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Patterns of spatial variability between contrasting substrata: a boulder-field study

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ABSTRACT

Boulder-fields are complex habitats in which many species coexist and are important contributors to coastal biodiversity. These habitats experience important natural disturbances due to wave action, over which anthropogenic stressors, such as hand-fishing and urban sprawl, can be added. Despite their particularity and vulnerability, there have been few attempts to disentangle the processes that actually structure boulder-field communities at different scales. In order to help direct future research in boulder-field systems, diversity, community structure as well as the patterns of variability were compared between boulder and bedrock habitats at a hierarchy of spatial scales (from 100s cm to 10s km) along approximately 100 km of shoreline in NW Brittany. Specifically, it was hypothesised (i) that difference in physical structure would produce greater variability on boulder than on the bedrock at small scales and (ii) that contrasting patterns of variability will emerge with increasing scales as the processes operating at large scale on the bedrock would be dampened on boulders undergoing physical disturbance. Overall, both hypotheses were rejected with regards to variability patterns in diversity, community structure and abundances of most functional groups, except for ephemerals in both shore heights and limpets in the low shore. Variability was generally concentrated at the smallest spatial scale, but bedrock showed greater patchiness than boulders for most of the response variables. With increasing spatial scales, the variability patterns were overall consistent between habitats. Among potential mechanisms, the interplay between grazing and physical disturbance over several spatial scales deserve further experimental scrutiny.

INTRODUCTION

Analyzing multi-scale patterns of variability in diversity, abundance and assemblage structure has been proven efficient to highlight the processes likely responsible for observable patterns in population and assemblage structures (Underwood & Chapman 1996, Benedetti-Cecchi 2001). On rocky shores and more specifically on bedrock substrates, such approaches inferred the significance of small-scale processes, such as biotic interactions (especially competition, facilitation and predation, incl. grazing) and substratum heterogeneity (e.g. Dayton 1971, McGuinness & Underwood 1986, Guichard & Bourget 1998, Blanchard & Bourget 1999, Coleman et al. 2006, Smale et al. 2010), generally resulting in larger variability at small scales (10s to 100s of centimeters). In contrast to small-scale patterns, the spatial variability at larger scales is generally lower, though processes acting across these scales can result in important differences in population and community structure (Broitman et al. 2001, Puente et al. 2017, Robuchon et al. 2017). These patterns can result from variation in coastal topography, wave exposure, upwelling, dispersal and recruitment, generally acting at the mesoscale, i.e. from a few to hundreds of kilometers, as well as climatic gradients, oceanography and geomorphology, which usually act at a broader scale, i.e. from hundreds to thousands of kilometers (see Fraschetti et al. 2005, Benedetti-Cecchi & Trussell 2014 for reviews). Since all these forces can overlap across spatial scales and interact among each other, identifying a characteristic scale of variation is a robust preliminary approach to determine which processes should be further investigated with thorough experiments. While consistent patterns of spatial variability emerged from general reviews on the topic or cross-system comparisons (e.g. Fraschetti et al. 2005, Dal Bello et al. 2017), there have been few attempts to compare these patterns between microhabitats shared by rocky shores across several spatial scales. Both the nature and the strength of the forces experienced by these habitats (e.g. bedrock more or less inclined, rock pools, and boulders) may however differ (e.g. Benedetti-Cecchi et al. 2000, Firth & Crowe 2010) and lead to contrasting patterns across spatial scales.

Boulder fields have long been proven to provide a useful framework to study ecological theories (e.g. Sousa 1979a, McGuinness 1984), and yet, rare have been the studies examining multi-scale patterns in these habitats (McKindsey & Bourget 2001, Chapman 2005). It has long been suggested that physical disturbance is one of the major forces influencing community structure in boulder fields (Osman 1977, Sousa 1979a, Littler & Littler 1984) (but see McGuinness 1987b). By overturning boulders at different rates (turnover), physical disturbance may create a mosaic of patches undergoing different stages of community development. Though the probability of overturning of individual boulders could be estimated by its size (McGuinness 1984, McGuinness 1987a), it does not necessarily reflect the intensity of disturbance actually operating on such heterogeneous habitats (Blanchard & Bourget 1999). In addition, the rate of boulder overturning may be locally increased by anthropogenic impacts such as seaweed and seafood harvesting (Le Hir & Hily 2005, Stagnol et al. 2013, Hily & Bernard 2014). While a huge boulder is unlikely to be overturned by wave action, a smaller boulder may experience an intermediate level of disturbance. When a boulder is overturned for a long period (several months), most of its sessile biota may be killed, and a new sequence of succession is to be started on the open space created upon its top surface (Sousa 1979b). Depending on its duration, the period of overturning will differently affect the ongoing succession sequence as some biota in place may either persist as reproductive or vegetative stages. By favouring the coexistence of a mosaic of successional stages and preventing dominance, an intermediate level of disturbance can thus be assumed to be associated with a greater species diversity (Osman 1977, Connell 1978, Sousa 1979b, 1980). Under heterogeneous disturbance, communities on boulder fields may therefore be naturally more variable at the patch scale than on more temporally-constant surrounding bedrock. Further processes interacting with physical disturbance (e.g. grazing) may however make such model more complicated and its outcomes may vary according to life form strategies and specific stress-resistance (Sousa 1980, Littler & Littler 1984).

The rare studies performed at a hierarchy of spatial scales in boulder fields suggested that less and less variability is explained by increasing spatial scale (e.g. McKindsey & Bourget 2001, Chapman 2005, Liversage & Kotta 2015). Though not jointly performed, similar studies conducted on the bedrock generally captured processes operating at larger scales, such as among shores (Benedetti-Cecchi 2001, Valdivia et al. 2011) or among regions (Dal Bello et al. 2017). If the disturbances acting upon boulders are sustained across several spatial scales, they may overwhelm processes coming into play with increasing spatial scales (e.g. wave exposure, recruitment) on the bedrock, and contrasting patterns of variability may thus be expected between habitats. Processes operating at larger spatial scales may however interact with these disturbances and the local influences (e.g. species pool) may change the outcomes of this model (Chapman & Underwood 1998), for example, boulder communities may tend to converge with bedrock in some place but not in others.

The present study aimed to compare boulder and bedrock substrata across different spatial scales and tidal heights in NW Brittany. In order to make both multivariate and univariate comparisons possible between habitats, bedrock was compared with the top of the boulders. Many fewer exclusive species occur in this stratum compared to habitats underneath boulders, therefore differences in multivariate variability would mainly result from differences in abundance of a common set of species rather than differences in identity. Beyond pattern descriptions, the following hypotheses were tested: first, it was expected that small-scale variability in richness, abundance of most taxa and community structure is lower on the bedrock than on boulders, which experience higher level of disturbance. Second, it was expected that contrasting patterns of variability between habitats will emerge from 10s m to 10s km as processes operating on the bedrock over increasing spatial scales are overwhelmed by the disturbance presumably undergone by boulders at small scale.

METHODS

Sampling design and data collection

The study was performed during November 2015 'Spring' tides along approximately 100 km of shoreline in NW-Brittany (Fig. 1, Appendix S1). In this mega-tidal region, the tidal range may reach 8.5-10 m (increasing along a W-E gradient). This portion of coastline is part of the same well-mixed water body and experiences relatively cold (mean about 12°C) and stable (yearly amplitude of 6-8°C) sea-surface temperatures throughout the year (Birrien et al. 1991, Gallon et al. 2014). The dominant rock formation is granite, though mixed with mica-schist at the westernmost part (locality A, Fig. 1), gneiss at northernmost (B) and gabbro (with pegmatite patches) at easternmost (D). The study region is generally exposed to WNW swell, varying on average from approximately 1.5 m in summer to 3.3 m in winter (with maxima up to 10.5 m), and showing a slight decrease along a W-E gradient (Appendix S). According to the coastline conformation and to the wave energy-gradients, coastal boulder-fields can be encountered either along headlands or embedded within rocky inlets (Le Duff & Hily 2001). All boulder-fields (sites) were selected according to the presence of both natural boulders densely clustered and stable bedrock along at least 300 m of shoreline, extending at least from the top fringe of the mid-shore (about. 6 m above chart datum) and the infra-littoral fringe (chart datum ± 1 m approximately). In addition, an operational criterion was adopted: the sampled boulders had to be large enough to be covered by a flexible 0.1 m^2-quadrat on their top part and light enough to be overturned manually by the present observer. These individual boulders were thus assumed to experience an intermediate level of disturbance due to wave action (Sousa 1979a) as well as potential disturbance from recreational fishing (Hily & Bernard 2014). Both habitats (boulders and bedrock) were sampled at two tide-levels (mid- and low-shore), adopting a hierarchical design comprising three random factors (locality, site and patch). Localities were haphazardly selected, 20-30 km apart within the region (Fig. 1). Within each locality, two study sites (the so-called boulder fields) were haphazardly selected 2-5 km apart. Finally, two patches (20-50 m wide) were placed 200-300 m apart within each site. While boulders tend to accumulate along the bedrock according to wave energy-gradients at the scale of a site, it was possible to find – generally on site edges – patches presenting a scattered arrangement of both habitats, hence avoiding confounding effects in habitat comparisons. Within a patch, the wave exposure experienced by these habitats was expected to be the same. Nonetheless, comparisons between patches or tidal heights may involve differences in wave exposure (see Appendix S1 for further details) owing to the site features (headland, island and inlets), and hence contrasting frequency and intensity of disturbance (McGuinness 1987a). Tidal heights were defined using a tide table: 2.0 ± 0.50 m above chart datum for the low-shore and 4.5 ± 0.50 m for the mid-shore. These heights were considered for both the upper side of boulder and the bedrock (i.e. sampled surface) to avoid confounding effect due to emersion period (McGuinness & Underwood 1986). Within each patch and at each tidal height, the stable bedrock (n = 16) and the top of the boulders (n = 16) were sampled using a flexible (plastic mesh) 0.1 m^2-quadrat.

Abundances were assessed for sessile organisms (seaweeds, sessile fauna) and mobile invertebrates (> 2 mm) using percentage covers and counts, respectively. Seaweed and sessile fauna percentage cover was assessed by summing over 25 sub-quadrats, within each an abundance score from 1 to 4 was given to each taxon (after Dethier et al. 1993). In order to take into account species layering, percentage cover was assessed for epiphytic, canopy and understorey species (after moving the canopy aside); therefore the total frequently exceeded 100%. All quadrats were photographed entirely and a series of close-ups (above and beneath canopy) were taken for double-checking in the laboratory. Given the important diversity and layering of low-shore assemblages, their diversity and assemblage structure were directly assessed on the field. As for mid-shore, their assemblages were visually assessed based on photographs later in the laboratory using the same method described above. Most specimens were visually (non-destructively) identified at the lowest taxonomic level possible (generally species). A few specimens were brought to the laboratory, preserved at – 20°C, before further identification under a dissecting microscope. Notably, it was operationally unmanageable to remove all limpets, from the genus *Patella* (a total of 10,866 ind.), from their substrate to allow identification based on foot and tentacle patterns; only the blue-rayed limpet *Patella* (formerly *Helcion*) *pellucida* L. could be identified based on superficial (shell) criteria. *P. vulgata* L., *P. depressa* Pennant and *P. ulyssiponensis* Gmelin were thus pooled into a single limpet group: *Patella* spp. Given the inefficiency in counting the cryptic periwinkle *Melarhaphe neritoides* L. from photographs (mid-shore bedrock), this species was not included in analyses.

Statistical analyses

General patterns in species diversity and distributions

Patterns in species richness, community structure (all taxa) and abundance of functional groups of algae (sheet-like, filamentous, coarsely branched, thick leathery canopy, jointed calcareous and crustose, Littler & Littler 1984), key faunal taxa (barnacles, limpets) and bare space – shared by both habitats and tidal levels – were examined with a five-way design (Fig. 1) using permutational multivariate (or univariate) analyses of variance (PERMANOVA, Anderson 2001), with 4999 permutations. Factors were ‘habitat’ (fixed, 2 levels: boulders and bedrock), ‘level’ (fixed, 2 levels: mid- and low-shore), ‘locality’ (random, 4 levels), ‘site’ (random, 2 levels nested within Locality) and ‘patch’ (random, 2 levels, nested within Site and Locality). Univariate analyses were based on Euclidian distance matrices whereas multivariate analyses were based on Bray-Curtis similarity matrices generated from either raw or transformed data. In order to down-weight the importance of most abundant species (and homogenize multivariate dispersion), multivariate data were square root-transformed. No transformation allowed homoscedasticity to be achieved in univariate data (PERMDISP analyses, unpresented). Given the balance of the design and the large number of samples (n = 16), univariate PERMANOVAs (analogous to ANOVAs) were considered robust enough to cope with this issue and were run on untransformed data (Underwood 1997). When appropriate, PERMANOVAs were followed by pairwise comparisons and *P*-values were estimated using Monte Carlo procedure. In order to examine the general patterns in habitat, vertical and horizontal distribution, a principal coordinate (PCO) analysis and a cluster analysis were jointly performed on centroid values computed from each combinations of Habitat × Level × Patch (Site (Locality)), i.e. from 16 replicates (Appendix S2). Subsequently, additional PCOs were performed on all samples and correlations of the variable to the axes were analysed in order to better explain these patterns. Since multivariate and most univariate PERMANOVAs showed a three-way interaction, separate graphics were presented for mid- and low-shore assemblages, respectively.

Patterns of spatial variability across horizontal scales, habitats and levels

Degrees of variability were independently estimated for all combinations of Habitat (boulder and bedrock) × Level (mid- and low-shore) × horizontal Scale (Patch, Site, Locality and Region). To this end, community structure, richness and abundances of functional groups of algae, barnacles, limpets and bare space in mid-shore boulders, mid-shore bedrock, low-shore boulders and low-shore bedrock were all examined separately using a fully nested three-way PERMANOVA, with Patch nested in Site and Site nested in Locality. For each response variable, these analyses were repeated on eight independent matrices, yielded from the random selection of two quadrats per patch. Untransformed data were used for all multivariate and univariate analyses, respectively calculating Bray-Curtis dissimilarities and Euclidean distances. Pseudo-variance components (or variance in the case univariate analyses) were extracted for each source of variation (within region: 10s km; within locality: 1000s m; within site: 10s m; and within patch: 100s cm) by setting equal the observed mean square to their expectations (Anderson et al. 2008). When occurring, any negative estimate was set to zero and the model was adjusted – by excluding the corresponding factor – to re-calculate the remaining estimates (Fletcher & Underwood 2002, Fraschetti et al. 2005). For each response variable, a total of 128 estimates of horizontal variability were thus obtained and examined using a balanced three-way analysis of variance (ANOVA). Factors (all fixed and orthogonal) were Habitat (boulder and bedrock), Level (mid- and low-shore) and Scale (Patch, Site, Locality and Region). Although pseudo-variance estimates were systematically log-transformed to reduce heterogeneity (Benedetti-Cecchi 2001), the homogeneity of variances could not be achieved (Levene's test). As such, a conservative level of significance ($\alpha = 0.01$) was applied (Underwood 1997, Fraschetti et al. 2005). Provided that components of variation of residuals – associated with large degree of freedom – are generally more accurately estimated than other terms in nested ANOVA, obtaining heterogeneous variances was not surprising. It should be noted that other procedures herein employed (one-way ANOVAs for each scale, variance or dissimilarity calculations for pairs of samples) led to similar results, and were thus unpresented. When appropriate, ANOVAs were followed by Student-Newman-Keuls (SNK) tests for multiple comparisons (with $\alpha = 0.05$). ANOVAs were performed using SigmaPlot, while PERMANOVAs, PCOs and PERMDISPs were performed using PRIMER 7 (Clarke & Warwick 2001).

RESULTS

During this study, a total of 114 taxa were identified (2 lichens, 49 seaweeds and 63 animals). Complete lists and species authorities are provided in Appendix S3. Cumulated richness was more than twice higher in the low-shore (104 taxa) than in the mid-shore (43 taxa). Average abundances (per sites) within the mid-shore and the low-shore are given for both habitats in Appendix S4 and S5, respectively. Across horizontal scales, the preliminary principal component analysis based on centroids suggested differences in assemblage structure among habitats and shore levels, with habitat discrimination seemingly level-dependent (Appendix S2).

Dissimilarities in diversity and assemblage structure between boulders and bedrock

Overall, boulders and bedrock were different, with some inconsistencies across scales and levels depending on the response variable considered (Appendix S6, Fig. 2). According to the PERMANOVAs and pairwise tests (Appendix S6), the more consistent result was regarding richness (interaction Habitat × Level), being about twice as high(average ± SD) on the bedrock than on boulders in the mid-shore (6.2 ± 2.3 vs 3.4 ± 1.4, respectively, Fig. 2A) and in the low-shore (13.2 ± 3.5 vs 7.2 ± 2.7, respectively, Fig. 2A'). Although contrasting between tidal levels, almost consistent results were observed for the abundance of *Patella* spp. (interaction Habitat × Level, Fig. 2B-B'), which was caused by abundances being similar between habitats in the mid-shore (overall 8.0 ± 6.7) but lower on the bedrock (6.9 ± 8.4) than on boulders (19.1 ± 12.5) in the low-shore. Contrasting and patch-dependent results were observed for the cover of barnacles: covers were lower on boulders than on the bedrock in 11 patches out of 16 in the mid-shore (Appendix S6, Fig. 2C) and greater on boulders than on the bedrock in 3 patches in the low-shore (Fig. 2C'). A three way-interaction (Habitat × Level × Patch (Site (Locality)), appendix S6) was observed for the bare space cover, but pairwise tests revealed relatively consistent results: bare space was lower on the bedrock than on boulders within 13 patches out of 16 in the mid-shore (on average 74.6 ± 24.4 vs 91.0 ± 14.3, Fig. 2D) and within 15 patches in the low-shore (9.8 ± 16.0 vs 54.4 ± 31.0, Fig. 2D'). In contrast, despite a three way-interaction (Habitat × Level × Site (Locality)), appendix S6), no significant differences could be observed regarding the cover of sheet-like seaweeds (here represented by ephemerals, such as *Ulva* and *Porphyra* spp., Appendix S4) between habitats in the mid- and low-shore at any site. This group seemed however to be more represented, though not very abundant and highly variable (up to 25.1 ± 24.2 % cover), on boulders than on the bedrock (Fig. 2E-E'). The percentage cover of filamentous algae tended to be greater on the rock than on boulders (Habitat × Level × Patch) in the low-shore (13 patches out of 16, Fig. 2F'), but less clearly in the mid-shore (4 patches, Fig. 2F). Similarly, coarsely branched algae displayed greater cover on the bedrock than on boulders (Habitat × Level × Patch) within 3 patches in the mid-shore (Fig. 2G) and within 14 patches in the low-shore (Fig. 2G'). Less abundant than other groups, jointed calcareous displayed greater cover on the bedrock than on boulders (Habitat × Level × Patch) in only 1 patch in the mid-shore and 8 in the low-shore (Fig. 2I-I'). No difference could be detected regarding the crustose group between habitats (Fig. 2J-J'). In contrast, canopy cover (i.e. thick-leathery seaweeds, Fig. 2H-H') was greater on the bedrock than on boulders (Habitat × Level × Patch) within 12 patches out of 16 in the mid-shore (12.0 ± 19.4% vs 2.2 ± 5.6%) and within 13 patches in the low-shore (36.7 ± 31.1% vs 3.8 ± 10.7%).

As for the community structure, differences between habitats appeared patch-dependent (three-way interaction, Appendix S6, Fig. 3), although pairwise tests indicated significant differences between habitats in all patches, either in the mid- and in the low-shore (Appendix S6). In the mid-shore, habitat appeared mainly discriminated by the first axis of PCO (30.9% of variation, Fig. 3A-B), highly correlated with the cover of bare space ($r = 0.8$), tending to be greater on boulders than on the bedrock. In the low-shore, samples appeared more scattered on the PCO and, in spite of some overlap, habitats were mostly discriminated by the first axis (41.0% of variation, Fig. 3C). Boulders tended to display greater cover of bare space and abundances of *Patella* spp. in comparison to the stable bedrock, characterized by greater canopy (especially *F. serratus*) cover and diverse associated species (Fig. 3D).

Horizontal patterns in diversity and assemblage structure within habitats

Important similarities in community structure were observed all along the studied area and no clear patterns in richness and abundances could be identified among localities (Fig. 2, Appendix S6). Some subtle differences could however be observed on the stable bedrock, but not on boulders. For instance, a three-way interaction Habitat × Level × Locality was revealed for community structure and discriminated the western locality “A” from the others on the stable bedrock at both shore heights, and the eastern locality “D” from the others in the mid-shore (Appendix S6). These differences are well illustrated on the PCOs, though explaining a limited amount of variation (Fig 3), as marked differences are also observed within sites (i.e. among patches, Appendix S6). In the mid-shore, the second axis (23.9%) tends to depict a balance between barnacles/limpets (eventually mussels) and fucoids, respectively more abundant in localities A/D and B/C (Fig. 4A-B, Appendix S4). Further variation (14.7 % on Axis 3, non-presented) discriminated patches partially covered by *Fucus vesiculosus* var. *linearis* to patches sheltering some *Ascophyllum nodosum* and accompanying species. Finally, dissimilarities among localities were also suggested from community structure of the stable bedrock in the low shore. The second PCO axis (9.8% of variation, Fig. 3C-D) tended to differentiate sites with *F. serratus* canopy to sites dominated by diverse red turf-forming seaweeds (e.g. *Osmundea pinnatifida*, *Chondracanthus acicularis*) and alternative canopy (e.g. *Himanthalia elongata*) (especially in locality A).

As for pooled morpho-functional groups, horizontal patterns were less evident from univariate analyses and the variability between patches was important within most of the sites, with contrasting patterns depending on the habitat as well as on the shore-height considered (Fig. 2, Appendix S6). Habitat × Level × Locality interactions were observed for the abundances of coarsely branched and crustose seaweeds as well as barnacles, but pairwise tests solely revealed logical groupings for the latter. Locality-to-locality differences in barnacle covers (fig. 2C-C') were limited to the bedrock in the low-shore (A > B = C = D), in the mid-shore (A = (B = C < D)) and to boulders in the mid-shore (A = B = C < D).

Patterns of spatial variability across horizontal scales, habitats and levels

Patterns of horizontal variability across scales appeared relatively consistent between habitats and shore levels – generally higher at the scale of patch – although depending on the response variable considered (Table 1-2, Fig. 4). While multivariate components of variability (community structure) displayed greater values on the bedrock than on boulders, it was consistently higher at the scale of the patch. Variability was equally distributed between site and locality, though it increased within the region. While these patterns seem to be driven by values observed on the bedrock (Fig. 4), no interaction (e.g. Scale × Habitat × Level) was significant at the level adopted ($\alpha < 0.01$, Table 1). Such interactions were significant for the abundance of *Patella* spp., the covers of bare space, barnacles and jointed calcareous algae (Table 1-2). Nonetheless, the only consistent logical grouping was greater variance values at the scale of patch at both shore levels, with the exception of bare surface in mid-shore bedrock. In only a few cases, within site-variability appeared higher than within locality, namely for jointed calcareous and crustose algae in the low-shore bedrock, and barnacles in the mid-shore. Patterns of increasing variability between the scales of locality and region – revealed with overall community structure – were also observed with the cover of barnacles in the mid- and the low-shore and with the cover of crustose algae in the low-shore.

Finally, greater values of horizontal variability were generally observed on the bedrock as compared to boulders (Fig. 4, Table 1-2), most likely due to difference in mean values (e.g. richness and abundance of most functional groups of seaweeds, Fig. 2). Greater variability on boulders as compared to bedrock were only revealed with the cover of sheet-like ephemeral algae within the scales of patch, site and locality, along with the cover of bare surface at the scale of locality in the mid-shore and limpet abundances in the low-shore (Fig. 4, Table 3).

DISCUSSION

Across the majority of sampling sites, boulders appeared to be devoid of most functional groups of seaweeds, found in abundance of the stable bedrock. In addition, the variability in abundance of most of these groups was lower on boulders than on the bedrock irrespective of the horizontal and vertical scales considered, except for jointed calcareous and sheet-like seaweeds. The latter group, dominated by ephemerals actually experienced larger variability in abundance on boulders than on the bedrock across three horizontal scales (from metres to kilometres). While these results could suggest that most replicate boulders were more disturbed than the surrounding bedrock, these differences did not translate to greater patchiness in algal abundances on boulders than on the bedrock. The opposite pattern was actually observed for all groups, except early successional species at both tidal heights and limpets in the low shore. First, this suggests that boulder patches do not necessarily represent a mosaic of successional stages, but could rather be dominated by individual boulders at an early stage of development. Second, this indicates that small-scale variability is pervasive within the studied communities, including on the comparatively ‘stable’ bedrock. While physical disturbance may contribute to the observed patterns, further processes (e.g. grazing pressure, habitat selection) are likely to operate at both tidal heights studied.

Small-scale patterns and variability

At both tidal heights, important variability occurred at the scale of the patch and was generally greater than any other spatial scale considered. This finding aligns with reviews on the topic (e.g. Fraschetti et al. 2005), regardless of the substrate type (boulder versus bedrock).

Contrary to expectations, patchiness was however generally greater on the bedrock than on boulders, except for ephemerals in both shore heights and limpets in the low shore. In parallel, boulders presented lower covers of barnacles, leathery fucoids and associated species – but higher densities of limpets in the low-shore – and were comparatively less biodiverse at the patch scale. This result may thus partially be explained by mean-variance relationship (Taylor 1961, Benedetti-Cecchi 2003), although further mechanisms could be invoked.

Small scale variability is a common feature of rocky shore communities from moderately to highly exposed conditions and can be influenced by various interplaying processes such as substratum heterogeneity, species behaviour and biotic interactions (Dayton 1971, Connell 1972, Raffaelli & Hawkins 1996, Underwood & Chapman 1996, Guichard & Bourget 1998, Raimondi et al. 2000, Fraschetti et al. 2005). NW European mid-shores are generally characterized by clumps of either *Ascophyllum*, *Fucus* or *Mytilus* (all observed in the present study), whose formation depends on hydrodynamic forces acting at the scale of hundreds of meters and biotic interactions at the patch scale. For instance, in moderately exposed conditions, *Fucus vesiculosus* may establish within dense clusters of barnacles, which provide substratum and refuge from grazing by limpets. Adult plants may reduce further settlement of barnacles through sweeping while favouring aggregations of limpets and barnacle-predators under the canopy, and in turn limit additional plants and barnacles to establish at the vicinity (Hawkins & Hartnoll 1983, Hartnoll & Hawkins 1985). Through habitat-formation (Jenkins et al. 1999, Moore et al. 2007), both richness and species interactions are promoted at the patch scale, hence increasing the small scale variability in richness and overall community structure on the bedrock. In the low shore, diverse assemblages of seaweeds and associated invertebrates were observed. The abundance of canopy species varied among shores and some differences in community structure were detected on the bedrock. Nonetheless, there was no dominance of a single canopy species (thick leathery cover varied from 4 to 76% cover per patch), nor exclusion of understorey seaweeds. The variability in the abundance of thick leathery groups was greater at the scale of the patch and this pattern was tracked by all seaweed functional groups, except sheet-like ephemerals. While dominant and monospecific canopy stands could eventually exclude most understorey species owing to shading, whiplash and scouring (Wernberg et al. 2005), such negative interactions may be dampened as environmental factors, such as the substratum heterogeneity (topography, sediments) and hydrodynamics, come into play (Connell 2003, Toohey & Kendrick 2008). A patchily distributed and/or multi-specific canopy would be more likely to create a mosaic of environmental conditions (light gaps, protection from physical stress) and to promote diverse assemblages within which multiple interactions (either direct or indirect; positive, neutral and negative) take place (Bertness et al. 1999, Irving & Connell 2006, Smale et al. 2011, Bulleri et al. 2012). Like in the mid-shore, the greater patchiness observed on the bedrock as compared to boulders could thus simply be explained by greater biological interactions as well as higher species diversity and abundances of almost all successional groups of seaweeds. In addition, the substratum complexity and the presence of dense boulders surrounding the bedrock may also affect the incident light and hydrodynamics (current velocity and turbulence) from centimetres to meters (Guichard & Bourget 1998, Guichard et al. 2001, McKindsey & Bourget

2001). Even more likely, given the close proximity of bedrock and boulders at the scale of patch, disturbance may also contribute to small-scale variability on the bedrock (Shanks & Wright 1986, Povey & Keough 1991). Bare space may be opened through boulders hitting bedrock, sand scouring and recreational fishing (seaweed and shellfish removal, stamping), hence providing settlement substrate and refuge from grazers to various seaweeds, regardless of their expected successional stages (Sousa 1980).

Seminal works on boulder fields supported the intermediate disturbance hypothesis (e.g. Osman 1977, Sousa 1979a) as greater diversity and patchiness (mosaic of successional stages) were observed on moderately disturbed boulders, while stable (or stabilized) boulders tended to be dominated by competitive dominants, such as *Gigartina* sp. (Sousa 1979a, 1980) excluding other species through competition for resources (light, substratum) and whiplash securing the open space. However, this model does not hold for all boulder fields, systems within which physical disturbance is unlikely to explain alone community dynamics (McGuinness & Underwood 1986, McGuinness 1987a, b). In the mid-shore, limpet abundances were statistically similar between habitats (Appendix S6). Since boulder overturning has not been thoroughly inferred in the present study, it could be hypothesised that physical disturbance is locally unimportant (Bishop & Hughes 1989) or – alternatively – that limpets are highly resistant to such disturbance, perhaps due to their anchoring capacity and mobility (Raffaelli & Hawkins 1996) and to boulder substratum heterogeneity (McGuinness & Underwood 1986). With limited substratum-facilitation and refuges from grazing (typically due to barnacles, which preferentially settle towards adult clumps) (e.g. Jenkins 2005), seaweeds may thus be less likely to establish on boulders. Though not statistically significant, the pattern observed in the Western site Ab may support this hypothesis (Fig. 2), which could be easily tested through limpet removals: likely due to extreme wave exposure in this site (Appendix S1, Le Duff & Hily 2001, Robuchon et al. 2017), limpets were virtually absent from most boulders, presenting a featureless/smooth aspect and upon which ephemerals and young *Fucus* were observed in abundance. In NE Atlantic, it is often considered that the grazing pressure of limpets decreases lower on the shore (Raffaelli & Hawkins 1996), as the ability of seaweeds to settle and grow (under decreasing stresses) becomes higher than limpet foraging. Indeed, the bedrock herein presented similar limpet densities between tidal heights, but the bare space was about seven-fold lower in the low-shore, where diverse assemblages of seaweeds and associated invertebrates were observed. In contrast, low-shore boulders were generally dominated by bare surface and only limpets and sheet-like ephemerals presented higher variability on boulders than on the bedrock at the scale of patch. Limpet abundance was up to 15-fold higher (× 3.9 on average per patch) on boulders than on the bedrock (and generally higher than on the mid-shore). Although this remains to be thoroughly tested, limpets when present may thus limit the establishment of a patchy seaweed assemblage, similar to surrounding bedrock. Interestingly, among the possible mechanisms regulating limpet abundance on boulders, habitat selection for substrate and food (e.g. biofilm growing on the apparent bare surface), survival due to lower predation and movement facilitated by bare surface (Underwood & Jernakoff 1981) may all be promoted by disturbance. While physical disturbance (e.g. boulders knocking together, overturning) likely contributes to the contrasting patchiness observed between habitats, it may be either directly (by creating bare space) or indirectly (by modulating important processes, such as grazing).

Patterns and variability at increasing spatial scales

Beyond patches, variability patterns were generally consistent between boulder and bedrock with increasing spatial scales, i.e. from tens of meters to tens of kilometres. As an exception, the abundance of ephemerals varied equally among all spatial scales examined on the bedrock but showed a trend in decreasing variability on boulders as the horizontal span increases. This pattern tends to support the initial hypothesis that disturbance operating at small-scale will lessen other processes – visible on the bedrock – at larger scales. Comparable trends were however observed irrespective of the substrate for several groups (thick leathery, crustose) or solely on the bedrock (jointed calcareous) in the low shore.

The within-site variability (10s m) was generally similar to within-locality (1000s m), but a few contrasting patterns were observed in the low shore (e.g. jointed calcareous on the bedrock, barnacles and crustose on both substrata). Although contrasting between habitats and shore heights, some patch-to-patch differences were observed for the community structure, the richness and the abundance of all groups, expect sheet-like and crustose seaweeds (which displayed some site-to-site differences). Given the coastal features of the study sites (distributed along headlands or within inlets), hydrodynamics are likely to interact with substratum heterogeneity at these intermediate scales, hence influencing many aspects of recruitment and post-recruitment processes (Blanchard & Bourget 1999).

Between the scales of locality to region (1-10s km), an increase in variability was observed for barnacle cover and community structure. These variables displayed differences, generally more pronounced on the bedrock than on boulders, between localities. On the bedrock, mid-shore communities ranged from fucoid- to suspension feeders-dominated, which could be due to gradients in wave exposure (Hartnoll & Hawkins 1985, Raffaelli & Hawkins 1996). In the low shore, the splash and spray resulting from waves may allow the development of uplifted communities (Raffaelli & Hawkins 1996), as herein observed westernmost location A (Fig. 3) probably undergoing greater swell than the others (Appendix S1). Should wave exposure be important in influencing bedrock communities among localities, it may also influence boulder communities, hence contributing to the similar variability patterns observed between habitats at this scale ($\alpha = 0.01$). In addition, within a single patch and at a given tidal height, both boulders and bedrock could be expected to experience a similar propagule supply, either originating from local or remote sources. It could be hypothesized that the number of species likely to settle, colonize and eventually establish would tend to be similar between the bedrock and virtually non-disturbed boulders at local scale (Sousa 1979b, 1980, Chapman & Underwood 1998), although post-settlement survival may be influenced by a series of habitat- and site-specific processes. Any discrepancy between biodiversity patterns of natural boulders and bedrock may thus emerge if the influence of these specific processes (e.g.. physical and biotic disturbance) prevails over those operating at larger scale. Across all studied patches, a positive correlation between boulders and bedrock richness was herein found on the low-shore, but not on the mid-shore (Fig. 5), and this may align with McGuinness (1987a) who found that the frequency and intensity of boulder overturning was generally higher on the shore. Although further work would be needed to disentangle putative mechanisms, disturbance is thus likely to prevail over a series of processes in influencing mid-shore boulders. Nonetheless, since boulder limpets may locally be excluded in favour of ephemerals' development (e.g. site Ab), the interaction between physical disturbance and biotic interactions may contribute to variability at large scales on boulders. In the low-shore, biodiversity patterns were generally more pronounced and involved a greater number of species than in the mid-shore. Through 'sampling effect', these patterns are more likely to co-vary between habitats, regardless of the disturbance (incl. grazing) seemingly stronger on boulders than on the bedrock. Like on the surrounding bedrock, all hydrodynamics, dispersal and recruitment processes may therefore contribute to large scale variability on boulders.

Beyond observations: implications and limitations

Overall, the present results suggest that several abiotic and biotic processes interact and may influence patterns at multiple spatial scales (Levin 1992, Benedetti-Cecchi & Trussell 2014, Dal Bello et al. 2017), even within two distinct microhabitats. While habitat properties may locally affect diversity and assemblages, such relationships are generally mediated, over a range of spatial and temporal scales, by the biological and environmental contexts (Tews et al. 2004, Matias 2013, Leclerc & Viard 2018). In the studied system, wave action and limpet grazing may have conspicuous influence on boulder field communities. Nonetheless, experimental manipulations would be needed to infer these processes and to define the spatial scales at which they operate (e.g. Benedetti-Cecchi et al. 2000). While the present study helps direct future research in boulder fields, its outcomes may depend on the specific temporal frame at which it was conducted (Benedetti-Cecchi 2001, Maggi et al. 2017). First, the intensity and the spatial extent of physical and biotic processes may vary over time (Osman 1977). The present study was performed in late fall, when tourism and associated recreational fishing are reduced, as compared to spring or summer holiday periods. Furthermore, the intensity of recreational fishing is unlikely to be even from site to site(Addessi 1994). As such, the balance between small- and intermediate-scale variability may be time-dependent. Should they contribute to physical disturbance, strong storms – operating at the scale of the region, though probably interacting with habitat heterogeneity at small scale – are less likely to occur during summer. Second, the nature and abundance of species interacting with these processes also likely change over time. For instance, most fleshy red algae grow and reproduce during the winter-spring period (Sousa 1979b), i.e. a few months after the sampling was performed. Unlike ephemeral algae (reproducing all the yearlong), these middle and late successional species could have displayed very different patterns of variability later in the year. Finally, since all natural and anthropogenic disturbances may vary throughout the year, incorporating a temporal level of variability would have been even more valuable than simply replicating the survey (Smale 2013, Leclerc et al. 2016). Given the spatially patchy nature of both boulders and bedrock, such direction may be promising to define indices of anthropogenic disturbance on the basis of variability (Warwick & Clarke 1993, Fraschetti et al. 2001, Chapman 2002) – an approach which has so far yielded conflicting results (e.g. Chapman et al. 1995). Nonetheless, variance analyses generally rely on independency and such temporal replication would be challenged by the limited number of boulders available per sampling units and risks of repetition should be considered.

CONCLUSIONS

In conclusion, important patchiness was revealed on either boulders or 'stable' bedrock, though generally higher on the bedrock than on boulders, except regarding the abundance of ephemeral algae. While the degree of spatial variability in this group could be useful to characterize physical disturbance on boulders, it is unlikely to disentangle between natural and anthropogenic causes from one shore to another, and even more likely to interact with additional sources of disturbance such as grazing, especially by limpets. Like within most rocky shores worldwide, intertidal communities of NW Brittany – regardless of substrate type – experience important sources of variability across multiple spatial scales (100s cm, 10s m, 1000s m and 10s km) which should be considered in sampling designs for both experimental and monitoring purposes.

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Table 1. Results of ANOVA tests for differences in multivariate and univariate pseudo-variance estimates across habitats, levels and spatial scales. **: $P < 0.01$, ***: $P < 0.001$, ^{a}: term not significant at $\alpha = 0.01$, level adopted given the heteroscedasticity of the data.

		Community structure		**Richness**		***Patella* spp.**		**Barnacles**		**Bare rock**	
Source of Variation	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Scale (Sca)	3	90.56	30.53***	12.02	48.93***	52.87	38.11***	56.03	44.89***	96.16	37.59***
Habitat (Hab)	1	59.39	20.02***	5.25	21.37***	2.14	1.54$^{\text{ns}}$	18.82	15.08***	3.89	1.52$^{\text{ns}}$
Level (Lev)	1	3.42	1.15$^{\text{ns}}$	5.48	22.30***	0.04	0.03$^{\text{ns}}$	61.30	49.12***	7.29	2.85$^{\text{ns}}$
Sca × Hab	3	9.90	3.34a	0.08	0.32$^{\text{ns}}$	1.34	0.96$^{\text{ns}}$	1.47	1.17$^{\text{ns}}$	9.69	3.79a
Sca × Lev	3	10.05	3.39a	0.65	2.66$^{\text{ns}}$	11.83	8.53***	5.90	4.73**	22.23	8.69***
Hab × Lev	1	1.16	0.39$^{\text{ns}}$	0.27	1.11$^{\text{ns}}$	6.24	4.50a	22.88	18.33***	16.42	6.42a
Sca × Hab × Lev	3	8.91	3.00a	0.38	1.53$^{\text{ns}}$	5.64	4.07**	0.83	0.67$^{\text{ns}}$	17.34	6.78***
Res	112	2.97		0.25		1.39		1.25		2.56	

Pairwise tests	*Scale:*	*Scale:*	*Scale × Habitat × Level:*	*Scale × Level:*	*Scale × Habitat × Level:*
	Pa > ((Si = Lo) < Re)	Pa > Si = Lo = Re	*Mid: (Scale × Habitat)*$^{\text{ns}}$	Mid: (Pa > Si > Lo < Re)	*Mid: (Scale × Habitat)****
			Pa > Si = Lo = Re	Low: Pa > (Si = Lo < Re)	B: Pa > Si = Lo = Re
	Habitat:	*Habitat:*	B = R		R: Pa = Si [> Lo] = Re
	B < R	B < R		*Habitat × Level:*	Pa : B = R
			Low: (Scale × Habitat)$^{\text{ns}}$	Mid: B < R	Si: B < R
		Level:	Pa > Si = Lo = Re	Low: B = R	Lo : B > R
		Mid < Low	B > R		Re B = R
					Low: (Scale × Habitat)$^{\text{ns}}$
					Pa > Si = Lo = Re
					B = R
Abreviations:	Scale: Patch (Pa), Site (Si), Locality (Lo), Region (Re); Habitat: Boulders (B), Bedrck (R); Level: Mid-shore (Mid), Low-shore (Low)				

Table 2. Results of ANOVA tests for differences in multivariate and univariate pseudo-variance estimates across habitats, levels and spatial scales. **: $P < 0.01$, ***: $P < 0.001$, ^{a}: term not significant at $\alpha = 0.01$, level adopted given the heteroscedasticity of the data.

		Sheet-like ephemerals		**Filamentous**		**Coarsely branched**		**Thick leathery**		**Jointed calcareous**		**Crustose**	
Source of Variation	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Scale (Sca)	3	36.84	40.05***	27.25	23.24***	68.32	40.51***	73.12	25.98***	5.87	28.27***	54.98	38.90***
Habitat (Hab)	1	90.66	98.54***	72.16	61.57***	17.28	10.25**	178.72	63.50***	15.03	72.35***	25.08	17.74***
Level (Lev)	1	0.12	0.13^{ns}	45.68	38.97***	133.81	79.35***	25.34	9.00**	29.22	140.66***	73.77	52.19***
Sca × Hab	3	15.66	17.02***	2.82	2.41^{ns}	3.80	2.25^{ns}	0.84	0.30^{ns}	2.15	10.37***	0.99	0.70^{ns}
Sca × Lev	3	5.21	5.66**	4.22	3.60a	33.02	19.58***	1.03	0.37^{ns}	5.24	25.24***	8.25	5.84***
Hab × Lev	1	1.69	1.83^{ns}	7.34	6.26a	0.64	0.38^{ns}	3.22	1.15^{ns}	13.69	65.92***	0.13	0.09^{ns}
Sca × Hab × Lev	3	3.23	3.51a	2.52	2.15^{ns}	3.10	1.84^{ns}	3.39	1.20^{ns}	1.93	9.27***	3.44	2.43^{ns}
Res	112	0.92		1.17		1.69		2.81		0.21		1.41	
Pairwise tests		*Scale × Level:* Mid: Pa > Si (= Lo) = Re Low: Pa > Si = Lo = Re *Scale × Habitat:* B: Pa > (Si = Lo) > Re R: Pa = Si = Lo = Re Pa : B > R Si: B > R Lo : B > R Re B = R		*Scale:* Pa > Si = Lo = Re *Habitat:* B < R *Level:* Mid < Low		*Scale × Level:* Mid: Pa > Si = Lo = Re Low: Pa > Si = (Lo > Re) *Habitat:* B < R		*Scale:* Pa > ((Si = Lo) > Re) *Habitat:* B < R *Level:* Mid < Low		*Scale × Habitat × Level:* *Mid: (Scale × Habitat)*^{ns} Pa > Si = Lo = Re B = R *Low: (Scale × Habitat)**** B: Pa > Si = Lo = Re R: Pa > Si > Lo > Re Pa : B < R Si: B < R Lo : B < R Re B = R		*Scale × Level:* Mid: Pa = Si = Lo = Re Low: Pa > (Si > Lo < Re) *Habitat:* B < R	
Abreviations:		Scale: Patch (Pa), Site (Si), Locality (Lo), Region (Re); Habitat: Boulders (B), Bedock (R); Level: Mid-shore (Mid), Low-shore (Low)											

Figure legends

Figure 1. Sampling design and maps indicating shores, sites and patches on the NW coast of Brittany where boulders and stable bedrock were sampled for the study. Intertidal areas appear in pale grey.

Figure 2. Univariate patterns in richness and abundances of various groups in mid-shore (left panels) and low-shore (right panels). Mean values (± SE, n = 16) for richness (A, A’), numerical abundance of *Patella* spp. (B, B’), covers of barnacles (C, C’), bare space (D, D’), ephemeral (E, E’), filamentous (F, F’), coarsely branched (G, G’), canopy (H, H’), jointed calcareous (I, I’) and crustose algae (J, J’) are indicated for each habitat with patch.

Figure 3. Principal coordinate analyses describing mid-shore (A, B) and low-shore assemblage structure (C, D). Vector plots of variable correlated with the PCO axes are indicated on right panels ($r > 0.4$), with font varying with r values (see legend in the figure).

Figure 4. Pseudo-variance estimates (mean ± SE, n = 8, logarithmic scale) in various multivariate and univariate descriptors of the assemblages depending on habitats and shore levels within four spatial scales (Patch, Site, Locality and Region).

Figure 5. Relationship between the observed combined richness on boulder and on the bedrock per patch in the mid- and in the low-shore (i.e. total number of species identified within a total of 16 quadrats). Only significant regression (within low shore) is depicted.

Supplementary information

Appendix S1. Study site names and patch description (coordinates and apparent exposure).

Appendix S2. Preliminary analyses of multivariate assemblage structure.

Appendix S3. Complete list of taxa (with authority) identified during this study.

Appendix S4. Abundance distribution of taxa and space occupiers within sites in the Mid-shore.

Appendix S5. Abundance distribution of taxa and space occupiers within sites in the Low-shore.

Appendix S6. Results of PERMANOVAs (with pairwise tests) testing for differences in species abundance distribution and richness for the complete set of species and main groups across habitats (B, R), levels (mid-shore, low-shore) and spatial scales (patch, site and shore) within the studied region.

Fig. 1

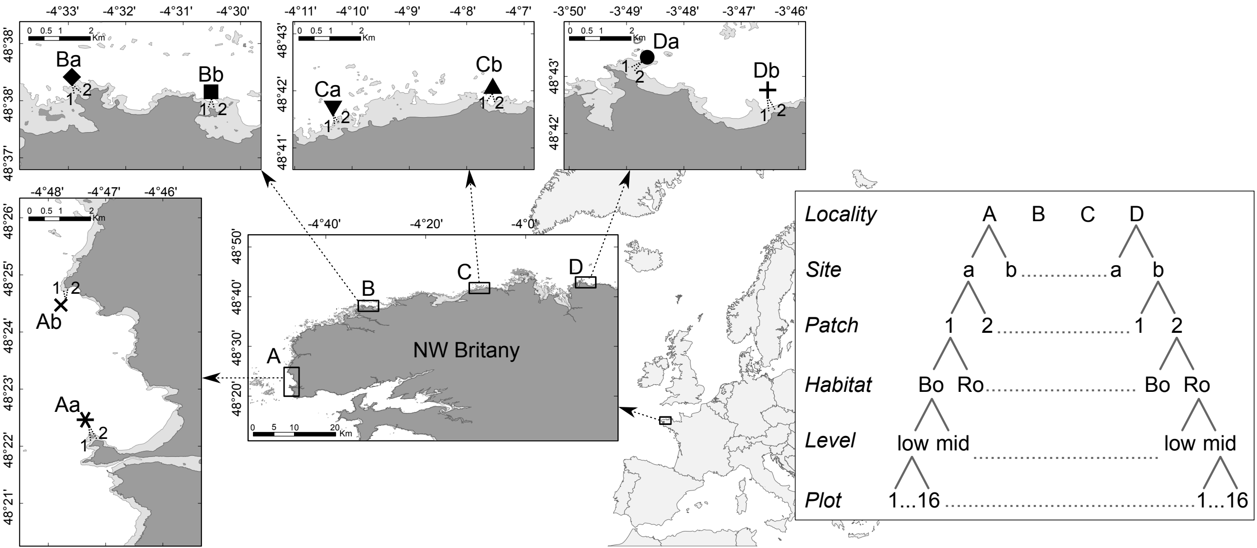

-4°33' -4°32' -4°31' -4°30'
48°38' 48°38' 48°37'
0 0.5 1 2 Km
Ba
Bb
1 2
-4°11' -4°10' -4°9' -4°8' -4°7'
48°43' 48°42' 48°41'
Ca
Cb
-3°50' -3°49' -3°48' -3°47' -3°46'
48°43' 48°43' 48°42'
Da
Db
-4°48' -4°47' -4°46'
48°26' 48°25' 48°24' 48°23' 48°22' 48°21'
Aa
Ab
-4°40' -4°20' -4°0'
48°50' 48°40' 48°30' 48°20'
0 5 10 20 Km
A
B
C
D
NW Britany
Locality
Site
Patch
Habitat
Level
Plot
A B C D
a b a b
1 2 1 2
Bo Ro Bo Ro
low mid low mid
1…16 1…16

Fig. 2

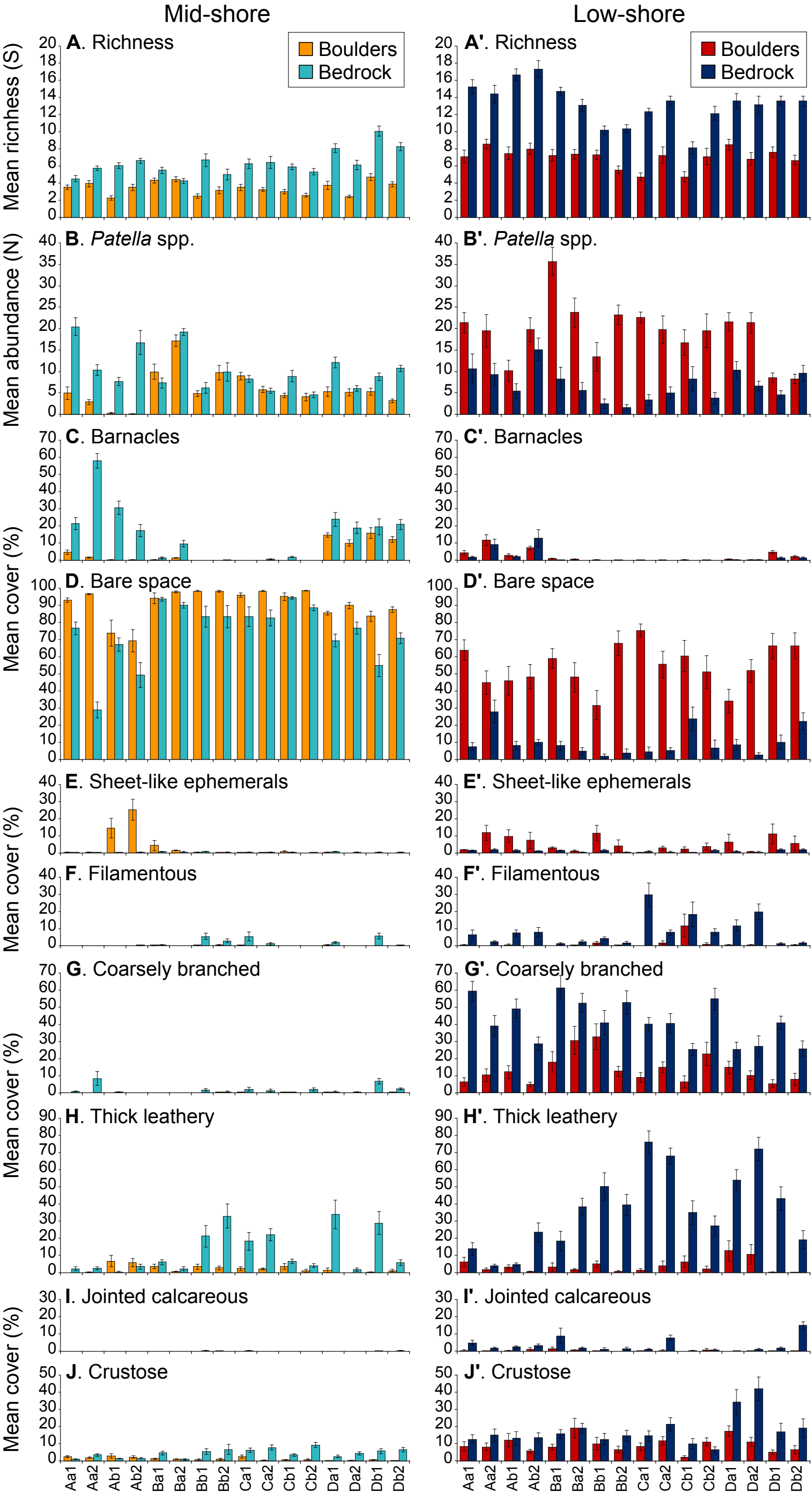

Mid-shore
Low-shore
Mean richness (S)
A. Richness
A'. Richness
Boulders
Bedrock
0
2
4
6
8
10
12
14
16
18
20
Mean abundance (N)
B. *Patella* spp.
B'. *Patella* spp.
0
5
10
15
20
25
30
35
40
Mean cover (%)
C. Barnacles
C'. Barnacles
0
10
20
30
40
50
60
70
D. Bare space
D'. Bare space
0
10
20
30
40
50
60
70
80
90
100
Mean cover (%)
E. Sheet-like ephemerals
E'. Sheet-like ephemerals
F. Filamentous
F'. Filamentous
0
10
20
30
40
Mean cover (%)
G. Coarsely branched
G'. Coarsely branched
0
10
20
30
40
50
60
70
H. Thick leathery
H'. Thick leathery
0
10
20
30
40
50
60
70
80
90
Mean cover (%)
I. Jointed calcareous
I'. Jointed calcareous
0
10
20
30
J. Crustose
J'. Crustose
0
10
20
30
40
50
Aa1
Aa2
Ab1
Ab2
Ba1
Ba2
Bb1
Bb2
Ca1
Ca2
Cb1
Cb2
Da1
Da2
Db1
Db2

Fig.3

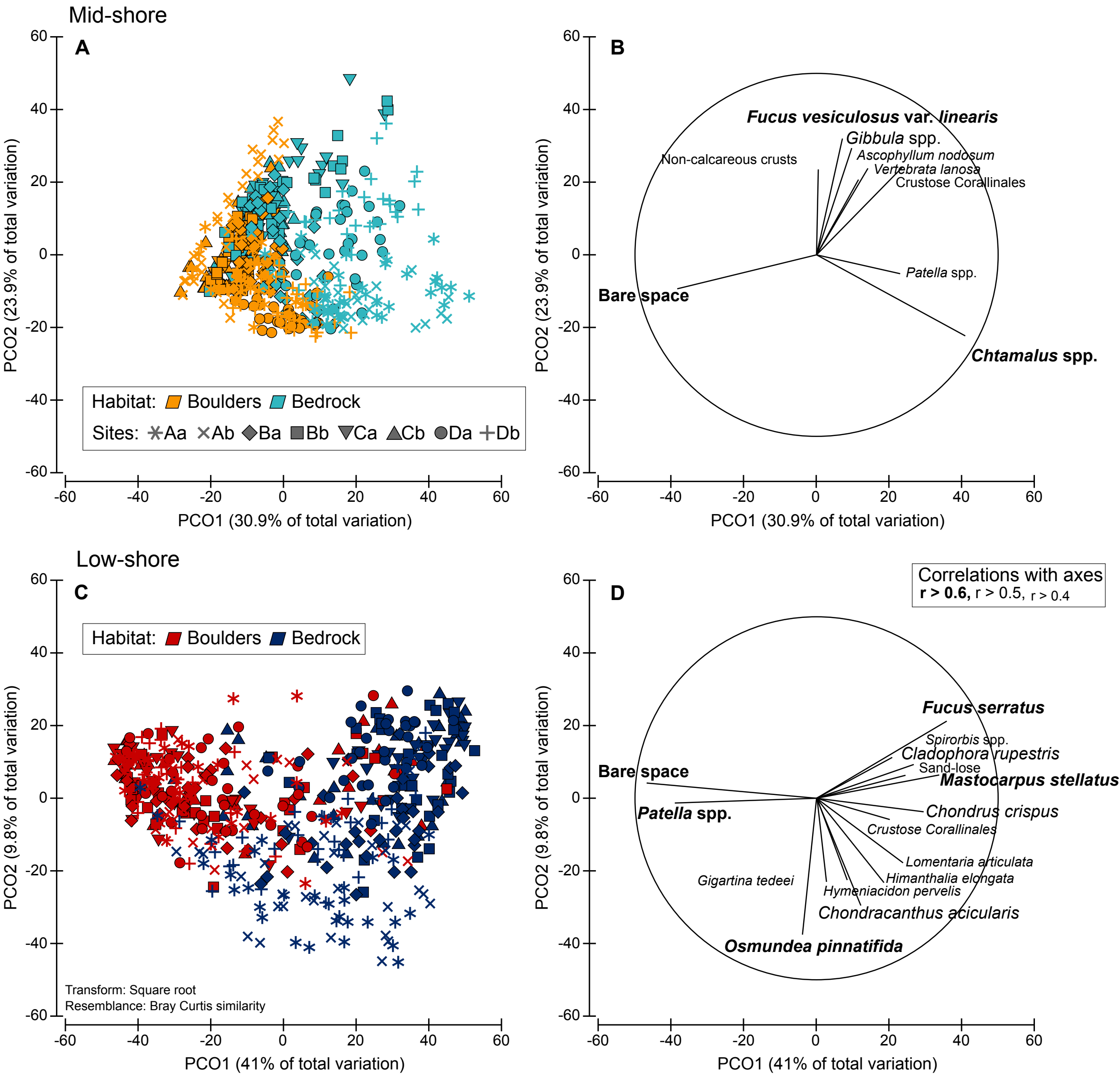

Mid-shore
A
60
40
20
0
-20
-40
-60
PCO2 (23.9% of total variation)
-60
-40
-20
0
20
40
60
PCO1 (30.9% of total variation)
Habitat: Boulders Bedrock
Sites: Aa Ab Ba Bb Ca Cb Da Db
B
Fucus vesiculosus var. linearis
Gibbula spp.
Ascophyllum nodosum
Vertebrata lanosa
Crustose Corallinales
Non-calcareous crusts
Patella spp.
Bare space
Chtamalus spp.
Low-shore
C
PCO2 (9.8% of total variation)
PCO1 (41% of total variation)
Habitat: Boulders Bedrock
Transform: Square root
Resemblance: Bray Curtis similarity
D
Correlations with axes
r > 0.6, r > 0.5, r > 0.4
Fucus serratus
Spirorbis spp.
Cladophora rupestris
Sand-lose
Mastocarpus stellatus
Bare space
Patella spp.
Chondrus crispus
Crustose Corallinales
Lomentaria articulata
Himanthalia elongata
Gigartina tedeei
Hymeniacidon pervelis
Chondracanthus acicularis
Osmundea pinnatifida

Fig. 4

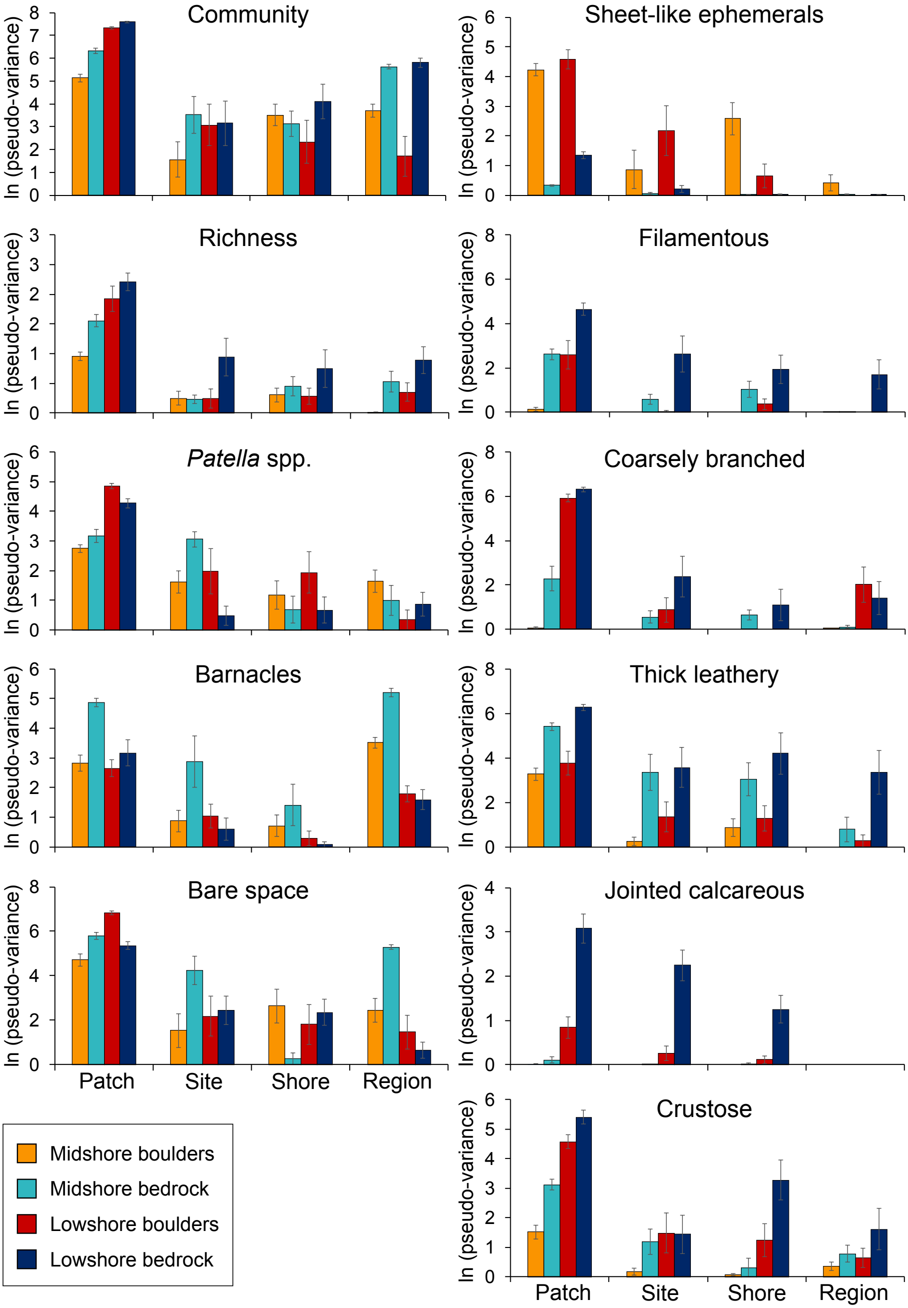
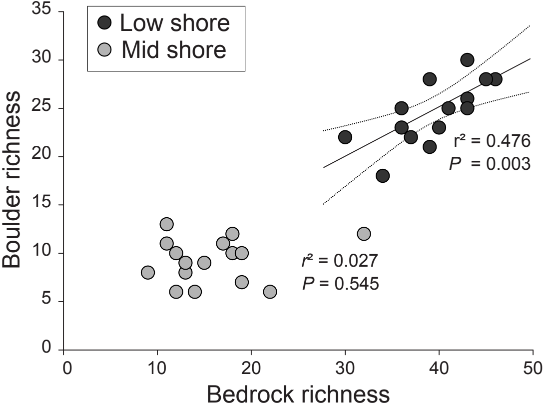

Community
Sheet-like ephemerals
Richness
Filamentous
Patella spp.
Coarsely branched
Barnacles
Thick leathery
Bare space
Jointed calcareous
Crustose
ln (pseudo-variance)
Patch
Site
Shore
Region
Midshore boulders
Midshore bedrock
Lowshore boulders
Lowshore bedrock

Fig. 5



● Low shore
● Mid shore
Boulder richness
Bedrock richness
0
5
10
15
20
25
30
35
0
10
20
30
40
50
r² = 0.476
P = 0.003
r² = 0.027
P = 0.545