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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 level 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 (≈ 6 ind m^{-2}), low
16 taxa richness (≈ 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 (≈ 35 and 67 ind m^{-2}), high taxa richness
20 (≈ 26 and 39 taxa) and high metabolic activity (GPP ≈ 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) but few
54 studies have explicitly measured changes in community primary production through succession from
55 opportunistic ephemerals to dense canopy. A species-specific productivity decrease with increasing
56 successional status is predictable but differences in the productivity of component species, measured
57 per unit biomass, do not necessarily scale to the productivity of the community as a whole (Noël et al.,
58 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 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 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⁻² h⁻¹ and respiration in the range 100-500 mg C m⁻² h⁻¹, 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 (CO₂) fluxes at the air-slab interface inside benthic chambers, at
101 the onset of emersion period of spring tides (around midday). Each benthic chamber, which is made
102 of a transparent Perspex® dome with a transparent air-tight Perspex® base, has a covering surface of
103 0.3 × 0.3 m and a total volume of 17.7 or 26.5 L (depending on the amount of *Fucus* settled on the
104 slabs). It was sealed to the slab (using bungees) and was connected to an infrared CO₂ gas analyzer
105 (LiCor Li-820) in a closed air circuit (with a flow of about 1 L min⁻¹). CO₂ air concentration (μmol_{CO₂}
106 mol_{air}⁻¹) was recorded every 15 s for 5 to 15 min during incubation to calculate CO₂ fluxes as described
107 in Migné *et al.* (2002). Net community production (NCP) and community respiration (CR) were
108 examined successively in ambient light and in darkness (by covering the chamber), respectively.
109 Photosynthetically available radiations (PAR, in μmol of photons m⁻² s⁻¹) were measured close to the
110 incubation chambers, using a planar sensor (Li-Cor QuantumSA-190). PAR were recorded every minute
111 to ensure that measurements in ambient light were performed under saturating irradiance, assuming
112 that the onset of light saturation for coastal macroalgal communities is reached, on average, at 291
113 μmol_{photons} m⁻² s⁻¹ (Middelboe, Sand-Jensen, & Binzer, 2006). Benthic chambers were opened between
114 two consecutive incubations to renew the ambient air. Gross community production (GCP) was
115 calculated as the sum of NCP and CR. Metabolic rates were calculated according to the covering surface
116 of incubation chambers (i.e. 0.09 m²) and expressed in carbon units (mg C m⁻² h⁻¹) assuming a molar
117 volume of 22.4 L mol⁻¹ at standard temperature and pressure and a molar mass of 12 g C mol_{CO₂}⁻¹.

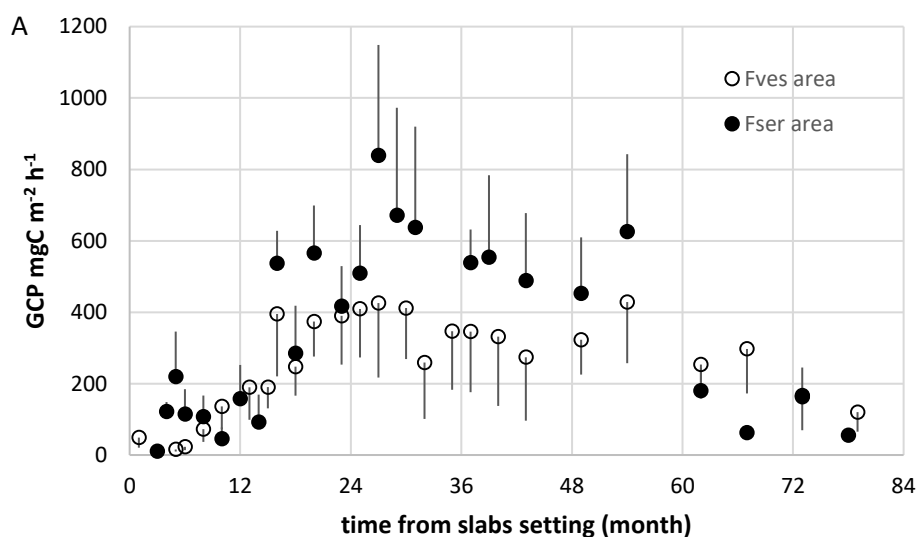
118 Macrobenthic community structure

119 The survey of the structure of settled communities started as far as some settled *Fucus* were
120 identifiable to the species level, that was in September 2013 (i.e. seven months after the setup of slabs)
121 and continued until March 2023 (i.e. 121 months, 10 years, after the setup of slabs). Non-destructive
122 sampling of biota colonising the slabs was conducted during low tide, every 3 months until September
123 2016 and then every 6 months (leading to a total of 25 sampling dates in each area). Algae and
124 invertebrates were identified in the field to the lowest possible taxonomic level, being usually the
125 species level but genus, family, or order level for some colonial invertebrates (e.g. bryozoans,
126 ascidians) and morphologically similar taxa (e.g. ectocarpales, amphipods). Density was determined
127 for *Fucus* identifiable to the species level and for countable invertebrates (e.g. gastropod species).
128 Identification and count were done on all available slabs (i.e. not detached and returned during the
129 survey) in the *F. vesiculosus* area (21 slabs until March 2017 and 17 to 14 slabs from September 2017
130 to March 2023), on all available slabs in the *F. serratus* area (20 slabs until June 2015 and 19 to 15 slabs
131 from March 2018 to March 2023) or on 9 to 12 haphazardly chosen slabs at the period of the highest
132 colonisation by *Fucus* (from September 2015 to September 2017).

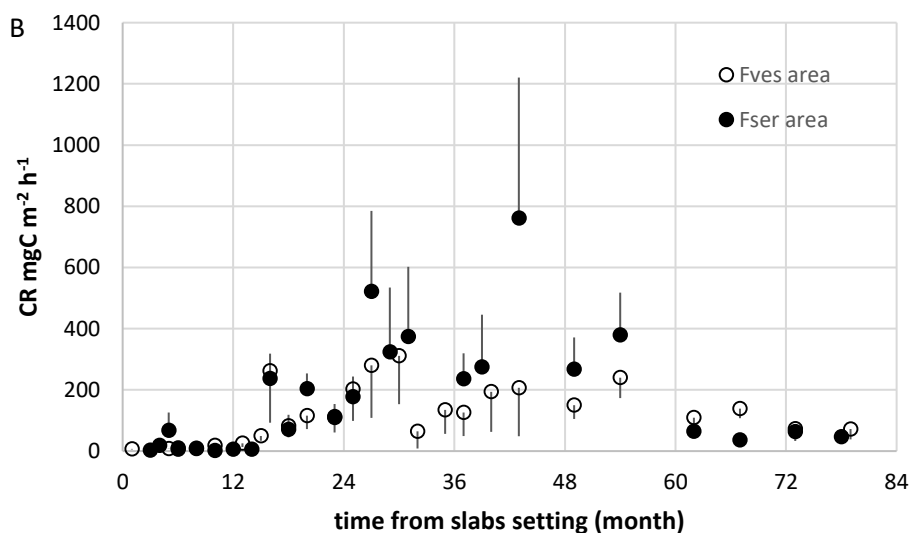
133 Before any data analysis, the sampling effort was homogenised by randomly selecting 9 slabs among
 134 the slabs on which the structure of the macrobenthic community was assessed at each sampling date,
 135 in each area. Shannon diversity and Pielou evenness were calculated based on abundance data of
 136 countable invertebrates obtained after pooling the 9 slabs (representing a sampling surface of 1.44
 137 m²) at each sampling date in each area. The occurrence of each taxa was measured as the number of
 138 slabs bearing the taxa among the 9 slabs and similarities (using Bray-Curtis coefficient) between every
 139 pair of samples were calculated on the occurrence data (in a 72 taxa x 50 samples matrix). Samples
 140 were then grouped by hierarchical clustering (group-average link) based on the Bray-Curtis similarities
 141 to explore spatio-temporal structuring.

142 Results

143 Macrobenthic community metabolism



144



145

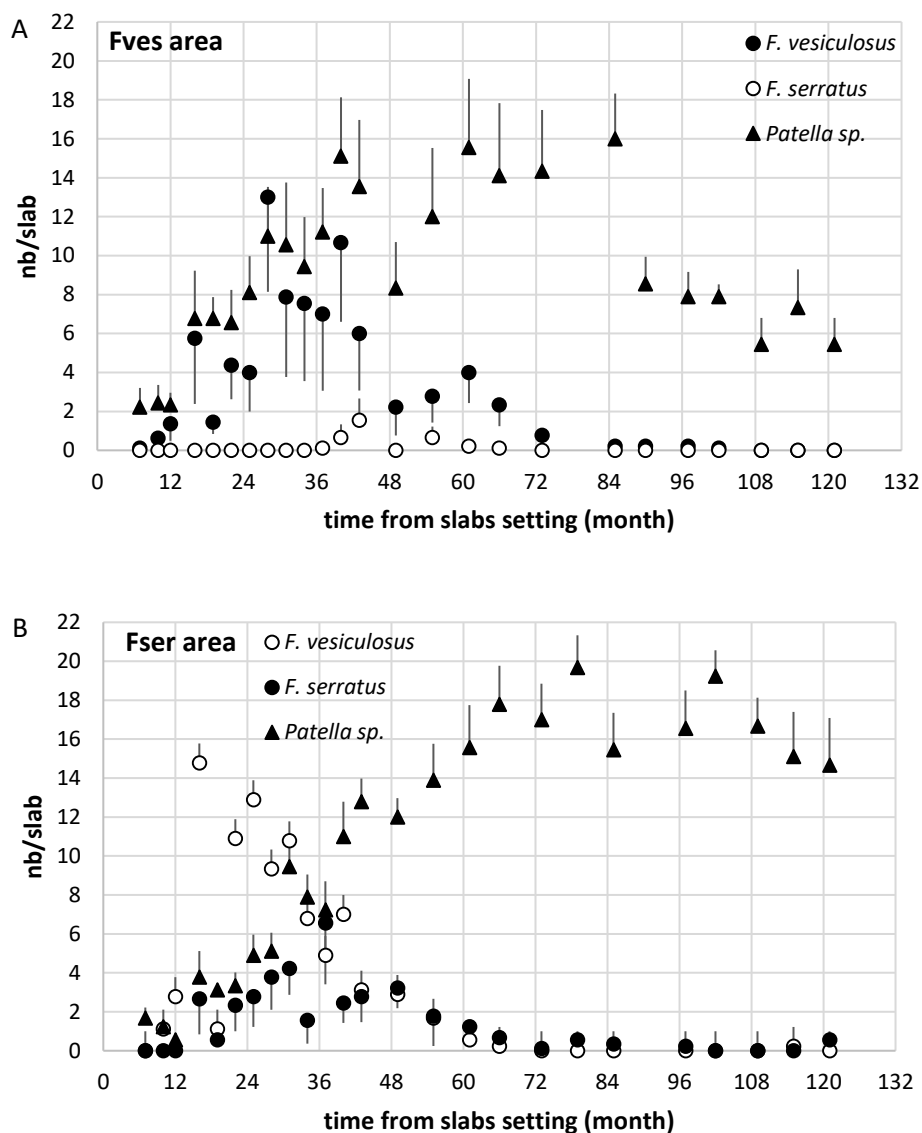
146 **Figure 1.** Mean gross community primary production (GCP, A) and community respiration (CR, B) measured over time on
 147 slabs set in the *Fucus vesiculosus* (Fves) and *Fucus serratus* (Fser) areas. Error bars indicate standard errors ($3 \leq n \leq 7$)

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

151 Mean (\pm se) gross community production (GCP) measured on slabs set at mid-intertidal level in the *F.*
 152 *vesiculosus* area ranged from 15.53 ± 5.72 to 428.58 ± 171.35 mg C m⁻² h⁻¹. The minimum and the
 153 maximum were observed 5 and 54 months after the slabs setting respectively (Figure 1A). Mean GCP
 154 measured on slabs set at low mid-intertidal level in the *F. serratus* area ranged from 10.60 ± 8.70 to
 155 839.44 ± 309.13 mg C m⁻² h⁻¹. The minimum and the maximum were observed 3 and 27 months after
 156 the slabs setting respectively (Figure 1A).

157 Mean (\pm se) community respiration (CR) measured on slabs set at mid-intertidal level in the *F.*
 158 *vesiculosus* area ranged from 5.80 ± 0.92 to 311.08 ± 157.76 mg C m⁻² h⁻¹. The minimum and the
 159 maximum were observed 6 and 30 months after the slabs setting respectively (Figure 1B). Mean CR
 160 measured on slabs set at low mid-intertidal level in the *F. serratus* area ranged from 1.25 ± 0.75 to
 161 761.02 ± 459.58 mg C m⁻² h⁻¹. The minimum and the maximum were observed 10 and 43 months after
 162 the slabs setting respectively (Figure 1B).

163 Macrobenthic community structure



164

165

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

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

176 Few *Fucus serratus* individuals settled on slabs set in the *F. vesiculosus* area (with a mean in the range
177 0.1-1.6 ind/slab during the period 37-66 months after the slabs setting, Figure 2A). *F. serratus*
178 individuals were identifiable on slabs set in the *F. serratus* area 16 months after the slabs setting, at a
179 mean density of 3 ± 2 ind/slab (Figure 2B). Their mean density increased to 7 ± 3 ind/slab 37 months
180 after the slabs setting and then decreased to less than 1 ind/slab 66 months after the slabs setting
181 (Figure 2B).

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

189 Mean taxa richness per slab (\pm se), including macroalgae and invertebrates, varied over the survey in
190 the range 3.4 ± 0.4 - 16.4 ± 3.3 in the *F. vesiculosus* area and in the range 5.4 ± 1.0 - 21.9 ± 3.7 in the *F.*
191 *serratus* area. The maximum was observed in June 2016 (40 months after the slabs setting) in both
192 areas. On the 9 pooled slabs (i.e. sampling surface of 1.44 m²), total taxa richness (S_{total}) varied in the
193 range 6 - 39 in the *F. vesiculosus* area and in the range 7 - 51 in the *F. serratus* area, with a maximum
194 observed in June and September 2016 (40 and 43 months after the slabs setting) in the *F. vesiculosus*
195 area (Figure 3A) and in September 2016 in the *F. serratus* area (Figure 3C). Richness in countable
196 invertebrates (S_{count}) varied in the range 3 - 15 in the *F. vesiculosus* area (Figure 3A) and in the range 5
197 - 19 in the *F. serratus* area (Figure 3C), with a maximum observed in June 2016 in both areas. Shannon
198 diversity (H') and Pielou's evenness (J), calculated based on countable invertebrate taxa on the 9
199 pooled slabs, tended to decrease over the survey in the *F. vesiculosus* area with maximum values of
200 2.54 and 0.81 observed 10 and 7 months after the slabs setting, respectively, and minimum values of
201 0.73 and 0.37 observed 109 months after the slabs setting (Figure 3B). In the *F. serratus* area, H'
202 remained higher than 2.00 until September 2017 then decreased to values around 1.00 since March
203 2020 while J decreased over the survey with a maximum value of 0.82 observed 12 months after the
204 slabs setting and a minimum value of 0.27 observed 102 months after the slabs setting (Figure 3D).

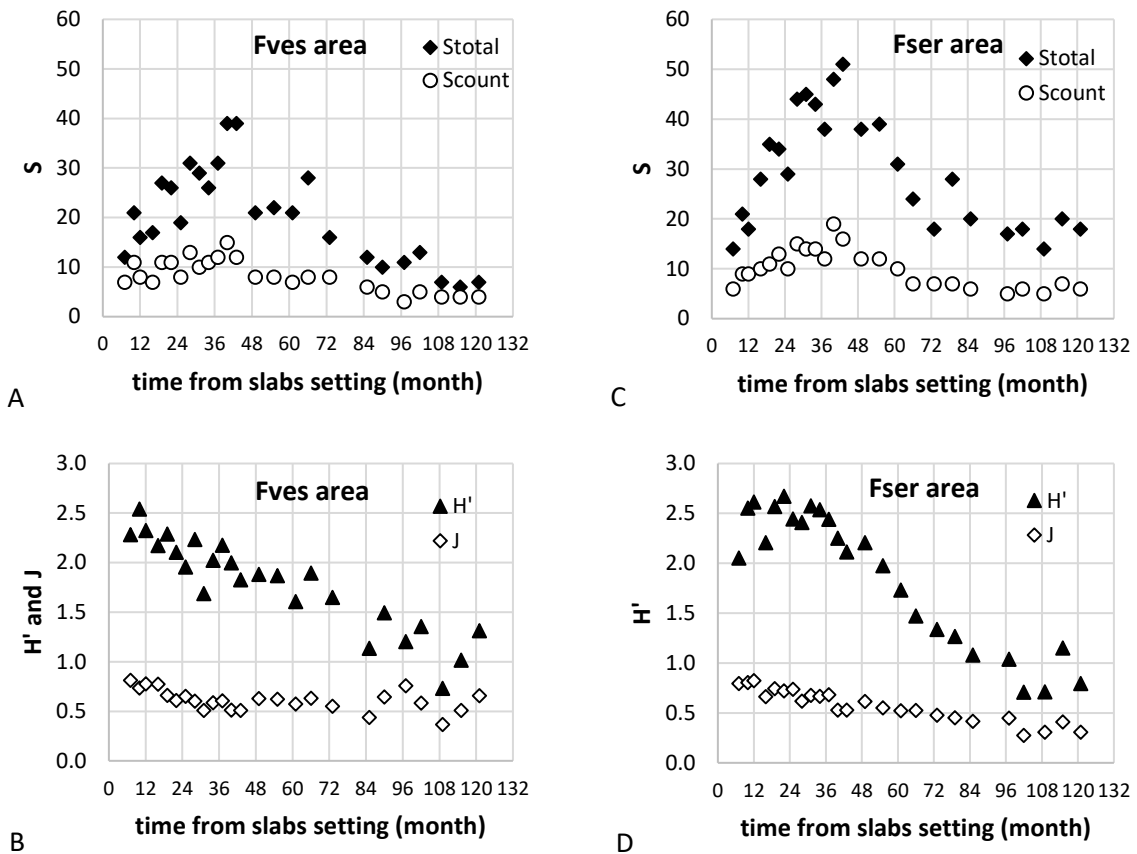
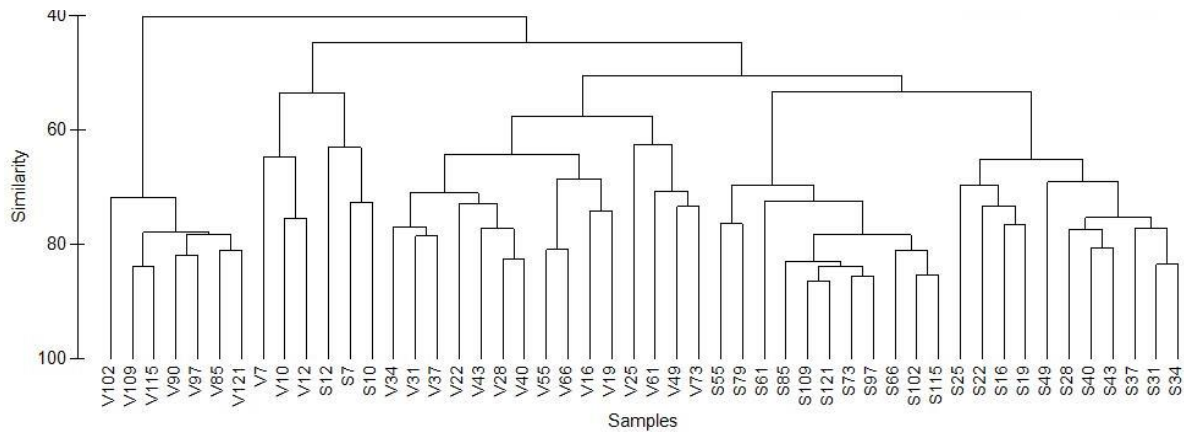


Figure 3. Total number of taxa (S_{total}) and number of countable invertebrate taxa (S_{count}) on the 9 pooled slabs, Shannon diversity index (H') and Pielou's evenness (J) calculated based on countable invertebrate taxa on the 9 pooled slabs observed over time in the *Fucus vesiculosus* (Fves, A and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

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206
207
208

209 A total of 72 taxa were identified along the survey, including 27 algae and 45 invertebrates, most being
210 observed in both areas (23 algae and 31 invertebrates). Among taxa commonly observed but only in
211 one area, there were the barnacle *Austrominius modestus* in the *F. vesiculosus* area and the brown
212 alga *Ascophyllum nodosum*, the gastropod *Calliostoma zizyphinum* and the bryozoan *Flustrellidra*
213 *hispidia* in the *F. serratus* area. The hierarchical clustering based on Bray-Curtis similarity between
214 occurrence of taxa on slabs through time showed five groups of samples (Figure 4). Four groups were
215 formed by samples performed in the same area during a certain period: from 16 to 73 and from 85 to
216 121 months after the slabs setting (grouped, respectively, at a 57 and 72% similarity level) in the *F.*
217 *vesiculosus* area and from 16 to 49 and from 55 to 121 months after the slabs setting (grouped,
218 respectively, at a 65 and 69% similarity level) in the *F. serratus* area. The fifth group were formed (at a
219 53% similarity level) by the samples performed during the first year of the survey in both areas.

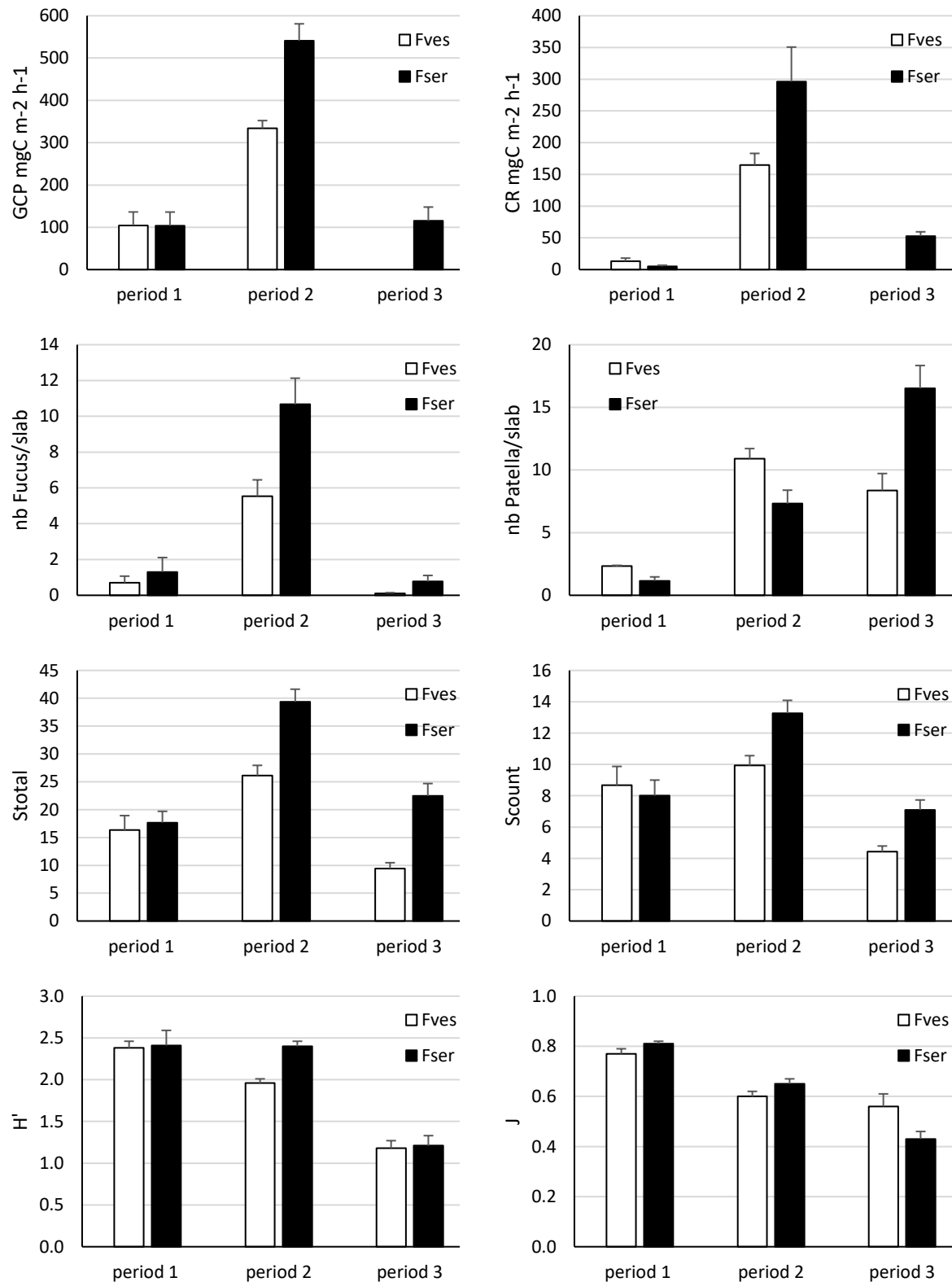


220
 221 **Figure 4.** Dendrogram obtained by hierarchical clustering (average linkage) based on Bray-Curtis similarity between
 222 occurrence of taxa on slabs through time (from 7 to 121 months after setting) in the *Fucus vesiculosus* (V7-V121) and *Fucus*
 223 *serratus* (S7-S121) areas

224 Discussion

225 Primary succession at two tidal levels of a rocky shore

226 The present 10-year survey of the structure of communities established on bare substrata at two tidal
 227 levels on a rocky shore showed three distinct periods. The first period corresponded to the first year
 228 following the availability of bare substrata at both tidal levels. The second period was longer at the
 229 higher tidal level, about 6 years in the *Fucus vesiculosus* area at mid-intertidal versus 4 years in the
 230 *Fucus serratus* area at low mid-intertidal level. The third period corresponded to the last years of the
 231 survey: from about the seventh and fifth year after bare substrata was available at mid-intertidal and
 232 low mid-intertidal level respectively. While of different duration, these three periods presented similar
 233 characteristics at the two tidal levels (Figure 5). During the first period, communities with a low density
 234 of *Fucus* (averaging 6 ind m⁻²) and a rather low richness of taxa (about 17 taxa observed in an area of
 235 1.44 m²) exhibited low metabolic activity (gross primary production about 100 mg C m⁻² h⁻¹ and
 236 respiration about 10 mg C m⁻² h⁻¹). During the second period, communities with a high density of *Fucus*
 237 (averaging 35 and 67 ind m⁻² in the *F. vesiculosus* and the *F. serratus* area respectively) and a rather
 238 high richness of taxa (about 26 and 39 taxa in the *F. vesiculosus* and the *F. serratus* area respectively)
 239 exhibited high metabolic activity (gross primary production about 350 and 550 mg C m⁻² h⁻¹ and
 240 respiration about 150 and 300 mg C m⁻² h⁻¹ in the *F. vesiculosus* and the *F. serratus* area respectively).
 241 During the third period, communities with a low density of *Fucus* (less than 5 ind m⁻²) and a rather low
 242 richness of taxa (about 9 and 22 taxa in the *F. vesiculosus* and the *F. serratus* area respectively)
 243 exhibited low metabolic activity (gross primary production about 100 mg C m⁻² h⁻¹ and respiration
 244 about 50 mg C m⁻² h⁻¹ in the *F. serratus* area, no data for the *F. vesiculosus* area). During the second
 245 period, that is after recruitment and growth of *Fucus*, the structure and metabolism of the
 246 communities set on the slabs were then similar to the structure and metabolism of the communities
 247 established at each tidal level (Bordeyne, 2016; Bordeyne et al., 2015). The transition between the
 248 second and the third period was marked by the loss of *Fucus* individuals. The loss of the foundation
 249 species (either *F. vesiculosus* or *F. serratus*) was accompanied by a decline in taxa richness as well as a
 250 decline in diversity of mobile invertebrates (Figure 5). During the first and the second periods, the
 251 dominant mobile invertebrate, accounting for about 30% of the total abundance of counted
 252 invertebrates, was a top shell or a periwinkle (*Phorcus lineatus* and *Steromphala umbilicalis* in the
 253 *F. vesiculosus* area the first and second period respectively; *Steromphala pennanti* and *Littorina obtusata*
 254 in the *F. serratus* area the first and second period respectively). During the third period, the dominant
 255 mobile invertebrate was a limpet (*Patella sp.*) accounting for about 75% of the total abundance of
 256 counted invertebrates in both areas.



257 **Figure 5.** Comparison of the means of the various parameters measured over the 3 periods of succession observed on slabs
 258 set in *Fucus vesiculosus* (Fves) and *Fucus serratus* (Fser) areas: gross community primary production (GCP), community
 259 respiration (CR), number of individuals of *Fucus* per slab, number of *Patella* per slab, total number of taxa on the 9 pooled
 260 slabs (Stotal), number of countable invertebrate taxa on the 9 pooled slabs (Scount), shannon diversity index calculated
 261 based on countable invertebrate taxa on the 9 pooled slabs (H') and Pielou's evenness calculated based on countable taxa
 262 on the 9 pooled slabs (J). Error bars indicate standard errors (GCP and CR: n = 2, 17 and 0 for period 1, 2 and 3 in the *F.*
 263 *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 and 3 in the
 264 *F. vesiculosus* area and 3, 11, 1

265 Insights from long-term survey

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

305 Communities established on slabs versus surrounding communities

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

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

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338 Conflict of interest disclosure

339 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
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