



# Biogeography and biodiversity change on coastal communities at continental scales

Storyline 36



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## Introduction to FutureMARES

The EU Horizon project FutureMARES (2020-2024) was designed to develop science-based advice on viable actions and strategies to safeguard biodiversity and ecosystem functions to maximise natural capital and its delivery of services from marine and transitional ecosystems in a future climate. The program investigates effective habitat restoration, conservation strategies and sustainable harvesting at locations across a broad range of European and other marine and transitional systems. The restoration of habitat-forming species (plants or animals) and habitat conservation (e.g. marine protected areas, MPAs) represent two nature-based solutions (NBS) defined by the EU as "resource efficient actions inspired or supported by nature to simultaneously provide environmental, social and economic benefits that help to build resilience to change". A third action that will interact with these two NBS and have positive effects on marine biodiversity is nature-inclusive harvesting (NIH) such as the sustainable farming of plants and animals at the base of marine food webs and ecosystem-based management practices for traditional (artisanal) and commercial fisheries.

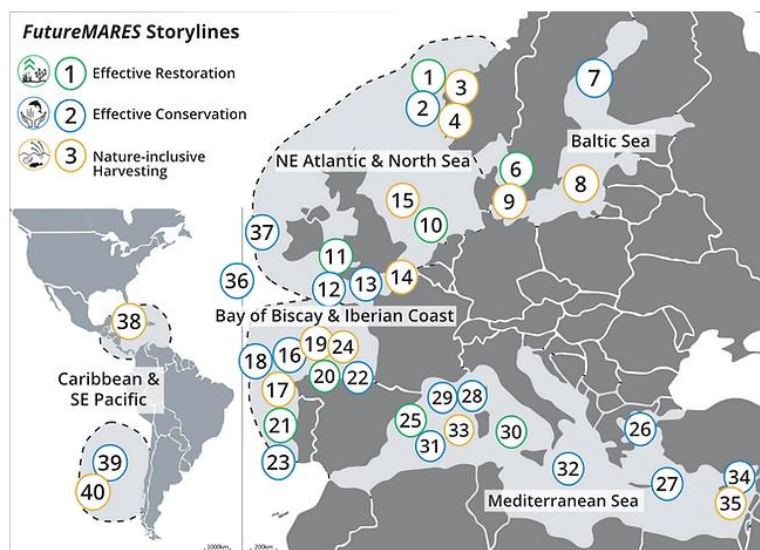


Figure 1: Overview of FutureMARES Storylines

FutureMARES was designed to:

- advance the state-of-the-art forecasting capability for species of high conservation value,
- explore new and less carbon intensive aquaculture production methods,
- perform modelling analyses geared towards informing the development of climate-smart marine spatial planning approaches, and
- provide an assessment of ecosystem services based on scenarios of climate change and the implementation of NBS and NIH.

This document provides a summary of activities conducted in FutureMARES in a specific area on specific NBS and/or NIH. The activities are multi-disciplinary and include marine ecology (analyses of historical time series and experiments performed in the field and laboratory), climate change projection modelling (future physical, biogeochemical and ecological changes), economic analyses and social-ecological risk assessments. Many of these components and analyses were co-developed with local and regional stakeholders through regular engagement activities. The work presented in this Storyline document represent activities conducted by a large number of FutureMARES project partners. Broader comparisons and syntheses (across regions and/or topics) are provided in the FutureMARES deliverable reports submitted to the European Commission ([www.futuremares.eu](http://www.futuremares.eu)).

## Regional Storyline Context

There is mounting awareness about the threat that climate change poses to global biodiversity, and that addressing it requires a better understanding of the link between climate and biodiversity. This is certainly the case of marine thermal refugia – which organisms can exploit to escape from the effects of climate change. The extent to which thermal refugia matters for biodiversity at continental and decadal scales remains largely unaddressed, though, because of a lack of simultaneously detailed and wide coastal temperature and biodiversity datasets. Temperature data at scales matched to those of organisms is lacking due to previously unsurmountable technical limitations, severely reducing the impact of most analyses and forecasts (Helmuth et al. 2014). We have, however, recently developed a new family of miniaturized autonomous loggers (Chan et al. 2016, Lima & Wethey 2009, Gandra et al. 2015) which are key for collecting temperature at organismal scales over continental spans.

Intertidal systems, located in the area between the high and low tide levels, offer unparalleled advantages to address these questions. They are inhabited by marine organisms which must withstand terrestrial conditions during low tide (Harley 2008, Denny & Wethey 2000), and which are regarded as especially sensitive indicators of the effects of climate variability and climate change (Helmuth et al. 2006). In the intertidal, solar radiation is the dominant component of the energy balance, and during low tide its influence can exceed that of seasons or latitude (Seabra et al. 2011). Thus, geomorphology determines the availability of refugia and influences metabolic costs and sublethal and lethal stress (Lima et al. 2016). Coastal upwelling further increases thermal complexity (Seabra et al. 2019). During summer, cold and warm-water pockets alternate at regional scales, and owing to wind stress variability, sea temperature may experience oscillations of 5-10 °C in a few days.



**Figure 2:** Extraordinary biodiversity in the low intertidal of NW Iberia. This sort of luxuriant algae cover was once abundant towards the south, but many of the canopy-forming algae are now retreating, leaving behind much less diverse communities. In some, few locations, however, these highly diverse communities are still present. We want to understand why. Are they exploiting thermal refugia? Credit: Fernando Lima

Interestingly, along the European coast, there is an alternation between stressful and non-stressful environments across a variety of scales, ranging from a few meters to hundreds of kilometres. Often these patterns overlap across spatial scales, amplifying or dampening their combined effect. Quantifying the availability of thermal refugia and understanding how it can buffer the deleterious effects of climate change is fundamental for understanding the mechanisms setting biogeographic limits and forecast changes in biodiversity. This information is extremely valuable to prioritize conservation efforts and to inform on the ideal spatial arrangement of marine protected areas.

In this storyline, we are compiling quantitative abundance data of more than 200 species of rocky intertidal organisms (e.g., algae, molluscs, crustaceans) collected by our research team more than 15 years ago at a series of microhabitats at 22 locations on the Atlantic coast of Europe (from Morocco to Scotland). We are downloading and compiling long-term temperature profiles measured at the scale of the organisms and at the same microhabitats by autonomous data-loggers developed specifically for this purpose by our team. These loggers have been installed in 2010 and have been collecting temperature at 1h resolution since then. Additionally, we are currently re-assessing biodiversity in the field at the same coastal locations surveyed in the past. Biodiversity changes are being compared with temperature patterns and with temperature changing trends. We are looking at changes in the temperature affinity of native and invasive species, changes in their geographical span, abundance, and co-occurrence, at the same time we quantify thermal heterogeneity and identify and quantify thermal refugia from micro to continental scales.



**Figure 3 (left):** The cold-water adapted canopy-forming foundation species *Himanthalia elongata*, which has suffered a dramatic retreat of the southern distribution limit along the coast. It moved more than 400 km over ~150 years. Notably, in the last decade the species disappeared from the entire coast, with the exception of the relict population here depicted. Is it because this location provides refugia from warming? Credit: Rui Seabra.

**Figure 4 (right):** Field testing of a new smartphone app developed by us to aid on the acquisition of photo-quadrat data and metadata, important to contextualize biodiversity measurements in the field. Credit: Fernando Lima

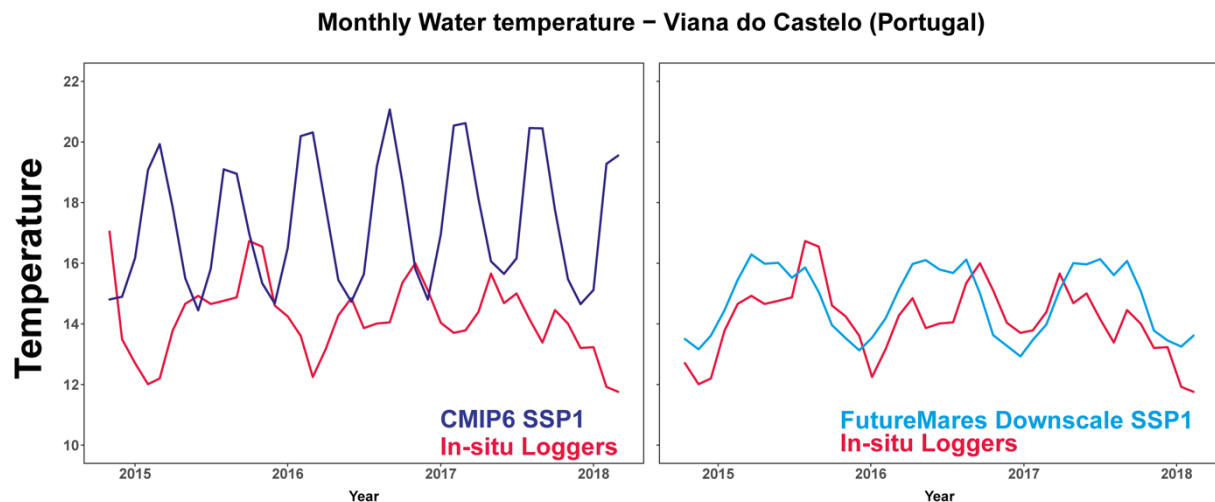
The evaluation of current and future distribution of thermal refugia along the European Atlantic coast will help us to generate robust forecasts of ecosystem sensitivity or resilience to climate change and, consequently, inform on the optimal placement of MPA in relation to climate change.

## Projected impacts of climate change

Climate change has already been linked to the global redistribution of species and biogeographical boundaries, a process with deep ecological, economic, and social consequences (Pecl et al. 2017). Our ability to address the processes that drive these changes is deeply dependent on a better understanding of the links between the spatial and temporal structures of temperature and community changes (Waldock et al. 2018). FutureMARES has made projections of physical and biogeochemical impacts of climate change in the region including three IPCC scenarios (SSP126, SSP 245 and SSP 585 (for background see [Deliverable Report 2.2](#)). Despite the fact that a substantial number of studies have been reporting major biodiversity changes in European intertidal communities in response to climate change (Lima et al. 2007, Burrows et al. 2020, Hawkins et al. 2009), few have focused on the importance of thermal refugia as a modulator of the effects of climate change (Lima et al. 2016, Lourenço et al. 2016, Bates et al. 2018). Thermal refugia may allow species to extend their distribution to areas otherwise uninhabitable, and may act as thermal buffers overriding the long-term warming trend. When acting upon key species (e.g., foundation species, Fig. 3) these processes have the potential to influence the entire community and drive (or prevent) pervasive change.

FutureMARES has made projections of physical and biogeochemical impacts of climate change for three IPCC scenarios (SSP1-2.6, SSP2-4.5 and SSP5-8.5). The projected data includes information on temperature, pH, oxygen, and salinity.

Here, we extracted the downscaled temperature for the shallowest depth (5 meters) to use in our modelling efforts in 2.6, where we tested how different populations of a intertidal macroalgae (*Ascophyllum nodosum*) responded to heat stress treatments, and used that information to predict the biogeographic consequences of future climates under different emission scenarios. Downscaled data vastly outperformed non-downscaled data (Fig 5).



**Figure 5:** Comparison between the accuracy of regular, non-downscaled SSP1 sea temperature from CMIP6 (on the left) and FutureMares downscaled SSP1 sea temperature (on the right), when ground-truthed against in situ temperature data collected by data-loggers at Viana do Castelo (where the southernmost population).

## Scenarios describing future society and economy

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FutureMARES developed three policy-relevant scenarios for NBS and NIH based on commonly used IPCC frameworks (for more details see hyperlink). These scenarios were regionalised based on stakeholder perspectives to guide activities such as model simulations and risk assessments.

### **(GS) Global Sustainability (SSP126)** - Low challenges to mitigation and adaptation

The world shifts gradually but pervasively to a more sustainable path, emphasising inclusive development that respects perceived environmental boundaries. Management of the global commons slowly improves, investments in educational and health accelerate lower birth and death rates, and the emphasis on economic growth shifts to an emphasis on human well-being.

### **(NE) National Enterprise (SSP385)** - High challenges to mitigation and adaptation

A resurgent nationalism, concerns about competitiveness and security, and regional conflicts push countries to focus on domestic or regional issues. Policies shift over time to be oriented more on national and regional security. Countries focus on achieving energy and food security goals within their own regions at the expense of broader-based development.

### **(WM) World Markets (SSP585)** - High challenges to mitigation, low challenges to adaptation

The world increasingly believes in competitive markets, innovation and participatory societies to produce rapid technological progress and train and educate people for sustainable development. The push for economic and social development is coupled with exploiting abundant fossil fuel resources and adopting resource and energy intensive lifestyles around the world.

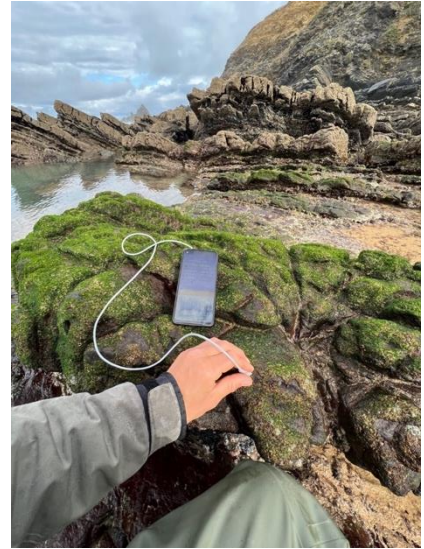


Figure 6: The three, broad scenarios that were regionalised to guide activities in FutureMARES.  
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## FutureMARES research needs

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While large amounts of data are available on large-scale temperature patterns, comparatively little is known about near coastal and intertidal zones that are crucial for a wide variety of ecosystem services. Obtaining temperature data at scales matched to those of organisms is crucial because it ultimately drives organism's physiology and performance (17). The consequences of those performances are then scaled-up to the community level. Thermal refugia, in particular at scales that effectively matter, still needs to be quantified. Those data need to be accompanied by simultaneously detailed and geographically-wide biodiversity datasets collected at decadal scales from which change and stasis can be accurately assessed.

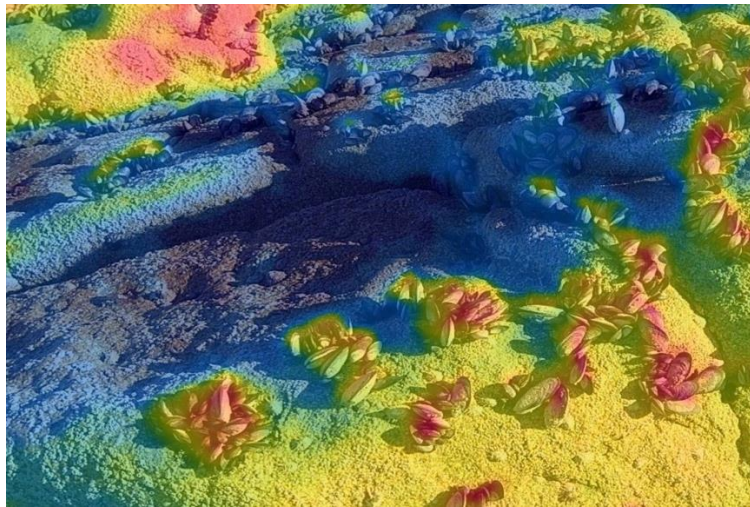


*Figure 7: Downloading a year's worth of hourly temperature data from an autonomous miniaturized logger previously deployed in the intertidal. These data are crucial to identify and, more importantly, quantify the distribution of thermal refugia along the entire geographical span of species. Credit: Rui Seabra.*

## FutureMARES research (T = Task – see program structure at [futuremares.eu](http://futuremares.eu))

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- **T1.1** Temporal trends in macroalgae and macroinvertebrate distribution and abundance across the Atlantic coast of Europe
- **T1.2** Identification of functional groups whose change can be associated with warming
- **T1.4** Engage stakeholders on FutureMARES scenarios to help define projection simulations
- **T2.1** Contribution with in-situ temperature data series for forecasts and hindcasts
- **T2.2** Contribution with in-situ temperature data series for uncertainty analyses
- **T2.3** Combination of biodiversity and temperature data to identify biodiversity hotspots and climate refugia in the Atlantic coast of Europe
- **T3.1** Team-up with CIIMAR to run experiments looking at the functions provided by canopy forming macroalgae at the southern limit of their distribution
- **T3.2** Team-up with CIIMAR to build a standardized experimental chamber that accurately replicates the intertidal thermal environment to assess the potential for local adaptation of selected species across the European Atlantic
- **T4.1** Provide data on range and abundance of seaweeds
- **T6.1** Produce climate readiness maps

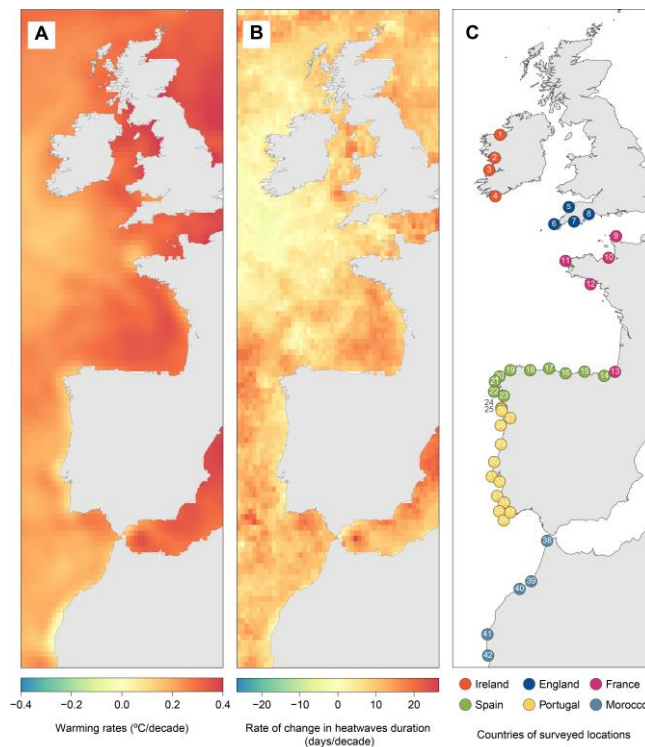


**Figure 8:** Thermal picture of the intertidal showing its immense thermal variability. We are quantifying how much thermal refugia and hotspots exist at a variety of scales from a few cm to continental scales, and their importance for the inhabiting life. Credit: Fernando Lima.

## 2. Research conducted

### 2.1 Temporal trends in macroalgae and macroinvertebrate distribution and abundance across the Atlantic coast of Europe (T1.1, T4.1)

We used 37 years of daily SSTs (1982–2018) from NOAA 1/4 arc-degree Daily Optimum Interpolation SST version 2 (dOISST.v2) (Banzon et al., 2016) to assess how global warming has impacted the ocean along the area of study (Fig. 9).



**Figure 9.** 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



Ocean warming was characterized both in terms of SST warming rates and the trend in the yearly duration of marine heatwaves. We used AVHRR-only data due to its long temporal span and because it has been shown to out-perform other datasets in coastal areas (Lima & Wethey, 2012). For each individual pixel, the climatology was obtained following (Schlegel & 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 & 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 & 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.

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; Fig. 9 C).

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 & Southward, 1958) scale (SACFOR: S\_extremely abundant; A\_abundant; C\_common; F\_frequent; O\_occasional; R\_rare). The currently accepted taxonomy was accessed through the World Register for Marine Species database (WORMS; <http://www.marinespecies.org/>). 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.

Species turnover was synthesized by a modified version of the (Helm et al., 2015) index, and hereby defined as the Novelty Index (*NI*), calculated as:

$$NI = \left[ \frac{e+i}{R} \right] * 100$$

, where *e* is the number of species extinct (i.e., representing the loss of 'characteristic diversity', the number of species belonging to habitat-specific pools, which we assume is the community composition during S1); *i* is the number of invading species, whereas the 'derived diversity', representing the pool of species that is novel to a community. The percentage of a community composition that is novel is, finally, obtained, by calculating the combined contribute between species loss (*e*) and gain (*i*) on the total number of species that can co-occur at each location (*R*), multiplied by 100, 'normalizing' the change in species composition among assemblages. Biodiversity reconfigurations at each location were quantified by the difference in Shannon Diversity Indices (*H*) (Shannon, 1948) between recent (S2) and past (S1) surveys, in this way summarizing the net outcome from the interplay between species gain, loss, and change in relative abundance.

The Community Temperature Index is the average of the thermal affinities of the species that co-occur in a community, weighted by their abundance. In this study, we investigate changes in 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. 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.

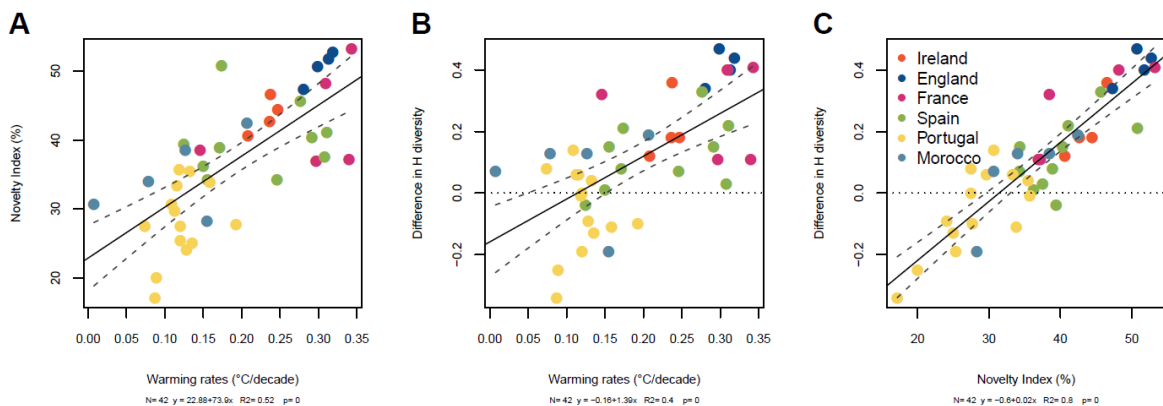
Seaweeds were also classified into four distinct functional groups according to the size of their thalli, morphological similarity, and on the basis of grouping systems commonly applied for intertidal species (e.g., (Arenas et al., 2006; Steneck & Dethier, 1994). 'Encrusting' species (e.g., *Lithophyllum incrustans*, *Codium adhaerens*) are characterized by crustose forms. 'Turfs-forming' species have limited vertical growth and include both filamentous and articulated calcareous species (< 5 cm; e.g., *Halopteris scoparia*, *Rhodothamniella floridula*, *Corallina* spp, *Ceramium* spp). 'Sub-canopies' can reach up to 20 cm in height and compose mainly a secondary cover in intertidal rocky shore areas (e.g., *Chondrus crispus*, *Mastocarpus stellatus*, *Bifurcaria bifurcata*). 'Canopies' species are the most sizable (> 20 cm and up to 60-80 cm; e.g., *Himanthalia elongata*, *Cystoseira* spp., *Laminaria* spp., *Fucus* spp.), forming a shading layer in intertidal ecosystems, hence why they are often addressed as 'forests' (e.g., kelp-forests are mainly composed of *Laminariales*). Animals were distinguished according to similarity in feeding traits between 'filter-feeders' (mainly mussels and barnacles), 'grazers' (e.g., limpets, *Steromphala* spp), 'predators' (e.g., *Nucella lapillus*, seastars) and 'others' (e.g., anemones, which are both carnivorous and detritivores). Per each location, the difference in the relative proportion of functional groups was calculated between surveys (S2-S1).

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. 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 of approximately 0.3 to 0.4 °C/decade since 1982. The SST rate of change emerged in these analyses is above the warming rates calculated by Lima (Lima & Wethey, 2012) on the same dataset but on a time-series of data extending 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 ( $R^2= 0.28$ ,  $p < 0.001$ ; Fig. S1).

The western margin of Ireland has also experienced consistent warming, although temperatures increased at a slower pace ( $0.2-0.3^\circ\text{C}/\text{decade}$ ). 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 & 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).

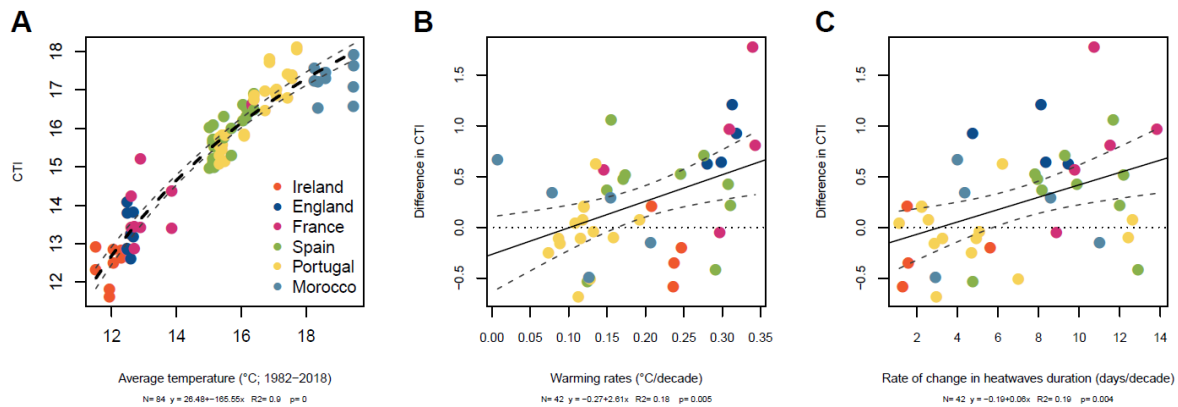
The intertidal communities surveyed in this study showed consistent changes in their compositions since their first assessment. In 15 years, a marked turnover of species occurred in all locations (Novelty Indices range: 17.14 - 53.25%), with the most novel communities being those where the highest warming rates were recorded (Fig. 10 A).



**Figure 10.** Patterns of change in the composition of the NE Atlantic intertidal communities foresee greater species turnover (A) and higher diversity (B) with increasing warming rates. Species turnover is leading to an increased diversity of intertidal communities in the NE Atlantic (C).

Communities' novelty is showed to be positively correlated with the warming rates experienced in the last decades ( $R^2= 0.52$ ,  $p < 0.001$ ; Fig. 10 A), and marginally to the increase in the yearly duration of marine heatwaves ( $R^2= 0.11$ ,  $p = 0.03$ ). Communities from regions that are warming the most are additionally showed to be more diverse than in the past ( $R^2= 0.4$ ,  $p < 0.001$ ; Fig. 9 B). Patterns of change in the NE Atlantic intertidal assemblages highlight that consistent changes in the sets of co-occurring species are taking place and that this is leading to increased biodiversity (Figure 10 C).

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; Fig. 11 A).



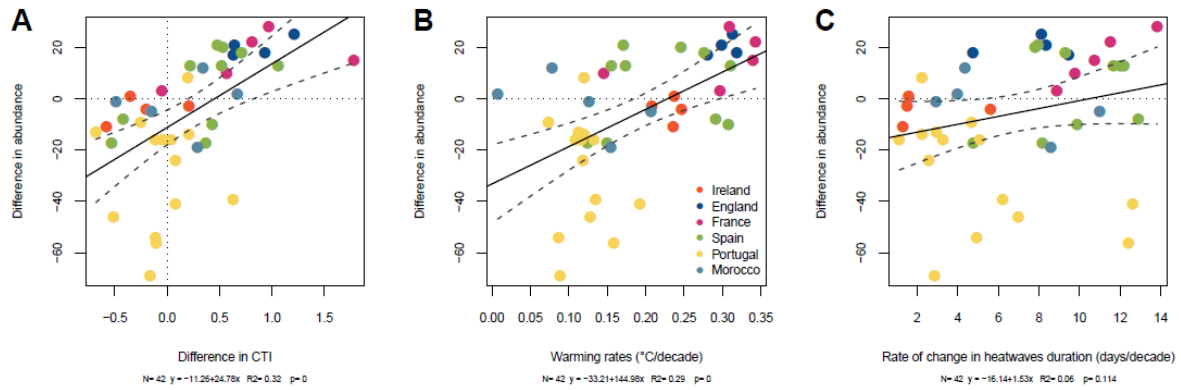
**Figure 11.** The CTI has emerged as a reliable metric for the tracking of reconfigurations in the NE Atlantic intertidal communities. (A) The values of CTI during both surveys were broadly in line with the longer-term trend in temperature of surveyed locations (1982–2018). A ‘thermophilization’ of 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. The coastline south of Morocco is characterized, for long distances, 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 ( $R^2 = 0.09$ ,  $p = 0.054$ ).

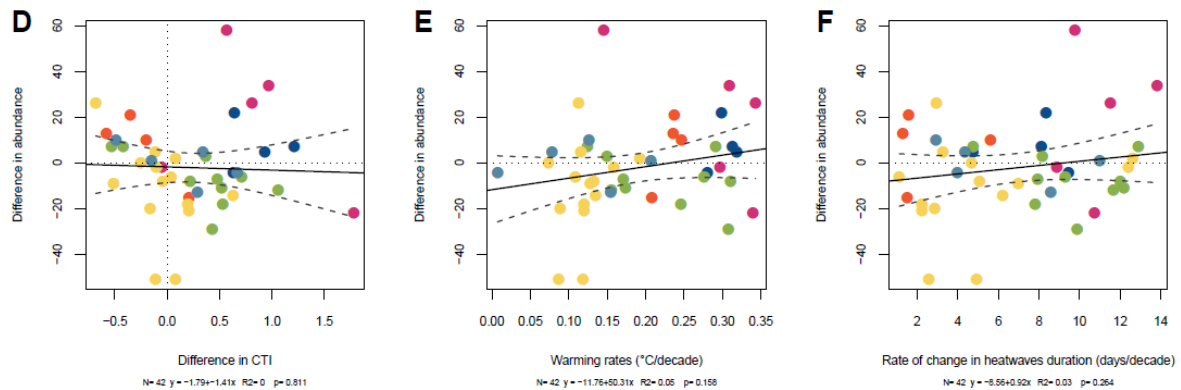
Changes in CTIs between surveys confirm that, in the majority of cases (26 out of 42), communities’ redistributions are going in the same direction of warming (range in CTI increase: 0.04–1.78 °C). The greatest positive shifts have occurred in those communities which experienced the highest warming rates ( $R^2 = 0.18$ ,  $p < 0.01$ , Fig. 10 B) and the greatest increase in heatwaves duration ( $R^2 = 0.19$ ,  $p < 0.01$ , Fig. 10 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; 50<sup>th</sup> 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 (Fig. 12 A and D).

### Warm-water species



### Cold-water species

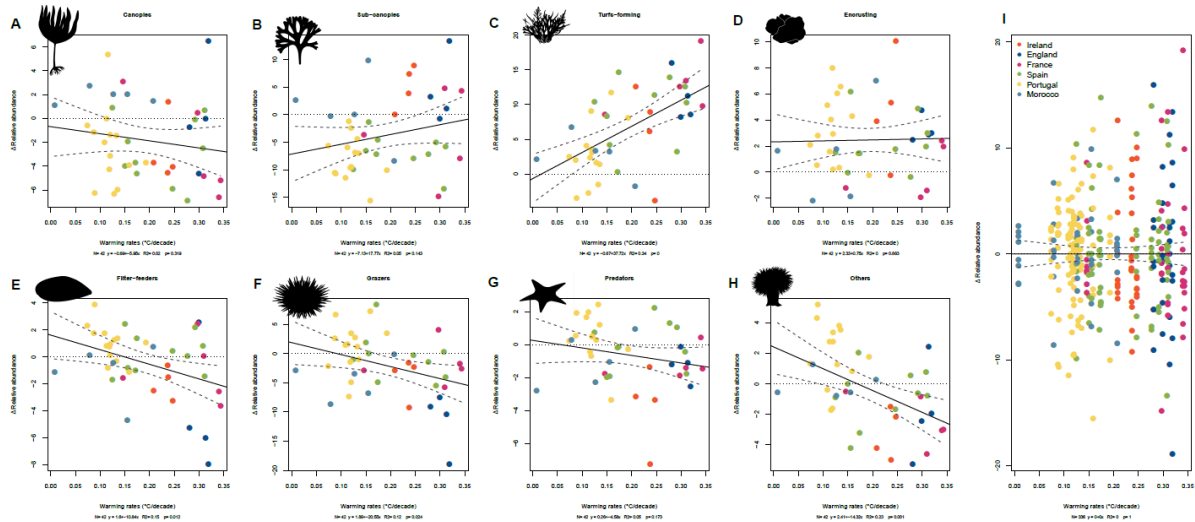


**Figure 12.** Positive shifts in the thermal affinity of the NE Atlantic intertidal assemblages are associated with an increase in the total abundance of warm-water species (A) rather than to a decrease in cold-water counterparts (D). Species with warm affinities increased in abundance mainly in those 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).

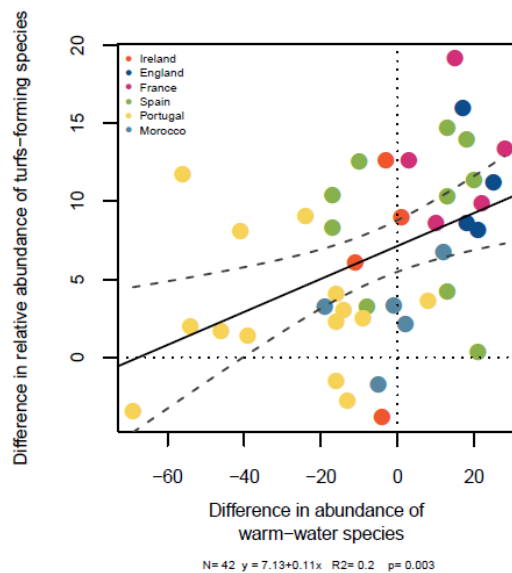
The total abundance of species with warm affinities increased mainly in those locations which experienced the highest warming rates ( $R^2 = 0.29$ ,  $p < 0.01$ , Fig. 12 B), and where a positive, despite non-linear, increase in the duration of heatwaves occurred ( $R^2 = 0.06$ ,  $p = 0.114$ , Fig. 12 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.

Changes in the composition of intertidal rock communities in the NE Atlantic are additionally leading to alterations in the communities’ structure. Functional groups redistributions are taking place and are noticeable mainly in the increase in the relative proportion of ‘turfs-forming’ species ( $6.56 \pm 5.68\%$ ) and in the reduced proportions of ‘sub-canopies’ ( $-3.73 \pm 6.83$ ). The increased frequency of occurrence of turfs is closely linked to warming rates ( $R^2 = 0.34$ ,  $p < 0.01$ ; Fig. 12 C) and to the increased occurrence of extreme events ( $R^2 = 0.17$ ,  $p < 0.01$ ), likely because of the warm-affinity of the species composing these low-lying mats (Fig. 13). Significant correlations between the reduced relative abundances of ‘sub-canopies’ and the thermal metrics calculated in this study did not emerge (warming rates:  $R^2 = 0.05$ ,  $p = 0.143$ ; the yearly trend in heatwaves duration:  $R^2 = 0.02$ ,  $p = 0.419$ ; Fig. 12 B). The rate of increase in SSTs has, additionally, been observed to be related to moderate decreases in the relative proportion of ‘grazers’ ( $-2.06 \pm 5.22\%$ ;  $R^2 = 0.12$ ,  $p = 0.024$ ; Fig. 12 E), and to neglectful reductions in ‘filter-feeders’ ( $-0.48 \pm 2.48\%$ ;  $R^2 = 0.15$ ,  $p = 0.012$ ; Fig. 12 D) and ‘others’

functional groups ( $-0.33 \pm 2.63$  %;  $R^2= 0.23$ ,  $p= 0.001$ ; Fig. 12 F). A flattening of the three-dimensional structure of seaweed assemblages is additionally seen in the increase, in almost all locations, of encrusting forms, which however is uncorrelated with warming rates experienced at each location ( $R^2= 0.00$ ,  $p= 0.083$ ; Fig. 12 D). Ultimately, the stability of communities in NW France, SW England and Spain was the one most affected, highlighting the greatest differences in the proportions among functional groups (Fig.12 I).



**Figure 12.** An increase in the proportion of ‘turfs-forming’ species occurred in almost all locations, and more intensely where warming rates were the highest (C). A decrease in the relative proportion of ‘filter-feeders’ (E), ‘grazers’ (F), and ‘others’ (G) functional groups were also found to be related to the rate of increase in SSTs. A marked decrease in the relative abundance of ‘sub-canopies’ species is instead observed across communities although it is not directly related to warming (B). Drawings by Adi Khen.



**Figure 13.** Redistributions of the NE Atlantic intertidal assemblages that occurred in the last 15 years have led towards changes in communities’ structure mainly observable in the increase in relative proportions of ‘turfs-forming’ species with warm-water affinities.

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 of 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; S. 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 & 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 furoids (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 & Wernberg, 2018; Voerman et al., 2013; Wernberg et al., 2010). Space availability due to canopies loss has, therefore, represented an opportunity for warm-adapted turfs to rapidly expand, and later inhibit the recolonization of larger size species, thus forming an alternative stable state (Feehan et al., 2019; Filbee-Dexter & Wernberg, 2018; Petraitis & Dudgeon, 2004).

In this study, the largest drops in site occupancy were detected in sub-canopies species (-0.32 to -15.09% in 30 of 42 communities), which were the dominant group in intertidal environments across the NE Atlantic (Fig. S5). Canopies proportions have also declined (reduced relative abundances of -0.12 to -6.62% in 26 of 42 surveyed communities) in most of the assemblages surveyed, despite to a less extent. Reduced abundances in kelps hereby documented, however, could be underestimated because our surveys are limited to intertidal environments, while many *Laminariales* species largely distribute in subtidal zones.

Space vacancy due to the declines of both macroalgal groups, and minimally of filter-feeders and 'others' groups, are thought to have triggered the observed shifts in warm-water turfs and encrusting algae distributions, but the reasons of such losses remain to be investigated. A close link between reduced proportions of canopies and sub-canopies and warming has not emerged, probably because the impact of rising temperatures is superimposed on many other anthropogenic disturbances at the coast, and that act with different intensity at the regional scale (S. D. Connell et al., 2008; Russell & Connell, 2012). A meta-analysis on the cumulative effects of local anthropogenic stressors) and other sources of disturbance (e.g., presence of competitors or grazers, removal of canopy algae, limiting or excessive light, low or high salinity, increasing temperature, high wave exposure, and high UV or CO<sub>2</sub>) in rocky temperate environments highlighted that eutrophication, and generally, poor water quality (due to heavy metal pollution, nutrient enrichment and high sediment loads) have major negative effects on the growth and survival of canopy-forming algae, while unaffected or even enhancing growth of mat-forming species (Strain et al., 2014).

Increased proportions of low-lying mats occurred also at the expense of grazers among intertidal assemblages. Herbivory is known to exert a key role in the control of seaweeds coverage across the NE Atlantic (Coleman et al., 2006). Exclusion experiments along the Portuguese and British coast have specifically demonstrated that grazers' partial or total removal lead towards rapid colonization from algal 'turfs' and the expansion of their upper limits

of distribution in the mid-littoral zone (Boaventura-Alexander et al., 2002). In this study, a moderate increase in grazers proportions were observed where lower warming rates were recorded (e.g., see assemblages in Portugal and some in northern Spain; Fig. 12 F). In these locations, invasions of new herbivores (Lima et al., 2006; Rubal et al., 2013) and higher metabolic rates induced by warming (Brown et al., 2004; O'Connor, 2009) might have led towards increased grazing pressure, targeting macroalgal assemblages (see yellow and green points in Fig. 12 A and B highlighting macroalgal depletions in the Portuguese and in some of the northern Spain assemblages) and favouring moderate replacement by turfs (Fig. 12 C). In warmer communities, however, reduced proportions of both consumers and resources (canopy-forming species) were observed, resulting counterintuitive. The observed pattern could represent a more advanced stage where turf covers are already stable and are outperforming on grazing top-down control.

Empirical tests under higher temperature conditions highlighted that herbivorous gastropods consumption peak earlier than the rate of growth of primary producers, resulting in an inability of grazers to keep up with turfs growth (Mertens et al., 2015). Other studies instead suggested that the trapping of fine sediments in turfs-mats can impair or inhibit the grazing-activity of the limpet *Patella vulgata* (a species abundantly found across the NE Atlantic), and even lead to individuals mortality (Airoldi & Hawkins, 2007). Further investigation on the causes and on the effects of human-induced transitions from complex three-dimensional structures to low-lying mats is urged. In just 15 years we witnessed a pervasive trend of flattening of temperate assemblages, despite at an early stage. Future warming projections and the increased frequency of occurrence of extreme hot events, however, will likely forward these patterns of change, leading to a gradual loss of the unique biodiversity that characterizes the cold NE Atlantic regions, and likely impairing the ecosystem goods and services that rely on them.

Canopy-forming macroalgae are crucial for the provision of protection, food, and habitat for intertidal organisms (Chapman, 1995; Dayton, 1985). The shading from their three-dimensional structure is, additionally, essential for the avoidance of physical stress, especially in the higher shore (Bennett et al., 2015; Teagle et al., 2017). Macroalgal assemblages, in general, support high primary productivity, provide nursery grounds, prevent erosion and are significant CO<sub>2</sub> sinkers (Muguerza et al., 2017). Degradation of the ecosystem towards flatter structures is therefore associated with loss of habitat, food, and productivity (S. Connell et al., 2014). Turf-mats alter the physical and biological structure of ecosystems, providing different ecological services. They tend to accumulate sediment and modify the chemical environment (e.g., reducing oxygen or concentrating contaminants (Airoldi & Hawkins, 2007; S. Connell et al., 2014). Their lack of vertical structure deprives intertidal organisms of the benefits described above. The monopolization of the substrate by turfs rapid vegetative propagation impedes spores of many larger species to recruit, or forces macroalgal species to overgrow on a carpet-like layer where they are much more unstable. As a result, local biodiversity cannot be reestablished (Feehan et al., 2019) and the ecological benefits associated to them are lost (Filbee-Dexter et al., 2016).

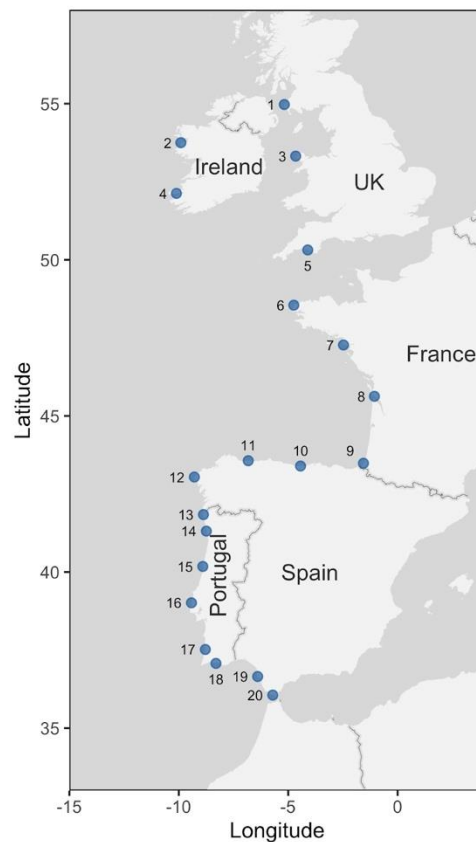
Solutions to prevent further loss of the NE Atlantic ecosystems composition and structure in the coming years should be pursued through a better understanding of the synergistic effects of both local and global drivers of change. Stress release from eutrophication or pollution at the coast, for instance, are more easily achievable in the short-term and could slow down this process if promptly implemented. Mitigation and restore strategies should, in any case, account for the superimposed effect of warming on coastal impacts and thus always couple ecological forecast with climate variability.



## 2.2 Identification of functional groups whose change can be associated with warming (T2.2)

The study area encompassed 20 exposed to moderately exposed rocky shores along the European Atlantic coast, from SouthWest Scotland to South Spain (with a span of approximately 20 degrees of Latitude, see Figure. 14). Throughout the study area climatic and oceanographic conditions vary greatly – there is a marked north to south cline in sea temperature during Winter, and an alternation between warm and cold coastal pockets in Summer.

We collected data from twenty rocky intertidal macroalgal communities on the European coastline from March to July 2022. At each location and during low tide, we surveyed conspicuous intertidal seaweed, totalizing 157 species. We identified them *in situ* to the lowest possible taxonomic level and assessed their abundance via a semi-quantitative estimation of abundance. We used a modified version of the scale established by Crisp and Southward (1958)

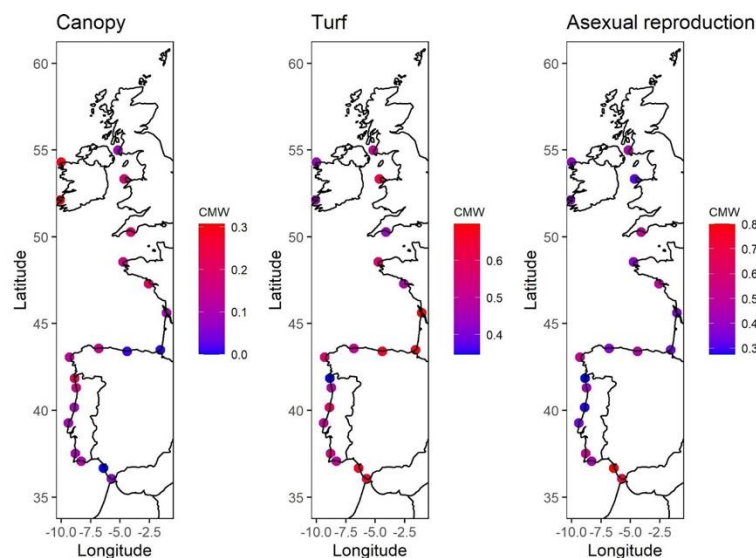


**Figure 14** Study area and sampling locations along the Atlantic coast of Europe: 1 - South Cairn, 2 - Emlagh, 3 - Holyhead, 4 - Minard Castle, 5 - Wembury, 6 - Landunvez, 7 - Le Croisic, 8 - Royan, 9 - Biarritz, 10 - San Vicente de la Barquera, 11 - Pormenande, 12 - Cabo Touriñan, 13 - Moledo, 14 - Mindelo, 15 - Buarcos, 16 - São Lourenço, 17 - Alteirinhos, 18 - Evaristo, 19 - Peginas, and 20 - Paloma.

This section investigates the spatial patterns and underlying environmental drivers of macroalgae community weighted trait means (CWM). We selected two categories from the vertical space trait that reflect contrasting ecological strategies (Martini et al. 2020), namely (i) turf and (ii) canopy. Turf was the dominant category within the trait and whole spatial dataset (always >50%, Figure 15). In this particular case, we did not consider the sub-canopy category as previously done in section 3.6, as this category had an extremely low CWM percentage. We focused on the “canopy” category, as it reflects higher structural complexity and investment in biomass growth, providing habitat for several associated species and blue carbon potential (Mauffrey et al. 2020). In comparison, “turf” species have a much more restricted three-dimensional structure due to their limited vertical height (Vranken et al., 2022). A community

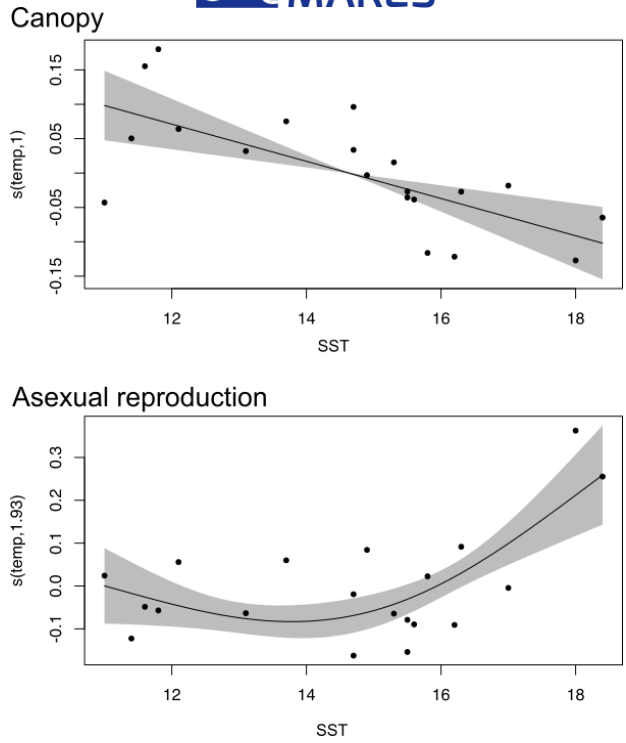
change from canopy-dominated to turf-dominated forms indicates a general shift between species that are structurally complex to species that have less structure and which grow fast and in an opportunistic way (Mauffrey et al. 2020). We also focused on a reproductive trait, namely the ability to perform “asexual reproduction”. This is also a trait associated with lower complexity which is considered advantageous under stressful conditions and which has the potential to promote rapid dispersion. First, we will provide an overview of the spatial changes in the selected CWMs, and then on their relationships with environmental conditions.

Spatial patterns on the CWM showed different trends along the European coast, depending on the trait (Fig. 15). Canopy CWM was higher at higher latitudes and in Northern Portugal, and decreased in the Bay of Biscay and further south along the Portuguese coast. This is in agreement with the above mentioned temperature trends in the area: due to the effects of Summer upwelling in NW Iberia, seawater temperature in the area is almost as cold as that at higher latitudes. Conversely, oceanic weather is much more “continental” in the Bay of Biscay, where summer temperatures reach much higher values (Seabra et al., 2015). Thus, canopy-forming species, such as those that dominate in kelp forests, are more abundant and generate higher biomass in colder waters (Smale, 2019). On the other hand, turf species are typical of warm-temperate and tropical areas probably due to competition release from kelps in those regions. This work shows that turf is highly dominant along the European coast, particularly in areas where canopy dominance is weaker. The capacity for asexual showed a less clear pattern. Still, it was more prevalent at the southernmost locations, and in some particular locations at higher latitudes (e.g., NW Iberia, S Brittany, SW England and S Scotland, Fig. 15).



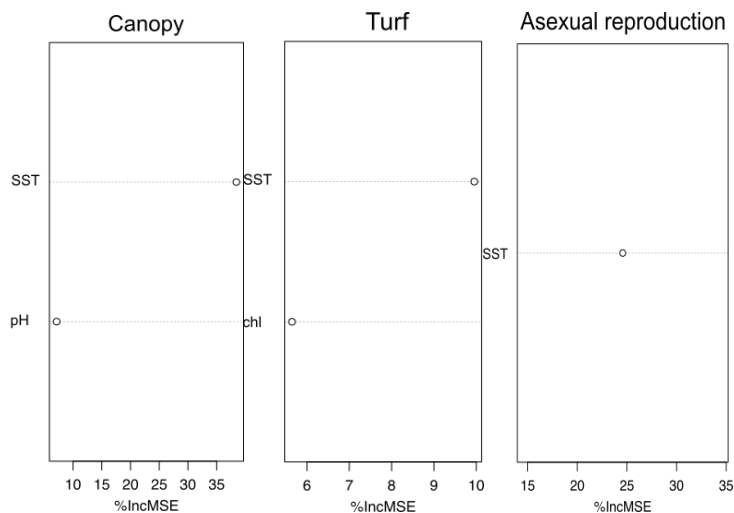
**Figure 15.** Maps of community weighted trait means (CWM) for “canopy”, “turf” and “asexual reproduction” categories across the study area.

This section reports on some of the individual responses of CWM traits (using the same trait selection as above) to the environmental predictors using both GAM and Random Forests (see section 2 for details regarding methods). Prior to these analyses, we analysed collinearity among environmental parameters and removed dissolved oxygen as it was highly correlated (correlation > 0.99) with sea surface temperature (SST). After a formal model selection routine comparing all combinations of predictors, the final GAM (i.e., that with the lowest AIC) identified SST as the main predictor contributing to “canopy” and “asexual reproduction” patterns. For the “turf”, however, none of the predictors was significant. For “canopy”, the model explained 44.9% of the variance, while for asexual reproduction, it explained 48.4%. A linear and negative relationship was observed between “canopy” and SST. As for the “asexual reproduction”, it generally increased non-linearly with temperature (Fig. 16).



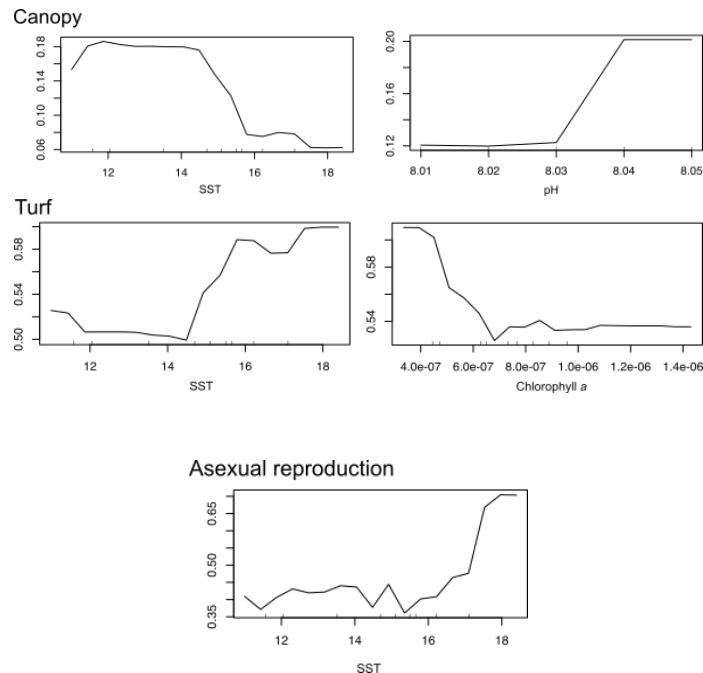
**Figure 16** Statistical relationships from GAM between the traits “canopy” and “asexual reproduction” and the significant predictor (SST). Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

The complementary analysis using Random Forest (RF) confirmed the GAM results but included other predictors for the “canopy” and a model for “turf”. The RF model explained 47.2% of the variance for the “canopy” CWM with two predictors (Figure 17), as chlorophyll-*a* did not affect the outcome. On the contrary, excluding temperature or pH could increase the prediction errors by up to ~35%. Canopy abundance decreased with increasing SST and increased with the increasing pH, yet within pH varied within small variation range (Figure 16). The model on the “turf” CWM only explained 4% of the variability, also with two predictors (Figure 17). An increase in the “turf” trait was associated with increasing SST and decreasing chlorophyll-*a* (Figure 17). This is in agreement with recent literature, which suggests that heat stress has been driving the extirpation of canopy-dominated forests, which are being replaced by turf-dominated communities (Filbee-Dexter and Wenrberg, 2018). For the “asexual reproduction” trait, SST was enough for the model, with an overall importance of about 25% (Figure 16).



**Figure 17** Variable importance for the predictors used in RF measured by the increase in the overall error (mean squared error, MSE) when predictors are, in turn, excluded from models.

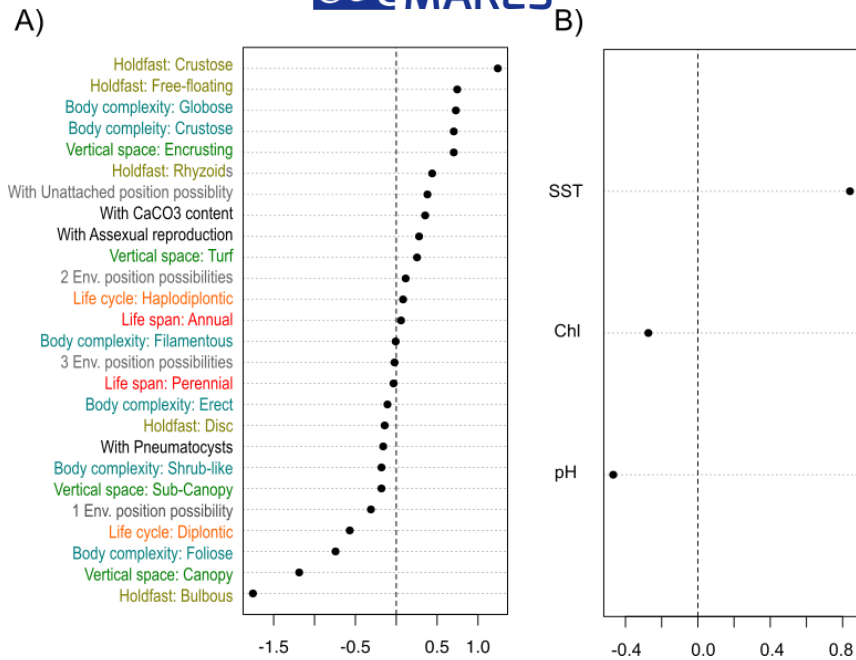
Overall, SST was the most determinant parameter for the trait-environment relationships from both models. The models suggest that communities should be dominated by canopy-forming species in cold waters, with their influence declining from 16 °C upwards (Figure 15, 17). This relationship, however, was not ascertained for turf species due their extremely low variability in the RF model. In other words, turf species were highly dominant across all sampling areas, which indubitably degraded the ability to detect subtle environmental effects. Yet, results still suggest that these species should increase in warmer waters. For asexual reproduction, we also found an increase with increasing SST for temperatures higher than 16 °C (Figure 18).



**Figure 18** Partial dependence plots based on the RF demonstrating the predicted responses of CWM for the “canopy”, “turf” and “asexual reproduction” trait categories to changes in their predictors.

### 3.7.4. Trait-environment relationships using RLQ

The total amount of co-inertia explained by the RLQ amounted to 0.23, with the first dimension (i.e., RLQ axis) contributing to 91.5% of the explained covariance. Hence, we only show the scores of the first axis (but a similar visualisation could be done for the subsequent axis). In terms of traits, RLQ1 demonstrate positive scores for more opportunistic traits, such as the possibility of asexual reproduction, free-living (unattachment) environmental position and holdfast, with encrusting species that privilege horizontal growth (in opposition to those that growth mostly vertically,, see Figure 19 A). These traits categories were associated with increasing SST, which was associated with the positive score (Figure 19 B). On the negative scores, the analysis highlighted categories of traits associated with higher complexity regarding the vertical space occupied and potential habitat provided (such as canopy and sub-canopy species with bulbous holdfast). These categories were associated with lower temperature scores. RLQ analyses also confirmed the patterns described above, stressing the importance of SST as a determinant parameter for the trait-environmental relationships. Overall, traits associated with higher complexity were linked to lower temperatures, while traits characteristic of opportunistic life cycles were linked to higher temperatures.



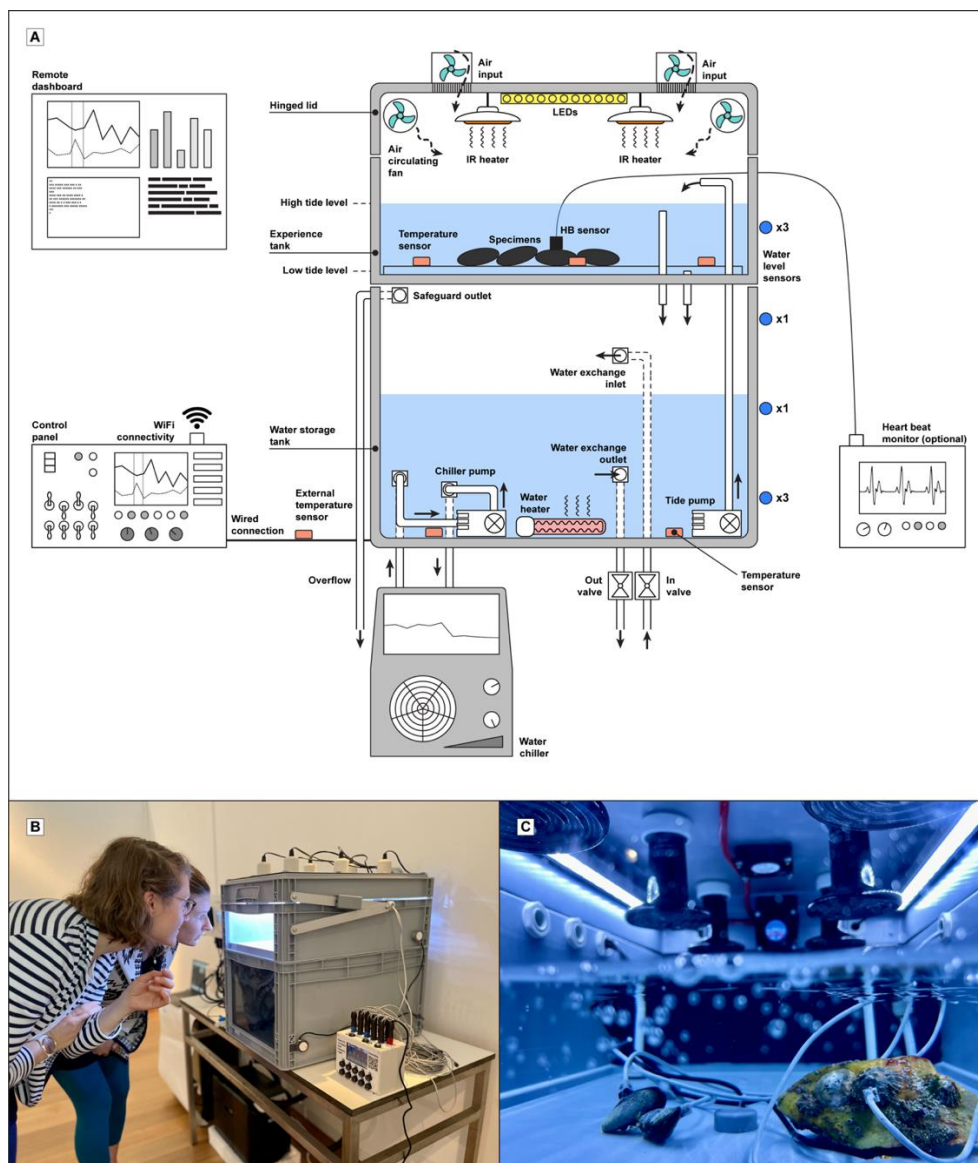
**Figure 19** Loadings of traits (categories and binary traits) (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores. Similar colours represent the categories within the categorical traits, while binary (0,1) traits are represented in black.

#### Summary of main findings:

- The primary traits explaining the observed spatial differentiation and abundance were mainly associated with vertical space occupied by the species (also a proxy of body size and structural complexity), holdfast and body form complexity, suggesting that these might be primary "response" traits for seaweeds at the spatial scale here considered.
- Overall, the investigation of the trait-environment relationship for intertidal seaweeds across the European rocky shores shows broadly consistent results across the three methods, indicating that findings are robust.
- The most important environmental variable explaining the distribution of the traits was temperature. Still, the variability explained by temperature was always below 50 %, suggesting that other environmental parameters may also play an important role driving species traits.
- Our results suggest that there is a continuous pattern from species with more opportunist traits associated to higher temperature (simple body forms with dispersal potential due to unattached position and asexual reproduction possibilities), to species with higher structural complexity across their body forms, holdfast and vertical space. These relationships with temperature seem to hold true at lower temperature values and higher chlorophyll.
- The relation between the dominance of canopy species and temperature were consistent with literature, showing a clear decline of this trait at higher temperatures.

**Team-up with CIIMAR to build a standardized experimental chamber that accurately replicates the intertidal thermal environment to assess the potential for local adaptation of selected species across the European Atlantic (T4.1)**

With the objective to develop a standardized, self-contained, modular and automatic experimental apparatus to precisely replicate temperature profiles in aquatic and intertidal environments, we developed the “Intertidal Simulation Chamber” (Fig. 20). The system has the ability to simulate the complex thermal conditions characteristic of the intertidal environment. Using multiple chambers, researchers can create “virtual common garden experiments” across large geographic spans. It plugs into a regular mains power outlet and controls other mains power devices (such as pumps and heaters) and 12 V (such as fans, LEDs, and water valves).



**Figure 20:** A: Schematic representation of the intertidal simulation chamber. B: The chamber in display. C: The experimental tank with several animals subjected to high tide. Credits: Fernando Lima.

The unit has two chambers: a top experimental chamber where organisms live and a bottom chamber which holds seawater during low tide. During low tide, heating is provided by six 50

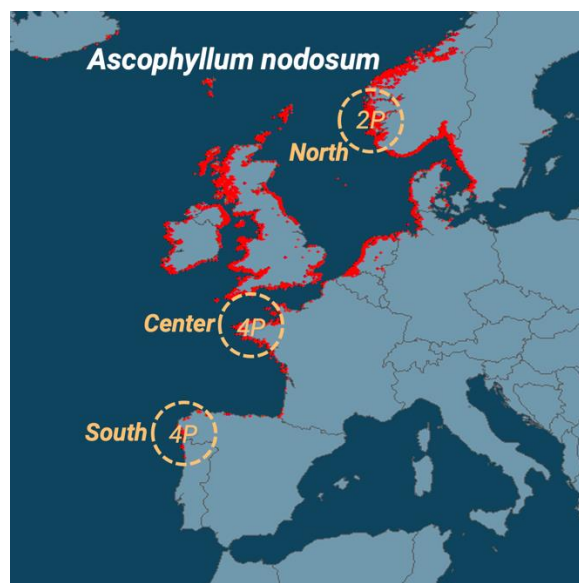
W infra-red lamps, which simulate natural solar heating. These lamps do not produce visible light, only heat. Wired EnvLoggers inside the chamber provide temperature feedback during low tide. IR is continuously and automatically adjusted to follow even the most complex thermal profiles. Computer-controlled fans provide cooling, swapping inner hot air with colder exterior air. Inside the chamber, air-circulating fans contribute to temperature homogenization during low tide. During low tide, seawater moves to the lower chamber and is pre-heated or cooled to the exact temperature required at the start of the next high tide. During high tide, water temperature is continuously monitored and adjusted.

Tide timings are programmable, and can be regular or change from one tide to the next. In addition, regular seawater changes can be programmed and done in an automated way. Visible light is independently provided by LED strips, producing 1130 lumens each. LED strips are easily swapped if needed. The number of stripes is also configurable to keep algae happy.

Intertidal chambers can be connected to WiFi, and experimental conditions can be remotely monitored and changed at any moment through a dedicated webpage. The machine also stores programmed profiles (i.e., what it should do) and sensor data (i.e., what it actually did) in an SD card for offline data transfer if WiFi is unavailable.

## 2.6 Produce climate readiness maps

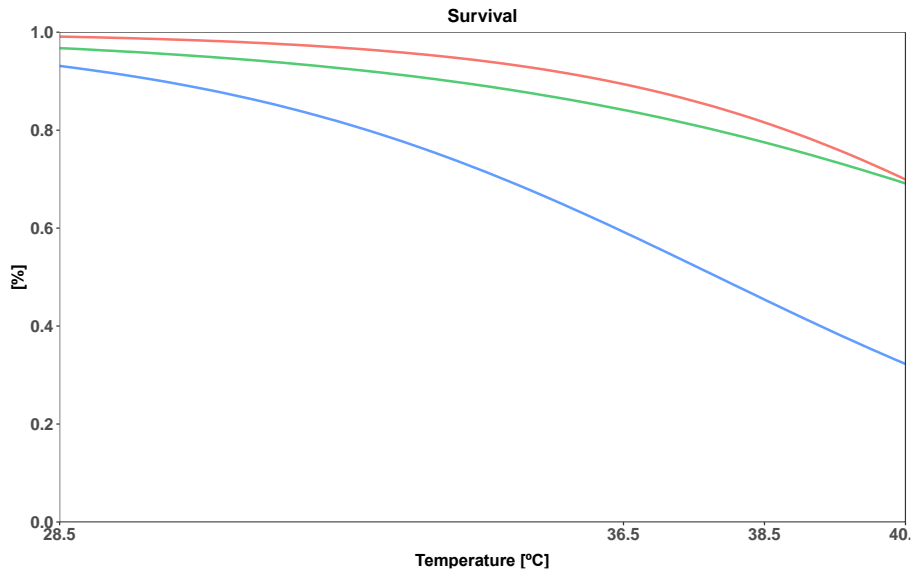
To understand how species will cope with future climate, we need to understand the resilience of their populations under the expected climate. In this study, we conducted a series of experiments to test whether different populations of the same species, collected across a large latitudinal gradient, displayed distinct physiological responses to intertidal temperatures. The primary objective was to discern any potential variation among different populations of the species *Ascophyllum nodosum*, producing geographically explicit forecasts that could aid stakeholders managing and protecting this species and its habitat. Specimens were collected from 10 populations from Portugal, Spain, France and Norway (Fig. 21).



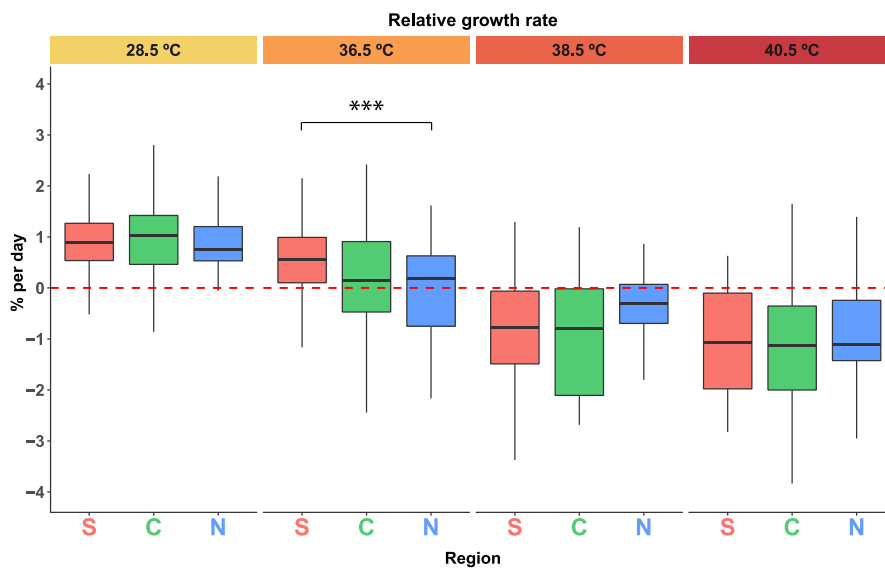
**Figure 21:** Populations of *Ascophyllum nodosum* that were collected for this study (4 in NW Iberia, 4 in Brittany, and 2 in Norway)

We used the standardized experimental intertidal chamber explained above to expose the algae at various realistic heatwaves, measuring their survival and growth rate. Survival

revealed greater susceptibility from the north populations to all heatwave treatments (peak temperatures 36.5°, 38.5 and 40.5°C), while central and southern populations appeared similarly affected (>0.6 survival rate, Fig. 22). Relative growth rate (% ww/day) showed significant results between northern and southern populations at the weakest heatwave treatment (36.5°C peak temperature). No other significant results were found in growth between populations at each heatwave treatment (Fig. 23).



**Figure 22:** Differential survival of the different populations (blue: Norway, green: Brittany, red: Iberia) to simulated intertidal temperatures.



**Figure 23:** Relative growth rates of the different populations (blue: Norway, green: Brittany, red: Iberia) to simulated intertidal temperatures.

In conclusion, resilience to emersion heat waves can be a decisive feature for this intertidal macroalgae. Climatic projection models suggest heatwaves are to become more intensive and frequent because of climate change. However, populations may endure such events differently. Our data strongly suggests that local adaptation can modulate populations' resilience to heatwaves. Data is now being analyzed and maps are being produced.



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