RESEARCH ARTICLE

Range-edge populations of seaweeds show niche unfilling and poor adaptation to increased temperatures

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Abstract

Aim: Global warming is affecting the distribution of species worldwide, but the level of adaptation of edge populations to warmer temperatures remains an open question. Here, we assess the thermal tolerance of populations of two habitat-forming seaweeds along their latitudinal range, using thermal niche unfilling to assess their resilience to global warming.

Location: European Atlantic coastline.

Taxon: *Ascophyllum nodosum* (Linnaeus) Le Jolis (Phaeophyceae) and *Chondrus crispus* Stackhouse (Rhodophyta).

Methods: We studied the ecotypic variation in upper survival temperatures (USTs) by measuring survival and growth of adults representing populations under a gradient of seawater temperature (12–30°C). Comparing the USTs with maximum seawater temperatures obtained from satellites, we investigated safety margins and niche unfilling states, both in recent history and under future climate scenarios.

Results: USTs (≈24°C) did not differ significantly between populations, except for higher values (27.9°C) for the northernmost populations (cold edge) of *A. nodosum*. Populations of both species had thermal safety margins over the last few decades (from 1982 to 2021). However, projections based on USTs showed that in several years these margins have been eliminated and will completely disappear in the Bay of Biscay under RCP4.5 and RCP6.0 2090–2100 IPCC scenarios for *C. crispus* and under RCP8.5 for both species, threatening the populations there.

Main Conclusions: Southern marginal populations were not better adapted to global warming than populations elsewhere. Both seaweed species tolerated higher temperatures than the ambient maxima, suggesting a thermal niche unfilling state with thermal safety margins in their recent history. However, those are being depleted by ongoing climate change and this trend is predicted to increase. Marine heat waves are important threats to these habitat-forming species, transiently reducing or even eliminating safety margins in the hottest parts of the European Atlantic coastline, contributing to explaining the distributional gap there.

1 | INTRODUCTION

Global warming already exceeds the physiological tolerance of many organisms and threatens their persistence (e.g. Root et al., 2003). Species with limited phenotypic plasticity and/or constrained genotypic adaptation are becoming locally extinct if unable to disperse and colonize new regions (Carpenter et al., 2008; Hoffmann & Sgró, 2011). In consequence, low-latitude distributional limits are contracting worldwide (e.g. Brown et al., 2016; Parmesan, 2006). However, the variation in physiological thresholds for changing temperatures across marine species' ranges is poorly studied (Jørgensen et al., 2022). Identifying latitudinal ecotypic variation in thermal tolerance thresholds allows us to characterize species' niche space filling and thermal safety margins (Guisan et al., 2014; Stuart-Smith et al., 2015) and, thus, to predict potential shifts in their distributions, and the effects on associated communities under current and future climate change scenarios (e.g. Sunday et al., 2012). Determining this variation is especially important for habitat-forming species which support other organisms, and whose decline compromises the biodiversity and resilience of ecological communities (Gunderson, 2000; Wernberg et al., 2016).

Range contractions do not necessarily reduce the range of a species, if compensated by pole-ward range expansions into regions that are becoming thermally suitable (e.g. Parmesan & Yohe, 2003). At range expansion fronts, niche unfilling is expected since the colonization progress takes time to occupy new locations with benign conditions until the species can fill their niches in those expansion areas (Petitpierre et al., 2012). In contrast, niche filling and the disappearance of safety is expected at contracting limits as environmental conditions reach the species' physiological thresholds (PTs) of tolerance, especially in the current climate change scenario with increasing temperatures margins (Petitpierre et al., 2012). There, the thermal safety margins, that is, the difference between the lethal thermal threshold of the species and the current maximum ambient temperature (Sunday et al., 2014), are small or absent. Niche filling is more common in the marine than the terrestrial environment because marine species generally have a higher dispersal capacity (Sunday et al., 2012). In the marine realm species are expected to be in equilibrium with the environment and, thus, to have narrow thermal safety margins and exhibit niche filling in range-edge populations. However, there has been little exploration of niche fill or unfill states in gaps within the species distribution, where the presence of the species may be excluded by extreme temperature itself (e.g. Helmuth et al., 2002) or other environmental constraints.

In the intertidal coastal zone, habitat-forming seaweeds play an important ecological role in providing shelter, resources, and food for accompanying organisms (Dayton, 1975), forming one of the most diverse and productive marine systems at temperate latitudes.

Nevertheless, a dramatic worldwide loss of habitat-forming intertidal and subtidal seaweed species has been explained by low physiological resilience to climate change (e.g. Smale, 2020; Wernberg et al., 2011). Little evidence of replacement by other habitat-forming organisms has been observed, suggesting a cascading deterioration of coastal rocky ecosystems (e.g. Wernberg et al., 2016). This marked decline is very noticeable in southern Europe, which is considered a biogeographical transition zone where many seaweeds reach their southern limit of distribution (Tuya et al., 2012).

Seaweed biogeography has historically been assumed to be mainly set by oceanic isotherms (reviewed in Lüning, 1990), because, as for marine ectotherms, seaweed metabolism depends closely on ambient temperature (Sunday et al., 2012). However, responses to climate change are particularly rapid and intense in intertidal systems (Sorte et al., 2010), given that the organisms are often already at their tolerance limits when emersed during low tide (Helmuth et al., 2002; Williams et al., 2008). Thus, several low tide stressors, air temperature in particular, have been recently included in species ecological niche models (e.g. Assis et al., 2015; Martínez et al., 2012).

In this study, we examined whether seaweed populations at their southern European distributional limits tolerate higher seawater immersion temperatures as compared with populations from higher latitudes. We used two model species with contrasting physiological plasticity and genetic variability, *Ascophyllum nodosum* (Linnaeus) Le Jolis (Phaeophyceae), a long-lived, morphologically invariant intertidal species with little between-population genetic differentiation (e.g. Olsen et al., 2010), and *Chondrus crispus* Stackhouse (Rhodophyta), a highly variable intertidal and shallow water species with wide morphological plasticity and extensive genetic variability (Collén et al., 2014; Provan & Maggs, 2011). For both species, we tested the variation in upper survival temperatures (USTs) (Bischoff-Bäsmann & Wiencke, 1996; Breeman, 1988) among populations along their latitudinal distributions. We expected the species to show contrasting levels of variation for USTs across their distributions—with *A. nodosum* showing uniform UST values and *C. crispus* showing variation in USTs according to population origin (i.e. higher USTs in southern populations). Variation in USTs would translate into population-specific differences in thermal resilience, also referred to as ecotypic differentiation (e.g. Bischoff-Bäsmann & Wiencke, 1996). In addition, by comparing the historical variation of the maximal sea surface temperature with the thermal fundamental niches based on experimental USTs, we estimated the thermal safety margins (from 1982 to 2021) for the studied populations along the latitudinal range, and for populations in the hottest area, which framed a big distribution gap. Finally, we developed projected maps of the thermal fundamental niche with respect to the upper thermal limit in the future (2090–2100) to estimate if the distribution of these species is expected to contract.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Adult nonreproductive fronds of *A. nodosum* and *C. crispus* were collected at low tide from eight and six populations, respectively, at least two for each marine region ("biotype") following the classification established in Ramos et al. (2012, 2014) (Table S1, Figure S1). These locations represent almost the entire European latitudinal range of *A. nodosum*, from 41° N in Viana do Castelo in northern Portugal to 67° N in Mørkved in central Norway, and about 75% of the European latitudinal range of *C. crispus* from 41° N in Aguda in northern Portugal, to 54° N in Groomsport in Northern Ireland (Araújo et al., 2009; Collén et al., 2014). Viana do Castelo represents the southernmost limit of *A. nodosum* while *C. crispus* reaches warmer areas in central Portugal, about 170 km further south (Collén et al., 2014). Both species inhabit the intertidal zone, occupying different shore heights, with *C. crispus* also extending subtidally, and they do not coexist locally.

Vegetative fronds from Iberian populations were transported to the Interdisciplinary Centre for Marine and Environmental Research (CIIMAR, Portugal) within 2 h, while fronds from elsewhere were transported in cool boxes, arriving within 3 days. Upon arrival, fronds were accommodated in laboratory conditions for almost 1 month in 150 L tanks at 16°C, supplied with aeration and under 135–150 μmol m^{-2} s^{-1} irradiance (PAR) with a 12 h photoperiod, in order to minimize environmental imprinting.

Three cultivation experiments each lasting 6 or 7 weeks were carried out from 2014 to 2017 (Table S1.1). In each experiment, 200 individual fronds per population were tagged and suspended from nylon strings inside 20 experimental tanks (20 L plastic boxes) at 10 seawater temperatures (12.4 ± 0.9, 13.9 ± 0.5, 15.9 ± 0.4, 18.3 ± 0.8, 20.0 ± 0.6, 22.0 ± 0.6, 23.8 ± 0.5, 25.9 ± 0.5, 27.9 ± 0.6, 29.8 ± 0.6°C; mean ± SD, $n = 1040$ replicate measurements per temperature). Each experimental temperature was replicated in two tanks, checked twice a day, and for fine control, boxes were isolated with polystyrene plates and submerged in water baths kept at constant temperatures (9, 15 and 23°C) using coolers. The water inside each tank was heated to the desired temperature with aquarium titanium heaters connected to Aqua Medic® AT Control System controllers with a programmed error of 0.2°C in the trials in 2014, and to Inkbird ITC-2000 thermostats with a lower instrumental error of 0.1°C thereafter.

Salinity was measured twice a day using a refractometer, maintained at 35 ‰ by adding fresh water when necessary and avoiding excessive evaporation by covering the tanks with Plexiglas lids. During the trials in 2014 and 2015, the water in the system was pumped from the big (1000 L) supply tank of the facility into the 20 L tanks in a recirculating system, therefore the water was enriched with NaNO$_3$ and N$_2$HPO$_3$ every second day, to a final optimal N concentration of about 42 mg L^{-1}, and of about 4 mg L^{-1} for P (as in Martínez et al., 2014). The system was improved in 2016 by relocating it to the shore and pumping water directly from the sea, thus removing the need for extra nutrients. To homogenize conditions, water in all tanks was completely changed weekly and kept agitated and oxygenated by bubbling air. This control system successfully maintained the variables at the desired values and no anomalies were observed in any phase of the experiment, so the treatments were always consistent and stable.

2.2 | Survival and growth

Each frond was weighed to the nearest 0.01 g at the beginning of the experiment and then weekly. The differences between fresh weight measurements at the different time periods were used to calculate growth or biomass loss due to thallus necrosis (as in Martínez et al., 2014). Survival was assessed by classifying fronds as dead or alive. Mortality indicators were obvious tissue depigmentation, slimy consistency, missing fragments, apical breakage and loss of biomass, resulting in a negative growth rate.

The relationship between survival vs temperature and growth vs temperature for the different populations was investigated by plotting the percentage of surviving individuals and the mean growth rates, respectively, for each experimental temperature for successive weeks. Data falling outside the mean ± 3 × SD were considered outliers (199 out of 2800 data points) and were excluded from the analysis (Sokal & Rohlf, 1969). From each population's survival response, we calculated by means of logistic regressions using generalized linear models (GLMs) the lowest temperature at which at least 50% of the fronds were dead, hereafter referred to as the upper survival temperature (UST$_{50}$, modified from Yarish et al., 1987). This UST$_{50}$ was used as the upper limit of the fundamental niche of tolerance to water temperature (Martínez et al., 2014).

To determine if UST$_{50}$ differed among the studied populations and at which level of significance (including marginally significant), we compared them using analysis of variance (ANOVA, Underwood, 1996). Homogeneity of variance was examined using Levene's test (Lim & Loh, 1996) and post hoc analysis was conducted using the Student–Newman–Keuls (SNK) post hoc test (Quinn & Keough, 2002). When differences were not significant, the lowest UST$_{50}$ was selected as proxy for each studied species. Though this may result in an overestimation of the effect of climate change, we adopted it as the most precautionary approach. We used linear models (LMs) to explore the relationship between the total net growth of each individual over the whole experiment and the UST$_{50}$ values. All statistical analyses were performed with R 4.0.5 software (R Development Core Team, 2021).

2.3 | Distribution records

All available records of occurrence of *A. nodosum* and *C. crispus* along the Atlantic coast of Europe were accessed through the Global Biodiversity Information Facility (GBIF.org (24 January 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.zamdm7 and

), and the Ocean Biogeographic Information System (OBIS.org (24 January 2022) OBIS Occurrence Download https://datasets.obis.org/downloads/ff030b06-2a94-414d-83e9-f38b5a1d05e8.zip and https://datasets.obis.org/downloads/1168796e-492b-4f69-905b-57532ba5b562.zip). Literature was consulted to verify uncertain records and to complete the databases (Appendix S2). To investigate possible distributional changes across time, we explored the data year by year, considering all the records available, even the historical ones and those included as herbarium records if they were well referenced and with concrete coordinates. We consulted with phycology experts in Spain to obtain more data on distributional changes at the species' southern limit. Records that were duplicated in different data sources were visualized using Google Earth and Geographic Information Systems (GIS, ArcGIS® 10.4.1., ESRI) and combined into a single occurrence.

A total of 8151 and 8654 reliable presences of *A. nodosum* and *C. crispus*, respectively, were obtained following the process explained above (7131 GBIF +1447 OBIS +108 literature records minus duplications for *A. nodosum* and 7829 GBIF +1770 OBIS +125 literature records minus duplications for *C. crispus*). The distribution of each species along the European Atlantic coast was assessed from these records displayed in GIS maps.

2.4 | Thermal safety margins

The evolution of thermal safety margins over time was evaluated for each studied population in relation to the UST_{50} values obtained by means of the ecophysiological experiments. A high resolution layer of the maximum sea surface temperature (SST_{max}) per year was created using a satellite-observation daily mean product (01/10/1981 to 31/10/2021 with a spatial resolution of 0.05°×0.05°) from Copernicus (https://resources.marine.copernicus.eu/products). To create the layer we used the ncdf4, raster and rgdal packages from R software, selecting all August days as comparable to the August isotherm used in the classic biogeographic studies of seaweeds (Lüning, 1990). This Copernicus product performs as a good proxy of the actual temperature in coastal systems when compared with 10 other sources (Meneghesso et al., 2020). Values of the resulting SST_{max} layer for each year were extracted for each studied population and then compared with the UST_{50} associated with the corresponding population to follow the evolution of the thermal safety margins from 1982 to 2021 and determine the thermal fundamental niche filling or unfilling state of the populations.

The Bay of Biscay is a distributional gap for both species, related both to temperature and lack of hard substratum. Populations on the Spanish side of this gap are the most threatened by temperature. As we did not have ecophysiological data for these particular populations, we studied the safety margins with the SST_{max} layers from 1982–2021 compared with the UST_{50} selected as proxy for each studied species following a conservative approach based on the UST_{50} obtained from the studied populations along the Atlantic European gradient of distribution.

2.5 | Projected species distribution using physiological thresholds

We created species presence-absence GIS map projections of thermal habitat suitability along the European coast, based on empirical evidence on the fundamental thermal niches obtained from our experiments. To do so, we classified each pixel of the SST_{max} layer in relation to the UST_{50} selected for each species, whereby $SST_{max} > UST_{50}$ was defined as unsuitable, and $SST_{max} < UST_{50}$ as suitable. Locations with maximum mean temperatures below 12°C, the lowest of our experimental temperatures, were left unclassified. We compared these maps of the species' thermal fundamental niches with the species' distributions.

To project the fundamental thermal niche of each species into the future, we again classified grid cells as either suitable or unsuitable, but this time based on the SST_{max} values projected under the four different Representative Concentration Pathways (RCPs) from the Intergovernmental Panel on Climate Change (IPCC) for the 2090–2100 period (https://www.ipcc.ch/report/ar5/wg1/). These environmental layers were downloaded from Bio-ORACLE v2.0 (http://www.bio-oracle.org), which offers GIS rasters providing geophysical, biotic, and environmental data for surface and benthic marine realms at a global scale with a spatial resolution of 5 arcmin (Assis et al., 2018).

3 | RESULTS

3.1 | Responses in growth, survival and UST_{50}

The reduction in growth at high temperatures was associated with an increase in mortality where at the highest experimental temperature none of the studied populations survived, and at 28°C only the Norwegian and French populations survived at all and few individuals were able to grow (Figure 1). Thus, mortality occurred differentially at the different temperatures studied for the two species over the duration of the experiments. For standardization, we used the final date of the experiment to calculate UST_{50} since at that time the response was stationary. For *A. nodosum*, there were significant differences in physiological thresholds between populations from different marine regions (ANOVA: $F3,4 = 37.36$, $p = .0022$; Table S1.2). Post-hoc tests revealed differences only between Norway populations (B22 region) and the other marine regions, while the remaining comparisons were not significant (Table S1.3). For *C. crispus*, differences were marginally significant ($F2,3 = 8.67$, $p = .0566$; Table S1.2), the French populations (B21a2b region) being the only ones with higher UST_{50} values, although this was not clearly detected by the post-hoc test (Table S1.3).

The UST_{50} values selected for each species were 23.9°C (Groomsport, United Kingdom) for *A. nodosum*, and 23.8°C (Aguda, Portugal) for *C. crispus* (Figure S1.2). These were used to estimate the species' fundamental thermal niches when projecting to an unstudied population or area. The only marine regions with higher (≈4°C)
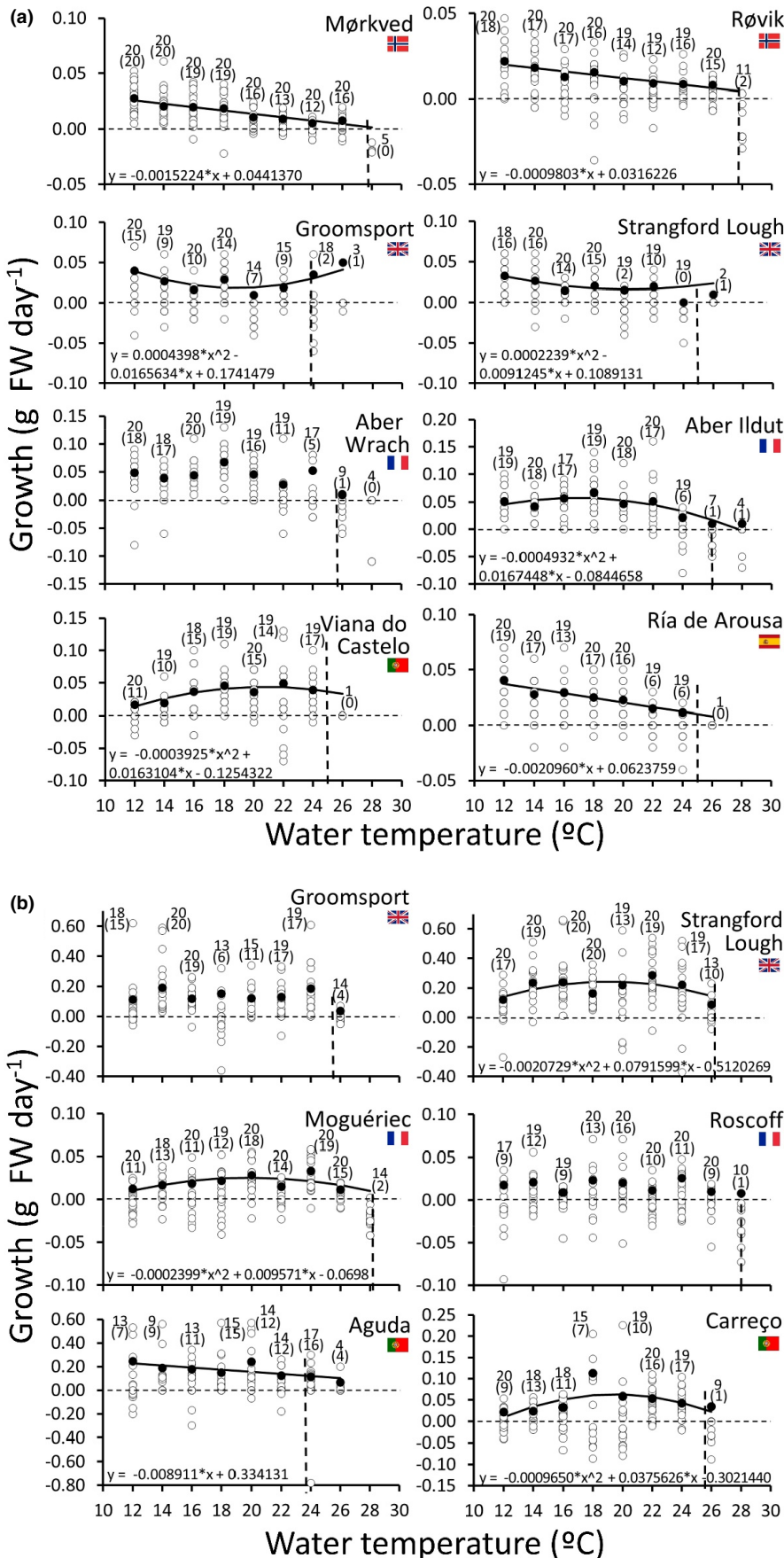
FIGURE 1 Growth functional responses of (a) *Ascophyllum nodosum* and (b) *Chondrus crispus* to the temperature of the seawater during the last week of experiment. White dots represent growth or loss of biomass for individual replicates, and black dots represent the means of growth data (positive values excluding zeros). Numbers above the dots denote the number of live algae and in brackets those showing growth ($n = 20$). Dashed vertical lines mark the UST_{50} obtained with the survival graphs (see Figure S1.2) which are used as physiological thresholds (PTs) for the species. Continuous black lines represent the relationship between growth and temperature from linear or quadratic models; equations are shown below if significant ($p < .05$). For *A. nodosum*, experiments ran for 42 days except for Viana do Castelo (51 days) and Ría de Arousa (39 days), and for *C. crispus* experiments ran for 42 days except for Aguda (49 days).

UST$_{50}$ values were the B22 (Norwegian populations) for *A. nodo-sum* and the B21a2b (French populations) for *C. crispus* (Figure S1.2, Table S1.3). However, these populations showed the lowest growth rates, which could indicate that the greater tolerance to heat stress results in reduced growth (compare axes in Figure 1). In agreement, for both species, UST$_{50}$ values were negatively correlated with total net growth (Figure S1.3, Table S1.4).

3.2 | Thermal safety margins and niche unfilling

Both species showed clear thermal niche unfilling over time (1982–2021) since UST$_{50}$ for the studied populations was not being sur-passed during the last few decades (Figure S1.4). Examining the SST$_{max}$ values of the pixels that the studied populations occupied in the field, we could detect the thermal latitudinal pattern of the dif-ferent marine regions represented by the selected populations. The southern ones were exposed to more thermal fluctuations shown by more frequent and higher heat peaks along the time series. The only exception was the Mørkved population of *A. nodosum* which experienced higher temperatures during 2002–2004 and 2006 com-pared with the other years and with the other Norwegian population studied (Røvik) (Figure S1.4a).

When we analysed the safety margins and evolution of the thermal niche filling of the distribution records in the Bay of Biscay, we found that maximal SST values correspond to temperatures of known marine heat waves (MHWs), such as 2003 and 2006 (e.g.

Meehl & Tebaldi, 2004; Smale et al., 2019), or others not so well documented in the literature (e.g. years 2013 or 2018). The histor-ical series suggests that temperature peaks of similar magnitude were observed in alternate years and seemed to become hotter and more frequent over time, as happened with the southern studied populations (Figure 2). In the Bay of Biscay the years 1984, 1993, and 2002 were especially cold, and in 2003, 2006, and 2018 sea surface temperatures were exceptionally high. Indeed, the safety margins were exceeded in some years: 2003 and 2020 for *A. nodo-sum* (Figure 2a), and 1992, 1997, 2003, 2006, 2013, and 2018 for *C. crispus* (Figure 2b).

3.3 | Projections of thermal fundamental niche

Our results indicated that *A. nodosum* and *C. crispus* do not fill their fundamental thermal niches, and when we projected that into a GIS map classifying the pixels of the SST$_{max}$ layer using the se-lected UST$_{50}$ of each species, the entire European Atlantic coastal area turned out to be favourable (green colour) for both (maps not shown). However, future temperature projections, based on the IPCC predictions for 2090–2100, suggested that for both species the values of UST$_{50}$ will be exceeded in the Bay of Biscay, threat-ening the survival of the populations present there today. These projections are based on emissions increases in the different IPCC scenarios, affecting the easternmost *C. crispus* populations from RCP4.5 IPCC scenario onwards, and *A. nodosum* under the RCP8.5
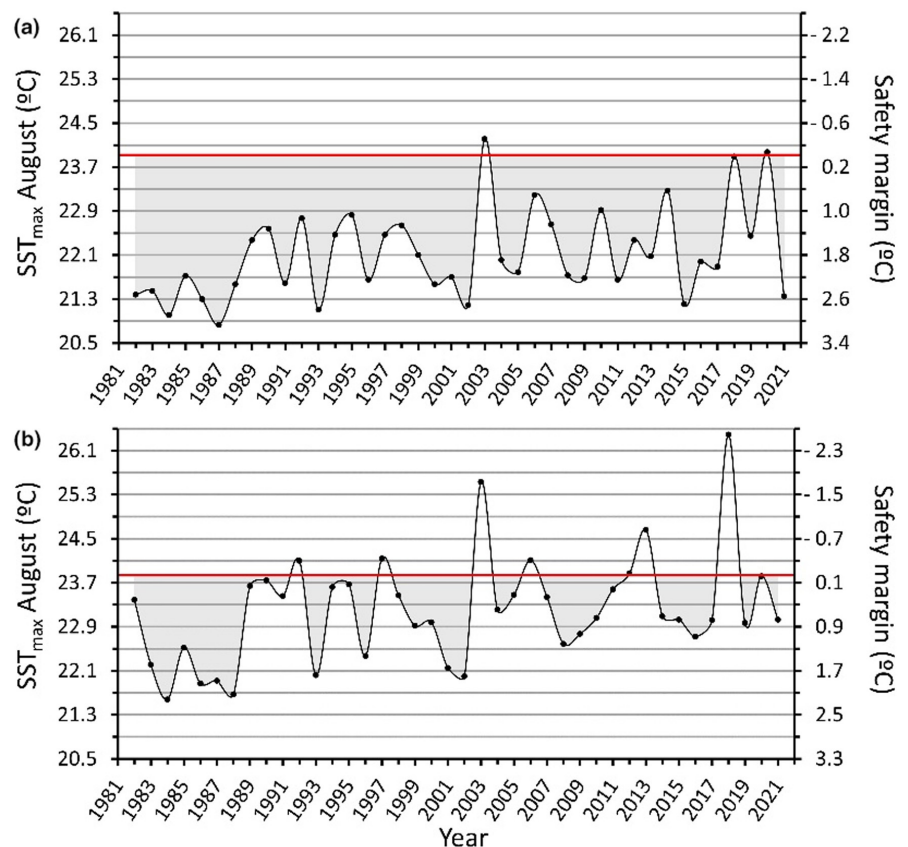

FIGURE 2 Time series of the yearly SST$_{max}$ (1982–2021) at the pixel that, for each species, contained the distributional record that has experienced the hottest temperatures, in the inner Biscay Bay (black dots and line, left axis). UST$_{50}$ values for each species following a precautionary approach (23.9 in *Ascophyllum nodosum* and 23.8 in *C. crispus*) are shown as red lines. Time variation of the difference between SST$_{max}$ and UST$_{50}$ representing the time trend of the thermal safety margins (shaded in grey, right axis) for (a) *Ascophyllum nodosum* and (b) *Chondrus crispus*.
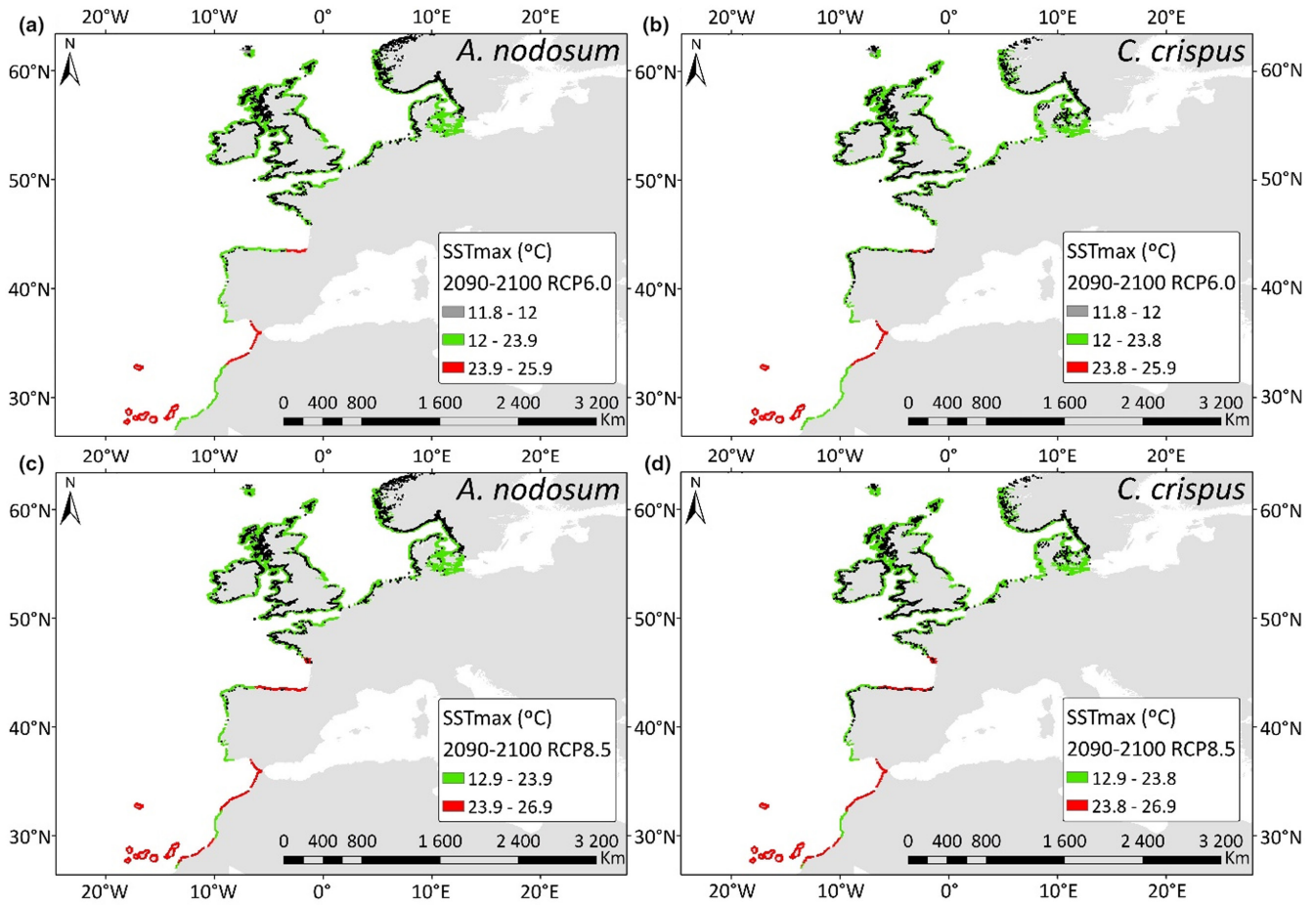
FIGURE 3 Maps of the fundamental thermal niches along the South and mid-European Atlantic coast, based on the UST_{50} values as thresholds to classify the SST_{max} projected layers: (a) 2090–2100 RCP6.0 scenario for *Ascophyllum nodosum*, (b) 2090–2100 RCP6.0 scenario for *C. crispus*, (c) 2090–2100 RCP8.5 scenario for *A. nodosum* and (d) 2090–2100 RCP8.5 scenario for *C. crispus*. Suitable thermal conditions, i.e. $SST_{max} < UST_{50}$, shown in green; unsuitable thermal conditions ($SST_{max} > UST_{50}$) in red; thermal conditions that do not fall in the range of our thermal experiments in grey; and sandy areas of unsuitable substratum for the species with no colour. The distribution records of each species are shown as black points. All georeferenced information is projected at the World Geodetic System 1984 (WGS84).

climate change scenario (Figure 3). According to current studies, the intermediate-high emission scenario is the most probable (Hausfather & Peters, 2020), corresponding to the RCP6.0 scenario in our study, where warm temperatures could eliminate the Biscay populations of *C. crispus* along a 236 km coastline by the end of this century (Figure 3b). Therefore, the current safety margins for the Bay of Biscay will disappear because the UST_{50} will be exceeded by $0.8 \pm 0.1°C$ (mean value). If we apply the worst climate change scenario, RCP8.5, the current populations of *A. nodosum* would also be affected with a retraction of 298 km since the UST_{50} would be exceeded by an average of $1.4 \pm 0.1°C$ (Figure 3c). In the case of *C. crispus*, the distributional shift would be 496 km and the UST_{50} would be exceeded by $2.3 \pm 0.1°C$ on average (Figure 3d).

4 | DISCUSSION

This study provides evidence that marginal southern populations of two habitat-forming seaweeds do not tolerate higher ocean temperatures than central or northern populations, although they have contrasting population dynamics, morphological plasticity, and genetic diversity. Only the northernmost cold populations of *A. nodosum*, the species with long generation times and limited between-population genetic differentiation, showed significantly higher upper survival thresholds (UST_{50}). Our results suggest that both species exhibit poor physiological plasticity and no local adaptation, reducing their ability to cope with global warming. Furthermore, the species' thermal safety margins seem to have been reduced over time (since 1982) and the future trend is that they will gradually disappear. In fact, through the analysis of the yearly SST_{max} values at the Bay of Biscay, where the most heat-threatened populations of the studied species occur, we saw that MHWs are becoming more frequent and have exceeded UST_{50} in several years over the last few decades. Thus, the results suggested a recent history of niche unfilling, in contrast to general predictions for marine ectotherms (e.g. Sunday et al., 2012). Nevertheless, our predictions forecast that safety margins will be completely exceeded in the Bay of Biscay under the RCP4.5 and RCP6.0 warming future

scenarios for *C. crispus* and under the RCP8.5 for both species by 2090–2100, which is likely to be exacerbated by more frequent and intense MHWs.

4.1 | Poor plasticity and no local adaptation in thermal tolerance at the warm edge

The selected UST_{50} values, obtained from the ecophysiological experiments, were ≈24°C for both species. Except for the Norwegian populations of *A. nodosum*, no significant differences between the UST_{50} for different populations were detected. The Norwegian northernmost *A. nodosum* populations and the French *C. crispus* populations (marginally significantly different from the rest) had the higher UST_{50} values. In both species, growth decreased with increasing UST_{50} values (69% reduction from optimal growth in *A. nodosum* and 91% in *C. crispus*). This could potentially be attributed to a carry-over effect from the environment or even to a higher allocation of resources to increase thermal tolerance at the expense of growth, as has been suggested in terms of reproduction versus growth for other algae and plants (Viejo et al., 2011; Wreede & Klinger, 1988). In concordance, individuals show a smaller threshold size for reproduction under unfavourable conditions, such as at range edges, as has been demonstrated for *A. nodosum* and other seaweeds (Araújo et al., 2015; Viejo et al., 2011). In our study, the reduction in growth cannot be explained by plasticity or local adaptation to increased thermal tolerance, given the detected large thermal safety margins (from 1982 to 2021) in northern and central localities, which had the highest UST_{50} (up to 15.4°C in Mørkved for *A. nodosum* and up to 12.6°C in Moguériec for *C. crispus*). So, the physiological variation observed here seems a random variation expected between different populations but unrelated to latitude.

The between-population differences in thermal tolerance were higher in our study than in other studies similarly using adults from the field. For example, European and Canadian populations of *C. crispus* showed differences in tolerance thresholds of only 1°C (Lüning et al., 1986). UST_{50} were not higher at the southern distributional limit of this species and other macroalgal species (e.g. *Fucus serratus*, Pearson et al., 2009), indicating that range edge populations at greater risk to die off due to climate change seemed not to be better adapted to the ongoing warming (Alsuwaiyan et al., 2021). Gene flow from central populations is unlikely to explain the lack of local adaptation of the edge populations in the Iberian Peninsula because of limited gene flow and relatively small population sizes subject to genetic drift (Araújo et al., 2011; Olsen et al., 2010). However, recent studies of *F. serratus* and other macroalgae have suggested ecotypic differentiation between populations from the European Atlantic coast (Ferreira et al., 2014; Jueterbock et al., 2014; King et al., 2019; Saada et al., 2016). The attribution of the differences observed among populations to the existence of ecotypes in many taxa is a subject that generates debate (e.g. marine fishes, Grabowski et al., 2011; cyanobacteria, Rodríguez et al., 2005). We did not find evidence of ecotypic differentiation in heat tolerance related to the species' biogeographic

limits, suggesting limited adaptation to climate change. The increased UST_{50} values in Norway for *A. nodosum* and in France for *C. crispus* could be related to the presence of unique and non-dominant genetic haplotypes (Olsen et al., 2010; Provan & Maggs, 2011), but exploring this possibility requires molecular studies.

4.2 | Thermal niche unfilling and safety margins

Both species tolerated higher water temperatures than those experienced in their current distribution since there was a thermal safety margin from 1982 to 2021 for both *A. nodosum* and *C. crispus*. Accordingly, they would be expected to encounter niche opportunities at lower unoccupied latitudes with favourable sea temperatures (Southern Portugal and Morocco), corresponding to a southward extension of the fundamental thermal niches. These results indicated that the species were in a current state of thermal niche unfilling, that is, temperatures at the species' distribution limits fell below those suggested by the fundamental niches according to UST_{50}. These safety margins must have existed at least since 1880, because the SST data since then suggested colder conditions (Merchant et al., 2019; Thompson et al., 2008). Moreover, we could extend this inference even further back in time since the Northern Hemisphere was in the Little Ice Age and temperatures were probably colder before 1880 (Savin, 1977).

In line with our observations, *F. serratus* was successfully transplanted eastward of its natural distributional limit in Northern Iberia during the 90s (Arrontes, 1993, 2002), suggesting that it did not fill its fundamental thermal niche in its recent history. Nevertheless, climate change-induced heat waves 3–5°C above average summer temperatures, which have been particularly intense in Europe since 2003 (Frölicher & Laufkötter, 2018; García-Herrera et al., 2010), have been linked to transient periods of distributional contractions for marine species (Filbee-Dexter et al., 2020; Smale et al., 2019). This was clearly observed in our southern populations and even for the safety margin projections in the Bay of Biscay. In fact, there has been evidence of a range contraction of about 180 km for *C. crispus* along open shores of the Iberian Peninsula over several decades (e.g. Fernández, 2016; Lima et al., 2007). Those edge populations, warm refugia during the Last Glacial Maximum (LGM, 20 ka ago), supported unique genetic variation (Provan & Maggs, 2011; Wang et al., 2008). In contrast, *A. nodosum* finds current refuge in embayment areas where conditions are locally colder (Baardseth, 1970; Salois et al., 2022), suggesting a persistent state of niche unfilling. Observing our graphs of the thermal safety margins for the study populations and for the projections in the Bay of Biscay, it was possible to see that those margins were greater for *A. nodosum* than for *C. crispus*, which supports this hypothesis.

4.3 | Biogeographic models

Traditional biogeographic models of macroalgae assume that species fill their fundamental thermal niches and consider their distributional

limitstobedirectlysetbyoceanisotherms(Breeman,1988;Lüning,1990; Müller et al., 2009; van den Hoek, 1982). Indeed, recent research suggests that most marine ectotherms, such as fishes or invertebrates, fill their fundamental thermal niches (Stuart-Smith et al., 2015; Sunday et al., 2012). Nevertheless, niche filling has seldomly been investigated in macroalgae, which differ from many taxa in their sessile nature and lower dispersal capacity of embryos (Kinlan & Gaines, 2003; Norton, 1992). Our results suggested that niche unfilling could be more common in foundational macroalgae than expected from intertidal ectotherm fauna (Sunday et al., 2012). However, ongoing and predicted climate change at the species southern distributional ranges is likely to remove the safety margins, causing range shifts and extinctions (e.g. Wernberg et al., 2011, 2016).

Alternatively, thermal niche unfilling in a climatic gradient can be explained by other stressors (Cefalì et al., 2016; Helmuth et al., 2002; Mineur et al., 2015). Among the factors that have been considered most relevant in the biogeography of macroalgae and other marine species are air temperature and wave exposure (e.g. Lima et al., 2007; Wethey et al., 2011). For example, the distribution of intertidal species inhabiting embayments, such as *A. nodosum*, is likely to be influenced also by atmospheric temperature and/or regional nutrient availability (Baardseth, 1970; Vadas et al., 1990). Biotic interactions and dispersion are other drivers that affect species distributions, but which seem to involve small-scale patterns, and it is not clear that these processes explain large-scale biogeographic patterns (Wiens, 2011). With statistical correlative approaches such as Species Distribution Models (SDMs) (e.g. Araújo & Guisan, 2006; Guisan & Thuiller, 2005), any environmental factors can be included in the algorithms to get realistic biogeographic models. Such approaches allow projections into future climate scenarios (e.g Elith et al., 2010), as used recently in phycology where temperatures played a key role in the models (e.g. Martínez et al., 2012, 2014, 2018; Westmeijer et al., 2019; Wilson et al., 2019). However, mechanistic approaches like those employed here allow the study of ecophysiological responses that are key to complementing such correlative approaches (Martínez et al., 2014; Rodríguez et al., 2019).

4.4 | Predicted contraction

The thermal safety margins are predicted to be surpassed in the Bay of Biscay by 2090–2100 under the climate change scenarios of RCP4.5 and RCP6.0 for *C. crispus* and under the RCP8.5 for both species. Considering the RCP6.0 as the most likely given current policies (Hausfather & Peters, 2020), this would result in a range reduction of ca. 235 km for *C. crispus*. However, based on the transient thermal niche filling state observed there, and on the contractions that are already taking place at the southern limit of *C. crispus* and many other species of macroalgae, the range contractions may be more drastic than in our estimates. The estimated range contractions under the RCP scenarios were based on average SST values, but other stressors could be affecting the species distribution as well.

For example, MHWs have been become more frequent, intense and longer and are likely to be increasingly so in future decades (Filbee-Dexter et al., 2020; Meehl & Tebaldi, 2004). Thus, the cause of the observed local or regional extinctions in *C. crispus* and in other species worldwide could be these thermal events that surpass the identified thermal safety margins (Filbee-Dexter et al., 2020; Smale et al., 2019; Smale & Wernberg, 2013). In fact, the *Climate Extremes Hypothesis* states that extreme thermal events, even if rare, are a key selection agent in evolution of thermal tolerance (Sunday et al., 2019).

Rising temperatures increase the risk of extinction of the southernmost populations because they rise too fast to allow for thermal adaptation (Calosi et al., 2016; Thomas et al., 2012). The loss of habitat-forming species, like the ones studied here, results in a decline of complexity and diversity of the associated ecological communities (Filbee-Dexter & Wernberg, 2018; Mineur et al., 2015; Tanaka et al., 2012; Wernberg et al., 2011, 2016). Unfortunately, distributional ranges are currently contracting for many taxa of temperate climates (e.g. Bates et al., 2014; Brown et al., 2016; Sunday et al., 2012).

4.5 | Conclusions

In contrast to what has been assumed in traditional biogeographical models of marine species (reviewed in Lüning, 1990), and shown for many marine ectotherms (Sunday et al., 2012), the two model macroalgae have had a historical (since ca. 1880) niche unfilling state relative to sea surface temperature. Variations in the UST_{50} among populations were observed but were not related to latitude and seemed to be random. The use of such upper survival thresholds to calculate the thermal safety margins over time allowed us to see the evolution of the recent state of thermal niche unfilling. Transient periods of niche filling were observed at the limit of one of the most relevant distributional gaps on the European Atlantic coast due to the influence of MHWs. Using UST_{50} as a threshold for habitat suitability for the climate change scenario projections for sea surface temperature predicted that the populations that are suffering from transient periods of niche filling will disappear. By comparing species distributions with their thermal fundamental niches, as in this study, niche filling or unfilling states and thermal safety margins can be identified, which are crucial in explaining and predicting the biogeography of the species.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Distribution records, Growth and Survival Data at https://datadryad.org/stash/share/tB92G0JocosyZ9-YzUEyQd-TypNfJ2bQY4-PutUVRaI, reference number https://doi.org/10.5061/dryad.dv41ns207.

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BIOSKETCH

Sandra Hernández is broadly interested in the biogeography of marine seaweeds along European coasts. This work represents a component of her PhD at Rey Juan Carlos University on the eco-physiological and distributional responses to Climate Change in seaweeds. She and the other authors collaborate on questions of algae distribution, taxonomy and ecophysiology in Europe.

Author contributions: All authors participated in the collection of vegetative fronds and the revision of the drafts giving their final approval for publication. Francisco Arenas provided the facilities where the experiments were developed. Ana G. García, Francisco Arenas, João N. Franco, M. Pilar Escribano, and Sandra Hernández participated in the experiment execution. Sandra Hernández performed the statistical analyses in collaboration with Ana G. García, Brezo D. C. Martínez and Francisco Arenas, Sandra Hernández and Brezo D. C. Martínez led the writing of the manuscript and its revision.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.