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Changes in the community composition of beach wrack macrophytes along thermal and latitudinal gradients

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ABSTRACT

Marine species and ecosystems are highly threatened by many anthropogenic drivers of biodiversity loss, among which the various components of climate change play a key role. Bending the curve of marine biodiversity loss requires the development of decision-making tools, such as indicators that provide information on community responses to climatic change. Although monitoring marine environments, such as benthic habitats, is highly challenging, beach wrack monitoring may provide an alternative and complementary approach to inform changes in proximate intertidal and subtidal habitats under anthropogenic threats. However, the relationship between macrophyte in beach wrack and benthic macrophyte is not fully understood. In particular, the composition of beach wrack macrophyte communities in relation with climate has not been explored yet, although such research is a prerequisite for investigating the ability of macrophyte communities in beach wrack to monitor composition changes of benthic macroalgal and seagrass communities in the face of climate change. Here, we assessed the thermal and spatial patterns of thermal affinity of macroalgae and seagrass communities (84 taxa) in beach wrack sampled at 172 sites (from Saint-Jean-de-Luz, latitude 43.39°N, to Calais, latitude 50.89°N) along the Channel and Atlantic French coast. We also investigated the contribution of taxa to these patterns, and evaluated the latitudinal patterns of abundance of the most and least contributing taxa. We found that thermal affinity of macrophyte communities in beach wrack increased with sea-surface temperature and decreased with latitude. Latitudinal patterns were also identified at smaller spatial scales. Our findings, that are consistent with previously documented macroecological patterns of benthic macrophytes, suggest that beach wrack might provide insights into proximate benthic macrophyte communities, especially their composition in light of climate warming. We recommend further investigations to ensure the relevance of developing indicators of benthic habitats based on beach wrack.

1. Introduction

Marine ecosystems have experienced increasing threats over the last century, most of which being attributable to marine and terrestrial anthropogenic activities, such as fishing, pollution, and climate change (Halpern et al., 2008, 2015). The latter has already been reflected in warming temperatures, deoxygenation, sea-level rise, ocean acidification, alteration of ocean currents, and increase in frequency and intensity of extreme weather events (Blowes et al., 2019; Doney et al., 2012; Jaureguiberry et al., 2022). Combined with other pressures, this has resulted in a global erosion of marine biodiversity, as shown by declining populations, increased risk of species extinction, and altered composition, structure, and function of marine and coastal ecosystems (Gascuel and Pauly, 2009; Johnston et al., 2015; McCauley et al., 2015).

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Yet, both the monitoring of marine ecosystems and their management in the face of global change is challenging.

Indicators are essential decision-making tools at the interface of science and policy (Mccool and Stankey, 2004; Turnhout et al., 2007). International environmental protection policies, such as the EU Marine Strategy Framework Directive (MSFD, 2008/56/EC), rely on the development of indicators to assess the state and dynamics of biodiversity (*e.g.*, the Living Planet Index, developed by WWF), the extent of anthropogenic pressures (*e.g.*, the average annual temperature), and the effectiveness of conservation measures (*e.g.*, percentage of land and sea protected, to inform the targets of the post-2020 Global Biodiversity Framework). Indicators are thus critical to inform policy decisions, and especially for underpinning conservation measures that may help to bend the curve of marine biodiversity loss (Palialexis et al., 2021). To develop and compute reliable and sensitive indicators, data is needed at large spatiotemporal scales and high resolution. However, quantifying ecosystem shifts, biodiversity decline, habitat loss, or human footprint in the marine environment is challenging (Borja, 2014; Borja et al., 2020).

Benthic habitats are essential for many marine and coastal species. However, they are generally difficult to access, strongly influenced by tides and currents that, together with depth, limit our access and monitoring abilities (Noble-James et al., 2023), hence the need to develop alternative monitoring approaches. These difficulties in monitoring marine benthic habitats *in situ*, together with the inherent costs, often limit the temporal and spatial resolution of monitoring outputs (Patrício et al., 2016). Remote methods, such as those based on photogrammetry, imagery, or robotics, offer encouraging prospects (McGeady et al., 2023). However, these methods usually do not enable species composition to be monitored, and their implementation is currently limited by the acquisition and use of advanced technological equipment. On the other hand, *ex situ* monitoring of benthic habitats through the monitoring of proximate beach-cast macrophytes originating from both intertidal and subtidal zones may provide a cost-effective, fast, and easy-to-implement complementary approach (Suursaar et al., 2014; Thibault et al., 2022).

Various studies have assessed the effects of climatic conditions on benthic macrophyte communities over the past decade (*e.g.*, Arriaga et al., 2023, 2024; Bates et al., 2017; Burrows et al., 2020; Chust et al., 2024; Jueterbock et al., 2013), demonstrating for instance that the thermal affinity of benthic macrophyte communities is driven by sea-surface temperature (Arriaga et al., 2023, 2024; Bates et al., 2017; Burrows et al., 2020). Researchers have also investigated the relationships between beach wrack and climate change, mainly through the lens of clean energy production from macrophytes wracks (*e.g.*, Kaspersen et al., 2016; Macreadie et al., 2017), their greenhouse gas emissions (*e.g.*, Lastra et al., 2018; Liu et al., 2019), and their role in sea-level rise adaptation (*e.g.*, Dugan and Hubbard, 2010; Innocenti et al., 2018). However, to our knowledge, research assessing the potential of beach wrack monitoring to produce *ex situ* indicators of benthic macrophyte communities has focused only on community diversity, cover, and composition (*e.g.*, Liebowitz et al., 2016; Reimer et al., 2018; Suursaar et al., 2014; Thibault et al., 2022), whereas the ability of macrophyte wracks to indicate changes in proximate benthic macroalgal and seagrass communities under climate change has not yet been investigated. Indeed, even the patterns of beach wrack composition with regard to climate have been overlooked to date, hindering the exploration of its potential as an indicator of the effects of climate change on benthic communities.

In this study, we assessed the spatial relationship between the composition of macrophyte communities in beach wrack and thermal conditions along the Channel and Atlantic French coast (from Saint-Jean-de-Luz, latitude 43.39°N, to Calais, latitude 50.89°N). As the thermal affinity of benthic macrophyte communities depends on sea-surface temperature (Arriaga et al., 2023, 2024; Bates et al., 2017; Burrows et al., 2020) and beach wrack macrophytes are closely related to proximate benthic communities (Liebowitz et al., 2016; Reimer et al., 2018; Suursaar et al., 2014; Thibault et al., 2022), we expected a linear increase in thermal affinity of macrophyte communities in beach wrack with sea-surface temperature. Because sea-surface temperatures linearly decrease with latitude along the European Atlantic coast (Baumann and Doherty, 2013), we also expected a linear decrease in thermal affinity of macrophyte communities in beach wrack with latitude. To test these hypotheses, we assessed the thermal and latitudinal patterns of thermal affinity (based on the Community Temperature Index, CTI) of macrophyte communities in beach wrack sampled at 172 sites. We also computed taxa contributions to the patterns of thermal affinity, and assessed the latitudinal patterns of abundance for the most and least contributing taxa in order to evaluate the ability of each taxon to provide information on changes in beach wrack macrophyte communities. Finally, we assessed latitudinal patterns of α-diversity of beach wrack macroalgae and seagrass communities.

2. Material and methods

2.1. Beach wrack sampling

To explore thermal and spatial patterns in the composition of beach wrack macroalgal and seagrass communities across a large spatial extent, we sampled 172 sites along the Channel and Atlantic French coast (latitude 43.39°N to 50.89°N, Fig. 1) comprising a wide variety of beach types and coastal marine habitats. Each site was sampled once, in April 2018 (n = 68) or in April 2019 (n = 104). No sites were sampled from 44°N to 46°N due to a lack of regular beach wrack deposition caused by the absence of benthic habitats suitable for the growth of algae and seagrass (sandy habitats) (Fig. 1). Large muddy estuaries were also excluded (*i.e.*, river Gironde, Loire, and Seine).

At each site, sampling was conducted on five 1 m^2 quadrats placed at 5 m intervals along a 25 m transect located on a line of fresh wrack. Within each quadrat, macroalgae and seagrass fragments were visually identified by five trained scientists to species level, when possible. The five observers all attended numerous training sessions and adopted common guidelines aimed at limiting the detection bias. When visual identification to species level was difficult (*e.g.*, fragments too degraded or small), macrophytes were identified to genus, when possible, or were categorised into groups based on their morphology (n = 22 taxa, 26.2 %, see full taxon list Table A.1). Macrophyte fragments belonging to the *Ulva* genus were classified into two groups based on their morphology: *Ulva* spp. – Foliose form, and *Ulva* spp. – Tubular form (previously classified as the *Enteromorpha* genus). The relative abundance of each taxon per quadrat was estimated using a 5-level ordinal scale (0: none; 1: very rare, one fragment; 2: rare, a few fragments; 3: common, many fragments; 4: dominant), as the absolute abundance of each taxon can be extremely difficult and time-consuming to assess.

2.2. Sea-surface temperature and taxa thermal niche

To assess the effects of sea-surface temperature (SST) on macrophyte communities in beach wrack, we extracted SST within a 2 km radius around each site using MARS3D model simulations of the "Modelling and Analysis for Coastal Research" (MARC) project, which provide SST for the French seas at a 2.5 km spatial resolution and a temporal resolution of 1 h (Lazure and Dumas, 2008). To reflect the different life cycles of species (*e.g.*, perennial vs. seasonal species), we used the SST of the twelve preceding months (SST_{1year}) and of the three preceding months ($SST_{3months}$).

The average thermal niche of species (Species Temperature Index, STI) were retrieved from the EMODnet Biology thermal traits dataset (Webb, 2018), which provides temperature affinity metrics for European marine species based on their global occurrences and a global sea temperature spatial database (Table A.1). For taxa identified to genus level, STI values were calculated as the mean STI of all species within that genus that are known to occur in the study zone and for which the

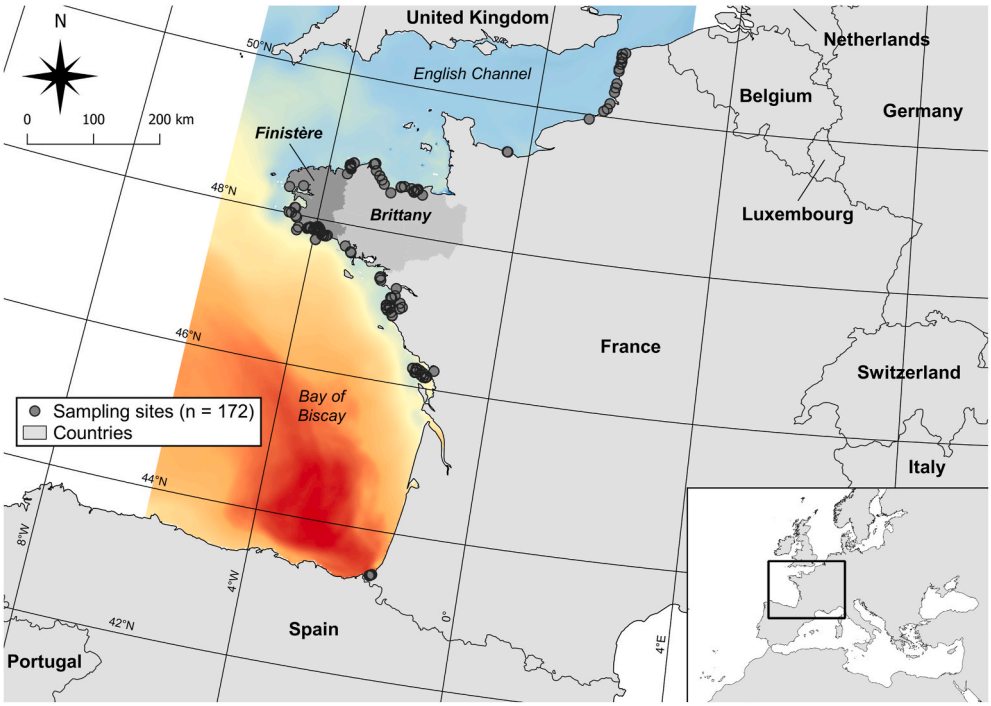

Fig. 1. Map of the 172 sampling sites. The colour gradient corresponds to the sea-surface temperature averaged over the twelve months preceding sampling in April 2019, derived from MARS3D model simulations of the "Modelling and Analysis for Coastal Research" (MARC) project (Lazure and Dumas, 2008). Country boundaries were extracted from the Natural Earth database (naturalearthdata.com). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

STI was based on more than 10 observations in the EMODnet database. Morphological groups (n = 3) were not assigned a STI value.

2.3. Community metrics

For each quadrat we calculated two thermal affinity indices (CTI_o and CTI_a) based on the Community Temperature Index, and two α-diversity indices (taxonomic richness and Shannon index). The CTI is a community weighted mean index (Díaz et al., 2007) that represents the average temperature niche of a community and was calculated as the average value of STIs across all taxa in a community (Devictor et al., 2008). Two versions of the CTI were computed: the CTI based on taxa occurrence (CTI_o), calculated as the mean STI from all macroalgae and seagrass taxa observed per quadrat, and the CTI based on taxa relative abundance (CTI_a), calculated as the mean STI from all taxa observed weighted by their relative abundance per quadrat. Taxa with no STI value (3 morphological groups and one species) were excluded for CTI calculations. Taxonomic richness was calculated as the number of identified taxa. Shannon index was calculated using the R *vegan* package (Oksanen et al., 2022).

2.4. Data analysis

2.4.1. Latitudinal and thermal patterns of CTI

We used generalized linear mixed models (GLMMs) to assess the spatial patterns of CTI_o and CTI_a computed at the quadrat scale using a Gaussian distribution and the latitude as predictor. These models also included: i) the year as a fixed effect, as two levels for a random effect is insufficient (Bolker et al., 2009; Silk et al., 2020); and ii) the site as a random intercept effect, to account for the hierarchical structure of our sampling design (*i.e.*, five quadrats per site) (Equation (1)). The longitude was not included because: i) the latitude and longitude variables were not independent; ii) we only had a strong hypothesis on the link between thermal affinity and latitude; and iii) the latitude is a better descriptor of the shape of the coastline of our study zone than the longitude, because it increases (or decreases) almost monotonically when following the coastline. GLMMs were selected as we expected a linear decrease of thermal affinity of macrophyte communities in beach wrack with latitude.

We also assessed the effect of sea-surface temperature on CTI by replacing latitude in Equation (1) by SST_{1year} or $SST_{3months}$ (Equation (2)). Furthermore, we assessed the effects of latitude and SST simultaneously by adding to Equation (1) one of the two SST metrics as a fixed effect (Equation (3)). Although the latitude and SST metrics were strongly to moderately correlated (Pearson correlation coefficient for SST_{1year}: 0.63; Pearson correlation coefficient for $SST_{3months}$: 0.40), the Variance Inflation Factors (VIFs) of the corresponding models were low (<2).

$$CTI_i = \alpha + \beta \times Latitude_i + \sum_j^J \left(\gamma_j \times Year_i\right) + \mu_k + \varepsilon_i \quad \text{(Equation 1)}$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

$$CTI_i = \alpha + \delta \times SST_i + \sum_j^J \left(\gamma_j \times Year_i\right) + \mu_k + \varepsilon_i \quad \text{(Equation 2)}$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

$$CTI_i = \alpha + \beta \times Latitude_i + \delta \times SST_i + \sum_j^J \left(\gamma_j \times Year_i\right) + \mu_k + \varepsilon_i \quad \text{(Equation 3)}$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

where CTI_i is the CTI (CTI_o or CTI_a) observed in quadrat i of site k at year j.

The sensitivity of our findings to rare taxa was assessed by carrying out these analyses including only taxa observed in more than 10 quadrats (n = 56). To ensure that these results were not sensitive to the spatial scale considered, these analyses were also run at two smaller scales to complement the national scale (*i.e.*, including only sites in the Brittany region, and sites in the "Finistère" department), and after excluding sites in the South of the Bay of Biscay to remove the important latitudinal gap in our beach wrack sampling. Furthermore, we also ran these analyses including only non-buoyant taxa (n = 73) since they may have limited dispersal capacity and are more likely to originate from proximate benthic habitats (Thibault et al., 2022), whereas buoyant macrophytes can drift over long distances (Harwell and Orth, 2002).

Latitudinal and thermal patterns of CTI were also assessed at the algae type level (*i.e.*, brown, green, and red algae) and algae source level (*i.e.*, intertidal, subtidal, and both intertidal and subtidal habitats), by including in a single model the algae type or source as a fixed effect and its interaction with latitude or SST to test for potential different patterns per algae type or source (Equation (4)). Quadrats with null taxa richness (n = 105) were excluded from all the above-mentioned analyses.

$$CTI_i = \alpha + \beta \times Latitude_i + \sum_j^J \left(\gamma_j \times Year_i\right) + \sum_l^L \left(\varphi_l \times Trait_i\right) + \sum_l^L \left(\omega_l \times Latitude_i\right) + \mu_k + \varepsilon_i \quad \text{(Equation 4)}$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

where CTI_i is the CTI (CTI_o or CTI_a) observed in quadrat i of site k at year j and for algae type or source l.

2.4.2. Taxa contributions to the patterns of the CTI

Furthermore, following Princé and Zuckerberg (2015), we assessed the extent to which each individual taxon contributed to the modelled latitudinal and thermal patterns of the CTI_o and CTI_a. To this end, we performed a jackknife analysis (Crowley, 1992): taxa were removed one by one (with replacement) from the initial dataset to recalculate the CTI values for each quadrat and we then reran the model (Equations (1) and (2)). Each taxon contribution was calculated as the difference (in %) between the absolute value of the latitude or SST coefficient in the model performed on the CTI with all taxa and that of the corresponding 'CTI minus one taxon model'. Therefore, a positive contribution of a taxon indicates that its inclusion in the computation of the CTI strengthens the expected decreasing pattern of the CTI with latitude or increasing pattern with SST, whereas a negative contribution of a taxon indicates that its inclusion in the computation of the CTI mitigates the decreasing pattern with latitude or increasing pattern with SST (Fig. 2).

2.4.3. Latitudinal patterns of taxa abundance

Then, we assessed the latitudinal patterns of abundance of each of the taxa that strongly influenced the latitudinal pattern of CTI_o or CTI_a (*i.e.*, taxa with absolute value of contribution ≥ 5 %) using Poisson GAMMs with a log link function (Equation (5)). The effect of latitude was modelled using a thin plate regression spline smoothing function instead of a linear predictor as a non-linear relation was expected for most species. These models also included the year as a fixed effect and the site as a random intercept effect. *Jania* spp. was not modelled due to insufficient number of observations (n = 12).

$$Abundance_i \sim Poisson(\lambda_i) \quad \text{(Equation 5)}$$

$$log(\lambda_i) = \alpha + f(Latitude_i) + \sum_j^J \left(\beta_j \times Year_i\right) + \mu_k + \varepsilon_i$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

where $Abundance_i$ is the taxa abundance observed in quadrat i of site k at year j.

2.4.4. Latitudinal patterns of α-diversity

To model the latitudinal patterns of α-diversity metrics (taxonomic richness and Shannon index) measured at the quadrat scale, we used generalized additive mixed models (GAMMs) using a Gaussian distribution and with the effect of latitude modelled using a thin plate regression spline smoothing function allowing to model a non-linear latitudinal pattern (Equation (6)), as we expected a peak of α-diversity in the Brittany region. The basis complexity of the smoothing function (*i.e.*, maximum allowed wiggliness, k) was set to default value ($k = 10$). These models also included the year as a fixed effect and the site as a random intercept effect. Latitudinal patterns of α-diversity metrics per algae type (*i.e.*, brown, green, and red algae) were also assessed using a single model with group-level smoothers allowing for separate smoothers with different wiggliness and intercept for each algae type (Pedersen et al., 2019), the year as a fixed effect, the interaction between algae type and year, and the site as a random intercept effect (Equation (7)). Seagrasses were not included due to the low number of taxa (n = 2). Quadrats with null taxa richness (n = 105; 12 %) were excluded from Shannon index analyses.

$$Diversity_i = \alpha + f(Latitude_i) + \sum_j^J \left(\beta_j \times Year_i\right) + \mu_k + \varepsilon_i \quad \text{(Equation 6)}$$

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

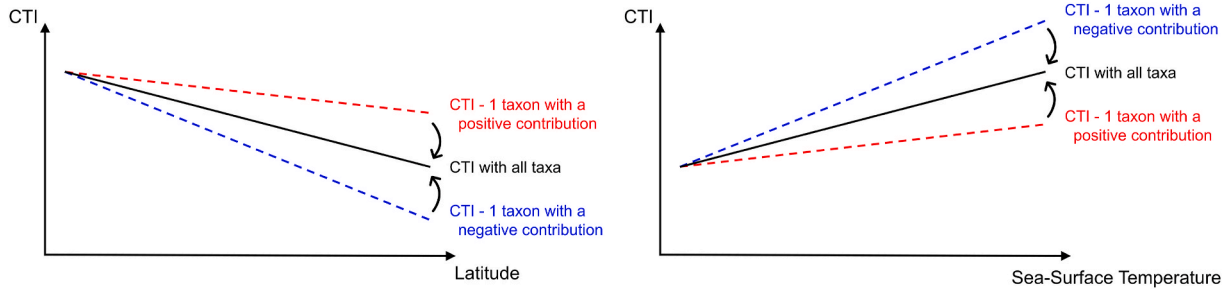

Fig. 2. Contribution (red: positive; blue: negative) of a taxon to the latitudinal pattern (left) and thermal pattern (right) of the Community Temperature Index (CTI). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$$Diversity_i = \alpha + \sum_{l}^{L} f_l(Latitude_i) + \sum_{j}^{J} (\beta_j \times Year_i) + \sum_{l}^{L} (\gamma_l \times Type_i) + \sum_{j}^{J} \sum_{l}^{L} (\varphi_{j,l} \times Year_i \times Type_i) + \mu_k + \varepsilon_i$$

(Equation 7)

$$\mu_k \sim N(0, \sigma)$$

$$\varepsilon_i \sim N(0, \sigma')$$

where $Diversity_i$ is the α-diversity (taxa richness or Shannon index) observed in quadrat *i* of site *k* at year *j* and for algae type *l*.

2.4.5. Statistical modelling

Statistical analyses were performed using R 4.3.2 (R Core Team, 2023). We fitted GAMMs with the *mgcv* package (Wood, 2011) and GLMMs with the *glmmTMB* package (Brooks et al., 2017) using Restricted Maximum Likelihood (REML) to estimate smoothing parameters and model coefficients. Statistical significance was assessed using 95 % confidence intervals for GLMMs and was set at $P < 0.05$ for GAMMs. Nakagawa's marginal (fixed predictors only) and conditional (fixed predictors and random factors) R^2 values (Nakagawa and Schielzeth, 2013) were obtained for GLMMs using the *performance* package (Lüdecke et al., 2021). In GLMMs that included an interaction effect between latitude and the factor 'algae type' or 'algae source', the slopes were assessed for each algae type or source with the package *emmeans* (Lenth, 2023). To ensure that model assumptions were met, we visually inspected model fit and residuals structure using the *performance* package for GLMMs, and the *mgcv* package for GAMMs. Spatial autocorrelation issues were assessed using the *DHARMa* package (Hartig, 2022). Maps were generated using QGIS 3.4.15 (QGIS Development Team, 2020).

Although the inclusion of the site as a random intercept effect addressed spatial autocorrelation issues—at least partially—in many models, these issues were sometimes difficult to overcome due to the structure of our data and our research questions. Indeed, i) latitude had to be included in the fixed part of some models, leading to potential difficulties when also including it in the spatial correlation structure; and ii) spatial correlation structures that include both latitude and longitude are not well adapted to coastal monitoring data, as two sites may have been much closer as the crow flies than by following the coastline (*e.g.*, between sites in South Brittany and North Brittany).

3. Results

We identified a total of 84 taxa in macrophyte wracks, of which 62 species, 17 genera (including the genus *Ulva* that was split into *Ulva* spp. – Foliose form, and *Ulva* spp. – Tubular form), 1 order, and 3 morphological groups (Table A.1). Of the identified taxa, 25 were brown algae (*Phaeophyceae*), 52 red algae (*Rhodophyta*), 5 green algae (*Chlorophyta*), and 2 seagrasses. A third of identified taxa were strictly subtidal (n = 29), 17 were strictly intertidal, and 33 could be found in both subtidal and intertidal habitats. Only 10 of the identified taxa were considered as buoyant, and one taxon comprised both buoyant and non-buoyant species.

3.1. Latitudinal and thermal patterns of CTI

The Community Temperature Index based on taxa abundance (CTI_a) significantly decreased with latitude, *i.e.*, its values were lower at northern latitudes (Table 1, Fig. 3). When assessing differences in latitudinal patterns between algae types, red algae displayed the strongest decline in CTI_a with increasing latitudes, followed by brown algae and

Table 1
Assessment of latitudinal and thermal patterns of CTI_a using GLMMs and various subsets. SE: standard error; 2.5 % and 97.5 %: 95 % confidence interval; R^2_m: marginal R^2 (fixed predictors); R^2_c: conditional R^2 (fixed predictors and random factors). Estimates significantly different from zero are in bold.

Response	Subset	Predictor	Estimate	SE	2.5 %	97.5 %	R^2_m	R^2_c
CTI_a	Full dataset	Latitude	**−0.327**	0.034	−0.394	−0.261	0.307	0.753
		Year: *2019*	**−0.226**	0.090	−0.402	−0.050		
		SST_{1year}	**0.252**	0.048	0.157	0.346	0.126	0.756
		Year: *2019*	0.016	0.102	−0.184	0.215		
		SST_{1year}	0.002	0.054	−0.102	0.106	0.308	0.756
		latitude	**−0.327**	0.044	−0.414	−0.241		
		Year: 2019	**−0.230**	0.094	−0.413	−0.048		
	Non-buoyant taxa only	Latitude	**−0.314**	0.037	−0.387	−0.242	0.283	0.807
		Year: *2019*	**−0.195**	0.097	−0.385	−0.006		
		SST_{1year}	**0.305**	0.048	0.212	0.398	0.186	0.808
		Year: *2019*	0.036	0.101	−0.161	0.233		
	Without rare taxa	Latitude	**−0.340**	0.034	−0.406	−0.274	0.327	0.759
		Year: *2019*	**−0.223**	0.090	−0.403	−0.054		
		SST_{1year}	**0.266**	0.049	0.171	0.361	0.139	0.762
		Year: *2019*	0.023	0.103	−0.178	0.223		
	Brittany only	Latitude	**−0.482**	0.119	−0.714	−0.251	0.133	0.474
		Year: *2019*	0.022	0.102	−0.177	0.221		
		SST_{1year}	−0.051	0.053	−0.153	0.052	0.057	0.479
		Year: *2019*	**−0.270**	0.089	−0.444	−0.097		
	Finistère only	Latitude	**−0.992**	0.328	−1.629	−0.355	0.105	0.616
		Year: *2019*	−0.042	0.102	−0.240	0.156		
		SST_{1year}	−0.237	0.138	−0.504	0.030	0.046	0.635
		Year: *2019*	−0.017	0.116	−0.243	0.208		
	Without the south of the Bay of Biscay	Latitude	**−0.225**	0.044	−0.311	−0.140	0.115	0.670
		Year: *2019*	**−0.192**	0.087	−0.362	−0.022		
		SST_{1year}	0.026	0.057	−0.085	0.137	0.002	0.674
		Year: *2019*	−0.046	0.092	−0.226	0.134		

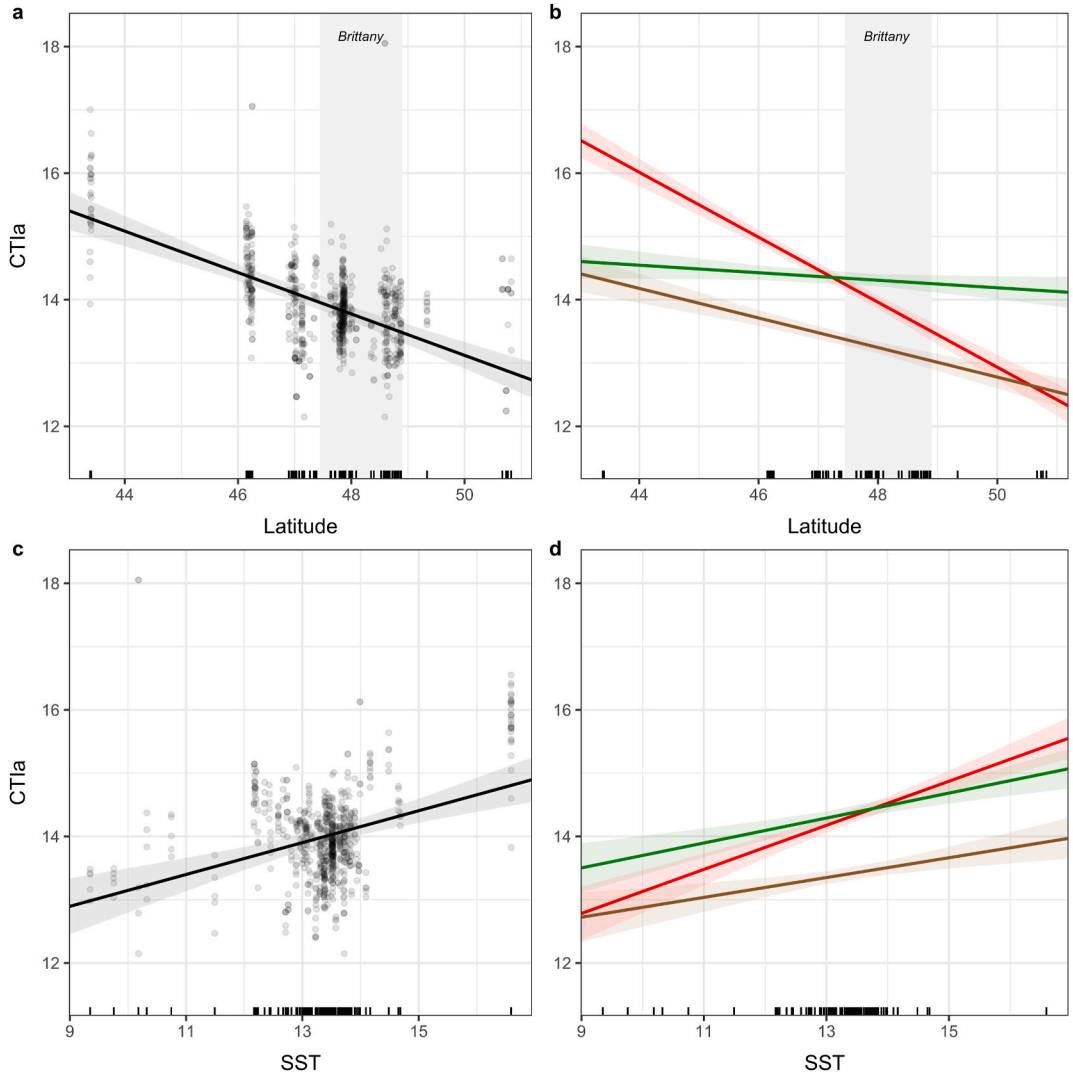

Fig. 3. Latitudinal patterns (upper panel) and thermal patterns (lower panel) of Community Temperature Index based on taxa abundance (CTI_a) with all taxa (left panel) and by algae type (right panel). For thermal patterns, we considered the sea-surface temperature averaged over the twelve months preceding sampling (SST_{1year}). Shaded areas represent 95 % confidence intervals. Predicted patterns were computed with year held constant at 2019 and the site with the median coefficient value. Observed values are depicted by small rings and were corrected by the estimate of the year effect. The difference between observed and predicted values thus represents marginal residuals. Black vertical bars at the bottom represent sampling sites. The latitudinal range of the Brittany region is depicted in light grey. Latitudinal and thermal patterns of the Community Temperature Index based on taxa occurrence (CTI_o) are provided in Figure A.1.

green algae (Fig. 3, Table A.2). The CTI_a of macrophytes originating strictly from intertidal habitats did not decrease significantly with latitude, contrary to that of macrophytes from subtidal habitats strictly and both intertidal and subtidal habitats (Figure A2). Latitudinal patterns were also identified when only taxa observed in more than 10 quadrats and non-buoyant taxa were considered, as well as at smaller spatial scales (*i.e.*, Brittany region and "Finistère" department) or when removing sampling sites with latitude <46°N (Table 1).

The CTI_a significantly increased with both metrics of sea-surface temperature (SST_{1year} or $SST_{3months}$) (Fig. 3, Table 1), although the increase and the R^2_m were lower with $SST_{3months}$ (Table A.3). Red algae displayed the strongest increase in CTI_a with increasing SST (Fig. 3, Table A.2). The CTI_a of macrophytes originating strictly from subtidal habitats did not increase significantly with SST_{1year}, contrary to that of macrophytes from intertidal habitats strictly and both intertidal and subtidal habitats (Figure A2). Thermal patterns were also identified when considering only taxa observed in more than 10 quadrats and non-buoyant taxa (Table 1). However, the effect of SST was not significant at smaller spatial scales or when removing sampling sites in the South of the Bay of Biscay (Table 1). Models including the SST had lower R^2_m than models including the latitude (Table 1, Table A.3). The effect of SST was no longer significant when associated with latitude (Table 1, Table A3).

Very similar results were found with the Community Temperature Index based on taxa occurrence (CTI_o), although the latitudinal and thermal patterns were slightly less marked than with the CTI_a (Table A.2; Table A.3; Figure A.1).

3.2. *Taxa contributions to the latitudinal and thermal patterns of the CTI*

More taxa contributed positively to the latitudinal patterns of the CTI_a (n = 50) than negatively (n = 30) (Table A.1). Taxa contributions were very similar between CTI_o and CTI_a, with only 4 taxa that had a positive contribution to the latitudinal patterns of the CTI_o and a negative contribution to that of the CTI_a, or vice versa (Table A.1).

Only 10 taxa had an absolute contribution higher than 5 % (CTI_o: 10; CTI_a: 6), of which three green algae taxa, one seagrass taxon, and one red algae taxon had a negative contribution (*i.e.*, their inclusion in the computation of the CTI mitigates its decreasing pattern with latitude), and three red algae taxa and two brown algae taxa had a positive contribution (Table 2). Among these 10 taxa, 3 were considered as

Table 2
Assessment of taxa contributions to the latitudinal patterns of CTI_o and CTI_a using a jackknife analysis. Only taxa with absolute contribution >5 % for CTI_o or CTI_a latitudinal patterns are shown. Full results are provided in Table A.1.

Taxon	Type	Buoyancy	STI	Contribution (%) to	
				CTI_o	CTI_a
Zostera marina	seagrass	yes	18.1	−24.49	−16.99
Ulva spp. – Foliose form	green algae	no	15.5	−9.03	−5.44
Corallina spp.	red algae	no	13.3	−7.48	−3.11
Ulva spp. – Tubular form	green algae	no	13.2	−6.51	−4.85
Cladophora spp.	green algae	no	14.9	−6.24	−8.18
Gelidium spp.	red algae	no	16.1	5.98	4.70
Jania spp.	red algae	no	18.6	8.58	3.64
Fucus vesiculosus	brown algae	yes	12.8	10.88	8.76
Halopithys incurva	red algae	no	16.3	14.57	16.36
Ascophyllum nodosum	brown algae	yes	12.1	15.47	13.59

buoyant: *Zostera marina*, *Fucus vesiculosus*, and *Ascophyllum nodosum*.

Among the 11 taxa that had an absolute contribution higher than 5 % to the thermal patterns of the CTI (CTI_o: 11; CTI_a: 7), 8 also had an absolute contribution higher than 5 % to the latitudinal patterns of the CTI and of the same sign (*i.e.*, positive or negative for both latitude and SST_{1year}) (Table A.4).

3.3. Latitudinal patterns of taxa abundance

Among the five taxa that contributed most negatively to the CTI latitudinal patterns, i) two had no significant latitudinal pattern of abundance (*Zostera marina* and *Cladophora* spp.), ii) two were more abundant at lower latitudes despite their medium and low STI respectively (*Ulva* spp. – Foliose form and *Corallina* spp.), and iii) one exhibited a non-monotonic latitudinal pattern of abundance but with lower abundance at the highest latitudes notwithstanding its low STI value (*Ulva* spp. – Tubular form) (Table 2, Fig. 4).

Conversely, among the five taxa that contributed most positively to the CTI latitudinal patterns, i) two are warm-dwelling taxa that were more abundant at lower latitudes (*Gelidium* spp. and *Halopithys incurva*) and ii) two are cold-dwelling taxa with less abundance at lower latitudes (*Fucus vesiculosus* and *Ascophyllum nodosum*) (Table 2, Fig. 4). The latitudinal pattern of *Jania* spp. abundance was not modelled due to the low number of observations (n = 12).

3.4. Latitudinal patterns of α-diversity

The latitudinal patterns of taxa richness and Shannon index were very similar: a more or less bell-shaped pattern with a peak between latitudes 47°N and 48°N, and the lowest values found for the highest latitudes (Fig. 5, Figure A.4). Patterns of brown and red algae α-diversity exhibited more wiggliness, the former with a plateau of maximum values between 46°N and 49°N, and the latter with an overall decrease with increasing latitude (Fig. 5, Figure A.4; Table A.5). Latitudinal patterns of green algae taxa richness and Shannon index were not significant (Table A.5).

4. Discussion

By investigating the composition of macrophyte communities in beach wracks along the Channel and Atlantic French coast, we demonstrated that their thermal affinity increased with sea-surface temperature and decreased with latitude. Both thermal and latitudinal patterns of thermal affinity were mainly driven by red and brown algae. We were also able to detect latitudinal variations in their α-diversity and identified its expected regional hotspot (peak between 47°N and 48°N). These results are a preliminary step towards further exploring the ability of beach wrack to develop *ex situ* indicators of changes in proximate benthic macrophyte communities under climate warming, in line with Thibault et al. (2022) that recently demonstrated the relationship between the composition of macrophyte communities in beach wracks and the composition of proximate benthic macrophyte communities.

4.1. Latitudinal and thermal patterns of CTI

The thermal affinity of macrophyte communities in beach wrack linearly decreased with latitude, and linearly increased with sea-surface temperature. These results are in line with latitudinal patterns of thermal affinity observed in intertidal macroalgal communities (Burrows et al., 2020), but also coastal sea-surface temperatures linearly decreasing with latitude along the European Atlantic coast (Baumann and Doherty, 2013), and thermal patterns of thermal affinity observed in benthic macrophyte communities (Arriaga et al., 2023; Bates et al., 2017; Burrows et al., 2020). Although a negative relationship between the thermal affinity of macrophyte communities in beach wrack and latitude and a positive relationship with SST may appear somewhat trivial at the scale of macrophyte species distributions, these results are much more interesting considering the national to local scales of our study, especially with the prospect of developing a local-scale indicator.

We also found that patterns of thermal affinity could be more strongly attributed to latitude than SST. This rather unexpected outcome may result from various non-mutually exclusive factors. First, we used SST averaged over three months or one year and within a 2 km radius around each site, which might not perfectly illustrate the climatic conditions experienced by the benthic communities of macroalgae and seagrass from which the macrophyte wracks originate. In addition, the magnitude of SST variations in our study zone may have been too weak. Furthermore, the thermal affinity indices calculated might not perfectly reflect the optimal thermal niche of the community. Indeed, STIs were computed using very large scale data, and without considering intra-annual variations of SST. Moreover, a quarter of taxa (n = 22) were not identified to species level, resulting in their thermal affinity being computed by averaging different STIs, which may not perfectly represent the thermal affinity of the different species comprising these taxa. Finally, although latitude was correlated with SST, the latitudinal gradient also captures other variables, such as the longitude and differences between biogeographical areas, that, according to our findings, may also play a key role at the spatial scale of this study.

The α-diversity of buoyant macrophytes in beach wrack does not reflect the heterogeneity of proximate benthic habitats (Thibault et al., 2022) as they can drift over long distances (Harwell and Orth, 2002). However, two of the most positively contributing taxa to the thermal and latitudinal patterns featured buoyancy structures (*Fucus vesiculosus* and *Ascophyllum nodosum*), and the observed patterns of thermal affinity were extremely similar when considering only non-buoyant taxa. This might be due to: i) the minor role played by drifting macrophytes events in shaping the community composition of distant beach wrack sampling sites at the spatial scale of this study compared with that of Thibault et al. (2022); and ii) the fact that sampling sites close to each other, that are thus most likely to receive drifting macrophytes from each other's donor site, also have very similar latitude and sea-surface temperature, with latitude being highly autocorrelated in space *per se*. As expected, the patterns of thermal affinity without rare taxa (*i.e.*, observed in 10 quadrats or less) were also extremely similar to that with all taxa. Furthermore, there was a negative effect of latitude on thermal affinity of macrophyte communities in beach wrack even at smaller spatial scales (*i.e.*, Brittany region and "Finistère" department). At these spatial scales, the latitudinal pattern of thermal affinity was stronger than when considering the whole geographical range, certainly due to the particular geography of these zones (sites at very similar latitudes can be located far apart along the coastline), but it also explained less of the

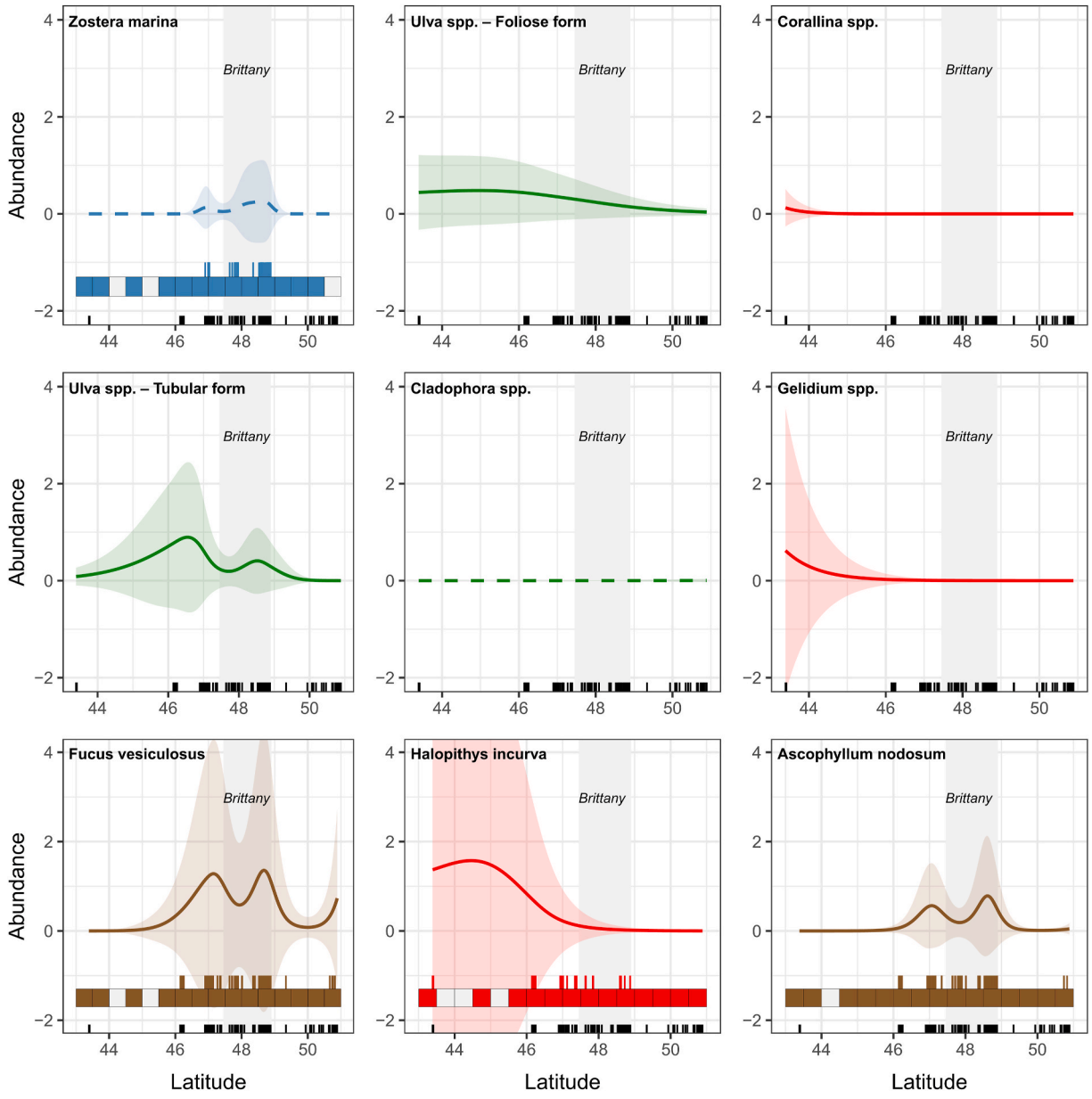

Fig. 4. Latitudinal patterns of abundance for taxa that strongly contributed to the Community Temperature Index (CTI) latitudinal pattern (*i.e.*, absolute contribution ≥5 %). Shaded areas represent 95 % confidence intervals. Non-significant patterns are depicted by dashed lines. Predicted patterns were computed with year held constant at 2019 and the site with the median coefficient value for each model. For taxa identified at species level, tiles represent 0.5° latitude zones in France, with coloured ones corresponding to zones with occurrence of the species in the Global Biodiversity Information Facility database (GBIF, 2025), and white ones without occurrence of the species. Black vertical bars at the bottom represent sampling sites and coloured vertical bars directly above tiles represent sampling sites with occurrence of the species. The latitudinal range of the Brittany region is depicted in light grey. Distribution ranges of taxa were not provided because of their much larger scale than that of our study zone. Latitudinal patterns of abundance for the same taxa when removing sampling sites with latitude <46°N are provided in Figure A.3.

variation in thermal affinity (lower R^2), which was also expected at these spatial scales where local factors are more likely to drive the composition of macroalgal and seagrass communities. Thermal patterns of thermal affinity were not identified at smaller scales nor after removing sampling sites with latitude <46°N, which reinforces the hypothesis that other local factors play a key role at these scales. Finally, we also observed the negative latitudinal pattern of thermal affinity after removing sampling sites of the south of the Bay of Biscay, thereby confirming that this trend is not only driven by those sites or biogeographic areas, nor influenced by the important latitudinal gap in our beach wrack sampling. All these alternative analyses emphasise the robustness of our findings, as well as their potential transferability to other study zones.

4.2. *Taxa contributions to the patterns of the CTI and latitudinal patterns of taxa abundance*

Thermal affinity of strictly subtidal macrophytes was not affected by spatial changes in SST, which may be due to the lower statistical power of these analyses, but also to the use of the sea-surface temperature that might be less appropriate than the sea-bottom temperature for subtidal organisms, especially in stratified areas such as the north of the Brittany (Gaudin et al., 2018).

The decrease in thermal affinity with latitude and increase with SST

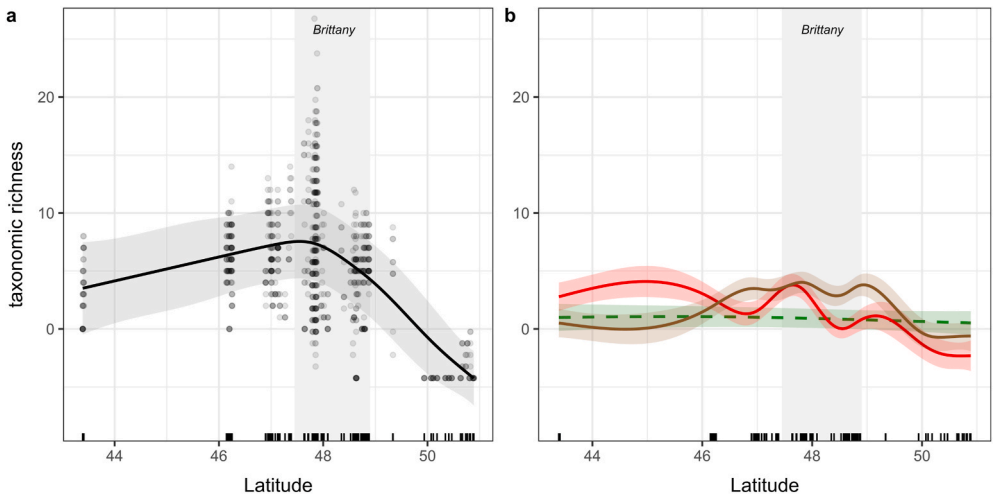

Fig. 5. Latitudinal patterns of taxonomic richness: a) with all taxa; b) by algae type. Shaded areas represent 95 % confidence intervals. Non-significant patterns are depicted by dashed lines. Predicted patterns were computed with year held constant at 2019 and the site with the median coefficient value. Observed values are depicted by small rings and were corrected by the estimate of the year effect. The difference between observed and predicted values thus represents marginal residuals. Black vertical bars at the bottom represent sampling sites. The latitudinal range of the Brittany region is depicted in light grey. Latitudinal patterns of the Shannon index are provided in Figure A.4. Latitudinal patterns of taxonomic richness when removing sampling sites with latitude <46°N are provided in Figure A.5.

were mainly driven by red algae, in accordance with Gallon et al. (2014), and, to a lesser extent, by brown algae. These findings are consistent with the analysis of taxa contributions to the latitudinal patterns of thermal affinity, from which we identified three green algae taxa among the five most negatively contributing taxa, and three red and two brown algae taxa among the five most positively contributing taxa. The sign of contributions (*i.e.*, positive or negative) of these taxa were overall consistent with their latitudinal pattern of abundance and thermal affinity. For instance, *Gelidium* spp. and *Halopithys incurva* were more abundant in southern France, as expected given their high thermal affinity, hence their strongly positive contribution to latitudinal patterns of thermal affinity. Finally, interpreting the southern part of latitudinal patterns of taxonomic abundance must be done with great caution due to the large gap in our sampling of the Bay of Biscay.

4.3. Latitudinal patterns of α-diversity

We found that taxa richness and Shannon index of macrophyte communities in beach wrack were highest between latitudes 47°N and 48°N, corresponding roughly to the stratified waters of the south of the Brittany region (Derrien-Courtel et al., 2013), with a peak in brown algae α-diversity, then strongly decreased towards higher latitudes, driven by a low diversity in red and brown algae in northern France. This regional peak of macrophyte diversity is difficult to compare with the latitudinal patterns of marine and algae species richness at global (Chaudhary et al., 2016; Kerswell, 2006) and European scales (Santelices and Marquet, 1998) due to their coarse spatial resolution. Nevertheless, this pattern has been reported from underwater samplings along the Brittany coastline and is supported by the mosaic of benthic habitats in this region, its location in a biogeographic transition area (Gallon et al., 2017), and its heterogeneity in abiotic conditions (*e.g.*, exposure, turbidity, temperature) (Derrien-Courtel et al., 2013; Gallon et al., 2014). Green algae diversity did not vary with latitude, as this group comprises only five taxa, none of which was identified to species level, but also because their abundance is mainly driven by processes at local scale, such as eutrophication caused by nutrient inputs to coastal waters from human activities (*e.g.*, agriculture, aquaculture) (Streicher et al., 2021; Teichberg et al., 2010). The wiggliness of α-diversity latitudinal patterns for brown and red algae in Brittany might be due to the high concentration of sampling sites in this area, some of which might differ in their characteristics, but also to this region's coastline that is less accurately described by the latitude (*i.e.*, latitude does not increase monotonically from the south of Brittany to the north). Finally, similarly to the latitudinal patterns of taxonomic abundance, caution must be applied when interpreting the latitudinal patterns of α-diversity over the southern part of the study zone due to the important gap in our sampling below 46°N.

4.4. Beach wrack monitoring to produce indicators of benthic macrophyte communities

Our results, which are consistent with macroecological and physico-chemical patterns described in the literature (Arriaga et al., 2023; Bates et al., 2017; Baumann and Doherty, 2013; Burrows et al., 2020; Derrien-Courtel et al., 2013; Gallon et al., 2014, 2017), contribute to assessing whether the thermal affinity of macrophyte communities in beach wrack could potentially be used as an *ex situ* indicator of the thermal affinity of benthic macrophyte communities, even at a local scale. They also indicate that beach wrack could be used to detect changes in abiotic conditions, such as changes in SST. Finally, our results reinforce the claim formulated by Thibault et al. (2022) that beach wrack monitoring could be used to provide information on the diversity of benthic habitats. We believe that these conclusions can be transposed to other geographic areas. However, only a spatial application of this indicator has been suggested so far. Therefore, it is crucial to continue to sample macrophyte wracks every year, as well as monthly at a restricted number of sites, in order to explore the ability of beach wrack to provide information on inter- and intra-annual changes in the composition of benthic macroalgal and seagrass communities under climate change, changes in these communities that have already been documented in recent publications (*e.g.*, Arriaga et al., 2023, 2024; Bates et al., 2017; Burrows et al., 2020; De Azevedo et al., 2023; Soler et al., 2022). Yet, our results represent a first step towards exploring the relevance of beach wrack monitoring to detect changes in proximate benthic macrophyte communities and in all marine and coastal species that are likely to be affected by SST.

Establishing beach wrack macrophyte communities as an *ex situ* indicator of the thermal affinity of benthic macrophyte communities would enable the development of vulnerability indicators of benthic habitats to climate change. Such indicators can be based on thermal affinity metrics of macrophyte communities in beach wrack, such as the Community Thermal Bias, computed from CTI of benthic macroalgal

communities and current SST in Burrows et al. (2020). Indicators of vulnerability to climate change can also combine future projections of climate warming and thermal affinity metrics using a trait-based Climate Change Vulnerability Assessment (CCVA) framework (Foden et al., 2019; Pacifici et al., 2015) (*e.g.*, Verniest et al., 2023).

While here we focused on spatial changes derived from thermal conditions, this approach might also be extended to other drivers of change affecting benthic communities such as biological invasions or chemical pollution. Considering the cost-effectiveness and logistical ease of beach wrack sampling in various conditions, beach-cast macrophytes may thus represent valuable opportunities for *ex situ* monitoring of coastal and marine ecosystems.

Finally, beach wrack monitoring appeared an excellent candidate for citizen science initiatives (*e.g.*, Vázquez-Delfín et al., 2024). Therefore, we have co-developed with environmental education and teaching partners a citizen science program named "ALAMER" targeting school children (https://www.plages-vivantes.fr/alamer/edito/le-protocole-alamer). This program will ultimately greatly enhance the sampling effort, thereby expand the range of current coastal ecosystem monitoring and improve our ability to inform on the dynamics of benthic macrophyte communities under global change at multiple spatial and temporal scales. It is also used as a sensitisation tool to raise awareness on the functioning of the beach ecosystem and its vulnerability to multiple anthropogenic pressures, such as beach wrack collection and sea-level rise, thereby increasing the acceptance of beach wrack by users. Finally, expanding this protocol to other audiences, such as conservation practitioners, could help to address more local questions (*e.g.*, comparison of local benthic macrophyte communities with those of the network of sites). Nevertheless, the development of such initiative requires overcoming many challenges, such as defining the number and identity of taxa to be monitored, developing adapted monitoring tools and training courses, identifying the target audience, and ensuring their long-term commitment (Thibault et al., 2022; Vázquez-Delfín et al., 2024).

CRediT authorship contribution statement

Fabien Verniest: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Elisa Alonso Aller:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Pauline Poisson:** Writing – review & editing, Investigation, Data curation. **Martin Thibault:** Writing – review & editing, Methodology. **Isabelle Le Viol:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Christian Kerbiriou:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109342.

Data availability

Data will be made available on request.

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