oliver et al., 2019). Biological and ecological impacts derived from MHW occurrence have been thoroughly reported worldwide, which range from population regime shifts and algal blooms to coral bleaching, mass mortality and re-structuring of entire ecosystems. (Ummenhofer and Meehl, 2016). Specifically, MHW impacts upon macroalgae communities and their repercussions have been widely addressed in literature (Smale and Wernberg, 2013; Wernberg et al., 2016; Arafeh-Dalmau et al., 2019; Smale et al., 2019; Benthuysen et al., 2020). Although the distribution changes experienced by coastal seaweed populations off the coast of northern Spain in recent years have been widely addressed (Fernández and Anadón, 2008; Müller et al., 2009; Fernández, 2011, 2016; Viejo et al., 2011; Duarte et al., 2013; Voerman et al., 2013; Piñeiro-Corbeira et al., 2016; Casado-Amezúa et al., 2019; Des et al., 2020), the influence of extreme temperature events upon them has not yet been assessed. Thus, abrupt changes in the abundance and distribution of habitat-forming seaweed communities recently documented in the literature provide good candidates to assess the impact of MHWs in the Cantabrian Sea.

Viejo et al. (2011) documented a general decrease in the reproductive capacity of *Fucus serratus* and a dramatic increase in their mortality from 2005 to 2006 towards the west of Cape Peñas. Fernández (2011) observed a progressive abundance decrease and growth issues in *Saccharina polyschides* populations in the central Cantabrian coast from the year 2000 on and reported the disappearance of reproductive plants by 2006. Duarte et al. (2013) observed a sharp decline in the abundance of *Fucus serratus* in the area west to Cape Peñas, as well as a 130 km westwards retreat of *Himanthalia elongata* between 2004-2006 and 2008–2009. Finally, Voerman et al. (2013) detected a massive decline of nearly ~1400 ha of *Laminaria ochroleuca* west of Cape Peñas in 2007. All of the former population shifts were reported to occur between 2005 and

2009 and seem to coincide with MHW incidence periods (Fig. 5). Nearly 30% of the total MHWs detected in the present study took place within these years (23/78 MHWs; 14 at Oleiros and 9 at La Franca), half of them during 2006 (12/24 MHWs; 5 at Oleiros and 7 at La Franca). Straub et al. (2019) recently argued that the differential responses over time and space of macroalgae species to the effect of a MHW are likely subjected to a number of factors (*e.g.*, physiological versatility, ecological resilience and genetic diversity of macroalgae populations, MHW extent and magnitude; see Wernberg et al., 2018). Thus, MHW impacts upon macroalgae communities may not be immediately evident and might even present long time-lags. This implies that the extreme temperatures derived from the occurrence of MHWs probably contributed to the range shifts and abundance decreases in the canopy-forming algae communities documented in the literature above.

SSTs in the Bay of Biscay have been warming at a considerable rate since the 1970s (deCastro et al., 2009). The disappearance of canopy-forming algae species in the Cantabrian Sea began to be described from that moment on (Fernández, 2016), although it has been especially noticeable since the turn of century (Fernández, 2011; Casado-Amezúa et al., 2019). Alongside with human-derived pressures, a number of environmental agents have been described in the Bay of Biscay that can influence the maintenance of canopy-forming macroalgae populations (*i.e.*, temperature, sunlight, wave exposure, storms, changes in biogeochemical cycles; see Borja et al., 2013, 2018), although temperature is usually the main factor used to assess distribution change scenarios (Franco et al., 2017). Temperature is known to strongly influence the spatial distribution of canopy-forming algae species, with extreme temperatures directly affecting their physiological and ecological performance (Straub et al., 2019). Species distributions might indeed be more sensitive to extreme conditions than to average longer-term trends (Sanz-Lázaro, 2016), considering the rapid shifts and long-term impacts that discrete events drive in ecosystems (O'Leary et al., 2017; Smale et al., 2019). Hence, the recently documented shifts in macroalgal communities in the central Cantabrian Sea may be related to the incidence of MHWs reported here, especially during 2005–2009. Extreme temperatures associated with MHWs erode the resilience of seaweeds adapted to cool conditions like *Fucus serratus* and may ultimately lead to their eventual loss as their biogeographical distribution range continues to shrink.

The results in this study are unavoidably conditioned by the short duration and narrow spatial extent of our analysis, which represent a major weakness of our approach. Though Oleiros and La Franca provide the longest and most complete *in situ* temperature record in an intertidal rocky shore in the central Cantabrian Sea, a spatiotemporally longer, more comprehensive record should provide a broader perspective and reveal different trends both in SST and MHW incidence in the region (see Izquierdo et al., 2022), considering the general warming trend that affects the Bay of Biscay and the world oceans (Chust et al., 2022; Fox-Kemper et al., 2021). Our findings suggest, nonetheless, a warming trend in central Cantabrian Sea manifested as a steady increase in water temperature and through prolonged MHWs with extreme temperatures. Moreover, the positive association between MHW incidence and the EA implies that large scale patterns of atmospheric forcing may act dominating variability in the incidence of MHWs. However, further research is needed on how the EA pattern may be operating on local-scale oceanic physical processes to prompt MHW conditions (i.e., air-sea heat fluxes or ocean advection; Schlegel et al., 2017). Future investigations might consider taking into account other European modes of climate variability to look into their influence on the occurrence of MHWs in the Bay of Biscay (Borja et al., 2019). Finally, the match between recently documented shifts in the abundance and distribution of canopy-forming macroalgae and severe MHW episodes suggests that MHWs might have played a part in the regression of macroalgae species in the coast of northern Spain in recent years. Under the escalating pressure of global warming, and in light of the ecological consequences reported in the scientific literature (Smale et al., 2019), our study stresses the need to

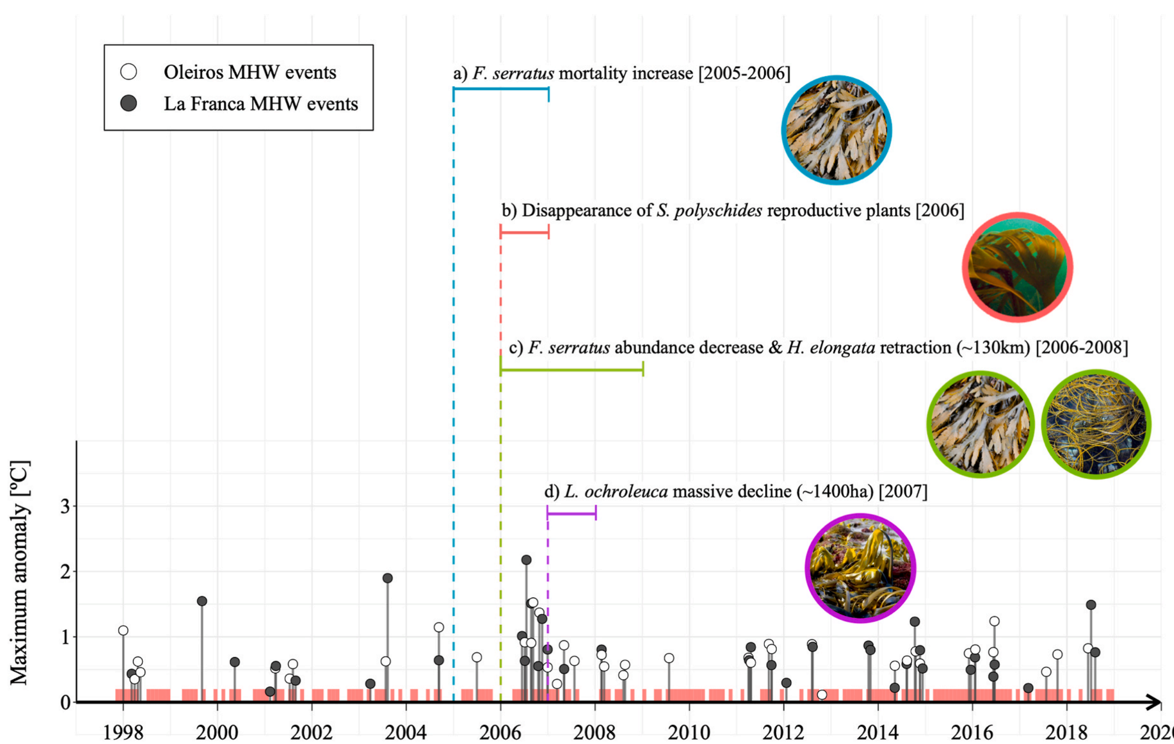

Fig. 5. Maximum temperature anomaly -interpreted as the temperature exceeding the 90th percentile threshold, not the climatological baseline- of the marine heatwaves detected in the time series from Oleiros (open dots) and La Franca (solid dots) overlapped with periods of severe population shifts of local macroalgae communities documented in (a) Viejo et al. (2011), (b) Fernández (2011), (c) Duarte et al. (2013) and (d) Voerman et al. (2013). Red bars at the bottom represent the positive phases of the East Atlantic pattern. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

reinforce coastal monitoring efforts to analyze the impact of extreme temperature events like MHWs.

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CRediT authorship contribution statement

Paula Izquierdo: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing, Visualization. **José M. Rico:** Conceptualization, Resources, Supervision. **Fernando González Taboada:** Methodology, Visualization, Writing – review & editing. **Ricardo González-Gil:** Methodology, Visualization, Writing – review & editing. **Julio Arrontes:** Data curation, Investigation, Resources, Writing – review & editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107923.

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