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1 Long-term survey of intertidal rocky shore macrobenthic community metabolism and structure after  
2 primary succession

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7 Short title Succession in intertidal rocky shore

8 Abstract

9 Ecological succession involves the transition from opportunistic ephemeral species, which display a  
10 minimal variation in functional traits, to slow growing, more functionally diverse, perennial species.  
11 The present study aimed in measuring the functional effect of changes in the community structure  
12 through succession and to compare the timing of successional sequences in communities dominated  
13 by canopy-forming algae established at two levels of the emersion gradient in a rocky shore. Granite  
14 slabs were set at two tidal levels, in the *Fucus vesiculosus* and *F. serratus* areas, in February 2013.  
15 Communities settled on the slabs during the first year exhibited low *Fucus* density ( $\approx 6$  ind  $m^{-2}$ ), low  
16 taxa richness ( $\approx 17$  taxa) and low metabolic activity (gross primary production, GPP, about 100 mg C  
17  $m^{-2} h^{-1}$ ) at both levels. Communities established on the slabs were similar to the surrounding  
18 communities for the 5 and 3 following years in the *F. vesiculosus* and *F. serratus* area respectively.  
19 Communities were then characterized by high *Fucus* density ( $\approx 35$  and  $67$  ind  $m^{-2}$ ), high taxa richness  
20 ( $\approx 26$  and  $39$  taxa) and high metabolic activity (GPP  $\approx 350$  and  $550$  mg C  $m^{-2} h^{-1}$ ). However, *Fucus*  
21 populations did not persist on slabs on which communities turned into limpet dominated, with low  
22 *Fucus* density, low taxa richness and low metabolic activity. 10 years after the slabs setting, limpet  
23 densities averaged 34 and 92 ind  $m^{-2}$ . Given the long life-span of *Fucus* and *Patella*, the survey needs  
24 to be pursued to test for cyclical changes of dominance.

25 Key words

26 Field experiment; Temporal scale; Canopy forming macroalgae; Emersion gradient; Biotic interactions

27 Introduction

28 Rocky shores are naturally disturbed environments where secondary and tertiary successions occur  
29 due, notably, to direct and indirect action of waves removing biota (Hawkins, Pack, Hyder, Benedetti-  
30 Cecchi, & Jenkins, 2020). Patchiness is thus a fundamental feature of most rocky shores where  
31 macrobenthic communities correspond to mosaics of species assemblages on various spatial scales in  
32 different succession stages, from cleared rock to complete cover by a dominant species (Raffaelli &  
33 Hawkins, 1999). Primary succession, the colonization of virgin substrata, can also be initiated on rocky  
34 shores, either naturally by flaking of the rock or artificially by the placement of human-made  
35 structures. The early physicochemical events occurring over very short time periods allow the rapid  
36 colonisation of bare substrata by bacteria and diatoms. After this microbiotic phase, the macrobiotic  
37 succession on rocky shores typically involves a transition from a suite of opportunistic and ephemeral  
38 species which display minimal variation in functional traits, to a more functionally diverse mature,  
39 more or less stable, community including slow-growing perennial species (Noël et al., 2009). This  
40 general pattern and the mechanisms implied in the replacement of species are influenced by a number  
41 of physical and biological factors. Macrobiotic succession on rocky shores is thus highly variable and  
42 context dependent. Furthermore, on most rocky shores, it is likely that succession never stops with  
43 small-scale disturbances opening up resources all the time (Raffaelli & Hawkins, 1999) and the

44 perception of the establishment of a stable community is largely temporal scale dependent (Jenkins &  
45 Uya, 2016).

46 On sheltered and semi-exposed intertidal rocky shores, the mature community is often characterized  
47 by canopy-forming brown algae. Canopy-forming algae are foundation species that play a pivotal role  
48 by mitigating stressful abiotic conditions (Bulleri, 2009) and constitute highly productive systems  
49 (Mann, 1973). Loss or reduction of canopy-forming algae, as a consequence of local and global  
50 stressors, have direct and indirect effects on benthic communities, reflected in diversity and  
51 abundance reductions, shifts in composition and ecosystem functioning (Mineur et al., 2015). There is  
52 thus a clear need to understand the mechanisms that control their establishment and persistence.  
53 Succession has been the focus of intensive research on rocky shores (Hawkins et al., 2020 and  
54 references therein) but few studies have explicitly measured changes in community primary  
55 production through succession from opportunistic ephemerals to dense canopy. A species-specific  
56 productivity decrease with increasing successional status is predictable but differences in the  
57 productivity of component species, measured per unit biomass, do not necessarily scale to the  
58 productivity of the community as a whole (Noël et al., 2009).

59 The present study associates long-term macrobenthic community primary production measurements  
60 and community structure assessments over succession initiated experimentally by placing bare  
61 substrata in a semi-exposed intertidal rocky shore. The experiment was conducted in two communities  
62 adjacent over the emersion gradient, the mid and low-mid intertidal communities dominated by  
63 canopy-forming algae, *Fucus vesiculosus* and *Fucus serratus* respectively. These communities consist  
64 of dense and complex assemblages composed of *Fucus spp* with associated epibiont and understory  
65 algae and invertebrates. Both communities exhibit high metabolic activity, gross community primary  
66 production reaching  $1 \text{ gC m}^{-2} \text{ h}^{-1}$  during spring and summer midday emersions (Bordeyne, Migné, &  
67 Davoult, 2015). Experimental bare substrata units consisted on slabs built with materials of the same  
68 nature of the rock and which surface was made rough as surrogates of the natural habitat. Those slabs  
69 were spread out in winter in the established communities to be influenced by the same local  
70 environmental variation and supply of propagules. With this survey, we intended to measure the  
71 functional effect of changes in the community structure through succession and to compare the timing  
72 of successional sequences at two levels of the emersion gradient in a rocky shore system. We  
73 hypothesized that, due to harsher environmental conditions, the timing of successional sequences  
74 would be slower in the mid intertidal than in the low-mid intertidal.

75

## 76 Materials and Methods

### 77 Study site and experiment set up

78 This experiment was conducted on an intertidal boulder reef (Karreg Ar Vraz) located in front of the  
79 Roscoff Marine Station (48°43.754'N, 3°59.420'W) in the southwestern part of the English Channel.  
80 This semi-exposed shore is subjected to a semi-diurnal tidal cycle, with a maximal range of about 9 m.  
81 It presents a typical vertical distribution of communities dominated by canopy-forming brown algae.  
82 The mid-intertidal level (3.0 to 4.0 m above chart datum) is characterized by a *Fucus vesiculosus*  
83 community and the low mid-intertidal level (2.5 to 3.0 m above chart datum) is characterized by a  
84 *F. serratus* community. At the mid-intertidal level, *F. vesiculosus* density is about  $45 \text{ ind m}^{-2}$ , accounting  
85 for 2 to  $5 \text{ kg}_{\text{FW}} \text{ m}^{-2}$  according to the season (Bordeyne, 2016). At the low mid-intertidal level, *F. serratus*  
86 density is about  $70 \text{ ind m}^{-2}$  accounting for 2 to  $12 \text{ kg}_{\text{FW}} \text{ m}^{-2}$  (Bordeyne, 2016). Both communities are  
87 known to exhibit high metabolic activity year-round: gross primary production in the range 400-1000

88 mg C m<sup>-2</sup> h<sup>-1</sup> and respiration in the range 100-500 mg C m<sup>-2</sup> h<sup>-1</sup>, when measured at the beginning of  
89 emersion period (Bordeyne et al., 2015).

90 In February 2013, bare granite slabs (0.4 × 0.4 m) with rough surface were haphazardly attached (as  
91 flat as possible) to large boulders of the mid-intertidal level in the *F. vesiculosus* area and of the low  
92 mid-intertidal level in the *F. serratus* area of the Karreg Ar Vraz site. Slabs (21 in the *F. vesiculosus* area,  
93 20 in the *F. serratus* area) were arranged to be 1 to 3 m away one from each other within areas, and  
94 were separated by a distance of approx. 30 m between areas.

#### 95 Macrobenthic community metabolism

96 The metabolism of settled communities was assessed from March 2013 to September 2019 (i.e. from  
97 one month to 78 months, 6.5 years, after the setup of slabs), with a delay between two sampling dates  
98 varying from 1 to 7 months (leading to a total of 25 sampling dates). At each sampling date, metabolism  
99 of settled communities was assessed on 3 to 7 randomly chosen slabs in each area. Metabolism was  
100 assessed by measuring carbon dioxide (CO<sub>2</sub>) fluxes at the air-slab interface inside benthic chambers, at  
101 the onset of emersion period of spring tides (around midday). This period has previously been shown  
102 to be the most favourable for primary production of such intertidal furoid stands (Migné, Duong,  
103 Menu, Davoult, & Gévaert, 2021). Each benthic chamber, which is made of a transparent Perspex®  
104 dome with a transparent air-tight Perspex® base, has a covering surface of 0.3 x 0.3 m and a total  
105 volume of 17.7 or 26.5 L (depending on the amount of *Fucus* settled on the slabs). It was sealed to the  
106 slab (using bungees) and was connected to an infrared CO<sub>2</sub> gas analyzer (LiCor Li-820) in a closed air  
107 circuit (with a flow of about 1 L min<sup>-1</sup>). CO<sub>2</sub> air concentration (μmol<sub>CO<sub>2</sub></sub> mol<sub>air</sub><sup>-1</sup>) was recorded every 15  
108 s for 5 to 15 min during incubation to calculate CO<sub>2</sub> fluxes as described in Migné *et al.* (2002). Net  
109 community production (NCP) and community respiration (CR) were examined successively in ambient  
110 light and in darkness (by covering the chamber), respectively. Photosynthetically available radiations  
111 (PAR, in μmol of photons m<sup>-2</sup> s<sup>-1</sup>) were measured close to the incubation chambers, using a planar  
112 sensor (Li-Cor QuantumSA-190). PAR were recorded every minute to ensure that measurements in  
113 ambient light were performed under saturating irradiance. That is PAR levels above the onset of light  
114 saturation which was previously determined to vary seasonally between 250 and 800 μmol m<sup>-2</sup> s<sup>-1</sup> for  
115 the *F. vesiculosus* community and between 200 and 500 μmol m<sup>-2</sup> s<sup>-1</sup> for the *F. serratus* community  
116 (Bordeyne, 2016). Benthic chambers were opened between two consecutive incubations to renew the  
117 ambient air. Gross community production (GCP) was calculated as the sum of NCP and CR. Metabolic  
118 rates were calculated according to the covering surface of incubation chambers (i.e. 0.09 m<sup>2</sup>) and  
119 expressed in carbon units (mg C m<sup>-2</sup> h<sup>-1</sup>) assuming a molar volume of 22.4 L mol<sup>-1</sup> at standard  
120 temperature and pressure and a molar mass of 12 g C mol<sub>CO<sub>2</sub></sub><sup>-1</sup>.

#### 121 Macrobenthic community structure

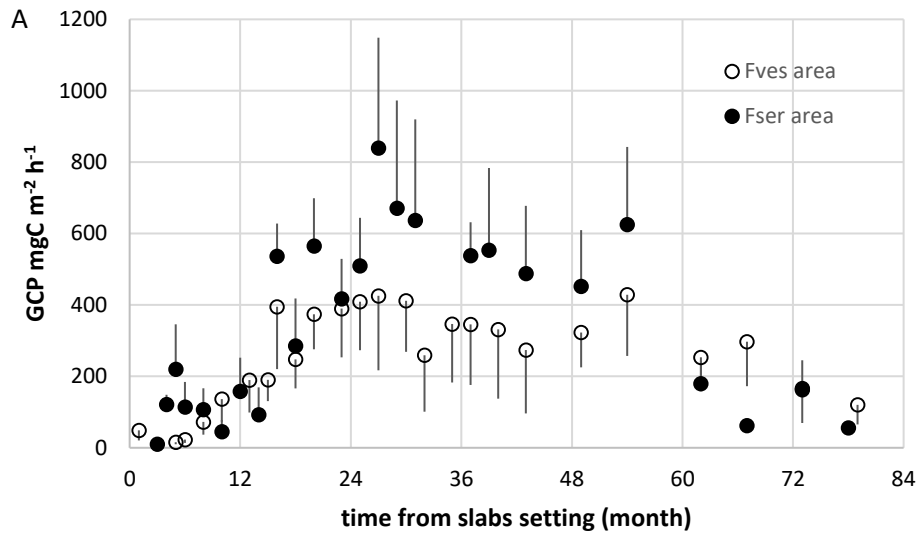
122 The survey of the structure of settled communities started as far as some settled *Fucus* were  
123 identifiable to the species level, that was in September 2013 (i.e. seven months after the setup of slabs)  
124 and continued until March 2023 (i.e. 121 months, 10 years, after the setup of slabs). Non-destructive  
125 sampling of biota colonising the slabs was conducted during low tide, every 3 months until September  
126 2016 and then every 6 months (leading to a total of 25 sampling dates in each area). Algae and  
127 invertebrates were identified in the field to the lowest possible taxonomic level, being usually the  
128 species level but genus, family, or order level for some colonial invertebrates (e.g. bryozoans,  
129 ascidians) and morphologically similar taxa (e.g. ectocarpales, amphipods). Density was determined  
130 for *Fucus* identifiable to the species level and for countable invertebrates (e.g. gastropod species).  
131 Identification and count were done on all available slabs (i.e. not detached and returned during the  
132 survey) in the *F. vesiculosus* area (21 slabs until March 2017 and 17 to 14 slabs from September 2017

133 to March 2023), on all available slabs in the *F. serratus* area (20 slabs until June 2015 and 19 to 15 slabs  
134 from March 2018 to March 2023) or on 9 to 12 haphazardly chosen slabs at the period of the highest  
135 colonisation by *Fucus* (from September 2015 to September 2017).

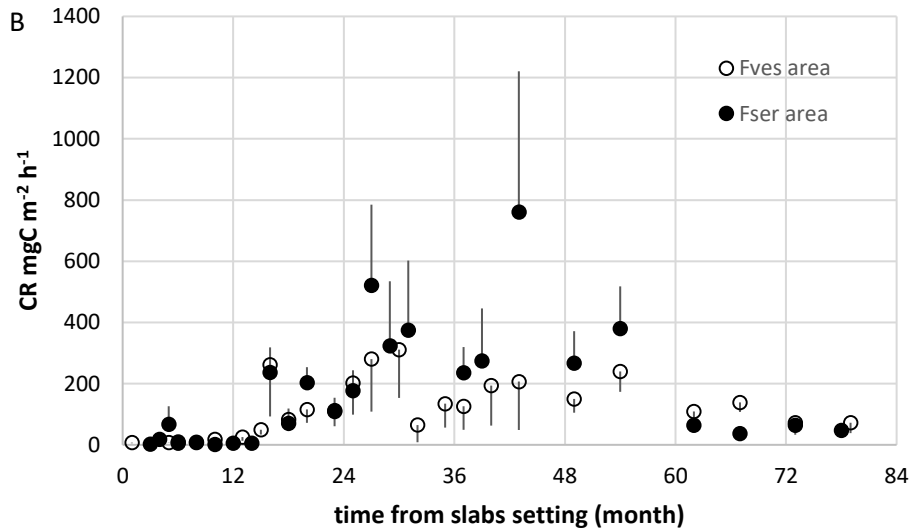
136 Before any data analysis, the sampling effort was homogenised by randomly selecting 9 slabs among  
137 the slabs on which the structure of the macrobenthic community was assessed at each sampling date,  
138 in each area. Given the small size of the slabs and the high small spatial scale variability on rocky shores,  
139 data were pooled for the 9 slabs (representing a sampling surface of 1.44 m<sup>2</sup>) to better highlight the  
140 temporal variability of diversity metrics in each area. Shannon diversity and Pielou evenness were  
141 calculated based on abundance data of countable invertebrates obtained after pooling the 9 slabs at  
142 each sampling date in each area. Pooling the data for the 9 slabs also allowed to calculate the  
143 occurrence of each taxa (as the number of slabs bearing the taxa among the 9 slabs) and to analyse  
144 similarities between sampling dates and areas based on quantitative data for all the observed taxa.  
145 Bray-Curtis similarity was calculated between every pair of samples (in a 72 taxa x 50 samples matrix  
146 using the software PRIMER). Samples were then grouped by hierarchical clustering (group-average  
147 link) based on the Bray-Curtis similarities to explore spatio-temporal structuring.

148 Results

149 Macrobenthic community metabolism



150



151

152 **Figure 1.** Mean gross community primary production (GCP, A) and community respiration (CR, B) measured over time on  
 153 slabs set in the *Fucus vesiculosus* (Fves) and *Fucus serratus* (Fser) areas. Error bars indicate standard errors ( $3 \leq n \leq 7$ )

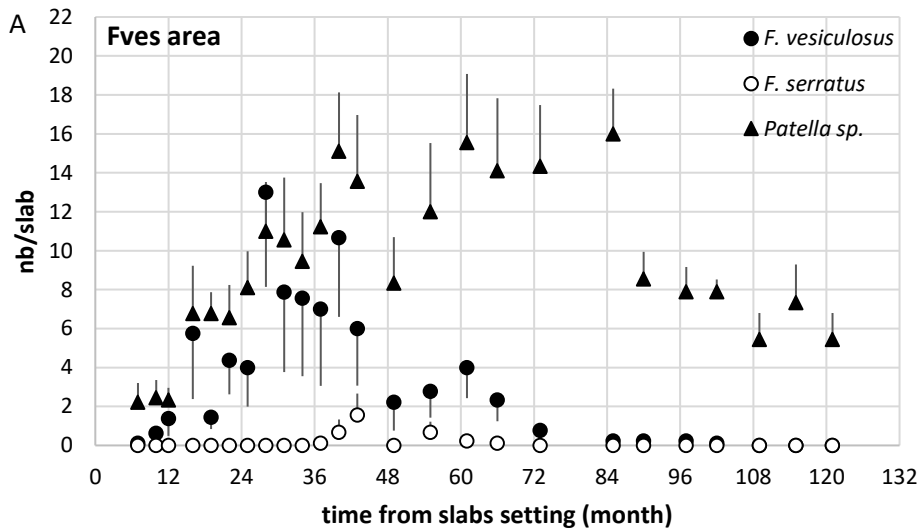
154 Metabolism of the macrobenthic communities settled on the slabs over the 6.5-year survey showed  
 155 the same global temporal trend at the two intertidal levels, reaching higher rates in the lower level  
 156 (i.e. in the *Fucus serratus* area, Figure 1).

157 Mean ( $\pm$  se) gross community production (GCP) measured on slabs set at mid-intertidal level in the *F.*  
 158 *vesiculosus* area ranged from  $15.53 \pm 5.72$  to  $428.58 \pm 171.35$  mg C m<sup>-2</sup> h<sup>-1</sup>. The minimum and the  
 159 maximum were observed 5 and 54 months after the slabs setting respectively (Figure 1A). Mean GCP  
 160 measured on slabs set at low mid-intertidal level in the *F. serratus* area ranged from  $10.60 \pm 8.70$  to  
 161  $839.44 \pm 309.13$  mg C m<sup>-2</sup> h<sup>-1</sup>. The minimum and the maximum were observed 3 and 27 months after  
 162 the slabs setting respectively (Figure 1A).

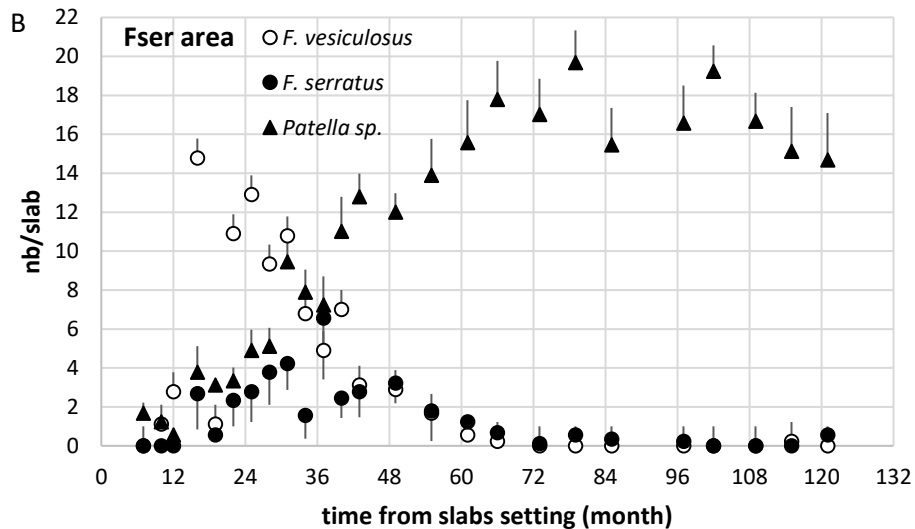
163 Mean ( $\pm$  se) community respiration (CR) measured on slabs set at mid-intertidal level in the *F.*  
 164 *vesiculosus* area ranged from  $5.80 \pm 0.92$  to  $311.08 \pm 157.76$  mg C m<sup>-2</sup> h<sup>-1</sup>. The minimum and the  
 165 maximum were observed 6 and 30 months after the slabs setting respectively (Figure 1B). Mean CR  
 166 measured on slabs set at low mid-intertidal level in the *F. serratus* area ranged from  $1.25 \pm 0.75$  to

167 761.02 ± 459.58 mg C m<sup>-2</sup> h<sup>-1</sup>. The minimum and the maximum were observed 10 and 43 months after  
168 the slabs setting respectively (Figure 1B).

169 Macrobenthic community structure



170



171

172 **Figure 2.** Mean number of individuals of *Fucus vesiculosus*, *Fucus serratus* and *Patella sp.* observed over time per slab (0.4 x  
173 0.4 m) set in the *F. vesiculosus* (Fves, A) and *F. serratus* (Fser, B) areas. Error bars indicate standard errors (n = 9)

174 First *Fucus* individuals settled on slabs that were identifiable to the species level were *Fucus vesiculosus*  
175 individuals in both areas (7 and 10 months after the slabs setting in the *F. vesiculosus* and *F. serratus*  
176 area respectively). Their density increased rapidly to reach a mean (± se) of 13 ± 5 ind/slab (28 months  
177 after the slabs setting) in the *F. vesiculosus* area (Figure 2A) and of 15 ± 4 ind/slab (16 months after the  
178 slabs setting) in the *F. serratus* area (Figure 2.B.). The *F. vesiculosus* density then decreased in both  
179 areas with mean less than 1 ind/slab since March 2019 (72 months after the slabs setting) in the *F.*  
180 *vesiculosus* area (Figure 2A) and since March 2018 (61 months after the slabs setting) in the *F. serratus*  
181 area (Figure 2B).

182 Few *Fucus serratus* individuals settled on slabs set in the *F. vesiculosus* area (with a mean in the range  
183 0.1-1.6 ind/slab during the period 37-66 months after the slabs setting, Figure 2A). *F. serratus*

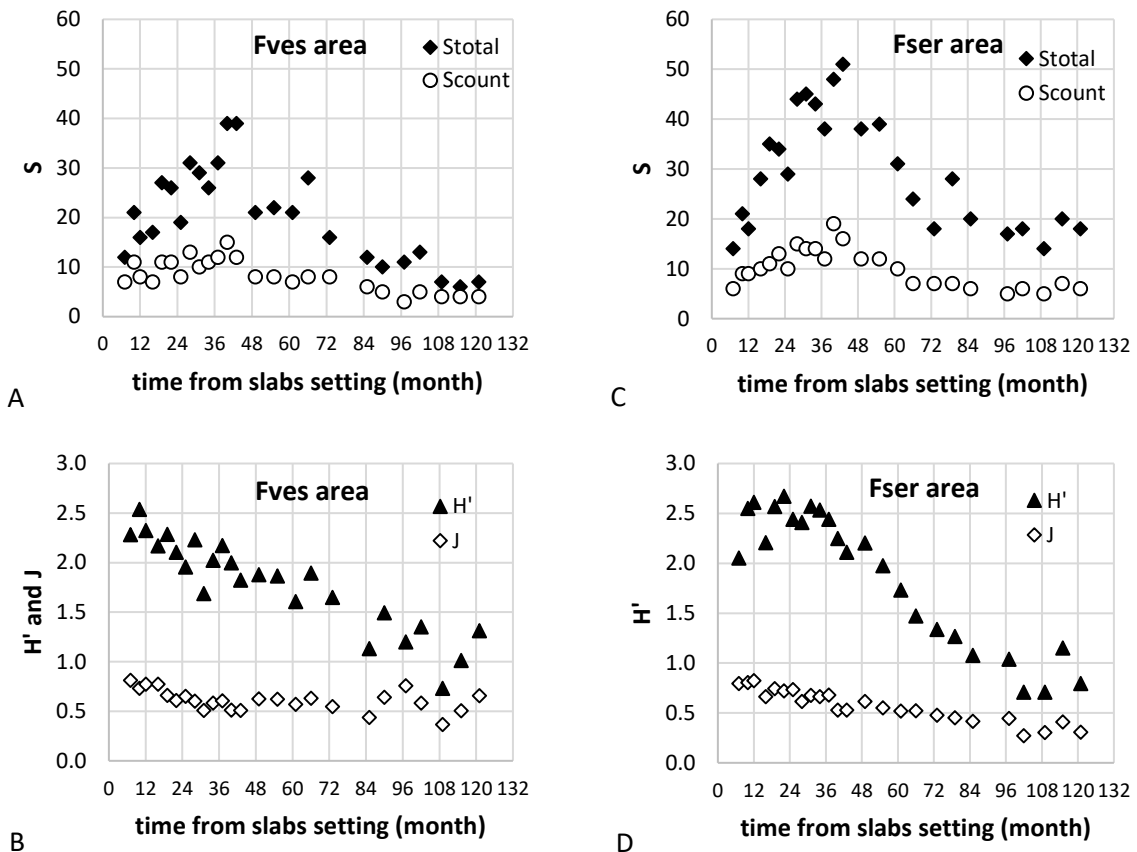
184 individuals were identifiable on slabs set in the *F. serratus* area 16 months after the slabs setting, at a  
185 mean density of  $3 \pm 2$  ind/slab (Figure 2B). Their mean density increased to  $7 \pm 3$  ind/slab 37 months  
186 after the slabs setting and then decreased to less than 1 ind/slab 66 months after the slabs setting  
187 (Figure 2B).

188 At the beginning of the survey, the *Patella sp.* density increased concurrently with the *F. vesiculosus*  
189 density on slabs in the *F. vesiculosus* area and with *F. serratus* density on slabs in the *F. serratus* area.  
190 The *Patella sp.* density continued to increase when *Fucus* densities decreased and its mean reached a  
191 maximum of 16 ind/slab (85 months after the slabs setting) in the *F. vesiculosus* area (Figure 2A) and  
192 of 20 ind/slab (79 months after the slabs setting) in the *F. serratus* area (Figure 2B). The *Patella sp.*  
193 density decreased at the end of the survey and, 121 months after the slabs setting, its mean was 5  
194 ind/slab in the *F. vesiculosus* area (Figure 2A) and 15 ind/slab in the *F. serratus* area (Figure 2B).

195 Mean ( $\pm$  se) taxa richness per slab (0.4 x 0.4 m), including macroalgae and invertebrates, varied over  
196 the survey in the range  $3.4 \pm 0.4$  -  $16.4 \pm 3.3$  in the *F. vesiculosus* area and in the range  $5.4 \pm 1.0$  -  $21.9$   
197  $\pm 3.7$  in the *F. serratus* area. The maximum was observed in June 2016 (40 months after the slabs  
198 setting) in both areas. On the 9 pooled slabs (i.e. sampling surface of 1.44 m<sup>2</sup>), total taxa richness ( $S_{total}$ )  
199 varied in the range 6 - 39 in the *F. vesiculosus* area and in the range 7 - 51 in the *F. serratus* area, with  
200 a maximum observed in June and September 2016 (40 and 43 months after the slabs setting) in the *F.*  
201 *vesiculosus* area (Figure 3A) and in September 2016 in the *F. serratus* area (Figure 3C). Richness in  
202 countable invertebrates ( $S_{count}$ ) varied in the range 3 - 15 in the *F. vesiculosus* area (Figure 3A) and in  
203 the range 5 - 19 in the *F. serratus* area (Figure 3C), with a maximum observed in June 2016 in both  
204 areas. Shannon diversity ( $H'$ ) and Pielou's evenness ( $J$ ), calculated based on countable invertebrate  
205 taxa on the 9 pooled slabs, tended to decrease over the survey in the *F. vesiculosus* area with maximum  
206 values of 2.54 and 0.81 observed 10 and 7 months after the slabs setting, respectively, and minimum  
207 values of 0.73 and 0.37 observed 109 months after the slabs setting (Figure 3B). In the *F. serratus* area,  
208  $H'$  remained higher than 2.00 until September 2017 then decreased to values around 1.00 since March  
209 2020 while  $J$  decreased over the survey with a maximum value of 0.82 observed 12 months after the  
210 slabs setting and a minimum value of 0.27 observed 102 months after the slabs setting (Figure 3D).

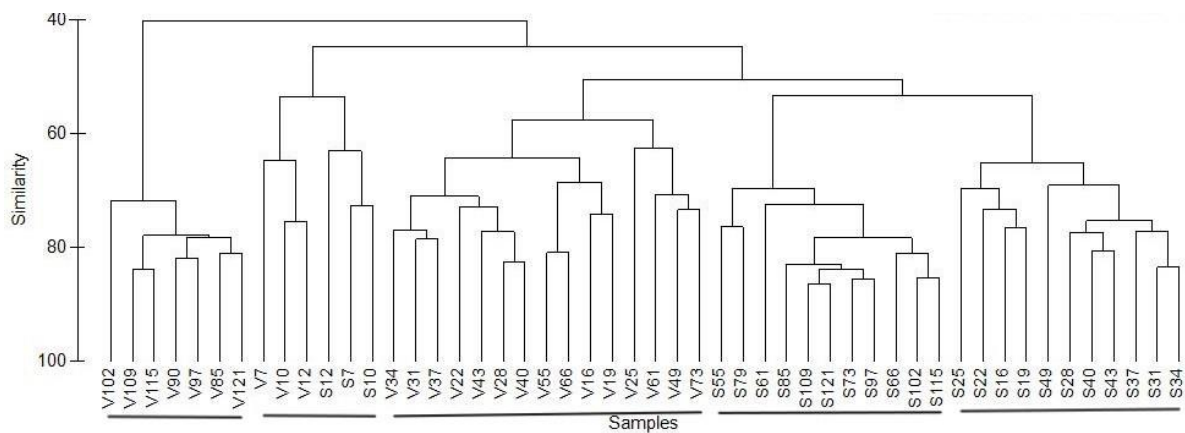
211





213 **Figure 3.** Total number of taxa ( $S_{total}$ ) and number of countable invertebrate taxa ( $S_{count}$ ) on the 9 pooled slabs (1.44 m<sup>2</sup>),  
 214 Shannon diversity index ( $H'$ ) and Pielou's evenness ( $J$ ) calculated based on countable invertebrate taxa on the 9 pooled  
 215 slabs observed over time in the *Fucus vesiculosus* (Fves, A and B) and *Fucus serratus* (Fser, C and D) areas  
 216

217 A total of 72 taxa were identified along the survey, including 27 algae and 45 invertebrates, most being  
 218 observed in both areas (23 algae and 31 invertebrates). Among taxa commonly observed but only in  
 219 one area, there were the barnacle *Austrominius modestus* in the *F. vesiculosus* area and the brown  
 220 alga *Ascophyllum nodosum*, the gastropod *Calliostoma zizyphinum* and the bryozoan *Flustrellidra*  
 221 *hispidia* in the *F. serratus* area. The hierarchical clustering based on Bray-Curtis similarity between  
 222 occurrence of taxa on slabs through time showed five groups of samples (Figure 4). Four groups were  
 223 formed by samples performed in the same area during a certain period: from 16 to 73 and from 85 to  
 224 121 months after the slabs setting (grouped, respectively, at a 57 and 72% similarity level) in the *F.*  
 225 *vesiculosus* area and from 16 to 49 and from 55 to 121 months after the slabs setting (grouped,  
 226 respectively, at a 65 and 69% similarity level) in the *F. serratus* area. The fifth group were formed (at a  
 227 53% similarity level) by the samples performed during the first year of the survey in both areas.



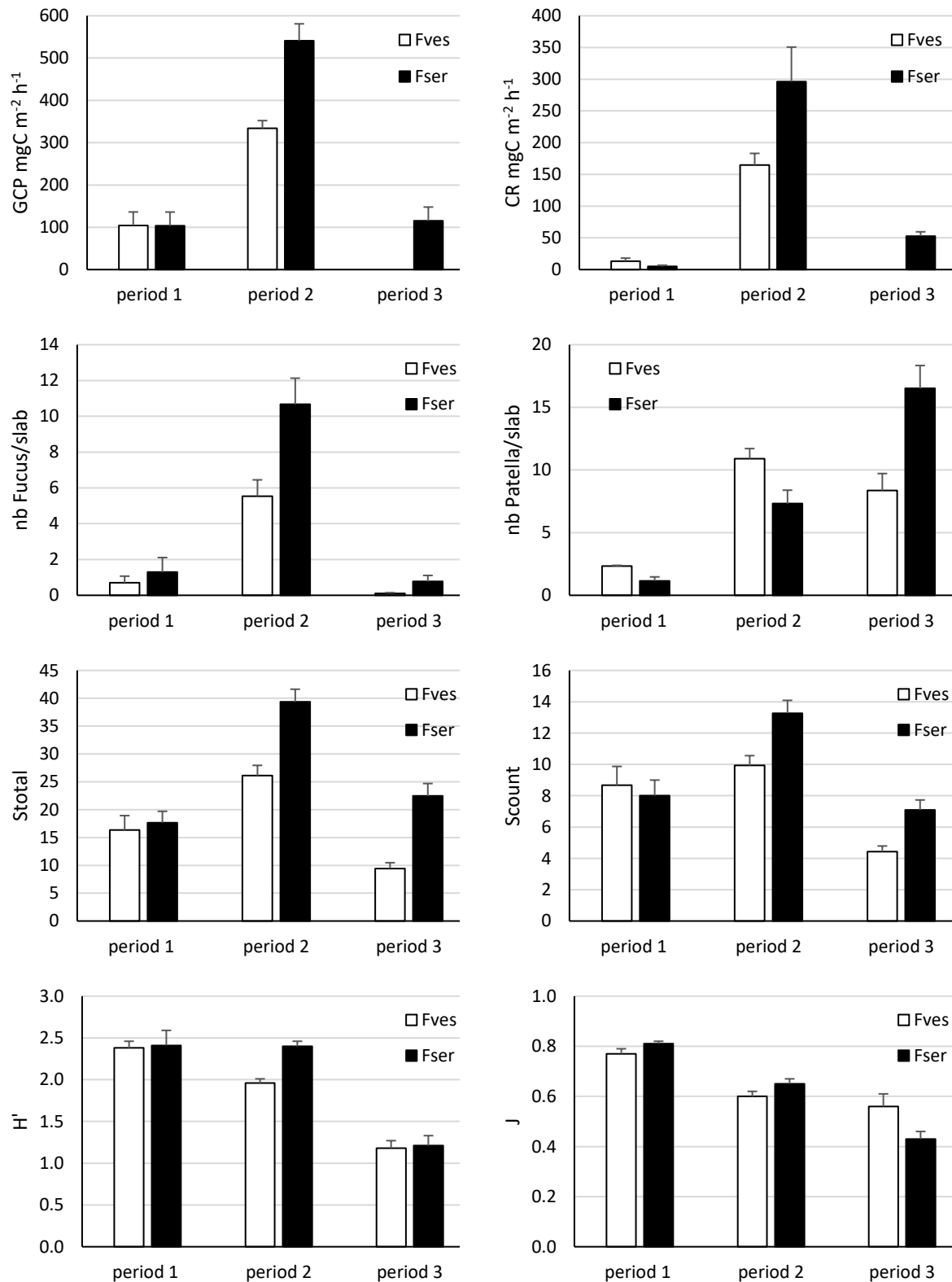
**Figure 4.** Dendrogram obtained by hierarchical clustering (average linkage) based on Bray-Curtis similarity between occurrence of taxa on 9 slabs through time (from 7 to 121 months after setting) in the *Fucus vesiculosus* (V7-V121) and *Fucus serratus* (S7-S121) areas

228  
229  
230  
231

## 232 Discussion

### 233 Primary succession at two tidal levels of a rocky shore

234 The present 10-year survey of the structure of communities established on bare substrata at two tidal  
235 levels on a rocky shore showed three distinct periods. The first period corresponded to the first year  
236 following the availability of bare substrata at both tidal levels. The second period was longer at the  
237 higher tidal level, about 6 years in the *Fucus vesiculosus* area at mid-intertidal versus 4 years in the  
238 *Fucus serratus* area at low mid-intertidal level. The third period corresponded to the last years of the  
239 survey: from about the seventh and fifth year after bare substrata was available at mid-intertidal and  
240 low mid-intertidal level respectively. While of different duration, these three periods presented similar  
241 characteristics at the two tidal levels (Figure 5). During the first period, communities with a low density  
242 of *Fucus* (averaging 6 ind m<sup>-2</sup>) and a rather low richness of taxa (about 17 taxa observed in an area of  
243 1.44 m<sup>2</sup>) exhibited low metabolic activity (gross primary production about 100 mg C m<sup>-2</sup> h<sup>-1</sup> and  
244 respiration about 10 mg C m<sup>-2</sup> h<sup>-1</sup>). During the second period, communities with a high density of *Fucus*  
245 (averaging 35 and 67 ind m<sup>-2</sup> in the *F. vesiculosus* and the *F. serratus* area respectively) and a rather  
246 high richness of taxa (about 26 and 39 taxa in the *F. vesiculosus* and the *F. serratus* area respectively)  
247 exhibited high metabolic activity (gross primary production about 350 and 550 mg C m<sup>-2</sup> h<sup>-1</sup> and  
248 respiration about 150 and 300 mg C m<sup>-2</sup> h<sup>-1</sup> in the *F. vesiculosus* and the *F. serratus* area respectively).  
249 During the third period, communities with a low density of *Fucus* (less than 5 ind m<sup>-2</sup>) and a rather low  
250 richness of taxa (about 9 and 22 taxa in the *F. vesiculosus* and the *F. serratus* area respectively)  
251 exhibited low metabolic activity (gross primary production about 100 mg C m<sup>-2</sup> h<sup>-1</sup> and respiration  
252 about 50 mg C m<sup>-2</sup> h<sup>-1</sup> in the *F. serratus* area, no data for the *F. vesiculosus* area). During the second  
253 period, that is after recruitment and growth of *Fucus*, the structure and metabolism of the  
254 communities set on the slabs were then similar to the structure and metabolism of the communities  
255 established at each tidal level (Bordeyne, 2016; Bordeyne et al., 2015). The transition between the  
256 second and the third period was marked by the loss of *Fucus* individuals. The loss of the foundation  
257 species (either *F. vesiculosus* or *F. serratus*) was accompanied by a decline in taxa richness as well as a  
258 decline in diversity of mobile invertebrates (Figure 5). During the first and the second periods, the  
259 dominant mobile invertebrate, accounting for about 30% of the total abundance of counted  
260 invertebrates, was a top shell or a periwinkle (*Phorcus lineatus* and *Steromphala umbilicalis* in the *F.*  
261 *vesiculosus* area the first and second period respectively; *Steromphala pennanti* and *Littorina obtusata*  
262 in the *F. serratus* area the first and second period respectively). During the third period, the dominant  
263 mobile invertebrate was a limpet (*Patella sp.*) accounting for about 75% of the total abundance of  
264 counted invertebrates in both areas.



265 **Figure 5.** Comparison of the means of the various parameters measured over the 3 periods of succession observed on slabs  
 266 (0.4 x 0.4 m) set in the *Fucus vesiculosus* (Fves) and *Fucus serratus* (Fser) areas: gross community primary production (GCP),  
 267 community respiration (CR), number of individuals of *Fucus* per slab, number of *Patella* per slab, total number of taxa on  
 268 the 9 pooled slabs (Stotal), number of countable invertebrate taxa on the 9 pooled slabs (Scount), Shannon diversity index  
 269 calculated based on countable invertebrate taxa on the 9 pooled slabs (H') and Pielou's evenness calculated based on  
 270 countable taxa on the 9 pooled slabs (J). Error bars indicate standard errors (GCP and CR: n = 2, 17 and 0 for period 1, 2 and  
 271 3 in the *F. vesiculosus* area and 3, 12, 4 in the *F. serratus* area; nb Fucus, nb Patella, S, H', J: n = 3, 15 and 7 for period 1, 2  
 272 and 3 in the *F. vesiculosus* area and 3, 11, 1 for period 1, 2 and 3 in the *F. serratus* area)

273 Insights from long-term survey

274 Placing bare substrata in two communities adjacent over the emersion gradient, we hypothesized that  
275 the timing of successional sequences would be slower in the mid intertidal than in the low-mid  
276 intertidal. Surprisingly, first *Fucus* individuals identifiable to the species level were observed 3 months  
277 sooner in the *F. vesiculosus* area (mid intertidal) than in the *F. serratus* area (low-mid intertidal).  
278 Moreover, those individuals belonged to the *F. vesiculosus* species in both areas and, at low-mid  
279 intertidal level, first *F. serratus* individuals were observed only 6 months after *F. vesiculosus* individuals.  
280 However, the two species fulfilled the same functional role in the community and one year after the  
281 slabs setting, as the surrounding communities, communities established on the slabs were  
282 characterized by high *Fucus* density, high taxa richness and high metabolic activity at both tidal levels.  
283 The transition between the first and the second period pointed above for this 10-year survey was  
284 concomitant in the two areas, that could invalidate our hypothesis. Nevertheless, the transition  
285 between the second and third period pointed above appeared later in the mid intertidal than in the  
286 low-mid intertidal (that is respectively 6- and 4-years post deployment of fouling plates). This  
287 confirmation of our hypothesis would not have been possible within the duration of most intertidal  
288 field experimental studies (Jenkins & Uya, 2016). The long-term observations made here following the  
289 provision of bare substrata revealed late transition from communities dominated by canopy-forming  
290 algae to grazing limpet dominated communities. Furoid algae and grazing patellid limpet interactions  
291 are known to be greatly variable and to have various effects on the community structure of intertidal  
292 rocky shores of north west Europe (Jenkins et al., 2005). The present survey suggests that *Fucus sp.*  
293 and *Patella sp.* interactions changed over succession time, depending on the life-stage of the species  
294 and the development stage of the populations, and owing to the plasticity of the diet of the grazer  
295 (Schaal & Grall, 2015). *Fucus sp.* and *Patella sp.* interactions had direct and indirect effects on the  
296 structure and functioning of the whole macrobenthic communities, which also varied over succession  
297 time. During the first period, the few small individuals of *Patella sp.* that had recruited on slabs could  
298 either have had no effect on *Fucus sp.* recruitment or have facilitated it by grazing pioneer ephemeral  
299 algae. During the second period, *Patella sp.* and *Fucus sp.* individuals and populations grew on slabs  
300 concurrently until algae naturally decayed (the *Fucus* life-span being about 3 years). The limpet  
301 individuals and populations growth at that time could have been facilitated on slabs by the dampening  
302 effect of the *Fucus* canopies at emersion (amelioration of tide-out temperatures and relative  
303 humidity), particularly at the mid-intertidal level. In parallel, diverse flora and fauna also benefited  
304 from the canopies, due either to the shelter or to the substratum complexification they provided.  
305 Finally, community primary productivity was high during this second phase. The detachment of the  
306 *Fucus sp.* individuals from the slabs was thus accompanied by community taxa richness and primary  
307 productivity reductions, and also by a limpet mortality on slabs in the mid intertidal level. In the low-  
308 mid intertidal level, the emersion stress was weaker and limpets were still protected on slabs by the  
309 denser surrounding canopy. The numerous large individuals of *Patella sp.* on slabs were not suspected  
310 to outcompete *Fucus sp.* for space, but rather to prevent subsequent *Fucus sp.* recruitment by grazing  
311 germlings. Indeed, bare substrata persisted on slabs over the survey and the only *Fucus sp.* individuals  
312 remaining on slabs after 10 years had settled and developed on *Patella sp.* shells.

313 Communities established on slabs versus surrounding communities

314 Even made of natural materials and with enhanced roughness, artificial hard substrata are known to  
315 constitute poor surrogates of natural habitats that support assemblages different to those found on  
316 natural shores (Cacabelos et al., 2016). In particular, the experimental slabs used here offered less  
317 refuges for furoid germlings to escape grazing than the surrounding natural boulder reef. At the end  
318 of the 10-year survey, communities established on slabs were dominated by limpets and differed from

319 the surrounding communities dominated by furoid algae at both tidal levels. The last year of the  
320 survey, the *Patella sp.* density was higher on slabs at mid-tidal level (about 40 ind m<sup>-2</sup>) than in the  
321 surrounding *Fucus vesiculosus* community (averaging 28 ind m<sup>-2</sup> over the whole 10-year period,  
322 unpublished data) and much higher on slabs at mid-low tidal level (about 93 ind m<sup>-2</sup>) than in the *F.*  
323 *serratus* surrounding community (averaging 8 ind m<sup>-2</sup>, unpublished data). Limpets have long been  
324 shown to control Furoid recruitment (Jones, 1946), and their important community regulating role as  
325 grazer has been widely documented on European rocky shores (Coleman et al., 2006). This community  
326 regulating role involves a complex series of interactions and depends on local environmental  
327 conditions. The threshold density beyond which limpets prevent the establishment of *Fucus sp.* might  
328 have been surpassed here on the experimental slabs (Jonsson et al., 2006). Further settlement of *Fucus*  
329 might thus depend upon a decrease in the limpet population as the adult limpets die off, and long-  
330 term cyclical changes of dominance between these two organisms, as documented in the Lough Hyne  
331 Marine Reserve of Ireland (Little et al., 2017), could occur. However, the peculiar environmental  
332 conditions experienced on artificial substratum potentially influence the structure of the colonising  
333 populations. For example, recent studies in the Irish Sea showed that dislodgement of *Fucus*  
334 *vesiculosus* was higher and that limpets were larger on artificial structures than on natural shores (Earp  
335 et al., 2023; Farrugia Drakard et al., 2021). Such effects could allow the limpet dominance to persist on  
336 the experimental slabs. Given the relatively long life-span of *Fucus* (about 3 years) and *Patella* (up to  
337 15 years), very long-term (i.e. multi-decades) data series are required to test for cyclical changes of  
338 dominance. The persistence of limpet dominated communities or the alternance of limpet and furoid  
339 dominated communities on the experimental slabs should then be checked by going on the survey for  
340 a further decade.

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#### 348 Conflict of interest disclosure

349 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in  
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#### 351 Data accessibility

352 Data are available on line (<https://doi.org/10.5281/zenodo.10401814>).

#### 353 References

- 354 Bordeyne, F. (2016). *Production primaire et fonctionnement de communautés intertidales à canopée*  
355 *de Fucus*. (PhD), Paris VI University, France.
- 356 Bordeyne, F., Migné, A., & Davoult, D. (2015). Metabolic activity of intertidal *Fucus spp.* communities:  
357 evidence for high aerial carbon fluxes displaying seasonal variability. *Marine Biology*, 162(10),  
358 2119-2129. <https://doi.org/10.1007/s00227-015-2741-6>
- 359 Bulleri, F. (2009). Facilitation research in marine systems: state of the art, emerging patterns and  
360 insights for future developments. *Journal of Ecology*, 97(6), 1121-1130.  
361 <https://doi.org/10.1111/j.1365-2745.2009.01567.x>

362 Cacabelos, E., Martins, G. M., Thompson, R., Prestes, A. C. L., Azevedo, J. M. N., & Neto, A. I. (2016).  
363 Material type and roughness influence structure of inter-tidal communities on coastal  
364 defenses. *Marine Ecology-an Evolutionary Perspective*, 37(4), 801-812.  
365 <https://doi.org/10.1111/maec.12354>

366 Coleman, R. A., Underwood, A. J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J., . . . Hawkins,  
367 S. J. (2006). A continental scale evaluation of the role of limpet grazing on rocky shores.  
368 *Oecologia*, 147(3), 556-564. <https://doi.org/10.1007/s00442-005-0296-9>

369 Earp, H. S., George, R., Brooks, P. R., Drakard, V. F., Thompson, B. J., Fisher, B., . . . Moore, P. J. (2023).  
370 The population structure, sex ratio and reproductive potential of limpets (*Patella* spp.) on  
371 natural shores and artificial structures in the Irish Sea. *Marine Environmental Research*, 184.  
372 <https://doi.org/10.1016/j.marenvres.2022.105853>

373 Farrugia Drakard, V., Brooks, P., Crowe, T. P., Earp, H. S., Thompson, B., Bourke, N., . . . Moore, P. J.  
374 (2021). *Fucus vesiculosus* populations on artificial structures have potentially reduced  
375 fecundity and are dislodged at greater rates than on natural shores. *Marine Environmental*  
376 *Research*, 168. <https://doi.org/10.1016/j.marenvres.2021.105324>

377 Hawkins, S. J., Pack, K. E., Hyder, K., Benedetti-Cecchi, L., & Jenkins, S. R. (2020). Rocky shores as  
378 tractable test systems for experimental ecology. *Journal of the marine biological Association*  
379 *of the United Kingdom*, 100(7), 1017-1041. <https://doi.org/10.1017/s0025315420001046>

380 Jenkins, S. R., Coleman, R. A., Della Santina, P., Hawkins, S. J., Burrows, M. T., & Hartnoll, R. G. (2005).  
381 Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine*  
382 *Ecology Progress Series*, 287, 77-86. <https://doi.org/10.3354/meps287077>

383 Jenkins, S. R., & Uya, M. (2016). Temporal scale of field experiments in benthic ecology. *Marine Ecology*  
384 *Progress Series*, 547, 273-286. <https://doi.org/10.3354/meps11659>

385 Jones, N. S. (1946). Browsing of *Patella*. *Nature*, 158(4016), 557-558.  
386 <https://doi.org/10.1038/158557b0>

387 Jonsson, P. R., Granhag, L., Moschella, P. S., Aberg, P., Hawkins, S. J., & Thompson, R. C. (2006).  
388 Interactions between wave action and grazing control the distribution of intertidal  
389 macroalgae. *Ecology*, 87(5), 1169-1178.

390 Little, C., Trowbridge, C. D., Pilling, G. M., Stirling, P., Morritt, D., & Williams, G. A. (2017). Long-term  
391 fluctuations in intertidal communities in an Irish sea-lough: Limpet-fucoid cycles. *Estuarine*  
392 *Coastal and Shelf Science*, 196, 70-82. <https://doi.org/10.1016/j.ecss.2017.06.036>

393 Mann, K. H. (1973). Seaweeds: their productivity and strategy for growth. *Science*, 182(4116), 975-981.  
394 <https://doi.org/10.1126/science.182.4116.975>

395 Migné, A., Davoult, D., Spilmont, N., Menu, D., Boucher, G., Gattuso, J.-P., & Rybarczyk, H. (2002). A  
396 closed-chamber CO<sub>2</sub>-flux method for estimating intertidal primary production and respiration  
397 under emersed conditions. *Marine Biology*, 140(4), 865-869. <https://doi.org/10.1007/s00227-001-0741-1>

398

399 Migné, A., Duong, G., Menu, D., Davoult, D., & Gévaert, F. (2021). Dynamics of *Fucus serratus* thallus  
400 photosynthesis and community primary production during emersion across seasons: canopy  
401 dampening and biochemical acclimation. *Peer Community Journal*, 1, e32.  
402 <https://doi.org/10.24072/pcjournal.42>

403 Mineur, F., Arenas, F., Assis, J., Davies, A. J., Engelen, A. H., Fernandes, F., . . . De Clerck, O. (2015).  
404 European seaweeds under pressure: Consequences for communities and ecosystem  
405 functioning. *Journal of Sea Research*, 98, 91-108.  
406 <https://doi.org/10.1016/j.seares.2014.11.004>

407 Noël, L. M. L. J., Griffin, J. N., Moschella, P. S., Jenkins, S. R., Thompson, R. C., & Hawkins, S. J. (2009).  
408 Changes in diversity and ecosystem functioning during succession. In M. Wahl (Ed.), *Marine*  
409 *Hard Bottom Communities*: Springer-Verlag Berlin Heidelberg.

410 Raffaelli, D., & Hawkins, S. (1999). *Intertidal ecology*. Dordrecht, Boston, London: Kluwer Academic  
411 Publishers.

412 Schaal, G., & Grall, J. (2015). Microscale aspects in the diet of the limpet *Patella vulgata* L. *Journal of*  
413 *the marine biological Association of the United Kingdom*, 95(6), 1155-1162.  
414 <https://doi.org/10.1017/s0025315415000429>

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416