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FutureMARES Project

FutureMARES - Climate Change and Future Marine Ecosystem Services and Biodiversity is an EU-funded research project examining the relations between climate change, marine biodiversity and ecosystem services. Our activities are designed around two Nature-based Solutions (NBS) and Nature-inclusive Harvesting (NIH):



We are conducting our research and cooperating with marine organisations and the public in Case Study Regions across Europe and Central and South America. Our goal is to provide science-based policy advice on how best to use NBS and NIH to protect future biodiversity and ecosystem services in a future climate.

FutureMARES provides socially and economically viable actions and strategies in support of nature-based solutions for climate change adaptation and mitigation. We develop these solutions to safeguard future biodiversity and ecosystem functions to maximise natural capital and its delivery of services from marine and transitional ecosystems.

To achieve this, the objectives of FutureMARES defined following goals:





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List of symbols, abbreviations and a glossary

CC	Climate change
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- Tn.x Task a sub-component of a work package where "n" is a number of the work package and "x" is a number of the task within this work package
- WP Work Package
- NBS Nature-based Solutions
- CTI Community Temperature Index



Executive summary

This report, undertaken within FutureMARES Task 1.1, addresses historical shifts in marine biodiversity in European seas in relation to climate change.

Defining the Challenge

The effect of global warming on the oceans, the acidification, and the rise in mean sea level derived from climate change and greenhouse gases emissions are challenges that society must face promptly to avoid additional, unwanted impacts in the coming decades. The Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) highlighted scenarios of global sea level rise higher than previous assessment reports, and an ocean transition to unprecedented conditions, with warming seas, acidified water, a decrease in oxygen and an alteration in primary production, impelling a global redistribution of life on Earth. As a consequence, marine ecosystems are experiencing trophodynamic changes, commercial fishes and scientific surveys have demonstrated body size reductions, poleward shifts and phenological alterations. There is a prompt need to understand these changes at regional scales for proposing adaptation and mitigation measures.

The aim of this report is to analyse, contribute and synthesize the current marine biodiversity shifts in European seas in relation to climate change. The specific objectives are: 1) reporting the existing monitoring programmes specifically dedicated to biotic climate change indicators, 2) analysing trends and regime shifts in main groups (phytoplankton, zooplankton, benthic communities, fish, megafauna), 3) undertaking a comparison of the ecological response to ocean warming, acidification and other climate regime shifts among the biological groups across different European regional seas and in terms of tolerance ranges, abundance, poleward shift, phenological change, and identification of gaps and uncertainties in the knowledge and monitoring programmes, and 4) a cross-region and cross-taxa comparison of community response to warming, using a common metric based on the Community Temperature Index (CTI).

Approach

This report is structured in case studies grouped by Storylines in three marine regions (North-East Atlantic, Baltic Sea and Mediterranean Sea), where analysis and results of current marine biodiversity shifts in European seas in relation to climate change are summarised. Two approaches for each storyline have been followed: 1) Community Temperature Index (CTI) analysis, which enabled to compare the response to warming of benthic macroalgae and invertebrates, and demersal and pelagic fish communities across regions. CTI is a measure of the average thermal affinity of ecological communities, weighted by the species relative abundance. CTI analyses and exploration of the underlying processes (i.e., tropicalization and borealization) were performed using the R statistical package in three sequential scripts which use local data (from metadata catalogue we built) and public databases on species occurrence and sea temperature. R codes were provided to all partner participants of Task 1.1 to run the analysis on their time series data, where data was appropriate in terms of time series length and species representativity of the community. 2) Depending on data availability and focus of the Storyline, specific and *ad hoc* analyses were conducted in some regions and for some biological groups to more thoroughly examine biodiversity shifts in relation to climate change,



Contribution to the project

This report addressed the current marine biodiversity shifts in relation to climate change of 20 storylines encompassing main trophic levels (phytoplankton, zooplankton, macroalgae, invertebrates, fish, cephalopods, marine reptiles) and covering most European marine regions (NE Atlantic, Baltic Sea, Mediterranean Sea). A substantial ongoing impact of CC on community shifts has been identified in the cross-region comparison of biodiversity trends and drivers. Results indicated that a significant part of biological communities and sites showed a clear response to ongoing sea warming (0.28°C/decade) with several examples of favoured warm-water species (tropicalization) with decreases in cold-water species (deborealization).

Across the broad European region examined here, most biodiversity hotspots occurred in the coastal areas around the Scandinavian Peninsula, UK, Azores, Madeira and Canary Islands, Iberian Peninsula, and the northernmost areas of the Western and the Central Mediterranean Sea (including Balearic, Tyrrhenian and Adriatic Seas). These results suggested a northwestern-to-southeastern gradient of species richness that widely concur which likely respond to analogous trends in marine productivity. However, there are important data gaps (for example in the Black Sea). In particular, the availability of phytoplankton and zooplankton time series data is sparse with the available data indicating a tropicalization trend with the most marked increase in the CTI in the Kattegat. In terms of marine forests and seagrasses, the CTI increased and the process of deborealization was stronger than tropicalization during the last 15 years in Portuguese coastal waters. However, a longer-term analysis shows a temperature increase of 0.1°C per decade which might be driving a turnover of species with perennial kelps replaced by annual species. In the Baltic Sea, major declines in eelgrass depth distribution have occurred due to recent warming (0.5°C per decade, 1985-2018), bottom trawling and eutrophication despite current management efforts to reduce nutrient inputs. Future management must reduce both eutrophication and bottom trawling to help eelgrass reach deeper, cooler refugia, to increase resilience toward ongoing and further warming. In macroinvertebrates and macroalgae from coastlines of the UK and Bay of Biscay, tropicalization was the dominant processes. In the Mediterranean, the CTI also increased, but showing deborealization. In terms of Mediterranean coralligenous species, the analysis of CTI assemblage of Marseille revealed a significant sea warming (0.21°C per decade) indicating tropicalization. Moreover, marine heatwaves have caused long-term alterations to the functional trait composition of coralligenous assemblages in the observed in both Scandola and Port-Cros Mediterranean sites. Demersal fish have been studied in the NE Atlantic and W Mediterranean Sea with significant increases in CTI observed in most regions related to increasing trends in SST in the last decades. The underlying processes contributing to the observed changes in CTI differ slightly between regions, but the predominant process overall is tropicalization. Conversely, in pelagic community and estuarine fishes, deborealization prevailed. Specific species responses indicate that horse mackerel advanced the timing of spawning (11.7 days/°C of warming) from 1992 to 2019, whilst Atlantic mackerel shifted poleward (369 km/°C of warming). Thermal conditions of green turtle nests in the Mediterranean (Turkish beaches) are linked to a reduction in population recruitment.

In summary, results indicated that a significant portion of each of the biological communities and sites examined demonstrated a clear response to ongoing sea warming which, in some cases, favouring warm-water species (tropicalization) with decreases in cold-water species (deborealization), in contrast to borealization and detropicalization. The relative importance between tropicalization and deborealization of communities appeared to depend on biological traits of species, geomorphology of regional sea / area, and anthropogenic activities.



Dissemination and Exploitation

The results described in this report are being exploited within the *FutureMARES* project (Task 1.2, 1.3, and all Tasks in WP4). The work contributes to 20 Storylines documents. The work undertaken within Task 1.1 and presented in this deliverable report has contributed to 8 published papers and 6 articles in preparation or already submitted (see list below). Moreover, the research collaboration among partners in Task 1.1 provides the basis for a high-impact publication comparing biodiversity trends in relation to warming across European regional seas and coasts that will be prepared for journal submission in the next months (see below Chust et al. In prep).

FutureMARES recognizes the importance of translating these results to policymakers. In the future, the information contained in this report will form the content of one or more policy briefs highlighting changes in marine biodiversity with warming and the regional similarities of the response. The work will also be communicated to the public using our FutureMARES website and newsletter.

Published articles:

- Chust, G., M. González, A. Fontán, M. Revilla, P. Alvarez, M. Santos, U. Cotano, M. Chifflet, A. Borja, I. Muxika, Y. Sagarminaga, A. Caballero, I. de Santiago, I. Epelde, P. Liria, L. Ibaibarriaga, R. Garnier, J. Franco, E. Villarino, X. Irigoien, J. A. Fernandes-Salvador, A. Uriarte, X. Esteban, D. Orue-Echevarria, T. Figueira, and A. Uriarte. 2022. Climate regime shifts and biodiversity redistribution in the Bay of Biscay. *Science of the Total Environment* 803:149622. https://doi.org/10.1016/j.scitotenv.2021.149622
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- 8. Turkozan, O., Almpanidou, V., Yılmaz, C., Mazaris, A.D. 2021. Extreme thermal conditions in sea turtle nests jeopardize reproductive output. *Climate Change*, *167*, *30*.



Articles submitted or in preparation:

- 1. Chust et al. (In Preparation) Cross-taxa and cross-region comparison of Community Temperature Index. *In preparation*, expected submission on Autumn 2022.
- 2. Chust, G., F. González Taboada, P. Alvarez, L. Ibaibarriaga (In Preparation) Acclimatization pathways in marine species to track ocean warming.
- 3. Garrabou, J., et al. (Submitted). Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology*.
- 4. Monteiro C., Pereira J., Seabra R, Lima F.P. (Submitted). Fine-scale survey of intertidal macroalgae reveals recent changes in a cold-water biogeographic stronghold. *Frontiers in Marine Science.*
- 5. Ramírez F., Villarino E., Sbragaglia V., Chust G., Coll M. (In Preparation) Changes in fishing catch composition respond to local climate change velocities in the Northwestern Mediterranean Sea. Expected submission on Summer 2022.
- 6. Turkozan, O., Can Yılmaz, C., Almpanidou, V., Godfrey, H.M., Mazaris, A.D. (Submitted) Thermal conditions of the green turtle, *Chelonia mydas*, nests in the largest rookery of eastern Mediterranean. *Endangered species research*.



1. Introduction

1.1. Ocean warming and acidification

The effect of global warming on the oceans, the acidification, and the rise in mean sea level derived from climate change and greenhouse gases emissions are challenges that society must face promptly to avoid additional, unwanted impacts in the coming decades. The Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) (IPCC, 2019), highlighted scenarios of global sea level rise higher than previous assessment reports, and an ocean transition to unprecedented conditions, with warming seas, acidified water, a decrease in oxygen and an alteration in primary production, impelling a global redistribution of life on Earth (Pecl et al., 2017). As a consequence, marine ecosystems are experiencing trophic changes, commercial fishes show body size reduction, poleward shifts and phenological alterations. There is a prompt need to understand these changes at regional scales for proposing adaptation and mitigation measures (Kebede et al., 2018).

The main physical and biogeochemical trends observed in European regional seas in relation to climate change and CO₂ atmospheric concentration are sea warming, acidification, deoxygenation, and changes in salinity. The large geomorphological and ecological differences among the major European seas (north-eastern Atlantic / North Sea, Baltic Sea and Mediterranean Sea) are important considerations when interpreting why physical, biogeochemical and biological climate change effects vary within and among these areas (EEA, 2017). In the North Sea and greater NE Atlantic, the coastal sea surface temperature warmed from 1982 to 2010 at rates of 0.2-0.3 °C/decade in the southwest European coast and up to 0.3-0.7 in the Norwegian and North Seas (Lima and Wethey, 2012). In the Bay of Biscay, warming trends started from the 1980s onwards and varied between 0.10 to 0.25 °C/decade (Costoya et al., 2015; deCastro et al., 2009), with the greater increase at the surface and a deepening of the 14 °C isotherm (Valencia et al., 2019). The Baltic Sea temperature has also increased at a rate of 0.4 °C/decade (1978-2007) (Kniebusch et al., 2019). In the Mediterranean, there has been an increasing trend of in situ Sea Surface Temperature (SST) of 0.9 °C/decade, which corresponds well with the 0.6 to 0.8 °C/decade estimates from remote sensing / satellite data (Salat et al., 2019). These trends have been accompanied by an increase in water column stratification (0.02 °C/year in summer temperature difference between 20 and 80 m).

1.2. Impacts on populations, communities and biodiversity

Global climate change is redistributing life on Earth (Baudron et al., 2020; Pecl et al., 2017). Concerning specifically the response of species to global warming, three universal ecological responses have been outlined at the biogeographical scale (Daufresne et al., 2009): Poleward distribution shifts, adjustments in phenology, and reductions in mean body size. The first two responses can be explained by changes in temperature triggering changes in habitat use of species with specific ecological thermal niches, also called niche tracking (Bruge et al., 2016b; Monahan and Tingley, 2012; Pinsky et al., 2013), whilst the body size reduction is a complex and debated process that could involve physiological and/or eco-evolutionary responses (Audzijonyte et al., 2020; Queirós et al., 2018; Verberk et al., 2021). Due to the general trend of decreasing water temperature with increasing latitude (and depth), a distribution shift poleward (or to increased depth) is the displacement (either active or passive) of populations that corresponds to species thermal preferences (Poloczanska et al., 2013a). Adjustments in



the phenology (i.e., altered migration timing and changes in spawning onset and duration (Asch et al., 2019; Poloczanska et al., 2013a; Poloczanska et al., 2016)) are triggered by the advancement in seasonal cues used by species to schedule life history events. In fish, spawning adults and embryos consistently have a narrower range in tolerable temperatures than late-stage larvae/ juveniles and nonreproductive adults and are most vulnerable to climate warming (Dahlke et al., 2020). Body size reduction at warmer temperatures agrees with observations made on ectotherms across latitudes / locations with different mean and seasonal temperatures (Gardner et al., 2011; Pauly and Cheung, 2018), at different levels of organisation (individuals, population, and community). Trends related to warming in ectothermic aquatic organisms from bacteria, plankton, and fish indicate an increase in the proportion of small-sized individuals, species and young age classes and a decrease in size-at-age, in accordance with the ecological rules dealing with the temperature–size relationships (i.e., Bergmann's rule, James' rule and Temperature–Size Rule) (Daufresne et al., 2009). The specific mechanism by which the size of fish decreases with temperature is the subject of intense scientific debate (Lefevre et al., 2017; Pauly and Cheung, 2018).

Although evidence associated with marine species responses to climate change is extensive for some groups and in some regions such as fish in the north Atlantic Ocean (Peck and Pinnegar, 2018), observations and assessments of climate impacts are scarce for groups such as phytoplankton, benthic invertebrates, and marine mammals (Poloczanska et al., 2016), and for processes such as body size reduction.

1.3. Objectives

Our aim is to analyse, contribute and synthesize the current marine biodiversity shifts in European seas in relation to climate change. The specific objectives are: 1) reporting the existing monitoring programmes specifically dedicated to biotic climate change indicators, 2) analysing trends and regime shifts in main groups (phytoplankton, zooplankton, benthic communities, fish, megafauna), 3) undertaking a comparison of the ecological response to ocean warming, acidification and other climate regime shifts among the biological groups across different European regional seas and in terms of tolerance ranges, abundance, poleward shift, phenological change, and identification of gaps and uncertainties in the knowledge and monitoring programmes, and 4) a cross-region and cross-taxa comparison of community response to warming, using a common metric based on the Community Temperature Index (CTI).



2. Data and Metadata catalogue

2.1. Marine biodiversity metadata catalogue

Marine monitoring includes the sampling of different physical, chemical and biological ecosystem components for a well-defined purpose (Borja and Elliott, 2021; Borja and Elliott, 2013; McLusky and Elliott, 2004). In this line, most of the national monitoring programs on marine issues focus on short to mid-term temporal scales, such as weather forecast and emergency prevention, water quality and pollution, biological conservation, and fisheries stock assessment (Philippart et al., 2011). The collection of data from those programs might be valuable for other purposes such as the surveillance of climate change. To achieve this, specific indicators of climate change need to be defined from local monitoring variables and integrated within a regional network.

The aim of this study was to build a metadata catalogue of European long-term marine biodiversity monitoring programmes in relation to climate change, from all partners involved in Task 1.1 to contribute to the WP1 in general, and in particular to T1.1. Available monitoring data was compiled on species of different trophic compartments of marine ecosystems, from plankton to top predators, and across European seas. Different fields have been defined in an excel sheet to easily collect information on long-term ecological time series data, as well as contacts (See Annex 1).

Fields defined:

Contact name
email
Contact organisation
Species
Data type
Sampling method
Geographic area
Start date
End date
Recording frequency
Number of stations
Available biological traits
WP1 task in which data will be analysed
Links to NBS 1,2 &/or 3
Links to Storylines
Can the partner analyse the data in R-language?
Data origin
Stressor
Open access (link)
Reference (detailing dataset description)



2.2. Global Biodiversity Information databases

2.2.1. GBIF and OBIS

Public databases on species occurrence data are increasingly used for multiple purposes such as conservation planning, climate change assessments, habitat modelling, and fisheries management. Two main sources of species occurrence are: 1) GBIF (Global Biodiversity Information Facility) open database (GBIF.org (2021)), and OBIS (Ocean Biogeographic Information System; <u>www.iobis.org</u>).

R packages implemented for OBIS *robis* (Provoost and Bosch, 2019) and GBIF *rgbif* (Chamberlain et al., 2022) can be used to download massive amounts of information on presences and absences of species with geographic and temporal associated data such as: longitude, latitude, date, and depth. GBIF and OBIS often compile data from the same source, hence duplicates need to be removed.

2.2.2. Testing completeness of GBIF data in European Seas

Within the context of climate change, biodiversity knowledge integration is urgently required to evaluate and monitor marine ecosystems and to support suitable responses to underpin a sustainable future. Here, we reviewed existing findability, accessibility, interoperability, and reusability (FAIR) biodiversity data coming from one of the most reliable online information systems: the Global Biodiversity Information Facility (GBIF).

<u>This study has been published in</u>: *Frontiers in Marine Science* as "Challenges for Marine Ecological Assessments: Completeness of Findability, Accessibility, Interoperability, and Reusability Biodiversity Data in European Seas" by Francisco Ramírez, Valerio Sbragaglia, Karen Soacha, Marta Coll and Jaume Piera". doi: 10.3389/fmars.2021.802235.

Background

Reliable and systematic biodiversity assessments are challenging in the vast and remote oceans. The first large-scale, multidisciplinary and multinational assessments on marine biodiversity date back only to the 90s, with the Census of Marine Life (CoML, spanning the 2000-2010 period) likely being the most extensive of all of them (Costello et al., 2010). A decade after, and coinciding with the steep increase of digitalization of our society, FAIR (Findable, Accessible, Interoperable, and Reusable) digital data and online information systems may offer a means for marine biodiversity assessments at an unprecedented extent and spatial, temporal and taxonomical resolutions (Jarić et al., 2020); while contributing to our understanding of the processes, patterns and mechanisms underlying the ongoing contemporary biodiversity crisis (Meyer et al., 2015; Ball-Damerow et al., 2019). However, digital biodiversity databases are still in the initial stages of developments (Ariño, 2018; Ball-Damerow et al., 2019). As such, completeness of biodiversity digitized data is likely biased; with remote regions and 'less common' taxa being under-sampled or completely unrepresented (Boakes et al., 2010; Meyer et al., 2015, 2016b; Ruete, 2015). These biases directly influence opportunities for inference and application of biodiversity digitized data (Katsanevakis et al., 2015; Meyer et al., 2015, 2016).

Objectives

We assessed existing FAIR biodiversity data for the European Seas (Figure 1) available on GBIF (Global Biodiversity Information Facility). We evaluated the completeness of available



FAIR digitized datasets with respect the CoML benchmark, along with progresses in understanding spatial patterns of marine biodiversity in the European Seas.

Methods

Based on data from GBIF, we evaluated spatial-temporal patterns in the number of occurrences and individual species per cell within a 1° x 1° grid map, as proxies of 'sampling effort' and species richness, respectively. We distinguished among four basins: Atlantic EU, Baltic Sea, Black Sea and Mediterranean Sea (Figure 1). We also evaluated the data taxonomical completeness by comparing the total number of species per taxa and basin, with analogous results reported by Costello et al., (2010) and, hence, for the CoML.

Results and Discussion

Our proxies to sampling effort (i.e. total number of occurrences per cell) and species richness (i.e. total number of species per cell) heterogeneously distributed spatially, with most biodiversity hotspots occurring in the Atlantic basin and particularly in the North Sea, the coastal areas around the Scandinavian Peninsula and the UK. Other 'biodiversity hotspots' with relatively high values of species richness emerged in the Macaronesia (including Azores, Madeira and Canary Islands), the coastal areas around the Iberian Peninsula, and the northernmost areas of the Western and the Central Mediterranean Sea (including Balearic, Tyrrhenian and Adriatic Seas; Figure 1). These results suggested a northwestern-to-southeastern gradient of species richness that widely concur with those for previous biodiversity assessments (based on CoML), and may likely respond to analogous trends in marine productivity (Coll et al., 2010; Narayanaswamy et al., 2013).

Besides the ecological/environmental mechanisms underlying the spatial gradients in marine biodiversity, observed patterns may be also partially driven by the heterogeneous distribution of available data (driven by heterogeneous sampling effort and/or data mobilization) and the gaps in our knowledge of the biota (or the lack of information mobilization) along the southern and the eastern rims (Coll et al., 2010; Narayanaswamy et al., 2013; Levin et al., 2014).

Overall, the total number of species reported in GBIF was higher than those previously reported in Costello et al., (2010), with the exception of the less conspicuous species (e.g., Protozoa, Annelida and Platyhelminthes), which might be partially driven by species traits that affect detection and collection probabilities (Figure 2). These taxonomical biases can prevent from biodiversity comparisons among areas and periods, and imply that completeness pattern of a single-taxon is a poor predictor for un-assessed taxa and highlights the need to identify taxon-specific information gaps (Vale and Jenkins, 2012; Meyer et al., 2015).

Conclusions

Information on species distributions in space and time is a central aspect of biodiversity knowledge that is needed for the effective management of biodiversity and associated ecosystem services in a rapidly changing world (Whittaker et al., 2005; Butchart et al., 2010; Levin et al., 2014). FAIR biodiversity data available in GBIF provide vital information about where and when species occur and are widely used in ecology, evolution and conservation



research (Ball-Damerow et al., 2019). This information has the potential to contribute and inform actions towards multiple research questions and conservation targets at the global level.



Figure 1. (a) Study area. Following Costello et al., (2010) we distinguish among four basins: Atlantic EU, Baltic Sea, Black Sea and Mediterranean Sea. Note that the 'Atlantic EU' considered in Costello et al. (2010) was smaller than what we consider as the whole Atlantic EU area. To evaluate spatial patterns in the total number of occurrences (b) and individual species (c), we consider a 1° x 1° grid map covering the whole study area.

However, our assessments suggests that severe spatial and taxonomical gaps and biases exist in FAIR biodiversity information, even for the comparatively well-known European Seas; and these require careful consideration when developing conservation research and applications. For instance, the pervasive lack of biodiversity data for the south-easternmost marine areas (including the Black Sea) indicates that there are not sufficient occurrence (available) data to facilitate modelling approaches. National to international join efforts aimed at generating and/or mobilizing biodiversity data should focus on data-deficient areas, periods and taxa.





Figure 2. Bar plot showing the difference between the total number of species per taxa reported in GBIF with respect analogous results from Costello et al., (2010). Positive values indicate a higher number of species reported in GBIF. What we consider here as Atlantic EU (Whole area) differ from Costello et al. (2010) in that we also include marine waters around the Macaronesia (including Azores, Madeira and Canary Islands), and the northernmost Atlantic waters (see Fig. 1). For comparative purposes, we also consider the same Atlantic EU area than Costello et al. (2010). Note also that Costello et al. (2010) did not report biodiversity data for the Black Sea.



3. Methods

3.1. Defining climate change indicators

A key and priority step for developing a climate change marine observatory is to define potential indicators of climate change (EEA, 2017). There are, in general, two types of indicators, those describing the physical state of the climate system and its historical development, and those looking at future impact, risk and adaptation (GCOS, 2017). To select a potential climate change indicator to be monitored in a particular region, a set of criteria should be followed and applied to both data and variables. Here, to define the indicators of Climate Change (iCC) in the marine environment, we have selected some of the criteria used by U.S. Environmental Protection Agency (EPA, 2016): 1) data available to show trends over time, 2) data consist of actual measurements, 3) data representative of the region, 4) data credible, reliable, peer-reviewed and published, 5) sources of variability and uncertainty available, 6) the relationship between the indicator and climate change is supported by published, peer-reviewed science and data, and 7) data and analysis are founded on scientifically objective and transparent methods.

3.2. Biodiversity climate change indicators

3.2.1. Distribution shifts

Historical trend analyses of species distribution might be limited due to the nature of the raw data used (Chust et al., 2014). When data have non-homogeneous spatial and temporal coverage (e.g. most fishing data, historical collections), the conventional estimators such as the abundance-weighted average (AWA) indices (e.g. CoG or distribution boundaries), may confound changes in the distribution of sampling effort with changes in species distribution (Thorson et al., 2016). Data from research surveys are considered more homogeneous and consistent to use in historical trend analyses than catch or collection data (Green and Green, 1979). However, in some cases, scientific survey data do not have homogeneous spatiotemporal coverage (e.g. Bruge et al. (2016a), Erauskin-Extramiana et al. (2019b), due to variations in the spatial distribution of sampling through time. Properly characterizing changes in the spatial distribution of sampling through time. Properly characterizing changes in the spatial distribution of sampling effort is essential to accurately identify range shifts over time, and to identify their potential drivers (Erauskin-Extramiana et al., 2020). To avoid introducing biases in our analyses due to spurious trends in sampling effort, we followed a simplified approach from that developed by Erauskin-Extramiana et al. (2020).

3.2.2. Phenology changes

As the oceans warm, species must simultaneously face changes in the timing and in the magnitude of seasonal temperatures. Phenological adjustments are responses to warming consisting in advance the timing of seasonal migrations and the onset and duration of the spawning season (Poloczanska et al., 2013a; Poloczanska et al., 2016)). Though it is well known that spawning phenology varies across the latitudinal range of fish species (Qasim, 1956), potential acclimatization pathways are commonly addressed as independent responses. For instance, the length of the spawning season spans several months to exploit prolonged growing seasons at low latitudes (Vila-Gispert et al., 2002), but the short window faced by species shifting poleward may constrain potential spawning output (Slesinger et al., 2021). This scenario completes the set of three alternative acclimatization pathways for species



adjusting their reproductive strategies to changing temperature conditions: (*i*) a poleward shift in distribution, (*ii*) a change in phenology, or (*iii*) a combination of both responses. Here, we aim to test whether the phenological activities respond to sea warming, and to partition the relative contribution of the distributional shifts versus phenological adjustments to explain the thermal niche tracking. This has been applied in fish species (see section on mackerel below).

3.2.3. Species turnover: Community Temperature Index

As a consequence of the latitudinal shift in populations resulting from the response to warming, the abundance in each latitude range (more specifically, in each thermal range) may vary. However, the movement of a species may be the result of other factors not related to climate change such as the exploitation of commercial species. Therefore, studying the response of a group of species (community) to warming is a more complete and reliable analysis strategy for attributing the causes. To this end, a methodology at community level was used to test whether changes in the composition of species in a community correspond to their thermal preferences, using the CTI, a measure of the average thermal affinity of ecological communities, weighted by the relative abundance (Devictor et al., 2008; Stuart-Smith et al., 2015):

$$CTI = \sum_{s=1}^{n} Temp.pref_s \times Relative.Abundance_s$$

where the number of species in the community is n and each species (s) has a temperature preference (*Temp.pref*) and a relative abundance (the species' abundance divided by the abundances of all species) in the community.

By comparing the inter-annual changes in CTI with local temperature trends, inferences of community tracking to warming can be made. The thermal preferences were determined for each species by matching occurrence records collected from OBIS (Ocean Biogeographic Information System; www.iobis.org) with annual means of GODAS local SST during the 1982–1999 period, Webb et al. (2020). Then, the midpoint between the 5th and 95th percentile of the temperature distribution occupied by each species was calculated, as a measure of central tendency of their realized thermal distribution (Stuart-Smith et al., 2015). Subsequently, CTI was calculated at each station using the thermal midpoint values for each species recorded weighted by their *log*(abundance + 1) (Stuart-Smith et al., 2015). We estimated the CTI per each time unit for time series of communities identified at species level. The trend of CTI has been analysed linear model for yearly data.

Tropicalization and borealization of communities

The intensity of the ecological processes underlying the change in CTI has been also examined following the four aspects defined in McLean et al. (2021): (i) tropicalization of the community (an increase in the number of warm species); (ii) borealization (an increase in the number of cold species); (iii) de-tropicalization (a decrease in the number of warm species); (iv) and de-borealization (a decrease in cold species). Increases in CTI are expected to occur when the combination of tropicalization and de-borealization is stronger than the combination of borealization.

<u>This methodology has been published in</u>: McLean, M., D. Mouillot, A. A. Maureaud, T. Hattab, M. A. MacNeil, E. Goberville, M. Lindegren, G. Engelhard, M. Pinsky, and A. Auber. 2021. Disentangling tropicalization and deborealization in marine ecosystems under climate change. *Current Biology* 31:4817-4823.e4815. <u>https://doi.org/10.1016/j.cub.2021.08.034</u>



R codes

CTI analysis and process behind (i.e. tropicalization and borealization) have been coded in R language (R-Core-Team, 2014) in three scripts to run sequentially, and provided to all partner participants of Task 1.1:

- Script 1: Get local potential temperature from GODAS
- Script 2: Estimate Thermal optimal from OBIS
- Script 3: Analyze CTI trends over time and process behind

3.2.4. Body size

Body size in marine ectotherm individuals is inversely related to the warming of the sea (Daufresne et al., 2009; Gardner et al., 2011; Pauly and Cheung, 2018). Temperature increases initial growth but decreases adult body size (Atkinson, 1994; Atkinson and Sibly, 1997). In fish, body size is decreasing due to climate change (Perry et al., 2005), but also because of other factors such as fishing pressure and density-dependence factors.

Here, we analysed trends of fish body size and tried to disentangle the causal factors.

3.3. Time series statistical methods

Most time series methods decompose the temporal data into the following components: cyclical fluctuation, trend, and random error (Mudelsee, 2019). The most adequate statistical method for time series analysis depends on: 1) Regularity of the data. The classic methods of time series analysis usually assume that the data are regular through time. However, sampling often result in irregular time series. It is therefore necessary to use time series analysis methods adapted for irregular data such as Generalized Additive Models (GAMs) (Simpson, 2018). 2) Type of series: univariate or multivariate. A data series measured at a single spatial point can be defined as univariate and is the simplest case. An indicator (e.g., salinity) can be measured at several stations or depths simultaneously, and therefore we are in the case of multivariate series. In this case, we can estimate the general trend of the variable taking into account each station or depth as a random effect, and the year and seasonality as fixed effects, using mixed effects models (Zuur et al., 2009). 3) Objective of the study (average, extremes, seasonality). The simplest case is when the objective is to study changes in the mean values of the variable. To address extreme events, an appropriate metric needs to be defined (e.g., intensity, duration or frequency of the event) before the trend analysis. A complex case is the study of changes in seasonality, which in classical decomposition methods is assumed to be constant over the years.

Climatic and biological variables often have probability distributions that differ from Gaussian and observations may be autocorrelated. Both non-normality (non-Gaussian) and temporal autocorrelation in the error must be considered to correctly estimate uncertainty (Mudelsee, 2019), and the use of parametric methods may underestimate the error. In the case of an autocorrelated variable with irregular sampling that also presents a complex and unknown seasonal cycle (difficult to adjust to a predetermined model such as the sinusoidal one), methods based on GAMMs are a suitable alternative (Simpson, 2018). GAMMs provide a suitable tool that allows a statistical test to be carried out on the significance of each of the terms analysed (Dominici et al., 2002).

For those reasons, here we have used GAMMs to analyse the trend of iCCs and develop a code in R to analyse time series (Figure 3). A GAM generalizes a Generalized Linear Model



(GLM) so that the linear predictor depends linearly on non-parametric smoothing regression functions, which allow the study of non-linear relationships between the response variable and the explanatory variables (Hastie and Tibshirani, 1990; Wood, 2006). As in GLMs, GAMs can model a wide range of probability distributions including Gaussian, binomial, Poisson and gamma distributions, among others. A GAMM goes a step further and allows the inclusion of random effects and spatio-temporal correlation structures. To analyse the time-series of physicochemical and biological iCCs, we constructed GAMMs that included terms accounting for linear trends along time, cyclical fluctuations within the year and temporal correlation.



Figure 3. Decomposition method of time series with GAMMs.

<u>This methodology has been published in</u>: Chust, G., M. González, A. Fontán, M. Revilla, P. Alvarez, M. Santos, U. Cotano, M. Chifflet, A. Borja, I. Muxika, Y. Sagarminaga, A. Caballero, I. de Santiago, I. Epelde, P. Liria, L. Ibaibarriaga, R. Garnier, J. Franco, E. Villarino, X. Irigoien, J. A. Fernandes-Salvador, A. Uriarte, X. Esteban, D. Orue-Echevarria, T. Figueira, and A. Uriarte. 2022. Climate regime shifts and biodiversity redistribution in the Bay of Biscay. *Science of the Total Environment* 803:149622.



4. Case studies of long-term biodiversity trends

The case studies were grouped by marine regions with storylines as defined in *FutureMARES* (North-East Atlantic and North Sea, Baltic Sea, Bay of Biscay and Iberian coast, and Mediterranean Sea) (Figure 4). The biological group coverage is not uniform in all case studies and depends on data availability and the specific analysis of the storylines in each area, except for the CTI analysis which enabled to compare the response to warming of benthic and fish communities across regions.



Figure 4 FutureMARES Storyline locations among five, broad regions.



4.1. North-East Atlantic

4.1.1. Rocky intertidal macroalgal communities in Atlantic coast of Europe

Introduction and objective

Along NE Atlantic coastline, high warming rates have been recorded in the last decades, although with a marked variability among regions (Lima and Wethey, 2012). Ocean circulation, but also local topography and the regional occurrence of oceanographic processes such as upwelling, are among the reasons leading to different warming of surface waters in this area (Seabra et al., 2019; Varela et al., 2018). As a result, species responses are variable among regions and large-scale predictions on the repercussions for coastal biodiversity cannot be inferred. Along the strong latitudinal thermal gradient that characterizes this margin, a shift between cold- and warm-water intertidal floras and faunas occurs (Boaventura et al., 2002). This north-to-south distinctive gradient in the composition of coastal communities, however, seems to be weakening with climate change. Many studies have documented recent depletions and local extinctions of cold-water species occurring especially at the southern margins of their distributions, and increased abundances and poleward invasions of many warm-water counterparts (Hawkins et al., 2009; Lima et al., 2006; Mieszkowska et al., 2014; 2006). In the long-term, this could lead towards a shift in the composition of cold north-European communities (assemblages of cold-species) towards configurations that resemble much more those present at lower latitudes (assemblages of warm-species; (Bartsch et al., 2012; Hawkins et al., 2009; Müller et al., 2009), triggering a series of cascading effects along entire ecosystems and potentially impairing their anthropogenic consumption (Worm et al., 2006).

In this study, we provide a synoptic view of warming and of the dominant patterns of change in 42 intertidal communities (Figure 5) displaced along an area of the NE Atlantic spanning 24° of latitude (from the north of Ireland to Morocco). The occurrence and abundance of 173 species, from seaweeds to marine invertebrates, has been re-assessed 15 years after a first survey of the same areas. In particular, driven by the need to understand the net outcome from the interplay between species gains, losses and changes in abundance recently observed, we investigate whether a climate-induced 'thermophilization' of assemblages (i.e., a shift in the composition of assemblages from being mainly composed of cold-water to warm-water species (De Frenne et al., 2013) is occurring across the NE Atlantic. This was done through the calculation of a Community Temperature Index (CTI) (Devictor et al., 2008), the weighted average of the thermal affinities of the species that co-occur in each community. Circumstantial evidence of the impacts of warming is assessed by relating the biological changes described above with SST warming rates and the trend in the yearly duration of marine heatwaves (1982-2018).





Figure 5. Examples of surveyed intertidal communities. Left: typical cold-water community dominated by kelp in the upwelling-dominated NW Iberia. Right: typical warm-water community dominated by algae turfs, in Southern Portugal.

Study area and data description

We used 37 years of daily SSTs (1982-2018) from NOAA 1/4 arc-degree Daily Optimum Interpolation SST version 2 (dOISST.v2 and referred as 'NOAA OI' in this study; (Banzon et al., 2016) to assess how global warming has impacted the ocean along the area of study (Figure 6). Ocean warming was characterized both in terms of SST warming rates and the trend in the yearly duration of marine heatwaves. We used data derived from AVHRR due to their long temporal span and because AVHRR has been shown to out-perform other remotely sensed datasets in coastal areas (Lima and Wethey, 2012). For each individual pixel, the climatology was obtained following (Schlegel and Smit, 2018). Average warming rates were then calculated as the slope of the linear regression of seasonally detrended SST (obtained after subtracting the climatology) versus time (Lima and Wethey, 2012). To compute the rate of change in the yearly duration of marine heatwaves, we first detected marine heatwaves (90th percentile as threshold) following (Schlegel and Smit, 2018), then summed the number of heatwave days per year and finally calculated the slope of the linear regression of the total of heatwave days versus time. In a final step, SST warming rates and the trend in the yearly duration of marine heatwaves from pixels overlapping surveyed locations were, extracted, and their relationships with changes in the composition and structure of communities (described below) were investigated through Pearson's correlations.

Two surveys, set about 15 years apart, were carried out in 42 rocky shores displaced between the north of Ireland and Morocco (2003/05-2017/19; Figure 6C). Operators differed between the two assessments, but were cross-calibrated, thus helping to ensure estimates were comparable. The logistics required for the sampling of such an extensive geographic area prevented the collection of a time-series of data. Sampling sessions were always scheduled during spring tides, thus ensuring maximum emersion of the intertidal area, and were carried out from the low tide level zone, delimited by the occurrence of red seaweeds (Rhodophyta), through the mid-tide zone, where mussel beds are usually distributed, to the high tide zone, where mussels cease to exist and barnacles, limpets and few seaweeds species subsist. The same methodology was used during all assessments. The composition and abundance of each community was synthesized from a) 15 quadrats haphazardly-placed in the low tide zone (50X50 cm) for seaweeds coverage estimation, with b) 10 quadrats (30X30 cm) randomly placed in the mid-tide zone for the estimation of both the percentage of cover of mussels and barnacles, and for the individual counting of all other co-occurring marine invertebrates, and c) with 30 minutes ad libitum transects where a semi-quantitative estimation of species abundance was done following a modified version of (Crisp and Southward, 1958) scale (EACFOR: E_extremely abundant; A_abundant; C_common; F_frequent; O_occasional; R rare). Species percentage of coverage was later converted into semi-quantitative



abundance estimations following (Hiscock, 1981), and, for each species, the highest EACFOR category assigned between the different sampling methods was preserved. Seaweed thalli or animals of dubious classification, and especially turf covers, were collected and classified in the laboratory with the help of a stereomicroscope and taxonomic guides. The taxonomy currently accepted of all species was accessed through the World Register for Marine Species database (WORMS; http://www.marinespecies.org/). Percentages of the cover of species which have recently been reclassified as one (e.g., *Acrosorium uncinatum* is now referred as *Cryptopleura ramosa*) were summed. A total of 173 taxa were identified (Plantae: 93, Chromista: 36, Animalia: 41, Fungi: 2, Bacteria: 1), providing a baseline from which tracking future changes in communities' composition also for areas which floras and faunas had been overlooked.

Methods: 'Thermophilization' of intertidal assemblages

We investigated changes in Community Temperature Indices (CTIs) to test the hypothesis of 'thermophilization' of communities (De Frenne et al., 2013) across the NE Atlantic. If warming is inducing a proportionally greater increase in the frequency of occurrence of warm-water species on cold-water counterparts, temporal changes in CTIs are expected to be positive and correlated with regional warming. Community Temperature Indices were based on a subset of 139 species (Plantae: 71, Chromista: 31, Animalia: 37). We have excluded from calculations species *i*) present in less than 10% of surveyed locations, *ii*) classified only by genera (e.g., Corallina sp), *iii*) with dubious classification and very different ranges of distributions (e.g., *Gelidium pulchellum* and *Gelidium pusillum*), *iv*) that cannot be discriminated without genetic analysis (e.g., *Mytilus edulis* from *Mytilus galloprovincialis*), given the inability to define their global distributions with accuracy.

Calculations followed Burrows et al. (2019)'s methodology for rocky shore communities, where a species thermal affinity (STI) is defined by the median of the average coastal temperatures within its ranges of distribution. The global distribution of each species was derived from the Ocean Biogeographic Information System (OBIS; https://obis.org/), the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), literature reports on species occurrence, and our surveys data. Within range temperatures were obtained by averaging NOAA OI daily SST (Banzon et al., 2016) from 1982 to 2018 from pixels adjacent to the coastline. Quantiles of within-range temperatures were weighted by pixels area using the cosine of the latitude.

Changes in the thermal affinity of intertidal assemblages were, finally, obtained by subtracting CTIs (based on data collected during the second survey) based on communities' most recent compositions (S2) to that in the past (S1). The different contributions of cold and warm water species to changes in CTIs were also investigated. An increase in CTI only informs that a greater contribution of warm-water species relative to the total abundance of species in the communities has occurred, but not if it is the outcome of an increase in the total abundance of warm-water species or of a decrease in cold-water counterparts. A species affinity to cold or warm waters is defined with respect to the time and location where it occurred. A positive difference between a species STI and local temperature define the species' warm-affinity, and vice-versa. NOAA OI daily SSTs from pixels overlapping surveyed locations were extracted for the calculation of local temperatures, defined as the average of SSTs recorded during the 5 years antecedent to the year when each location was surveyed.

Results

<u>Coastal warming in the NE Atlantic</u> - Coastal warming was characterized for the area of the NE Atlantic that extends from the British Isles to northern Morocco (latitudinal range: 30°-60°;



Fig.1 A and B), revealing marked regional variability in both the rate of SST change and in the trend in the yearly duration of marine heatwaves.



Figure 6. Ocean warming in the NE Atlantic is characterized in this study both in terms of A) SST warming rates, and B) the trend in the yearly duration of marine heatwaves (NOAA OI; 1982-2018). C) The area of study. The composition and abundance of species present in 42 intertidal rock communities (circles) displaced in six different countries (colors) were surveyed twice, about 15 years after their first assessment (2003/05 and 2017/18).

The areas warming the most were, respectively, the Irish Sea, the English Channel (especially in the French margin), the Bay of Biscay and southern Portugal, where temperatures have increased by approximately 0.3 to 0.4 °C/decade since 1982. The SST rate of change that emerged in these analyses is above the warming rates calculated by Lima (Lima and Wethey, 2012) on the same dataset but on a time-series of data extending only to 2010, highlighting that a marked increase in water temperatures likely occurred in the last 8 years, the period at the end of which our second survey took place. Along scattered areas of the coast of these same regions, and mainly in the Bay of Biscay and southern Iberia Peninsula, a marked increase in the duration of extreme hot events has also emerged (10 - 25 days/decade), significantly contributing to the warming pattern observed in these areas (R^2 = 0.28, p < 0.001).

The western margin of Ireland has also experienced consistent warming, although temperatures increased at a slower pace (0.2-0.3°C/decade). Weak or no warming, and much lower trends in the increase in the yearly duration of extreme events were instead recorded in Brittany and along the western margins of the Iberian Peninsula and Morocco, where upwelling occurs (Alvarez et al., 2011; Froidefond et al., 1996; Kämpf and Chapman, 2016). Recent climate-impacts studies focusing on this oceanographic process highlighted that a periodic uplift of cold waters is linked to reduced warming nearshore, thus suggesting a buffering effect of upwelling at the coast (Seabra et al., 2019; Varela et al., 2018).



<u>'Thermophilization' of the NE Atlantic intertidal communities</u> - The CTI has emerged as a reliable metric for the tracking of reconfigurations in the NE Atlantic intertidal communities. Values of CTI during both surveys were broadly in line with the longer-term trend in temperature of surveyed locations (1982-2018; Figure 7A).



Figure 7. The CTI has emerged as a reliable metric for the tracking of reconfigurations in the NE Atlantic intertidal communities. (A) The values of CTI during both surveys were broadly in line with the longer-term trend in temperature of surveyed locations (1982-2018). A 'thermophilization' of the NE Atlantic intertidal communities is occurring in the direction of warming. A majority of communities (26 of 42) present increased CTI values than in the past, with warmer affinities in assemblages which experienced the highest increase in SST change (B and C).

At temperatures above 18° C, however, the CTI ability to detect changes in communities' thermal affinities is partially lost. This could be consequent to an inaccurate definition of the southern ranges of distribution of warm-water species because of an unbalanced effort in the study of intertidal communities in sub-tropical regions than in northern Europe. The thermal affinities of those species which are typically encountered in north Africa and in the Mediterranean could, therefore, be underestimated. On the other side, the reason behind this pattern could be merely biological. Large portions of the coastline south of Morocco is characterized by a sandy substratum. It is possible that rocky shore species with even warmer affinities than the ones encountered in the southernmost locations surveyed in this study occur at distances above their dispersal abilities. Finally, it is possible that communities in northern Morocco are more stable than those at higher latitudes, and that higher warming rates are necessary for inducing perceptible redistributions. If that would have been the case, however, a significant correlation between differences in CTIs and long-term trends in temperatures would have emerged (R²= 0.09, p= 0.054).

Changes in CTIs between surveys confirm that, in the majority of cases (26 out of 42), communities' redistributions are going in the same direction of warming (range in CTI increase: 0.04-1.78 °C). The greatest positive shifts have occurred in those communities which experienced the highest warming rates (R²= 0.18, p< 0.01, Fig. 2 B) and the greatest increase in heatwaves duration (R²= 0.19, p< 0.01, Fig. 2 C). Curiously, the remaining communities evidenced an overall affinity towards colder temperatures, although with lower absolute values of change (CTI decrease: 0.04 to 0.68°C; 50th quantile: -0.25°C).

An increase and a decrease in the abundance of both cold and warm-water species occurred in the past 15 years. Positive shifts in CTIs, however, resulted from an increment in the total abundance of warm-water species rather than in the loss of cold-water counterparts (Figure 8 A and D).



Warm-water species



Figure 8. Positive shifts in the thermal affinity of the NE Atlantic intertidal assemblages are associated with an increase in the total abundance of warm-water species (A) rather than to a decrease in cold-water counterparts (D). Species with warm affinities increased in abundance mainly in those locations which experienced the highest warming rates (B), and where a positive, despite non-linear, increase in the duration of heatwaves occurred (C). Increased and decreased abundances of cold-water species were observed across locations but are not explicable through warming metrics (E-F).

The total abundance of species with warm affinities increased mainly in those locations which experienced the highest warming rates (R^2 = 0.29, p < 0.01, Fig. 3 B), and where a positive, albeit non-linear, increase in the duration of heatwaves occurred (R^2 = 0.06, p = 0.114, Fig. 3 C). Redistributions of intertidal assemblages in SW England, NW France, and northern Spain, the areas of the NE Atlantic which have warmed the most since 1982, are therefore in line with climate-impact hypothesis of 'thermophilization' of assemblages induced by global warming.

Discussion

The composition and structure of the NE Atlantic intertidal communities have markedly changed in the past 15 years. Species turnover has occurred in all assemblages, and some of them have lost up to 50% of their previous pool of species. Local biodiversity is being replaced by novel anthropogenic systems that are more diverse but characterized by a dominance of warm-water, turfs-forming species. Shifts towards low-lying mat structures were found to be linked to warming, and to have occurred along those regions of the NE Atlantic where average temperatures have increased at least 0.6-0.8 °C since 1982, and extremely hot temperatures have occurred 10 to 25 days more each decade (SW England, France, northern Spain, mainly). The observed patterns of change are in line with the intrinsic definition of 'turfs': multispecies assemblages of short algae which share an extensive low-lying morphology, and that tend to be fast-growing, opportunistic, and higher stress-tolerant compared with macroalgae (Airoldi, 1998; Connell et al., 2014). Their rapid vegetative propagation is suggested to determine their



success in competitive interactions for space and in the resistance to disturbance (Airoldi, 1998).

An increasing number of studies are reporting global expansions of turf-forming species at the expense of canopy-forming algae (Feehan et al., 2019; Filbee-Dexter et al., 2016; Filbee-Dexter and Wernberg, 2018; Muguerza et al., 2017; Smale, 2019; Voerman et al., 2013; Wernberg et al., 2016). In localized areas of the N Atlantic, for instance, coastal warming has induced consistent declines of fucoids (Order *Fucales*) and kelps (mainly species of the Order *Laminariales*) by directly or indirectly affecting their survival and resilience (Feehan et al., 2019; Filbee-Dexter and Wernberg, 2018; Voerman et al., 2013; Wernberg et al., 2010). Space availability due to the loss of canopy has, therefore, represented an opportunity for warm-adapted turfs to rapidly expand and subsequently inhibit the recolonization of larger size species, thus forming an alternative stable state (Feehan et al., 2019; Filbee-Dexter and Wernberg, 2018; Petraitis and Dudgeon, 2004).

4.1.2. Rocky intertidal communities in UK coastline

Objective

The MarClim project is tracking changes in the population abundances and biogeographic range limits of 82 species of intertidal invertebrates and macroalgae of boreal, Lusitanian, and invasive origins around the coastline of the UK and northern France in response to climate change.

Study area and data description

Approximately 100 rocky shores are surveyed annually around the UK Regional Seas and the Brittany coastline of France. All MarClim survey locations are located in areas of extensive, exposed intertidal rocky reef or artificial, hard, coastal structures/defences away from areas of coastline that are heavily developed or utilized for social or economic purposes, and avoiding riverine and estuarine outputs. This reduced the likelihood of acute anthropogenic factors skewing the data and masking any potential climate change signals. Sites were also selected to fall within, or adjacent to marine SACs, SSSIs, Ramsar sites, EMSs and MCZs where possible to provide additional information for use by site managers. All existing MarClim sites were locations surveyed in the 1950s and/or subsequent decades.

At every MarClim site, categorical SACFOR abundance scores are recorded for a suite of 82 species including 49 species of ectothermic invertebrate and 33 species of macroalgae from boreal 'coldwater', Lusitanian 'warmwater' and invasive non-native geographic ranges.

At each of the three shore levels, high hshore (upper eulittoral), mid-shore (mid eulittoral) and low shore (lower eulittoral), six digital photographs are taken of 5x5 cm quadrats at each shore height to record barnacles present on the shore on the flattest possible areas of bedrock. Species counts have been subsequently undertaken for all individuals > 2 mm in the laboratory using digital image analysis. Statistical analyses and modelling have shown that 6 replicates at each shore height is the required number to permit multivariate analysis of species-level changes and use for general linear regression modelling (Burrows et al. 2006).

Ten replicate 0.25 m² quadrats are randomly placed within the midshore zone on areas of bedrock or large boulders with homogeneous surfaces (Figure 3). Pools, cracks and crevices and patches of macroalgae were avoided. The slope of the rock, percentage cover of adult barnacles, algae and mussels are recorded in each quadrat. All limpets greater than 10 mm in size are counted and identified to species level.



Three replicate searches of either 1, 2, 5, or 15 minutes duration, depending on the population density, were made separately for the Lusitanian warmwater species *Phorcus lineatus* and *Steromphala umbilicalis* in the area of the shore where each of the two warmwater indicator species were most abundant. Cobble and small boulders were turned to ensure all individuals were collected, and returned to their original orientation after the search. The maximum basal diameter of every individual was measured in mm to 2 decimal places and population size frequencies calculated from the data. No counts were done at the northeast England sites as neither species occurs that far north.

Results

The dataset has been grouped in 4 regions (Figure 9). In 2 out of 4 sea regions, CTI increase significantly (Figure 10). In the two cases, tropicalization is the dominant processes.



Figure 9. Regions considered in the analysis of rocky intertidal communities.





Figure 10. CTI analysis of rocky intertidal communities of UK coastline.

4.1.3. Demersal fish in the North-East Atlantic

Introduction and objective

Fish communities worldwide are responding to global warming through shifts in mean thermal affinity, which can be represented by the community temperature index (CTI). Using long-term monitoring of marine demersal fishes across the North Atlantic, we decomposed CTI changes into four underlying processes: tropicalization (increasing warm-affinity), deborealization (decreasing cold-affinity), borealization (increasing cold-affinity), and detropicalization (decreasing warm-affinity), for which we examined spatial variability and drivers.

<u>This study has been published in:</u> McLean, M., D. Mouillot, A. A. Maureaud, T. Hattab, M. A. MacNeil, E. Goberville, M. Lindegren, G. Engelhard, M. Pinsky, and A. Auber. 2021. Disentangling tropicalization and deborealization in marine ecosystems under climate change. *Current Biology* 31:4817-4823.e4815. <u>https://doi.org/10.1016/j.cub.2021.08.034.</u>

Below, we describe the data we selected for the North-East Atlantic, and analysis undertaken to be subsequently compared with other regions and taxa.

Study area and data description

Freely available long-term monitoring data on marine fish communities from six bottom-trawl surveys were downloaded from DATRAS-ICES (the Database of Trawl Surveys¹). These surveys encompass a range of marine eco-regions across the North Atlantic were we examined changes in the CTI. The bottom-trawl surveys included the North Sea (NS-IBTS), Baltic Sea (BITS) and the Scottish (SWC-IBTS) International Bottom Trawl Surveys, the French Surveys (EVHOE) in the NE Bay of Biscay and the Spanish Surveys (SP-NORTH and SP-PORC) in the southern Bay of Biscay². All surveys use standardized sampling protocols, where bottom trawls are towed for an average of 30 min and the species composition and

¹ <u>https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx</u>

² <u>https://datras.ices.dk/home/descriptions.aspx#FRA</u>



abundances of all captured fishes are identified and recorded to the finest taxonomic level possible. The spatial coverage and resolution differed across surveys, and we therefore aggregated trawl surveys to $1x1^{\circ}$ spatial grid cells. The length of time series also differed between surveys, and we therefore examined the period 1980–2015, which maximized temporal overlap between surveys. The arithmetic mean of each single species abundance was calculated for each year on each ecoregion. Within each region, only grid cells with > 20 years observations were selected for further analysis.

Results

Results indicated that CTI closely tracked changes in SST, increasing in 72% of locations. However, 31% of these increases in CTI were primarily due to decreases in cold-affinity species, thus reflecting a process of deborealization. However, increases in warm-affinity species were also prevalent, but not ubiquitous. More specifically, tropicalization was stronger in areas that were initially warmer, experienced higher rates of warming, or were generally deeper. Conversely, deborealization was stronger in areas that were closer to human population centers or that had higher community thermal diversity. When CTI (and temperature) increased, species that decreased were more likely to be living closer to their upper thermal limits or to be commercially exploited. Additionally, warm-affinity species that increased in abundance had smaller body sizes that are linked to environmental conditions, human impacts, community structure, and species characteristics in terms of key life history traits.

The analysis of the same data limited to North-eastern Atlantic and grouped in 4 regions, yield the following results. The surveys BITS, EVHOE, NS-IBTS and SWC-IBTS were represented by 118, 183, 179 and 105 demersal fish species, respectively. Significant increases in CTI were observed in all ecoregions: BITS (0.024°C/year), NS-IBTS (0.026°C/year), EVHOE (0.024°C/year) and SWC-IBTS (0.035°C/year (Figure 11b). Similarly, increasing trends in SST were observed in all ecoregions (Table 1). Despite the increasing trends in CTI and SST, significant correlations between SST and CTI were found only for NS-IBTS and SWC-IBTS (Figure 11c). The underlying processes contributing to the observed changes in CTI differ slightly between regions, but the predominant process overall involve tropicalization: BITS (71%), EVHOE (53%), NS-IBTS (76%) and SWC-IBTS (72%) (Figure 11a).

Desian	period	period	SST_ch	SST_cha	ST100m_	ST100m_c	CTI_ch	CTI_cha	tropicali	deboreal	boreali	detropica	r2,CTI_v
Region	_init	_ena	ange	nge_p	cnange	nange_p	ange	nge_p	zation	Ization	zation	lization	5_551
North East Atlantic BITS (Baltic Sea)	1991	2020	0.033	0.002	0.029	0.138	0.024	0.000	0.715	0.033	0.246	0.007	0.123
North East Atlantic EVHOE (N Bay of													
Biscay French+South UK)	1997	2019	0.006	0.321	-0.011	0.035	0.024	0.002	0.535	0.196	0.169	0.100	0.056
North East Atlantic NS-IBTS (North													
Sea)	1981	2020	0.028	0.000	0.012	0.050	0.026	0.000	0.766	0.081	0.138	0.016	0.419
North East Atlantic SWC-IBTS	1985	2010	0.034	0.000	0.027	0.000	0.035	0.000	0.724	0.171	0.069	0.035	0.316

Table 1. Trends of SST and CTI for demersal fish of the NE Atlantic by ecoregions.





Figure 11. CTI trends of demersal fish in NE Atlantic.

4.1.4. Pelagic fish distribution and phenology in NE Atlantic waters

Introduction and objective

Poleward distributional shifts and phenological adjustments are universal ecological responses to ocean warming. Though they are commonly addressed as independent processes, phenology usually depends on the latitudinal location where an organism lives. Such interaction can mask the actual impacts of warming and may even constrain the ability of a species to cope with ocean warming. Here, we propose a framework to analyse alternative acclimatization pathways that accounts for pure distributional shifts, pure phenological adjustments, and mixed, intermediate pathways balancing both responses.

The specific objective was to analyse the patterns of spawning activity of horse mackerel (*Trachurus trachurus*) and Atlantic mackerel (*Scomber scombrus*) in the northeast Atlantic during the last three decades (1992-2019). Our main objective is to test whether the spawning activity of these two pelagic species have been affected by interannual changes in sea temperature, and to partition the relative contribution of the distributional shifts *versus* phenological adjustments to explain the thermal niche tracking.

<u>This study is summarised below, and a detailed version has been submitted in:</u> Chust, G., F. González Taboada, P. Alvarez, L. Ibaibarriaga. Acclimatization pathways in marine species to track ocean warming. Submitted to *Fish and Fisheries* in May 2022.

Study area and data description

Temperature data of the sea surface - We characterized the potential impact of climate warming on the spawning activity of horse mackerel and Atlantic mackerel in the North East Atlantic margin using daily retrievals of the temperature of the ocean surface from NOAA



Optimum interpolation 0.25° daily sea surface temperature analysis (DOISST version 2.1, Sep. 1981–present) (Huang et al., 2021). We retrieved data from the Advanced Very High-Resolution Radiometer (AVHRR)-only product from the Pathfinder Version 5 dataset (Casey et al., 2010), which ensures temporal homogeneity of satellite observations (Reynolds and Chelton, 2010).

Spawning data from scientific surveys - We analysed changes in the spawning activity of horse mackerel and Atlantic mackerel based on the triennial Mackerel and horse mackerel Eggs Surveys (MEGS) (ICES, 2020b), which have been sampling the abundance and distribution of their planktonic eggs (count per m²) along the Northeast Atlantic since 1977 (Figure 12). To ensure a homogeneous survey coverage and prevent biases, we excluded data from earlier surveys and focused our analyses on the period 1992 to 2019. The surveys coordinate several vessels to simultaneously sample the entire spawning grounds of both species. Surveys start in January in the southern end to match the earlier seasonal onset of spawning in warmer waters, and continue until July by gradually allocating sampling effort northwards as the spawning season progresses.



Figure 12. Average abundance of horse mackerel and Atlantic mackerel eggs, pooled across development stages, based on the triennial MEGS surveys conducted between 1992 and 2019. The grey crosses are true absences. Orange square corresponds to the defined window to ensure a constant latitudinal coverage during each survey (see text for detailed explanation).

Observed egg counts of all developmental stages were converted to density estimates following standard procedures to adjust for differences in gear characteristics, sampling depth and filtered volume during each tow (ICES, 2019; Smith and Richardson, 1977). During the survey, samples are examined onboard to enable each vessel to adjust survey extent to changes in the distribution of spawning areas within each season and between years. *A priori*, each vessel continues sampling on the same grid line until it accumulates two consecutive zero counts for Atlantic mackerel eggs or larvae, although some years this rule is not achieved (Bruge et al., 2016b).

Methods

We first explored the potential covariation between the phenology and spatial extent of spawning grounds, using data surveyed triennially by the Working Group on Mackerel and horse mackerel Egg Surveys (WGMEGS) from 1992 to 2019 (ICES, 2020b). These scientific


surveys provide fishery independent data used to assess population abundance and temporal trends in both species. Then, we analysed the magnitude of phenological and latitudinal changes in spawning activity in relation to interannual sea temperature variation. If a species responds to warming period with respect to cold years, the spawning is expected to shift northward or/and adjust the timing earlier in the year. Finally, we explored the potential contribution of density dependent and other environmental factors to explain the distinct response of the two species.

Results

The spawning habitat of horse mackerel and Atlantic mackerel along the Northeast Atlantic European shelf experienced significant surface warming in spring (Apr-Jul) during the last four decades (0.223 ± 0.048 °C per decade, Figure 13). MEGS survey years covered a wide range of conditions, with an average difference in mean seasonal temperature of half a degree between cool, normal and warm years, and a difference above one degree between the coolest (2013) and the warmest (2007) years in the record. The pace of the seasonal cycle also varied with latitude and between survey years, with an advance up to one month between cool and warm years in the onset of temperatures above 10° C (*i.e.* a lower bound of optimal spawning conditions for both species, Figure 13).



Figure 13. Average temperature of the ocean surface over the potential spawning areas of horse mackerel and Atlantic mackerel along the Northeast Atlantic European shelf during the last four decades (1982-2021). Areal weighted averages were calculated for each year during the peak of spawning season (Apr-Jul) based on daily sea surface temperature (SST) data from the NOAA Optimum interpolation 0.25° daily sea surface temperature analysis (OISST version 2.1, Sep. 1981–present, see Huang et al. 2021 and <u>www.ncdc.noaa.gov/oisst</u> for further details). Survey years are highlighted with a text label and by a colour that codes whether they correspond to a cool, normal, or warm year according to the relative ranking of their seasonal temperatures. The grey line corresponds to the linear trend estimate at the bottom of the panel.

To explore changes in the latitudinal and timing centre of gravity of each species, we analysed the response to environmental drivers grouping MEGS surveys into cool, normal and warm seasons (Figure 14). The grouping based on the thermal characteristic of each season resulted in separated classes that confirmed the contrasting response of each species to interannual changes in temperature (Figure 14). Variability in the centre of gravity of horse mackerel for different thermal conditions aligned preferentially along the phenological axis, with an average advance of 20 days that is consistent with the difference of ~0.5 °C between cool and warm seasons. On the other hand, the arrangement of the centre of gravity of Atlantic mackerel under different thermal conditions aligned along the latitudinal axis and was consistent with a



poleward displacement in response to temperature (~280 km poleward in warm vs cool seasons).



Figure 14. Spawning activity of horse mackerel and Atlantic mackerel grouped according to the thermal regime of MEGS survey years. The centre of gravity of spawning activity was characterized by the distribution of egg abundance in the niche space defined by their spatial location (latitude) and phenology (day of the year) in the corresponding year. Survey years are highlighted with a text label and by a colour that codes whether they correspond to a cool, normal, or warm year according to the relative ranking of their seasonal temperatures (Figure 3). The dots correspond to the centre of gravity estimated for each survey year, and the ellipses enclose a 75th of the distribution for each thermal class.

Discussion

The two species showed contrasting responses to warming; horse mackerel advanced the timing of spawning (11.7 days / °C of warming), whilst Atlantic mackerel shifted poleward (369 km / °C of warming). The narrower reproductive thermal niche of horse mackerel resulted in a tight coupling between latitude and timing of spawning and small-scale distributional shifts that are consistent with geographical attachment, and an acclimatization strategy constrained to an advanced earlier phenology. Atlantic mackerel shifted its distribution due to its wider thermal reproductive niche, which enables prolonged migrations and widespread, almost synchronous spawning at all latitudes along the Atlantic margin. These results support our framework underpinning that acclimatization pathways to warming can combine, or exclude, timing and poleward shift. The strategy selected by the species probably depends on its biological traits such as migration patterns. These new insights are useful for fisheries management and to improve species habitat projections under climate change.

4.2. Bay of Biscay and Iberian coast

4.2.1. Marine forests in North Iberian Peninsula

Introduction and objective

Marine seaweed forests are together with seagrasses, the foundation of submerged vegetated ecosystems of coastal waters worldwide. Seaweed forests species include habitat-forming primary producers such as large canopy species like kelps (*orders of Laminariales and Tilopteridales*) and intertidal fucoids (eg. *Fucus* spp, *Ascophyllum nodosum*) (Wernberg and



Filbee-dexter, 2019). These species often dominate intertidal and shallow subtidal rocky coasts and are key components of coastal ecosystems, contributing to their biodiversity, structure and functioning (Smale et al., 2013). Marine forests provide food, shelter and habitats for a variety of organisms such as apex predators (sea mammals and seabirds), fish, invertebrates and other seaweeds, and support complex food webs in coastal zones, promoting healthy artisanal fisheries (Bertocci et al., 2015). Marine forest may lessen coastal erosion by buffering waves and reducing the movement of sand and pebbles (Løvås and Tørum, 2001). Additionally, the role of marine forests as a carbon sink has been highlighted as a climate change mitigation strategy. Accordingly, their carbon sequestration capacity should not be neglected (Froehlich et al., 2019). Furthermore, marine forests could also act as rescuers of climate change-sensitive species by ameliorating environmental harnesses (Bulleri et al., 2018). In this context, marine seaweed forests are highly relevant natural capital in all rocky shores. These biodiversity-rich ecosystems are gaining recognition as cost-effective nature-based solutions (NBS) to tackle some of the threats imposed by climate change (Krause-Jensen and Duarte, 2016).

The coast of northern Portugal hosts the southernmost North Atlantic seaweed forests of several cold-adapted species like *Laminaria hyperborea, Saccharina latissima, Ascophyllum nodosum* or *Fucus serratus*. Iberian upwelling is probably key in maintaining those northerly communities at these latitudes by provisioning cold and nutrient-enriched oceanic waters during the summer season. In the Northern littoral, they have been traditionally used with stranded seaweeds used to fertilize orchards for centuries ("masseiras"). Yet, an abrupt local extirpation and fragmentation of populations has been reported (Casado-Amezúa et al., 2019), mostly linked to recent climate change (Franco et al., 2017). Typical of cold waters, marine forest species are highly sensitive to ocean warming, particularly in their distribution edges where species are more often in suboptimal conditions and suffer the effects of multiple accumulative stressors (Steneck, 1982).

Unfortunately, there is a general scarcity of monitoring programs able to provide long-term evidence of changes in the abundance and distribution of these species (Krumhansl et al., 2016). Additionally, we lack a good understanding on the causes driving their decline and this baseline information is urgently needed in order to promote effective management and restoration actions (Araújo et al., 2016).

Here, we explore the changes in abundances of intertidal (5 locations) and subtidal assemblages (5 reefs from a rocky coastal area) from Northern Portugal.

Study area and data description

The study was undertaken in the Northern Portugal coast, considering 5 beaches at low intertidal rocky shore, i.e., Carreço, Praia Norte, Amorosa (Viana do Castelo), Eléctricos (Vila do Conde) and Aguda; and 5 subtidal reefs in the region of Viana do Castelo to Esposende (Table 2).



 Table 2. Localities considered in Northern Portugal coast study for the intertidal and subtidal seaweed communities, with indication of coordinates, time frame of the CTI analyses and main characteristics.

Beaches	Coordinates	Time frame	Measurement unit considered	Main characteristics
Carreço (Viana do Castelo)	41.741982 -8.878258	Winter 2006-2008, 2019, 2021	Cover (%)	low level Intertidal 8 to 21 species, 15±3 for whole period Dominant species: turf <i>Chondracanthus</i> <i>acicularis</i>
Praia Norte (Viana do Castelo)	41.696783 -8.853827	Winter 2006-2008, 2019, 2021	Cover (%)	low level Intertidal 5 to 21 species, 13±3, decreasing trend over time Dominant species: increasing trend for theturf <i>Chondracanthus acicularis</i>
Amorosa (Viana do Castelo)	41.643418 -8.826093	Winter 2006-2008, 2019, 2021	Cover (%)	low level Intertidal, 5 to 24 species, 15±4, decreasing trend over time Dominant species: increasing trend for the turf <i>Chondracanthus acicularis</i>
Eléctricos (Vila do Conde)	41.309672 -8.741715	Winter 2006-2008, 2019, 2021	Cover (%)	low level Intertidal 5 to 24 species, 14±4, decreasing trend over time
Aguda (Aguda - Gaia)	41.045092 -8.653918	Winter 2006-2008, 2019, 2021	Cover (%)	low level Intertidal 7 to 18 species, 13±2 Note: different species composition compared to other 4 intertidal localities
Viana do Castelo- Esposende region	41.5 °	Summer 2012 2018	Biomass (g wet weight per 0.25 m2)	Subtidal, 5 random reefs 26 to 41 species Dominant species changed over time, the kelp <i>Laminaria hyperborea</i> was dominant in 2012; yet, declined in 2018, while <i>Saccorhiza</i> <i>polyschides</i> increased

Assemblages from the low intertidal were sampled in the winter-spring from 2006 to 2008, (February/March or beginning of April) and again from 2019 and 2021 (March/April). At each beach, 15 quadrats, 50 x 50 cm in size (0.25 m²), were haphazardly selected on the rocky shore to visually assess the cover of percentage of sessile macroalgae and invertebrates. Sampling was carried out using a plastic frame divided into 25 sub-quadrats and giving each taxon a score of 0 (absent), 1 (occupation of 1/4 of the sub-quadrat), 2 (occupation of 1/2 of the sub-quadrat), 3 (occupation of 3/4 of the sub-quadrat) or 4 (occupation of the entire sub-quadrat) to each sub-quadrat. The final percentage covers were calculated by summing over the 25 sub-quadrats (Araújo et al., 2016). All species were characterized to species-level, as much as possible, or to the genre level (e.g., *Ulva* spp., *Ceramium* sp., *Codium* sp.).

Assemblages from the subtidal were surveyed through diving campaigns conducted in the summers of 2012 and 2018. In each year, five rocky reefs from Viana do Castelo to Esposende coast were selected and sampled. In each reef, six quadrats of 50×50 cm (0.25 m²) haphazardly deployed on the top of the horizontal bottom reef, using SCUBA diving. In each quadrat, all macroalgae were collected using scrapers. Samples were labeled and transported to the laboratory in cool boxes and frozen until processing (Tuya et al., 2012). Seaweeds within each sample were identified to the lowest feasible taxonomic level, mostly species, and weighed (wet weight after removing excess water by shaking).



Kelp forest densities were examined in these reefs using 25 m long and 4 m wide transects where the density of kelp individuals was recorded. In a similar approach to the protocol described above, 5 transects were done per reef.

Methods: CTI analyses

Analyses of changes in CTI were performed to the macroalgae communities for each surveyed locality/beach, considering the winter periods for the different years (Table 1), using the codes provided by Task 1.1 leaders. Some individuals were only identified to the genus level (e.g. *Ulva* spp.). Yet, for CTIs' analyses, only species level was considered, meaning that, on average, 20% of the community abundance was not considered.

Results

CTI - Considering the intertidal sampling localities, there was a statistically significant increase in the CTI over time from 2006 to 2021 in Praia Norte and Amorosa (slope = 0.061 and 0.08, p < 0.01; respectively), corresponding to almost 1 °C increase for a 15-year time span. Although without statistical significance, there was an increase of CTI in Carreço and Eletricos (slope = 0.04 and 0.03, respectively, p > 0.05). For Aguda, located at the lowest latitude, a negative tendency was observed (slope = -0.01, p > 0.05). Contributing for these differences in the higher latitude beaches is the declining trend of species, such as *Chondrus crispus*, *Mastocarpus stellatus and Cryptopleura ramosa*, with affinity to colder waters, together with the increasing one of the turf *Chondracanthus acicularis*, *Codium tomentosum*, and the opportunist *Ulva rigida*, all warm-water species. Indeed, *Chondracanthus acicularis* has become a dominating species in recent years, particularly in Praia Norte and Amorosa.

Time could explain the variation in CTI at all locations (Adjusted $R^2 = 0.92$). Although not significant, at all locations seawater temperature tended to decrease with time (p > 0.05). Likewise, there was no significant correlation between the annual temperature and the CTI. The increase in CTI over time was mostly the result of a slight decrease in cold affinity species (deborealization), such as those mentioned above in all localities with an exception of Aguda, where there was an increase of cold affinity species (borealization) coupled with a decrease of warm adapted ones (detropicalization, Figure 15). Interestingly, despite the proximity of the beaches, whose distance among them varies within 8 to 90 km, there were differences in the mean CTI, with the beach located most to the south, Aguda, presenting the lowest mean CTI score. We would expect higher mean CTI at this beach, yet, species composition also confirms this trend since it is considerably different than other beaches, still presenting a high cover of species such as *Mastocarpus stellatus, Lomentaria articulata, Callithamnion tetricum and Calliblepharis jubata* (Rushel-Pires *per. com.*), with cold water affinity. A detailed study on local temperature dynamics along this coastal stretch is therefore imperative.

Deliverable D1.3– (Report on cross-region long-term monitoring of the marine biodiversity in relation to climate change and variability)





Figure 15. Contribution of single species to the different processes underpinning changes in CTI for the intertidal communities (Carreço, Praia Norte, Amorosa, Eléctricos and Aguda) and subtotal communities (Viana). Cold-affinity and warm-affinity are at the left and right side of the vertical line. Blue = Borealization; Yellow = Deborealization; Red = Tropicalization; Purple = Detropicalization.

Regarding subtidal communities, there was a slight decrease in CTI from 2012 to 2018 in kelp communities of Viana do Castelo. As there are only two time periods, it was not possible to get a statistical significance for it using the methodology proposed. Yet, there is a difference of almost 1°C in the temperature of water both at the surface but also at to 100 m depth.

Highly contributing to this result in a 6-year period is the decline of the boreal kelp species *Laminaria hyperborea*, as documented by Franco et al. (2017) and the increase of the *Laminaria ochroleuca*, a species with affinity for warmer temperatures.

Overall, results showed that the structure of seaweed assemblages along North Portugal seashores changed in the last decade. This evidence reinforces the idea that coastal communities are responding quickly to climate change (Poloczanska et al., 2016), even when environmental drivers do not show obvious trends.

Kelp forest abundance changes - Figure 16 shows the observed changes in abundance of the kelp species in the area of North Portugal. Abundance patterns show positive trend when all the kelp species are pooled (*Saccorhiza polyshides, Laminaria ochroleuca, Laminaria hyperborea and Phyllariopsis* spp.). This trend is dictated by similar positive trend in annual kelp species (*Saccorhiza polyshides* and *Phyllariopsis* spp.) with higher abundance (Figure 16B) and disguise the decline of the perennial kelp species (*Laminaria ochroleuca, Laminaria hyperborea*), that showed a negative trend (Figure 16C).



Similar to the whole assemblage study, the results of the monitoring program of kelp densities during the last decade in the area shows a temporal turnover of species. In this case, perennial kelps are being replaced by annual species with unexplored effects on the functioning of the whole ecosystem. These trends emerge despite the annual variability habitual in these type of assemblages (Araújo et al., 2016).

Kelp forest declining trend in these Southernmost populations of Europe is recognized as a threat to coastal ecosystems in this area and recently OSPAR (de Bettignies et al., 2021) has launched a recommendation for further protection of these habitats³.



Figure 16. Temporal trends (2011-2021) of kelp abundance at the Northern region of Portugal, Viana do Castelo. (A) All kelp species, (B) Annual kelp species and (C) Perennial kelp species. Solid circles are the observed mean values, solid lines represent mean of the model fits for abundance ok kelp individuals in the frame of individual transects (n=25) using negative binomial regression, and shading is the SEM of models fitted (Franco et al. in prep.).

³ <u>https://www.ospar.org/documents?v=46286</u>



4.2.2. Climate regime shift and biodiversity redistribution in the Bay of Biscay

Introduction and objective

The marine ecosystems of the Bay of Biscay (North-eastern Atlantic) and its littoral have been extensively studied in relation to climate change, e.g., (Chust et al., 2011; Gimeno et al., 2011; Hemery et al., 2008; Le Marchand et al., 2020; Le Treut, 2018). However, this bay lacks of integrative and continuous surveillance connecting multiple observations from physics to biodiversity within the context of climate change, and covering from monitoring to future scenarios. The vulnerability of the coasts of the Bay of Biscay to the combination of extreme events and potential change in present climate regimes (de Santiago et al., 2021; Liria et al., 2011; Marcos et al., 2012) is increased by anthropogenic activities such as the urban and industrial discharges, water treatment, the exploitation of marine resources, tourism, marine traffic, oil spills, and the high human use of the marine space (Borja et al., 2019). Coastal biotic communities have already changed according to sea warming rates, e.g. macroalgae (Casado-Amezúa et al., 2019), mammals and seabirds (Hemery et al., 2008). Similarly, commercial fish species in the bay, such as anchovy, mackerel, and tuna, are experiencing responses to sea warming with expected changes on latitudinal distribution and migration (Bruge et al., 2016b; Caill-Milly et al., 2018; Chust et al., 2019; Erauskin-Extramiana et al., 2019a).(Bruge et al., 2016b; Caill-Milly et al., 2018; Chust et al., 2019; Erauskin-Extramiana et al., 2019a). Implementing an integrated system for monitoring climate change and its effects through the selection of the main climate change indicators and their standardization would allow continuous monitoring of trends, and generation and validation of projection models. This is key to define the best adaptation criteria that must be carried out at specific coasts to face future threats such as flooding, and revise management actions on environmental conservation and local fisheries within the climate change context.

The main objective of this study is the temporal trend analysis of physicochemical and biological variables in the Bay of Biscay, including specifically the Basque coast (northern Spanish coast), within the context of ongoing climate change. The specific objectives are: 1) to define potential indicators of Climate Change (iCC) in the marine and coastal environment and identification of available time series, 2) to develop and apply the time-series analysis methodology based on Generalized Additive Mixed Models (GAMMs), and 3) to interpret the iCC trends within the context of climate change and other potential drivers. These specific objectives will enable in the future to develop and improve potential scenarios for impacts of climate change by means of downscaled models, as well as defining adaptation strategies. The objective of this study was to undertake a time-series analysis of climate change indicators within the Bay of Biscay, including the Basque coast. We used an integrated and flexible methodology, based on Generalized Additive Mixed Models, to detect trends on 19 indicators (including marine physics, chemistry, atmosphere, hydrology, geomorphology, biodiversity, and commercial species).

This study is summarised below, and a detailed version has been published in: Chust, G., M. González, A. Fontán, M. Revilla, P. Alvarez, M. Santos, U. Cotano, M. Chifflet, A. Borja, I. Muxika, Y. Sagarminaga, A. Caballero, I. de Santiago, I. Epelde, P. Liria, L. Ibaibarriaga, R. Garnier, J. Franco, E. Villarino, X. Irigoien, J. A. Fernandes-Salvador, A. Uriarte, X. Esteban, D. Orue-Echevarria, T. Figueira, and A. Uriarte (2022). Climate regime shifts and biodiversity redistribution in the Bay of Biscay. *Science of the Total Environment*, 803, 149622. doi: https://doi.org/10.1016/j.scitotenv.2021.149622.



Study area and data description

At the Bay of Biscay, and in particular on the Basque coast, there are various monitoring programmes for physicochemical and biological variables with specific purposes: weather forecast and emergency prevention, hydrographic monitoring, water quality, biological conservation, fisheries stock assessment, and sustainable management of the coastal erosion. These programmes, together with earth observation monitoring programmes, collect multiple variables that we used here to derive the specific indicators for the marine climate change monitoring.

Below, we detailed the most relevant in terms of biodiversity shifts.

<u>Phytoplankton community data</u>: phytoplankton species abundance (cell L⁻¹) during a 13-year period (2008-2020) were employed to calculate the CTI. These data had been obtained in surface waters of the southeastern Bay of Biscay (Muñiz et al., 2020). To calculate the CTI the mean of two stations were used: the onshore station L-OK10 (located on a depth of 30 m) and the offshore station L-RF10 (on 110 m); these were the stations with the longest data series, among those with the lowest anthropogenic nutrient pressure. Field work involved quarterly sampling of surface (0-1 m) water. Cell counting and identification were conducted under an inverted microscope following the Utermöhl technique (Muñiz et al., 2020). Only the identifications that reached the species level were considered for the CTI. Phytoplankton cells consist of micro- and nanophytoplankton (2-200 μ m). These included diatoms, dinoflagellates, and other groups, such as, chlorophytes, cryptophytes, euglenophytes, haptophytes and ochrophytes. The arithmetic mean of each single species abundance was calculated for each year.

<u>Hard bottom macrobenthic community data</u>: Rocky benthic communities including hard bottom macroinvertebrates, lichens and macroalgae were analysed during 2002-2020. Samples were collected every 3 years in 26 intertidal transects along the Basque coast, perpendicular to the shoreline. A semi-quantitative sampling of surface coverage similar to Braun-Blanquet³ was carried out across the transects, scaled from 1 (low coverage) to 7 (high coverage). The arithmetic mean of each single species abundance was calculated for each year.

<u>Soft bottom macrobenthic community</u>: Soft-bottom macroinvertebrates were sampled with a van Veen grab and identified to species level to estimate abundance (ind/m²) and community composition at all stations along the coast within "Littoral Water Quality Monitoring and Control Network". The sampling of most of the stations started in 1995. At each station, an annual sample was taken in winter, consisting of 3 replicates. The data used in the calculation of CTI includes stations with the lowest anthropogenic impact. The arithmetic mean of each single species abundance was calculated for each year.

<u>Fish body size</u>: Three monitoring programmes for fish stock assessment in the Bay of Biscay were used for deriving indicators for fish body size of European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*): 1) BIOMAN surveys (BIOMass of ANchovy) (Erauskin-Extramiana et al., 2019a; Santos et al., 2018) on anchovy spawning. Egg abundance and weight-at-age of adult anchovy data have been collected annually during these surveys, between 1989 and 2019. 2) JUVENA surveys on juvenile anchovy (Boyra et al., 2013). Anchovy juveniles were sampled since 2003 in September. Randomly sampled juvenile specimens were measured to the nearest mm for standard length (SL) to determine the length-frequency distribution in 0.5 cm length classes (Aldanondo et al., 2016). Juvenile length was transformed to weight according to a size-length allometric relationship (weight = $0.0027(\text{length})^{3.3066}$). 3) The monitoring programme PELGAS in the Bay of Biscay is an integrated ecosystem survey conducted by Ifremer (Doray et al., 2018; ICES, 2020a; Véron et



al., 2020), which was used for deriving indicators for weight-at-age of sardine from 2000 to 2019.

Methods

We computed the Community Temperature Index (CTI, see section 3.2.3) and used Generalized Additive Mixed Models (GAMMs) to analyse time series (see section 3.3 Time series statistical methods).

Results

The results of all time series trends are indicated in rates per decade (= dec⁻¹) and shown in Table 3. Below, we detailed also the most relevant in terms of biodiversity shifts and its potential drivers: sea temperature, CTI, body size.

Table 3. Indicators of Climate Change (iCC) and time series analysis. CTI: Community Temperature Index. BoB: Bay of Biscay. LM: Linear Model. GAMM: Generalized Additive Mixed Model; MNES: Monitoring Network of the Ecological Status; St: station; Basque: Bq; Bilbao-V: Bilbao-Vizcaya. In all GAMMs, fixed effects are a linear term of the variable Year in decimals and a seasonal component of the variable day of the year (Day) fitted with a smoothing term (s, with a maximum of degrees of freedom of k=6), and imposing cyclicality (bs="cc"), whilst random effects (REff) are indicated in the corresponding time series.

iCC	Time series	Zone	Units	Period	Trend (/dec)	р
Sea Temperature	At surface	Bq coast	С°	1946-1980	-0.216	0.0001
	At surface	Bq coast	°C	1980-2019	0.232	0.0000
	At surface (Satellite)	BoB	°C	2003-2019	0.106	0.0092
	At surface (reanalysis)	BoB	°C	1986-2019	0.252	0.0000
	At different depths (0-100 m)	Bq coast	°C	1986-2019	0.154	0.0002
Salinity	Integrated (0-100 m)	Bq coast		1986-2019	-0.022	0.1620
	Integrated (0-100 m)	Bq coast		1993-2019	-0.015	0.4810
	At different depths (0-100 m)	Bq coast		1993-2020	-0.030	0.0095
Structure of water column	14 °C isotherm depth	Bq coast	m	1993-2019	-5.038	0.0167
	14 °C isotherm depth (April to December)	Bq coast	m	1993-2019	-2.426	0.3165
	Thermal stratification	Bq coast	°C/m	1993-2019	-0.011	0.7240
	Thermohaline stratification	Bq coast	kg.m⁻ ³/m	1993-2019	0.015	0.3528
	Winter mixed layer depth	Bq coast	m	1986-2019	-21.39	0.0391
Dissolved oxygen	At surface	Bq coast	mg/l	1995-2019	0.144	0.0000
	At 25 m	Bq coast	mg/l	1995-2019	0.090	0.0000
	At 100 m	Bq coast	mg/l	1995-2019	-0.253	0.0001
Nutrients	NH4	Bq coast	µmol/l	1995-2019	0.171	0.0227
	PO4	Bq coast	µmol/l	1995-2019	0.013	0.0080
	NO2	Bq coast	µmol/l	1995-2019	-0.005	0.1998
	NO3	Bq coast	µmol/l	1995-2019	0.279	0.0038
	SiO4	Bq coast	µmol/l	1995-2019	0.447	0.0000
Sea level	Tide gauge	BoB	cm	1992-2019	1.534	0.0407
	Tide gauge	BoB	cm	1943-1990	2.481	0.0000
	Tide gauge	BoB	cm	1995-2019	0.375	0.5053
	Tide gauge	BoB	cm	1992-2019	1.800	0.0000
	Tide gauge	BoB	cm	1915-2016	1.860	0.0000
	Tide gauge	BoB	cm	1846-2019	1.253	0.0000
	Tide gauge	BoB	cm	1992-2019	2.481	0.0000
	Tide gauge	BoB	cm	1992-2019	3.532	0.0000
	Tide gauge	BoB	cm	1943-2019	1.968	0.0000
	Tide gauge	Bq coast	cm	1992-2019	2.965	0.0000
	Satellite	BoB	cm	1993-2019	2.418	0.0000
Wave	Hs	Bq coast	cm	1991-2019	1.791	0.5709
	Pw	Bq coast	kW/m	1991-2019	0.504	0.6492
	Hs90	Bq coast	cm	1991-2019	16.799	0.0373
Air Temperature	Daily mean	Bq coast		1928-2019	0.1947	0.0000
	Daily mean	Bq coast		1980-2019	0.3057	0.0562
	Daily mean	Bq coast		1971-2017	0.3693	0.0000
	Daily mean	Bq coast		1980-2017	0.2480	0.0000
Sunshine hours	Daily sunshine hours	Bq coast	h	1947-2019	0.0462	0.0031
	Daily sunshine hours	Bq coast	h	1980-2019	0.2615	0.0000

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iCC	Time series	Zone	Units	Period	Trend (/dec)	р
Wind	Daily mean speed	BoB	m/s	1998-2019	0.2497	0.0043
	Daily maximum speed	BoB	m/s	1998-2019	0.3630	0.0012
	Daily mean U	BoB	m/s	1998-2019	-0.0658	0.7728
	Daily mean V	BoB	m/s	1998-2019	-0.1934	0.1520
Precipitation	Annual accumulated	Bq coast	mm	1980-2019	34.530	0.2630
	Annual accumulated	Bq coast	mm	1980-2019	78.650	0.0667
	Annual extreme P75	Bq coast	day	1980-2019	0.214	0.1870
	Annual extreme P75	Bq coast	day	1980-2019	0.542	0.0108
River flow	Annual accumulated	Bq coast	m ³ s ⁻¹	1997-2019	0.155	0.0065
	Annual accumulated	Bq coast	m ³ s ⁻¹	1992-2019	0.086	0.0738
	Annual accumulated	Bq coast	m ³ s ⁻¹	1999-2019	0.115	0.0741
	Annual accumulated	Bq coast	m ³ s ⁻¹	1996-2019	0.033	0.5242
	Annual accumulated	Bq coast	m ³ s ⁻¹	1995-2019	0.024	0.6177
	Annual accumulated	Aquitaine	m ³ s ⁻¹	1967-2019	-0.066	0.0001
	Annual extreme P90	Bq coast	m ³ s ⁻¹	1997-2019	15.8	0.001
	Annual extreme P90	Bq coast	m ³ s ⁻¹	1992-2019	12.8	0.000
	Annual extreme P90	Bq coast	m ³ s ⁻¹	1999-2019	14.3	0.009
	Annual extreme P90	Bq coast	m ³ s ⁻¹	1996-2019	9.1	0.040
	Annual extreme P90	Bq coast	m ³ s ⁻¹	1995-2019	8.4	0.056
	Annual extreme P90	Aquitaine	m ³ s ⁻¹	1967-2019	n.sig.	>0.05
Beach coastal line	Low tide	Bq coast	m	2010-2019	17.180	
	High tide	Bq coast	m	2010-2019	-4.490	
Beach area	Supratidal area	Bq coast	m2	2010-2019	-1535.1	0.8437
	Intertidal area	Bq coast	m2	2010-2019	30544.1	0.0023
Zooplankton (copepods)	Total biomass	BoB	mg/m ³	1998-2019	2.27	<0.001
Hard-bottom benthos	CTI	Bq coast	°C	2002-2019	0.2700	0.0030
Soft-bottom benthos	CTI	Bq coast	°C	1995-2019	0.1600	0.0320
Fish	Weight juveniles (anchovy)	BoB	cm	2003-2019	-1.399	<0.001
	Weight age 1 (anchovy)	BoB	g	1987-2019	-2.5	<0.001
	Weight age 2 (anchovy)	BoB	g	1987-2019	-3.3	<0.001
	Weight age 1 (sardine)	BoB	g	2000-2019	-1.20	<0.001
	Weight age 2 (sardine)	BoB	g	2000-2019	-1.27	<0.001
	Weight age 3 (sardine)	BoB	g	2000-2019	-1.42	<0.001
	Weight age 4 (sardine)	BoB	g	2000-2019	-1.35	<0.001
	Weight age 5 (sardine)	BoB	g	2000-2019	-1.35	<0.001
	Weight age 6 (sardine)	BoB	g	2000-2019	-1.09	0.0005

<u>Sea temperature</u>: The filter and trend change analysis of the historical time series of SST of the Aquarium of Donostia-San Sebastián (1946-2019) identified a trend reversal in 1980. The analysis of trends in each of the periods with GAMMs provided the following estimates: 1) a decreasing trend at a rate of -0.22 ± 0.06 °C dec⁻¹ from 1946 to 1980, and 2) an increasing trend in the most recent period (1980-2019) at a rate of 0.23 ± 0.04 °C dec⁻¹ (Figure 17). The analysis of the time series of satellite-based SST of the Bay of Biscay for the period 2003-2019 indicated a significant increasing trend with a rate of 0.11 ± 0.04 °C dec⁻¹ (p=0.00923). The analysis of reanalysis-based SST in May in the Bay of Biscay in the period 1986-2019 showed a significant increase with a rate of 0.25 ± 0.05 °C dec⁻¹ (p=0.00923). The sea temperature in the water column (0-100 m depth) (from 1986 to 2019) at the L-RF10 (D2) station showed an increasing trend of 0.15 ± 0.04 °C dec⁻¹.





Figure 17. Analysis of Sea Surface Temperature (SST) of the Donostia-San Sebastián Aquarium in the period 1980-2019 with GAMMs: decomposition into seasonal component and trend. A) Original data of the time series; B) Partial residuals throughout the year (points) and seasonal component of the model (blue line). C) Partial residuals of the time series after removing the seasonal component (i.e., deseasonalized, grey points) and the linear trend component of the model (blue line with red confidence interval). The partial residuals have been scaled up by adding the average SST of the whole series.

<u>Community Temperature Index</u>: Concerning, **phytoplankton community**, 149 species were analyzed. The results show a slight decrease in the CTI over time, not significant (-0.104 °C/year) and a predominance of tropicalization (36%) and borealization (27%) of the phytoplankton community (Figure 18). **Hard bottom macrobenthic community**: 146 species were analyzed. The results indicated a slight non-significant increase in CTI over time (0.008 °C/year) as well as with SST (Figure 181b). The ecological processes that predominate in the hard substrate benthic community were the tropicalization (41%) and borealization (37%) (Figure 18). **Soft bottom macrobenthic community**: 579 species were analysed. The CTI results for soft-bed benthic macroinvertebrates are very much in line with the results for hard-bed benthos: a small non-significant increase in CTI over time (0.010 °C/year) was detected (Figure 18b). The ecological processes that predominate in the soft substrate benthic community are tropicalization (46%) and borealization (42%) (Figure 18a).





Figure 18. CTI trends in phytoplankton, hard-bottom and soft bottom benthic communities in the Basque coast (Bay of Biscay).

<u>Fish body size</u>: The analysis of annual mean weight at age of anchovy in the Bay of Biscay showed a general decrease (1.3-3.3 g dec⁻¹) for the three age classes (age 1-2 from BIOMAN survey and juveniles from JUVENA survey) and particularly for recent years (Figure 19). The break-point detection analysis has detected a change in trend in 2005 for ages 1 and 2; beyond this year, weight decreases substantially. A sharp decline starts in 2011 for all ages. The trend analysis of annual mean weight at age of sardine in the Bay of Biscay from PELGAS showed a general decrease (1.1-1.4 g dec⁻¹) for the six age classes.





Figure 19. Variability over time of the mean weight at age of the Bay of Biscay for anchovy and sardine. Anchovy data from Bioman – adults – and JUVENA – juveniles – surveys. Sardine data from PELGAS Survey of Ifremer, taken from: (Doray et al., 2018; ICES, 2020a). For anchovy, the fishery was closed between 2005 and 2010 (vertical bars).

Discussion

The results of 87 long-term time series analysed (~512,000 observations), in the last four decades, indicate four groups of climate regime shifts: 1) A gradual shift associated with CC starting in the 1980s, with a warming of the sea surface down to 100 m depth in the bay (0.10-0.25 °C per decade), increase in air temperature and insolation. This warming may have impacted on benthic community redistribution in the Basque coast, favouring warm-water species relative to cold-water species. Weight at age for anchovy and sardine decreased in the last two decades. 2) Deepening of the winter mixed layer depth in the south-eastern bay that probably led to increases in nutrients, surface oxygen, and chlorophyll concentration. Current increases on chlorophyll and zooplankton (i.e., copepods) biomass are contrary to those expected under CC scenarios in the region. 3) Sea-level rise (1.5-3.5 cm per decade since 1990s), associated with CC. 4) Increase of extreme wave height events of 16.8 cm per decade in the south-eastern bay, probably related to stormy conditions in the last decade, with impacts on beach erosion. Estimating accurate rates of sea warming, sea-level rise, extreme events, and foreseeing the future pathways of marine productivity, are key to define the best adaptation measures to minimize negative CC impacts in the region.

4.2.3. Estuarine fish communities of La Gironde (Bay of Biscay)

Study area and data description

The Gironde estuary, located SW France is one of the largest European estuary (Lobry et al., 2003). Its surface area is approximately 625 km² at high tide. Between the ocean (seaward of a transect drawn between Pointe de Grave and Pointe de Suzac; Figure 20) and the upstream salinity limit (Bec d'Ambes), it is 76 km long. The watershed covers 81,000 km² and the mean annual rate of freshwater discharge is now around 800 m³.s⁻¹ (Chevillot et al., 2019; Pierre and Lobry, 2021).





Figure 20. Location of the sampling stations in the Gironde estuary. T2 = Transect 2. From Lobry et al. (2006).

The dataset comes from the Blayais Power Plant monitoring program. In the frame of this program, fish sampling surveys are conducted monthly since the late 1970s. Data from 1985 was selected since the sampling protocol is considered stable and standardized from this date.

Three sampling sites are located along four transects (Figure 20). On each site, simultaneously, one fishing sample is made near the surface and one near the bottom. Surface samples are taken using two 4.0×1.0 m rectangular frame nets fitted both sides of the boat. The subconical nets have a stretched mesh size of 18 mm in the main section and 2.8 mm in the terminal section. For the benthic samples, a 2.0×1.2 m frame is used with runners keeping the frame 0.2 m above the bed. The net meshes are identical to those used for surface samplings. A sampling lasts five to seven minutes and is performed in daytime, between the halfway stage of the flood tide and high tide slack, with the gear being towed against the current. Details in the sampling protocol can be found in (Lobry et al., 2006) and (Chevillot et al., 2017).

The monitored fauna consists mainly of small fish species and juveniles of larger species. 47 species are considered in the analysis. They can be divided into 4 ecological guilds (Marine M, Freshwater FW, Diadromous DIA and Estuarine Resident ER) following (Franco et al., 2008) and (Courrat et al., 2011).

SST temperatures were extracted at the mouth of the estuary (45.57, -1.25) considering a range of 2 degrees for both latitude and longitude.

Results

Analysing our entire estuarine fish community, we observed a significant increase of our CTI (Figure 21), mainly through deborealisation (75%, Figure 22). The CTI change was estimated to 0.043 and the SST one to 0.015 (both significant).





Figure 21. Evolution of the CTI between 1985 and 2020 for fish community of the Gironde estuary.



Figure 22. Processes involved in the CTI trend for fish community of the Gironde estuary.

It seems that warming leads to a disappearance of the cold affinity fish species in the Gironde estuary. The seven orange points correspond to *Platichthys flesus, Pomatoschistus minutus, Gasterosteus aculeatus, Alosa fallax, Anguilla anguilla, Osmerus eperlanus* thus, mainly diadromous fishes suffer deborealisation. Indeed, warming plays a role in their disappearance but many other factors may exacerbate their decline as they share their lifecycle between sea and freshwater (e.g., pollution, habitat degradation).

As our fish community is a mix of marine and freshwater species, we wonder if a focus on the marine species would lead to the same trend. Indeed, maybe freshwater species could have been more sensitive to warming as they cannot escape from their habitat. This hypothesis was not confirmed, removing the freshwater fish community (12 species) from our analysis leads to the same trend: a significant CTI change of 0.04, 74% due to deborealisation.

4.3. Baltic Sea

4.3.1. Seagrasses: Eutrophication, trawling and warming challenges eelgrass recovery

Introduction and objective

Global losses over the 20th century placed seagrass ecosystems among the most threatened ecosystems in the world, with eutrophication, and associated deterioration of the submarine light environment identified as the main driver. Growing appreciation of the ecological and



societal benefits of healthy seagrass meadows has stimulated efforts to protect and restore them, largely focused on reducing nutrient input to coastal waters.

Here, we analyzed a unique data set spanning 135 years on eelgrass (*Zostera marina*), the dominant seagrass of the northern hemisphere. Due to the importance of eelgrass in the region, which was already acknowledged around 1900, a unique long-term data set on eelgrass depth limits is available from Danish coastal waters. The data represent nation-wide information from around 1900 and 1930-1940, scattered information over the following decades, and yearly monitoring from the Danish national monitoring program since 1989. Long-term data on eutrophication, trawling and water temperature is also available from the region and allowed an analyses of long-term eelgrass trends in relation to changing stressors(Krause-Jensen et al., 2021).

<u>This study is summarised below, and a detailed version has been published in</u>: Krause-Jensen, D., C. M. Duarte, K. Sand-Jensen, and J. Carstensen. 2021. Century-long records reveal shifting challenges to seagrass recovery. *Global Change Biology* 27:563-575.

Study area and data description

Danish coastal waters are located in the transition zone between the brackish Baltic Sea and the saline North Sea. The region is characterized by extensive areas with shallow sandy seafloor in relatively protected microtidal, brackish waters, which offer ideal conditions for eelgrass. The region is, and used to be, a key distribution area for eelgrass in the Baltic Sea (Boström et al., 2014). The historical distribution area of eelgrass in Danish coastal waters was about 6700 km² around the year 1900 with most coastal areas covered by eelgrass to large depths (down to 11 m) (Petersen, 1914). The current distribution area is not quantified but is lower than 2200 km², which is the modelled potential distribution area (Staehr et al., 2019). The lower colonization depth (depth limit) of eelgrass meadows, which is ultimately governed by water clarity, is a key indicator of ecological status, as it defines the edge of the eelgrass distribution area and the associated ecological functions.

Results and discussion

The long-term analysis showed major declines in eelgrass depth distribution, relative to the historic (1890–1910) situation, due to the wasting disease in the 1930s followed by eutrophication peaking in the 1980s, which reduced water clarity, and trawling, which has disturbed the seafloor (Figure 23). The analyses further highlighted that the meadows have only shown modest improvement in depth limits since then despite major mitigation of eutrophication, representing a halving of nitrogen inputs since the 1980s (Krause-Jensen et al. 2020). Moreover, across the past century, the Danish eelgrass meadows exhibited generally shallower colonization depth for a given submarine light penetration and, hence, increased apparent light requirements for eelgrass growth relative to the historic situation). This finding suggest that eelgrass recovery is limited by stressors in addition to shading caused by eutrophication, stressors which prevents eelgrass from growing as deep at light levels would allow.





Figure 23. Long-term means of eelgrass depth limits, Secchi depths, and eelgrass pressures in Danish waters. (a) eelgrass depth limits (EDLs) and (b) Secchi depths (SDs) for the open coastal areas (8 units) and estuaries (Limfjorden and "other estuaries/smaller straits"), (c) Nitrogen (N) input from land, (d) mean summer (June– August) surface water temperature, and (e) mussel landings (fresh biomass) as total and for the main harvesting areas with insert showing a close-up for Samsø Belt and Little Belt. Lines are 5-year moving averages. From Krause-Jensen et al. (2020).

The analysis indicates that bottom trawling, e.g. for mussels, as well as intense recent warming (0.5°C per decade, 1985–2018) may suppress eelgrass from fully recovering from eutrophication (Krause-Jensen et al., 2021). Hence, for a given light setting, trawled areas often had shallower eelgrass meadows than non-trawled areas). Warming and associated heat waves may hamper eelgrass meadows as temperatures above 25°C cause a negative carbon balance and increased mortality. Warming was most severe in eutrophic, turbid waters, where the meadows remained confined to very shallow waters. By contrast, clear-water areas appeared to offer eelgrass refugia from warming in deeper, cooler waters if trawling did not prevent the meadows from reaching those refugia (Krause-Jensen et al., 2021).





Figure 24. Representation of the relationship between eelgrass depth limit and water transparency and stressors. Arrows show that eutrophication and trawling force eelgrass populations toward shallower waters where they are increasingly exposed to warming, which also stresses the populations. Management to control eutrophication and trawling reverse the arrows, and can be supported by restoration effort. From Krause-Jensen et al. 2020.

The study concluded that efforts to reduce nutrient input and thereby improve water clarity have been instrumental for avoiding a catastrophic loss of eelgrass (Figure 24). However, future management must reduce both eutrophication and bottom trawling to help eelgrass reach deeper, cooler refugia, which will increase resilience toward realized and further warming (Figure 25) (Krause-Jensen et al., 2021). Moreover, restoration is increasingly explored as means to accelerate eelgrass recovery in target habitats (Flindt et al., 2020).

4.4. Mediterranean Sea

4.4.1. Systematic review of climate change effects in the Western Mediterranean Sea

Introduction and objective

Climate change has strong ecological and socioeconomic effects worldwide (Mooney et al., 2009) and can have profound impacts on the state and distribution of coastal and oceanic habitats and marine organisms (Johnson and Lyman, 2020). The Mediterranean Sea is a global hotspot of marine biodiversity (Myers et al., 2000), and it is extremely vulnerable to human impacts, including human-driven climate change (Coll et al., 2010). In fact, the Mediterranean Sea is warming faster than any other area in the world, which may indicate that climate change effects can be very severe, such as what it occurs with heatwaves and mass mortality events (Garrabou et al., 2019; Ibrahim et al., 2021). In this context, the Western Mediterranean Sea is an interesting area of study due to the important biological, ecological, and socio-economic gradients of the region, the dependencies of human populations on marine resources, and the relatively large amount of information available about marine resources and their spatial-temporal dynamics (Coll et al., 2010; Margalef, 1985).

We aimed to start a systematic review to summarize available information on the environmental and biological effects of climate change in the Western Mediterranean Sea, while we identify gaps in knowledge. In this contribution, we present preliminary results.



Methods

We first conducted a literature review following a systematic approach, based on filtering and screening published articles from Scopus selected through the query: "climate change" AND "Mediterranean Sea" (query run on the 3rd of November 2021); and focused on the Western Mediterranean.

We then analysed the search results with the R package "*litsearchr*" following the steps described in (Grames et al., 2019), which allowed the automatic identification of search terms for our systematic review topic using keyword co-occurrence networks. We assigned a strength to each keyword in the network. In particular, when we arranged the terms in ascending order of strength, we discovered that "Western Mediterranean" showed one of the highest strengths in the network. Therefore, we did filter for all the papers containing "Western" in the abstract and screened their full text, in order to prepare the data for screening and be more specific in terms of the study area. Then, we selected only those papers that were related to our topic of interest "the effect of climate change on marine ecosystem" and geographic scope "Western Mediterranean", and considered any location within this geographical area.

During the screening of selected papers, we searched, among others, for information about geographic scope (e.g., local, NW Mediterranean, W Mediterranean, and whole Mediterranean), specific location of the study, methods to collect the data (e.g., experimentation, observations, remote sensing, modelling), data used for the study (e.g., environmental data, and biota), type of biota studied (e.g., fish, seabirds, corals, sponges, molluscs, phytoplankton, and zooplankton), habitat studied (e.g., pelagic, demersal, and benthic), main topic of the publication (e.g., fisheries, Marine Protected Areas (MPAs), and others) and Nature-Based Solutions involved (restoration, conservation, and harvesting).

Results and discussion

The first query on Scopus provided a total of 1994 published papers. We analysed the search results and identified the most important keywords that were related to our systematic review. Low levels of strength keywords mean that they have a low probability of relevance for the systematic review (Figure 25).





Figure 25. Strength analysis of the network of keywords identified in the abstracts of the papers. It is important to note that we removed "climate change" and "Mediterranean Sea" from the figure because they were the original terms of our query on Scopus and they were the two keywords with the highest rank.

We applied a filter in the abstract with the word "western" (see methods for more details), and we retrieved a total of 452 papers. After the screening of the full text form these 452 papers, we ended up with 226 papers for the review and discarded the others (e.g., that focused on the Eastern Mediterranean, Atlantic Ocean).

Results showed that the date of the studies ranged was from 1996 to 2022, and we found an increasing temporal trend in the number of papers published regarding the topic of interest (Figure 26A). Almost half of the papers (49%) characterized local dynamics, while 30% of the papers provided evidence for the entire W Mediterranean (Fig. 2B). Regarding the methods, 50% of the papers screened were based on observations, 29% were focused on modelling, 20% used remote sensing, and only 1% performed experiments (Figure 26C). The most common variables considered were environmental variables 74%, while 26% of the papers focused on biota (Figure 26D).

The most common focus of the publications that dealt with biota was about fish (40% of papers), followed by phytoplankton (30%), and zooplankton (10%; Figure 26E). Regarding the habitat of focus, 50% of the papers dealt with the pelagic environment, 30% were focused on the benthic one, and 20% were targeting the demersal habitat (Figure 26F). A total of 44% of the papers analysed related to fisheries issues and 6% dealt with Marine Protected Areas (MPA) (Figure 26G). Regarding the association with NBS, 65% of the publications were focused on conservation, 22% on harvesting, and 13% on restoration (Figure 26H).





Figure 26. Summary diagram of the studies considered in this review. A) Number of included papers per year of climate change effects in the Western Mediterranean Sea from 1996 to 2022; B) Geographical scope (local, NW Mediterranean, W Mediterranean, whole Mediterranean); C) Methods (experimentation, observations, remote sensing, modelling); D) Type of data (biota, environment); E) Type of Biota (fish, seabirds, corals, sponges, molluscs, phytoplankton, zooplankton); F) Habitat (pelagic, demersal, benthic); G) Topic of the publication (fisheries, MPAs, others); H) Nature-Based Solutions (restoration, conservation, harvesting).

This review aimed to summarize the available information regarding climate change in the Western Mediterranean Sea. Our preliminary results highlight an increasing temporal trend in the number of papers published regarding our topic of interest. As a geographical scope, half of the papers characterized local dynamics. Likewise, half of the papers were based on observations as a method. The available works are mostly focused on evaluating climate-driven impacts on environmental conditions, while the potential responses by biota have comparatively received less attention. Most of the papers dealt with the pelagic environment as a habitat; while the main topics of the papers were related to fisheries as a major concern among the scientific community; while conservation measures are proposed as the most plausible alternative to mitigate the impacts of climate change on marine ecosystems of the western Mediterranean. Overall, our preliminary review illustrates that currently available knowledge in the Western Mediterranean Sea has the potential to inform about climate change



effects. This knowledge can also be used to identify gaps of information and future research priorities in the region.

4.4.1. Non-native seaweed Caulerpa cylindracea

Introduction and objective

Fluctuations in abiotic conditions play a key role in regulating the abundance and distribution of marine species, including invasive ones (Brown et al., 2020; Burrows et al., 2020; Rilov et al., 2020). As the oceans are rapidly changing due to anthropogenic activities, long-term information on species abundance along with abiotic variables are essential to predict shift in species distributions and their ecological effects on ecosystem structure and functioning. Biological invasions are among the major threats to biodiversity and ecosystem functioning (Simberloff et al., 2013; Strayer, 2012). A large research effort has been devoted to identify the drivers of invasion success (Stachowicz et al., 2002; Levine et al., 2003; Lockwood et al., 2013; Bulleri et al., 2020), but the mechanisms underpinning temporal dynamics of invasive species have seldom been investigated. The establishment and spread of non-native species generally occur in areas with climatic and environmental conditions similar to those of their native range, however, seasonal and interannual fluctuations in abiotic conditions can alter invader performance, thus influencing their population dynamics (Bulleri et al., 2020; Levine et al., 2003; Stachowicz et al., 2002), but the mechanisms underpinning temporal dynamics of invasive species have seldom been investigated. The establishment and spread of non-native species generally occur in areas with climatic and environmental conditions similar to those of their native range, however seasonal and interannual fluctuations in abiotic conditions can alter invader performance, thus influencing their population dynamics (Brown et al., 2020; Chefaoui et al., 2019; Forsström et al., 2018; Menke et al., 2018; Murphy et al., 2017). Identifying the abiotic drivers regulating temporal patterns of abundance and distribution of non-native species is crucial for pinpointing areas most vulnerable to invasion and to predict how invader populations will respond to future climatic conditions.

The invasive macroalga, *Caulerpa cylindracea*, has become a common component of benthic assemblages in the Mediterranean sea, being able to colonize both rocky and sandy bottoms, from intertidal to subtidal habitats (Piazzi et al., 2016). This species shows strong seasonal fluctuations in abundance, alternating a period of vegetative growth in summer and a resting phase in winter, primarily driven by temperature (Ruitton et al., 2005). *C. cylindracea* is often more abundant in wave-sheltered areas (Iveša et al., 2015; Vaselli et al., 2008) and preferentially colonized complex biogenic substrata, such as those formed by algal turf and dead matte of *Posidonia oceanica*, which may favour the trapping and anchoring of its fragments under wave stress (Bulleri et al., 2011; Ruitton et al., 2005). In addition, an increase in seawater nutrient concentration throughout the year has been shown to positively influence *C. cylindracea* cover at the peak of its growing season (summer/early fall) (Uyà et al., 2017).

Here, we used data on *C. cylindracea* abundance, sampled repeatedly between 2005 and 2020, to assess whether interannual variations in environmental conditions affect the alga at the peak of its growing season, in both intertidal and subtidal habitats in the NW Mediterranean. The set of environmental conditions used for the analysis included seawater temperature, wave intensity and rainfall regime, which are likely to play an important role in determining the abundance and distribution of this species.



Data description and analyses

Data on *C. cylindracea* abundance were collected within the framework of descriptive and experimental studies, carried out between 2005 and 2020. The percentage cover of this species was estimated in shallow subtidal sites, at depths varying from 6 to 8 m, along an exposed rocky shore between the urban city of Livorno and Calafuria (NW Mediterranean, 43°30'N, 10°20'E). Data on *C. cylindracea* cover were collected every 1-2 years between 2005 and 2013 and again in 2020 (8 sampling years in total). Along the coast of Calafuria, *C. cylindracea* cover was also assessed in rockpools, between 2005 and 2020. We used data collected every 1-2 years between 2005 and 2010 and again in 2020 (6 sampling years in total).

For both subtidal habitat and rockpools, *C. cylindracea* cover was visually estimated in the field, during late summer-early fall, corresponding to the period in which *C. cylindracea* peaks in abundance, by means of a plastic frame subdivided into 25 sub-quadrats. A score from 0 to 4 was given to *C. cylindracea* in each sub-quadrat and the percentage cover was obtained by summing over the entire set of sub-quadrats. In 2008, benthic assemblages (including *C. cylindracea*) in subtidal habitat were photographed underwater, and images were processed in the laboratory to extract from each quadrat the percentage cover of each species, using the same method described above.

For the environmental variables, data on hourly seawater temperature (°C) and wind speed (m/s) were collected from the Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA, www.mareografico.it; station located in Livorno). Onshore winds (between 180 and 360° for the study sites) were used as a proxy of wave height, which was assumed to be positively correlated to wind speed intensity. Data on daily rain (mm) were collated from the Servizio Idrologico Regionale (SIR, www.sir.toscana.it; station located in Livorno). Data were divided into four periods throughout the year, each corresponding to a different phase of the life cycle of *C. cylindracea* (declining phase = October – November; resting phase = December – March; early-growing phase = April – June; fast-growing phase = July – August). We calculated mean and maximum daily values for seawater temperature and wind speed, while, for rainfall, we calculated maximum monthly values from total daily precipitation. Within each year, an average value of each metric (mean and maximum daily seawater temperature and wind speed and mean daily and maximum monthly precipitation) was calculated for each period of *C. cylindracea* growth.

Since the mean and maximum metrics of each environmental variable, within each period of *C. cylindracea* growth, were highly correlated, we performed statistical analyses separately for the mean and maximum metrics, for both habitats. For each metric, we, then, tested the collinearity of environmental variables by means of the variance inflation analyses (VIF) and discarded those variables with a VIF > 5. The final sets of uncorrelated environmental variables used in our analyses are reported in Table 4.



Table 4. Environmental variables with VIF < 5 for A) subtidal habitat and B) rockpools, separately for mean and maximum values. These variables are included as explanatory variables in the models.

Environmental variables	VIF
<u>(A) Subtidal habitat</u> Mean	
Fast-growing phase seawater temperature	4.431
Fast-growing phase wind speed	1.549
Fast-growing phase rainfall	3.056
Early-growing phase seawater temperature	1.319
Early-growing phase rainfall	2.074
Declining phase _ wind speed	2.156
Maximum	
Fast-growing phase seawater temperature	4.431
Fast-growing phase wind speed	1.576
Fast-growing phase rainfall	3.265
Early-growing phase wind speed	1.550
Early-growing phase rainfall	2.479
Declining phase _ wind speed	2.703
(\mathbf{D}) $\mathbf{D}_{\mathbf{r}}$, let $\mathbf{r} \in \mathbf{I}_{\mathbf{r}}$	
<u>(B) Rockpools</u> Mean	
Fast-growing phase seawater temperature	2.523
Fast-growing phase wind speed	1.885
Fast-growing phase rainfall	2.108
Early-growing phase rainfall	1.751
Maximum	
Fast-growing phase wind speed	1.069
Early-growing phase seawater temperature	1.158
Early-growing phase wind speed	2.652
Declining phase wind speed	2.694

For subtidal habitats, generalized linear mixed models (GLMM), assuming negative binomial distribution, were used to model the relationship between temporal patterns of abundance of *C. cylindracea* and explanatory variables (Table 5A). The environmental variables were included in the fixed part of the model, while the plot was included as a random effect in the model, as a subset of plots was repeatedly sampled through years. In the analysis of data from rockpools, zero-inflated GLMMs, assuming a gaussian distribution, were used to model the relationship between temporal patterns of *C. cylindracea* abundance and the selected environmental variables (Table 5B). The environmental variables were included in the fixed part of the model, while the pool was included in the random part of the model to deal with temporal autocorrelation (a subset of pools was repeatedly sampled through years). The GLMMs for both habitats were run using the *glmmTMB* R package (Brooks et al. 2017). The minimum adequate models (MAM) were generated by means of a step-backward selection procedure, using the Akaike information criteria.

Results

<u>Temporal patterns of C. cylindracea cover in the subtidal habitat</u> - Regarding the mean values of environmental variables, the MAM retained rainfall and wind speed, from early-growing (April – June) and declining (October – November) phases, respectively (Table 5A). The peak



abundance of *C. cylindracea* was positively related with increasing mean daily wind speed intensity in the period of its declining growth and with rainfall in the period of its early-growth (Table 5A, Figure 27a,b). The MAM fitted with maximum values of environmental variables retained seawater temperature from fast-growing phase (July – August), as explanatory variable (Table 5B). Peak *C. cylindracea* cover was negatively related with increasing maximum daily seawater temperature in the fast-growth period (Table 5B, Figure 27c).

Table 5. Results from GLMM used to assess temporal patterns of C. cylindracea cover in relation to A) mean and B) maximum values of environmental variables, during different growing periods, in the subtidal habitat. Coefficients, standard errors (SE) and p-values for explanatory variables retained in the minimum adequate model (MAM) are reported for the fixed effects, while estimates of variance (σ^2) and standard deviations (SD) are reported for the random effects.

Effect	Estimate	SE or	р
	or σ^2	SD	
(A) MAM model: mean values			
Fixed effects	Estimate	SE	
Intercept	-1.683	0.5	< 0.001
Early-growing phase _ rainfall	0.430	0.07	< 0.0001
Declining phase _ wind speed	1.412	0.2	< 0.0001
Random effects	σ^2	SD	
Plot	1.62 e ⁻⁰⁹	$4.02 e^{-05}$	
(B) MAM model: maximum values			
Fixed effects	Estimate	SE	
Intercept	24.02	1.85	< 0.0001
Fast-growing phase _ seawater temperature	-0.83	0.07	< 0.0001
Random effects	σ^2	SD	
Plot	2.32 e ⁻⁰⁹	$4.82 e^{-05}$	

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Figure 27. Relationship between C. cylindracea cover at the peak of the growing season (late August/early October) and (a) mean wind speed intensity (m/s) during the decay phase (autumn), (b) mean cumulative precipitation (mm) during the early-growth period (spring) and (c) maximum seawater temperature (°C) during the fast-growth period (summer) of the seaweed, in the subtidal habitat. Dots represent the observed values (mean \pm SE) in each year, whereas the black line represents the fitted line obtained by the negative binomial GLMM model.

<u>Temporal patterns of C. cylindracea cover in rockpools</u> - The MAM fitted with mean values of environmental variables retained seawater temperature from the fast-growing period (July-August), as explanatory variable (Table 6A). For maximum values, seawater temperature from the early-growing period (April-June) was included as explanatory variable (Table 6B). The

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peak abundance of *C. cylindracea* was negatively related with increasing mean and maximum daily seawater temperature in the fast- and early-growth periods, respectively (Table 6A,B; Figure 28a,b).

Table 6. Results of the GLMM used to assess temporal patterns of C. cylindracea cover in relation to A) mean and B) maximum values of environmental variables, during different growing periods, in the rockpools. Coefficients, standard errors (SE) and p-values for explanatory variables retained in the minimum adequate model (MAM) are reported for the fixed effects, while estimates of variance (σ^2) and standard deviations (SD) are reported for the random effects.

Effect	Estimate	SE or	р
	or σ^2	SD	_
(A) MAM model: mean values			
Fixed effects	Estimate	SE	
Intercept	99.241	25.17	< 0.001
Fast-growing phase _ seawater temperature	-3.847	1.03	< 0.0001
Random effects	σ^2	SD	
Pool	7.76	2.79	
Residual	41.66	6.46	
(B) MAM model: maximum values			
Fixed effects	Estimate	SE	
Intercept	297.63	83.99	< 0.001
Early-growing phase seawater temperature	-14.78	4.24	< 0.001
Random effects	σ^2	SD	
Pool	8.59	2.93	
Residual	42	6.48	

Figure 28 Relation between C. cylindracea cover at the peak of the growing season (late August/early October) and (a) mean seawater temperature (°C) during the fast-growth period (summer) and (b) maximum seawater temperature (°C) during earlygrowth period (spring) of the alga, in rockpools. Dots represent the observed values (mean \pm SE) in each year, whereas the black line represents the fitted line obtained by the gaussian GLMM model.





Discussion

Our analysis provides insights into the environmental conditions shaping the invasion dynamics of the well-established *C. cylindracea* in the NW Mediterranean. The subtidal population appears to be influenced positively by an increase in the spring cumulative precipitation and autumn wave intensity and negatively by high seawater temperature in the summer period. Similarly, warmer seawater in the spring-summer period negatively affected peak *C. cylindracea* cover in rockpools.

Temperature is one of the most important factors shaping species distribution and range limits (Eggert, 2012; Parmesan and Yohe, 2003). In marine systems, seawater temperature can affect physiological performance (e.g., reproduction, growth rate, body size) and survival limits of a variety of organisms, including seaweeds (Chefaoui et al., 2019; Murphy et al., 2017). Thus, the effects of temperature on different life stages of non-native species may regulate their performance once a new region has been colonized and may, subsequently, impact their long-term population dynamics and viability (Chefaoui et al., 2019; Forsström et al., 2018; Keller and Shea, 2021; Murphy et al., 2017). The negative influence of warmer seawater on the peak abundance of C. cylindracea documented in our analysis is in line with previous studies, showing a peak in the occurrence of the alga at about 20 °C and a sharp decrease at higher seawater temperature (Verbruggen et al., 2013). This seaweed displays a broad distribution in its native range, spanning from the temperate water of the western Australian coasts to the tropical waters of northern Australia (Sauvage et al., 2013; Verlaque et al., 2003). Thus, a negative influence of warmer seawater on peak C. cylindracea cover could indicate a reduced temperature tolerance range for introduced populations. Ocean warming due to climate change is predicted to shift seaweed abundance and distribution (Chefaoui et al., 2019; García Molinos et al., 2016). For instance, poleward expansions of species at cold range boundaries and retreats at warm edges have been documented in many areas around the globe (Chefaoui et al. 2019; Beas-Luna et al. 2020; Burrows et al. 2020). Our results suggest that the predicted seawater warming under future climate scenarios may change the distribution of C. cylindracea, with a potential retreat from currently occupied areas and a northward shift, as also predicted for other invasive seaweeds in temperate regions (Chefaoui et al., 2019).

Variation in the peak abundance of subtidal *C. cylindracea* was explained by cumulative precipitation during spring-growing phase. This could be the result of increased nutrient inputs to the subtidal habitat, due to run-off from overtopping cliffs during heavy rains. In line with previous experiments (Gennaro et al., 2015; Uyà et al., 2017), our results suggest that this species can take advantage of nutrients throughout different life stages of its seasonal growth, ultimately fostering its abundance at the summer peak. In addition, temporal patterns of subtidal *C. cylindracea* were also positively related to an increase in mean wind intensity during the decay season (fall). This result suggests that an increase in wave intensity in autumn, when thalli are fully grown, may enhance the generation and dispersion of high-quality propagules (e.g., fragments with stolon, fronds and rhizomes), sustaining the next season generation.

In rockpools, the peak abundance of *C. cylindracea* was influenced neither by rainfall nor by wind speed intensity. A recent experiment showed that nutrient enrichment during the resting phase could promote the spring regrowth of *C. cylindracea*, but there was no carry over effect on the summer peak in abundance (Uyà et al. 2017). In addition, patterns of invasion of rockpools are likely to be much more dependent on subtidal populations of surrounding areas, which may replenish rockpools with algal propagules, rather than variations in seasonal wind speed condition.

Our analysis highlights the importance of long-term monitoring data to identify factors regulating invasion dynamics and to predict future patterns of spread. To date, most long-term



observations of biological variables and environmental conditions are restricted to a limited number of key functional groups or limited to some geographical regions (Miloslavich et al., 2018). Including biological invasions into long-term monitoring programs can help to assess how invasive species can respond to environmental drivers and to identify areas most vulnerable to invasions, with the goal of implementing management and adaptive strategies. Finally, the identification of the mechanisms underpinning invasion dynamics is key to predict future spread of invaders under climate change (Chefaoui et al. 2019; Keller and Shea 2021). Our results indicate a possible reduction in the abundance and distribution of *C. cylindracea* in both subtidal and intertidal habitats under future climatic conditions, in response to seawater warming. Such negative effects might be partially offset by the increasing amount of rainfall and the intensity and frequency of storms which could provide *C. cylindracea* with greater nutrient availability and facilitate its dispersal.

4.4.2. Coralligenous habitats

Introduction and objective

Coralligenous assemblages are one of the biodiversity-richest ecosystems in the Mediterranean Sea, hosting more than 1,600 species (up to 10% of the Mediterranean marine biodiversity) (Ballesteros, 2006). Rather than a unique habitat, coralligenous assemblages represent a mosaic of different habitats allowing the development of assemblages ranging from the dominance of calcareous algae to invertebrates such as corals, sponges, bryozoans or tunicates. Beyond the inherent natural value of their exceptional biodiversity, coralligenous assemblages are an important source of ecosystem services for human societies, such as the provision of food, pharmaceutical products, or beautiful landscapes for diving and inspiration. Moreover, they serve as indicators for environmental change, reduce the turbidity of the water by retaining nutrients and sediments, and may have an active role as carbon sink (Paoli et al., 2017). Overfishing, habitat degradation, damage from recreational diving, mucilaginous algal aggregates and algal invasions have been known to impact coralligenous assemblages for long (Balata et al., 2007; Montero-Serra et al., 2015; Piazzi et al., 2018). Yet, ocean warming and marine heatwaves (hereafter, MHWs) have emerged in recent decades as the most important threat for Mediterranean coralligenous assemblages (Cerrano et al., 2000; Garrabou et al., 2009; Garrabou et al., 2019).





Figure 29. Map showing the three locations and dates where ecological and temperature data were collected to explore the ecological trajectories in marine heatwave-impacted vs. non impacted coralligenous assemblages (Studies i and ii).

Previous studies had provided fundamental insights regarding the resistance of individuals, populations and species of coralligenous assemblages to MHWs at local and regional scales (Cerrano et al., 2000; Gómez-Gras et al., 2019). Moreover, these previous studies had also provided hints about how the responses of organisms to MHWs cascade down to cause structural changes at the community level in these marine ecosystems, leading to changes in biodiversity (Verdura et al., 2019). However, the influence of MHWs on functional aspects of coralligenous habitats is much less clear, as it is the recovery capacity of key components of the coralligenous habitats in the long-term. Similarly, the lack of collaborative schemes has hindered the understanding of the spatiotemporal scales of MHW impacts across the Mediterranean basin, in spite of the accelerating warming trends.

Within the FutureMARES project, we have contributed to narrowing the above-mentioned knowledge gaps by: i) Using functional traits to link MHW-induced temporal changes in assemblage structure to potential effects on the ecosystem functioning in coralligenous assemblages. ii) Exploring the long-term (>15 years) recovery capacity from MHWs of populations of key habitat-forming octocoral species of these habitats. iii) Creating an open-access, standardized database on mass mortality records occurred across the Mediterranean basin since 1970 (MME-T-MEDNet database). iv) Assessing and integrating sea surface and in situ temperature data with mass mortality records across the Mediterranean basin during the exceptionally warm 2015-2019 period.

The first two studies were conducted in three MPAs of the NW Mediterranean Sea (Scandola NR, Port-Cros NP and Calanques NP; Figure 29), whereas the latter study was collaboratively conducted in 142 monitoring areas located across the entire basin (Figure 30). Thus, our results have provided the most updated view into the impacts of extreme events such as MHWs on Mediterranean coralligenous assemblages.





Figure 30. Map showing the 142 Monitoring areas where mass mortality surveys were conducted over the 2015-2019 period. Monitoring areas were considered as geographic areas (10-25 km coastline, e.g., a marine protected area and the nearby coast) sharing common environmental features. For those areas that have been monitored from 1-3 years, the size of the circles represents the number of monitoring years and their transparency is related to a mortality ratio on those areas. For areas with more than three years of monitoring, pie-charts have been used to represent the temporal trends in each of the four/five years of the study.

Several studies were conducted within the framework of FutureMARES project regarding the impacts of MHWs on populations, community and biodiversity of Mediterranean coralligenous habitats. <u>These studies on Mediterranean coralligenous habitats related to Task 1.1 and</u> summarised below have been published (or submitted) in:

- 1. Gómez-Gras, D., et al. (2021a). Ecol. Lett. 24(5), 1038-1051. <u>https://doi.org/10.1111/ele.13718</u>
- 2. Gómez-Gras D., et al. (2021b). Proc. R. Soc. B., 288, 20212384. https://doi.org/10.1098/rspb.2021.2384
- 3. Garrabou, J., et al. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. Submitted to *Global Change Biology*.

Results and discussion

<u>Impacts of MHWs</u> - Results demonstrate that MHWs have caused long-term alterations to the functional trait composition of coralligenous assemblages, leading to marked functional changes (Gómez-Gras et al. (2021b)). In particular, we first examined temporal trends of functional richness and functional identity (complementary facets of the biodiversity-ecosystem function relationship) on assemblages exposed to MHWs to different extents in Scandola and Port-Cros MPAs (Figure 29, Figure 30), and found that while non-impacted sites had remained functionally stable over the monitored periods, MHW-impacted ones had suffered long-term changes in their functional identity. Finally, we explored the trajectories of different functional groups and found a general MHW-driven collapse in a critical functional group related to the provision of structural complexity; the one of habitat-forming octocorals. Overall, these results demonstrate that MHWs are currently triggering long-term, systemic changes in the functioning



of coralligenous assemblages and exemplify how the stability of biodiversity-rich benthic assemblages can be compromised by the decline of just one or few pivotal species belonging to critical functional groups.

In addition, our results revealed that gorgonians, which are some of the most important habitatformers of the coralligenous assemblages, have a generally low recovery capacity from MHWs, even in the long-term (> 15 years) (Gómez-Gras et al. (2021a)). In particular, we observed a population collapse (in terms of biomass and density) in 5 out of the 5 populations that were monitored in our study after being impacted by a MHW in Scandola MPA in 2003. For the red gorgonian *Paramuricea clavata*, we found a biomass loss of about 75% from 2003, whereas for the *Corallium rubrum* monitored population, the biomass loss was higher than 90% of the initial one.

Interestingly, recurrent MHWs were observed in both Scandola and Port-Cros sites during the studied periods, which has likely contributed to both the functional changes and the lack of recovery observed. Worryingly, since MHWs are expected to become more frequent and severe in the Mediterranean Sea (Darmaraki et al., 2019), the observed patterns could become common in the future in many areas of the Mediterranean Sea.

Nevertheless, there could also be some areas of the Mediterranean where, due to specific oceanographical conditions, the recurrence of MHWs could be lower. This could favor the recovery of the populations and habitats in case of impact, which could be key to avoid the collapse trajectory. In fact, some recent (unpublished) results that we have obtained within the FutureMARES project point towards such possibility. In Calanques NP, a MHW decimated octocoral populations in 1999, which could have potentially led to subsequent changes in taxonomic and functional biodiversity, as observed in Scandola and Port-Cros. However, our preliminary results indicate that populations and coralligenous habitats from Calanques are nowadays in an overall good condition and far from having suffered a collapse. Since no recurrent MHWs were observed in Calanques since 1999, the recovery of the impacted populations seems to have been facilitated by the lack of recurrent climatic impacts. Finding and protecting such kind of climatic refugia would be essential to ensure the conservation of coralligenous assemblages in the Mediterranean.

Finally, our two last contributions to the FutureMARES project are related to the creation and posterior updating and capitalization of a pan-Mediterranean database of Mass Mortality Events (MME-T-MEDNet database; (Garrabou et al., 2019)). With this database, we have been able to establish a permanent pan-Mediterranean network of collaborators, assemble and standardize existing information on MMEs, identify geographic gaps that need to be addressed through future monitoring and research efforts, such as the case of the North of Africa, assess species vulnerability to MMEs, identify observation taxonomic gaps, foster the analysis of the relationship between MMEs and marine heatwaves and provide information for the assessment of the impact of MMEs on the biodiversity and socio-economic activities. Moreover, by updating collaboratively updating the mass mortality database to the 2015-2019 period within the FutureMARES project, we have also been able to demonstrate that the Mediterranean Sea has experienced exceptional thermal conditions during the 2015-2019 period resulting in the onset of five consecutive MMEs across the basin. Our results, which have been recently submitted to Global Change Biology journal (Garrabou et al. 2022), show that MMEs affected a wide range of taxa (50), phyla (8), main habitats (5) and depths from the surface down to 45 m depth and over thousands of kilometres of coastlines. Moreover, they show a significant relationship between the incidence of MMEs and the heat exposure associated with MHWs, both at the surface and along depth. Overall, our findings reveal that the Mediterranean Sea is experiencing an acceleration of the ecological impacts of MHWs which poses an unprecedented threat to its ecosystems' health and functioning.



<u>CTI</u> - A significant warming trend (slope = 0.021, p < 0.001) was observed in the waters of Marseille over the 2008-2020 period. However, the warming trend was not accompanied by a statistically significant change in the CTI of the studied coralligenous assemblage over the same time period (p > 0.05). This shows that, from a CTI perspective, the coralligenous community has not been reactive to the steady changes in SST, with species with affinity for warm water not having significantly increased in abundance in comparison with colder water species. These results are in line with previous studies in coralligenous assemblages, which show that recurrent warming events such as MHWs, rather than long-term warming itself, is responsible for most community changes observed in these Mediterranean communities (Gómez-Gras et al., 2021a; Gómez-Gras et al., 2021b; Verdura et al., 2019). Moreover, the changes observed so far in these communities are mainly caused by changes in species abundance within the community, rather than arrival or more warm-affinity species, or the disappearance of more temperate ones.

The lack of CTI temporal trends in the studied community can also be also explained by the occurrence of multiple, but small changes in species abundances leading to all borealization, deborealization, tropicalization and detropicalization processes (Figure 31, Table 7).



Figure 31: Representation of the processes occurring in the studied community as a consequence of the increases and losses of abundances in the present species, and their thermal affinity. Specifically; red dots located in the upper right corner indicate tropicalization (i.e., species with warm affinity that are increasing), purple dots in the lower right corner indicate detropicalization (e., species that with warm affinity that are decreasing in abundance), blue dots in the upper left corner indicate borealization (i.e., species with cold affinity that are increasing), orange dots in the lower left corner indicate deborealization (i.e., species with cold affinity that are decreasing).



Table 7. Table showing the specific temporal changes (slope of the linear models) observed for each of the sampled species, together with their thermal optimum and the associated community process.

Species	Change	sst_MP	process
Agelas oroides	0.10007	19.57	Tropicalization
Cliona viridis	0.02865	23.01	Tropicalization
Flabellia petiolata	0.01191	18.74	Tropicalization
Halimeda tuna	0.007442	22.86	Tropicalization
Myriapora truncata	0.048363	18.72	Tropicalization
Palmophyllum crassum	0.049107	22.76	Tropicalization
Womersleyella setacea	0.918899	22.46	Tropicalization
Axinella polypoides	-0.00446	19.66	Detropicalization
Chondrosia reniformis	-0.02902	21.8	Detropicalization
Eunicella cavolini	-0.02865	19.24	Detropicalization
Halocynthia papillosa	-0.01711	18.66	Detropicalization
Caryophyllia (Caryophyllia) inornata	0.00632	15	Borealization
Cellaria salicornioides	0.04092	15.5	Borealization
Clavelina lepadiformis	0.00744	11.43	Borealization
Crambe crambe	0.21242	18.53	Borealization
Dictyota dichotoma	0.00930	13.76	Borealization
Filograna implexa	0.00037	15.3	Borealization
Leptopsammia pruvoti	0.13988	16.27	Borealization
Parazoanthus axinellae	0.03757	16.01	Borealization
Pentapora fascialis	0.03125	15.57	Borealization
Reteporella grimaldii	0.02121	16.75	Borealization
Serpula vermicularis	0.00223	15.3	Borealization
Axinella damicornis	-0.05018	15.41	Deborealization
Corallium rubrum	-6.87E-05	18.55	Deborealization
Disporella hispida	-0.00298	11.64	Deborealization
Exidmonea atlantica	-0.01302	13.36	Deborealization
Paramuricea clavata	-1.04948	18.55	Deborealization
Schizomavella (Schizomavella) linearis	-0.01488	11.62	Deborealization

However, despite there were not clear evidences of any of these processes being more important than the other regarding the number of species affected, the largest changes in terms of relative abundance were clearly related to the increase of *Womersleyella setacea* (a species of red algae with warm-water affinity) and the decrease of *Paramuricea clavata* (a species of habitat-forming octocoral with boreal affinity). Therefore, the processes of tropicalization and deboralization were more important than the others in terms of changes in relative abundance.

Overall, this indicates that, despite CTI not being reactive yet, the future trajectories of the coralligenous assemblages of Marseille could be associated with more tropical (and less boreal) communities, with both the increase of abundance of warm-affinity species and the loss of cold affinity ones. Remarkably, the ongoing changes could also potentially lead to changes in ecosystem functioning (Gómez-Gras et al., 2021a), as the species that are being reduced (e.g., *Paramuricea clavata*) have key roles (e.g., formation of 3D- habitats) that cannot be replaced by the species that are taking its their place (e.g., *Womersleyella setacea*). This, in turn, could likely lead to the loss of associated ecosystem services (Smith et al., 2021).

4.4.3. Rocky benthos in the Ligurian Sea

Objective

We analysed temporal changes in CTI of low intertidal assemblages along the coast of the Ligurian Sea.



Study area and data description

The study was undertaken along the coast of the Island of Capraia (43.048 N, 9.828 E), about 40 miles off the west coast of Italy, in the Ligurian Sea (northwest Mediterranean). Low intertidal assemblages (0 and -0.3 m above mean low water level) are dominated by belts of the canopy-forming fucoid *Ericaria amentacea* (previous name *Cystoseira amentacea Bory* var. *stricta Montagne*) (Figure 32) which alternate with patches occupied by algal turfs, encrusting coralline algae or bare rock, varying in size between tens to hundreds of cm² (Bulleri et al., 2002; Tamburello et al., 2013).

Assemblages were sampled annually in summer, from 2007 to 2016, in 64 contiguous quadrats, 50 x 50 cm in size, that were marked permanently using epoxy putty on two randomly chosen shores (Tamburello et al. 2013). The abundance of sessile macroalgae and invertebrates was assessed visually in 20 x 20 cm quadrats that were placed in the center of each 50 x 50 cm quadrat along each transect. Sampling was carried out using a plastic frame divided into 25 sub-quadrats and giving each taxon a score of 0 (absent), 1 (occupation of 1/4 of the sub-quadrat), 2 (occupation of 1/2 of the sub-quadrat), 3 (occupation of 3/4 of the sub-quadrat) or 4 (occupation of the entire sub-quadrat) to each subquadrat. The final percentage covers were calculated by summing over the 25 sub-quadrats (Dethier et al., 1993). We recorded a total of 68 taxa, which except for 5, were classified at the species level.

Analyses of changes in CTI were performed using the protocol and codes defined in methods (section 3.2.3) for 44 species (Table 8).



Figure 32. Rocky benthic community in the Ligurian Sea.

Results

There was a statistically significant increase in the CTI over time in the 2007-2016 period (slope = 0.10467, p < 0.001; Figure 33). This clearly shows that the community is changing and that species with affinity for warm water have significantly increased in abundance in comparison with colder water species. Indeed, time could explain about 77% of the variation in CTI (Adjusted R² = 0.772).
Deliverable D1.3– (Report on cross-region long-term monitoring of the marine biodiversity in relation to climate change and variability)





Figure 33. CTI trend of the rocky benthic community in the Ligurian Sea.

There was a trend for increasing sea temperature with time, but it was not statistically significant (slope = 0.059, p = 0.1135). Likewise, there was no significant correlation between the annual temperature and the CTI (slope = 0.271; p = 0.478).

The increase in CTI over time was mostly the result of an increase in the abundance of warm water affinity (tropicalization), coupled with a slight decrease in cold affinity species (deborealization) (Figure 34).

	Genus	Species	Change	Mean SST (°C)
1	Acetabularia	acetabulum	0.0025	17.86
2	Aglaozonia		0.0056	18.29
3	Amphiroa	rigida	-0.0018	23.69
4	Anadyomene	stellata	-0.0016	23.46
5	Ascidia		0.0000	13.50
6	Actinia	equina	-0.0338	13.74
7	Balanus	perforatus	0.0100	17.26
8	Rivularia		-0.0004	12.81
9	Cystoseira	amentacea	0.0126	18.86
10	Caryophyllia	smithii	0.0002	14.55
11	Caulerpa	cylindracea	-0.0006	19.36
12	Cystoseira	compressa	-0.0035	18.30
13	Champia	parvula	0.0001	19.89
14	Chthamalus	stellatus	-0.0026	15.17
15	Cladophora	prolifera	-0.0125	17.41
16	Cladophora	pellucida	0.0009	15.58
17	Codium	bursa	-0.0001	18.37
18	Corallina	officinalis	-0.0105	12.58
19	Lithothamnion		-0.0031	16.01
20	Cutleria	multifida	-0.0001	14.43
21	Didemnum	candidum	0.0524	20.43
22	Diplosoma	spongiforme	0.0619	17.96
23	Falkenbergia	rufolanosa	-0.0008	15.52
24	Ceramium	rubrum	-0.0587	10.50
25	Flabellia	petiolata	-0.0002	18.41
26	Stramonita	haemastoma	0.0010	23.47
27	Gelidium	pusillum	0.0512	19.88
28	Chondracanthus	acicularis	-0.0017	20.03
29	Halimeda	tuna	-0.0022	22.85
30	Hypnea	musciformis	-0.0012	22.88
31	Jania	rubens	-0.0332	18.65

Table 8.	Species,	abundance	change	and	estimated	thermal	mean.
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32	Laurencia	obtusa	-0.0018	20.64
33	Osmundea	pinnatifida	0.0006	13.35
34	Mytilus	galloprovincialis	-0.0007	16.61
35	Osilinus	turbinatus	0.0001	19.08
36	Padina	pavonica	0.0004	20.98
37	Peyssonnelia	polymorpha	0.0063	17.75
38	Pomatoceros	triqueter	0.0046	11.86
39	Spirorbis		0.0005	17.70
40	Ircinia	muscarum	0.0027	18.93
41	Sarcotragus	foetidus	-0.0323	18.93
42	Dictyota	implexa	0.0044	23.37
43	Vermetus	triquetrus	0.0057	18.88
44	Valonia	utricularis	0.0328	23.10



Figure 34. Processes of CTI.

Discussion

The results of our analyses indicated that, in just one decade, the CTI of intertidal rocky assemblages increased about 1°C. Our analyses found no significant increase in SST with time and, although there was a positive trend, the correlation between CTI and local mean SST was not significant. However, the relationship between CTI and temperature change is not necessarily linear since species thermal performance curves can be asymmetrical and thermal preferences can be either lower or higher than those recorded in a given region (Stuart-Smith et al., 2015). In addition, species may respond to temperature maxima or variability rather than its mean. For example, inter-annual fluctuations in the abundance of the invasive seaweed, Caulerpa cylindracea, are correlated with spring and summer maximum temperatures (Ravaglioli et al., in press, this report). In this sense, increasing intensity of extreme events, such as marine heatwaves, rather than increases in the mean SST could underpin the increasing CTI. Analyses from WP2 indicate that in the past three decades, both the intensity and trend of marine heatwaves in the study area has exceeded the 50th percentile of values for the whole Mediterranean; indeed, the intensity has exceeded the 75th percentile threshold. Thus, the island of Capraia represents a hotspot for marine heatwaves in the NW Mediterranean. In addition, seawater temperature can affect species abundance indirectly via the regulation of species interaction (Bates et al., 2014; Bates et al., 2017). Thus, changes emerged in the CTI could be the results of changes in the abundance an/or metabolism of



species that are not permanently associated with macroalgal canopies. In particular, it is worth noting that our data are limited to sessile species.

The increasing trend in CTI appears to be mostly the result of an increase in the abundance of species characterized by affinity for warmer water. Such a phenomenon, termed as tropicalization, has been previously documented in subtidal rocky systems of the NW Mediterranean. For example, the frequency of observations and the abundance of warm water native species, previously restricted to southern sectors, such as the fishes *Sphyraena viridensis* and *Thalassoma pavo*, has increased in the period 2009-2015 (Bianchi et al., 2018). Likewise, a decline in the abundance of the Mediterranean native purple sea urchin, *Paracentrotus lividus*, a species sensitive to seawater warming has been recorded in the Tuscan Archipelago (Benedetti-Cecchi et al).

The rocky assemblage investigated is dominated by the fucoid Ericaria amentacea which forms a lush canopy at low intertidal levels and provides habitat to a variety of macroalgae and sessile invertebrates (Benedetti-Cecchi et al., 2001; Bulleri et al., 2002). Although species belonging to the genus Cystoseira sensu lato are declining throughout the Mediterranean as a consequence of climate change, increased rates of nutrient loading and sediment deposition (Strain et al., 2014; Thibaut et al., 2015), there is no evidence of significant changes in the distribution and abundance of this species at the study site in the last two decades. This species, with a preferential mean temperature of 18.85°C showed a small negative change in abundance (i.e., 0.013). The species with colder water affinity that underwent a greater decline in abundance were the red macroalga Ceramium rubrum and the anemone Actinia equina. While, to the best of our knowledge, there is no information on the response of C. rubrum to thermal stress, a loss of biomass in A. equina due to reduced growth and pedal disk shrinking, has been documented during summer, suggesting impaired metabolism during warmer months (Chomsky et al., 2004). The warmer water affinity species which showed a marked increase in abundance were the macroalgae Gelidium pusillum and Valonia utricularis and the didemnid Didemnum candidum. A warming-induced decline of other species of Gelidium has been documented along the northern coast of Tenerife, an island of the Canaries Archipelago (i.e. G. canariensis and G. arbuscula) (Alfonso et al., 2021), in the Bay of Biscay (Borja et al., 2018), suggesting large variation of thermal preference within the genus Gelidium. By contrast, V. utricularis is a species with a tropical to warm-temperate distribution and achieving maximum growth at temperature exceeding 25° C (Pakker and Breeman, 1996). The colonial ascidian D. candidum has been recorded in harbours in southern India suggesting affinity for tropical waters (Ali et al., 2014).

In conclusion, although the majority of the species composing low shore assemblages showed little changes in their relative abundance, we found trend of deborealization and tropicalization. Building on these results, which have been produced using a relatively short time series (i.e., 10 years) suggests that intertidal habitats formed by *Cystoseira* species could undergo major changes under future climate scenarios.

4.4.4. Soft bottom benthos in the Ionian Sea

Objective

We analysed temporal changes in CTI of soft bottom benthic assemblages in Amvrakikos Gulf of the Ionian Sea.



Study area

Amvrakikos Gulf (Figure 35) is located in Western Greece in the Ionian Sea (38.9853 N, 20.9634 E). The Gulf has a narrow opening on the west side, the maximum depth reaches 63 m and accepts the inflows of three large rivers: Arachthos, Louros and Vouvos (Kapsimalis et al., 2005). There is a wide network of lagoons around the coasts of the Amvrakikos Gulf. The Gulf often suffers from hypoxic events followed by mass mortalities of the fauna inhabiting the area. However, the causes that trigger hypoxic events are not completely apparent. Studies conducted in the area are linking these events with human activities, topography and climatic conditions (Ferentinos et al., 2010; Georgiou et al., 2021; Kormas et al., 2001; Kountoura and Zacharias, 2011; Reizopoulou and Nicolaidou, 2007). The formation history of Amvrakikos Gulf was similar to the formation of the Mediterranean and Black Seas, in that there were periods of complete or partial (via narrow straits) isolation of the Gulf from the Ionian Sea (Avramidis et al., 2014). This eventful geological history of Amvrakikos Gulf might have influenced the macrofaunal populations living in the Gulf.



Figure 35. Amvrakikos wetlands (from Google maps).

The lagoonal complex on the northern side of Amvrakikos Gulf is one of the largest wetlands in Greece. The nutrient load is mainly transferred by the rivers and deposited in the Gulf, therefore the concentration rates are observed to change seasonally following the freshwater inflows (Kormas et al., 2001). Aquaculture installations are located in the eastern part of the Gulf, while the lagoons are also used for semi-extensive aquacultures.

Data description

A number of studies have been completed in Amvrakikos Gulf. The benthic data from the area were obtained during different sampling expeditions in 1980 (Nicolaidou et al., 1983), 1993-1995 (Nicolaidou et al., 2006; Reizopoulou et al., 1996) and 2010-2011 (Reizopoulou et al., 2016). Data were collected at various temporal scales (either annually or seasonally), from different lagoons and from several stations/locations within the Gulf. In order to create a more concrete and enriched dataset for performing the CTI analysis, the assumption that all benthic samples were collected from one area (i.e., the wider area of Amvrakikos wetlands) was made, the annual averages were calculated (when possible) and the CTIs per year were compared.

The samples were collected from soft sediment (mud, sand) using different types of box-corers in order to study the macrobenthic communities. The samples were sieved using a 0.5 mm mesh sieve, preserved in 5% formaldehyde buffered with seawater and stained with Rose Bengal, and identified down to the lowest possible taxonomic level (species in most cases). The final dataset on which a CTI analysis was performed included species abundances (individuals per m²) per sampling event (year or season).



Results

The results of the CTI analysis showed that there is neither a clear nor significant trend (p>0.05) (Table 1). From 1980 until 1995, there was an increase in CTI due to changes in the species composition (Figure 36). However, in the years between 1995 and 2010 the opposite trend was observed, where a decreased CTI was shown. This can be explained due to the increase of both the species abundances as well as the number of species during the specific time frame. This fact would imply that the temperature changes occurring in the Amvrakikos Gulf were within the species' temperature preference and, even if some species were replaced by others, the latter were also species with similar temperature preference. Since our data are derived from a lagoonal/wetland ecosystem, the macrobenthic species present in the area are already tolerant in highly fluctuating environmental conditions in terms of salinity and temperature; species' temperature preferences covary with other species traits which may affect their response to several environmental variables and not only temperature alone (Bowler and Böhning-Gaese, 2017).



Figure 36. Community Temperature Index (CTI) in relation to time (year) and surface sea temperature for the dataset (1980 - 2011) of the Amvrakikos wetlands (Ionian Sea, Western Greece).



When looking into the species abundance change vs the species thermal preference (Figure 37), it is clear that there are more data points in Borealization (increasing abundance of cold-affinity species), followed by Tropicalization (increasing abundance of warm-affinity species). In addition, the sum of Borealization + Detropicalization (increasing abundance of cold-affinity species + decreasing abundance of warm-affinity species) is higher than the sum of Tropicalization + Deborealization (increasing abundance of warm-affinity species + decreasing abundance of warm-affinity species). This is expected since the CTI decreased over time (Figure 37).



Figure 37. Species abundance change in relation to the species thermal preference for the dataset (1980 - 2011) of the Amvrakikos wetlands (Ionian Sea, Western Greece).

4.4.5. Catch Thermal Index from the Catalan Sea (western Mediterranean)

Introduction and objective

Overall, marine communities worldwide are responding to global warming through increasing trends in mean thermal affinity, which can be represented by increasing values for the Community Temperature Index (CTI) (McLean et al., 2021). This can be translated into changes in global catches with increasing representations of thermophilic species in the catch



(Cheung et al., 2013). However, a key and largely unresolved question so far is whether trends in CTI in highly impacted marine areas are primarily due to: (i) increasing abundance of warmaffinity species (tropicalization), (ii) decreasing abundance of cold-affinity species (deborealization), (iii) increasing abundance of cold-affinity species (borealization), or (iv) decreasing abundance of warm-affinity species (detropicalization) (McLean et al., 2021).

The Mediterranean Sea is widely considered as largely endangered or threatened marine ecosystems. Water temperature within the Mediterranean Sea is increasing faster than the global average rate (Burrows et al., 2011; Coll et al., 2012; Micheli et al., 2013; Ramírez et al., 2017; Salat et al., 2019). Furthermore, the presence of the European landmass north of the basin poses an important limitation for species adaptation to increasing temperatures in the Mediterranean Sea, as it constrains the movement of species and blocks their poleward shift when dispersing while searching for more favourable conditions (Poloczanska et al., 2013b). Climate change poses, therefore, a serious threat for Mediterranean marine communities that will certainly increase in severity in the future, in line with regional and world-wide predictions.

Concurrently, most fish stocks in the Mediterranean Sea are exploited at unsustainable levels (FAO, 2020; Rousseau et al., 2019). This high fishing pressure may exacerbate climate impacts on the Mediterranean marine communities by speeding up the climate-driven displacement of marine species distribution through resource depletion and population crashes at the trailing edge (Lenoir et al., 2020).

Based on highly-detailed landing information for fisheries operating along the Catalan Sea (North-western Mediterranean, Figure 38), we evaluated trends in CTI for the pelagic and benthic communities, and quantified the relative contributions of the four underlying processes driving CTI changes.

Study area and data description

Daily data on landings span the 2000-2020 period and come from 23 different fishing ports scattered along the Catalan Sea (Figure 38). Raw data were grouped by species, gear, port and year. Here, we exclusively considered main fishing gears in the area: purse-seiners and bottom trawlers (hereafter trawlers). Purse-seiners operate through the water column and target pelagic fish species (mostly anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus*). Therefore, their catches can mainly inform about the pelagic fish community. Bottom trawlers operate near the bottom and integrate the benthic and demersal community. Whereas purse-seiners mainly target pelagic fish and few cephalopod species, landings from trawlers are taxonomically diverse, including many species of fish and invertebrates. Here, we considered two main groups of species for trawlers: fish and invertebrates (crustaceans and cephalopods).





Figure 38. Study area (North-western Mediterranean). Data on landings span the 2000-2020 period and come from 23 different fishing ports scattered along the Catalan Sea. Source: Institut Català de Recerca per a la Governança del Mar (ICATMAR). State of Fisheries in Catalonia 2020. Part 1: Methods and Results (ICATMAR, 21-02), Barcelona.

Methods

Trends in CTI and the relative contributions of the four different underlying processes (i.e., tropicalization, deborealization, borealization and detropicalization) were evaluated by aggregating daily landing data into annual values. We first considered all the ports in the study area simultaneously. Then, fishing ports were grouped within three main subregions: North, Central and South (Figure 38). For comparative purposes, we also considered those ports occurring in what M. Hidalgo in this repot considered the Northern region of the Western Mediterranean (latitude > 41°) when analysing data from MEDITS (Figure 38).

Results and discussion

Overall, CTI significantly increased over the study period (Table 9 and Figure 39 to Figure 41). However, these positive trends spatially differed according to the fishing gear considered. Landing data from purse-seiners revealed that increasing trends in CTI were particularly important in the northernmost regions. This spatial pattern concurs with previous regional assessments on climate change velocity suggesting more rapid increasing trends in water temperature for the northernmost regions of the Catalan Sea (Ramírez et al., 2021). Analogously, the magnitude of contemporary climate velocity is relatively faster in the surface (<200 m depth) than in the mesopelagic layer (200-1000 m depth (Brito-Morales et al., 2020), which could, at least partially, explain the weaker CTI trends when considering trawlers' landing data and, hence, when dealing with the benthic/demersal community (Table 9).



The Southernmost region of the Catalan Sea was the only region showing significant increasing CTI trends for trawlers' landing data. In this region, the continental shelf is particularly large due to the influence of the Ebro River (Figure 38). Thus, while trawlers from the North and Central Catalan Sea operate mainly on the mesopelagic layer, vessels from the South Catalan Sea largely occur in surface layer where the climate-driven change in water temperature is likely faster (Brito-Morales et al., 2020). Combined, these results suggest that changes in the community thermal affinities can respond to local trends in environmental conditions and can be translated to long-term chance in catch composition in the study area.

Table 9. Long-term (2000-2020) CTI change (slope of the linear regressions and significances), along with the relative contributions of the four underlying processes contributing to changes in CTI (i.e., tropicalization -Trop-, deborealization -Debore-, borealization -Bore- and detropicalization -Detrop-). Results are shown for the different fishing gears and regions considered in the study (see Fig. 1). The Catalan Sea category incorporates all regions, whereas Latitude > 41° refers to what M. Hidalgo considered the Northern region of the Western Mediterranean when analysing data from MEDITS. Redder colours indicate higher contributions. Contributions are only showed when CTI trends were significant.

	Таха	Region	CTI change	Trop	Debore	Bore	Detrop
All gear	All	Catalan Sea	0.014 *	0.34	0.27	0.23	0.16
Purse-seiners	All	Catalan Sea	0.038 **	0.13	0.54	0.03	0.31
		North	0.039 **	0.13	0.52	0.03	0.32
		Central	0.027 **	0.17	0.47	0.03	0.33
		South	0.025				
Trawlers	All	Catalan Sea	0.014 *	0.33	0.27	0.23	0.17
		North	-0.002				
		Central	0.005				
		South	0.018 *	0.43	0.16	0.30	0.10
		Latitude > 41°	0.008 *	0.19	0.38	0.15	0.29
	Fish	Catalan Sea	0.018 **	0.33	0.30	0.17	0.19
		North	0.001				
		Central	0.005				
		South	0.021 *	0.45	0.16	0.28	0.11
		Latitude > 41°	0.010 *	0.18	0.39	0.12	0.31
	Invertebrates	Catalan Sea	0.000				
		North	-0.010				
		Central	0.000				
		South	0.014 *	0.46	0.17	0.33	0.04
		Latitude > 41°	-0.002				

** p-value<0.001

* *p-value<0.05*

The prevailing process underlying CTI increases differed among fishing gear, but was fairly consistent among regions and taxa (in the case of bottom trawlers). Tropicalization was the main process behind CTI changes associated to trawlers (benthic community). In the case of purse-seiners (i.e., pelagic community), deborealization prevailed (Table 9, Figure 39 to Figure 41). This process could be partially explained by decreasing trends in the abundance of highly important, cold-affinity species such as the European sardine (*Sardina pilchardus*) (Pennino et al., 2020; Piroddi et al., 2017; Van Beveren et al., 2016). Population declines have been mostly attributed to the combined effects of climate impacts and fishing pressure (Coll et al., 2019; Pennino et al., 2020; Saraux et al., 2019). Because of their commercial value and ecological role within marine communities, emigration or mortality of this cold-affinity species could result in population crashes or local functional extinctions with important socio-economic consequences through the impact of fisheries (Coll et al., 2019; FAO, 2018; Palomera et al., 2007; Ramírez et al., 2018; Ramírez et al., 2021).





Figure 39. Long term (2000-2020) trends in CTI when considering all fishing gear (a), purse-seiners (b) and bottom trawlers (c). Significant linear trends and 95% confidence intervals are represented in blue lines and grey shadows. The four underlying processes contributing to changes in CTI (i.e., tropicalization, deborealization, borealization and detropicalization) are represented by plotting changes in species abundances through the study period vs. species-specific thermal preferences (d to f). Vertical lines represent the average thermal preferences for the whole community, whereas horizontal dashed lines indicate no change in species abundances.





Figure 40. Long term (2000-2020) trends in CTI estimated from landing data associated to purse-seiners (a-c) and bottom trawlers (d-i). Fishing ports were grouped within three main subregions: North (a, d, g), Central (b, e, h) and South Catalan Sea (c, f, i, see Fig. 1). Landing data for purse-seiners consider all species, whereas data for trawlers were grouped according to two main taxonomical groups: fish (d, e, f) and invertebrates (g, h, i; crustaceans and cephalopods).



Figure 41. Changes in species abundances through the study period vs. species-specific thermal preferences Points are coloured according to the four underlying processes contributing to changes in CTI: tropicalization, deborealization, borealization and detropicalization. Vertical lines represent the average thermal preferences for the whole community, whereas horizontal dashed lines indicate no change in species abundances. Data for purse-seiners consider all species (a, b, c), whereas data for trawlers were grouped according to two main taxonomical groups: fish (d, e, f) and invertebrates (g, h, i; crustaceans and cephalopods). Fishing ports were grouped within three main subregions: North (a, d, g), Central (b, e, h) and South Catalan Sea (c, f, i, see Fig. 1).





Figure 42. Long term (2000-2020) trends in CTI estimated from landing data associated to bottom trawlers (a-c). For comparative purposes, we exclusively accounted for those ports occurring in what M. Hidalgo (this report) considered the Northern region of the Western Mediterranean (latitude > 41°) when analysing data from MEDITS. Significant linear trends and 95% confidence intervals are represented in blue lines and grey shadows. The four underlying processes contributing to changes in CTI (i.e., tropicalization, deborealization, borealization and detropicalization) are represented by plotting changes in species abundances through the study period vs. species-specific thermal preferences (d to f). Vertical lines represent the average thermal preferences for the whole community, whereas horizontal dashed lines indicate no change in species abundances.

4.4.6. Demersal Fish in western Mediterranean

Objective

We analysed temporal changes in CTI of demersal fish assemblages in western Mediterranean.

Study area and data description

The MEDITS program started in 1994 in the Mediterranean with the cooperation among research institutes from four countries: France, Greece, Italy and Spain. MEDITS consist of series of bottom trawl surveys that routinely provide abundance indices of target species for tuning stock assessment models of intermediate complexity (Spedicato et al., 2019). The data to calculate the CTI in this study includes annual means of species abundance (km/m²) of demersal fish and benthic crustaceans and molluscs (cephalopods) sampled from May to July



during the 1994-2019 period in the western Mediterranean Sea, specifically within Geographical Sub Area 6 (GS6) as established by General Fisheries Commission for the Mediterranean. The analysis was carried out in three subregions of the GS6 area: (i) North at > 41° latitude north (North of Ebro Delta), (ii) Centre within 41-39.2° latitude north and (iii) South at < 39.2° latitude north. The division of these three areas show different ocean warming velocities.

Data have been kindly shared by M. Hidalgo (Spanish Institute of Oceanography, Balearic Oceanographic Centre).

Results

SST increased significantly in the three regions and period analysed (Table excel). No significant correlations between SST and CTI were found in any biological group and region analysed (Figure 43c).

<u>Crustacean community</u> – The north, central and southern regions were represented by 67, 66 and 84 species, respectively. A significant decrease in CTI over time (-0.030 °C/year) was observed in the southern community and no trend was found in the central and northern crustacean communities (Figure 43b). The deborealization ecological process dominated in the north (30%) and the borealization in the central (40%) and southern communities (52%) (Figure 43a).

<u>Fish community</u> – The north, central and southern regions were represented by 136, 138 and 159 species, respectively. A significant increase in CTI over time at a rate of 0.011 °C/year was observed in the northern fish communities. However, no trend was found in the central and southern communities (Figure 43b). The tropicalization was the main ecological driver in the north (37%) while the borealization dominated in the central (36%) and southern (35%) fish communities (Figure 43a).

<u>Mollusk (cephalopods) community</u> – The north, central and southern regions were represented by 48, 49 and 51 species, respectively. A significant decrease in CTI over time at a rate of -0.013 °C/year in the north and at a rate of -0.021 °C/year in the central regions was found in the cephalopod communities. However, in the southern regions no trend was observed (Figure 43b). The detropicalization was the strongest underlying CTI driver in the northern cephalopod communities (47%) and the borealization in the central (33%) and southern (44%) regions (Figure 43a).





Figure 43. Trends in CTI and processes for fish, mollusc, and crustaceans from western Mediterranean.

4.4.1. Fish in Balearic Islands associated to Posidonia

Introduction and objectives

The evolution of fish communities associated to *Posidonia Oceanica* were analysed to identify trends and potential climate drivers. We concentrated on compiling data of fish communities associated to *P. oceanica* in a close-by area, Palma Bay, one of the Mediterranean areas with the longest historical data on fish communities associated to *P. oceanica* (Deudero et al., 2008; Díaz-Gil et al., 2019).

Study area and data description

For the first time, we compiled data from 1914 to date, in order to detect potential changes in the fish community associated to climate change-related variables, among others (Figure 44). We compiled and analysed the fish communities associated to *P. oceanica* in Palma Bay in relation to climate change impacts. We explored if changes in the fish community could be associated to climate change-related variables. Palma Bay has a surface of 217 km² and an average depth of 28.5 m. P. oceanica covers a large portion down to 35 m depth. The evolution of the meadows is not well known and historical data collection on associated fish communities has occurred irregularly in space and time with varying sampling gears. We based our analyses on 10 studies, starting 1914, plus one conducted within FutureMARES in 2021 (Figure 37). The data were either retrieved from published articles or from other records and unpublished literature. We selected studies using a comparable non-damaging light beam trawl "ganguil" (versions of that described in Catalan et al. (2014)). Abundance and biomass of each species was calculated, in some instances converting from length to biomass via published length weight relationships. Data were standardized to surface area swept by the sampling gear. A large effort was devoted to the reconstruction of tow positions, standardization and extraction of covariates.





Figure 44. Map of Palma Bay, and location of stations of the different surveys in the historical time-series. Type of bottom is included.

Statistical analyses followed several steps within a multivariate framework, frequently resulting in loss of information to aid standardization. We analysed variations in abundance, biomass, size and presence/absence, in relation to year, depth, cardinal point and width of the net. Environmental variables included mean, maximum and minimum temperature of the main Mediterranean Species.



Figure 45. shows the sampling sites and some preliminary data on the distribution of dominant fish species along the measured depth gradient collected in 2021.

Results and discussion

Our analyses based on data compiled in the last 105 years suggest a relatively stable community and no clear changes associated to the effect of increasing temperature. For the few environmental parameters that could be tested, a large part of the variability is related to



the depth and intra-year temporal variability. Also, as our database is highly fragmented in time, interannual variability was not well captured. Although the difficulty in the analyses of our data has precluded drawing solid conclusions, the compiled dataset will enable to continue the historical study of these communities, centred on comparable sub-sets.



Figure 46. nMDS on the presence-absence resemblance matrix of benthic species associated to P. oceanica in Palma Bay, using trawls between 1914-2021. To the left, vectors include species with correlations over 0.5. To the right, vectors are average distributional temperature for each species, with a correlation >0.4. In these sets, problems arise in the use of some species being aggregated at the genus level in the oldest surveys, and in within-year differences in the surveys.

	Sum	nmer		18
Año S	N	d	H'(loge)	Ê
1977 16	55	3,736	2,404	» (د ۲
2000 21	33	5,717	2,357	8
2002 31	89	6,676	2,214	
2018 28	210	5,047	2,132	8
2021 22	93	4,636	2,142	13
		C.		
1980 25	36	6,693	2,209	(j)
1991 29	119	5,855	2,614	Ę
2006 26	68	5,916	2,118	

Figure 47. Left, comparison of the number of species (S), average number of individuals (N), Margelef's diversity (d) and Shannon's diversity (H) for comparable (standardized surveys). Between 1977 and 2021 (summer and spring). Right, size evolution of the average size of two common species, Diplodus annularis and Symphodus ocellatus.

4.4.1. Bottom trawling fishery in Levant (Israel)

Introduction and objective

The rapidly warming and highly invaded South-Eastern Mediterranean Sea is an ideal location to examine the relationship between community-level changes to rising water temperature. It is a hot spot for marine alien species in the Mediterranean, and probably also globally due to a major conduit of tropical invaders from the Indo-Pacific: the Suez Canal. In recent years, Ocean warming has been increasing the expansion rate of tropical species into the Mediterranean and has been facilitating their establishment and proliferation.



The objective is to test shifts in CTI on soft bottom trawling fishery assemblages in Levant (Israel), hypothesizing that the continuous invasion and spread of tropical species into the region will contribute to a considerable increase in CTI in the region.

Study area and data description

For the Levant case study 35, we have identified a large bottom trawling fishery-independent time series data provided by the Israel fishery Department. It covers a period from the early 1990s to recent years with some gaps mostly in the first two decades.

Results and discussion

A total of 145 species of benthic fish were analyzed. Results indicate a significant ocean warming in the 1990-2020 area, and the community of benthic fish appears to track their thermal niches over time, as seen in the significant CTI increase at rate of 0.054 °C/year (Figure 48). Significant correlations between SST and CTI were also found. The main drivers underlying the CTI changes over time are the deborealization (36%), that is, decrease of cold species, and the tropicalization (33%), that is, increase of warm species. Eastern Mediterranean is known to be a region exposed to an invasion of species of Red Sea origin, extreme climate change, and high fishing pressure (Givan et al., 2018). Thus, the deborealization trend found here can be a product of competition of native species with the alien species with similar traits or niches, and/or the warming itself that reduce the fitness of thermally-sensitive native species. A recent study suggests that the latter maybe be more important than the former (Givan et al., 2018).



Figure 48. Trends in CTI and processes for bottom trawling fishery from Levant (Eastern Mediterranean).



4.4.2. Long-term sampling of the fish community in the western Wadden Sea, The Netherlands

Objective

We analysed temporal changes in CTI of fish assemblages in western Wadden Sea.

Study area

The Wadden Sea is a large, shallow, marine ecosystem located along the coasts of The Netherlands, Germany, and Denmark. It represents one of the largest continuous, intertidal wetlands and is a UNESCO World Heritage Site. The area is connected with the North Sea through gullies and deeper channels. With its shallow depth, large intertidal areas, and its many inlets from the North Sea, this ecosystem provides an important stopover and feeding site for migratory birds as well as an important young juvenile nursery area for fish species spawning and foraging as adults in the North Sea. In line with global trends, this marine coastal zone has been heavily impacted by anthropogenic pressures (van der Veer et al., 2015) and the biomass of the fish community has severely declined since 1980. These trends are consistent across the entire Dutch Wadden Sea (Tulp et al., 2017).

In the western Wadden Sea, the fish community is comprised of several guilds, with residents, juvenile marine migrants, seasonal marine visitors and some rare vagrants and diadromous species (van der Veer et al., 2015). The dynamics in the fish community has been documented through a long-term sampling program that is carried out with traditional fishing gear. Sampling takes place at the western-most, largest inlet to the North Sea, the Marsdiep, a location at the threshold between the Wadden Sea and the North Sea (Figure 49). Using fixed gear, these catches have a combination of pelagic, demersal species, and benthopelagic species, with juvenile fish entering the Wadden Sea area in spring and young-of-the-year migrating out in the autumn (van der Veer et al., 2015).

On the basis of this long-term sampling program, previous analyses revealed that the overall fish biomass has decreased by ninety percent compared to the early 1980s and the mean individual body size (wet mass) of fish in the catch decreased from 150 to 20 g (van der Veer et al., 2015). In addition to these reductions, both the relative abundance and phenology of species, as well as the overall trophic level of the community, has changed in the last decades (Poiesz et al., 2020; Tulp et al., 2017; van Walraven et al., 2017). The strong decline of overall biomass is driven by a reduction in the abundance of juveniles of several marine species such as plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*), Atlantic cod (*Gadus morhua*), and sole (*Solea solea*) (Tulp et al. 2017).

Data description

The Royal Netherlands Institute for Sea Research (NIOZ) has collected data on the Wadden Sea fish community using traditional fixed gear at a specific location (Lat 59.9°N, Long 4.7°E) since 1960. The fixed gear is known as a 'kom-fyke' is a passive fish trap consisting of a 200-m net running from the beach towards deeper waters (the stretched mesh size is 20 mm) that guides migrating fish towards 2 chambers / traps and into a fyke where they can be collected (Figure 50). This gear is emptied each day in the spring (late March to early July) and autumn (late August to early November) and is removed in the summer (due to algae) and winter (due to storms). Fish captured each day are identified to species, total length is measured, and a subset of the catch is collected for subsequent morphological and/or biochemical analyses.

For the purpose of CTI analysis, the average yearly catch per species was corrected for effort (number of fishing days) and the data were filtered for the period 1980-2021. Temperature



data (SST) were collected by the NIOZ for the same time period and yearly averages based on daily measurements at 8AM were used for the analysis.



Figure 49. Location (blue circle) of the long-term sampling site of the Wadden Sea fish community established in 1960 by the Royal Netherlands Institute for Sea Research on the Island of Texel.



Figure 50. Aerial photograph of the traditional "komfyke" fishing gear. The long next extends to the beach (not shown, bottom left).

Results

SST increased significantly (0.035 °C/year) in the Wadden Sea during 1980-2021. 76 Fish species were included in the analysis. A significant increase in CTI over time was found in Wadden Sea fyke fish community (0.013 °C/year). Significant correlations between CTI and SST were also observed, meaning that the fish community is tracking their thermal niches well over time (Figure 51). The deborealization (51%), detropicalization (31%), and tropicalization (17%) were the dominant ecological drivers governing the CTI variations over time.



Figure 51. Trends in CTI and processes for fyke catches fish in Wadden Sea.



4.4.3. Thermal conditions of green turtle nests in the Mediterranean

Introduction and objective

The thermal environment during the incubation period is known to influence morphological, physiological, and behavioral traits of vertebrates. For instance, in many reptile species, the sexual differentiation of gonads is driven by incubation temperatures during a critical period of embryonic development (Pieau, 1996), while thermal nest conditions can impact offspring phenotype and survival (Noble et al., 2018). For marine turtles, high incubation temperatures tend to produce smaller hatchlings with slower crawling and swimming speeds (Booth and Astill, 2001; Booth et al., 2004; Booth and Evans, 2011), which may affect fitness in the long term (Noble et al., 2018). High incubation temperatures and prolonged exposure to extreme thermal conditions can also result in death (Hays et al., 2017; Howard et al., 2014). The maximum thermal tolerance of sea turtle embryos ranges from 33 to 35°C (Howard et al., 2014). Recent work provided evidence that sea turtle embryos may show some resilience to extreme incubation temperatures when the extremes are relatively short in duration (Türkozan et al., 2021). Precise information on incubation temperatures of sea turtle eggs may therefore provide a foundation for many fields of research such as the predicted impact of climate change (Hawkes et al., 2007).

All marine turtles exhibit temperature-dependent sex determination (TSD), with the middle third of embryonic development being the thermosensitive period (Girondot and Kaska, 2014). The constant incubation temperature, where a balanced (1:1) sex ratio occurs, is called pivotal temperature and has been estimated to be close to 29°C, for nearly all species and populations of sea turtles (Yntema and Mrosovsky, 1980)(Miller and Limpus, 1981; Ackerman, 1997). Higher temperatures produce more females, while cooler temperatures produce more males. Yet, an update of critical thermal thresholds (e.g., pivotal temperature) could facilitate more realistic models for deriving sex ratio patterns and projecting sex ratios under different climate change scenarios.

Still, this critical baseline information on the thermal environment of sea turtles is not always available for all species in all regions, hampering our ability to design analyses that could direct future management and conservation actions. Such is the case for green turtles in the Mediterranean, which nest in many different sites but few of which have had their thermal environment documented in detail.

Supported by FutureMARES and collaborating with researchers from Aydın Adnan Menderes University Turkey, Hakkari University, Turkey, and the Duke Marine Laboratory, USA, the objective of this work was to provide baseline information on the thermal conditions of green turtle nests in the Mediterranean. Yet, we compared nest and sand temperatures to various incubation metrics (e.g., duration, success). Concurrently, we explored metabolic heat and its potential contribution to incubation temperatures that could surpass the lethal limit for successful embryonic development.

This study is summarised below, and a detailed version has been published, or submitted to:

- Turkozan, O., Almpanidou, V., Yılmaz, C., Mazaris, A.D. 2021. Extreme thermal conditions in sea turtle nests jeopardize reproductive output. *Climate Change*, *167*, *30*.
- Turkozan, O., Can Yılmaz, C., Almpanidou, V., Godfrey, H.M., Mazaris, A.D. Thermal conditions of the green turtle, Chelonia mydas, nests in the largest rookery of eastern Mediterranean (under review). **Endangered species research**.



Study area and data description

Data presented here were collected over a 5-year period at Akyatan beach, Turkey, one of the most important nesting sites for green turtles in the Mediterranean and accounts for almost 25% of all Mediterranean green turtle reproductive effort. We recorded temperature in 225 nests of green turtles and 12 control sites (15, 30, and 45 m distance from high tide line between 2010-2013) at 75 cm depth. The design of the study, data collection and field surveys were leaded by Prof Oguz Turkozan; data were collected under a protocol between the 7th District of Forest and Water Ministry of Turkey and WWF-Turkey. These efforts were supported by MAVA Foundation, Garanti Bank, UNDP-GEF Small Grant Programme (SGP), the Dutch Embassy in Turkey, and individual supporters of the Adopt a Marine Turtle Programme of WWF Turkey.

Results and Discussion

The results of this analysis demonstrate that high nest temperatures are linked to a reduction in population recruitment, see also Türkozan et al. (2021). This highlights a growing threat that could be triggered by projected warming conditions in the Mediterranean and thus deserves more attention when defining research priorities and conservation actions. Nest temperature and sand temperature at nest depth were strongly correlated ($r^2 = 0.69$, p < 0.01) through the season. Sand temperatures during the reproductive season were characterized by a sharp increase from the start of the nesting season, followed by a slight decline at the end of the egg incubation period. Our analysis demonstrated a strong significant negative correlation between nest temperature and incubation duration ($r^2 = 0.48$, p < 0.01) (Figure 52).



Figure 52. The relationship between nest temperature during the entire incubation duration and incubation duration. Dashed lines show the 95% confidence interval for the prediction of linear model.



A GAM model suggested a significant effect of mean nest temperature upon hatching success (adjusted $r^2 = 0.18$, p < 0.01) (Figure 53), further revealing reduced hatching success when temperature approached 32°C. These findings imply that ongoing climate change is likely to jeopardize reproductive efficiency. Indeed, in a recent study that we conducted using the same dataset (Türkozan et al., 2021), we found projected that under a moderate climate scenario (RCP 4.5), the number of days above lethal thresholds (i.e., 35 °C; (Howard et al., 2014)) would increase from 1% at the year that the study was conducted to 19.3% in 2100. Therefore, it seems that although sea turtles have survived through past climate changes, these projections raise concerns about future recruitment success and the persistence of sea turtle populations.



Mean Nest Temperature

Figure 53. The relationship, derived from the generalized additive model, which illustrates the response between smoothed components of hatching success (%) (y-axis) against mean nest temperature (°C). Shaded gray area indicates 95% confidence intervals.

The sand temperature rose above the pivotal temperature in July and August and cooled in September but remained above pivotal temperature (Figure 54). The metabolic heat (i.e. heat generated by incubating eggs within the nest) (estimated as 1.1 ± 0.7 °C (n = 204, range from -0.8°C to 3.2°C) increased gradually throughout the incubation duration and was the highest during the final third of the incubation duration. Considering that July and August correspond to the peak of the hatching period, with the majority of nests already laid by early August, these conditions are likely to contribute to a female biased hatchling sex ratio (~ 2:1 female: male, based on Turkozan, unpublished data). Therefore, acknowledging the variation of upper thermal limits for successful incubation among different populations, our results suggest that current conditions for incubating eggs of Mediterranean green turtles are approaching the critical threshold that would jeopardize their reproductive success. Using these solid background data, calculated projections at a given site could direct the attention of conservationists towards carefully reviewing local conditions prior to developing specific mitigation measures. The combination of information collected in the field with projected data is critical towards establishing an early warning system to direct management intervention. In this context, decisions on actions towards cooling the nests (e.g. by planting vegetation, artificial shading, sprinkling water on the nests) should be based on a critical evaluation of several components (climate dynamics) and documented local conditions. The analysis of this collaborative effort highlights increased incubation temperatures at a critical green turtle nesting site in the Mediterranean, suggesting that management intervention may be required to preserve this population.





Figure 54. The relationship between pivotal temperature (horizontal black line) and mean sand temperatures (\pm standard deviation) over the main nesting season during 2010-2013 at a) 15 m (green line), b) 30 m (purple line) and c) 45 m (blue line) perpendicular distance from high tide line. All temperatures are for 75 cm depth.

4.5. Zooplankton communities across European seas

Introduction and objective

Zooplankton monitoring through long-term time series is useful for examining climateecosystem interactions. Zooplankton population dynamics and physiological rates are tightly linked to temperature (Richardson, 2008), which results in a fast species response to environmental change. Zooplankton dynamics studies are also of particular interest since zooplankton constitute a key link between primary producers and large predators, supporting commercially important fisheries (Orlova et al., 2005). Zooplankton time series extending >10 yr are now available for many regions, carried out as part of different monitoring and research programs (Mackas & Beaugrand, 2010), however, across-site studies comparing time series trends are scarce.

Here, we analysed temporal changes in CTI of zooplankton assemblages in different European seas.

Study area and data description

The dataset used here includes zooplankton time-series data collected at 3 sites in the eastern North Atlantic (Bay of Biscay and the Kattegat Sea) and the Mediterranean Sea (Gulf of Saronikos). The Kattegat is a sub-area of the North Sea (56.95° N, 11.30° E), which is a transition zone between the Baltic Sea and the North Sea, with a substantially higher salinity range than the 2 sea areas it connects. The estuary of Urdaibai (43° 22' N, 2°43'W) is a temperate estuary located on the Basque coast and the sampling location corresponds to the mouth of the estuary, in the southern Bay of Biscay. The Gulf of Saronikos is located in the eastern Mediterranean Sea. More details on the dataset can be found in (*Villarino et al., 2020*).



Results and discussion

SST increased significantly in the Kattegat and Saronikos, but not in Urdaibai (short time series from 1999-2013). Significant correlations between SST and CTI were found in the Kattegat, but not in Urdaibai and Saronikos (Figure 55c).

The number of copepod species analysed were 17, 25 and 45 in the Kattegat, Urdaibai and the Mediterranean Sea, respectively. A significant increase in CTI over time at a rate of 0.039 °C/year was found in the Kattegat. However, in the Urdaibai and Saronikos no trend was observed (Fig. 4b). CTI temporal trends varied across sites. The thermal preferences of members of the Kattegat copepod community are significantly changing over increasing local SST. In fact, a significant increase of CTI over time was observed, governed by a strong and significant local SST increase. As hypothesized, a significant positive correlation between local SST and CTI was found in the Kattegat. These results confirm that the copepod communities in the Kattegat are following their thermal niches, as the community is shifting towards one with a greater proportion of warm species. We found that ,in the Kattegat, the significant CTI increase over time is associated with a strong local sea temperature change (Kordas et al., 2011; Berline et al., 2012), which indicates that copepod communities are tracking their thermal niches. According to the results of underlying processes, this CTI increase in the Kattegat is due mainly to the increase of relative abundances of the warm-adapted species. In temperate latitudes within the western Bay of Biscay, we found no ocean warming during the biological time series period and a low yet negative correlation between SST and copepod community composition variability. We consider that in the Urdaibai other factors such as dispersal limitation or biotic interactions are playing a more important role than SST in driving temporal change in community composition.

The tropicalization was the strongest underlying CTI driver in all three sites, with the strongest intensity in the Kattegat (77%), followed by Saronikos (45%) and Urdaibai (37%) (Figure 55a).



Figure 55. CTI trends for zooplankton time series in Bay of Biscay, Kattegat Sea and Gulf of Saronikos.



5. Cross-region and cross-taxa comparison of the long-term marine biodiversity trends in relation to climate change and variability

Here we present a comparison of CTI analysis of benthic and fish communities across regions and taxa, which includes 35 time series analysed in the previous section (3 zooplankton, 3 benthos, 29 fish) (Figure 56).

Overall, nearly all sites are experiencing warming in the last decades (SST mean = 0.278 °C/decade) (Figure 57).

In most of sites, biological communities showed an increase in CTI through time (CTI mean = 0.101 °C/decade (-0.064 to 0.249). In particular, 29 out of 35 sites showed positive increase, 13 out of 35 positive and significant, and 4 out of 35 negative and significant (Figure 57). By sea, Baltic and NE Atlantic showed a higher CTI trend (Figure 58). By community type, CTI trend was highest for hard bottom (rocky shore) communities, followed by fish, and lowest in mollusks (Figure 58). CTI increase obeys to dominance of tropicalization and deborealization (56%) relative to detropicalization and borealization (44%) (Figure 59). Among processes explaining CTI increase, tropicalization is the dominant process (33%, with respect to 23% on deborealization). However, this general pattern varies across regions and biotic groups. For instance, in the fish trawling community in the NE Atlantic, tropicalization is highly dominant, while in most of fish trawling in Mediterranean Sea and in estuarine fish, deborealization is the dominant process.

This suggests that in semi-enclosed seas such as the Mediterranean Sea and communities with low recolonization rates such as estuaries, the process behind CTI increase in fishes is the loss of cold-affinity species probably because those species have dispersal constraints there, while in open seas, warm-affinity species increase dominates probably because those species can respond faster to warming.



Figure 56. Study area with location of the 35, long-term time series that were analysed with respect to change in their CTI (3 zooplankton, 3 benthos, 29 fish).





Figure 57. Frequency of SST change (left) and CTI change (right) for all time-series locations. SST Mean = 0.278 °C/decade. CTI Mean = 0.101 °C/decade; 1st 3rd Q = -0.064 to 0.249; 29/35 positive, 13/35 positive and significant, 4/35 negative and significant.



Figure 58. CTI trend by sea (left) and by community type (right).



Figure 59. Percentage (number of sites/total) of CTI process.





Figure 60. CTI process according to different fish community.



6. Biodiversity changes in response to ocean acidification in mesocosm experiments

Introduction and experimental design

Between 2010 and 2015, we conducted a series of experiments with the Kiel Off-Shore Mesocosms for Future Ocean Simulations covering a latitudinal gradient from the Arctic to the Subtropics and diverse pelagic ecosystems/environments. The mesocosms enclosed the natural plankton communities occurring in the different study regions. Future ocean acidification (OA) scenarios were simulated in the mesocosms by adding different amounts of filtered CO₂-saturated seawater into the mesocosms according to (Riebesell et al., 2013). CO₂ perturbations were performed at the beginning of each experiment and were usually repeated during the course of the studies to keep carbonate chemistry within target levels.

The experimental design and the range of established CO_2 levels in the mesocosms varied between the different studies (Table 10). Either a pCO₂-gradient was established or two different pCO₂-concentrations were replicated. Phyto-, microzoo-, and mesoplankton was regularly sampled over the entire experiment duration with integrated water samplers and Apstein nets (55 or 100 µm), respectively. Preservation and enumeration of plankton samples was according to standard methods down to species, genus or to the highest taxonomic level possible and was consistent within each study. Detailed information on the study locations, plankton collection and abundance determination can be found in the corresponding publications listed in Table 10.

In order to investigate for possible OA-effects on biodiversity, plankton data sets (abundances) were analysed for OA-related changes in biodiversity metrics using the *adiv* package in R (Pavoine, 2020). To account for the range of variation between rare and abundant species and the resulting impact on biodiversity measures estimated from a data set, we used the Hill index for the calculation of species diversity and evenness and its parameter q. The Hill index increases with species richness and evenness in abundance so that q = 0 means species richness (i.e. equal importance to all species), and with increasing q increasing importance is given to rare species (Pavoine, 2020). Hence, investigating the Hill index as a function of q allows for in-depth analysis of how biodiversity metrics (diversity, evenness) vary along the "abundance gradient" which is of particular importance the larger the range of abundance variability between species/categories in a community is. Hill diversity and evenness was estimated as a function of the Hill parameter q from mesocosm specific average species/taxon abundances across all sampling days.

Results and Discussion

Based on bootstrap confidence intervals, some significant OA effects on biodiversity are suggested for the plankton communities in Svalbard, Norway (2011), and Finland (Figure 61). For the remaining studies and plankton communities, no OA effects on biodiversity became apparent (Table 11). In Svalbard 2010, diversity and evenness of the phytoplankton community suggested for some significant difference between the ambient treatment and both elevated pCO₂ treatments which show up already at relatively low q numbers ($\sim < 0.2$), i.e. these differences were not due to only a few dominant species. With increasing q, diversity decreased from around 28 (q=0) to around 7 in the ambient treatment and to around 4.5 in the elevated treatments. For the phytoplankton community studied in Norway in 2011, some significant response to pCO₂ levels projected for > year 2100 are revealed in evenness at q numbers > ca. 0.8 compared to the communities exposed to ambient and end of century projected pCO₂. Interestingly, OA impact on mesozooplankton diversity in the Finland study is



not straightforward, here diversity is increasingly smaller at q > 2 at end of century projected pCO₂ conditions compared to the equally higher diversity of the ambient and > year 2100 projected pCO₂ treatments (3.1 and 4.1, respectively, at q=4).

In summary, based on preliminary analysis, we have little experimental evidence for OAinduced changes on biodiversity of plankton communities of different oceanographic regions from the Arctic to the Subtropics. However, it needs to be kept in mind that we performed only short-term experiments (33–113 days) and OA effects on biodiversity of plankton communities may only reveal after longer exposure times to elevated pCO_2 conditions as was observed in the Svalbard mesocosm study where CO_2 effects developed slowly but steadily with time (Schulz et al., 2013). This is especially applicable for zooplankton with generally longer generation times compared to phyto- and microzooplankton. Thus, our short-term mesocosm experiments probably were not long enough to capture complete life cycles of many zooplankton species. Based on the fact that differences in biodiversity revealed only at larger q, we assume that elevated pCO_2 conditions probably provided an adaptive advantage to a few particular species stimulating their proliferation and increasing dominance of the plankton community in terms of abundance, i.e. few(er) species accomplishing better. Further analyses shall aim at identifying species responsible for these OA-related "biodiversity shifts" in the different mesocosm studies.

Table 10. Overview of the different OA mesocosm experiments performed between 2010 and 2015. For each of the experiments, the applied pCO2 range as well as the average pCO2 of the undisturbed (ambient) and OA manipulated mesocosm is given. Corresponding publications indicate where study-specific abundance data of the different plankton communities are published (Phyto: phytoplankton abundance data, MiZP: microzooplankton abundance data).

Location	Biome	Year	Month, Duration	Design	Mesocosms	pCO_2	pCO_2	pCO ₂	Corresponding Publications
					[n]	$[\mu atm]$	$[\mu atm]$	$[\mu atm]$	
Svalbard	Arctic	2010	June–July, 33 days	gradient	9	190–1000	$^{210\pm20}_{(n=3)}$	850 ±150 (n=3)	Phyto: Aberle et al. (2013) MiZP: Aberle et al. (2013) McZP: Niehoff et al. (2013) Overview: Schulz et al. (2013)
Norway	Temperate	2011	May-June, 36 days	gradient	8	310-1600	$^{340\pm30}_{(n=2)}$	790 ± 120 (n=3)	Phyto: no yet published MiZP: no yet published MeZP: not yet published Overview: not yet published
Finland	Temperate	2012	June–August, 48 days	gradient	6	350-1120	350 ± 5 (n=2)	840 ± 80 (n=2)	 Phyto: Paul et al. (2015), Bermúdez et al. (2016) MiZP: Bermúdez et al. (2016), Lischka et al. (2017) MeZP: Lischka et al. (2017) Overview: Paul et al. (2015)
Sweden	Temperate	2013	March-June, 113 days	replicated treatment levels	10	380-760	380 ± 20 (n=5)	760 ± 20 (n=5)	Phyto: Horn et al. (2016) MiZP: Horn et al. (2016) McZP: Algueró-Muñiz et al. (2017) Overview: Bach et al. (2016)
Gran Canaria	Subtropic	2014	September–December, 62 days	$\operatorname{gradient}$	8	400-1190	400 ± 5 (n=2)	900 ± 120 (n=3)	Phyto: Taucher et al. (2018) MiZP: Algueró-Muñiz et al. (2019) MeZP: Algueró-Muñiz et al. (2019), MeZP: Lischka et al. (2018) Overview: Taucher et al. (2017)
Norway	Temperate	2015	May-June, 53 days	replicated treatment levels	8	314-1700	328 ±23 (n=4)	$^{1996~\pm~200}_{(n=4)}$	Phyto: Dörner et al. (2020) MiZP: Dörner et al. (2020) MeZP: no yet published Overview: Spisla et al. (2021)

Table 11. Summary table showing for which of the different plankton groups of the various mesocosm experiments significant effects (based on bootstrap confidence intervals) of diversity and/or evenness in response to OA conditions as a function of the Hill number q are suggested.



	Phyto	Phytoplankton		oplankton	Mesozooplanktor	
Experiment	Diversity Evenness		Diversity	Evenness	Diversity	Eveness
Svalbard 2010	yes	yes	no	no	no	no
Norway 2011	no	yes	no	no	no	no
Finland 2012	no	no	no	no	yes	no
Sweden 2013	no	no	no	no	no	no
Gran Canaria 2014	no	no	no	no	no	no
Norway 2015	no	no	no	no	no	no



Figure 61. **Svalbard 2010**: phytoplankton diversity (a) and evenness (b), Norway 2011: phytoplankton evenness (c), **Finland 2012**: mesozooplankton diversity (d) as a function of the Hill parameter q. Error bars are 95% bootstrap confidence intervals.



7. Conclusions

Overall, 20 long-term case studies distributed across all European seas (North-East Atlantic, Bay of Biscay and Iberian coast, Baltic Sea, and Mediterranean Sea) and covering a wide variety of marine taxa (phytoplankton, zooplankton, macroinvertebrates, macroalgae, fish, marine turtles) and habitats (rocky shore, soft-bottom, pelagic, demersal) have been reported here. A summary of main conclusions of community changes in relation to climate change derived sea warming (0.28°C/decade, stronger in Mediterranean than in NE Atlantic) and other environmental and anthropogenic drivers are as follows.

On plankton communities:

• Few long-term plankton communities have been analysed in order to make definitive conclusions and consistent comparisons with other taxa. Only one phytoplankton time series have been analysed, with no clear trends. In the three zooplankton time series analysed, the tropicalization was the strongest underlying process explaining the community trend, although only in Kattegat showed a significant increase in CTI.

On marine forests:

- Five beaches at low intertidal rocky shore with marine forests in Northern Portugal coast were analysed from 2006 to 2021. In most of them, CTI increased, with deborealization process stronger than tropicalization, while sea temperature decreased in this period. However, sea temperature trend estimated from 1980 to 2020 increased at 0.1°C per decade. Further analysis on local temperature and marine forests response lag is needed.
- A monitoring program focused on kelp densities during the last decade in Portugal coastline showed a temporal turnover of species, with perennial kelps replaced by annual species.

On seagrasses:

• The long-term analysis in the Baltic Sea showed major declines in eelgrass depth distribution, relative to the historic (1890–1910) situation, is due to the wasting disease in the 1930s followed by eutrophication peaking in the 1980s, which reduced water clarity, and trawling, which has disturbed the seafloor. The analysis indicates that bottom trawling and recent warming (0.5°C per decade, 1985–2018) may suppress eelgrass from fully recovering from eutrophication. Management efforts to reduce nutrient input and thereby improve water clarity have been instrumental for avoiding a catastrophic loss of eelgrass. Future management must reduce both eutrophication and bottom trawling to help eelgrass reach deeper, cooler refugia, to increase resilience toward ongoing and further warming.

On rocky benthic communities (macroinvertebrates and macroalgae):

 Rocky inter-tidal benthic communities from the coastlines of the UK, the Bay of Biscay, and from the Mediterranean Sea were analysed. The strongest processes of community change were tropicalization in some cases, and deborealization in others. Along the UK coast, the CTI increased significantly in 2 out of 4 locations, where tropicalization was the dominant processes. In the Bay of Biscay, the ecological processes that predominate in the hard substrate benthic community were tropicalization, followed by borealization. In Mediterranean coastal areas, a community in the Ligurian Sea showed an increase in the CTI with deborealization as the main process in 2007-2016 period.



On soft-bottom benthos (macroinvertebrates):

• Few data time series were available, one in the Bay of Biscay and one in Ionian Sea. In the case of the Ionian Sea, the number of years sampled were too limited to make definitive conclusions.

On coralligenous habitats:

- Observations in western Mediterranean Sea showed that marine heatwaves have caused long-term alterations to the functional trait composition of coralligenous assemblages, leading to marked functional changes, such as a critical functional group related to the provision of structural complexity; the one of habitat-forming octocorals. Gorgonians, which are some of the most important habitat-formers of the coralligenous assemblages, have a generally low recovery capacity from marine heatwaves, even in the long-term (> 15 years). Recurrent marine heatwaves were observed in both Scandola and Port-Cros sites during the studied periods, which has likely contributed to both the functional changes and the lack of recovery observed.
- The analysis of CTI on coralligenous assemblage of Marseille over the 2008-2020 period of significant sea warming (0.21°C per decade) indicated that tropicalization was more important than other processes in terms of changes in relative abundance.

On fish communities:

- Demersal fish have been studied in the NE Atlantic and W Mediterranean Sea. In NE Atlantic, significant increases in CTI were observed in all ecoregions, related to increasing trends in SST in the last decades. The underlying processes contributing to the observed changes in CTI differ slightly between regions, but the predominant process overall involve tropicalization. In the W Mediterranean, only 1 out 3 regions showed significant CTI increase.
- Catch fish data has been studied in the Catalan Sea (W Mediterranean). CTI significantly increased over the last decades with spatial variations. Landing data from purse-seiners revealed that increasing trends in CTI were particularly important in the northernmost regions. Tropicalization was the main process behind CTI changes associated to trawlers (benthic community), whilst in the case of purse-seiners (i.e., pelagic community), deborealization prevailed.
- Fish associated to *Posidonia* habitat was studied based on data compiled in the last 105 years (since 1914) suggest a relatively stable community and no clear changes associated to the effect of increasing temperature.
- Significant ocean warming in eastern Mediterranean in 1990-2020 triggered the community of benthic fish to track their thermal niches over time, as seen in the significant CTI increase at rate of 0.054 °C/year. The deborealization trend can be a product of competition of native species with the alien species with similar traits or niches, and/or the warming itself that reduce the fitness of thermally-sensitive native species.
- Estuarine fish community showed a significant increase of CTI in the last decades, mainly through deborealisation process.
- We proposed a framework to analyse alternative acclimatization pathways that accounts for pure distributional shifts, pure phenological adjustments, and mixed, intermediate pathways balancing both responses. We applied this framework to fish species that showed contrasting responses to warming; horse mackerel advanced the timing of spawning (11.7 days/°C of warming) from 1992 to 2019, whilst Atlantic mackerel shifted poleward (369 km/°C of warming). These results support our framework underpinning that acclimatization pathways to warming can combine, or



exclude, timing and poleward shift, and the strategy selected by the species probably depends on its biological traits.

On marine reptiles:

 Thermal conditions of green turtle nests in the Mediterranean (Turkish beaches) have been studied in 225 nests and 12 control sites by comparing nest and sand temperatures during 5-year period. The results showed that high nest temperatures are linked to a reduction in population recruitment, suggesting that current conditions for incubating eggs of Mediterranean green turtles are approaching the critical threshold that would jeopardize their reproductive success.

On biodiversity response to acidification:

 Mesocosm experiments from the Arctic to the Subtropics, identified biodiversity responses (lower diversity with OA) for the plankton communities (phytoplankton and mesozooplankton) in Svalbard and Finland. Elevated pCO₂ conditions probably provided adaptive advantage to a few particular species stimulating their proliferation to increasingly dominate the plankton community. For the remaining studies (Gran Canaria, Norway, Sweeden) and plankton communities (microzooplankton), no OA effects on biodiversity became apparent.

Concerning the methodology developed and employed, we contributed in two main aspects:

- We undertook a Community Temperature Index (CTI) analysis, which enabled to compare the response to warming of marine biodiversity communities across regions and taxa. CTI analysis and process behind (i.e., tropicalization and borealization) have been coded in R language (R-Core-Team, 2014) in sequential scripts which use local data (from metadata catalogue we built) and public databases on species occurrence and sea temperature. R codes were provided to all partner participants of Task 1.1 to run the analysis in its storyline time series data.
- We developed a GAMM methodology to decompose time series of indicators of climate change into linear trends along time, cyclical fluctuations within the year, that has been coded in R language. GAMMs can model a wide range of probability distributions and allows the inclusion of random effects and spatio-temporal correlation structures.

In summary, results indicated that a significant portion of each of the biological communities and sites examined demonstrated a clear response to ongoing sea warming which, in some cases, favoured warm-water species (tropicalization) with decreases in cold-water species (deborealization) in contrast to borealization and detropicalization. The balance between tropicalization and deborealization in responding communities seems to depend on biological traits, geomorphological characteristics and constraints of the sea area, and co-varying anthropogenic activities.



Indexes

7.1. Index of figures

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