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# Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial carbon fluxes displaying seasonal variability

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1 TITLE: Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial  
2 carbon fluxes displaying seasonal variability.

3

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18

19 ABSTRACT

20 Semi-sheltered rocky shores are characterized by a typical succession of Phaeophyceae-  
21 dominated communities where canopy-forming algae are assumed to be very productive.

22 However, metabolic activity of whole communities, integrating the main interactions that  
23 occur in these assemblages, still needs to be investigated more deeply, especially when

24 communities are emerged. Thus, the metabolism of the mid-intertidal *Fucus vesiculosus* and

25 *Fucus serratus* communities was surveyed once a month throughout a year in the Bay of

26 Morlaix (France). *In situ* measurements of primary production and respiration were carried  
27 out at the onset of emersion periods, using benthic chambers coupled to CO<sub>2</sub>-infrared gas  
28 analysers. Benthic measurements were performed successively on whole communities and  
29 after canopy removal, to assess the contribution of the canopies to the communities' carbon  
30 fluxes. Concurrently, nitrogen and organic carbon contents of the two *Fucus* species were  
31 evaluated monthly. Both communities exhibited high metabolic activity year-round  
32 (community gross primary production: 400-1 000 mgC m<sup>-2</sup> h<sup>-1</sup>; community respiration: 100-  
33 500 mgC m<sup>-2</sup> h<sup>-1</sup>), with canopies accounting for 77-97% of the global CO<sub>2</sub> fluxes. However,  
34 this relative canopies' contribution to global CO<sub>2</sub> fluxes did not follow seasonal fluctuations,  
35 whereas both metabolic activities and nitrogen and carbon contents did, confirming the  
36 importance of light and temperature in the regulation of metabolic processes. A nutrient  
37 limitation was also suggested to occur in summer, when seawater was nutrient-depleted.  
38 Finally, the *Fucus vesiculosus* community, located upper on the shore, exhibited lower  
39 photosynthetic activity than the *Fucus serratus* community, being consistent with the vertical  
40 zonation rules of intertidal habitats.

41

## 42 INTRODUCTION

43 Communities dominated by canopy-forming Phaeophyceae are particularly widespread along  
44 intertidal rocky shores of temperate regions. Such communities are usually considered to be  
45 very productive, although their metabolism has rarely been studied at the community scale  
46 (Goll ty et al. 2008; Tait and Schiel 2010). Yet, these communities are constituted of  
47 numerous species (Rindi and Guiry 2004; Kersen et al. 2011; Mign  et al. 2015b), giving rise  
48 to many interactions. For instance, numerous trophic relationships occur in these systems  
49 (Goll ty et al. 2010; Duarte et al. 2015), as well as competition for light and space  
50 (Underwood 2000). Such interactions could lead to large variability in the metabolism of

51 primary producers. They must for instance synthesise defence molecules against grazers,  
52 epibionts and/or biofilms (Brock et al. 2007; Wahl 2009) or are subjected to a reduced light  
53 due to epibionts, leading to a reduction of photosynthetic activity (Sand-Jensen 1977; Oswald  
54 et al. 1984). On the contrary, Tait and Schiel (2011) demonstrated that the structural  
55 differences of primary producers, but also their location in the community assemblage could  
56 lead to an enhancement of the global primary production. Therefore, all these interactions  
57 play a fundamental role and need to be accounted for when investigating community  
58 metabolism, as highlighted by Migné et al. (2015a).

59 These communities also experiment large changes in abiotic conditions at various temporal  
60 scales. The most drastic change occurs at the tidal scale, due to the alternation of immersion  
61 and emersion periods. Although usually thought as stressful for intertidal organisms, emersion  
62 periods can, however, be a very useful time for algae to do photosynthesis (Golléty et al.  
63 2008), with some of them exhibiting the major part of their production when emersed (Quadir  
64 et al. 1979). Thus, investigations of intertidal communities' metabolic activity should not  
65 neglect the low tide periods.

66  
67 The study of Golléty et al. (2008) is to our knowledge the first one dealing with *in situ*  
68 metabolic activity of Phaeophyceae dominated communities under emersed conditions. This  
69 pioneer study showed that primary production and respiration rates of the sheltered mid-  
70 intertidal *Ascophyllum nodosum* community followed a seasonal trend related to changes in  
71 light availability and temperature, and that the canopy and its epibionts were responsible for  
72 the huge majority of community' carbon fluxes.

73 Following the principles of the intertidal zonation of canopy-forming species and the general  
74 relationship between diversity of marine species and tidal level (Raffaelli and Hawkins 1999;  
75 Molina-Montenegro et al. 2005), it could be expected that the tidal level at which the

76 communities are established is of paramount importance in controlling the magnitude and the  
77 seasonal variability of their metabolism, as well as the contribution (and its seasonal  
78 variability) of the canopy to the total metabolism. Furthermore, the hydrodynamism to which  
79 the communities are exposed and specific environmental conditions (e.g. nutrient depletion),  
80 could as well have an influence on these parameters. In the current context of harvesting of  
81 Phaeophyceae along European West coasts (Jacob et al. 2012), it appears crucial to better  
82 understand the year-round dynamic of the communities they form, but also the way these  
83 canopy-forming species contribute to this dynamic.

84 In addition, some essential information on algae-environment interactions could be obtained  
85 considering the elemental composition of canopy-forming Phaeophyceae, which was shown  
86 to reflect both assimilation and use of nutrients and organic compounds by the algae  
87 (Chapman and Craigie 1977; 1978). This appears to be particularly attractive in intertidal  
88 systems since algae have to rely on their own nitrogen reserves when emerged (Pedersen and  
89 Borum 1997).

90

91 Mid- and low-mid intertidal communities dominated respectively by canopy-forming algae  
92 *Fucus vesiculosus* Linnaeus and *Fucus serratus* Linnaeus are particularly widespread along  
93 European coasts (Jueterbock et al. 2013). This study focused on the metabolic activity of  
94 these two adjacent communities, using *in situ* carbon fluxes measurements performed at the  
95 onset of emersion periods, under saturating irradiance. We hypothesized that (1) while  
96 following temporal variations, their gross primary production and respiration remained  
97 substantial all over the year, that (2) canopies consistently acted as the major contributor of  
98 total carbon fluxes in the communities, with this contribution following seasonal pattern, and  
99 that (3) the nitrogen and organic carbon contents of the canopies also varied with seasons and  
100 environmental conditions. Finally, we also hypothesized that (4) the lower shore community

101 exhibited a higher metabolic competitiveness than the upper shore community, in accordance  
102 with the principles of vertical zonation of canopy species.

103

## 104 MATERIALS & METHODS

### 105 *Study site*

106 This study was performed on *F. vesiculosus* and *F. serratus* communities established on an  
107 intertidal semi-sheltered boulder reef located in front of the Station Biologique de Roscoff  
108 (Brittany, France) (48°43.743'N, 3°59.407'W), in the southwest part of the English Channel.  
109 On this reef, these communities form dense and multi-layer assemblages which frequently  
110 cover 100% of the substratum, making it an ideal place to study their metabolism. This shore  
111 is subjected to semi-diurnal tidal cycle with maximal range of about 9 m. It presents a typical  
112 vertical distribution of communities dominated by canopy-forming Phaeophyceae, where *F.*  
113 *vesiculosus* community is characteristic of the mid-intertidal (3.0 to 4.0 m above chart datum,  
114 corresponding to an annual emerged time of 20-35%) while *F. serratus* community is  
115 characteristic of the low mid-intertidal (2.5 to 3.0 m above chart datum, corresponding to an  
116 annual emerged time of 15-20%).

117

### 118 *Environmental conditions*

119 This site, located in the temperate part of Northern hemisphere, displays a seasonal day:night  
120 cycle varying from 9:15 in late December to 16:8 in late June. It is also subjected to seasonal  
121 variations of irradiance and temperature. The weather station of Brest-Guipavas (located at  
122 approx. 40 km of our study site) provided monthly maximal instantaneous irradiance ( $\text{Max}_{\text{irr}}$ ,  
123 in  $\text{W m}^{-2}$ ) and monthly mean air temperature ( $T_{\text{air}}$ , in °C) datasets (October 2012 – December  
124 2013). The SOMLIT network (sampling site: Estacade, Roscoff, located at approx. 600 m of  
125 our study site) provided monthly mean seawater temperature ( $T_{\text{seawater}}$ , in °C) and monthly

126 means seawater nutrient concentrations ( $\text{NH}_4^+$ ,  $\text{NO}_3^{2-}$ ,  $\text{NO}_2^-$  and  $\text{PO}_4^{3-}$ , in  $\mu\text{mol L}^{-1}$ ) datasets  
127 (October 2012 – December 2013).

128

### 129 *Benthic metabolism measurements and sampling*

130 Measurements of benthic metabolism of *F. vesiculosus* and *F. serratus* communities were  
131 performed once a month from October 2012 to December 2013, with the exception of  
132 December 2012. They were always done at the onset of emersion of a spring tide (around  
133 midday) to avoid a desiccation effect on metabolic rates. At each occasion, three intra-site  
134 replicates (2 to 5 m distance between each) of a 0.09 m<sup>2</sup> rock area were haphazardly selected  
135 for both communities (only two replicates in November 2013 for *F. serratus* community). A  
136 replicate included one to several *Fucus* thalli (> 25 cm long) with the associated community,  
137 which was essentially made-up of *Fucus* epibionts (i.e. algae and sessile invertebrates directly  
138 attached to the *Fucus*, see Wahl 2009) and biofilms, as well as sub-canopy and encrusting  
139 macroalgae, rocky and sedimentary microphytobenthos and invertebrates, including the  
140 mobile ones on *Fucus* fronds. Each area was then enclosed in a custom-built incubation  
141 chamber (17.7 L) made of clear Plexiglas, connected to an infrared CO<sub>2</sub> gas analyzer (LiCor  
142 Li-820) in closed air circuit. Air motion of 1 L min<sup>-1</sup> was ensured by a pump in this closed  
143 circuit. CO<sub>2</sub> fluxes measurements were performed at the rock-air interface, as described by  
144 Migné et al. (2002), at ambient light and in darkness by covering up the chambers. These  
145 measurements allowed estimating the total community net primary production (NPP<sub>t</sub>) and the  
146 total community respiration (CR<sub>t</sub>), respectively, assuming that CO<sub>2</sub> fluxes measured in  
147 darkness after abrupt transition from ambient light reflected the respiration activity of the  
148 communities (del Giorgio and Williams 2005). Incubations were sufficiently short (i.e. 5 - 10  
149 min) to avoid feedback of temperature and gas concentration changes on metabolic rates.  
150 Total community gross primary production (GPP<sub>t</sub>) was calculated as  $\text{GPP}_t = \text{NPP}_t + \text{CR}_t$ . CO<sub>2</sub>

151 fluxes were calculated from recorded data using the slope of CO<sub>2</sub> concentration ( $\mu\text{mol}_{\text{CO}_2}$   
152  $\text{mol}_{\text{air}}^{-1}$ ) against time (min). Therefore, GPP<sub>t</sub> and CR<sub>t</sub> were expressed in carbon unit ( $\text{mgC m}^{-2}$   
153  $\text{h}^{-1}$ ) assuming a molar volume of 22.4 L mol<sup>-1</sup> at standard temperature and pressure and a  
154 molar mass of 12 gC mol<sub>CO<sub>2</sub></sub><sup>-1</sup>. Finally, the community metabolic balance was calculated each  
155 month for both communities as the ratio of CR<sub>t</sub> to GPP<sub>t</sub>.

156 After performing this first set of light and dark incubations, *Fucus* thallus and the associated  
157 epibionts and biofilms were removed from the incubation chambers, while mobile fauna being  
158 on the fronds was left inside of the chambers with the remaining organisms (including algae  
159 and invertebrates). A second set of light and dark incubations was performed on this residual  
160 community, in order to estimate residual community net primary production (NPP<sub>r</sub>) and  
161 residual community respiration (CR<sub>r</sub>). Residual community gross primary production (GPP<sub>r</sub>)  
162 was calculated following the formula used previously ( $\text{GPP}_r = \text{NPP}_r + \text{CR}_r$ ). These  
163 measurements allowed to determine the contribution of the canopy to the carbon fluxes of the  
164 community ( $\text{GPP}_{\text{can}} = \text{GPP}_t - \text{GPP}_r$ ;  $\text{CR}_{\text{can}} = \text{CR}_t - \text{CR}_r$ ).

165 Removed canopies were brought back to the laboratory to measure their dry masses after  
166 drying for 48 h at 60 °C. Dry masses were used to calculate the respiration rate of canopies  
167 ( $\text{R}_{\text{can}}/\text{DM}_{\text{can}}$ ) and their productivity ( $\text{GPP}_{\text{can}}/\text{DM}_{\text{can}}$ ) expressed in  $\text{mgC g}_{\text{DM}}^{-1} \text{h}^{-1}$ .

168  
169 Incident photosynthetically available radiation (400-700 nm) was recorded (LiCor  
170 QuantumSA-190,  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) close to the incubation chambers. Mean values during  
171 measurements at ambient light varied from 465  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  in December 2013 to  
172 2094  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  in June 2013. Measurements were thus assumed to be done under  
173 saturating irradiance, based on the average value of 291  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  given for the  
174 onset of light saturation of coastal macroalgal communities (Middelboe et al. 2006).

175

176 *Carbon and nitrogen content*

177 Just before drying the removed canopies as mentioned previously, samples ( $\approx 1$  g of fresh  
178 weight) were taken from *Fucus* fronds of each replicate, to assess their C and N contents.  
179 These sampling were done from January to December 2013. Samples were rinsed with  
180 distilled water before being dried (60°C, 48 h) and ground to a fine powder using a mortar and  
181 pestle. C and N mass percentages were determined at the Station Biologique de Roscoff using  
182 a Flash EA 1112 CHN analyzer (ThermoFinnigan) calibrated against nicotinamide and  
183 acetanilide reference materials.

184

185 *Statistical analysis*

186 Seasonal patterns of  $GPP_t$ ,  $CR_t$ ,  $CR_t/GPP_t$ ,  $GPP_{can}/DM_{can}$ ,  $R_{can}/DM_{can}$ , C and N contents were  
187 highlighted by fitting a sinusoidal curve to the monthly mean values:

188 
$$y = a + b \sin\left(\frac{2\pi}{365}x + c\right)$$

189 where  $y$  is the predicted value of the considered parameter, and  $x$  the time in days.  $F$ -test was  
190 used to test the fit, using R software, version 3.1.2 (R Core Team, 2014).

191 Comparisons of the two communities (community metabolism, canopy metabolism and C and  
192 N contents) were done using Wilcoxon signed rank test on the mean values for each month,  
193 performed with the R software, version 3.1.2 (R Core Team, 2014).

194 Correlations between monthly maximal instantaneous irradiance and PAR recorded during  
195 light incubations, and between N contents and seawater N-nutrients pool, were tested with  
196 Pearson coefficient using the R software, version 3.1.2 (R Core Team, 2014).

197 For both communities, the relationship between  $GPP_t$  or  $CR_t$  and environmental variables was  
198 analysed by linear multiple regression (Best procedure and AIC selection criteria) with  $p$ -  
199 values obtained by permutation, using PRIMER software, version 6.1.12 associated with  
200 PERMANOVA+ for PRIMER, version 1.0.2. Predictor variables of  $GPP_t$  consisted of

201 monthly maximal instantaneous irradiance, monthly means of air and seawater temperature  
202 and of nutrients seawater concentrations ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$  and  $\text{PO}_4^{2-}$ ), and canopy dry mass.  
203 Predictor variables of  $\text{CR}_t$  consisted of monthly means of air and seawater temperature, and  
204 canopy dry mass.

205

## 206 RESULTS

### 207 *Environmental conditions*

208 Monthly maximal instantaneous irradiance followed seasonal trend, with values ranging from  
209  $311 \text{ W m}^{-2}$  in December 2012 to  $1000 \text{ W m}^{-2}$  in May 2013 (Fig 1). Our records of incident  
210 photosynthetically available radiation during light incubations (data not shown) were  
211 significantly correlated with these values ( $r = 0.885$ ,  $p < 0.001$  for the *F. vesiculosus*  
212 community and  $r = 0.784$ ,  $p < 0.001$  for the *F. serratus* community). Monthly mean air and  
213 seawater temperatures also followed seasonal trends, with values ranging respectively from  
214  $5.8 \text{ }^\circ\text{C}$  in February 2013 to  $18.2 \text{ }^\circ\text{C}$  in July 2013 and from  $9.3 \text{ }^\circ\text{C}$  in March 2013 to  $16.5 \text{ }^\circ\text{C}$  in  
215 August 2013 (Fig 1). Nitrates ( $\text{NO}_3^-$ ) dominated the seawater N-nutrient pool throughout the  
216 year, with concentration ranging from  $0.19 \text{ } \mu\text{mol L}^{-1}$  at the end of July 2013 to  $12.45 \text{ } \mu\text{mol L}^{-1}$   
217 at the beginning of February 2013 (Fig 2a). Ammonium ( $\text{NH}_4^+$ ), nitrites ( $\text{NO}_2^-$ ) and  
218 phosphates ( $\text{PO}_4^{2-}$ ) seawater concentrations also fluctuated throughout the year, but remained  
219 lower than  $0.75 \text{ } \mu\text{mol L}^{-1}$  (Fig 2b).

220

### 221 *Benthic metabolism*

222 *Fucus vesiculosus* community exhibited a gross primary production ( $\text{GPP}_t$ , mean  $\pm$  SE)  
223 ranging from  $341.6 \pm 41.0 \text{ mgC m}^{-2} \text{ h}^{-1}$  in March 2013 to  $962.9 \pm 195.4 \text{ mgC m}^{-2} \text{ h}^{-1}$  in June  
224 2013 and respiration ( $\text{CR}_t$ , mean  $\pm$  SE) ranging from  $102.8 \pm 27.1 \text{ mgC m}^{-2} \text{ h}^{-1}$  in February  
225 2013 to  $562.7 \pm 117.1 \text{ mgC m}^{-2} \text{ h}^{-1}$  in August 2013.  $\text{GPP}_t$  of the *Fucus serratus* community

226 ranged from  $440.0 \pm 80.6 \text{ mgC m}^{-2} \text{ h}^{-1}$  in January 2013 to  $1104.4 \pm 101.9 \text{ mgC m}^{-2} \text{ h}^{-1}$  in  
227 August 2013 and  $\text{CR}_t$  ranged from  $74.3 \pm 7.9 \text{ mgC m}^{-2} \text{ h}^{-1}$  in January 2013 to  $475.9 \pm 65.8$   
228  $\text{mgC m}^{-2} \text{ h}^{-1}$  in August 2013 (Fig 3). Both  $\text{GPP}_t$  and  $\text{CR}_t$  of *F. vesiculosus* and *F. serratus*  
229 communities followed a seasonal pattern significantly fitted by sinusoidal curves (Table 1),  
230 with minimal values occurring during winter and maximal values occurring during summer,  
231 even though a metabolic depression was observed in July. While they followed the same  
232 seasonal fluctuations, the *F. vesiculosus* community exhibited significantly lower  $\text{GPP}_t$  than *F.*  
233 *serratus* community (20% lower in average) but significantly higher  $\text{CR}_t$  (25% higher in  
234 average) (Table 2). The metabolic balance (i.e.  $\text{CR}_t/\text{GPP}_t$ ) was always lower than 1 during our  
235 measurements under saturating light conditions. It followed a significant seasonal pattern too  
236 (Table 1) with minimal values in winter and maximal values during late summer and early fall  
237 (from 0.23 to 0.73 for *F. vesiculosus* community and from 0.16 to 0.45 for *F. serratus*  
238 community) (Fig 4). The metabolic balance was significantly higher for the *F. vesiculosus*  
239 community (Table 2), in agreement with the observed differences for both  $\text{GPP}_t$  and  $\text{CR}_t$  of  
240 these communities.

241 The variability of  $\text{GPP}_t$  was best explained by  $\text{NO}_3^-$  seawater concentration and  $\text{DM}_{\text{can}}$  taken  
242 together for the *F. vesiculosus* community whereas it was best explained by  $\text{Max}_{\text{irr}}$ ,  $T_{\text{air}}$  and all  
243 seawater nutrient concentrations for the *F. serratus* community (Table 3). The variability of  
244  $\text{CR}_t$  was best explained by the three predictor variables taken together ( $T_{\text{air}}$ ,  $T_{\text{seawater}}$  and  
245  $\text{DM}_{\text{can}}$ ) for the *F. vesiculosus* community whereas it was best explained by  $T_{\text{air}}$  alone for the *F.*  
246 *serratus* community (Table 3).

247

248 The metabolism of these two communities was consistently dominated by the canopies (i.e.  
249 the dominant species and their epibionts) since they accounted for the huge majority of the  
250 global  $\text{CO}_2$  fluxes (77-97% of  $\text{CR}_t$  and 83-95% of  $\text{GPP}_t$ ). Nevertheless, no seasonal pattern

251 was observed for the relative contribution of canopies, neither for respiration nor for primary  
252 production (F-test,  $p > 0.05$ ). The productivity ( $GPP_{can}/DM_{can}$ , mean  $\pm$  SE) of *F. vesiculosus*  
253 canopy ranged from  $0.172 \pm 0.029$  mgC  $g_{DM}^{-1} h^{-1}$  in November 2013 to  $0.473 \pm 0.072$  mgC  
254  $g_{DM}^{-1} h^{-1}$  in June 2013 and its respiration rate ( $R_{can}/DM_{can}$ , mean  $\pm$  SE) from  $0.043 \pm 0.010$   
255 mgC  $g_{DM}^{-1} h^{-1}$  February 2013 to  $0.217 \pm 0.053$  mgC  $g_{DM}^{-1} h^{-1}$  in June 2013. The productivity  
256 of *F. serratus* canopy ranged from  $0.083$  mgC  $g_{DM}^{-1} h^{-1}$  in November 2013 to  $0.740 \pm 0.112$   
257 mgC  $g_{DM}^{-1} h^{-1}$  in April 2013 and its respiration rate from  $0.040 \pm 0.008$  mgC  $g_{DM}^{-1} h^{-1}$  in  
258 November 2012 to  $0.240 \pm 0.027$  mgC  $g_{DM}^{-1} h^{-1}$  in June 2013 (Fig 5). As for whole  
259 communities, both productivity and respiration rate of the canopies followed a significant  
260 seasonal pattern (Table 1), except for the *F. vesiculosus* productivity (F-test,  $p > 0.05$ ). Finally,  
261 the productivity of *F. vesiculosus* was significantly lower than the one of *F. serratus* (30%  
262 lower in average). No significant difference was found for respiration rate (Table 2).

263

#### 264 *Carbon and nitrogen contents*

265 C and N contents measured from *Fucus* thallus samples exhibited a seasonal pattern  
266 significantly fitted by sinusoidal curves (Fig 6, Table 1). For both *Fucus* species, C content  
267 was the lowest in autumn and the highest in summer, ranging from 37.5 to 39.7% of DM for  
268 *F. vesiculosus* and from 37.8 to 41.7% of DM for *F. serratus*. On the contrary, N content was  
269 the lowest in summer and the highest in spring, ranging from 0.88 to 2.39% of DM for *F.*  
270 *vesiculosus* and from 0.99 to 2.16% of DM for *F. serratus* (Fig 6). *F. serratus* held  
271 significantly higher C content but lower N content than *F. vesiculosus* (Table 2). N content  
272 was significantly correlated with seawater N-nutrient pool, both for *F. vesiculosus* ( $r = 0.694$ ,  
273  $p = 0.012$ ) and *F. serratus* ( $r = 0.665$ ,  $p = 0.018$ ).

274

275 DISCUSSION

276 By measuring *in situ* metabolism of intertidal *Fucus vesiculosus* and *F. serratus* communities  
277 under saturating irradiance, this study highlights that, whatever the season, these communities  
278 display a substantial metabolic activity at the beginning of emersion periods. Our results of  
279 metabolic activity overlapped those previously obtained for *Ascophyllum nosodum*  
280 community (188–846 mgC m<sup>-2</sup> h<sup>-1</sup> for GPP<sub>t</sub> and 122–616 mgC m<sup>-2</sup> h<sup>-1</sup> for CR<sub>t</sub>, Golléty et al.  
281 2008). Consequently, in such latitudes, intertidal Phaeophycean-dominated communities  
282 appear to be photosynthetically active and efficient throughout the year, even though  
283 measurements were performed under emerged conditions, which are often considered to be  
284 very stressful (Wahl et al. 2011, and references therein). This study also confirms that  
285 Phaeophycean-dominated communities are the most productive systems of intertidal habitats.  
286 Indeed, *F. vesiculosus* and *F. serratus* communities displayed considerable higher year-round  
287 mean GPP<sub>t</sub> (in mgC m<sup>-2</sup> h<sup>-1</sup>) than those obtained in studies using the same *in situ* measurement  
288 method, i.e. 7 to 9 times higher than a *Zostera noltei* bed (Ouisse et al. 2010), 15 to 20 times  
289 higher than a muddy-sand community (Migné et al. 2004) or 35 to 44 times higher than a  
290 sandy beach community (Hubas et al. 2006). All these studies were conducted at the  
291 community scale, integrating the interactions between species and their responses to a broad  
292 range of local conditions, especially of incident light (Middelboe et al. 2006; Tait and Schiel  
293 2011; Migné et al. 2015a), and accounting for the contribution of biofilms which is known to  
294 be highly significant, both for autotrophic and heterotrophic activities (Golléty and Crowe  
295 2013).

296

297 As expected, both GPP<sub>t</sub> and CR<sub>t</sub> exhibited a seasonal pattern, with minima in winter and  
298 maxima in summer, in each community. Such seasonal pattern is in agreement with the  
299 general idea that light availability and temperature act as the major drivers of community  
300 metabolism (Davison 1991; Golléty et al. 2008; Ouisse et al. 2010; Kemp and Testa 2011).

301 However, inorganic seawater nutrient concentrations also act as a key factor of metabolic  
302 regulation of marine systems. Photosynthesis can be limited by low nutrient concentrations  
303 which affect algal growth and lead to changes in the structure and the food webs of the  
304 communities (Bosman et al. 1987). In this study, a gross primary production depression was  
305 observed in July for both *F. vesiculosus* and *F. serratus* communities and matched with the  
306 lowest records in seawater nutrient concentrations close to the study site, suggesting that a  
307 nutrient limitation has occurred during this period. The same depression in primary  
308 production was observed in summer for the *A. nodosum* community (Golléty et al. 2008), also  
309 matching with the lowest seawater nutrient concentrations (SOMLIT network data),  
310 strengthening this nutrient limitation hypothesis. Furthermore, the multiple correlations  
311 analyses showed that the variability of  $GPP_t$  was best explained by incident light, air  
312 temperature and seawater nutrient concentrations in *F. serratus* community, and by  $NO_3^-$   
313 concentration and canopy dry mass in *F. vesiculosus* community. Surprisingly, neither incident  
314 light nor temperature appeared in the best model of regressions for  $GPP_t$  of *F. vesiculosus*  
315 community. It can be hypothesized that as the *F. vesiculosus* community is located upper on  
316 the shore than the *F. serratus* community, it has a more restricted access to seawater nutrients,  
317 inducing a higher susceptibility to nutrient limitation, and particularly to nitrates, which  
318 dominate the nutrient pool.

319 The  $GPP_t$  depression observed in July could also be related to the highest irradiances as an  
320 excess of light could act as significant stress for photo-autotrophic organisms (e.g. Huppertz  
321 et al. 1990; Häder and Figueroa 1997; Bischof et al. 2000). However, Creis et al. (2015) have  
322 demonstrated that the exposition of *F. vesiculosus* individuals to UV-B conditions  
323 approximately two times more important than the maximal conditions occurring in Brittany  
324 only led to a slight reduction in the maximal efficiency of PSII after 1 and 4 weeks of chronic  
325 exposure. In addition, as we were working at the community scale, only the upper layer of the

326 community (mainly composed of *Fucus* spp.) was exposed to high light, and could have  
327 suffer from it. This layer acted as a protective layer for the other components of the  
328 community, which benefited from the attenuation of incident light and could have maintained  
329 a high metabolic activity. The canopy biomass appeared to be a good predictor of metabolic  
330 variations of the *F. vesiculosus* community  $GPP_t$ . Binzer and Sand-Jensen (2002)  
331 demonstrated that at high density, photosynthetic tissues have the ability to fully use incident  
332 light. This would imply an optimal distribution and utilisation of incident light among all  
333 photosynthetic tissues in the community. Nevertheless, at very high canopy density,  
334 photosynthetic activity could be limited under high light due to uneven distribution of photons  
335 (Binzer and Sand-Jensen 2002).

336 During our measurements, *F. vesiculosus* and *F. serratus* communities always performed as  
337 autotrophic entities, with a  $CR_t/GPP_t$  ratio strictly lower than 1. Interestingly, this metabolic  
338 balance fluctuated according to a seasonal pattern, as did photosynthesis and respiration. Such  
339 pattern could be related to the seasonal fluctuations of the biomass of these communities, as  
340 the metabolic balance was maximal in summer when maximal biomass accumulation  
341 occurred. Indeed, community gross primary production is limited at high canopy density  
342 while its respiration rate is linearly related to its density (Binzer and Sand-Jensen 2002).

343 Finally, this seasonal variation implies that metabolic balance has to be used with caution if  
344 measured punctually, particularly when dealing with the annual carbon budget of an  
345 ecosystem.

346

347 By removing *F. vesiculosus* and *F. serratus* canopies, we showed that they were responsible  
348 for the great majority of  $CO_2$  fluxes (77-97% of  $CR_t$  and 83-95% of  $GPP_t$ ). This confirms that  
349 the role of canopy-forming macroalgae in the community is not restricted to facilitation for  
350 associated species, but is also fundamental in the community metabolism, all over the year.

351 No seasonal pattern emerged however, even though diversity and abundance of epibionts and  
352 others species, like the opportunistic ones, are known to exhibit a strong seasonal variability  
353 (e.g. Rindi and Guiry 2004). Being substantial productive entities, canopy-forming algae can  
354 control the community processes they dominate, to constitute one of the major suppliers of  
355 organic carbon for coastal food webs (Paine 2002; Golléty et al. 2008). By this way, the  
356 global current decline of canopy-forming macroalgae (Airoidi and Beck 2007; Duarte et al.  
357 2013) and the predicted shift of European *F. vesiculosus* and *F. serratus* communities  
358 northward (Jueterbock et al. 2013; 2014) are likely to have dramatic effects on the dynamics  
359 of coastal ecosystems (Thompson et al. 2002).

360

361 As major metabolic component of their communities, the *F. vesiculosus* and *F. serratus*  
362 canopies rationally exhibited high productivity and respiration rate (in  $\text{mgC g}_{\text{DM}}^{-1} \text{h}^{-1}$ ). These  
363 rates were found to be in the same range as those obtained for other slow-growing  
364 Phaeophyceae (e.g. Quadir et al. 1979; Williams and Dethier 2005; Golléty et al. 2008). Yet,  
365 some previous studies on *Fucus* spp. indicated productivity 2 to 10 times higher than our  
366 results (Brinkhuis et al. 1976; Maberly and Madsen 1990; Kawamitsu and Boyer 1999)  
367 whereas respiration rates were quite similar. These high productivities might be explained by  
368 the use of fucoids segments under laboratory conditions, contrasting with our *in situ*  
369 conditions, where the canopies consisted of multi-layer assemblages subjected to strong self-  
370 shading, at least for the basal layers. Furthermore, canopies were considered as a multi-  
371 specific complex, composed of *Fucus* thalli associated with their epibionts (e.g. Chlorophyta,  
372 Rhodophyta, Bryozoa, Tunicates, etc.) and biofilms. These species probably acted as  
373 productivity inhibitors due to light attenuation, at least for the heterotrophic ones, as  
374 demonstrated by Sand-Jensen (1977) on eelgrass leaves. Considering this, our results  
375 appeared to be realistic about what really happened on the field. As for whole communities, a

376 seasonal pattern of productivity and respiration rate was observed, except for *F. vesiculosus*  
377 productivity, confirming the previous hypothesis about metabolic drivers. The C contents of  
378 both species followed a clear seasonal pattern, as those well described for *Laminaria* species  
379 (e.g. Gagné et al. 1982; Gevaert et al. 2001), with the highest C content in summer, when C  
380 assimilation by photosynthesis exceeds C requirements, leading to a storage of carbohydrates  
381 (Gomez and Wiencke 1998; Lehvo et al. 2001) and the lowest in winter when photosynthesis  
382 was not sufficient to supply C requirements, leading to a gradual use of carbohydrate reserves  
383 (Hatcher et al. 1977; Lehvo et al. 2001). Any variation in C content due to reproduction  
384 investment was detected while both species are known to exhibit seasonal trend in their  
385 reproductive strategy (Knight and Parke 1950; Brenchley et al. 1998). Yet, this reproductive  
386 process is known to be spread over several months (Knight and Parke 1950), with resources  
387 investment rarely exceeding 55% and fertile individuals found year-round (Brenchley et al.  
388 1998). The N contents also followed seasonal variations, which are well documented in the  
389 literature too (e.g. Asare and Harlin 1983; Carlson 1991; Brenchley et al. 1998; Young et al.  
390 2007). For both species, N content was highest in winter and lowest in summer, and was  
391 significantly correlated with seawater N-nutrient concentrations, as already observed by  
392 Young et al. (2007). This is also consistent with the N turnover rate of approximately 2 to 3  
393 weeks exhibited by *F. vesiculosus* (Viana et al. 2015). High seawater nutrient availability in  
394 winter allowed a substantial N assimilation and storage by *Fucus* species. Stored N is  
395 gradually used to support an active growth during spring and summer, when N-seawater is  
396 depleted. Nutrients limitation of metabolic activity, supposed to occur at community scale, is  
397 strengthened by N contents values. Indeed, Pedersen and Borum (1997) have calculated a  
398 critical N tissue content of 1.71% of DM to support maximum growth rate for *F. vesiculosus*.  
399 Lower contents were observed during several months in our *F. vesiculosus* and *F. serratus*  
400 individuals. Yet, we could expect a seasonal fluctuation of critical N concentration and/or N-

401 requirements for these species, which could restrict N-limitation during summer months,  
402 when both N tissue and seawater nutrient concentrations were the lowest.

403

404 This study allowed the comparison of the metabolism, at the beginning of the emersion period  
405 and under saturating irradiance, of two adjacent communities along the vertical zonation. The  
406 upper community exhibited the lowest  $GPP_t$  and the highest  $CR_t$ , and as a consequence, the  
407 highest metabolic balance. The canopy productivity was also lower for *F. vesiculosus* than for  
408 *F. serratus*. This is consistent with the C content values, significantly lower in *F. vesiculosus*  
409 than in *F. serratus*. Differences in C content were particularly pronounced during summer and  
410 fall, when a higher net primary production for *F. serratus* was observed. Moebus et al. (1974)  
411 have evidenced that lower C contents in upper species could be a consequence of a higher  
412 organic C release during low tide in response to a higher desiccation degree. Finally, *F.*  
413 *serratus* appeared to be more competitive than *F. vesiculosus* in a metabolic point of view, in  
414 agreement with the vertical zonation rules (Raffaelli and Hawkins 1999). The latter species  
415 has probably achieved more efficient, but costly, protecting mechanisms to deal with abiotic  
416 stresses, such as temperature or desiccation, to the detriment of its competitiveness. This  
417 could cause high differences in the annual carbon balance of adjacent communities and needs  
418 to be investigated in details further.

419

#### 420 *Conclusion and perspectives*

421 This study showed that the two widespread *Fucus vesiculosus* and *F. serratus* communities  
422 exhibited high rates of both gross primary production and respiration all over a year,  
423 confirming their importance in the intertidal area. Nevertheless, as our measurements were  
424 achieved at the beginning of emersion for each community, further investigations need to be  
425 performed, using complementary methods, to survey the metabolism of these intertidal

426 communities during tidal and daily cycles. This is essential to assess accurately the annual  
427 carbon balance of such Phaeophycean-dominated systems to bring some insights about their  
428 functional ecology, but also to carry on such measurements with the prospect to get  
429 fundamental information about ecosystem functioning modifications due to the large and  
430 complex changes that occur on the biosphere (Staeher et al. 2012).

431

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440

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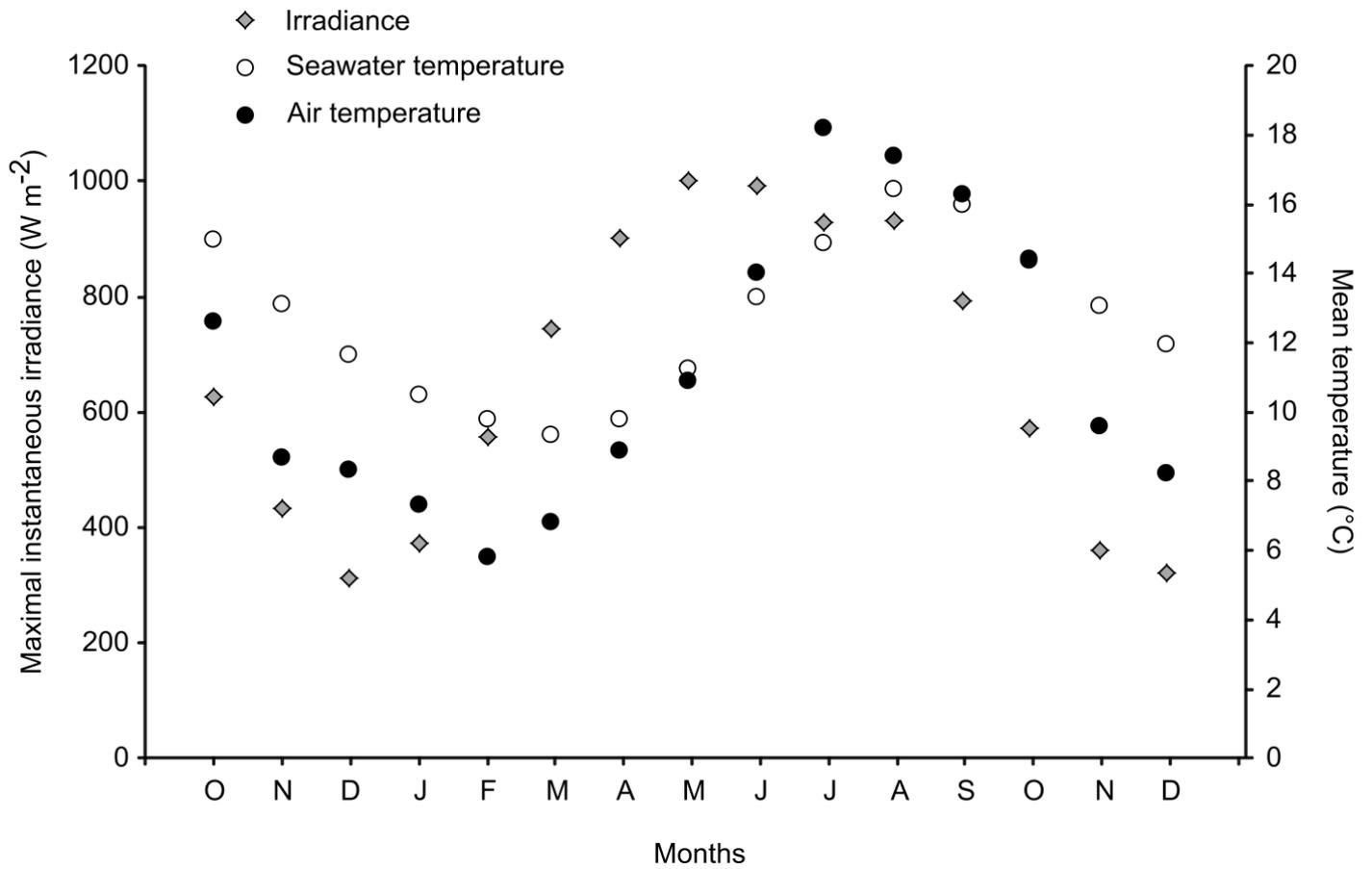
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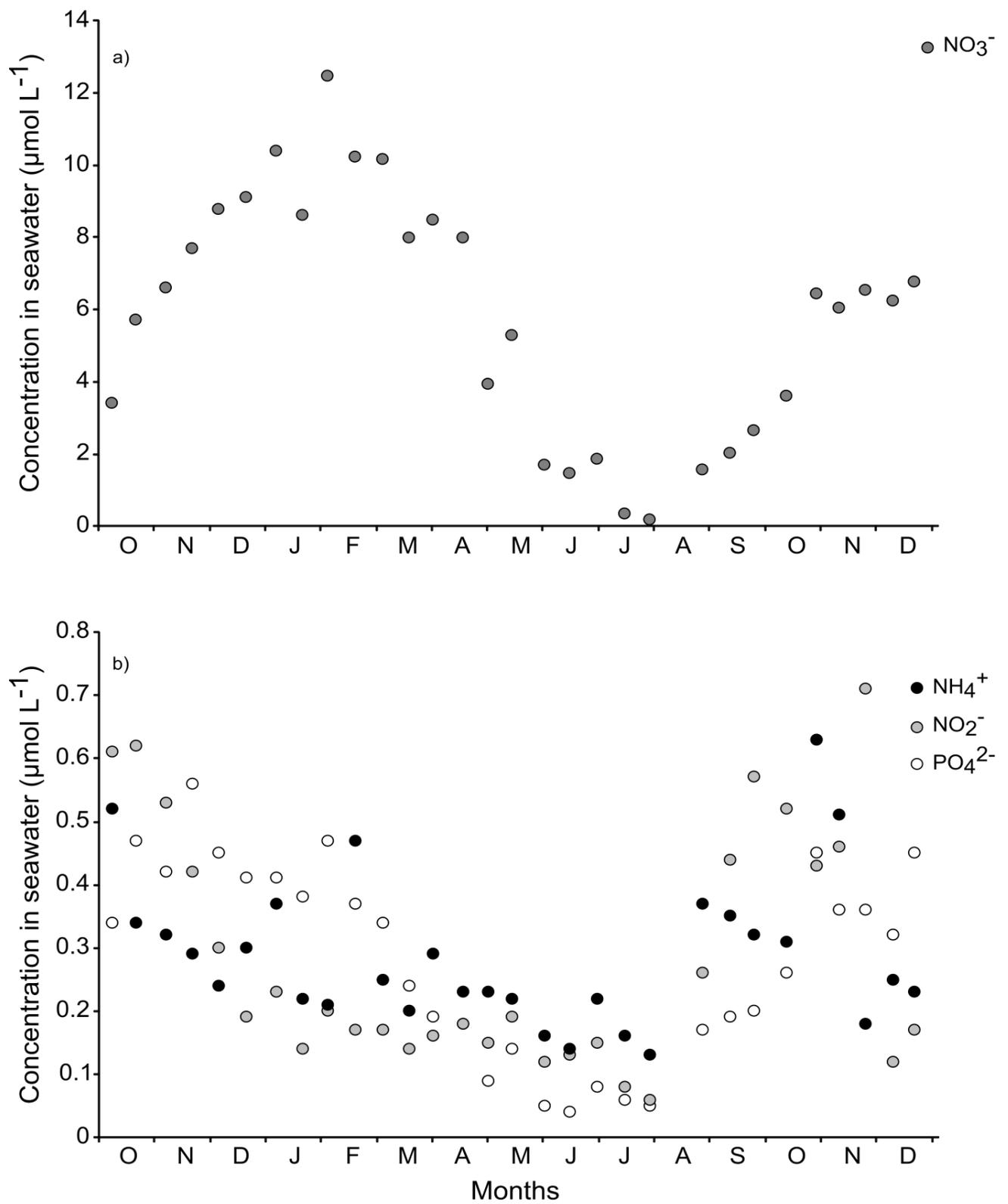
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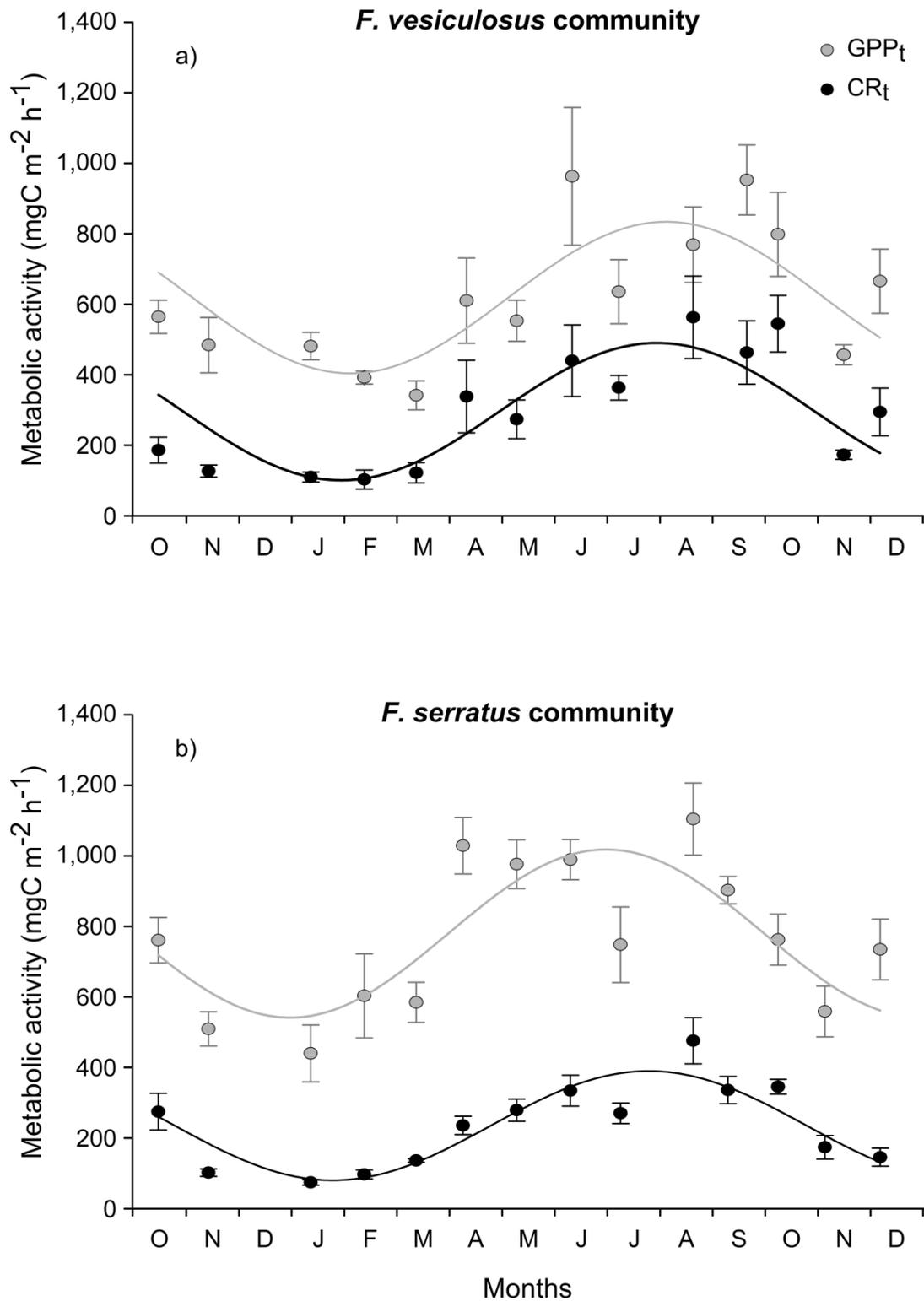
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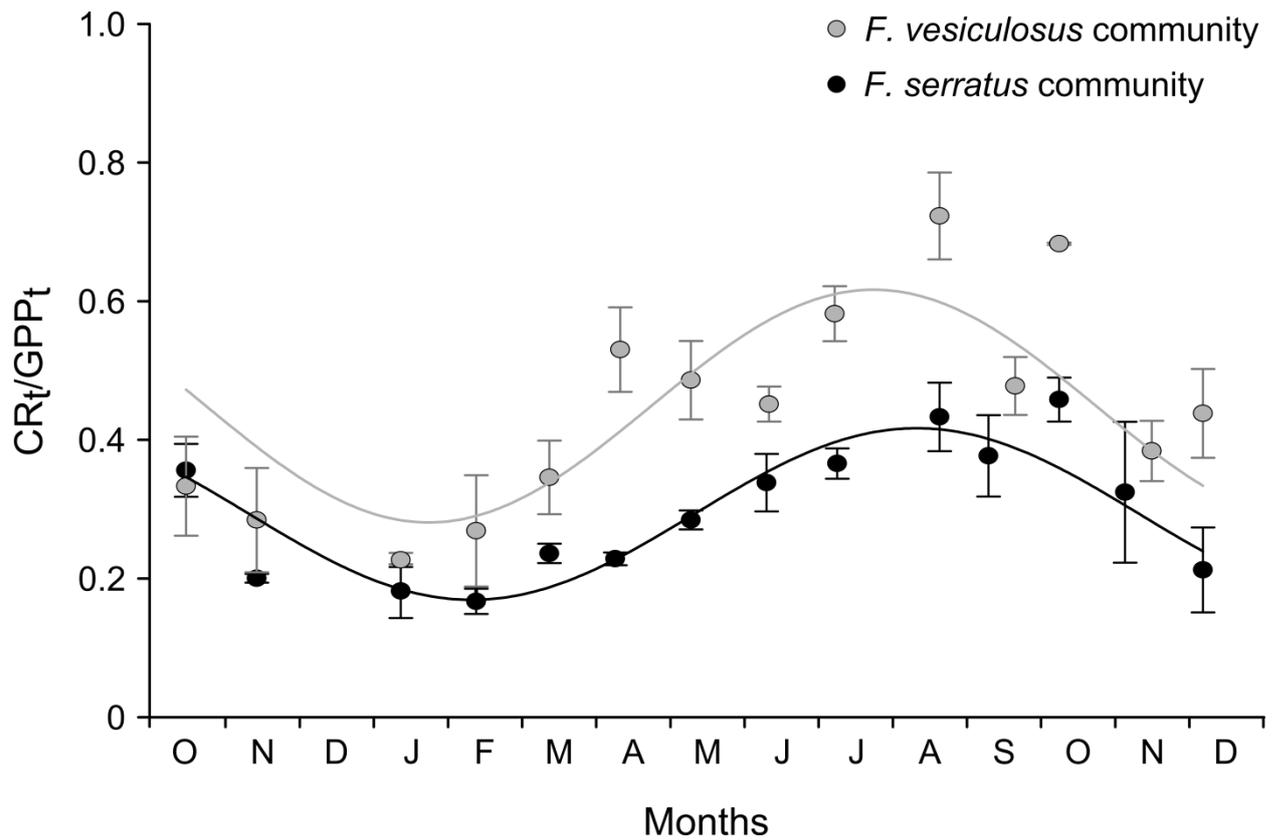
**Fig. 1** Monthly maximal instantaneous irradiance, expressed in  $\text{W m}^{-2}$ , and monthly mean of seawater and air temperatures, both expressed in  $^{\circ}\text{C}$ , as a function of time



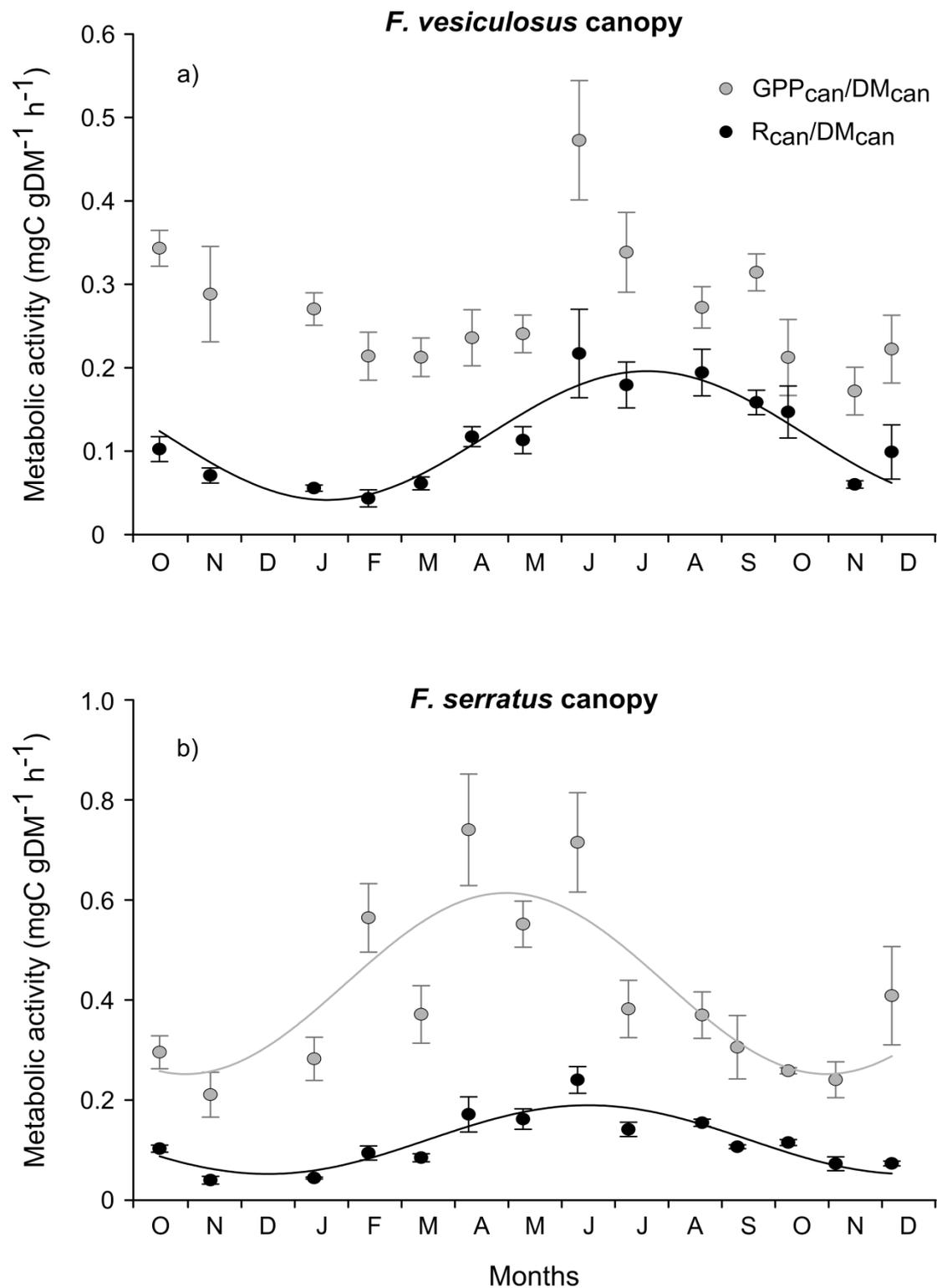
**Fig. 2** Seawater concentration of (a) nitrates ( $\text{NO}_3^-$ ) and (b) ammonium ( $\text{NH}_4^+$ ), nitrites ( $\text{NO}_2^-$ ) and phosphates ( $\text{PO}_4^{2-}$ ), expressed in  $\mu\text{mol L}^{-1}$ , as a function of time



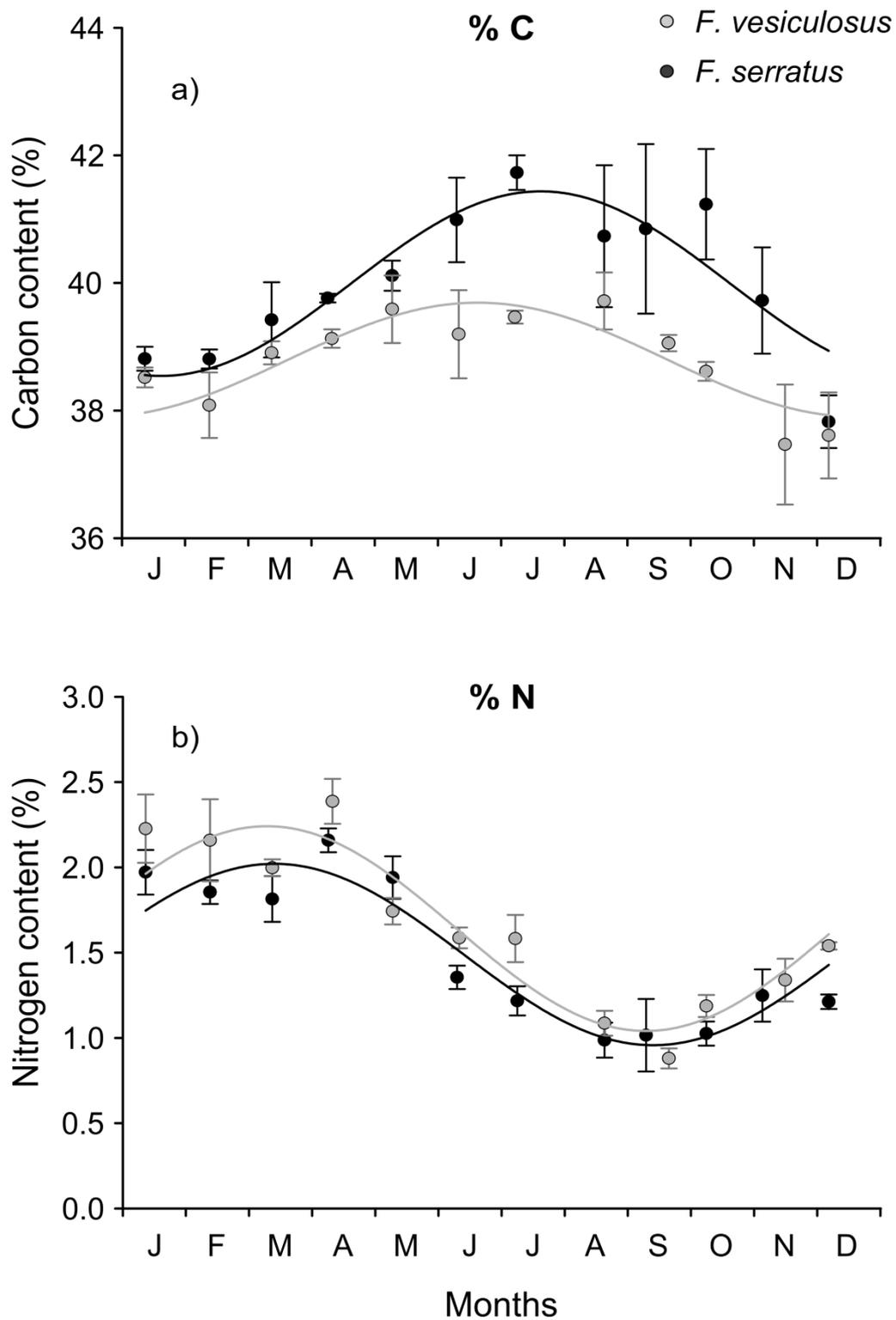
**Fig. 3** Mean ( $\pm$  SE) community gross primary production (GPP<sub>t</sub>) and respiration (CR<sub>t</sub>), both expressed in mgC m<sup>-2</sup> h<sup>-1</sup>, as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus* (b) communities. Grey and dark lines represent the sinusoidal curves fitted on GPP<sub>t</sub> and CR<sub>t</sub> data sets, respectively



**Fig. 4** Mean ( $\pm$  SE) metabolic balance, calculated as  $CR_t/GPP_t$ , as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark) communities. Grey and Dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* communities metabolic balance data sets, respectively



**Fig. 5** Mean ( $\pm$  SE) gross canopy productivity ( $\text{GPP}_{\text{can}}/\text{DM}_{\text{can}}$ ) and canopy respiration rate ( $\text{R}_{\text{can}}/\text{DM}_{\text{can}}$ ), both expressed in  $\text{mgC gDM}^{-1} \text{h}^{-1}$ , as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus* (b) canopies. Grey and dark lines represent the sinusoidal curves fitted on productivity and respiration data sets, respectively



**Fig. 6** Mean ( $\pm$  SE) C content (a) and N content (b), both expressed in % of  $DM_{can}$ , as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark). Grey and dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* data sets, respectively

Table 1: Sinusoidal curve parameters ( $n$ ,  $a$ ,  $b$ ,  $c$  and  $R^2$ ) and F-test significant level (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ) for *Fucus vesiculosus* and *Fucus serratus* community gross primary production ( $GPP_t$ ), community respiration ( $CR_t$ ), metabolic balance ( $CR_t/GPP_t$ ), canopy productivity ( $GPP_{can}/DM_{can}$ ), canopy respiration rate ( $R_{can}/DM_{can}$ ), C content (% C), N content (% N).

	Community/canopy	$n$	$a$	$b$	$c$	$R^2$	$p$
$CR_t$	<i>F. vesiculosus</i>	14	295.6	-194.8	7.4	0.634	**
	<i>F. serratus</i>	14	235.2	154.8	4.3	0.787	***
$GPP_t$	<i>F. vesiculosus</i>	14	618.9	-214.9	7.3	0.555	*
	<i>F. serratus</i>	14	779.7	238.2	17.3	0.604	*
$CR_t/GPP_t$	<i>F. vesiculosus</i>	14	0.4487	0.1678	4.3259	0.556	*
	<i>F. serratus</i>	14	0.2930	0.1238	4.0211	0.804	***
$R_{can}/DM_{can}$	<i>F. vesiculosus</i>	14	0.1187	-0.0772	1.2554	0.851	***
	<i>F. serratus</i>	14	0.1210	-0.0686	1.8345	0.779	***
$GPP_{can}/DM_{can}$	<i>F. serratus</i>	14	0.4330	0.1810	-0.5001	0.668	**
% C	<i>F. vesiculosus</i>	12	38.80	0.89	4.91	0.766	**
	<i>F. serratus</i>	12	39.99	1.45	4.39	0.807	**
% N	<i>F. vesiculosus</i>	12	1.64	-0.60	3.52	0.873	***
	<i>F. serratus</i>	12	1.49	-0.53	3.46	0.878	***

Table 2: Wilcoxon signed rank test results ( $V$ ,  $p$ ) for differences between *Fucus vesiculosus* and *Fucus serratus* in mean community gross primary production ( $GPP_t$ ), community respiration ( $CR_t$ ), metabolic balance ( $CR_t/GPP_t$ ), canopy productivity ( $GPP_{can}/DM_{can}$ ), canopy respiration rate ( $R_{can}/DM_{can}$ ), C content (% C), N content (% N).

	<b>V</b>	<b>p</b>
<b><math>CR_t</math></b>	15	<b>0.017</b>
<b><math>GPP_t</math></b>	12	<b>0.009</b>
<b><math>CR_t/GPP_t</math></b>	3	<b>&lt; 0.001</b>
<b><math>R_{can}/DM_{can}</math></b>	50	0.903
<b><math>GPP_{can}/DM_{can}</math></b>	13	<b>0.011</b>
<b>% C</b>	78	<b>&lt; 0.001</b>
<b>% N</b>	9	<b>0.016</b>

Table 3: Results of linear multiple regressions ( $R^2$ ,  $p$ ) analyzing relationships between  $GPP_t$  or  $CR_t$  and environmental variables, for both community.  $Max_{irr}$  = monthly maximal instantaneous irradiance;  $T_{air}$  = monthly mean air temperature;  $T_{seawater}$  = monthly mean seawater temperature;  $NO_3^-$  = monthly mean nitrates concentration in seawater;  $NO_2^-$  = monthly mean nitrites concentration in seawater;  $NH_4^+$  = monthly mean ammonium concentration in seawater;  $PO_4^{2-}$  = monthly mean phosphates concentration in seawater;  $DM_{can}$  = canopy dry mass.

	<b>Community</b>	<b>Environmental variables</b>	<b>R<sup>2</sup></b>	<b>p</b>
<b>GPP<sub>t</sub></b>	<i>F. vesiculosus</i>	$NO_3^-$ , $DM_{can}$	0.684	<b>0.002</b>
	<i>F. serratus</i>	$Max_{irr}$ , $T_{air}$ , $NO_3^-$ , $NO_2^-$ , $NH_4^+$ , $PO_4^{2-}$	0.840	<b>0.016</b>
<b>CR<sub>t</sub></b>	<i>F. vesiculosus</i>	$T_{air}$ , $T_{seawater}$ , $DM_{can}$	0.898	<b>&lt; 0.001</b>
	<i>F. serratus</i>	$T_{air}$	0.749	<b>&lt; 0.001</b>