Changes In The Community Composition Of Bach Wrack Macrophytes Along Thermal And Latitudinal Gradients

Verniest Fabien ^{1, *}, Alonso Aller Elisa ¹, Poisson Pauline ¹, Thibault Martin ^{1, 2}, Le Viol Isabelle ¹, Kerbiriou Christian ¹

¹ Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Station Marine de Concarneau, Place de la croix BP 225, 29182 Concarneau Cedex, France ² UMR ENTROPIE (UR-IRD-IFREMER-CNRS-UNC), Labex-CORAIL, 98800 Nouméa, New Caledonia

* Corresponding author : Fabien Verniest, email address : fabien.verniest@mnhn.fr

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.

Highlights

► Thermal affinity of beach wrack macrophytes increases with sea-surface temperature ► Thermal affinity of macrophyte communities in beach wrack decreases with latitude ► The latitudinal pattern is identified from a national scale to a local scale ► Patterns are consistent with earlier research on benthic macrophytes ► We suggest further exploring beach wrack's ability to inform on benthic macrophytes

Keywords : Climate change, Community Temperature Index, Diversity, Ecological Indicator, Macroalgae, Seagrass, Thermal affinity

54 INTRODUCTION

55 Marine ecosystems have experienced increasing threats over the last century, most of which 56 being attributable to marine and terrestrial anthropogenic activities, such as fishing, pollution, 57 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 58 59 currents, and increase in frequency and intensity of extreme weather events (Blowes et al., 60 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, 61 62 increased risk of species extinction, and altered composition, structure, and function of marine and coastal ecosystems (Gascuel & Pauly, 2009; Johnston et al., 2015; McCauley et 63 al., 2015). Yet, both the monitoring of marine ecosystems and their management in the face 64 65 of global change is challenging.

Indicators are essential decision-making tools at the interface of science and policy 66 (Mccool & Stankey, 2004; Turnhout et al., 2007). International environmental protection 67 68 policies, such as the EU Marine Strategy Framework Directive (MSFD, 2008/56/EC), rely on 69 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 70 average annual temperature), and the effectiveness of conservation measures (e.g., percentage 71 72 of land and sea protected, to inform the targets of the post-2020 Global Biodiversity 73 Framework). Indicators are thus critical to inform policy decisions, and especially for 74 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 75 76 needed at large spatiotemporal scales and high resolution. However, quantifying ecosystem 77 shifts, biodiversity decline, habitat loss, or human footprint in the marine environment is 78 challenging (Borja, 2014; Borja et al., 2020).

79	Benthic habitats are essential for many marine and coastal species. However, they are
80	generally difficult to access, strongly influenced by tides and currents that, together with
81	depth, limit our access and monitoring abilities (Noble-James et al., 2023), hence the need to
82	develop alternative monitoring approaches. These difficulties in monitoring marine benthic
83	habitats in situ, together with the inherent costs, often limit the temporal and spatial
84	resolution of monitoring outputs (Patrício et al., 2016). Remote methods, such as those based
85	on photogrammetry, imagery, or robotics, offer encouraging prospects (McGeady et al.,
86	2023). However, these methods usually do not enable species composition to be monitored,
87	and their implementation is currently limited by the acquisition and use of advanced
88	technological equipment. On the other hand, ex situ monitoring of benthic habitats through
89	the monitoring of proximate beach-cast macrophytes originating from both intertidal and
90	subtidal zones may provide a cost-effective, fast, and easy-to-implement complementary
91	approach (Suursaar et al., 2014; Thibault et al., 2022).
92	Various studies have assessed the effects of climatic conditions on benthic
93	macrophyte communities over the past decade (e.g., Arriaga et al., 2023, 2024; Bates et al.,
94	2017; Burrows et al., 2020; Chust et al., 2024; Jueterbock et al., 2013), demonstrating for
95	instance that the thermal affinity of benthic macrophyte communities is driven by sea-surface
96	temperature (Arriaga et al., 2023, 2024; Bates et al., 2017; Burrows et al., 2020). Researchers
97	have also investigated the relationships between beach wrack and climate change, mainly
98	through the lens of clean energy production from macrophytes wracks (e.g., Kaspersen et al.,
99	2016; Macreadie et al., 2017), their greenhouse gas emissions (e.g., Lastra et al., 2018; Liu et
100	al., 2019), and their role in sea-level rise adaptation (e.g., Dugan & Hubbard, 2010; Innocenti
101	et al., 2018). However, to our knowledge, research assessing the potential of beach wrack

102 monitoring to produce *ex situ* indicators of benthic macrophyte communities has focused

103 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 104 105 wracks to indicate changes in proximate benthic macroalgal and seagrass communities under 106 climate change has not yet been investigated. Indeed, even the patterns of beach wrack 107 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. 108 109 In this study, we assessed the spatial relationship between the composition of 110 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). 111 112 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 113 wrack macrophytes are closely related to proximate benthic communities (Liebowitz et al., 114 115 2016; Reimer et al., 2018; Suursaar et al., 2014; Thibault et al., 2022), we expected a linear 116 increase in thermal affinity of macrophyte communities in beach wrack with sea-surface 117 temperature. Because sea-surface temperatures linearly decrease with latitude along the 118 European Atlantic coast (Baumann & Doherty, 2013), we also expected a linear decrease in 119 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 120 Community Temperature Index, CTI) of macrophyte communities in beach wrack sampled at 121 122 172 sites. We also computed taxa contributions to the patterns of thermal affinity, and 123 assessed the latitudinal patterns of abundance for the most and least contributing taxa in order 124 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 125 126 wrack macroalgae and seagrass communities.

127 MATERIAL AND METHODS

128

129 Beach wrack sampling

130 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 131 and Atlantic French coast (latitude 43.39°N to 50.89°N, Figure 1) comprising a wide variety 132 133 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 134 135 regular beach wrack deposition caused by the absence of benthic habitats suitable for the growth of algae and seagrass (sandy habitats) (Figure 1). Large muddy estuaries were also 136 excluded (i.e., river Gironde, Loire, and Seine). 137

138 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 139 seagrass fragments were visually identified by five trained scientists to species level, when 140 141 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 142 was difficult (e.g., fragments too degraded or small), macrophytes were identified to genus, 143 when possible, or were categorised into groups based on their morphology (n = 22 taxa, 144 145 26.2%, see full taxon list Table A.1). Macrophyte fragments belonging to the Ulva genus 146 were classified into two groups based on their morphology: Ulva spp. – Foliose form, and 147 *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: 148 149 very rare, one fragment; 2: rare, a few fragments; 3: common, many fragments; 4: dominant), 150 as the absolute abundance of each taxon can be extremely difficult and time-consuming to 151 assess.

152

153 Sea-surface temperature and taxa thermal niche

154 To assess the effects of sea-surface temperature (SST) on macrophyte communities in beach 155 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 156 provide SST for the French seas at a 2.5 km spatial resolution and a temporal resolution of 1 157 158 hour (Lazure & 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 159 160 three preceding months (SST_{3months}). The average thermal niche of species (Species Temperature Index, STI) were 161 retrieved from the EMODnet Biology thermal traits dataset (Webb, 2018), which provides 162 163 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, 164 STI values were calculated as the mean STI of all species within that genus that are known to 165 occur in the study zone and for which the STI was based on more than 10 observations in the 166 EMODnet database. Morphological groups (n = 3) were not assigned a STI value. 167

168

169 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 (CTIa), calculated as the mean STI from all taxa observed weighted by their

177

178	relative abundance per quadrat. Taxa with no STI value (3 morphological groups and one
179	species) were excluded for CTI calculations. Taxonomic richness was calculated as the
180	number of identified taxa. Shannon index was calculated using the R vegan package
181	(Oksanen et al., 2022).
182	
183	Data analysis
184	Latitudinal and thermal patterns of CTI
185	We used generalized linear mixed models (GLMMs) to assess the spatial patterns of CTI_0
186	and CTIa computed at the quadrat scale using a Gaussian distribution and the latitude as
187	predictor. These models also included: i) the year as a fixed effect, as two levels for a random
188	effect is insufficient (Bolker et al., 2009; Silk et al., 2020); and ii) the site as a random
189	intercept effect, to account for the hierarchical structure of our sampling design (i.e., five
190	quadrats per site) (Equation 1). The longitude was not included because: i) the latitude and
191	longitude variables were not independent; ii) we only had a strong hypothesis on the link
192	between thermal affinity and latitude; and iii) the latitude is a better descriptor of the shape of
193	the coastline of our study zone than the longitude, because it increases (or decreases) almost
194	monotonically when following the coastline. GLMMs were selected as we expected a linear
195	decrease of thermal affinity of macrophyte communities in beach wrack with latitude.
196	We also assessed the effect of sea-surface temperature on CTI by replacing latitude in
197	Equation 1 by SST _{1year} or SST _{3months} (Equation 2). Furthermore, we assessed the effects of
198	latitude and SST simultaneously by adding to Equation 1 one of the two SST metrics as a
199	fixed effect (Equation 3). Although the latitude and SST metrics were strongly to moderately

200 correlated (Pearson correlation coefficient for SST_{1year} : -0.63; Pearson correlation coefficient

201	for SST _{3months} : -0.40), the Variance Inflation Factors (VIFs) of the corresponding	g models
202	were low (< 2).	
203		
204	$CTI_i = \alpha + \beta \times Latitude_i + \sum_{j}^{J} (\gamma_j \times Year_i) + \mu_k + \varepsilon_i$	(Equation 1)
205	$\mu_k \sim N(0,\sigma)$	
206	$\varepsilon_i \sim N(0, \sigma')$	
207		
208	$CTI_{i} = \alpha + \delta \times SST_{i} + \sum_{j}^{J} (\gamma_{j} \times Year_{i}) + \mu_{k} + \varepsilon_{i}$	(Equation 2)
209	$\mu_k \sim N(0,\sigma)$	
210	$\varepsilon_i \sim N(0, \sigma')$	
211		
212	$CTI_{i} = \alpha + \beta \times Latitude_{i} + \delta \times SST_{i} + \sum_{j}^{J} (\gamma_{j} \times Year_{i}) + \mu_{k} + \varepsilon_{i}$	(Equation 3)
213	$\mu_k \sim N(0,\sigma)$	
214	$\varepsilon_i \sim N(0, \sigma')$	
215		
216	where CTI_i is the CTI (CTI ₀ or CTI _a) observed in quadrat <i>i</i> of site <i>k</i> at ye	ar j.
217		
218	The sensitivity of our findings to rare taxa was assessed by carrying out these an	alyses
219	including only taxa observed in more than 10 quadrats ($n = 56$). To ensure that t	hese results
220	were not sensitive to the spatial scale considered, these analyses were also run at	two smaller
221	scales to complement the national scale (<i>i.e.</i> , including only sites in the Brittany	region, and
222	sites in the "Finistère" department), and after removing sites in the South of the	Bay of
223	Biscay to remove the important latitudinal gap in our beach wrack sampling. Fur	rthermore, we

dispersal capacity and are more likely to originate from proximate benthic habitats (Thibault

226	et al., 2022), whereas buoyant macrophytes can drift over long distances (Harwell & Orth,
227	2002).
220	

228	Latitudinal and thermal patterns of CTI were also assessed at the algae type level (<i>i.e.</i> ,
229	brown, green, and red algae) and algae source level (i.e., intertidal, subtidal, and both
230	intertidal and subtidal habitats), by including in a single model the algae type or source as a
231	fixed effect and its interaction with latitude or SST to test for potential different patterns per
232	algae type or source (Equation 4). Quadrats with null taxa richness ($n = 105$) were excluded
233	from all the above-mentioned analyses.
234	
235	$CTI_i = \alpha + \beta \times Latitude_i + \sum_{j}^{J} (\gamma_j \times Year_i) + \sum_{l}^{L} (\varphi_l \times Trait_i) + $
236	$\sum_{l}^{L} (\omega_l \times Latitude_i) + \mu_k + \varepsilon_i $ (Equation 4)
237	$\mu_k \sim N(0,\sigma)$
238	$\varepsilon_i \sim N(0, \sigma')$
239	
240	where CTI_i is the CTI (CTI _o or CTI _a) observed in quadrat <i>i</i> of site <i>k</i> at year <i>j</i> and for
241	algae type or source <i>l</i> .
242	
243	Taxa contributions to the patterns of the CTI
244	Furthermore, following Princé & Zuckerberg (2015), we assessed the extent to which each
245	individual taxon contributed to the modelled latitudinal and thermal patterns of the CTI_{0} and
246	CTI _a . To this end, we performed a jackknife analysis (Crowley, 1992): taxa were removed
247	one by one (with replacement) from the initial dataset to recalculate the CTI values for each

- 248 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
- 250 coefficient in the model performed on the CTI with all taxa and that of the corresponding

251	'CTI minus one taxon model'. Therefore, a positive contribution of a taxon indicates that its
252	inclusion in the computation of the CTI strengthens the expected decreasing pattern of the
253	CTI with latitude or increasing pattern with SST, whereas a negative contribution of a taxon
254	indicates that its inclusion in the computation of the CTI mitigates the decreasing pattern with
255	latitude or increasing pattern with SST (Figure 2).
256	
257	Latitudinal patterns of taxa abundance
258	Then, we assessed the latitudinal patterns of abundance of each of the taxa that strongly
259	influenced the latitudinal pattern of CTIo or CTIa (i.e., taxa with absolute value of
260	contribution \geq 5%) using Poisson GAMMs with a log link function (Equation 5). The effect
261	of latitude was modelled using a thin plate regression spline smoothing function instead of a
262	linear predictor as a non-linear relation was expected for most species. These models also
263	included the year as a fixed effect and the site as a random intercept effect. Jania spp. was
264	not modelled due to insufficient number of observations $(n = 12)$.
265	
266	$Abundance_i \sim Poisson(\lambda_i) $ (Equation 5)
267	$log(\lambda_i) = \alpha + f(Latitude_i) + \sum_{j}^{J} (\beta_j \times Year_i) + \mu_k + \varepsilon_i$
268	$\mu_k \sim N(0,\sigma)$
269	$\varepsilon_i \sim N(0, \sigma')$
270	
271	where Abundance _{<i>i</i>} is the taxa abundance observed in quadrat <i>i</i> of site <i>k</i> at year <i>j</i> .
272	
273	Latitudinal patterns of α -diversity
274	To model the latitudinal patterns of α -diversity metrics (taxonomic richness and Shannon

275 index) measured at the quadrat scale, we used generalized additive mixed models (GAMMs)

275 using a Gaussian distribution and with the effect of latitude modelled using a thin plate
277 regression spline smoothing function allowing to model a non-linear latitudinal pattern
278 (Equation 6), as we expected a peak of
$$\alpha$$
-diversity in the Brittany region. The basis
279 complexity of the smoothing function (*i.e.*, maximum allowed wiggliness, *k*) was set to
280 default value ($k = 10$). These models also included the year as a fixed effect and the site as a
281 random intercept effect. Latitudinal patterns of α -diversity metrics per algae type (*i.e.*, brown,
282 green, and red algae) were also assessed using a single model with group-level smoothers
283 allowing for separate smoothers with different wiggliness and intercept for each algae type
284 (Pedersen et al., 2019), the year as a fixed effect, the interaction between algae type and year,
285 and the site as a random intercept effect (Equation 7). Seagrasses were not included due to
286 the low number of taxa (n = 2). Quadrats with null taxa richness (n = 105; 12%) were
287 excluded from Shannon index analyses.
288
289 Diversity_l = $\alpha + f(Latitude_l) + \sum_{j}^{l}(\beta_{j} \times Year_{l}) + \mu_{k} + \varepsilon_{l}$ (Equation 6)
290 $\mu_{k} \sim N(0, \sigma)$
291 $\varepsilon_{l} \sim N(0, \sigma')$
292
293 Diversity_l = $\alpha + \sum_{i}^{k} f_{i} (Latitude_{i}) + \sum_{j}^{l}(\beta_{j} \times Year_{l}) + \sum_{i}^{k}(\gamma_{l} \times Type_{l}) +$
294 $\sum_{j}^{l} \sum_{i}^{l} (\varphi_{j,l} \times Year_{i} \times Type_{l}) + \mu_{k} + \varepsilon_{i}$ (Equation 7)
295 $\mu_{k} \sim N(0, \sigma)$
296 $\varepsilon_{i} \sim N(0, \sigma')$
297
298 where Diversity_i is the α -diversity (taxa richness or Shannon index) observed in
299 quadrat *i* of site *k* at year *j* and for algae type *l*.

301 Statistical modelling

302 Statistical analyses were performed using R 4.3.2 (R Core Team, 2023). We fitted GAMMs 303 with the *mgcv* package (Wood, 2011) and GLMMs with the *glmmTMB* package (Brooks et 304 al., 2017) using Restricted Maximum Likelihood (REML) to estimate smoothing parameters and model coefficients. Statistical significance was assessed using 95% confidence intervals 305 for GLMMs and was set at P < 0.05 for GAMMs. Nakagawa's marginal (fixed predictors 306 only) and conditional (fixed predictors and random factors) R^2 values (Nakagawa & 307 Schielzeth, 2013) were obtained for GLMMs using the *performance* package (Lüdecke et al., 308 309 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 310 package emmeans (Lenth, 2023). To ensure that model assumptions were met, we visually 311 312 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 313 DHARMa package (Hartig, 2022). Maps were generated using QGIS 3.4.15 (QGIS 314 315 Development Team, 2020). 316 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 317 difficult to overcome due to the structure of our data and our research questions. Indeed, i) 318 319 latitude had to be included in the fixed part of some models, leading to potential difficulties 320 when also including it in the spatial correlation structure; and ii) spatial correlation structures 321 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., 322

323 between sites in South Brittany and North Brittany).

324 **RESULTS**

325

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

334

335 Latitudinal and thermal patterns of CTI

336 The Community Temperature Index based on taxa abundance (CTI_a) significantly decreased 337 with latitude, *i.e.*, its values were lower at northern latitudes (Table 1, Figure 3). When 338 assessing differences in latitudinal patterns between algae types, red algae displayed the 339 strongest decline in CTI_a with increasing latitudes, followed by brown algae and green algae 340 (Figure 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 341 342 habitats strictly and both intertidal and subtidal habitats (Figure A2). Latitudinal patterns 343 were also identified when only taxa observed in more than 10 quadrats and non-buoyant taxa 344 were considered, as well as at smaller spatial scales (*i.e.*, Brittany region and "Finistère" 345 department) or when removing sampling sites with latitude $< 46^{\circ}N$ (Table 1). 346 The CTI_a significantly increased with both metrics of sea-surface temperature $(SST_{1year} \text{ or } SST_{3months})$ (Figure 3, Table 1), although the increase and the R^{2}_{m} were lower 347

348 with SST_{3months} (Table A.3). Red algae displayed the strongest increase in CTI_a with

349	increasing SST (Figure 3, Table A.2). The CTI_a of macrophytes originating strictly from
350	subtidal habitats did not increase significantly with SST_{1year} , contrary to that of macrophytes
351	from intertidal habitats strictly and both intertidal and subtidal habitats (Figure A2). Thermal
352	patterns were also identified when considering only taxa observed in more than 10 quadrats
353	and non-buoyant taxa (Table 1). However, the effect of SST was not significant at smaller
354	spatial scales or when removing sampling sites in the South of the Bay of Biscay (Table 1).
355	Models including the SST had lower R^{2}_{m} than models including the latitude (Table 1, Table
356	A.3). The effect of SST was no longer significant when associated with latitude (Table 1,
357	Table A3).
358	Very similar results were found with the Community Temperature Index based on
359	taxa occurrence (CTIo), although the latitudinal and thermal patterns were slightly less
360	marked than with the CTI_a (Table A.2, Table A.3, Figure A.1).

361

<u>Table 1:</u> 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; R²_m: marginal R²
 (fixed predictors); R²_c: conditional R² (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	Latitude	-0.225	0.044	-0.311	-0.140	0.115	0.670
the Bay of Biscay	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		

366

367

368 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 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).

383

384 <u>Table 2:</u> Assessment of taxa contributions to the latitudinal patterns of CTI_0 and CTI_a using a 385 jackknife analysis. Only taxa with absolute contribution > 5% for CTI_0 or CTI_a latitudinal 386 patterns are shown. Full results are provided in Table A.1.

T.	T.	D	OTI	Contribution (%) to		
laxon	Туре	Buoyancy	511	CTIo	CTIa	
Zostera marina	seagrass	yes	18.1	-24.49	-16.99	
<i>Ulva</i> spp. – Foliose form	green algae	no	15.5	-9.03	-5.44	
Corallina spp.	red algae	no	13.3	-7.48	-3.11	
<i>Ulva</i> 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	

³⁸⁷

388

389 Latitudinal patterns of taxa abundance

390 Among the five taxa that contributed most negatively to the CTI latitudinal patterns, i) two

391 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

393 (*Ulva* spp. – Foliose form and *Corallina* spp.), and iii) one exhibited a non-monotonic

394 latitudinal pattern of abundance but with lower abundance at the highest latitudes

notwithstanding its low STI value (*Ulva* spp. – Tubular form) (Table 2, Figure 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, Figure 4). The latitudinal pattern of *Jania* spp. abundance was not modelled due to the low number of observations (n = 12).

402

403 Latitudinal patterns of α-diversity

404 The latitudinal patterns of taxa richness and Shannon index were very similar: a more or less

405 bell-shaped pattern with a peak between latitudes 47°N and 48°N, and the lowest values

406 found for the highest latitudes (Figure 5, Figure A.4). Patterns of brown and red algae α -

- 407 diversity exhibited more wiggliness, the former with a plateau of maximum values between
- 408 46°N and 49°N, and the latter with an overall decrease with increasing latitude (Figure 5,
- 409 Figure A.4, Table A.5). Latitudinal patterns of green algae taxa richness and Shannon index
- 410 were not significant (Table A.5).
- 411

Johnal

412 **DISCUSSION**

413

414	By investigating the composition of macrophyte communities in beach wracks along the
415	Channel and Atlantic French coast, we demonstrated that their thermal affinity increased with
416	sea-surface temperature and decreased with latitude. Both thermal and latitudinal patterns of
417	thermal affinity were mainly driven by red and brown algae. We were also able to detect
418	latitudinal variations in their α -diversity and identified its expected regional hotspot (peak
419	between 47°N and 48°N). These results are a preliminary step towards further exploring the
420	ability of beach wrack to develop ex situ indicators of changes in proximate benthic
421	macrophyte communities under climate warming, in line with Thibault et al. (2022) that
422	recently demonstrated the relationship between the composition of macrophyte communities
423	in beach wracks and the composition of proximate benthic macrophyte communities.
424	
425	Latitudinal and thermal patterns of CTI

426 The thermal affinity of macrophyte communities in beach wrack linearly decreased with 427 latitude, and linearly increased with sea-surface temperature. These results are in line with 428 latitudinal patterns of thermal affinity observed in intertidal macroalgal communities (Burrows et al., 2020), but also coastal sea-surface temperatures linearly decreasing with 429 430 latitude along the European Atlantic coast (Baumann & Doherty, 2013), and thermal patterns 431 of thermal affinity observed in benthic macrophyte communities (Arriaga et al., 2023; Bates 432 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 433 434 with SST may appear somewhat trivial at the scale of macrophyte species distributions, these 435 results are much more interesting considering the national to local scales of our study, 436 especially with the prospect of developing a local-scale indicator.

437	We also found that patterns of thermal affinity could be more strongly attributed to
438	latitude than SST. This rather unexpected outcome may result from various non-mutually
439	exclusive factors. First, we used SST averaged over three months or one year and within a 2
440	km radius around each site, which might not perfectly illustrate the climatic conditions
441	experienced by the benthic communities of macroalgae and seagrass from which the
442	macrophyte wracks originate. In addition, the magnitude of SST variations in our study zone
443	may have been too weak. Furthermore, the thermal affinity indices calculated might not
444	perfectly reflect the optimal thermal niche of the community. Indeed, STIs were computed
445	using very large scale data, and without considering intra-annual variations of SST.
446	Moreover, a quarter of taxa ($n = 22$) were not identified to species level, resulting in their
447	thermal affinity being computed by averaging different STIs, which may not perfectly
448	represent the thermal affinity of the different species comprising these taxa. Finally, although
449	latitude was correlated with SST, the latitudinal gradient also captures other variables, such
450	as the longitude and differences between biogeographical areas, that, according to our
451	findings, may also play a key role at the spatial scale of this study.
452	The α -diversity of buoyant macrophytes in beach wrack does not reflect the
453	heterogeneity of proximate benthic habitats (Thibault et al., 2022) as they can drift over long
454	distances (Harwell & Orth, 2002). However, two of the most positively contributing taxa to
455	the thermal and latitudinal patterns featured buoyancy structures (Fucus vesiculosus and
456	Ascophyllum nodosum), and the observed patterns of thermal affinity were extremely similar
457	when considering only non-buoyant taxa. This might be due to: i) the minor role played by
458	drifting macrophytes events in shaping the community composition of distant beach wrack
459	sampling sites at the spatial scale of this study compared with that of Thibault et al. (2022);
460	and ii) the fact that sampling sites close to each other, that are thus most likely to receive
461	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, 462 the patterns of thermal affinity without rare taxa (*i.e.*, observed in 10 quadrats or less) were 463 also extremely similar to that with all taxa. Furthermore, there was a negative effect of 464 465 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 466 latitudinal pattern of thermal affinity was stronger than when considering the whole 467 468 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 469 variation in thermal affinity (lower R^2), which was also expected at these spatial scales where 470 471 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 472 473 after removing sampling sites with latitude $< 46^{\circ}$ N, which reinforces the hypothesis that other 474 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, 475 476 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 477 analyses emphasise the robustness of our findings, as well as their potential transferability to 478 other study zones. 479

480

481 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 were mainly 487 driven by red algae, in accordance with Gallon et al. (2014), and, to a lesser extent, by brown 488 489 algae. These findings are consistent with the analysis of taxa contributions to the latitudinal 490 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 491 492 most positively contributing taxa. The sign of contributions (*i.e.*, positive or negative) of 493 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 494 495 France, as expected given their high thermal affinity, hence their strongly positive 496 contribution to latitudinal patterns of thermal affinity. Finally, interpreting the southern part 497 of latitudinal patterns of taxonomic abundance must be done with great caution due to the 498 large gap in our sampling of the Bay of Biscay.

499

500 Latitudinal patterns of α-diversity

501 We found that taxa richness and Shannon index of macrophyte communities in beach wrack 502 were highest between latitudes 47°N and 48°N, corresponding roughly to the stratified waters 503 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 504 505 and brown algae in northern France. This regional peak of macrophyte diversity is difficult to 506 compare with the latitudinal patterns of marine and algae species richness at global 507 (Chaudhary et al., 2016; Kerswell, 2006) and European scales (Santelices & Marquet, 1998) 508 due to their coarse spatial resolution. Nevertheless, this pattern has been reported from 509 underwater samplings along the Brittany coastline and is supported by the mosaic of benthic 510 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-511

512 Courtel et al., 2013; Gallon et al., 2014). Green algae diversity did not vary with latitude, as 513 this group comprises only five taxa, none of which was identified to species level, but also 514 because their abundance is mainly driven by processes at local scale, such as eutrophication 515 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 516 latitudinal patterns for brown and red algae in Brittany might be due to the high concentration 517 518 of sampling sites in this area, some of which might differ in their characteristics, but also to 519 this region's coastline that is less accurately described by the latitude (*i.e.*, latitude does not 520 increase monotonically from the south of Brittany to the north). Finally, similarly to the 521 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 522 important gap in our sampling below 46°N. 523

524

Beach wrack monitoring to produce indicators of benthic macrophyte communities 525 526 Our results, which are consistent with macroecological and physico-chemical patterns 527 described in the literature (Arriaga et al., 2023; Bates et al., 2017; Baumann & Doherty, 2013; Burrows et al., 2020; Derrien-Courtel et al., 2013; Gallon et al., 2014, 2017), 528 contribute to assessing whether the thermal affinity of macrophyte communities in beach 529 530 wrack could potentially be used as an *ex situ* indicator of the thermal affinity of benthic 531 macrophyte communities, even at a local scale. They also indicate that beach wrack could be 532 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 533 534 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 535 536 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

544 in all marine and coastal species that are likely to be affected by SST.

545 Establishing beach wrack macrophyte communities as an *ex situ* indicator of the thermal affinity of benthic macrophyte communities would enable the development of 546 547 vulnerability indicators of benthic habitats to climate change. Such indicators can be based on 548 thermal affinity metrics of macrophyte communities in beach wrack, such as the Community 549 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 550 551 projections of climate warming and thermal affinity metrics using a trait-based Climate 552 Change Vulnerability Assessment (CCVA) framework (Foden et al., 2019; Pacifici et al., 2015) (*e.g.*, Verniest et al. 2023). 553

554 While here we focused on spatial changes derived from thermal conditions, this 555 approach might also be extended to other drivers of change affecting benthic communities 556 such as biological invasions or chemical pollution. Considering the cost-effectiveness and 557 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. 558 559 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 560 561 environmental education and teaching partners a citizen science program named "ALAMER"

562 targeting school children (https://www.plages-vivantes.fr/alamer/edito/le-protocole-alamer). 563 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 564 565 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 566 567 ecosystem and its vulnerability to multiple anthropogenic pressures, such as beach wrack 568 collection and sea-level rise, thereby increasing the acceptance of beach wrack by users. 569 Finally, expanding this protocol to other audiences, such as conservation practitioners, could 570 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 571 572 initiative requires overcoming many challenges, such as defining the number and identity of 573 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; 574 575 Vázquez-Delfín et al., 2024).

576 ACKNOWLEDGEMENTS

- 577 We thank two anonymous reviewers for comments that significantly improved the quality of
- 578 the manuscript. We acknowledge M. Hourcade and M. Pronost for their contribution to beach
- 579 wrack monitoring. We are also grateful to S. Derrien-Courtel and J. Fournier-Sowinski for
- the interesting references they provided. Finally, we thank to J-F. Le Roux for providing
- support on the MARS3D data.
- 582

583 FUNDING SOURCES

584 This work was supported by grants from the Fondation de France and the Région Bretagne

585 (Elisa Alonso Aller grand number 18031) and corporate sponsorship from CITEO and Crédit

586 Agricole.

587

588 DECLARATION OF COMPETING INTEREST

- 589 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.

591

592 DATA STATEMENT

- 593 Data will be made available on request.
- 594

595 CREDIT AUTHOR STATEMENT

- 596 Fabien Verniest: Conceptualization, Methodology, Formal analysis, Writing Original
- 597 Draft, Writing Review & Editing, Visualization. Elisa Alonso Aller: Conceptualization,
- 598 Methodology, Formal analysis, Writing Original Draft, Writing Review & Editing,
- 599 Visualization. **Pauline Poisson**: Investigation, Data Curation, Writing Review & Editing.
- 600 Martin Thibault: Methodology, Writing Review & Editing. Isabelle Le Viol:

- 601 Conceptualization, Methodology, Investigation, Writing Original Draft, Writing Review &
- 602 Editing, Supervision, Project administration, Funding acquisition. Christian Kerbiriou:
- 603 Conceptualization, Methodology, Investigation, Writing Original Draft, Writing Review &
- 604 Editing, Supervision, Project administration, Funding acquisition.

builter

605 **REFERENCES**

- 606 Arriaga, O., Wawrzynkowski, P., Ibáñez, H., Muguerza, N., Díez, I., Pérez-Ruzafa, I.,
- 607 Gorostiaga, J. M., Quintano, E., & Becerro, M. A. (2023). Short-term response of
- 608 macroalgal communities to ocean warming in the Southern Bay of Biscay. *Marine*
- 609 Environmental Research, 190, 106098.
- 610 <u>https://doi.org/10.1016/j.marenvres.2023.106098</u>
- 611 Arriaga, O., Wawrzynkowski, P., Muguerza, N., Díez, I., Gorostiaga, J. M., Quintano, E., &
- 612 Becerro, M. A. (2024). The thermal journey of macroalgae: Four decades of
- 613 temperature-induced changes in the southeastern Bay of Biscay. *Marine*
- 614 Environmental Research, 195, 106351.
- 615 <u>https://doi.org/10.1016/j.marenvres.2024.106351</u>
- 616 Bates, A. E., Stuart-Smith, R. D., Barrett, N. S., & Edgar, G. J. (2017). Biological
- 617 interactions both facilitate and resist climate-related functional change in temperate
- 618 reef communities. *Proceedings of the Royal Society B: Biological Sciences*,
- 619 284(1856), 20170484. <u>https://doi.org/10.1098/rspb.2017.0484</u>
- 620 Baumann, H., & Doherty, O. (2013). Decadal Changes in the World's Coastal Latitudinal
- 621 Temperature Gradients. *PLoS ONE*, 8(6), e67596.
- 622 <u>https://doi.org/10.1371/journal.pone.0067596</u>
- 623 Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F.,
- 624 Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler,
- 625 D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L.
- 626 M., ... & Dornelas, M. (2019). The geography of biodiversity change in marine and
- 627 terrestrial assemblages. *Science*, *366*(6463), 339–345.
- 628 <u>https://doi.org/10.1126/science.aaw1620</u>

629	Bolker	ΒM	Brooks	ΜE	Clark	CI	Geange S	W Pou	lsen I R	Stevens	мнн
025	DUIKCI,	, D. 1	, DIOOKS.	, IVI. L.,	Ciain,	C. J.,	Ocunge, D.	, , I UU	13011, J. IX.		, 181. 11. 11.,

- 630 & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for
- ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135.
- 632 <u>https://doi.org/10.1016/j.tree.2008.10.008</u>
- 633 Borja, A. (2014). Grand challenges in marine ecosystems ecology. *Frontiers in Marine*

634 *Science*, *1*. <u>https://doi.org/10.3389/fmars.2014.00001</u>

Borja, A., Andersen, J. H., Arvanitidis, C. D., Basset, A., Buhl-Mortensen, L., Carvalho, S.,

636 Dafforn, K. A., Devlin, M. J., Escobar-Briones, E. G., Grenz, C., Harder, T.,

- 637 Katsanevakis, S., Liu, D., Metaxas, A., Morán, X. A. G., Newton, A., Piroddi, C.,
- 638 Pochon, X., Queirós, A. M., ... & Teixeira, H. (2020). Past and Future Grand
- 639 Challenges in Marine Ecosystem Ecology. *Frontiers in Marine Science*, 7, 362.

640 <u>https://doi.org/10.3389/fmars.2020.00362</u>

- 641 Brooks, M., E., Kristensen, K., Benthem, K., J., van, Magnusson, A., Berg, C., W., Nielsen,
- A., Skaug, H., J., Mächler, M., & Bolker, B., M. (2017). glmmTMB Balances Speed
- and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed

644 Modeling. *The R Journal*, 9(2), 378. <u>https://doi.org/10.32614/RJ-2017-066</u>

645 Burrows, M. T., Hawkins, S. J., Moore, J. J., Adams, L., Sugden, H., Firth, L., &

646 Mieszkowska, N. (2020). Global-scale species distributions predict temperature-

647 related changes in species composition of rocky shore communities in Britain. *Global*

648 *Change Biology*, 26(4), 2093–2105. <u>https://doi.org/10.1111/gcb.14968</u>

- 649 Chaudhary, C., Saeedi, H., & Costello, M. J. (2016). Bimodality of Latitudinal Gradients in
- 650 Marine Species Richness. *Trends in Ecology & Evolution*, *31*(9), 670–676.
- 651 <u>https://doi.org/10.1016/j.tree.2016.06.001</u>
- 652 Chust, G., Villarino, E., McLean, M., Mieszkowska, N., Benedetti-Cecchi, L., Bulleri, F.,
- 653 Ravaglioli, C., Borja, A., Muxika, I., Fernandes-Salvador, J. A., Ibaibarriaga, L.,

654	Uriarte, A., Revilla, M., Villate, F., Iriarte, A., Uriarte, I., Zervoudaki, S., Carstensen,
655	J., Somerfield, P. J., & Lindegren, M. (2024). Cross-basin and cross-taxa patterns
656	of marine community tropicalization and deborealization in warming European seas.
657	Nature Communications, 15(1), 2126. <u>https://doi.org/10.1038/s41467-024-46526-y</u>
658	Crowley, P. H. (1992). Resampling Methods for Computation-Intensive Data Analysis in
659	Ecology and Evolution. Annual Review of Ecology and Systematics, 23(1), 405–447.
660	https://doi.org/10.1146/annurev.es.23.110192.002201
661	De Azevedo, J., Franco, J. N., Vale, C. G., Lemos, M. F. L., & Arenas, F. (2023). Rapid
662	tropicalization evidence of subtidal seaweed assemblages along a coastal transitional
663	zone. Scientific Reports, 13(1), 11720. https://doi.org/10.1038/s41598-023-38514-x
664	Derrien-Courtel, S., Le Gal, A., & Grall, J. (2013). Regional-scale analysis of subtidal rocky
665	shore community. Helgoland Marine Research, 67(4), 697–712.
666	https://doi.org/10.1007/s10152-013-0355-2
667	Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. (2008). Birds are tracking climate
668	warming, but not fast enough. Proceedings of the Royal Society B: Biological
669	Sciences, 275(1652), 2743-2748. https://doi.org/10.1098/rspb.2008.0878
670	Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007).
671	Incorporating plant functional diversity effects in ecosystem service assessments.
672	Proceedings of the National Academy of Sciences, 104(52), 20684–20689.
673	https://doi.org/10.1073/pnas.0704716104
674	Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A.,
675	Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J.,
676	Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate Change Impacts on
677	Marine Ecosystems. Annual Review of Marine Science, 4(1), 11–37.
678	https://doi.org/10.1146/annurev-marine-041911-111611

- Dugan, J. E., & Hubbard, D. M. (2010). Loss of Coastal Strand Habitat in Southern
- 680 California: The Role of Beach Grooming. *Estuaries and Coasts*, 33(1), 67–77.

681 <u>https://doi.org/10.1007/s12237-009-9239-8</u>

- Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A.,
- 683 Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G.,
- 684 Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., &
- 685 Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley*

686 *Interdisciplinary Reviews: Climate Change*, 10(1), e551.

- 687 <u>https://doi.org/10.1002/wcc.551</u>
- 688 Gallon, R. K., Lavesque, N., Grall, J., Labrune, C., Gremare, A., Bachelet, G., Blanchet, H.,
- 689 Bonifácio, P., Bouchet, V. M. P., Dauvin, J.-C., Desroy, N., Gentil, F., Guerin, L.,
- Houbin, C., Jourde, J., Laurand, S., Le Duff, M., Le Garrec, V., De Montaudouin, X.,
- 691 ... & Gauthier, O. (2017). Regional and latitudinal patterns of soft-bottom
- 692 macrobenthic invertebrates along French coasts: Results from the RESOMAR
- database. *Journal of Sea Research*, *130*, 96–106.
- 694 <u>https://doi.org/10.1016/j.seares.2017.03.011</u>
- Gallon, R. K., Robuchon, M., Leroy, B., Le Gall, L., Valero, M., & Feunteun, E. (2014).
- Twenty years of observed and predicted changes in subtidal red seaweed assemblages
- along a biogeographical transition zone: Inferring potential causes from
- 698 environmental data. *Journal of Biogeography*, 41(12), 2293–2306.
- 699 https://doi.org/10.1111/jbi.12380
- Gascuel, D., & Pauly, D. (2009). EcoTroph: Modelling marine ecosystem functioning and
- 701 impact of fishing. *Ecological Modelling*, 220(21), 2885–2898.
- 702 https://doi.org/10.1016/j.ecolmodel.2009.07.031

- 703 Gaudin, F., Desroy, N., Dubois, S. F., Broudin, C., Cabioch, L., Fournier, J., Gentil, F., Grall,
- J., Houbin, C., Le Mao, P., & Thiébaut, É. (2018). Marine sublittoral benthos fails to
- track temperature in response to climate change in a biogeographical transition zone.
- 706 *ICES Journal of Marine Science*, 75(6), 1894–1907.
- 707 <u>https://doi.org/10.1093/icesjms/fsy095</u>
- 708 GBIF (2025). GBIF.org (28 February 2025) GBIF Occurrence Downloads :
- 709 <u>https://doi.org/10.15468/dl.24cny9</u>; <u>https://doi.org/10.15468/dl.qcht6v</u>;
- 710 <u>https://doi.org/10.15468/dl.76nj4d</u>; <u>https://doi.org/10.15468/dl.zf76kv</u>.
- Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J.
- 712 S., Rockwood, R. C., Selig, E. R., Selkoe, K. A., & Walbridge, S. (2015). Spatial and
- temporal changes in cumulative human impacts on the world's ocean. *Nature*
- 714 *Communications*, 6(1), 7615. <u>https://doi.org/10.1038/ncomms8615</u>
- 715 Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C.,
- 716 Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan,
- 717 H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., &
- 718 Watson, R. (2008). A Global Map of Human Impact on Marine Ecosystems. *Science*,
- 719 *319*(5865), 948–952. <u>https://doi.org/10.1126/science.1149345</u>
- 720 Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
- 721 *Regression Models.* R package version 0.4.6, <u>https://CRAN.R-</u>
 722 project.org/package=DHARMa.
- Harwell, M. C., & Orth, R. J. (2002). Long-distance dispersal potential in a marine
- 724 macrophyte. *Ecology*, 83(12), 3319–3330. <u>https://doi.org/10.1890/0012-</u>
- 725 <u>9658(2002)083[3319:LDDPIA]2.0.CO;2</u>

- 726 Innocenti, R. A., Feagin, R. A., & Huff, T. P. (2018). The role of Sargassum macroalgal
- wrack in reducing coastal erosion. *Estuarine, Coastal and Shelf Science, 214, 82–88.*

728 <u>https://doi.org/10.1016/j.ecss.2018.09.021</u>

- Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S.,
- Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A.
- 731 (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science*

732 *Advances*, 8(45), eabm9982. <u>https://doi.org/10.1126/sciadv.abm9982</u>

- Johnston, E. L., Mayer-Pinto, M., & Crowe, T. P. (2015). REVIEW: Chemical contaminant
- effects on marine ecosystem functioning. *Journal of Applied Ecology*, 52(1), 140–
- 735 149. <u>https://doi.org/10.1111/1365-2664.12355</u>
- 736 Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J. A., Olsen, J. L., & Hoarau, G.
- 737 (2013). Climate change impact on seaweed meadow distribution in the North Atlantic
 738 rocky intertidal. *Ecology and Evolution*, *3*(5), 1356–1373.
- 739 <u>https://doi.org/10.1002/ece3.541</u>
- 740 Kaspersen, B. S., Christensen, T. B., Fredenslund, A. M., Møller, H. B., Butts, M. B., Jensen,
- 741 N. H., & Kjaer, T. (2016). Linking climate change mitigation and coastal
- 742 eutrophication management through biogas technology: Evidence from a new Danish
- bioenergy concept. *Science of The Total Environment*, *541*, 1124–1131.
- 744 <u>https://doi.org/10.1016/j.scitotenv.2015.10.015</u>
- Kerswell, A. P. (2006). Global biodiversity patterns of benthic marine algae. *Ecology*, 87(10),
- 746 2479–2488. <u>https://doi.org/10.1890/0012-9658(2006)87[2479:GBPOBM]2.0.CO;2</u>
- 747 Lastra, M., López, J., & Rodil, I. F. (2018). Warming intensify CO 2 flux and nutrient release
- from algal wrack subsidies on sandy beaches. *Global Change Biology*, 24(8), 3766–
- 749 3779. <u>https://doi.org/10.1111/gcb.14278</u>

- Lazure, P., & Dumas, F. (2008). An external–internal mode coupling for a 3D
- 751
 hydrodynamical model for applications at regional scale (MARS). Advances in Water

752 *Resources*, *31*(2), 233–250. <u>https://doi.org/10.1016/j.advwatres.2007.06.010</u>

- Lenth, R. (2023). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package
 version 1.8.8, https://CRAN.R-project.org/package=emmeans
- Liebowitz, D. M., Nielsen, K. J., Dugan, J. E., Morgan, S. G., Malone, D. P., Largier, J. L.,
- Hubbard, D. M., & Carr, M. H. (2016). Ecosystem connectivity and trophic subsidies
 of sandy beaches. *Ecosphere*, 7(10), e01503. <u>https://doi.org/10.1002/ecs2.1503</u>
- 758 Liu, S., Trevathan-Tackett, S. M., Ewers Lewis, C. J., Ollivier, Q. R., Jiang, Z., Huang, X., &
- 759 Macreadie, P. I. (2019). Beach-cast seagrass wrack contributes substantially to global
- 760 greenhouse gas emissions. *Journal of Environmental Management*, 231, 329–335.
- 761 <u>https://doi.org/10.1016/j.jenvman.2018.10.047</u>
- 762 Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021).
- 763 performance: An R Package for Assessment, Comparison and Testing of Statistical
- 764 Models. Journal of Open Source Software, 6(60), 3139.
- 765 <u>https://doi.org/10.21105/joss.03139</u>
- 766 Macreadie, P. I., Trevathan-Tackett, S. M., Baldock, J. A., & Kelleway, J. J. (2017).
- 767 Converting beach-cast seagrass wrack into biochar: A climate-friendly solution to a
- coastal problem. *Science of The Total Environment*, *574*, 90–94.
- 769 <u>https://doi.org/10.1016/j.scitotenv.2016.09.021</u>
- 770 McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R.
- 771 (2015). Marine defaunation: Animal loss in the global ocean. *Science*, *347*(6219),
- 772 1255641. <u>https://doi.org/10.1126/science.1255641</u>

- 773 Mccool, S. F., & Stankey, G. H. (2004). Indicators of Sustainability: Challenges and
- 774 Opportunities at the Interface of Science and Policy. *Environmental Management*,

775 *33*(3), 294–305. https://doi.org/10.1007/s00267-003-0084-4

- 776 McGeady, R., Runya, R. M., Dooley, J. S. G., Howe, J. A., Fox, C. J., Wheeler, A. J.,
- 577 Summers, G., Callaway, A., Beck, S., Brown, L. S., Dooly, G., & McGonigle, C.
- 778 (2023). A review of new and existing non-extractive techniques for monitoring
- marine protected areas. *Frontiers in Marine Science*, *10*, 1126301.
- 780 <u>https://doi.org/10.3389/fmars.2023.1126301</u>
- 781 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from
- generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2),

783 133–142. <u>https://doi.org/10.1111/j.2041-210x.2012.00261.x</u>

- Noble-James, T., Bullimore, R., McBreen, F., O'Connor, J., Highfield, J., McCabe, C.,
- 785 Archer-Rand, S., Downie, A.-L., Hawes, J., & Mitchell, P. (2023). Monitoring
- benthic habitats in English Marine Protected Areas: Lessons learned, challenges and
- future directions. *Marine Policy*, 157, 105852.
- 788 https://doi.org/10.1016/j.marpol.2023.105852
- 789 Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.,
- Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker,
- B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista,
- H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L.,
- 793 McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., &
- Weedon, J. (2022). *vegan: Community Ecology Package*. R package version 2.6-4,
- 795 https://CRAN.R-project.org/package=vegan
- 796 Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M.,
- 797 Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley,

798	B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P.,
799	Pearson, R. G., Williams, S. E., & Rondinini, C. (2015). Assessing species
800	vulnerability to climate change. Nature Climate Change, 5(3), 215–224.
801	https://doi.org/10.1038/nclimate2448
802	Palialexis, A., Kousteni, V., Boicenco, L., Enserink, L., Pagou, K., Zweifel, U. L., Somma,
803	F., Cheilari, A., & Connor, D. (2021). Monitoring biodiversity for the EU Marine
804	Strategy Framework Directive: Lessons learnt from evaluating the official reports.
805	Marine Policy, 128, 104473. https://doi.org/10.1016/j.marpol.2021.104473
806	Patrício, J., Little, S., Mazik, K., Papadopoulou, KN., Smith, C. J., Teixeira, H., Hoffmann,
807	H., Uyarra, M. C., Solaun, O., Zenetos, A., Kaboglu, G., Kryvenko, O., Churilova, T.,
808	Moncheva, S., Bučas, M., Borja, A., Hoepffner, N., & Elliott, M. (2016). European
809	Marine Biodiversity Monitoring Networks: Strengths, Weaknesses, Opportunities and
810	Threats. Frontiers in Marine Science, 3. https://doi.org/10.3389/fmars.2016.00161
811	Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized
812	additive models in ecology: An introduction with mgcv. PeerJ, 7, e6876.
813	https://doi.org/10.7717/peerj.6876
814	Princé, K., & Zuckerberg, B. (2015). Climate change in our backyards: The reshuffling of
815	North America's winter bird communities. Global Change Biology, 21(2), 572–585.
816	https://doi.org/10.1111/gcb.12740
817	QGIS Development Team (2020). QGIS Geographic Information System. Open Source
818	Geospatial Foundation Project. http://qgis.osgeo.org
819	R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation
820	for Statistical Computing, Vienna, Austria. <u>http://www.R-project.org</u>
821	Reimer, J., Hacker, S., Menge, B., & Ruggiero, P. (2018). Macrophyte wrack on sandy
822	beaches of the US Pacific Northwest is linked to proximity of source habitat, ocean

- upwelling, and beach morphology. *Marine Ecology Progress Series*, 594, 263–269.
- 824 <u>https://doi.org/10.3354/meps12565</u>
- 825 Santelices, B., & Marquet, P. (1998). Seaweeds, latitudinal diversity patterns, and Rapoport's
- 826 Rule. *Diversity and Distributions*, 4(2), 71–75. <u>https://doi.org/10.1046/j.1472-</u>
- 827 <u>4642.1998.00005.x</u>
- 828 Silk, M. J., Harrison, X. A., & Hodgson, D. J. (2020). Perils and pitfalls of mixed-effects
- regression models in biology. *PeerJ*, 8, e9522. <u>https://doi.org/10.7717/peerj.9522</u>
- 830 Soler, G. A., Edgar, G. J., Barrett, N. S., Stuart-Smith, R. D., Oh, E., Cooper, A., Ridgway,
- 831 K. R., & Ling, S. D. (2022). Warming signals in temperate reef communities
- following more than a decade of ecological stability. *Proceedings of the Royal Society*
- 833 *B: Biological Sciences*, 289(1989), 20221649. <u>https://doi.org/10.1098/rspb.2022.1649</u>
- 834 Streicher, M. D., Reiss, H., & Reiss, K. (2021). Impact of aquaculture and agriculture
- nutrient sources on macroalgae in a bioassay study. *Marine Pollution Bulletin*, 173,

836 113025. <u>https://doi.org/10.1016/j.marpolbul.2021.113025</u>

- 837 Suursaar, Ü., Torn, K., Martin, G., Herkül, K., & Kullas, T. (2014). Formation and species
- 838 composition of stormcast beach wrack in the Gulf of Riga, Baltic Sea. *Oceanologia*,

839 56(4), 673–695. https://doi.org/10.5697/oc.56-4.673

- 840 Teichberg, M., Fox, S. E., Olsen, Y. S., Valiela, I., Martinetto, P., Iribarne, O., Muto, E. Y.,
- 841 Petti, M. A. V., Corbisier, T. N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P.,
- Freitas, H., Zitelli, A., Cardinaletti, M., & Tagliapietra, D. (2010). Eutrophication and
- 843 macroalgal blooms in temperate and tropical coastal waters: Nutrient enrichment
- experiments with *Ulva* spp. *Global Change Biology*, *16*(9), 2624–2637.
- 845 <u>https://doi.org/10.1111/j.1365-2486.2009.02108.x</u>

- Thibault, M., Alonso Aller, E., Poisson, P., Kerbiriou, C., & Le Viol, I. (2022). Reading the
- 847 heterogeneity and spatial structuring of benthic habitats in macrophyte wracks.

848 *Ecological Indicators*, *142*, 109279. <u>https://doi.org/10.1016/j.ecolind.2022.109279</u>

- Turnhout, E., Hisschemöller, M., & Eijsackers, H. (2007). Ecological indicators: Between the
 two fires of science and policy. *Ecological Indicators*, 7(2), 215–228.
- 851 <u>https://doi.org/10.1016/j.ecolind.2005.12.003</u>
- 852 Vázquez-Delfín, E., Galindo-De Santiago, C., Paredes-Chi, A., Ríos-Vázquez, A.,
- 853 Benavides-Lahnstein, A., Khatun, K., & Brodie, J. (2024). Marine macrophyte
- 854 strandings in the Yucatán peninsula: Citizen science as a potential tool for long-term
- 855 monitoring. *Aquatic Botany*, *190*, 103728.
- 856 <u>https://doi.org/10.1016/j.aquabot.2023.103728</u>
- 857 Verniest, F., Le Viol, I., Julliard, R., Dami, L., Guelmami, A., Suet, M., Abdou, W., Azafzaf,
- 858 H., Bendjedda, N., Bino, T., Borg, J. J., Božič, L., Dakki, M., El Hamoumi, R.,
- 859 Encarnação, V., Erciyas-Yavuz, K., Etayeb, K., Georgiev, V., Hamada, A., ... &
- 860 Galewski, T. (2023). Anticipating the effects of climate warming and natural habitat
- 861 conversion on waterbird communities to address protection gaps. *Biological*
- 862 *Conservation*, 279, 109939. <u>https://doi.org/10.1016/j.biocon.2023.109939</u>
- 863 Webb, T. J. (2018). *EMODnet Biology thermal traits*.
- 864 <u>https://github.com/EMODnet/EMODnet-Biology-thermal-traits</u>
- 865 Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood
- 866 estimation of semiparametric generalized linear models. *Journal of the Royal*
- 867 *Statistical Society* (*B*), 73(1).

1	FIGURE CAPTIONS
2	
3	Figure 1: Map of the 172 sampling sites. The colour gradient corresponds to the sea surface
4	temperature averaged over the twelve months preceding sampling in April 2019, derived
5	from MARS3D model simulations of the "Modelling and Analysis for Coastal Research"
6	(MARC) project (Lazure & Dumas, 2008). Country boundaries were extracted from the
7	Natural Earth database (naturalearthdata.com).
8	
9	Figure 2: Contribution (red: positive; blue: negative) of a taxon to the latitudinal pattern (left)
10	and thermal pattern (right) of the Community Temperature Index (CTI).
11	
12	Figure 3: Latitudinal patterns (upper panel) and thermal patterns (lower panel) of Community
13	Temperature Index based on taxa abundance (CTIa) with all taxa (left panel) and by algae
14	type (right panel). For thermal patterns, we considered the sea-surface temperature averaged
15	over the twelve months preceding sampling (SST1year). Shaded areas represent 95%
16	confidence intervals. Predicted patterns were computed with year held constant at 2019 and
17	the site with the median coefficient value. Observed values are depicted by small rings and
18	were corrected by the estimate of the year effect. The difference between observed and
19	predicted values thus represents marginal residuals. Black vertical bars at the bottom
20	represent sampling sites. The latitudinal range of the Brittany region is depicted in light grey.
21	Latitudinal and thermal patterns of the Community Temperature Index based on taxa
22	occurrence (CTI ₀) are provided in Figure A.1.
23	
24	Figure 4: Latitudinal patterns of abundance for taxa that strongly contributed to the

25 Community Temperature Index (CTI) latitudinal pattern (*i.e.*, absolute contribution \geq 5%).

26 Shaded areas represent 95% confidence intervals. Non-significant patterns are depicted by 27 dashed lines. Predicted patterns were computed with year held constant at 2019 and the site 28 with the median coefficient value for each model. For taxa identified at species level, tiles 29 represent 0.5 degree latitude zones in France, with coloured ones corresponding to zones with occurrence of the species in the Global Biodiversity Information Facility database (GBIF, 30 31 2025), and grey ones without occurrence of the species. Black vertical bars at the bottom 32 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 33 34 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 35 removing sampling sites with latitude $< 46^{\circ}$ N are provided in Figure A.3. 36

37

Figure 5: Latitudinal patterns of taxonomic richness: a) with all taxa; b) by algae type. 38 Shaded areas represent 95% confidence intervals. Non-significant patterns are depicted by 39 dashed lines. Predicted patterns were computed with year held constant at 2019 and the site 40 with the median coefficient value. Observed values are depicted by small rings and were 41 42 corrected by the estimate of the year effect. The difference between observed and predicted 43 values thus represents marginal residuals. Black vertical bars at the bottom represent 44 sampling sites. The latitudinal range of the Brittany region is depicted in light grey. 45 Latitudinal patterns of the Shannon index are provided in Figure A.4. Latitudinal patterns of taxonomic richness when removing sampling sites with latitude $< 46^{\circ}N$ are provided in 46 Figure A.5. 47

48











HIGHLIGHTS

- Thermal affinity of beach wrack macrophytes increases with sea-surface temperature
- Thermal affinity of macrophyte communities in beach wrack decreases with latitude
- The latitudinal pattern is identified from a national scale to a local scale
- Patterns are consistent with earlier research on benthic macrophytes
- We suggest further exploring beach wrack's ability to inform on benthic macrophytes

Journal Prevention

Declaration of interests

☑ 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.

□ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Presson