
Clear-cut wave height thresholds reveal dominance shifts in assemblage patterns on rocky shores

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Abstract :

Physical constraints, and particularly hydrodynamics, are major drivers of macroalgal canopy-dominated rocky shore communities. The abundance of habitat-forming seaweeds decreases with increasing wave exposure, triggering cascading effects on their associated communities. This study aims at describing the structure of benthic communities along a hydrodynamic gradient and understanding the role of wave height in structuring the ecological transition from macroflora to macrofauna dominance. In situ wave height was measured together with biological communities (macroalgae, macrograzers and sessile fauna) along an exposure gradient on 3 rocky shores of western Brittany. Results showed that Fucales cover and the abundance of several understory organisms are negatively correlated to in situ wave height, except for barnacles and limpets which were positively correlated. Results revealed the occurrence of a wave height threshold at approximately 80 cm from high to mid-shore levels. Beyond this threshold, we observed a large dominance of barnacles, while below this threshold, Fucales and the associated organisms abounded. A similar threshold was observed on low shore habitats, for barnacle cover only. The results of this study challenge the commonly accepted paradigm of a gradual shift from seaweed-dominated to sessile fauna-dominated zones with increasing wave exposure on rocky shores. Finally, this study sheds new light onto interspecific interactions which drive the structure of rocky shore-associated communities.

Keywords : Hydrodynamics, Threshold, Rocky shore, Fucoids, Barnacles, Wave exposure, Benthic assemblage

19 **1. INTRODUCTION**

20 Ecosystem engineers are species structuring an habitat and influencing the associated
21 community (Jones et al. 1994). They allow ecological facilitation, *i.e.* by helping associated
22 species resisting to environmental stresses due to their presence (Brooker et al. 2008). These
23 species also act as habitat stabilizers by buffering environmental stress gradients (Crain &
24 Bertness 2006) and regulating the effects of predation and competition (Menge & Sutherland
25 1976). In coastal environments, ecosystem engineers such as seagrasses, macroalgae, bivalves,

1 cirripeds or polychaetes are able to alter their surrounding biophysical conditions by modifying
2 small-scale hydrodynamics, sediment deposition and lowering competition for space (Umanzor
3 et al. 2017).

4 On temperate rocky shores, hydrodynamics is considered to be one of the main environmental
5 factors generating horizontal gradients at local scale, and might be assessed either by modelling
6 (Bird et al. 2013) or by *in situ* measurements (Burel et al. 2019). Such gradients induce highly
7 contrasted patterns in macroalgal – macrofaunal assemblages depending on the intensity of
8 hydrodynamics (Christofoletti et al. 2010, Raffaelli & Hawkins 1999). These patterns are
9 typically used as biological scales to assess the degree of wave exposure (Ballantine 1961).
10 Indeed, increasing wave exposure is known to dislodge macroalgae (Bell 1999) and to affect
11 the cover of canopy forming macroalgae (Burel et al. 2019), while barnacles and other sessile
12 fauna appear to be better adapted to wave action (Marchinko & Palmer 2003, Neufeld & Palmer
13 2008). Organisms may adapt their morphology, physiology and behavior to these gradients
14 (Denny & Blanchette 2000, Knight & Parke 1950, Le Pennec et al. 2017, Stiger & Payri 1999),
15 while beyond a certain level of turbulence, environmental conditions can be too harsh for a
16 species to develop (Schiel & Lilley 2007). This is especially true for macroalgal engineer
17 species such as furoids, which are dominant on sheltered to semi-exposed rocky shores,
18 structuring macroalgal communities (Eriksson et al. 2007, Kay et al. 2016). The global structure
19 of seaweed communities may be affected by canopy loss, often leading to a severe reduction of
20 habitat complexity and affect drop of the associated diversity through cascading effects (Jenkins
21 et al. 1999a, Seed 1996).

22 In the North-East Atlantic, both barnacles and Fucales are considered as ecosystem engineers
23 (Barnes 2003, Bulleri et al. 2012). Upper and mid intertidal levels of the rocky shores are
24 dominated by either perennial species of Fucales forming dense canopies or by sessile
25 invertebrates, according to wave exposure (Ballantine 1961, Coppejans 1995, Lüning 1990). In

1 the intertidal zone, species of dominating Fucales are vertically distributed. They develop into
2 linear populations or belts of the species, from high to low shore, *Pelvetia canaliculata* (L.)
3 Decaisne & Thuret, *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jolis and *Fucus serratus*
4 L. (Johnson et al. 1998). A similar vertical zonation has been described for barnacles
5 (Southward 1976), as well as for associated organisms such as understorey macroalgae (Lewis
6 1964), gastropods (Boaventura et al. 2002, Tagliarolo et al. 2013) and sessile animals (Foster
7 1971). Although the usual distinction between typically exposed *versus* sheltered facies is based
8 on the relative abundance of vegetation *versus* sessile fauna and bare bedrock, little is known
9 on the quantitative relationship between wave exposure and the seaweed *vs* sessile fauna
10 dominance on rocky shores (Lindegarth & Gamfeldt 2005). Previous studies have revealed that
11 the metric scale variability in wave height within a sheltered rocky shore has an effect on
12 community structure (Burel et al. 2020), suggesting that the transition from seaweed-dominated
13 to sessile fauna-dominated habitats might be gradual. The relationship between fetch influence
14 and the composition of rocky shore assemblages reported in Burrows et al. (2008) and Burrows
15 (2012) also suggests such a gradual relationship. Because canopy-forming Fucales provide
16 shelter from hydrodynamics to diversified algal and animal assemblages (Hawkins & Hartnoll
17 1983a, Parker et al. 2001), the same gradual trend should be observed for the whole seaweed-
18 associated communities, though no empirical evidence has been reported so far.

19 Distribution patterns of rocky shores communities have been heavily studied, taking into
20 account both horizontal and vertical variations (Benedetti-Cecchi 2001). In recent studies
21 conducted on macroalgal-dominated habitats on the coast of Brittany, Burel et al. (2020) have
22 showed that at shore scale, spatial patterns in the communities were mostly explained by
23 vertical variations. While previous studies have evaluated qualitatively wave exposure at a
24 given shore level, showing limited effects on the community structure (Archambault & Bourget
25 1996), quantitative data obtained by Burel et al. (2019) revealed that hydrodynamics appeared

1 to be the major factor influencing the horizontal structure of communities at a given bathymetric
2 level. Other works have successfully linked community structure with hydrodynamics using
3 fetch data (*e.g.* Burrows et al. 2008). However, this approach does not allow for taking into
4 account the small-scale variability in wave exposure which occurs within every shore and the
5 effects this scale of variability might have on biological communities. We tested the effect of
6 different drivers on horizontal patterns, by coupling *in situ* wave height measurements and GIS
7 small-scale changes in topography together with community structure assessment. The present
8 study thus aims at providing a first quantitative assessment of the relationship between
9 hydrodynamics and patterns of rocky shore assemblages, along a wave exposure gradient at the
10 shore scale.

11 **2. MATERIAL AND METHODS**

12 **2.1. Sampling sites and levels**

13 The study area was located in western Brittany, on three sites in a 15 km range: Porsal
14 (48°33.848'N/4°42.309'W), Porspoder (48°28.876'N/4°46.293'W) and Segal
15 (48°26.330'N/4°47.376'W). The three locations were considered as site replicates due to their
16 high similarity in terms of physical and chemical traits. They were located in fully marine
17 conditions, open to the North-East Atlantic, and belong to the same water body (FRGC-13 in
18 the monitoring of the European Water Framework Directive; E.C. 2000). All sites present a
19 striking gradient between zones of extensive canopy forming *Fucales* landward to sessile fauna
20 dominated ones seaward. A classical pattern of vertical zonation was also observed in all sites,
21 with maximal tidal ranges of 8.35, 8.15 and 8.00 m respectively. Four bathymetric levels were
22 considered, corresponding to *Fucales*-dominated communities in sheltered zones (hereafter
23 named after the initials of the canopy-former): (1) the uppermost level corresponding to
24 *Pelvetia canaliculata* (*Pc*), (2) the second one to *Fucus spiralis* (*Fspi*), (3) the third one around
25 mid-tide level to *Ascophyllum nodosum* – *Fucus vesiculosus* (*An* – *Fves*) and (4) the last one to

1 *Fucus serratus* (*Fser*). The lowest tidal zone, dominated by either *Himanthalia elongata*,
2 *Bifurcaria bifurcata* or *Laminaria digitata* in this geographic area, was not integrated in the
3 present investigation since changes from macroflora to macrofauna dominance are uncommon
4 at this level (see Ballantine 1961).

5 **2.2. Assemblage sampling**

6 To assess the horizontal variability of the four bathymetric levels, alongshore transects
7 consisting of 12 sampling spots ranging from clearly sheltered facies (sampling spots n°1) to
8 clearly exposed ones (n°12) were performed in each of the three sites. Sampling points were
9 positioned by GPS and reference photos (Figure 1). Sampling was carried out once for each
10 level at different periods of the year: from 30th January to 6th February 2018 for *Pc*, from 15th
11 to 22nd February 2018 for *Fspi*, from 6th to 13th March 2018 for *An – Fves* and from 23rd to
12 30th April 2018 for *Fser*. The sampling of assemblages was performed at low tide, using a
13 mobile plastic grid structure of 1.65 * 1.65 m consisting of 25 quadrats of 33 * 33 cm. We used
14 the undisturbed sampling method described in Burel et al. (2019) to appreciate the cover of
15 animal and vegetal dominating species of the shore. We also used the upright profile sampling
16 method defined in Burel et al. (2019): the cover of all seaweeds and sessile fauna taxa was
17 estimated in three randomly chosen quadrats of the structure. In parallel, macrograzers (> 5mm)
18 were counted in the same quadrats. Whenever necessary, specimens were brought back to the
19 laboratory for identification.

20 **2.3. Data monitoring and analysis**

21 *In situ* wave height, an estimator comparable to the Significant Wave Height, was used as a
22 proxy of hydrodynamics (Burel et al. 2019). Within each sampling spot, simultaneously with
23 biological assemblages assessment, a 9 cm long Mini-Diver© recorder was attached to the
24 substratum (Figure 2 a.). Mini-Diver© sensors were programmed to measure the pressure every

1 25s during a one-week period (12 to 14 tide cycles for each recording period). A total of 36
2 recorders were distributed on the same assemblage sampling spots, and deployed
3 simultaneously during each sampling period, *i.e.* 12 per site. At the end of the recording period,
4 Mini-Divers© were removed from the sampling spots and brought back to the laboratory.
5 Pressure data was downloaded from each recorder, using Diver-Office software. The data
6 acquired correspond to the absolute pressure equal to the addition of the atmospheric pressure
7 and the water pressure (Figure 2 b.). To subtract the atmospheric pressure (~ 20 km away from
8 the sampling sites), a control recorder was deployed in the laboratory during the sampling
9 period. A second order polynomial regression was applied on each tide period in order to
10 remove the tide oscillation and extract raw pressure variations generated by waves (Figure 2
11 c.). The twenty highest and the twenty lowest pressure values were selected to determine the *in*
12 *situ* wave height (Figure 2 d.). Since absolute height values differed from a site to another, they
13 were standardized allowing a global comparison of biological characteristics per level and to
14 get normal values (Burel et al. 2019). At the same time, Mini-Diver© sensors recorded
15 alternately seawater and air temperatures depending on the tide oscillation. GIS treatment was
16 performed using QGIS open-source software (<https://www.qgis.org/>). Sampling spots were
17 positioned by GPS and added as a vector layer (point) in the GIS project. The digital terrain
18 model Litto3D (<https://diffusion.shom.fr/>) allowed for a precise, *ca.* 20 cm vertical accuracy as
19 estimation of the elevation (*i.e.* altitude above chart datum) of biological samples. Each Litto3D
20 cell was imported to the QGIS project as a raster layer. The vertical elevation was defined for
21 each sampling spot in order to quantify the small variations of elevation at a given bathymetric
22 level. The Raster Terrain Analysis plugin was used to calculate the influence of additional
23 processes that were liable to explain differences in small-scale horizontal patterns (*ca.* 20 cm),
24 such as local shore slope corresponding to the altitudinal difference of neighboring pixels (in

1 degrees), and the Ruggedness Index (dimensionless) as a proxy of terrain heterogeneity (Riley
2 et al. 1999). Again, slope and Ruggedness Index were determined for each sampling spot.

3 All data were analyzed using the R environment (R version 4.0.3, R Development Core Team
4 2020). Pearson's r coefficients were calculated, using the “corrplot” package (Wei & Simko
5 2017), to test correlations between *in situ* wave height, slope, ruggedness index and biological
6 data (covers of intertidal species and bare rock). A piecewise regression (segmented regression)
7 was used to analyze the dataset using R “segmented” package (Muggeo 2008) and evidence
8 potential conspicuous relationships between wave heights and biological patterns giving
9 potential estimated break-point and corresponding F values (Muggeo 2003).

10 **3. RESULTS**

11 **3.1. Physical traits**

12 The bathymetric levels of the sampling spots were well differentiated by the digital terrain
13 model determined elevation \pm the standard deviation: (1) the Pc level was 6.26 ± 0.43 m above
14 chart datum, (2) the $Fspi$ level was 5.77 ± 0.43 m (3) the $An - Fves$ level was 3.83 ± 0.72 m
15 and (4) the $Fser$ level was around 2.67 ± 0.37 m. The elevation within a given bathymetric level
16 differed slightly between sites, with globally lower elevations at Segal (the site presenting the
17 lowest tidal range). Detailed datas are given site by site in Table A1. From the highest
18 bathymetric level to the lowest, the average slope determined by GIS for all sites was *ca.* 12° ,
19 10° , 6° and 11° , whereas the Ruggedness Index gave 0.72, 0.65, 0.44 and 0.50 (dimensionless),
20 respectively. Seawater temperature showed very little variations between sites for similar
21 sampling periods (0.5°C difference at most). The minimum temperature recorded by the sensors
22 was 9.2°C in early March, while the maximum was 12.3°C at the end of April. Air temperature
23 was more variable, with up to 15°C difference observed during the same week. Extreme
24 temperature values observed during the sampling periods were a minimum of 0.5°C recorded

1 in February to a maximum of 26.6°C at the end of April. *In situ* wave heights showed large
2 variations, ranging from 34.4 to 149.5 cm in *Pc*, from 42.3 to 106.8 cm in *Fspi*, from 24.5 to
3 108.7 cm in *An – Fves* and from 30.9 to 83.1 cm in *Fser*. Figure 1 summarizes the evolution of
4 wave heights along the transect axis, designed to follow an apparent exposure gradient. Not
5 surprisingly, *in situ* wave height values increased gradually seawards. *In situ* wave heights for
6 each sampling spot are given in Table A2.

7 **3.2. Relationships between physical traits and biological assemblages**

8 Slope values did not reveal any significant correlation with biological data in any of the
9 bathymetric levels considered. On the contrary, the Ruggedness Index did show a few
10 significant correlations for all levels. At the *Pc* and *Fspi* levels, the index was positively
11 correlated with the abundance of barnacles (respectively $r = 0.37$, p -value < 0.03 , and $r = 0.43$,
12 p -value < 0.009). In *Fspi*, a positive correlation was also observed with the density of the sea
13 snail *Littorina compressa* ($r = 0.35$, p -value < 0.04). In *An – Fves*, a positive correlation was
14 observed with the abundance of limpets ($r = 0.49$, p -value < 0.003). At *Fser*, a negative
15 correlation was found only with the cover of green macroalgae *Cladophora rupestris* ($r = -0.49$,
16 p -value < 0.003).

17 *In situ* wave height was the physical trait showing the highest number of correlations, compiled
18 in Table 1. The cover of dominating Fucales was negatively correlated to *in situ* wave height.
19 Significant correlations were found with Fucales in bathymetric levels where they dominate,
20 with high values of Pearson's r (up to $r = -0.82$ for *Pelvetia canaliculata*), as well as in
21 communities characterized by a different dominating species (for example $r = -0.5$ for *F.*
22 *spiralis* in *Pc*). The only case showing a positive correlation with increasing wave height was
23 with the cover of *Fucus vesiculosus* within the *Fucus serratus*-dominated bathymetric level (r
24 $= 0.49$).

1 Among Rhodophyta and Chlorophyta, most species were negatively correlated with wave
2 heights (Table 1), such as the crustose coralline *Phymatolithon lenormandii*, the filamentous
3 *Cladophora rupestris*, the turf-forming *Catenella caespitosa* or the cartilaginous tufts of
4 *Mastocarpus stellatus*. In the lowest community considered in this study (*Fser*), positive
5 correlation with wave height were observed, such as for the thin foliose *Porphyra dioica* and
6 the tubular *Ulva compressa*, as well as the filamentous *Erythrotrichia welwitschii*. The crustose
7 *Hildenbrandia rubra* revealed contrasted trends depending on the community considered, with
8 a negative correlation with wave heights in the upper intertidal zone, and a positive correlation
9 in the mid-intertidal.

10 Concerning the taxa of sessile fauna associated with macroalgal communities, only the cover
11 of barnacles was positively correlated to wave height (Table 1). On the contrary, sessile fauna
12 taxa from various phyla were rather negatively influenced by wave heights in the mid intertidal
13 level, such as sponges (*Hymeniacidon perlevis*), anemones (*Actinia equina*) as well as
14 polychaetes (spirorbids).

15 The abundance of limpets was negatively correlated with wave heights, showing a linear
16 regression, and increasing densities in *An – Fves* and *Fser*. *Littorina compressa* and
17 *Steromphala umbilicalis* were positively correlated with increasing wave heights or showed no
18 significant correlations, depending on the level of the shore. In contrast, *Littorina obtusata* and
19 *Steromphala pennanti* were negatively impacted by wave heights or showed no significant
20 correlation, depending also on the level.

21 **3.3. Evidence of a common wave height threshold for dominance shifts**

22 The abundance of canopy forming Fucales and barnacles was highly related to *in situ* wave
23 heights at all bathymetric levels (Figure 3). Piecewise regression allowed the identification of
24 estimated break-points in the relationship between the cover of Fucales and *in situ* wave height.

1 These break-points corresponds to threshold points (*cf.* Flores et al. 2019) quantified as
 2 standardized values of wave height (dimensionless). These values were 0.96 for *Pc* ($F = 2.52$),
 3 0.34 for *Fspi* ($F = 5.46$) and 0.25 for *An - Fves* ($F = 25.07$). A gradual negative relationship
 4 was found between canopy cover and wave height, until a threshold where they abruptly
 5 disappear. The only exception was *F. serratus*, for which even though a decrease in the cover
 6 was observed with increasing wave heights, the decrease was continuous throughout the wave
 7 height range, and the species was present at both the most exposed and the most sheltered sites.
 8 Piecewise regression applied to the barnacle abundance and *in situ* wave height showed a
 9 complex relationship. The threshold points showed a two-step change: 0.87 ($F = 8.99$) and 1.03
 10 ($F = 13.41$) for *Pc*, -0.01 ($F = 0.56$) and 0.22 ($F = 11.46$) for *Fspi*, -0.79 ($F = 0.46$) and 0.79 (F
 11 = 3.98) for *An - Fves*, -0.18 ($F = 3.27$) and 0.38 ($F = 0.99$) for *Fser*.

12 These thresholds as expressed in standardized values correspond to actual wave heights of *ca.*
 13 84 cm for *P. canaliculata*, 79 cm for *Fucus spiralis*, and 73 cm for *Ascophyllum nodosum*.
 14 Close limits were observed for several organisms in associated assemblages (Figure 4 to 6).
 15 Particularly, it was the case for the cover of macroalgal species in the three upper levels of the
 16 shore (in *Pc*, *Fspi* and *An - Fves*). For example, the crustose red alga *H. rubra* in *Pc* and *Fspi*
 17 and the small erect red *C. caespitosa* in *Fspi*. It was also the case in *An - Fves*, with the
 18 filamentous green *Cladophora rupestris*, the sponges *H. perlevis* and *Grantia compressa* and
 19 of the Rhodophyta *Membranoptera alata*, *Plumaria plumosa*, *Gelidium pusillum* and
 20 *Vertebrata lanosa*. On the contrary, the threshold does not seem to coincide to any shift of
 21 abundance for other species. This is especially the case for gastropods such as limpets in the 4
 22 communities considered, *L. compressa* in *Pc* and *Fspi* or *S. umbilicalis* in *An - Fves* and *Fser*.
 23 This is also the case for a few macroalgal species such as the Gigartinales *M. stellatus* in *An -*
 24 *Fves*. Similarly, to what was observed for the dominant Fucales, the decrease in abundance was
 25 continuous throughout the wave height range for the *Fser* associated communities.

1 Wave height threshold values were roughly the same for macroalgae and sessile fauna in the
2 three upper levels of the shore (Figure 3). Apart from the exception of *An - Fves*, we found no
3 quadrat where fucoids and barnacles co-occurred in *Pc* and *Fspi*. This illustrates the absence of
4 a gradual relationship between facies dominance and exposure.

5 **4. DISCUSSION**

6 This work offers new keys to understand the structuring of macroalgae / macrofauna dominance
7 patterns along wave exposure gradients. Different patterns were highlighted in the relationship
8 between hydrodynamics and the structure of rocky intertidal assemblages.

9 Slope is considered as a primary driver of horizontal variations and is known to modulate small-
10 scale hydrodynamics in the intertidal zone, with especially effects on barnacle populations
11 (Shanks et al. 2017). In the present study, no significant effect of slope on flora-fauna patterns
12 was identified, probably because of the limited range observed within a single bathymetric level
13 (Benedetti-Cecchi 2001). Another explanation may result from the way slope was evaluated. In
14 the literature, the slope may be calculated using various techniques, such as visual qualitative
15 estimation of the inclination (Benedetti-Cecchi et al. 2000, Vaselli et al. 2008). However, more
16 accurate results may be obtained using a GIS approach, either by digital elevation / terrain
17 modeling and the calculation of a transect slope including the entire intertidal zone (Chappuis
18 et al. 2014) or by a quadratic computing (Chust et al. 2008).

19 The Ruggedness Index was positively correlated with the abundance of barnacles and limpets
20 from high to mid-shore. Such animals are known to benefit from substratum complexity and
21 crevices to protect them (Aguilera et al. 2014). The Ruggedness Index developed for
22 topographic heterogeneity has been used for mapping marine habitat at large-scale (Rinde et al.
23 2004). To our knowledge this study is the first one using Ruggedness Index at small-scale,

1 giving interesting preliminary results on the link that may exist between terrain complexity and
2 the structure of intertidal assemblages.

3 Although a gradual pressure-response relationship between wave exposure and benthic
4 organisms could have been hypothesized (Burrows 2012), here we evidence that several species
5 do not follow this pattern. We found wave height thresholds delineating dominance shifts
6 between seaweed dominated and sessile invertebrates dominated (barnacles) facies, on a “on/off
7 mode”. Dominating Fucales of the mid to upper shore were absent above these thresholds,
8 whereas they displayed highly variable covers in more sheltered areas, in which a significant
9 negative relationship with wave height was observed. Surprisingly, these thresholds were
10 observed for absolute values of *in situ* wave height around 80 cm, whatever the bathymetric
11 level, the sampling site or the recording period. Unlike Fucales, a two-step relationship was
12 observed between the cover of barnacles and *in situ* wave height. Nevertheless, break-points
13 values roughly frame the threshold points revealed in the Fucales for the three upper levels of
14 the shore. A similar two-step relationship was also evidenced for the extension of barnacles in
15 *Fser*. The lack of barnacles below the threshold could result from a reduced water circulation,
16 damageable for the alimentation of these filter-feeding animals (Marchinko & Palmer 2003). In
17 addition, other biotic factors such as the sweeping by fucoids (Jenkins et al. 1999b) or the
18 predatory by dogwhelks, *Nucella lapillus* L. (Burrows & Hughes 1991), are known to
19 negatively affect the cover of barnacles and could explain this lack.

20 **4.1. Wave height effects on canopy-forming Fucales**

21 There are several reasons why the wave height gradient was expected to induce a linear and/or
22 gradual response in intertidal seaweeds. First, drag forces, which limit the survival of seaweeds
23 on the most exposed shores, are related to wave height (Denny & Gaylord 2002, Jones et al.
24 2015). Second, the fact that studies have successfully managed to link wave exposure proxies
25 to assemblage composition suggests that there is a gradual relationship between these two

1 variables (*e.g.* Burrows et al. 2008). Finally, such a gradual (either positive or negative)
2 relationship has been reported for subtidal macrophytes on the western Basque coast (Díez et
3 al. 2003). Consequently, any deviations from this expected pattern should be interpreted as
4 reflecting other processes, of biotic nature.

5 Competition for substratum between canopy-forming seaweeds and sessile fauna (*e.g.*
6 barnacles, mussels) and/or limpets has been repeatedly reported as one of the most structuring
7 process on rocky shores (*e.g.* Leonard 1999, O'Connor et al. 2011). Here, we found almost no
8 examples where canopy-forming algae did cohabitate with barnacles, suggesting that
9 competition might be an important factor triggering the binary pattern observed, even if there
10 was no direct evidence for it. In contrast, although the grazing of canopy-forming Fucales by
11 limpets has been reported on several occasions (Davies et al. 2008, Schaal & Grall 2015),
12 sometimes leading to canopies eradication (Davies et al. 2007, Le Roux 2005), limpets were
13 present from the most sheltered to the most exposed zones, suggesting that grazing is of
14 secondary importance in supporting the relationship between canopies and wave exposure. This
15 was somewhat unexpected, as limpets are known to increase their feeding activity with
16 increasing wave exposure, to cope with limited food availability (Jenkins & Hartnoll 2001),
17 which could result in sharp Fucales-limpets transition along the exposure gradient.

18 In contrast with other canopy-forming Fucales, whose extension towards the most exposed
19 areas was limited by a clear-cut wave height threshold, *Fucus serratus* was present on the whole
20 exposure gradient, and was characterized by a significant negative correlation with wave height.
21 This might be the consequence of a reduced emersion stress (Burel et al. 2020), since at that
22 bathymetric level, desiccation is considerably reduced because of short emersion times,
23 comprised between 25 % and 40 % of the total (Ar Gall & Le Duff 2014). This would imply
24 that desiccation during emersion and wave exposure are two factors which act synergistically
25 to limit the extension of mid-to-high shore canopies in exposed conditions. This hypothesis

1 would be in agreement with the fact that *F. serratus* did not colonize the most exposed areas in
2 the highest parts of its vertical distribution range (*i.e.* in the *An - Fves* assemblage) (Figure 6).
3 Beyond the combined effects of wave exposure and desiccation, *F. serratus* is known to be
4 more resistant to hydrodynamics than other Fucales (Lindegarh & Gamfeldt 2005), which
5 probably contributes to the observed pattern. However, one has to consider the possibility of
6 spatially confounding effects due to the absence of replicate transects on each of the 4
7 macroalgal communities within each of the 3 sites.

8 **4.2. Wave height effects on associated assemblages**

9 Different types of relationships between increasing *in situ* wave height and the abundance of
10 species were observed (Figures 4 to 7). Several understory algal species displayed a similar
11 pattern as canopy-forming algae (*e.g.* *Catenella caespitosa* in *Pc*, *Cladophora rupestris* in *Fspi*,
12 *Gelidium pusillum* in *An – Fves*). The brutal reduction of canopies also led to the drastic
13 decrease of abundance and even to the loss of several associated fauna, such as the sponge
14 *Hymeniacidon perlevis* or the periwinkle *Littorina obtusata* associated to *Ascophyllum*
15 *nodosum*. Structuring species like *Pelvetia canaliculata*, *Fucus spiralis* and *A. nodosum* provide
16 shelter for their own early stages (Andrew & Viejo 1998), as well as for understory species,
17 by protecting them from wave action during immersion and against both irradiance and
18 desiccation during emersion (Bertness & Leonard 1997, Hawkins & Hartnoll 1983a).
19 Consequently, by reducing the cover of dominating Fucales, hydrodynamics alter the buffer
20 capacity of macroalgal communities against abiotic factors and, in turn, accentuates the
21 disturbance inside assemblages (Bertocci et al. 2010). Besides, the density of limpets, as well
22 as their feeding rate, increase along the gradient, benefiting from extended available space (bare
23 rock) in wave-swept shores (Hawkins & Hartnoll 1983b, Jonsson et al. 2006). Therefore, waves
24 act on the structure and diversity of macroalgal community both (1) directly by reducing the

1 cover of the canopy and (2) indirectly by promoting the multiplication of limpets, leading to
2 enhanced grazing and competition for space.

3 We also found several species that showed different patterns from canopy-forming algae along
4 the wave height gradient. Some of them (*e.g. Hildenbrandia rubra* and *Littorina saxatilis* in *Pc*,
5 *Phymatolithon lenormandii* and *L. obtusata* in *An – Fves*) were negatively correlated to wave
6 height, though they were present on the whole gradient, or displayed a different threshold value
7 from canopy-forming algae. This suggests that although these species are affected by
8 hydrodynamics, this effect is not mediated through the loss of canopies, hence that
9 hydrodynamics can be considered as a proximal factor driving their abundance on rocky shores,
10 while it may be a distal one for previous species.

11 Finally, some species (beyond limpets) inhabiting canopies proved to be positively affected by
12 increasing wave height. These species were all gastropods (*Littorina compressa*, *Steromphala*
13 *umbilicalis*). Even though these species radulas allow them to feed on a variety of sources
14 (Steneck & Watling 1982), their common occurrence on unvegetated shores suggests that they
15 mostly feed on biofilm, though opportunistic feeding on allochthonous sources cannot be
16 excluded (Laurand & Riera 2006). Their occurrence under canopies raises the question of their
17 relationship to these canopies, which deserves further investigation.

18 Understorey species were apparently not impacted by the reduction of canopy in the *F. serratus*
19 level, differing from upper levels of the shore (Figure 7). Thus, understorey species in *Fser*
20 might not be as shelter-dependent as in the upper intertidal zone and they could even cope
21 locally with a global canopy loss (Bertolini 2018).

22 **4.3 Relationships communities – hydrodynamics and importance of thresholds**

23 Organisms can develop diverse responses to increasing environmental disturbance, which are
24 particularly conspicuous in intertidal environments (Bertness et al. 1999, Schiel & Lilley 2007).

1 Either increasing or decreasing abundance are observed for organisms facing increasing wave
2 exposure (McQuaid & Branch 1984). In the light of our results, we suggest the co-occurrence
3 on a given shore of four types of relationship between the abundance of species and
4 hydrodynamics (Figure 8): a) no relationship, for species withstanding hydrodynamics and
5 being competitive enough below macroalgal canopies, illustrated in this study by several
6 species growing in *Fser*, like the turf-forming species *Osmundea pinnatifida* and *Lomentaria*
7 *articulata*, which can survive well as independent patches. b) bell curved relationships, with
8 higher densities found at intermediate wave exposure, either for faunal species independent
9 from macroalgae for feeding but which may not withstand strong hydrodynamical conditions
10 or macroalgal species requiring moderate hydrodynamics, like *Mastocarpus stellatus* in *An –*
11 *Fves*. c) gradual response for species exhibiting a clear affinity for either sheltered or exposed
12 areas depending on their ecological limits, noticeably limpets, which abundances increased
13 progressively with increasing wave heights. A similar positive relationship was also evidenced
14 for structurally simple seaweeds such as the uniseriate filamentous *Erythrotrichia welwitschii*
15 or the monostromatic *Porphyra dioica*. d) occurrence of a threshold between the absence of
16 Fucales on one side, typically *P. canaliculata*, *A. nodosum* and *F. spiralis*, and the dominance
17 of sessile fauna on the other side. Some understorey species displayed contrasted patterns
18 depending on the bathymetric level of the shore / community (*cf.* Table 1). A striking example
19 was the crustose species *H. rubra*, since it was negatively impacted by wave heights in both *Pc*
20 and *Fspi*, whereas it was positively conditioned by hydrodynamics in *An – Fves*. This variety
21 of relationships reveal that waves can induce a critical shift from well-structured macroalgal
22 communities to less structured barnacle-dominated habitats, by an increase of only a few
23 centimeters of wave heights. While species in low intertidal levels are less sensitive to wave
24 exposure increases, others respond more abruptly when approaching a critical state, like Fucales
25 from high- to mid-shore. Such a paradigm has been evidenced for various environments by

1 Briske et al. (2010). This finding underlines the interest of the community / assemblage
2 approach, *i.e.* at given elevation / bathymetric levels, to study the effect of hydrodynamics on
3 intertidal species (Ar Gall et al. 2016).

4 The statement that physical thresholds may condition the abundance and even the occurrence
5 of intertidal organisms opens new perspectives to study dominance shifts on rocky shores
6 beyond classical paradigms based on biological data. It contributes to the definition of regime
7 shifts depending on hydrodynamics which are highly needed in ecological studies (Andersen et
8 al. 2009), particularly in the context of global change (Ramos et al. 2020). When compared to
9 a qualitative approach, the use of a quantitative monitoring of wave height makes possible a
10 precise evaluation of the hydrodynamic stresses supported by intertidal organisms (Lindegarth
11 & Gamfeldt 2005). It may be seen as a decisive step forward to understand the functioning of
12 intertidal macroalgal - macrofauna assemblages submitted to hydrodynamic pressure.

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21

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1 **Table**

2 Table 1: main significant correlations obtained between in situ wave heights and the abundance
 3 of intertidal organisms (cover for sessile organisms and density for vagile fauna) and bare rock
 4 (p -value < 0.05). Communities dominated by *Pelvetia canaliculata* and *Fucus spiralis* were
 5 situated in the upper shore, those dominated by *Ascophyllum nodosum* – *Fucus vesiculosus* in
 6 the middle shore, and by *Fucus serratus* were situated from mid to low shore. “n.s.” indicates
 7 a non-significant result while “-” indicates an absence of the taxon in the community
 8 considered.

Community	Upper shore		Mid to low shore	
	<i>P. canaliculata</i>	<i>F. spiralis</i>	<i>A. nodosum</i> – <i>F. vesiculosus</i>	<i>F. serratus</i>
Phaeophyceae				
<i>Pelvetia canaliculata</i>	-0.82	-0.37	-	-
<i>Fucus spiralis</i>	-0.5	-0.69	-	-
<i>Ascophyllum nodosum</i>	-	n.s.	-0.63	-
<i>Fucus vesiculosus</i>	-	-	n.s.	0.49
<i>Fucus serratus</i>	-	-	-0.44	-0.66
Rhodophyta				
<i>Catenella caespitosa</i>	-0.35	-0.46	-	-
<i>Hildenbrandia rubra</i>	-0.52	-0.48	0.42	-
<i>Phymatolithon lenormandii</i>	-	n.s.	-0.48	n.s.
<i>Mastocarpus stellatus</i>	-	n.s.	n.s.	-0.52
<i>Porphyra dioica</i>	-	-	n.s.	0.48
<i>Erythrotrichia welwitschii</i>	-	-	n.s.	0.53
Chlorophyta				
<i>Cladophora rupestris</i>	-	n.s.	n.s.	-0.55
<i>Ulva compressa</i>	-	n.s.	n.s.	0.59
Sessile Fauna				
Barnacles	0.49	0.62	0.65	0.38
<i>Hymeniacidon perlevis</i>	-	-	-0.49	-0.49
<i>Actinia equina</i>	-	n.s.	-0.36	n.s.
Spirorbids	-	-	-0.49	-0.42
Vagile Fauna				
Limpets	0.51	0.58	0.61	0.60
<i>Littorina compressa</i>	n.s.	0.51	n.s.	n.s.
<i>Littorina obtusata</i>	n.s.	-0.44	-0.36	n.s.
<i>Steromphala umbilicalis</i>	-	n.s.	n.s.	0.35
<i>Steromphala pennanti</i>	-	-	-	-0.38
Bare rock	0.61	n.s.	0.35	0.49

1 Figures

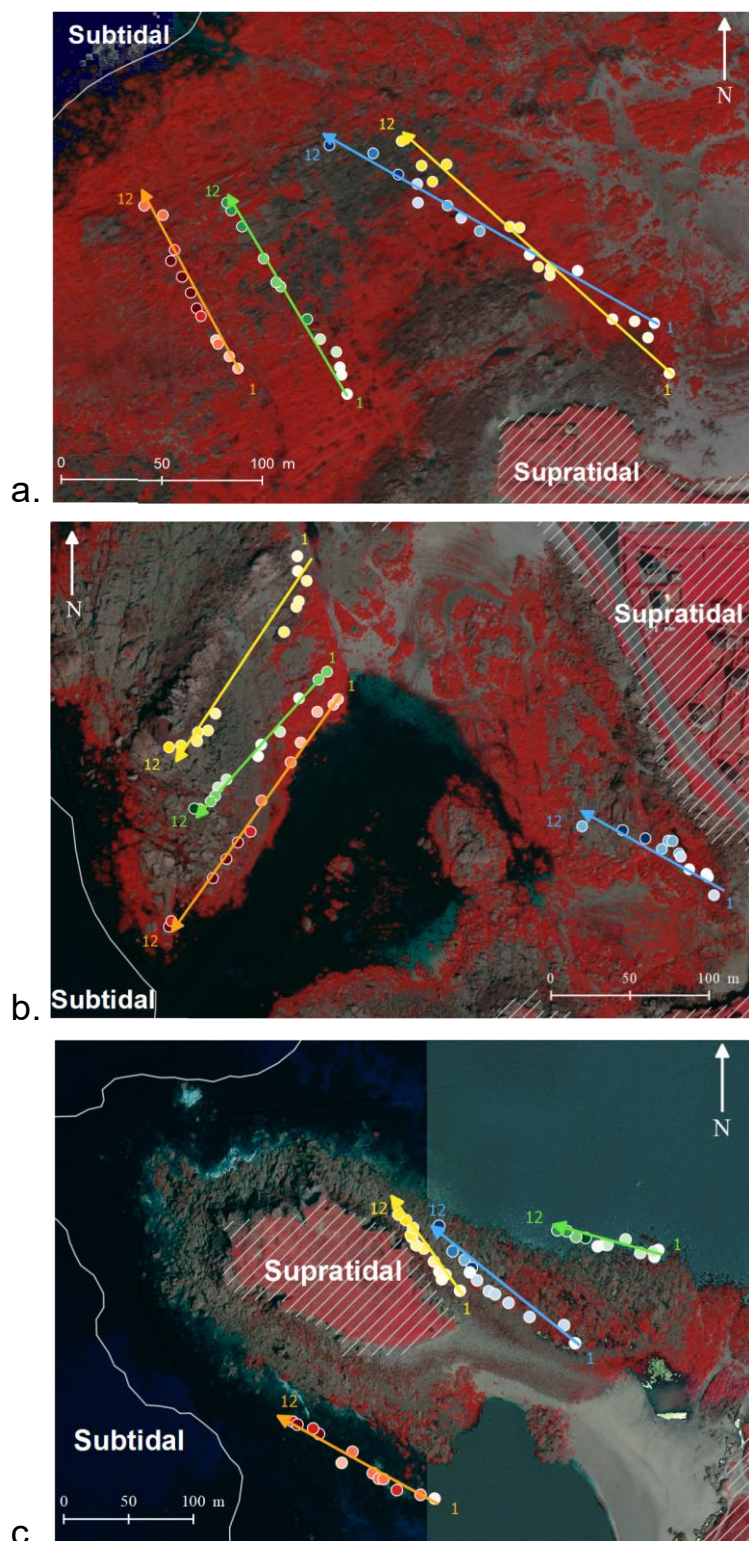
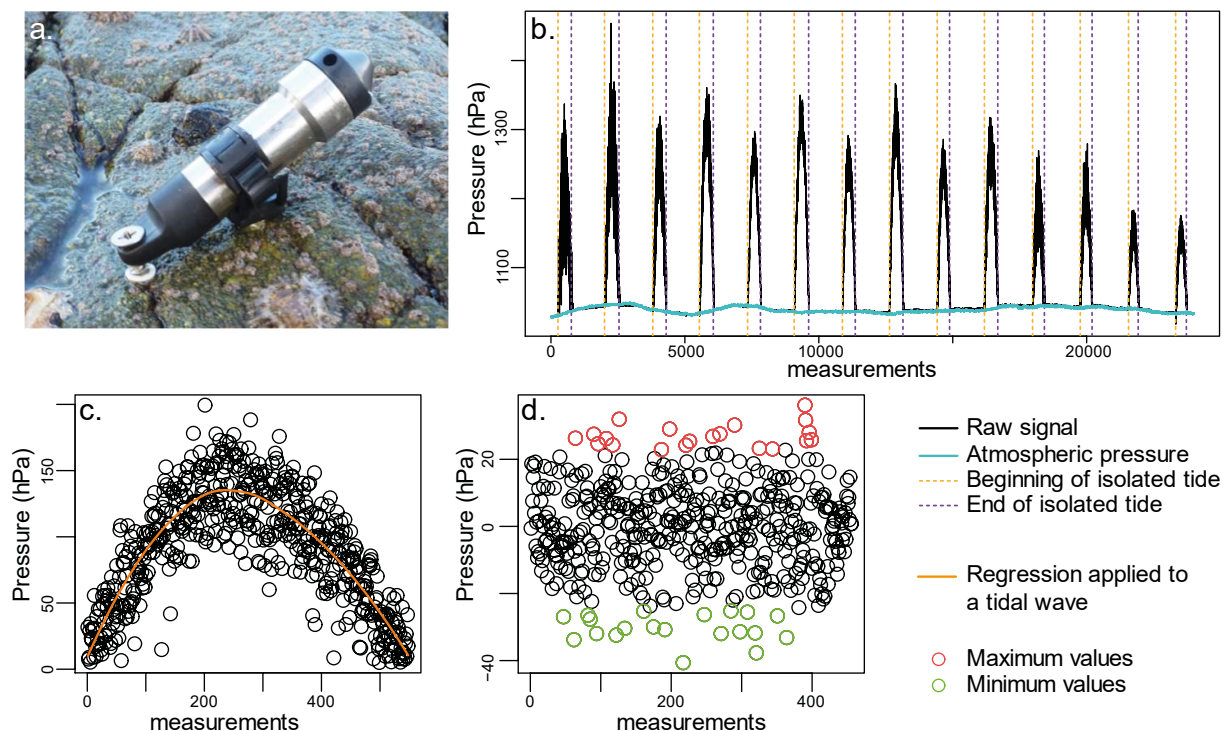
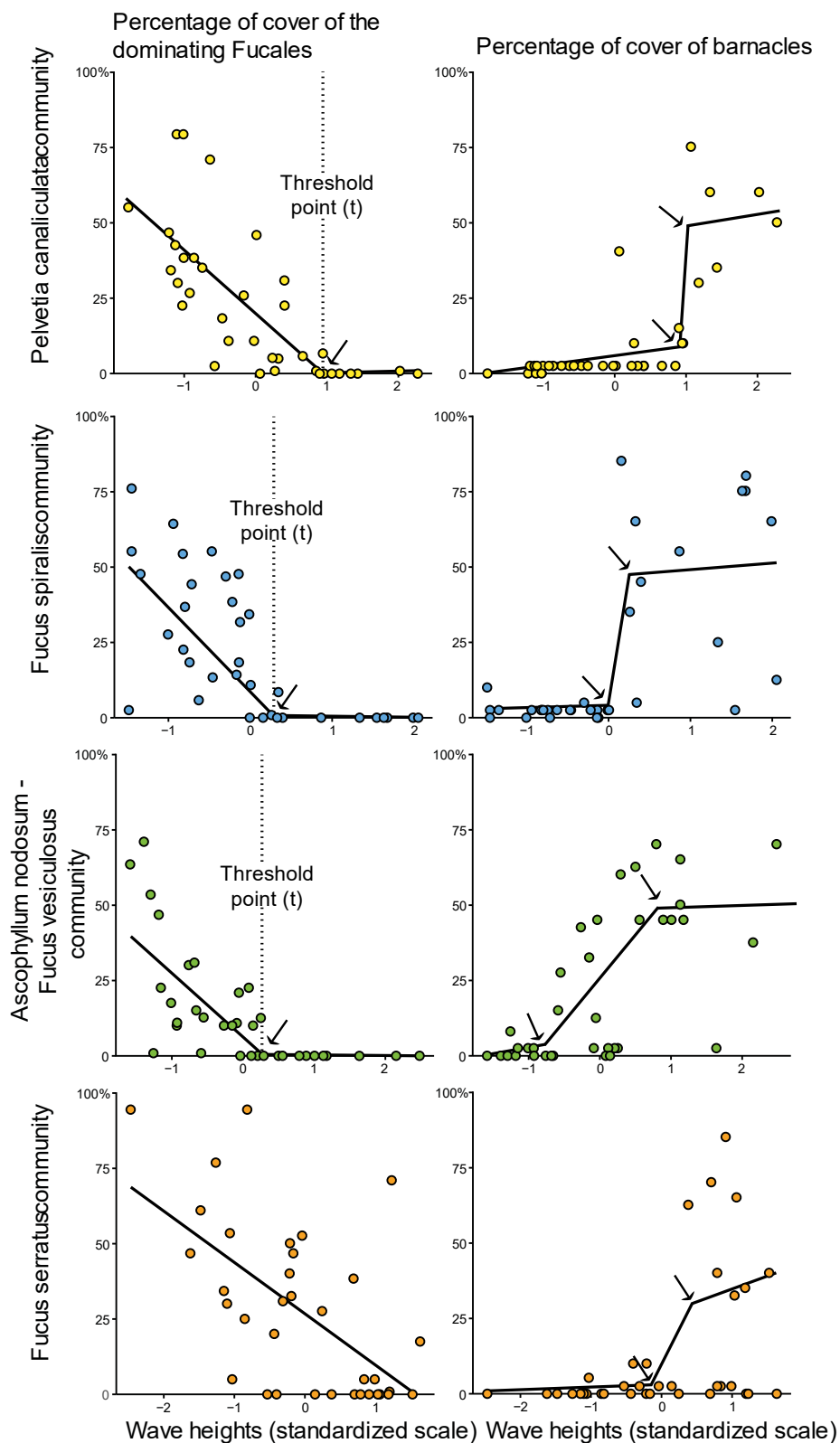


Figure 1: Images of the three studied sites showing the location of the transects and the sampling spots (colored dots). Transects range from area with small wave, represented with light colored dots to large waves with dark colored dots. Sites, **a**: Porsal, **b**: Porspoder, **c**: Segal. Transect color: yellow, *Pelvetia canaliculata*; blue, *Fucus spiralis*; green, *Ascophyllum nodosum*–*Fucus vesiculosus*; red, *Fucus serratus*. Numbers from 1 to 12 correspond to a landward to seaward transect. Background: infrared orthoimage from Finistère - Mégalis Bretagne with vegetation dominated area figured in red and macrofaunal dominated area or bare rock figured in grey. The supratidal zone is presented with dashed lines, whereas the limit of the subtidal zone is figured by a continuous line. *In situ* wave height values are available in Table A1.



1
 2 Figure 2: Presentation of the proxy *in situ* wave height, a. Mini-Diver© recorder placed on the
 3 rocky substratum within an invertebrate-dominated habitat, b. recording obtained for sampling
 4 spot n°1 in the community dominated by *Fucus spiralis* in Porsal between the 15th and the 22nd
 5 of February 2018 (Figure 1), c. example of one of the fourteen tidal cycles isolated for the
 6 calculation of the proxy; a regression is applied to remove the tide oscillation, d. flattened signal
 7 obtained after regression, the difference between the twenty highest (red) and lowest (green)
 8 pressure values are retained and averaged for the calculation of *in situ* wave height for available
 9 tidal cycles (here 14 cycles).

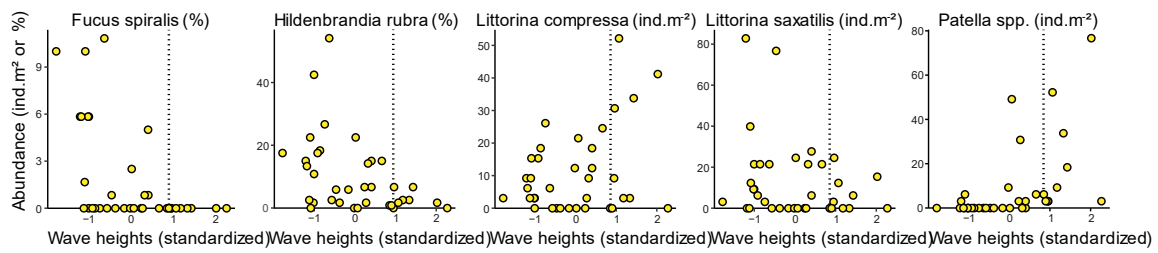
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2 Figure 3: Cover of engineer species on a landward to seaward transect according to *in situ* wave
 3 height on 3 sites of western Brittany. The cover of canopy-forming Fucal species (left column) and
 4 of barnacles (right column) are presented in the 4 studied bathymetric levels and correlated to
 5 normalized wave heights. The fits result from the piecewise regression analysis. Arrows
 6 correspond to estimated break-points and threshold points (t) are represented by dotted lines.

Pelvetia canaliculata community



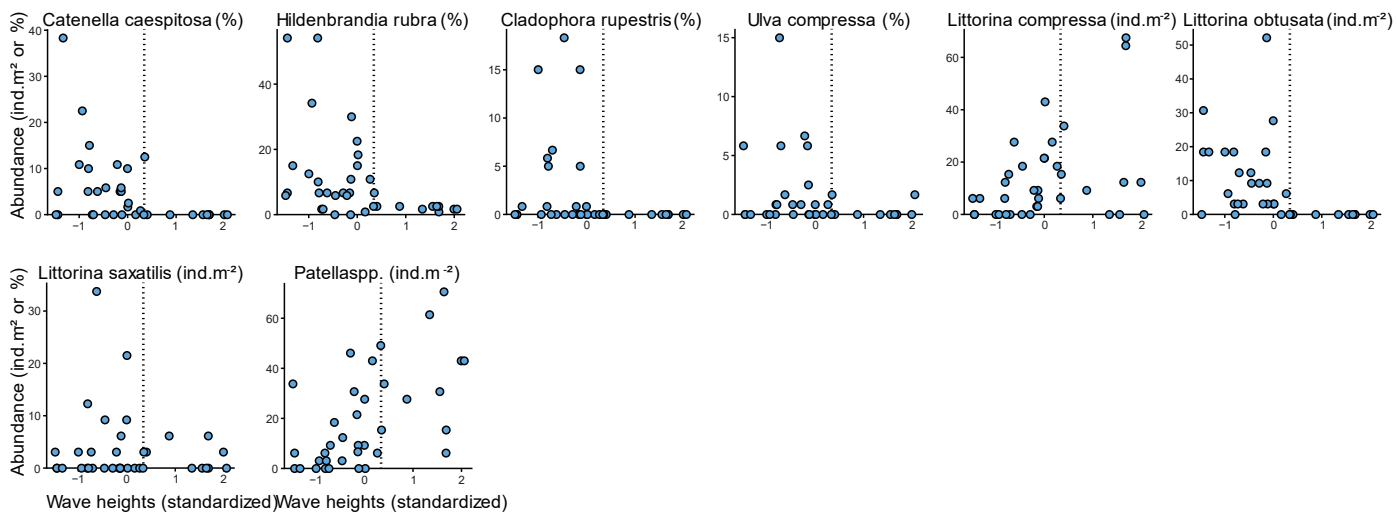
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2 Figure 4: Abundance of the most commonly encountered intertidal organisms in the *Pelvetia*
 3 *canaliculata*-dominated assemblages (6.26 m \pm 0.43, average elevation \pm SD above chart
 4 datum) correlated to normalized *in situ* wave heights. Abundance is given either in cover (%)
 5 or in density (ind.m⁻²). Doted lines delimit the wave height threshold above which *P.*
 6 *canaliculata* is present (*in situ* wave heights below *ca.* 84 cm).

7

1

Fucus spiralis community



2

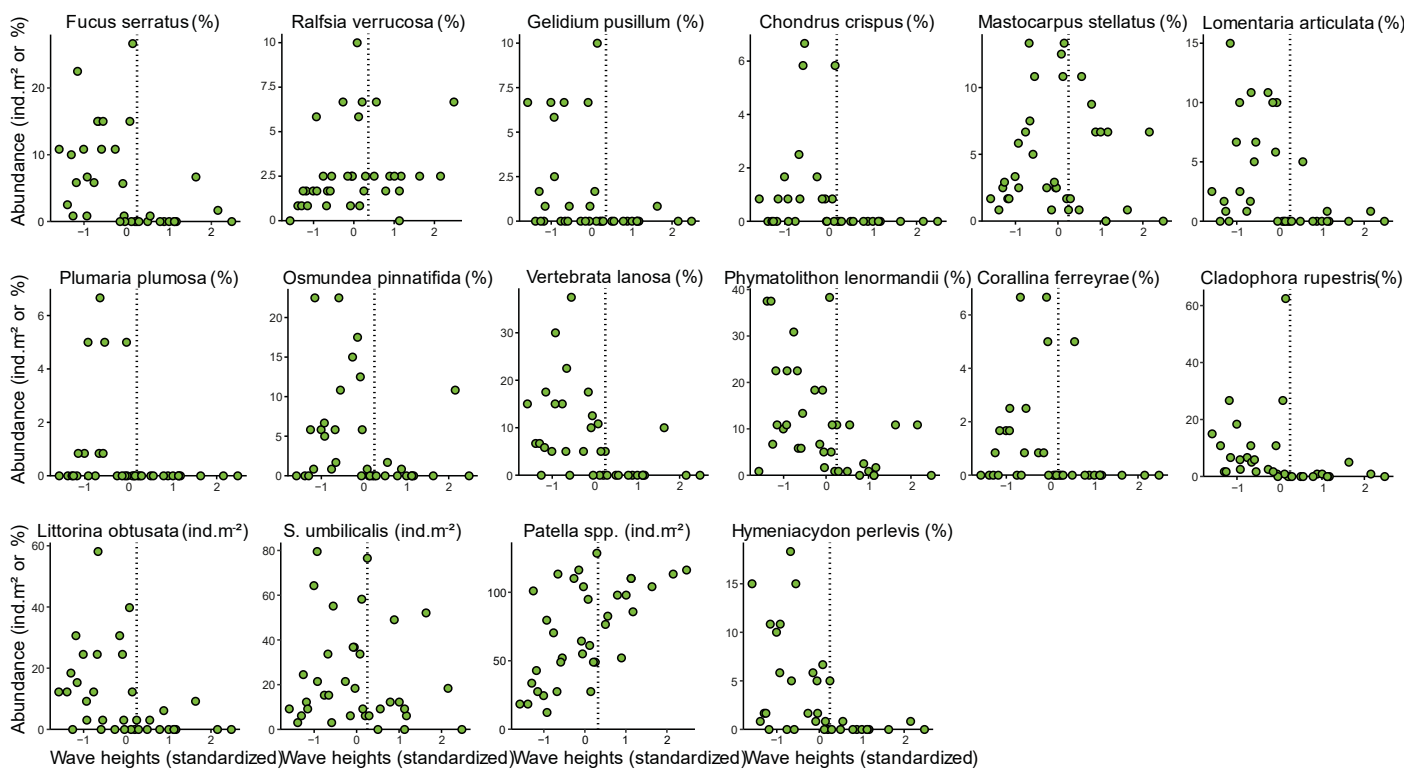
3 Figure 5: Abundance of the most commonly encountered intertidal organisms in the *Fucus*
 4 *spiralis*-dominated assemblage (5.77 m ± 0.43, average elevation ± SD above chart datum)
 5 correlated to normalized in situ wave heights correlated to normalized in situ wave heights.
 6 Abundance is given either in cover (%) or in density (ind.m⁻²). Doted lines delimit the wave
 7 height threshold above which *F. spiralis* is present (*in situ* wave heights below *ca.* 79 cm).

8

9

1

Ascophyllum nodosum - *Fucus vesiculosus* community



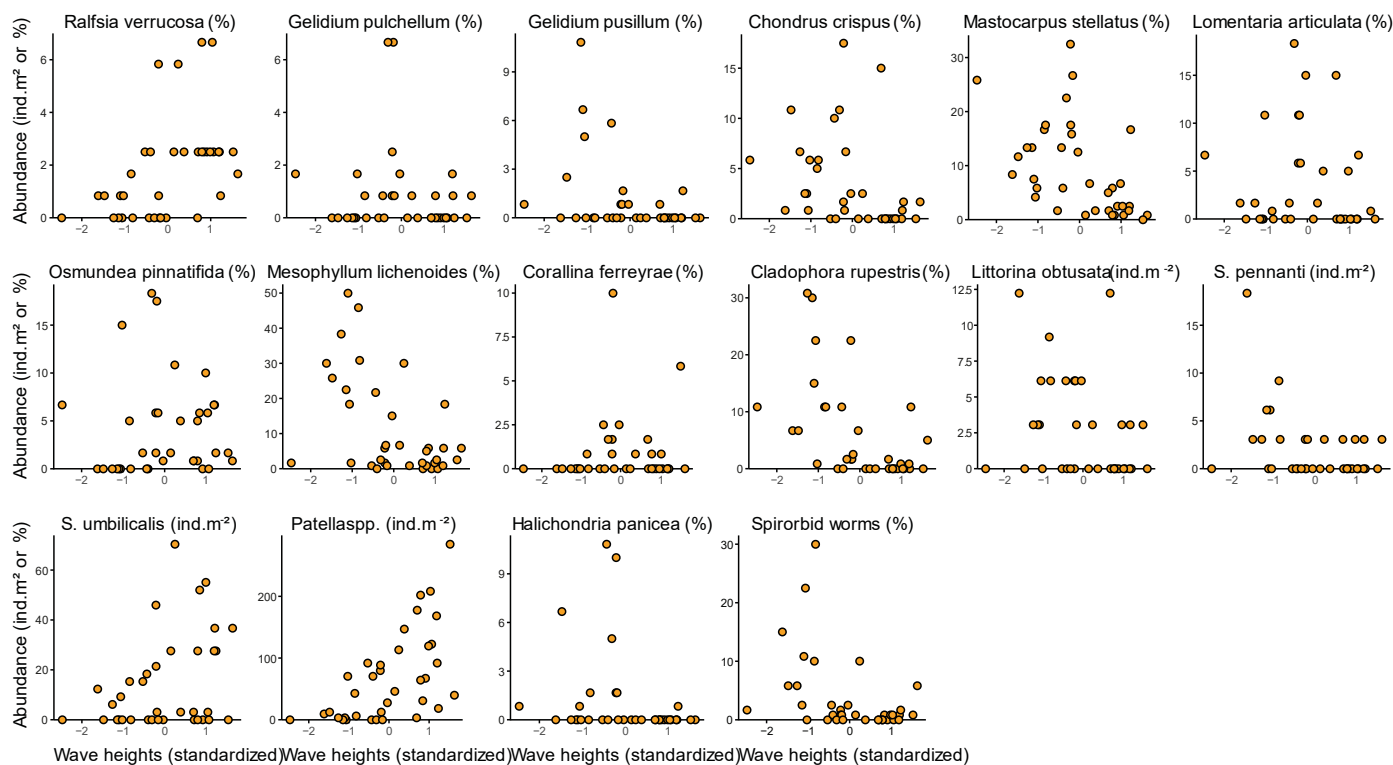
2

3 Figure 6: Abundance of the most commonly encountered intertidal organisms in the
 4 *Ascophyllum nodosum* – *Fucus vesiculosus*-dominated assemblages ($3.83 \text{ m} \pm 0.72$, average
 5 elevation \pm SD above chart datum) correlated to normalized in situ wave heights. Abundance
 6 is given either in cover (%) or in density (ind.m^{-2}). Dotted lines delimit the wave height threshold
 7 above which *A. nodosum* is present (*in situ* wave heights below *ca.* 73 cm).

8

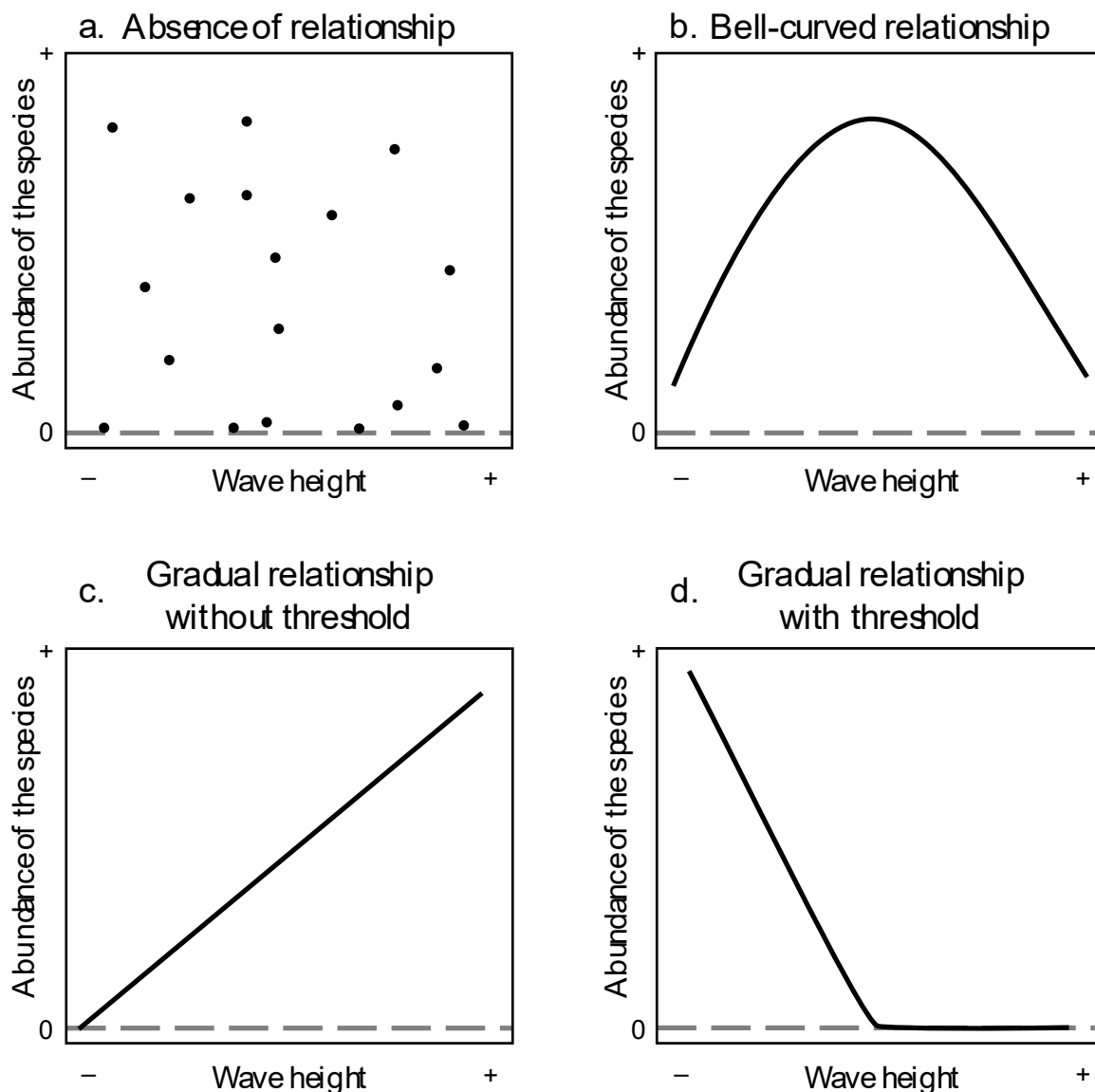
9

Fucus serratus community



1
 2 Figure 7: Abundance of commonly encountered intertidal organisms in *Fucus serratus*-
 3 dominated assemblages ($2.67 \text{ m} \pm 0.37$, average elevation \pm SD above chart datum) correlated
 4 to normalized *in situ* wave heights. Abundance is given either in cover (%) or in density (ind.m⁻²).
 5

6



1
2 Figure 8: Four types of relationship between the abundance of species and wave height. Species
3 or groups of species below are given for all communities in which they occur, unless specified,
4 a. Absence of relationship, *e.g.* *Steromphala umbilicalis* in *An - Fves* and *Lomentaria articulata*
5 in *Fser*. b. Bell-curved relationship, *e.g.* *Mastocarpus stellatus* in *An - Fves* c. Gradual
6 relationship, *e.g.* positive regression, limpets, *Littorina compressa*; negative: *Fucus serratus* d.
7 Gradual relationship with threshold, *e.g.* positive regression, barnacles; negative: *Pelvetia*
8 *canaliculata*, *Fucus spiralis*, *Ascophyllum nodosum*. The dotted line corresponds to an absence
9 of the taxon.

1 **Appendices**

1 Table A1: *in situ* wave heights obtained in each sampling spot per community and site during
 2 a one week-monitoring (24000 pressure data per sampling spot). Values corresponds to the
 3 difference between the average of the twenty highest and lowest pressure values of each
 4 flattened signal (between 12 and 14 tide cycles, see Figure 2). Wave height values are given in
 5 cm. Numbers in the first column correspond to a landward to seaward transect and refer to the
 6 numbers of Figure 1. *Pc* = *Pelvetia canaliculata*, *Fspi* = *Fucus spiralis*, *An - Fves* =
 7 *Ascophyllum nodosum* – *Fucus vesiculosus*, *Fser* = *Fucus serratus*.

n° Transect	Site	<i>Pc</i>	<i>Fspi</i>	<i>An - Fves</i>	<i>Fser</i>
1	a) Porsal	34.42	43.50	24.54	32.99
2	a) Porsal	44.36	42.28	25.58	34.11
3	a) Porsal	46.27	45.68	26.87	34.60
4	a) Porsal	57.47	45.83	31.56	34.54
5	a) Porsal	54.46	60.95	32.71	36.74
6	a) Porsal	65.86	58.07	58.26	38.72
7	a) Porsal	72.72	61.09	42.84	39.53
8	a) Porsal	72.68	49.38	42.34	38.67
9	a) Porsal	77.19	52.57	41.37	37.94
10	a) Porsal	82.38	90.28	53.12	36.54
11	a) Porsal	90.65	86.32	49.95	35.44
12	a) Porsal	88.97	98.58	51.25	35.18
1	b) Porspoder	50.39	75.15	70.36	35.10
2	b) Porspoder	50.31	53.84	71.34	37.36
3	b) Porspoder	58.29	51.91	43.77	38.25
4	b) Porspoder	54.79	51.91	58.21	30.86
5	b) Porspoder	52.95	74.91	52.94	51.31
6	b) Porspoder	90.51	77.44	54.20	55.57
7	b) Porspoder	63.54	83.36	68.15	75.32
8	b) Porspoder	87.99	81.86	68.45	79.19
9	b) Porspoder	106.55	84.28	73.68	83.06
10	b) Porspoder	89.04	106.67	77.05	80.65
11	b) Porspoder	116.40	106.76	81.67	73.65
12	b) Porspoder	149.51	80.10	108.65	77.67
1	c) Segal	60.74	62.76	61.70	39.78
2	c) Segal	58.11	65.86	62.23	43.71
3	c) Segal	59.11	63.54	64.14	45.17
4	c) Segal	59.68	68.94	63.07	43.46
5	c) Segal	74.84	68.20	63.72	43.93
6	c) Segal	77.17	67.46	63.99	43.67
7	c) Segal	71.33	63.29	62.99	43.63
8	c) Segal	92.98	56.28	61.46	42.24
9	c) Segal	92.20	89.64	69.24	44.64
10	c) Segal	78.57	73.37	65.60	46.60
11	c) Segal	110.61	78.46	66.90	45.76
12	c) Segal	94.97	85.69	66.90	45.34

1 Table A2: Maximum seawater and air temperatures determined through Mini-Diver©
 2 recorders, average values and standard deviations of elevation determined via GIS treatment
 3 with the corresponding recording periods per community and site. Assemblages dominated by:
 4 *Pc* = *Pelvetia canaliculata*, *Fspi* = *Fucus spiralis*, *An - Fves* = *Ascophyllum nodosum* – *Fucus*
 5 *vesiculosus*, *Fser* = *Fucus serratus*

Community	Site	Seawater temperature (°C)	Air temperature (°C)	Elevation (m)	Sampling period
<i>Pc</i>	Segal	9.7- 11.2	1.3 - 15.3	6.07 ± 0.45	30/01/18 to 06/02/18
	Porspoder	9.4 - 11.6	1.9 - 19.0	6.30 ± 0.34	
	Porsal	9.6 - 11.4	1.3 - 16.3	6.41 ± 0.40	
<i>Fspi</i>	Segal	9.7 - 10.6	1.2 - 21.2	5.66 ± 0.44	15/02/18 to 22/02/18
	Porspoder	9.2 - 10.7	0.5 - 21.0	5.72 ± 0.38	
	Porsal	9.3 - 10.5	1.3 - 21.9	5.93 ± 0.43	
<i>An - Fves</i>	Segal	9.2 - 10.2	6.4 - 16.7	3.31 ± 0.25	06/03/18 to 13/03/18
	Porspoder	9.4 - 10.2	6.4 - 16.4	3.44 ± 0.24	
	Porsal	9.2 - 10.2	6.4 - 20.0	4.74 ± 0.35	
<i>Fser</i>	Segal	11.2 - 12.3	5.8 - 21.6	2.60 ± 0.38	23/04/18 to 30/04/18
	Porspoder	11.1 - 12.3	6.0 - 26.6	2.85 ± 0.37	
	Porsal	11.3 - 12.1	6.6 - 20.0	2.56 ± 0.27	