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1 Multi-scale drivers of community diversity and composition across tidal

2 heights: an example on temperate seaweed communities

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18 Running title: Multi-scale community variation in Brittany kelp forests

19 Summary

Despite recent advances in understanding community assembly processes,
 appreciating how these processes vary across multiple spatial scales and
 environmental gradients remains a crucial issue in ecology.

2. This study aimed to disentangle the drivers of diversity and composition of 23 seaweed communities through a gradient of spatial scales based on a hierarchical 24 sampling design consisting of 19 sites distributed in four sectors along the Brittany 25 coastline. Using randomised community matrices and Moran's eigenvector maps 26 (MEMs), we compared i) the relative importance of deterministic and stochastic 27 processes, ii) the environmental correlates of community composition and iii) the 28 scale of variation in community composition for seaweed communities located at two 29 30 different tidal heights.

3. Processes shaping community patterns are expected to vary along a gradient of 31 tidal heights. Therefore, we specifically examined the following hypotheses: the 32 contribution of deterministic over stochastic processes as well as the relative 33 importance of environmental filtering over biotic interactions should be enhanced for 34 seaweed communities of the infralittoral fringe compared to subtidal ones, whereas 35 dispersal of propagules in the water column should be more restricted resulting in 36 finer-scale variation in community composition for seaweed communities of the 37 infralittoral fringe compared to subtidal communities. 38

4. Seaweed communities were largely shaped by deterministic processes, although
the relative importance of deterministic processes was greater for communities of the
infralittoral fringe than for subtidal communities. Sea surface temperature and
geophysical variables were correlates of community composition at the two tidal

heights; additionally, waves and current were correlated with the composition of the
communities of the infralittoral fringe while kelp density was correlated with the
composition of subtidal communities. Variation in community composition was
observed at a finer scale for infralittoral fringe than for subtidal communities.

Synthesis. Our results suggest that the relative importance of deterministic and stochastic processes in structuring seaweed communities varies across tidal heights. Furthermore, the MEMs framework highlights that the nature of environmental correlates and the spatial scale at which they were good correlates of community composition also vary across tidal heights and may therefore be useful to broaden our understanding of community assembly across vertical gradients.

53 Key-words

54 Brittany, community composition, determinants of plant community diversity and 55 structure, deterministic and stochastic processes, environmental filtering, kelp, 56 Moran's eigenvector map, multiple spatial scales, seaweed communities, tidal height

57 Introduction

Understanding how species assemble into communities is a key and highly debated 58 issue in ecology. The structure of communities has been traditionally explained as 59 the result of deterministic processes where species persistence in its environment is 60 determined by abiotic conditions and biotic interactions (Hutchinson 1957; Grime 61 1973; Tilman 1982). In 2001, Hubbell proposed an alternative view: the unified theory 62 of biodiversity and biogeography which considers the structure of communities as the 63 fruit of stochastic processes only (Hubbell 2001). Over the last fifteen years, 64 important efforts have been made to disentangle the relative contribution of 65 deterministic and stochastic processes in shaping community structure, including the 66 proposition of a theoretical framework (Leibold et al. 2004; Logue et al. 2011). It is 67 now widely recognised that both deterministic (i.e. environmental filtering and biotic 68 interactions) and stochastic processes (i.e. ecological drift and limited dispersal) 69 70 influence community structure (Leibold & McPeek 2006), however, there is no consensus regarding the relative importance of these two kinds of processes which 71 seem to differ both among different environmental conditions (Chase 2007; Chase & 72 Myers 2011) and across spatial scales (Cottenie 2005; Chase & Myers 2011; Logue 73 et al. 2011). 74

The consideration of multiple spatial scales to better understand patterns of 75 76 biodiversity and processes driving them has therefore become a cornerstone of modern ecology. Indeed, communities are organised at multiple scales and form a 77 network of communities that are connected by dispersal of multiple potentially 78 79 interacting species called metacommunities (see Leibold et al. 2004 for review). Connectivity among communities occur at various rates, depending on both species 80 dispersal abilities and landscape features. and affect the structure 81 of

metacommunities in interaction with ecological drift, environmental filtering and biotic 82 83 interactions. Yet, our knowledge regarding how biodiversity is structured across spatial scales varies greatly among ecosystems: most empirical support comes from 84 research on terrestrial ecosystems, in which dispersal distances are much easier to 85 estimate than in marine ecosystems. In the absence of robust dispersal estimates 86 and considering the fluid characteristics of the ocean, it has long been considered 87 that dispersal rates were greater in the marine realm compared to terrestrial 88 environments (Cowen 2000). However, the recent methodological advances in the 89 study of dispersal pathways and connectivity among marine populations have greatly 90 91 improved estimates of marine dispersal and challenge the simplicity of this longstanding paradigm. As such, in their review of propagule dispersal in marine and 92 terrestrial environments, Kinlan and Gaines (2003) have shown that marine 93 organisms displayed a huge variety in their mean dispersal distance ranging from a 94 few meters to nearly 1000 kilometres. 95

In cold to temperate waters, rocky subtidal assemblages are dominated by 96 kelps, brown seaweeds which form underwater forests and are of major ecological 97 importance since they provide habitat, food and protection to a myriad of other 98 marine organisms (Dayton 1985; Steneck et al. 2002). These kelp forests are one of 99 the most diverse and productive ecosystems worldwide (Mann 1973). Biodiversity 100 patterns of kelp-dominated communities have been described mostly at local scales 101 in different places of the world (e.g. Hawkins & Harkin 1985; Leliaert et al. 2000; 102 103 Christie et al. 2003; Graham 2004; Pehlke & Bartsch 2008; Leclerc et al. 2015), more rarely at regional scales (Wernberg, Kendrick & Phillips 2003; Derrien-Courtel, Le Gal 104 & Grall 2013; Robuchon et al. 2015) but to date, only Smale, Kendrick and Wernberg 105 106 (2011) looked at these patterns across multiple spatial scales. In their study of the

subtidal flora of the south-western Australia coastline, they showed that diversity and 107 turnover of communities varied considerably at all spatial scales, although small 108 scale variability contributed most to total variation. This important small scale 109 variability, a common pattern in rocky shores communities (Fraschetti, Terlizzi & 110 Benedetti-Cecchi 2005), was mainly attributed to the action of waves and habitat 111 heterogeneity while regional scale variability was attributed to climatic factors as most 112 species had cool-water affinities (Smale, Kendrick & Wernberg 2011). Despite 113 providing great insights in the understanding of multi-scale variability of kelp-114 dominated communities, the study of Smale, Kendrick and Wernberg (2011) did not 115 116 explicitly address the question of what are the underlying processes that explained the biodiversity patterns they documented. Addressing the relative contribution of 117 deterministic and stochastic processes driving biodiversity patterns of kelp-dominated 118 119 communities across multiple spatial scales remains an open issue.

120 In recent years, methods to analyse spatial ecological data across different scales have been improved, notably with the emergence of a set of methods now 121 called MEMs (Moran's eigenvector maps, Dray, Legendre & Peres-Neto 2006). 122 These methods can model structures at scales ranging from the broadest down to 123 the finest on the basis of a weighted matrix representing the degree of connection 124 between sampling sites, where the weighted matrix can take several forms from the 125 simplest (a binary matrix: sites are connected or not) to the most geographically 126 realistic (a matrix of geographic distances among sites). A principal coordinates 127 analysis (PCoA) is then performed on the truncated weighted matrix and the resulting 128 eigenvectors that model spatial correlation are used as spatial explanatory variables 129 in canonical ordination (Borcard, Gillet & Legendre 2011). Therefore, the MEMs 130 131 framework is a way to evaluate the importance of measured explanatory variables in

driving community patterns through a gradient of spatial scales as well as to identify significant residual spatial patterns that could arise from the omission of important unmeasured explanatory variables or processes (Dray *et al.* 2012).

In this study, our objective was to disentangle drivers of community diversity 135 and composition across multiple spatial scales for kelp-dominated seaweed 136 137 communities along ca 500 km of the Brittany coastline (France). This region harbours a hot spot of seaweed diversity (Kerswell 2006; Keith, Kerswell & Connolly 2014) 138 and, forms along the European Atlantic coastline a transition zone between two 139 biogeographic provinces, the warm temperate Lusitanian province in the south and 140 the cold temperate Northern European Seas province in the north (Spalding et al. 141 2007). We addressed this question in seaweed communities located at two different 142 tidal heights: i) Laminaria digitata understory communities, spanning the lower 143 intertidal (i.e. the infralittoral fringe) and upper subtidal zones and ii) Laminaria 144 hyperborea communities, found in the subtidal zone (i.e. the infralittoral zone). Note 145 that, even if *L. digitata* understory communities are located both in the infralittoral 146 fringe and the upper subtidal zone, they will be referred hereafter as infralittoral fringe 147 communities to facilitate the reading. Based upon these contrasted tidal heights, we 148 can formulate three hypotheses regarding the differences expected between 149 infralittoral fringe communities and subtidal ones in terms of relative importance of 150 deterministic processes, environmental drivers of community composition and 151 propagule dispersal distances (Fig. 1). First, some recent works have suggested that 152 153 the relative importance of deterministic processes in structuring communities was greater in disturbed compared to undisturbed environment (Chase 2007; Chase & 154 Myers 2011). The intertidal environment experiences frequent changes between 155 156 immersion and emersion and is exposed to waves; hence it is more disturbed than

the subtidal one which is always emerged (Raffaelli & Hawkins 1996). We can 157 therefore hypothesise that the relative importance of deterministic processes in 158 structuring communities is greater in infralittoral fringe communities than in subtidal 159 ones. Second, the relative importance of environmental filters over biotic interactions 160 in structuring littoral communities is known to increase with tidal height (Raffaelli & 161 Hawkins 1996). Therefore, the relative importance of abiotic over biotic variables in 162 driving community composition is expected to be greater (resp. lesser) in infralittoral 163 fringe communities compared to subtidal ones. Finally, third, infralittoral fringe 164 communities are located higher on the vertical gradient of tidal heights than subtidal 165 166 communities. Consequently, dispersal distances should be lower in these communities because they are less often immersed (which limits the dispersal of 167 propagules in the water column) but most importantly they experience osmotic and 168 169 thermic stresses during periods of emersion (which stimulate the simultaneous release of propagules at low tides and thus short-distance dispersal, Norton 1992). 170 171 Such differences in terms of propagule dispersal between the infralittoral fringe and the subtidal zone have recently been evidenced by comparing genetic connectivity of 172 L. digitata and L. hyperborea populations (Robuchon et al. 2014). Therefore, 173 variation in community composition should be observed at a finer spatial scale in 174 infralittoral fringe communities compared to subtidal ones. 175

Towards our objective, we conducted an extensive and quantitative survey of seaweed communities using a nested sampling design, characterised the variation of diversity indices and their deviations from null models at the different levels of our sampling hierarchy and investigated how environmental variables fitted community composition at multiple spatial scales using the MEMs framework.

181 Materials and methods

182 Study area and data sources

To determine the drivers of seaweeds' community structure across spatial scales, we 183 compiled data on floristic composition and environmental variables across 19 sites 184 distributed in four sectors of Brittany (France, Fig. 2). These sectors were chosen 185 because they display distinct features which characterised the environmental 186 heterogeneity of the Brittany coastline: St Malo Bay shows a more irregular 187 topography and is characterised by the presence of cyclonic and anticyclonic gyres 188 that increase the water mass residence times and may affect propagule dispersal 189 (Salomon & Breton 1993), water bodies of Southern Brittany are stratified (Le Fèvre 190 1987) and between these two regions, Iroise Sea and Morlaix Bay form a cold and 191 192 resilient water pocket (Gallon et al. 2014). Floristic composition was assessed during a survey of seaweed diversity conducted in winter 2011 by scuba-diving and 193 targeting the flora living beneath the canopy of Laminaria digitata and L. hyperborea, 194 which differ by their distributions along the tidal zone: L. digitata occupies the 195 infralittoral fringe, between + 1 and – 1 m depth whereas L. hyperborea occupies the 196 infralittoral zone between -1 and - 30 m (reviewed by Robuchon et al. 2014). This 197 difference in vertical distribution implies that L. digitata populations and associated 198 understory communities are sometimes emerged (83 hours over the year 2011 based 199 on the SHOM data - http://www.shom.fr/ - for the city of Roscoff, in Morlaix Bay) 200 whereas L. hyperborea populations and associated understory communities are 201 always underwater. At each site, six guadrats of 0.10 m² were randomly placed 202 203 among the kelps holdfasts at a few meters of distance (three among L. digitata and three among L. hyperborea) and sampled for all macroscopic specimens of 204 seaweeds (except crustose seaweeds) present in these quadrats. Then, specimens 205

were sorted by morphotype and identified using the floristic keys and field guides
available for the region (Dixon & Irvine 1977; Irvine 1983; Fletcher 1987; Burrows
1991; Maggs & Hommersand 1993; Irvine, Chamberlain & Maggs 1994; Brodie &
Irvine 2003; Cabioc'h *et al.* 2006). The number of individuals per morphotype within
each quadrat was counted, allowing generating one quadrat-by-species and one siteby-species abundance matrices.

We also built a site-by-environment matrix resulting from the compilation of 32 environmental variables (Table 1) related to the density of *Laminaria* individuals (measured during the floristic survey), geophysical and bioclimatic characteristics (extracted from MARSPEC layers, Sbrocco & Barber 2013) and sea-states characteristics (calculated from the HOMERE database, Boudière *et al.* 2013).

217 Hierarchical analyses of diversity indices

Species richness (SR) and Shannon diversity index based on loge (H', Shannon 218 1948) were calculated for the infralittoral fringe communities and the subtidal 219 communities at three spatial scales: sector (4 levels), site (19 levels) and quadrat (57 220 levels). Variability in SR and H' was examined at the different spatial scales with 221 nested analysis of variance (ANOVA) conducted with the R package BiodiversityR 222 (Kindt & Coe 2005). The design was fully hierarchical; sectors were fixed while 223 nested factors were treated as random. As neither SR nor H' fit the assumptions of 224 normality and homogeneity of variance, a dissimilarity matrix based on Bray-Curtis 225 coefficients (Bray & Curtis 1957) derived from untransformed SR and H' (using a 226 dummy variable equal to 1) was generated for the analyses, which used 999 227 permutations. 228

To examine if observed SR and H' at the three spatial scales of sampling hierarchy differed from results expected under a null-model, we performed an additive diversity partitioning following Crist *et al.* (2003) where mean values of α diversity at lower levels of a sampling hierarchy are compared to the total diversity in the entire data set, i.e. γ diversity. The expected diversity components were calculated 999 times by individual based randomisation of the community data matrix using the R package vegan (Oksanen *et al.* 2015).

236 Multivariate spatial analyses

To analyse spatial structures of seaweed communities across multiple spatial scales, 237 we used the approach proposed by Dray et al. (2012). It consists of examining how 238 the spatial pattern of beta diversity changes when considering the initial site-by-239 species abundance matrix (i.e. the community matrix), its approximation by 240 environmental variables (i.e. the fitted matrix) and its residual counterpart (i.e. the 241 residual matrix) on the one hand (McIntire & Fajardo 2009) and to estimate and test 242 at which spatial scale these beta diversity changes occur using Moran's eigenvector 243 maps (MEMs, Dray, Legendre & Peres-Neto 2006) on the other hand. 244

We carried out this approach independently for infralittoral fringe communities 245 and for subtidal communities. To that purpose, we considered two initial site-by-246 species abundance matrices, one for infralittoral fringe communities and one for 247 subtidal communities as well as the two corresponding site-by-environment matrices 248 249 containing explanatory environmental variables (i.e. the environmental matrices). The environmental matrices were generated by testing correlations among all variables 250 listed in Table 1 and removing variables driving absolute values of pair-wise 251 252 correlations superior to 0.75 using the R package caret (Kuhn & Contributions from Jed Wing 2015). The community matrices were transformed using the Hellinger transformation to put emphasis on abundant species as recommended by Rao (1995). Then, we performed a principal component analysis (PCA) to identify the main patterns in community data.

Redundancy analysis (RDA) was conducted to reveal the main structures in 257 community data explained by environmental variables (i.e. analysis of the two fitted 258 matrices) using a forward selection procedure to retain informative environmental 259 variables only, whereas partial residual analysis (PRA) was performed to identify the 260 structures in community data not explained by environmental variables (i.e. analysis 261 of the two residual matrices). To generate the spatial explanatory variables, we 262 conducted a classical distance-based MEMs approach (formally called Principal 263 Coordinates of Neighbour Matrices) following guidelines in Borcard, Gillet and 264 Legendre (2011): i) we computed a matrix of geographic distances among sites using 265 266 the shortest path by the sea, ii) we truncated the matrix using a distance threshold equal to the maximum distance between two consecutive sites across the coastline, 267 iii) we performed a principal coordinates analysis (PCoA) on the truncated distance 268 matrix and iv) we retained 18 eigenvectors that model spatial correlation as spatial 269 explanatory variables. Scalograms were computed for the community, the fitted and 270 the residual matrices by projecting the sites scores on the first two axes of the 271 different analyses (PCA, RDA, and PRA, respectively) onto the spatial basis formed 272 by the 18 MEMs, therefore representing a partitioning of the respective variances 273 274 across multiple spatial scales ranked from the broadest to the finest. They are represented in a smoothed version (as in Munoz 2009) with six spatial components 275 formed by groups of three successive MEMs, which is a way to avoid undesired 276 277 sampling artefacts at fine scales (aliasing effects, Platt & Denman 1975). The individual R² values that form the scalograms and correspond to the amount of variation explained by a given scale are expected to be uniformly distributed in the absence of spatial structure (Ollier, Couteron & Chessel 2006). To uncover significant spatial structure, we therefore tested if the maximum observed R² was significantly larger than values obtained in the absence of spatial structure using a permutation procedure with 999 repetitions.

All analyses were carried out in R (R Core Team 2015) and based on the script provided in Dray *et al.* (2012) and adapted to our data.

286 **Results**

In total, 5292 specimens corresponding to 69 species were identified from the 57 287 quadrat samples of the infralittoral fringe communities and 5179 specimens 288 corresponding to 68 species were identified from the 57 quadrat samples of the 289 subtidal communities. For both infralittoral fringe and subtidal communities, red 290 seaweeds constituted the most abundant and the most diverse seaweed lineage 291 (respectively 94% and 92% of total abundance/78% and 76% of total species 292 richness), followed by brown seaweeds (respectively 3.9% and 7.2% of total 293 abundance/ 14% and 18% of total species richness) and green seaweeds 294 (respectively 0.2% and 0.1% of total abundance/ 5.8% and 4.4% of total species 295 richness). 296

297 At the scale of sector and for both infralittoral fringe and subtidal communities, species richness (SR) was minimum in St Malo Bay and maximum in Iroise Sea 298 (equally maximum in Morlaix Bay for infralittoral fringe communities, Fig. 3a). 299 Shannon diversity (H') was also minimum in St Malo Bay for both infralittoral fringe 300 and subtidal communities; however, it reached its maximum in Southern Brittany for 301 302 infralittoral fringe communities and in Morlaix Bay for subtidal communities (Fig. 3b). At the scale of site and for both communities, SR encountered its minimum in site 4 303 (a site in St Malo Bay) and its maximum in site 19 (a site in Southern Brittany), and 304 could be markedly variable among sites within the same sector as reported in Morlaix 305 Bay and Iroise Sea (Fig. 3c). Finally, H' was minimum in sites of St Malo Bay and 306 very variable both among sites and between kelp communities (Fig. 3d). For both 307 308 infralittoral fringe and subtidal communities, nested ANOVA indicated that both SR and H' were considerably and significantly variable at all spatial scales (Table 2). In 309 all cases, the examination of variance components suggested that the relative 310

importance of fine scale variability (i.e. site and residuals) outweighed that of broadscale variability (i.e. sector), although the relative importance of broad-scale
variability was higher for SR than for H'.

Results of additive diversity partitioning indicated that in almost all cases, observed SR and H' were significantly different from expectations under a null-model for α and β diversities and at the three levels of sampling hierarchy (quadrat, site and sector) (Table 3). Specifically, α diversity was always lower than expected. The only exception was found for β diversity in subtidal communities for which among-sites differences in terms of SR did not differ from null expectations.

Regarding the computation of the environmental matrices, 10 out of 32 320 environmental variables were retained for the infralittoral fringe as well as for the 321 322 subtidal zone of which 8 are common to the two matrices (Table 1). After a forward selection procedure to retain environmental variables which best explained the 323 variations of the community matrices, 4 out of the 10 previously retained 324 environmental variables were selected for explaining the infralittoral fringe community 325 matrix (i.e. bathymetry, maximum monthly sea surface temperature, maximum 326 monthly wave energy flux and mean annual sea water velocity) and 4 out of the 8 327 previously retained environmental variables were selected for explaining the subtidal 328 community matrix (i.e. density of *L. hyperborea*, distance to shore, bathymetric slope, 329 annual range in sea surface temperature). 330

The environmental variables explained a significant proportion of the variation of both the infralittoral fringe community matrix ($R^2 = 0.457$, P = 0.001) and the subtidal community matrix ($R^2 = 0.461$, P = 0.001). The fitted matrix of the infralittoral fringe exhibited two prominent axes representing a total of 83.9 % of the total variance, correlating mainly with maximum monthly sea surface temperature (r = -0.79 for the first axis and -0.58 on the second axis) and bathymetry (r = -0.29 for the first axis and -0.52 on the second axis). Representing a total of 78.0% of the total variance, the first two axes of the subtidal fitted matrix correlated mainly with density of *Laminaria hyperborea* (r = -0.60 for the first axis and -0.78 on the second axis) and annual range in sea surface temperature (r = -0.83 for the first axis and 0.29 on the second axis).

Figures 4 to 6 show ordination of sites and the associated scalograms of the 342 main ordination axes for the community matrices (Fig. 4), the fitted matrices (Fig. 5) 343 and the residual matrices (Fig. 6). The scalograms for the first two axes exhibited 344 distinct shapes for the infralittoral fringe community matrix and the subtidal 345 community matrix, with variance accumulation in both broad - (axes 1 and 2) and 346 fine-scale (axis 1 only) components for the infralittoral fringe community matrix (Fig. 347 4a) and accumulation in broad-scale components only for the subtidal community 348 matrix (Fig. 4b). Indeed, the first axis of the infralittoral fringe community matrix 349 exhibited a fine-scale non-random spatial pattern ($R^2_{Max} = 0.53$, P = 0.008) and an 350 important but nonsignificant broad-scale component ($R^2_{Max} = 0.38$, P = 0.073) while 351 its second axis showed a broad-scale non-random spatial pattern ($R^2_{Max} = 0.47$, P = 352 0.007). In contrast, the main axis of the subtidal community matrix exhibited 353 significantly skewed distributions towards the broad-scale components solely (axis 1: 354 R^{2}_{Max} = 0.79, P = 0.001; axis 2: R^{2}_{Max} = 0.44, P = 0.023). These results regarding 355 community matrices signify that community variability is important at both broad and 356 fine scales for infralittoral fringe communities and at broad-scale only for subtidal 357 communities. 358

Regarding the fitted matrices (Fig. 5), scalograms of the first two axes 359 displayed a broad-scale non-random spatial pattern for both the subtidal fitted matrix 360 (axis 1: $R^2_{Max} = 0.47$, P = 0.011; axis 2: $R^2_{Max} = 0.68$, P = 0.004) and the infralittoral 361 fringe fitted matrix (axis 1: $R^2_{Max} = 0.76$, P = 0.001; axis 2: $R^2_{Max} = 0.37$, P = 0.048). In 362 addition, the first axis of the infralittoral fringe fitted matrix showed a fine-scale non-363 random spatial pattern ($R^2_{Max} = 0.47$, P = 0.013) while the second axis of the subtidal 364 fitted matrix exhibited an important but nonsignificant medium-scale component 365 $(R^{2}_{Max} = 0.32, P = 0.109)$. These results regarding fitted matrices are similar to those 366 observed for the community matrices and indicate that environmental variables well 367 explain community variability at broad spatial scales for both infralittoral fringe and 368 subtidal communities, and, additionally, at fine scale for infralittoral fringe 369 communities. 370

Finally, the scalograms for the first two axes of the residual matrices exhibited 371 distinct patterns for the infralittoral fringe fitted matrix (Fig. 6a), showing variation 372 accumulated mainly and significantly in broad-scale components (axis 1: R^2_{Max} = 373 0.37, P = 0.046; axis 2: R^2_{Max} = 0.52, P = 0.005), and the subtidal fitted matrix (Fig. 374 6b), displaying variation accumulated in medium-scale components (and only 375 significantly for axis 1: $R^2_{Max} = 0.41$, P = 0.043). Regarding infralittoral fringe 376 communities, this indicates that a significant broad-scale spatial pattern remained in 377 the data after the effects attributable to the measured environmental variables 378 (mainly a combination of maximum temperature and bathymetry) were partialled out. 379 Regarding subtidal communities, this reveals that a significant medium-scale spatial 380 pattern remained in the data after the broad-scale effects related to the measured 381 environmental variables (mainly temperature range and kelp density) were removed. 382

383 **Discussion**

In marine ecology, the variation of community patterns along the vertical gradient of 384 tidal heights is a longstanding issue (Raffaelli & Hawkins 1996) while its examination 385 along a gradient of multiple spatial scales is more recent and still scarce in major 386 coastal ecosystems such as kelp forests (but see Smale, Kendrick & Wernberg 387 2011). In this study of kelp-dominated seaweed communities, we sought to 388 understand how the relative roles of stochastic (i.e. ecological drift and limited 389 dispersal) and deterministic (i.e. environmental filtering and biotic interactions) 390 processes in structuring communities vary both along the vertical gradient of tidal 391 heights and across multiple spatial scales. Specifically, we highlight the crucial role of 392 deterministic processes in shaping these communities, we identify environmental 393 correlates of community composition and we show that the scale of variation in 394 community composition differs across tidal heights. 395

396 Relative importance of deterministic processes in structuring communities

Our results show that variability in α and β species diversity differed from 397 expectations under a null model at all spatial scales for infralittoral fringe 398 communities, indicating that they are largely shaped by deterministic processes at all 399 scales from the finest (the quadrats, separated by a few meters) to the broadest (the 400 sectors, separated by more than 60 km). The same pattern was observed for subtidal 401 communities, except for the variability in ß species richness which did not differ from 402 403 null expectations at the intermediate scale of sites (separated by more than 300 m), suggesting that variability in species richness between sites can be explained by the 404 405 action of stochastic processes only. Therefore, the relative importance of deterministic processes in structuring communities appears to be slightly greater in 406

infralittoral fringe communities than in subtidal ones. Such differences might be 407 408 related to the fact that infralittoral fringe communities inhabit a more disturbed environment than subtidal communities: the prevalence of deterministic processes in 409 disturbed environments has been advocated to explain variation in community 410 patterns along a gradient of disturbance in a variety of other organisms (i.e. small 411 freshwater ponds: Chase, 2007 and plants: Myers & Harms, 2011). Nevertheless, it 412 does not imply that deterministic processes do not structure subtidal communities. In 413 particular, α diversity was lower than expected for the three spatial scales and the 414 two diversity metrics examined. These results suggest that distribution of kelp 415 416 understory seaweeds is far from random and may be the result of species-specific factors such as biogeographic history and dispersal ability as well as deterministic 417 processes of environmental filtering and/or biotic interactions. 418

419 Environmental correlates of community composition

The relative importance of abiotic over biotic variables in driving community 420 composition established from the list of variables retained in our analysis was slightly 421 greater in infralittoral fringe communities compared to subtidal ones: four abiotic 422 423 variables correlated with composition of infralittoral fringe communities whereas a combination of one biotic and three abiotic variables correlated with composition of 424 subtidal communities. Community composition was correlated with variables related 425 426 to sea surface temperature for both infralittoral fringe and subtidal communities. This finding is consistent with previous studies on kelp forests showing that distribution of 427 understory red seaweeds was mainly driven by annual amplitude in sea surface 428 429 temperature (Gallon et al. 2014) and that large scale community variation was related to the differences in species temperature affinities (Smale, Kendrick & Wernberg 430 2011; Derrien-Courtel, Le Gal & Grall 2013). In agreement with recent reports 431

documenting the sensitivity of kelp species (e.g. Pehlke & Bartsch 2008; Oppliger *et al.* 2014) and associated communities (e.g. Gallon *et al.* 2014; Wernberg *et al.* 2016)
to rising temperatures, our study therefore suggests that kelp forests would be largely
affected by climate change.

Geophysical variables were also correlated with community composition and 436 more specifically bathymetry for infralittoral communities and slope for subtidal ones. 437 These results are not surprising since bathymetry and slope might capture the action 438 of other factors (not included in our study) important for the settlement and growth of 439 sessile organisms. For example, light availability decreases with bathymetry and 440 sediment burying decreases with slope and these two factors have been previously 441 described as influencing the composition of rocky subtidal communities (e.g. Miller & 442 Etter 2008). 443

Moreover, some variables were correlates of composition for infralittoral fringe 444 communities but not for subtidal ones, and vice versa. As such, current and wave 445 energy explained variation in composition for infralittoral fringe communities but not 446 for subtidal ones, a finding which is logical since infralittoral fringe communities are 447 448 located closer to the sea surface and are therefore more prone to be affected by the action of currents and waves than subtidal communities. A strong hydrodynamism 449 can affect kelp-dominated communities either directly through dislodgement of 450 individual kelps (Wernberg et al. 2008) or indirectly by modulating herbivores' 451 452 abundances (Vanderklift et al. 2009). Furthermore, kelp density explained variation in composition for subtidal communities but not for infralittoral fringe communities. 453 454 This outcome might reflect an interaction between L. hyperborea canopy and its understory community. Such canopy-understory interaction can be either competitive 455 or facilitative. Specifically, canopy formers may competitively exclude understory 456

457 species by shading their environment and scouring recruits or juveniles or facilitate 458 the recruitment and existence of other species by mitigating physical stress such as 459 hydrodynamic forces (e.g. Kain 1979; Wernberg, Kendrick & Toohey 2005; Bennett & 460 Wernberg 2014). As we recorded lower species diversity in sites characterised by a 461 high kelp density, the canopy-understory interactions we detected in subtidal 462 communities are likely dominated by competition.

Our results revealed that the measured environmental variables were good 463 correlates of community composition at both broad and fine scale for infralittoral 464 fringe communities, and at broad scale only for subtidal communities; however, 465 significant spatial patterns remained in the data after the effects attributable to the 466 measured environmental variables were partialled out. These remaining significant 467 spatial patterns could be attributed either to unmeasured environmental variables 468 (see the paragraph 'Study limitations and future directions') and/or to stochastic 469 processes such as ecological drift and limited dispersal. 470

471 Multi-scale variation in community composition

We found that variation in community composition was concentrated at both fine and 472 broad spatial scales in infralittoral fringe communities, and only at broad spatial 473 scales in subtidal ones. Expected lower dispersal distances in infralittoral fringe than 474 in subtidal communities may contribute to this difference, promoting finer scale 475 variation in community composition in the infralittoral fringe. In accordance to this 476 hypothesis, some studies have shown that genetic connectivity among populations 477 decreased with tidal height for different organisms of rocky shores (e.g. Engel, 478 Destombe & Valero 2004; Kelly & Palumbi 2010; Valero et al. 2011), including the 479 two kelps L. digitata and L. hyperborea (Robuchon et al. 2014). Alternatively, our 480

results also indicate that environmental variables were good correlates of community
composition at fine scale for infralittoral fringe communities. Thus, fine-scale
variability in the composition of infralittoral fringe communities may also be the result
of environmental filters acting at a fine scale.

485 Study limitations and future directions

Our study permitted the identification of environmental correlates of community 486 composition for infralittoral fringe and subtidal communities. Although this work could 487 be refined regarding the identification of variables driving community patterns, our 488 approach allowed us to test the correlation between observed community patterns 489 and a set of environmental variables possibly affecting these patterns. Additional 490 experimental approaches are needed to assess causal relationships among the 491 492 environmental correlates we identified and community composition. Furthermore, some potentially important variables were not included in our framework: despite 493 being important drivers of seaweed community structure, sea turbidity, nutrient 494 availability and herbivores' abundances were not included because data were not 495 available at a spatial resolution fine enough for our study. Nonetheless, other studies 496 497 on these omitted variables at a coarser spatial resolution indicate strong differences among regions that might contribute to regional differences in community structure; 498 for instance, sea turbidity is higher in St Malo Bay than in the other three regions 499 500 (Gohin 2011). This limitation was partially overcome because the geophysical and hydrodynamic variables that we included in our study may influence these omitted 501 variables. Nonetheless, future work investigating environmental drivers of kelp-502 503 dominated seaweed communities should include all pertinent variables at the appropriate scale, maybe by doing direct in situ measurements when remote sensing 504 data are not available. 505

Although our outcomes are coherent with individual processes known to vary 506 across a gradient of tidal heights, our study did not permit to identify how these local 507 processes act together to form the patterns we observed, neither to fully understand 508 the interplay between these local processes and biogeographic history of species. A 509 study including all tidal heights from the high intertidal to the subtidal and covering 510 entire biogeographic regions would be very helpful to further characterise how 511 ecological drift, environmental filtering, competition, facilitation and dispersal interact 512 with the biogeographic history of species to shape community patterns along the 513 whole gradient of tidal heights. Yet, even on a set of two neighbour tidal heights, the 514 515 MEMs framework permitted us to highlight that the nature of environmental correlates and the spatial scale at which they were good correlates of community composition 516 vary across tidal heights. Therefore, this framework seems promising to broaden our 517 518 understanding of community assembly across other vertical gradients, both in the sea and on land. 519

520 Author's Contributions

521 MR, MV and LL conceived the ideas and designed methodology; MR and LL 522 collected the data; MR analysed the data; ET critically interpreted the first results and 523 contributed to reorient the analyses; MR led the writing of the manuscript. All authors 524 contributed critically to the drafts and gave final approval for publication.

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537 Data accessibility

538 Data deposited in the Dryad repository: doi:10.5061/dryad.3s96n

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743 **Tables**

Table 1. Characteristics of the environmental variables used in this study

Name	Description	Туре	Source
(abbreviation)	(units)	(resolution)	
Density of Laminaria digitata	Density of <i>L. digitata</i> individuals	In-situ measure	This study
(Ld.density) ‡	(semi-quantitative measure ranging from 1		
	(low density) to 4 (high density))		
Density of Laminaria hyperborea	Density of L. hyperborea individuals	In-situ measure	This study
(Lh.density) ¶	(semi-quantitative measure ranging from 1		
	(low density) to 4 (high density))		
Bathymetry	Depth of the seafloor	Remotely sensed measure	MARSPEC*
(bathy)	(meters)	(30 arc-second)	
East/West aspect	Horizontal orientation of the seafloor on the	Derived from remotely sensed	MARSPEC*
(ew.aspect) ‡¶	East/West gradient	bathymetry	
	(radians)	(30 arc-second)	

North/South aspect	Horizontal orientation of the seafloor on the	Derived from remotely sensed	MARSPEC*
(ns.aspect) ‡ ¶	North/South gradient	bathymetry	
	(radians)	(30 arc-second)	
Plan curvature	Terrain curvature in the direction	Derived from remotely sensed	MARSPEC*
(pl.curv) ‡ ¶	perpendicular to the maximum slope	bathymetry	
	(none)	(30 arc-second)	
Profile curvature	Terrain curvature in the direction parallel to	Derived from remotely sensed	MARSPEC*
(pr.curv)	the maximum slope	bathymetry	
	(none)	(30 arc-second)	
Distance to shore	Distance to shore	Derived from remotely sensed	MARSPEC*
(shore.dist) ‡¶	(kilometres)	shoreline	
		(30 arc-second)	
Bathymetric slope	Slope of the seafloor	Derived from remotely sensed	MARSPEC*
(slope) ‡¶	(degrees)	bathymetry	
		(30 arc-second)	
Concavity	Slope of the bathymetric slope	Derived from remotely sensed	MARSPEC*

(concav)	(degrees)	bathymetry	
		(30 arc-second)	
Mean annual SSS	Mean sea surface salinity averaged over the	Derived from in-situ measures	MARSPEC*
(sss.mean)	period 1955-2006	(30 arc-second)	
	(psu)		
Minimum monthly SSS	Salinity of the least salty month averaged	Derived from in-situ measures	MARSPEC*
(sss.min)	over the period 1955-2006	(30 arc-second)	
	(psu)		
Maximum monthly SSS	Salinity of the saltiest month averaged over	Derived from in-situ measures	MARSPEC*
(sss.max)	the period 1955-2006	(30 arc-second)	
	(psu)		
Annual range in SSS	Annual range in sea surface salinity averaged	Derived from in-situ measures	MARSPEC*
(sss.range)	over the period 1955-2006	(30 arc-second)	
	(psu)		
Annual variance in SSS	Annual variance in sea surface salinity	Derived from in-situ measures	MARSPEC*
(sss.var)	averaged over the period 1955-2006	(30 arc-second)	

	(psu)		
Mean annual SST	Mean sea surface temperature averaged over	Derived from remotely sensed	MARSPEC*
(sst.mean) ‡ ¶	the period 1955-2006	measures	
	(°C)	(30 arc-second)	
Minimum monthly SST	Temperature of the coldest month averaged	Derived from remotely sensed	MARSPEC*
(sst.min)	over the period 1955-2006	measures	
	(°C)	(30 arc-second)	
Maximum monthly SST	Temperature of the warmest month averaged	Derived from remotely sensed	MARSPEC*
(sst.max)	over the period 1955-2006	measures	
	(°C)	(30 arc-second)	
Annual range in SST	Annual range in sea surface temperature	Derived from remotely sensed	MARSPEC*
(sst.range) ‡ ¶	averaged over the period 1955-2006	measures	
	(°C)	(30 arc-second)	
Annual variance in SST	Annual variance in sea surface temperature	Derived from remotely sensed	MARSPEC*
(sst.var)	averaged over the period 1955-2006	measures	
	(°C)	(30 arc-second)	

Mean annual CGE	Mean wave energy flux averaged over the	Derived from model outputs in	This study
(cge.mean) ‡	period 1994-2012	HOMERE database †	
	(kW. m ⁻¹)	(value from the nearest node)	
Minimum monthly CGE	Wave energy flux of the energy-calmest	Derived from model outputs in	This study
(cge.min)	month averaged over the period 1994-2012	HOMERE database †	
	(kW. m ⁻¹)	(value from the nearest node)	
Maximum monthly CGE	Wave energy flux of the energy-most agitated	Derived from model outputs in	This study
(cge.max) ¶	month averaged over the period 1994-2012	HOMERE database †	
	(kW. m ⁻¹)	(value from the nearest node)	
Annual range in CGE	Annual range in wave energy flux averaged	Derived from model outputs in	This study
(cge.range)	over the period 1994-2012	HOMERE database †	
	(kW. m ⁻¹)	(value from the nearest node)	
Mean annual number of CGE	Mean number of measures in wave energy	Derived from model outputs in	This study
extreme measures	flux exceeding 14 kW. m ⁻¹ averaged over the	HOMERE database †	
(cge.next.mean)	period 1994-2012	(value from the nearest node)	
	(none)		

Number of CGE extreme	Number of measures in wave energy flux	Derived from model outputs in	This study
measures within the 3 months	exceeding 14 kW. m ⁻¹ within the 3 months	HOMERE database †	
preceding the floristic survey	preceding the floristic survey	(value from the nearest node)	
(cge.next.3months)	(none)		
Mean annual CUR	Mean sea water velocity averaged over the	Derived from model outputs in	This study
(cur.mean)	period 1994-2012	HOMERE database †	
	(m. s ⁻¹)	(value from the nearest node)	
Minimum monthly CUR	Sea water velocity of the current-calmest	Derived from model outputs in	This study
(cur.min) ‡ ¶	month averaged over the period 1994-2012	HOMERE database †	
	(m. s ⁻¹)	(value from the nearest node)	
Maximum monthly CUR	Sea water velocity of the current-most	Derived from model outputs in	This study
(cur.max)	agitated month averaged over the period	HOMERE database †	
	1994-2012	(value from the nearest node)	
	(m. s ⁻¹)		
Annual range in CUR	Annual range in sea water velocity averaged	Derived from model outputs in	This study
(cur.range)	over the period 1994-2012	HOMERE database †	

	(m. s ⁻¹)	(value from the nearest node)	
Mean annual number of extreme	Mean number of measures in sea water	Derived from model outputs in	This study
CUR measures	velocity exceeding 0.15 m. s ⁻¹ averaged over	HOMERE database †	
(cur.next.mean)	the period 1994-2012	(value from the nearest node)	
	(none)		
Number of CUR extreme	Number of measures in sea water velocity	Derived from model outputs in	This study
measures within the 3 months	exceeding 0.15 m. s ⁻¹ within the 3 months	HOMERE database †	
preceding the floristic survey	preceding the floristic survey	(value from the nearest node)	
(cur.next.3months)	(none)		

* Sbrocco and Barber (2013); † Boudière *et al.* (2013); ‡ variable retained in E_Ld; ¶ variable retained in E_Lh

746	Table 2. Results of nested ANOVA for factor "site" nested in factor "sector" based on
747	Bray-Curtis dissimilarity coefficients derived from untransformed species richness
748	(SR) and Shannon diversity (H') using a dummy variable equal to 1; all tests used

749 999 permutations

	Df	SS	F	Р	Var. comp (%)	
a. SR, Infralittoral	a. SR, Infralittoral fringe communities					
Sector	3	0.942	9.64	0.001	44.9	
Sector:Site	15	0.489	1.85	0.040	23.3	
Residuals	38	0.669	0.02		31.9	
b. H', Infralittoral f	fringe co	ommunities				
Sector	3	0.198	5.82	0.004	36.5	
Sector:Site	15	0.170	2.45	0.009	31.3	
Residuals	38	0.175	< 0.01		32.2	
c. SR, Subtidal co	ommunit	ies				
Sector	3	0.778	6.37	0.006	40.9	
Sector:Site	15	0.611	3.02	0.005	32.1	
Residuals	38	0.512	0.01		26.9	
d. H', Subtidal co	mmuniti	es				
Sector	3	0.196	6.16	0.006	36.4	
Sector:Site	15	0.159	2.20	0.030	29.6	
Residuals	38	0.183	< 0.01		34.0	

750 Df = degrees of freedom, SS = sum of squares, F = F-ratio, P = p-value estimating

the significance of F-ratios; Var.comp = estimated relative contribution to total

752 variance

Table 3. Results of additive diversity partitioning from untransformed species richness (SR) and Shannon diversity (H') comparing simulated statistics under a nullmodel to observed statistics of α and β diversity at three levels of sampling hierarchy ("quadrat", "site" and "sector") as well as γ diversity of the entire dataset; all tests used 999 simulations

	Observed statistic	SES	Mean simulated statistic	Р	
a. SR, Infralitt	a. SR, Infralittoral fringe communities				
α. quadrat	9.05	- 72.30	25.02	0.001	
α. site	15.63	- 56.61	37.53	0.001	
a. sector	33.5	- 31.58	52.55	0.001	
Y	61.00	0.00	61.00	1.000	
β. quadrat	6.58	- 16.16	12.49	0.001	
β. site	17.87	4.36	15.07	0.015	
β. sector	27.50	31.58	8.50	0.001	
b. H', Infralitto	ral fringe communities				
α. quadrat	1.55	- 91.00	2.66	0.001	
α. site	1.88	- 89.98	2.90	0.001	
a. sector	2.43	- 155.69	3.02	0.001	
Y	3.03	0.00	3.03	1.000	
β. quadrat	0.33	7.89	0.24	0.001	
β. site	0.55	38.71	0.11	0.001	
β. sector	0.61	155.69	0.02	0.001	
c. SR, Subtida	al communities				
α. quadrat	9.81	- 63.83	22.36	0.001	

a. site	16.53	- 47.11	35.10	0.001
a. sector	35.50	- 27.12	53.10	0.001
γ	62.00	0.00	62.00	1.000
β. quadrat	6.72	- 16.67	13.42	0.001
β. site	18.97	1.34	19.32	0.171
β. sector	26.50	27.12	10.25	0.001
d. H', Subtidal	communities			
α. quadrat	1.64	- 76.16	2.57	0.001
a. site	1.98	- 74.74	2.79	0.001
a. sector	2.48	- 130.93	2.90	0.001
γ	2.92	0.00	2.92	1.000
β. quadrat	0.34	12.74	0.22	0.001
β. site	0.50	33.42	0.11	0.001
β. sector	0.44	130.93	0.02	0.001

759 SES = standardised effect sizes of the observed statistic quantifying the size of the

760 difference between expected and observed values, P = p-value of the statistic based

761 on simulations

762 Figures



Fig. 1. Diagram showing the different hypotheses of our study regarding the relative importance of deterministic processes, environmental filters, biotic interactions and dispersal distances in structuring seaweed communities at two tidal heights.



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Fig. 2. Map showing the 19 sampling sites distributed in the four sectors along the
Brittany coastline, France. Sites are: Guimereux (1), La Bigne (2), Nerput (3), Le
Moulin (4), Les Amas du Cap (5), Primel (6), Duons Est (7), Duons Ouest (8), Santec
2 (9), Santec 1 (10), Les Amiettes (11), Les Linious (12), Men Vriant (13), Klosenn
Malaga (14), Les Rospects (15), St Mathieu (16), Pointe du Grand Gouin (17), Houat
2 (18) and Houat 1 (19). For site coordinates, see Appendix S1.



Fig. 3. Comparison of species diversity estimates between infralittoral fringe communities and subtidal communities across space. (a) Species richness (SR) by sector, (b) Shannon diversity (H') by sector, (c) SR by site and (d) H' by site. For site names, see Fig. 2.



Fig. 4. Plots of site scores on the first two axes of the principal components analyses of site-by-species abundance matrices (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram (the 18 Moran's eigenvector maps [MEMs] are assembled in 6 groups) indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2 (in dark gray) is

- tested using 999 permutations of the observed values (P values are given). The 95%
- confidence limit is also represented by the line of plus signs.



Fig. 5. Plots of site scores on the first two axes of the redundancy analyses using the site-by-environment matrices as predictors (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram (the 18 Moran's eigenvector maps [MEMs] are assembled in 6 groups) indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2 (in dark gray) is

- tested using 999 permutations of the observed values (P values are given). The 95%
- confidence limit is also represented by the line of plus signs.

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Fig. 6. Plots of site scores on the first two axes of the partial principal component analysis using the site-by-environment matrices as co-variables (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram (the 18 Moran's eigenvector maps [MEMs] are assembled in 6 groups) indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2

- (in dark gray) is tested using 999 permutations of the observed values (P values are
- given). The 95% confidence limit is also represented by the line of plus signs.

807 Supporting information

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

809 Appendix S1. Taxonomic and geographic information on seaweed specimens

- 810 collected for the study
- 811 **Appendix S2.** Matrix of pairwise geographic distances among the sites of the study
- 812 Appendix S3. Site-by-environment matrix containing explanatory environmental
- 813 variables for infralittoral fringe communities
- 814 Appendix S4. Site-by-environment matrix containing explanatory environmental
- 815 variables for subtidal communities
- 816 **Appendix S5.** R script to reproduce the analyses using data of Appendices S1 to S4