



# Twenty years of observed and predicted changes in subtidal red seaweed assemblages along a biogeographical transition zone: inferring potential causes from environmental data

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## ABSTRACT

**Aim** To assess environmental changes within a marine biogeographical transition zone and how they have affected seaweed assemblages and distributions over the past two decades.

**Location** Brittany (western France, Europe) – a biogeographical transition zone between cold-temperate and warm-temperate regions.

**Methods** We assessed spatio-temporal variation for three environmental parameters [sea-surface temperature (SST), suspended inorganic matter and chlorophyll *a*] between 1992 and 2012 in five adjoining regions using generalized linear models. To investigate changes in assemblages and distributional patterns of red seaweeds based on sampling surveys conducted during two separate periods (1992–1998 and 2010–2012), we used two complementary approaches, multivariate data analysis and species distribution models (SDMs) with a set of modelling procedures.

**Results** Coastal water temperature in Brittany has increased by 0.7 °C on average over the past two decades (0.35 °C per decade). At a finer scale, changes in SST showed that Brittany constitutes a mosaic of contrasting conditions, with the western and north-western regions being colder and less affected by climate change than the other three regions. Our results suggest that increasing SST caused significant changes in subtidal red seaweed assemblages over the 20-year period. Between the two periods, SDMs predicted significant species shifts for seven out of ten representative species, and reductions in the distribution ranges of most species.

**Main conclusions** Our study confirmed important differences across the different regions of the studied biogeographical transition zone. Changes in abiotic parameters and red seaweed assemblages are expected to occur at varying extremes across these regions, with western and north-western Brittany representing the most stable zones that might constitute a potential refuge for certain species when responding to global changes.

## Keywords

Brittany, global change, macroalgal communities, North Atlantic, sea surface temperature, species distribution modelling.

## INTRODUCTION

The fourth report of the Intergovernmental Panel on Climate Change (IPCC) indicated that global sea-surface temperature

(SST) has increased by an average of 0.13 °C per decade over the last 50 years (Pachauri & Reisinger, 2008). These rapid shifts in temperature are expected to alter the survival of organisms, by affecting their physiology and phenology

(Hughes, 2000; Bellard *et al.*, 2012), leading to three non-exclusive responses: (1) acclimatization (at short time-scales) or adaptation (at long time-scales); (2) migration towards regions exhibiting suitable temperature ranges; and (3) extinction. Shifts in geographical ranges towards polar latitudes, higher elevation or deeper water are the most documented responses for various species in almost all natural systems worldwide (Parmesan, 2006).

Within this context of shifting species ranges, marine biogeographical transition regions represent an important focus area. In these regions, the response of a given species located at either the southern or northern limits of its range may be compared. Lima *et al.* (2007) investigated this by evaluating the direction and intensity of distribution changes of intertidal macroalgae located along the Portuguese coastline (eastern North Atlantic). The temperature in this region represents the main abiotic factor limiting seaweed growth and reproduction; thus, temperature directly controls the geographical boundaries of this group of organisms (reviewed by Eggert, 2012). In contrast to the expected general poleward shift, Lima *et al.* (2007) reported marked differences in the responses of cold-water and warm-water species. For instance, while the range of warm-water seaweeds has extended northwards, no significant change was observed for cold-water species. They demonstrated that single-species responses may be highly variable and that generalizations about poleward shifts, due to increasing temperature, should be made with caution.

There is increasing empirical evidence supporting northward shifts and/or changes in seaweed assemblages along European coasts. For instance, the brown seaweeds *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* are extending northwards along the British and Irish coasts (Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2006). Díez *et al.* (2012) detected substantial changes in the seaweed communities of the Cantabrian Sea (i.e. the Bay of Biscay, extending along the west coast of France to the Spanish border) during 1991–2008. These observed changes were confirmed by recent insights obtained from species distribution models (SDMs), which, benefiting from the development and the accessibility of recent and future environmental data, have been widely used to evaluate the potential impact of climate change on biodiversity and species distribution (e.g. Bellard *et al.*, 2012). SDMs have been applied to seaweeds, particularly the polar and cold-temperate communities of the North-eastern Atlantic (Müller *et al.*, 2009), intertidal brown seaweeds (Martínez *et al.*, 2012; Jueterbock *et al.*, 2013), and kelps (Bekkby & Moy, 2011; Raybaud *et al.*, 2013). These studies have generally predicted changes in species composition and abundance in response to temperature increases.

SDMs of seaweeds have traditionally used mean, minimum or maximum seawater temperature as predictors; however, various non-climatic factors might also act as the limiting factor in seaweed distribution, particularly at local scales. For example, nutrient concentration (estimated by chlorophyll *a* concentration) and water turbidity [estimated by the

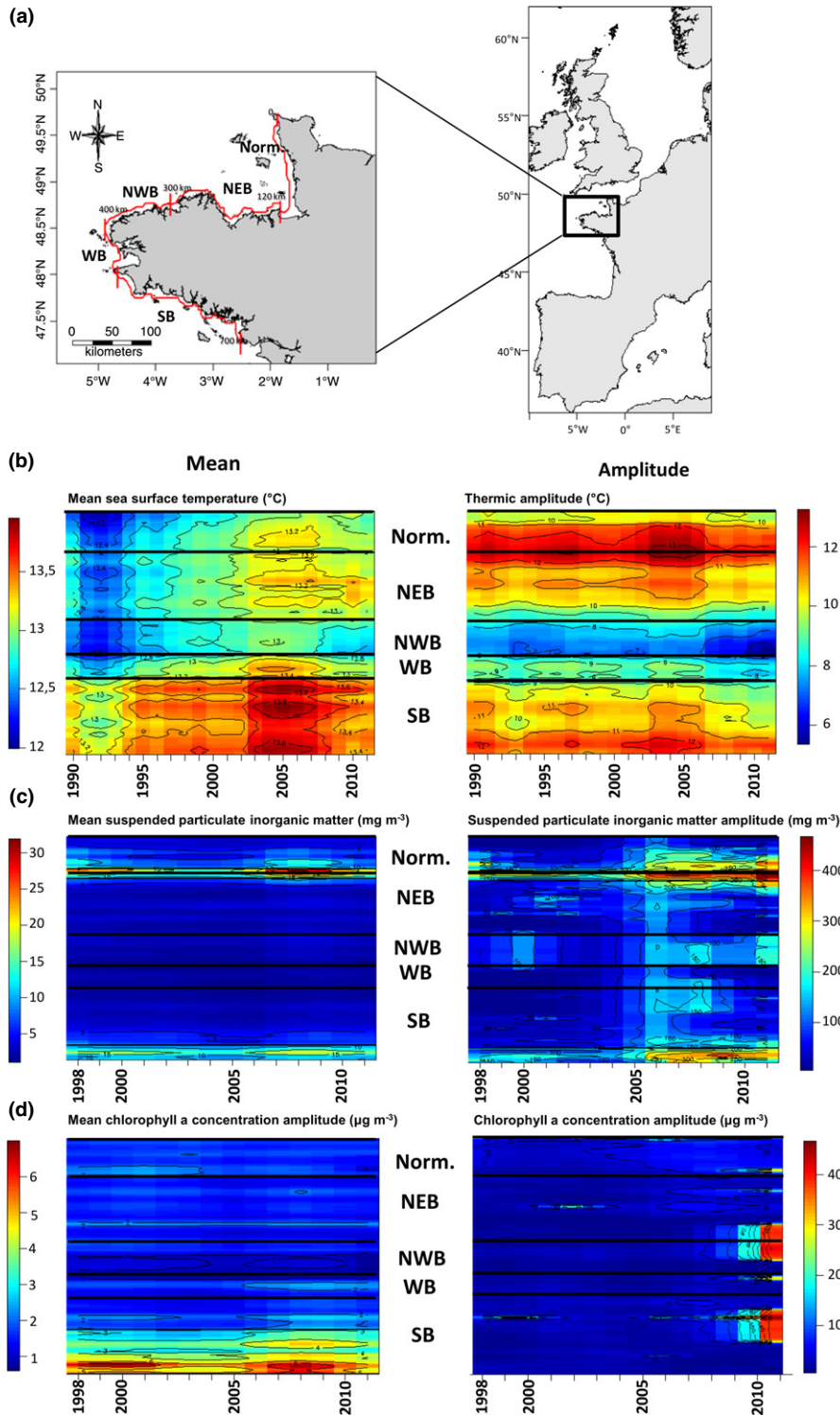
concentration of suspended particulate inorganic matter (SPIM)] may alter seaweed metabolism (particularly photosynthesis), and hence affect their performance and survival (Lobban & Harrison, 2000). While this difficulty in obtaining reliable predictions has been clarified for intertidal habitats exposed to extreme environmental conditions, it might not hold true for subtidal habitats, where the amplitude of abiotic variables is reduced (Helmuth *et al.*, 2002). However, information about subtidal communities inhabiting hard substrata remains scarce (Juanes *et al.*, 2008). Moreover, subtidal seaweed assemblages are mainly composed of red seaweeds, which have a higher species richness than brown seaweeds (Guiry & Guiry, 2013), offering the possibility of assessing a large range of species-specific responses.

This study investigated the environmental changes within a marine biogeographical transition zone (Brittany, France), and their impact on subtidal red seaweed assemblages and distributions over the last two decades (1992–2012). Brittany is a hotspot for seaweed species biodiversity (Kerswell, 2006; Santelices *et al.*, 2009), as well as a biogeographical transition zone between the Celtic Sea and the South European Atlantic Shelf ecoregions, and also between the Northern European Seas and Lusitanian provinces within the 'temperate Northern Atlantic' realm (Spalding *et al.*, 2007). Furthermore, the coastline of Brittany serves as a refugial zone for numerous species (Provan, 2013). Therefore, Brittany represents a highly relevant zone for studying the species range shifts of seaweeds. Here, we first assessed environmental changes in three biologically important factors for seaweeds (SST, concentration of SPIM, and chlorophyll *a*) over the last two decades. Second, we compared red seaweed assemblages that occur within kelp forests between two survey periods (1992–1998 and 2010–2012) along the Brittany coastline, to detect changes in assemblage composition in relation to changing environmental conditions. Third, we implemented SDMs based on both climatic and non-climatic predictors, to predict how red seaweed species have responded to environmental changes over the last two decades. By using both multivariate data analysis of actual data and robust SDMs, we sought to better explain the observed and predicted changes in red seaweeds in relation to environmental changes in the Brittany transition zone.

## MATERIALS AND METHODS

### Study area

The study area encompassed Brittany (approximately 600 km of coastline) and a portion of Normandy (France, north-eastern Atlantic; Fig. 1a). Within this study area, we delineated five regions: Normandy (Norm), north-eastern Brittany (NEB), north-western Brittany (NWB), western Brittany (WB), and southern Brittany (SB). Compared with the four regions of Brittany, Normandy is characterized by long and wide rocky shelves. Within Brittany,



**Figure 1** Position of the study area (a) and changes over time along the Brittany coastline for (b) sea-surface temperature (SST), (c) concentration of suspended particulate inorganic matter (SPIM), and (d) concentration of chlorophyll *a* (CHLa). ‘Average’ corresponds to the annual means, while annual ‘amplitude’ corresponds to the difference between the average annual minima and maxima. Time range: 1990–2012 for SST and 1998–2012 for SPIM and CHLa. Regions: Norm., Normandy; NEB, north-eastern Brittany; NWB, north-western Brittany; WB, western Brittany; and SB, southern Brittany.

NEB shows a more irregular topography and is more subject to cyclonic and anticyclonic gyres than other regions (Salomon & Breton, 1993). Water bodies of SB are more

stratified than those of WB and NWB (Le Fèvre, 1986), and WB is isolated from NWB by the Ushant front (Mariette & Le Corre, 1985) (Fig. 1a). All sites are located in

the upper subtidal zone and are characterized by rocky substratum, which, at these depths, hosts (1) kelp assemblages dominated by the two kelp species *Laminaria digitata* (Hudson) J.V. Lamouroux and *Laminaria hyperborea* (Gunnerus) Foslie, and (2) red seaweed assemblages located beneath the kelp canopy.

### Environmental data

Five environmental parameters were used to assess and model the distribution of red seaweed assemblages, including the mean and amplitude of SST, SPIM and chlorophyll *a*. SST, SPIM and chlorophyll *a* raw data were extracted at a 0.02° resolution from the CERSAT database (French ERS Processing and Archiving Facility, <http://cersat.ifremer.fr/>, data accessed in 2011; see Appendix S1 in Supporting Information). As some cells close to coastlines were lacking data, we applied a nearest-neighbour algorithm to assign to them the value of the nearest valued cell. The depth and the sea-floor substrate layers were used to create a mask selection; only the values on the bedrock and between 0 and -40 m were retained. All available data until 2012 were extracted, starting from 1992 for SST and 1998 for chlorophyll *a* and SPIM. Annual means and monthly averaged annual minima and maxima were calculated for each variable. We calculated 'amplitude' as the difference between monthly averaged annual minima and maxima.

### Red seaweed data

#### Sampling surveys

Occurrence records of red seaweeds were collected during three distinct diving surveys in the five previously defined regions. The first survey was conducted by divers from the 'Association pour la Découverte du Monde Sous-marin' (ADMS), who explored the entire Brittany coast during 1992–1998 (Castric-Fey, 2001). During this first survey, 163 sites were explored. The second survey targeted 39 sites distributed along the entire Brittany coastline, which were sampled by the present authors during August 2010–September 2011. At each site, seaweeds were collected from three to six 0.1-m<sup>2</sup> plots. Furthermore, additional samples were collected from 22 sites during a 10-minute visual census, conducted according to Gallon *et al.* (2013). Although not all sites were necessarily revisited during the second survey, all regions were revisited. Each specimen was identified using morphological criteria. Most specimens were identified to the species level, while the remainder were identified to the lowest taxonomic level possible (genus or family level). The third survey was performed within the framework of the CARTHAM project of the French Marine Protected Areas Agency. Twenty sites were sampled along the Brittany and Normandy coasts during July 2011–August 2012. To avoid biases due to rare species, singletons (i.e.

species sampled at only one site) were removed prior to the analyses.

In all three surveys, the dives were limited to depths of 40 m. The first two surveys (from SB to NEB) were used for multivariate data analyses, while all three surveys (from SB to Norm) were used for SDMs. To improve the performance of the models, we included species records from the OBIS database (Ocean Biogeographic Information System, <http://www.iobis.org/>, data accessed in 2011).

To link changing patterns with species ecological characteristics, we classified the species according to their affinity to cold or warm waters. We defined warm-water and cold-water species based on their presence or absence in the Mediterranean Sea, respectively.

### Data analyses

#### Evolution of abiotic variables

To map variations in SST, SPIM concentration and chlorophyll *a* concentration along the Brittany coastline, values were extracted for each cell located at 10 km from the coastline because the majority of sites were sampled between 5 and 10 km from the coast. Among the five defined regions, generalized linear models were computed to visualize trends between 1992 and 2012 for SST, and between 1998 and 2012 for SPIM concentration and chlorophyll *a* concentration.

#### Pre-treatment of databases

Some modifications were made to the original data to synchronize datasets. The substratum type at each site was checked, and sites that were not on rocky substratum were removed from the analyses. Specimens were identified to the species level, except for some genera where such identification was notoriously problematic (see Appendix S2). The taxonomic rank of identification varied between the first two surveys; therefore, some species were pooled into a single generic taxon (Appendix S1). As the sampling techniques used were not appropriate for collecting the encrusting algae, the group was removed from all datasets.

#### Evolution of biological data

We used several methods to test spatio-temporal variation of seaweed assemblages. First, we examined the sampler effect between 2010 and 2012 by testing whether data collected by R.K.G. and those collected by M.R. in the same region were different using a permutational multivariate analysis of variance (PERMANOVA, d.f. = 1, pseudo  $F = 1.152$ ,  $P$ -value = 0.076). We then used PERMANOVA to check whether: (1) assemblages differed between sampling periods; (2) assemblages differed between regions; and (3) there was an interaction between period and region. Second, when



differences were observed, we identified the species most contributing to these differences by using the similarity percentage analysis (SIMPER) routine (Clarke, 1993). Third, we performed constrained canonical analysis (CCA) to highlight relationships between changes in red seaweed assemblages and changes in the mean and amplitude of SST, SPIM and chlorophyll *a* concentrations. All analyses were based on a Bray–Curtis dissimilarity matrix, with presence/absence data calculated using the *VEGAN* package (Oksanen *et al.*, 2013) in R software (R Core Team, 2013).

## Species distribution modelling

### *Environmental predictor variables*

The 24 predictors used for SDMs were derived from the raw data of SST, SPIM and chlorophyll *a* (Appendix S1) by extracting for the two periods (1992–1998 and 2010–2011) the annual mean, amplitude, and monthly averaged annual minimum and maximum values, as well as mean, minimum, maximum and amplitude values during the period of seaweed growth (March–September). We restricted the predicted distributions of seaweeds to hard substrata between 0 and –40 m, using hard substratum and depth spatial layers (Appendix S1).

### *Modelled species*

We modelled the distributions of selected species based on two criteria: (1) species must be present during the three survey periods; and (2) at least 30 records per species are necessary for model training and evaluation (Wisz *et al.*, 2008). Ten taxa were selected: *Ahnfeltiopsis devoniensis* ( $n = 111$ ), *Calliblepharis ciliata* ( $n = 630$ ), *Calliblepharis jubata* ( $n = 261$ ), *Ceramium* spp. ( $n = 1480$ ), *Drachiella spectabilis* ( $n = 218$ ), *Gastroclonium ovatum* ( $n = 384$ ), *Kallymenia reniformis* ( $n = 540$ ), *Phyllophora pseudoceranoides* ( $n = 507$ ), *Plocamium* spp. ( $n = 1770$ ), and *Sphaerococcus coronopifolius* ( $n = 115$ ). [NB: Technically, two of these taxa are genus-level rather than species-level units, but for simplicity we refer to them as study species throughout.]

### *Modelling process*

Species records were aggregated into 0.02° cells, corresponding to the resolution of abiotic variables. We selected a set of variables that were not intercorrelated (Pearson's  $|r| < 0.70$ ; Dormann *et al.*, 2013) and best predicted the distribution for each species (see Leroy *et al.*, 2013). We modelled the species distributions using an ensemble modelling approach with seven modelling techniques implemented in the R package *BIOMOD2* (Thuiller *et al.*, 2009): generalized linear models, generalized additive models, generalized boosted models, classification tree analysis, multivariate adaptive regression splines, random forests and MaxEnt. As

the chosen models required data for both species presence and the available environmental conditions, we generated five sets of 1000 randomly selected pseudo-absences with equal weighting for presence and absence (Barbet-Massin *et al.*, 2012). Models were calibrated for the interval 1992–2012 using a larger area than our study region (area of Fig. 1b) to avoid overestimating effects of environmental changes (see Barbet-Massin *et al.*, 2010), and then were projected and analysed within our studied region only. Models were calibrated with 70% of data randomly selected and the predictive performance of each model was evaluated on the remaining 30% (Guisan & Thuiller, 2005) by using the true skill statistic criterion (TSS), generally considered to be the best criterion for presence-only models (Allouche *et al.*, 2006). This process was repeated five times to obtain an average value of model performances, and the final models were calibrated using all data. TSS scores (–1 to +1) that were above 0.7 were considered 'good' according to Landis & Koch (1977); models with TSS scores below 0.7 were removed. We computed response curves for each model based on the 'evaluation strip' method described by Elith *et al.* (2005). Background variables were fixed at the average value for the presence points of the species. Consensus distributions were obtained using the weighted average consensus (WAC) method (Thuiller *et al.*, 2009), which involves averaging model distributions with weights proportional to their TSS score.

## RESULTS

### Spatio-temporal changes in abiotic conditions

Abiotic variables (means and amplitudes) have significantly changed over the last 20 years (Table 1a); however, different local patterns were observed (Fig. 1b–d, Table 1b).

Over this 20-year period, the mean SST has increased across Brittany, from an average yearly increase of 0.025 °C for NWB, WB and SB, to an average yearly increase of 0.040 °C for Norm and NEB. The average increase across Brittany for the full period was 0.7 °C (0.35 °C per decade). SST amplitude increased for Norm and SB, but remained stable for NEB, NWB and WB. Rather than following a latitudinal gradient, changes in SST mean and amplitude revealed a mosaic of contrasting conditions, with a cold, resilient water body located in NWB and WB.

SPIM concentration was generally low and remained relatively stable along the coastline, except for two areas, the boundary of Norm with NEB, and in the southern part of SB, where a significant increase in SPIM concentration has been documented since 2006 (Fig. 1c). Average annual amplitude has increased in all regions; specifically, mean values have increased in Norm, NEB and NWB, whereas the mean values have remained stable in WB and SB (Fig. 1c, Table 2b).

**Table 1** Results of (a) the generalized linear model testing the factor 'region' for the different abiotic parameters averaged over the study period [1992–2012 for sea-surface temperature (SST) and 1998–2012 for suspended particulate inorganic matter (SPIM) and chlorophyll *a* (CHLa) concentrations], and (b) the average annual and amplitude changes in the different abiotic parameters within each region studied. Regions: Norm., Normandy; NEB, north-eastern Brittany; NWB, north-western Brittany; WB, western Brittany; and SB, southern Brittany.

(a)	d.f.	F-model	P-value		
Mean					
SST	4	705.5	< 0.001		
SPIM	4	217.45	< 0.001		
CHLa	4	401.24	< 0.001		
Amplitude					
SST	4	17.214	< 0.001		
SPIM	4	39.47	< 0.001		
CHLa	4	4.624	< 0.001		
(b)	Norm.	NEB	NWB	WB	SB
Mean					
SST	0.043	0.041	0.024	0.026	0.024
SPIM	0.046	0.028	0.027	-0.009	0.005
CHLa	-0.022	-0.012	-0.014	0.035	0.036
Amplitude					
SST	0.229	-0.002	-0.039	-0.051	0.262
SPIM	11.936	6.171	7.721	5.869	9.328
CHLa	5.775	3.011	7.716	0.624	1.339

Over the past two decades, higher chlorophyll *a* concentrations were recorded in SB ( $\sim 3\text{--}6 \mu\text{g m}^{-3}$ , with peaks in 1998–2001 and 2006–2009; Fig. 1d) than in the other four regions ( $\sim 1\text{--}3 \mu\text{g m}^{-3}$ ). Chlorophyll *a* concentrations also increased in WB and SB (Fig. 1d, Table 2b).

Of the five regions, WB was least impacted by changes in all the measured abiotic variables over the last 20 years.

### Spatio-temporal changes in red algal assemblages along the Brittany coastline

The PERMANOVA results highlighted significant differences between the two study periods and the five study regions (Table 2a). However, the variance explained by the factor 'period' (23.1%) was more than twice as high as the variance explained by the factor 'region' (8.6%). The interaction between period and region was also significant; hence, we analysed the differences within each region. Differences between sampling periods appeared significant in all of the Brittany regions (Table 2b). However, the magnitude of differences varied among regions. The magnitude was minimal for WB, intermediate for both NEB and NWB, and maximal for SB. The species that contributed the most towards discriminating between the two periods are presented in Appendix S2.

Across regions, different patterns emerged regarding changes in species occurrence frequencies (Table 3). First,

**Table 2** Summary of the permutational multivariate analysis of variance (PERMANOVA) results testing whether red seaweed assemblages differed between sampling periods and regions and their interaction. The factor 'period' corresponds to two periods of the survey (T1: 1992–1998 and T2: 2010–2012). The factor 'region' corresponds to the different regions that were surveyed (see Fig. 1). Both the global test (a) and the pairwise tests of the factor 'period' within each level of the factor 'region' (b) are presented. Regions: NEB, north-eastern Brittany; NWB, north-western Brittany; WB, western Brittany; and SB, southern Brittany.

	d.f.	F-model	Part of variance explained	P-value
(a)				
Period	1	71.1	0.231	< 0.001
Region	3	8.8	0.086	< 0.001
Period $\times$ Region	3	5.3	0.051	< 0.001
Residuals	194		0.631	
(b)				
Region NEB				
Period	1	28.1	0.342	< 0.001
Residuals	54		0.658	
Region NWB				
Period	1	12.2	0.367	< 0.001
Residuals	21		0.633	
Region WB				
Period	1	13.2	0.159	< 0.001
Residuals	70		0.841	
Region SB				
Period	1	36.0	0.424	< 0.001
Residuals	49		0.576	

the frequency of some species homogeneously decreased across the four Brittany regions between 1992–1998 and 2010–2012 (e.g. *Ceramium* spp., *Gastroclonium ovatum* and *Heterosiphonia japonica*). Second, some species present in the 1992–1998 period were absent in the 2010–2012 period (e.g. *Gracilaria gracilis*, *Seirospora seirosperma* and *Kallymenia requienii*). Third, the frequency of several species (e.g. *Cryptopleura ramosa*, *Phyllophora crispa*, *Corallina* spp., *Plocamium* spp. and *Heterosiphonia plumosa*) homogeneously increased across regions between the two periods. Fourth, one species was absent during the first sampling period and appeared in the four regions during the second sampling period (*Dilsea carnosus*). We observed an increase in cold-water species compared with warm-water species and a greater decrease in warm-water species compared with cold-water species (Table 4), indicating that assemblages gained cold-water species and lost warm-water species.

### Relationship between abiotic and biotic changes

The CCA (Fig. 2) displayed both spatio-temporal variations of red seaweed assemblages and the evolution of abiotic parameters between periods. Consistent with the PERMANOVA results, this CCA highlighted clear differences in biotic assemblages between the two study periods. Moreover, it

**Table 3** Reported distribution ranges and summary of changes in the occurrence frequencies between the two study periods, both over all Brittany regions and within each region, for red seaweed taxa contributing to more than 1% of global dissimilarity between the two periods according to the similarity percentage analysis (SIMPER) procedure. Regions: NEB, north-eastern Brittany; NWB, north-western Brittany; WB, western Brittany; and SB, southern Brittany.

Taxa	Distribution (latitudes and range)	Thermal affinity	Changes in occurrence frequencies between 1992–1998 and 2010–2012				
			Brittany	NEB	NWB	WB	SB
<i>Gracilaria gracilis</i>	60/30 (30) + MS	warm	↓	↓	↓	↓	↓
<i>Cryptopleura ramosa</i>	60/30 (30) + MS	warm	↑	↑	↑	↑	↑
<i>Phyllophora crispa</i>	70/35 (35) + MS	warm	↑	↑	↑	↑	↑
<i>Ceramium</i> spp.	N/A	N/A	↓	↓	↓	↓	↓
<i>Corallina</i> spp.	N/A	N/A	↑	↑	↑	↑	↑
<i>Gastroclonium ovatum</i>	60/30 (30) + MS	warm	↓	↓	↓	↓	↓
<i>Heterosiphonia japonica</i>	60/40 (20) Introduced	warm	↓	↓	↓	↓	↓
<i>Plocamium</i> spp.	N/A	N/A	↑	↑	↑	↑	×
<i>Heterosiphonia plumosa</i>	60/30 (30)	cold	↑	↑	↑	↑	↑
<i>Dilsea carnosa</i>	80/35 (45) + NWA	cold	↑	↑	↑	↑	↑
<i>Callophyllis laciniata</i>	65/35 (30)	cold	↑	↑	↑	↑	↑
<i>Seirospora seirosperma</i>	60/30 (30)	cold	↓	↓	↓	↓	↓
<i>Kallymenia reniformis</i>	60/30 (30)	cold	↑	↓	↑	↑	↑
<i>Kallymenia requienii</i>	35/30 (5) + MS	warm	↓	↓	↓	↓	↓
<i>Phyllophora sicula</i>	55/35 (20) + MS	warm	↓	↓	↓	×	×
<i>Calliblepharis ciliata</i>	60/30 (30)	cold	≈	↑	↑	×	×
<i>Gelidium corneum</i>	55/30 (25)	cold	↓	↓	↓	↑	↓
<i>Callithamnion tetragonum</i>	65/30 (35) + NWA	cold	↓	↓	↑	↑	↓
<i>Phyllophora pseudoceranoides</i>	70/40 (30) + NWA	cold	↓	↑	↓	↑	↓
<i>Phycodrys rubens</i>	80/35 (45) + NWA	cold	↑	↑	×	×	↑
<i>Meredithia microphylla</i>	60/30 (30) + MS	warm	↑	↑	×	×	×
<i>Cystoclonium purpureum</i>	70/40 (30) + NWA	cold	↓	↓	×	↓	↓
<i>Delesseria sanguinea</i>	70/40 (30)	cold	↑	×	↑	↑	≈
<i>Palmaria palmata</i>	70/30 (30) + NWA	cold	↑	↑	↑	×	×
<i>Chondrus crispus</i>	70/35 (35) + NWA	cold	↑	×	↑	↑	×
<i>Lomentaria articulata</i>	65/30 (35) + MS + NWA	warm	↑	×	↑	↑	↓
<i>Sphaerococcus coronopifolius</i>	60/30 (30) + MS	warm	↑	↑	↑	×	↓
<i>Polyneura bonnemaisonii</i>	55/40 (5)	cold	↑	↑	×	↑	×
<i>Aglaothamnion hookeri</i>	70/30 (40) + NWA	cold	↓	×	×	↓	↓
<i>Halurus equisetifolius</i>	55/30 (25) + MS	warm	↑	×	≈	↑	↑
<i>Rhodymenia holmesii</i>	55/30 (25)	cold	↑	↑	↑	×	×
<i>Calliblepharis jubata</i>	55/35 (20) + MS	warm	↓	↓	↑	×	×
<i>Porphyra</i> spp.	N/A	N/A	≈	×	×	×	×

Distribution is provided in degrees as the highest latitude/lowest latitude (latitude range); MS means that the species is also present in the Mediterranean Sea; NWA means that the species is also present in the north-western Atlantic; ×: no information; ≈ no change in occurrence frequencies.

**Table 4** Observed and predicted changes in relation to the thermal affinity of species that contributed to ≥ 1% of the global dissimilarity between the red seaweed assemblages sampled along the Brittany coastline in the periods 1992–1998 and 2010–2012.

	Observed increase in occurrence frequency	Observed reduction in occurrence frequency	Predicted northward shift	Predicted range contraction
Warm-water species ( $N_{\text{observed}} = 17$ and $N_{\text{predicted}} = 5$ )	50%	50%	100%	80%
Cold-water species ( $N_{\text{observed}} = 12$ and $N_{\text{predicted}} = 3$ )	62.5%	37.5%	33%	100%

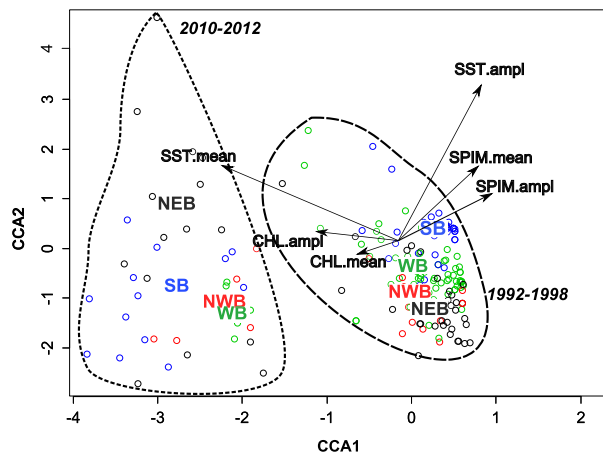
*N* is the number of species in each category.

Warm-water species: species occurring in the Mediterranean Sea.

Cold-water species: species not recorded in the Mediterranean Sea.

appeared that between the two study periods, the evolution of red seaweed assemblages was mainly correlated with the increase in mean SST. Across regions, assemblages appeared

to be distributed along a north–south gradient in 1992–1998, but not in 2010–2012, where the assemblages of NEB apparently became isolated from the other regions.



**Figure 2** Canonical correspondence analysis of red seaweed assemblages that were sampled during the periods 1992–1998 and 2010–2012 constrained by mean sea-surface temperature (SST.mean), amplitude of sea-surface temperature (SST.ampl), mean chlorophyll *a* concentration (CHL.mean), amplitude of chlorophyll *a* concentration (CHL.ampl), mean suspended particulate inorganic matter (SPIM.mean), and amplitude of suspended particulate inorganic matter (SPIM.ampl). The six environmental parameters contributed significantly towards explaining the observed pattern. Regions: NEB, north-eastern Brittany; NWB, north-western Brittany; WB, western Brittany; and SB, southern Brittany.

## Species distribution modelling

### Model performance

All calibrated models exhibited good prediction performances, with average TSS scores ranging from 0.517 for the GLM to 0.972 for the RF analyses (see Appendix S3).

### Species responses

A specific combination of variables was selected to model the distribution of each seaweed species (Table 5). Although the number and order of variables significantly explaining the distribution varied among species, the amplitude of SST (annual or during the growth period) were systematically the best predictors.

The 10 modelled species showed similar response patterns to SST variables (Fig. 3a,b). All of the species exhibited a peak in their probability of presence at an SST amplitude of approximately 1 °C, with probabilities collapsing to a minimum of 0–0.25 when the SST amplitude reached 2 °C (Fig. 3a). The values for all species remained low for their probability of presence beyond an SST amplitude of 2 °C, except for *Calliblepharis ciliata*, which exhibited a probability of presence beyond 0.50 at an SST amplitude of 6 °C. During the growth period, the effect of an increase in SST amplitude was also negative for all species, but was less important (Fig. 3b).

The probability of presence consistently varied for species sensitive to annual average concentrations of chlorophyll *a*

and decreased until the chlorophyll *a* concentration reached 2.5  $\mu\text{g m}^{-3}$  and remained constant beyond this value (Fig. 3c). Conversely, responses to chlorophyll *a* concentrations during the growth period were highly variable among species (Fig. 3d).

The modelled species were more sensitive to high SPIM concentrations during the growth period than during the entire year (Fig. 3e,f). Increasing SPIM concentrations greatly reduced the probability of presence for all modelled species (Fig. 3f).

### Latitudinal and coastline distributions

The models predicted a northward latitudinal shift for most species, with the notable exception of *Kallymenia reniformis*, *Phyllophora pseudoceranoides* and *Plocamium* spp. (Fig. 4a, Appendix S3). Furthermore, they predicted a considerable range contraction for most species, except *Plocamium* spp. and *Sphaerococcus coronopifolius*, the ranges of which were predicted to remain stable and to increase in size, respectively. The 2010–2012 coastline distribution projections were characterized by (1) a reduction in the potential distribution area for most species, particularly *Ahnfeltiopsis devoniensis*, *Drachiella spectabilis* and *Calliblepharis ciliata*, and (2) a shift towards NEB for seven of ten species (Fig. 4b, Appendix S3). The predicted shifts and range contractions were not related to the thermal water affinity of the species (Table 4).

## DISCUSSION

Sea-surface temperature (SST) has on average increased by 0.7 °C along the Brittany coastline of France over the last two decades, whereas suspended particulate inorganic matter (SPIM) concentrations have remained relatively stable and chlorophyll *a* concentrations have increased slightly during this period. Nevertheless, this global trend has concealed more complex environmental patterns, with the changes in various abiotic parameters varying greatly at a local scale. Assuming that these rapid environmental changes have affected the ecology of red seaweeds, we investigated changes in assemblages using multivariate analyses and changes in potential species distributions using SDMs over the past 20 years. Our results revealed strong changes in the distributions of both species and assemblages of red seaweeds during 1992–1998 and 2010–2012. Red seaweeds appear to be strongly dependent on SST, specifically, the mean temperature when considering assemblages, and the temperature amplitude when assessing single species responses. Therefore, we assumed that temperature was the main driver of the observed changes, supporting the findings of previous studies (Bartsch *et al.*, 2012).

### Recorded changes in abiotic conditions

The SST warming rate calculated in this study for Brittany (0.35 °C per decade) was slightly higher than but generally



**Table 5** Environmental variables selected for the species distribution modelling of each species of red seaweed sampled along the Brittany coastline. Numbers correspond to the order of importance in the consensus model. G is the growth period.

	SST					SPIM					Chlorophyll <i>a</i>						
	Ampl	Ampl G	Max	Max G	Mean	Mean G	Min	Min G	Ampl	Ampl G	Max	Max G	Mean	Mean G	Min	Min G	
<i>Ahrfeliopsis devoniensis</i>	1				2		9		8	6			3		5	4	7
<i>Calliblepharis ciliata</i>		1			3		9	10	7		4				8	5	6
<i>Calliblepharis jubata</i>	2					3	8	6	5						9	4	7
<i>Ceramium</i> spp.	1	2				3	8	10	9		5		4		9	4	6
<i>Drachiella spectabilis</i>	1	2			7		5	8	3						9	4	6
<i>Gastroclonium ovatum</i>	1	2				3	9	10	7		5				4	6	8
<i>Kallymenia reniformis</i>	2	1		3		3	8	10	5		6		4		9	7	7
<i>Phyllophora pseudoceranoides</i>	1	2				3	9	10	7		5		4		6	8	8
<i>Plocamium</i> spp.	2	1		3		3	9	10	7		5		4		10	6	7
<i>Sphaerococcus coronopifolius</i>	1	2		4		7					5	9		8	3	6	9

Ampl, amplitude.

consistent with values estimated by Lima & Wethey (2012) for the Eastern Atlantic coast ( $0.27 \pm 0.13$  °C per decade). At a finer scale, within Brittany, the average SST and the amplitude of SST together indicated that over the last 20 years, NWB and WB represent the regions least impacted by SST variations, whereas NEB and SB represent the regions most impacted by increasing SST and SST amplitude, respectively.

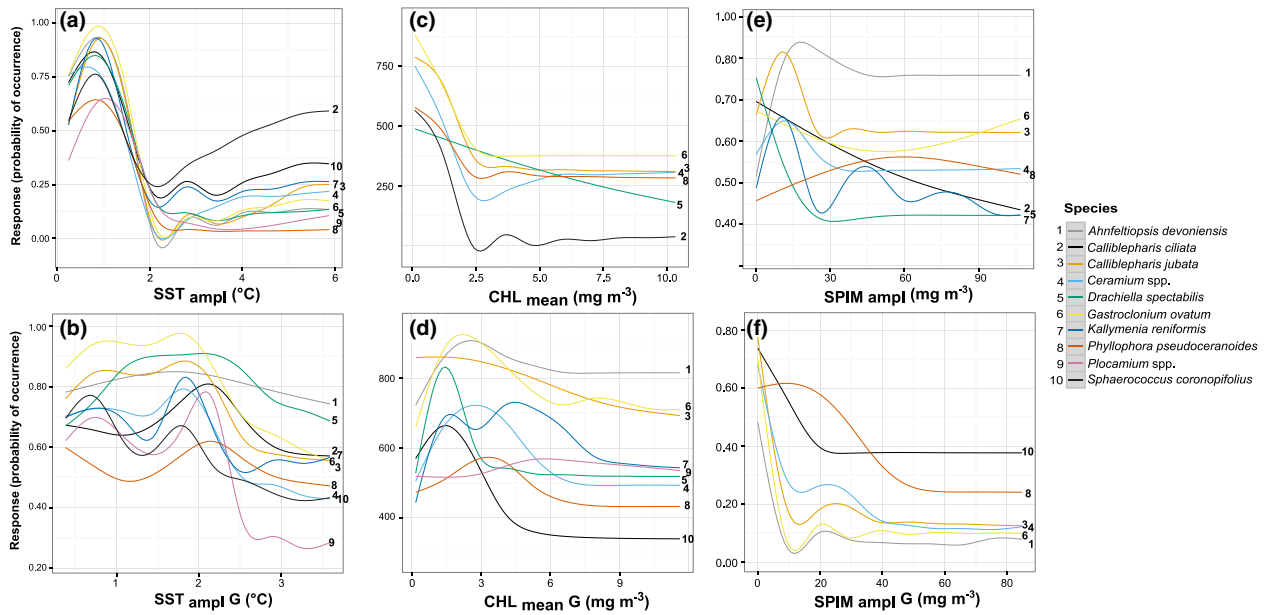
Changes in the other abiotic parameters were detected at a finer local scale. SPIM amplitude has increased in two areas since 2006 at the boundary of Norm with NEB, and in the southern part of SB. These two areas are known to receive a large amount of terrigenous material from drainage basins. The amplitude of chlorophyll *a* concentration has increased in two areas at the boundary between NEB and NWB, and in SB. These local increases correspond to zones where green tides (i.e. algal blooms) have been observed. Variations in SST and SPIM and chlorophyll *a* concentrations in Brittany were the least altered in WB over the past 20 years, which corroborates current knowledge about the hydrodynamic features of this region (Le Boyer *et al.*, 2009). The existence of the cold pocket of WB is mainly due to thermal and salinity fronts (the Ushant front) which isolate the water bodies.

**Observed changes in red seaweed assemblages**

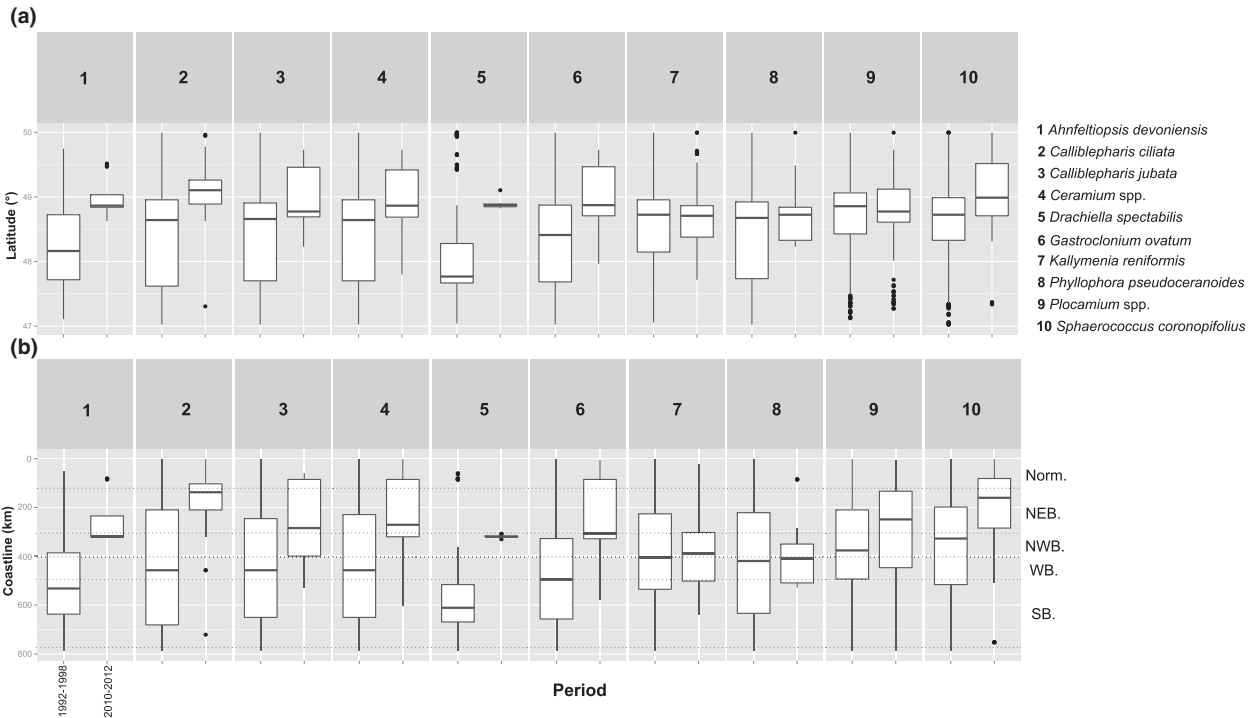
Our findings showed varying patterns of change in red seaweed assemblages across the four Brittany regions over the last two decades. The observed changes were strongly correlated with environmental shifts, particularly mean temperature. The strongest assemblage changes occurred in the region most impacted by temperature increase (SB). Conversely, the smallest assemblage changes occurred in WB, the least impacted region.

Specifically, we documented increases in the occurrence of several species (*Corallina* spp., *Cryptopleura ramosa*, *Dilsea carnosa*, *Heterosiphonia plumosa*, *Plocamium* spp. and *Phyllophora crispa*). Interestingly, some studies on recent changes in European seaweed communities obtained similar results for most of these species. For instance, Díez *et al.* (2012) did not find *P. crispa* in their 1991 survey, but found some specimens in their 2008 survey, with an observed increase in the frequencies of *C. ramosa*, *Corallina* spp., and *Plocamium* spp. between the two surveys. Similarly, Husa *et al.* (2008) described an increase in the frequency of *P. crispa* between their 1994 and 2008 surveys. These findings might indicate that these four species have benefited from recent environmental changes. These observations seem to be in accordance with previous studies for *Corallina* spp., which have shown that an increase in temperature could be beneficial for the calcification and growth of coralline seaweeds (e.g. Sun *et al.*, 2010).

We also recorded strong decreases in the frequency of *Ceramium* spp., *Gastroclonium ovatum* and *Heterosiphonia japonica* during 1992–1998 and 2010–2012. *Heterosiphonia japonica* is an invasive species from the western Pacific, with



**Figure 3** Response curves of all red seaweed taxa that were modelled along the Brittany coastline. Plain line: average predicted values for all models. Only the important variables are shown: (a) annual amplitude of sea-surface temperature (SST); (b) SST amplitude during the seaweed growth period; (c) annual mean chlorophyll *a* concentration (CHL<sub>a,mean</sub>); (d) CHL<sub>a,mean</sub> during the growth period; (e) amplitude of suspended particulate inorganic matter (SPIM); and (f) SPIM amplitude during the growth period. Growth values correspond to values extracted between March and October.



**Figure 4** Latitudinal distribution (a) and distribution along the coastline where Norm = Normandy, NEB = north-eastern Brittany, NWB = north-western Brittany, WB = western Brittany and SB = southern Brittany (b) for the 10 red seaweed taxa for which distribution was modelled between the two study periods (1992–1998 and 2010–2012). Values were extracted from the two projections (1992–1998 and 2010–2012). Dotted horizontal lines delimit the five regions.

other studies reporting an increase in its frequency during 1991–2008 on the Basque coast of Spain (Díez *et al.*, 2012), 1994–2003 in Norway (Husa *et al.*, 2008), and 1998–2011 in

Brittany (Derrien-Courtel *et al.*, 2013). *Heterosiphonia japonica* has been frequently observed in Brittany (L.L.G., pers. obs.); hence, the observed decrease in its occurrence

frequency in the present work was probably related to it primarily occurring epiphytically, rather than epilithically, while our sampling effort only focused on the latter habitat type.

We observed the disappearance of several species between 1992–1998 and 2010–2012. *Gracilaria gracilis* was not recorded in the 2010–2012 survey, whereas it was present at every site in the 1992–1998 survey. Like *H. japonica*, *G. gracilis* has been observed throughout Brittany, but not at our sampling sites (which were limited to epilithic species), indicating that these species no longer occur under the kelp canopy. *Kallymenia requienii* and *Seirospora seirosperma* were also not recorded in the 2010–2012 survey. The former is a cold-water species that has not been previously recorded in Brittany. To our knowledge, the latter species has not been observed in Brittany in recent years (Guiry & Guiry, 2013), but was observed in Norway in 2003 (Husa *et al.*, 2008) and was observed at low frequencies in Spain in 2008 (Díez *et al.*, 2012).

### Modelled changes in red seaweed distributions

For the 10 modelled species, the best predictor of distribution was SST amplitude, either for the whole year or just during the growth period, re-affirming the crucial role of temperature in shaping the patterns of seaweed distribution, as highlighted by previous studies (Jueterbock *et al.*, 2013; Raybaud *et al.*, 2013). The current results indicate that the distribution of red seaweeds seems to be limited by the temperature range they can tolerate, rather than the mean annual temperature.

The models developed here predicted both a northward shift and a contraction of the predicted suitable range for most species over the last two decades, based on the observed increase in SST. Our models predicted a northward shift of seven of ten species, with the distributions of the remaining three species either contracting or remaining stable. The lack of predicted northward range expansion might indicate that new environmental conditions further north of Brittany are not suitable for these species. Indeed, NEB is warmer and has been warming at a faster rate than the other Brittany regions over the last two decades; however, changes in temperature conditions in NWB and WB have been less drastic, which may have resulted in their isolation. This isolated status might serve as a refuge for many species and act as a barrier for warm-water species, explaining why the latter group were not predicted to expand their range within Brittany.

### Synthesis

We observed a correlation between the changes in environmental conditions over the last two decades and the documented changes in red seaweed communities. Similarly, when using the same environmental variables, strong changes were predicted from the species distribution models of a restricted species set. Three of the modelled species were

among those that best discriminated between the 1992–1998 and 2010–2012 surveys. *Plocamium* spp. was the only taxon not predicted to be subject to range contraction. This prediction may be corroborated by the observed increase in the occurrence frequency of this taxon between the 1992–1998 and 2010–2012 surveys. *Ceramium* spp. and *Gastroclonium ovatum* were predicted to be subject to strong range contraction. These predictions were corroborated by the observed decrease in their occurrence frequency between the two survey periods. Therefore, our predictions that environmental changes have had a strong impact on red seaweeds were strengthened by combining the two different approaches. We initially used multivariate analysis based on real but discrete data, which enabled detection of changes in whole species assemblages. These results were then combined with SDMs, which enabled prediction of the entire distribution for a reduced number of modelled species.

However, we did not observe the expected increase in warm-water species, and shifts were not predicted for all species. Therefore, we hypothesized that this complex pattern of responses to environmental changes might have two origins. First, species might track changes in environmental conditions, but not fast enough, resulting in a time lag between abiotic changes and the resulting changes in biotic assemblages. This pattern has already been observed for several taxa in the terrestrial realm (Devictor *et al.*, 2012). Second, environmental changes occur heterogeneously at very small spatial scales, resulting in complex global variations when species track these changes. These types of local changes are highly likely, given the mosaic of different environments recorded along the Brittany coastline in the current study. Similar outcomes have been documented for recent trends in the range shifts of marine taxa in North America; it has been suggested that marine species shift at different rates and in different directions because they closely track the complex mosaic of local climate velocities (Pinsky *et al.*, 2013).

### Study limitations

Here, we compared red seaweed assemblages that were sampled at an interval of 20 years. While important changes in red seaweed assemblages were revealed over this timeframe, several disadvantages were noted. First, the sampling scheme was not identical between the two periods; hence, we had to remove the details of or simplify the results of the most recent study to allow comparison with the sampling data of the first study.

Second, the presence of some taxa (i.e. *Ceramium* spp., *Corallina* spp. and *Plocamium* spp.) was evaluated at the generic level, so our results for these genera might not reflect the responses of individual species, as responses to climatic stress might differ within a genus (Harley *et al.*, 2006). Furthermore, the data used in this study are based on morphological identification, whereas global taxonomic knowledge has evolved since the 1990s, highlighting many cases of cryptic diversity, such as in the genera *Corallina* (Walker *et al.*,

2009; Hind & Saunders, 2013) and *Plocamium* (Saunders & Lehmkuhl, 2005). Third, if marine species track highly local environmental changes, as suggested by Pinsky *et al.* (2013), they might migrate not only along a latitudinal gradient but also along a depth gradient. In the present study, we did not have access to information on the depth at which the samples were collected; therefore, we could not test this hypothesis. Collecting pertinent local information about abiotic conditions, including the depth, to cover the entire ecological range of a species would contribute towards further accurately predicting species responses to global changes (Owens *et al.*, 2013).

## CONCLUDING REMARKS

The impact of environmental changes on red seaweeds in Brittany over the last two decades was determined using a combination of two different approaches. Changes in both biotic and abiotic conditions in this biogeographical transition zone were contrasted across adjoining regions. Changes in temperature conditions did not follow a latitudinal gradient. These changes were much milder in north-western and western Brittany, which potentially represent a refuge for red seaweeds of cold water affinity. In contrast, further drastic temperature changes were recorded in north-eastern Brittany, which potentially represents a thermal barrier to the northward migration of red seaweeds. In conclusion, we recommend both (1) extending the scope of observations to other parts of the European coastline, and (2) collecting data at a very fine scale, to better understand how red seaweeds track environmental changes, and therefore improve our understanding of the dynamics of marine biogeographical transition zones within the context of global change.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Information about abiotic and biotic data used in the study.

**Appendix S2** Occurrence frequencies and contribution to overall dissimilarity of the species between the two sampling periods.

**Appendix S3** Detailed information about the results of species distribution modelling.

## BIOSKETCHES

**Régis Gallon** and **Marine Robuchon** are PhD students working, respectively, on the functional diversity of Rhodophyta and the biodiversity of kelp forests.

Author contributions: R.K.G. and M.R. participated in conception of the study and data collection, carried out the analysis and wrote the first draft. B.L. improved the section on SDMs. L.L.G. and E.F. participated in the conception of the study and data collection. M.V. participated in the conception of the study. All authors contributed to the writing of the manuscript.

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