



HAL
open science

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

François Bordeyne, Aline Migné, Dominique Davoult

► To cite this version:

François Bordeyne, Aline Migné, Dominique Davoult. Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial carbon fluxes displaying seasonal variability. *Marine Biology*, 2015, 162 (10), pp.2119-2129. 10.1007/s00227-015-2741-6 . hal-01212165

HAL Id: hal-01212165

<https://hal.sorbonne-universite.fr/hal-01212165>

Submitted on 6 Oct 2015

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Authors:

5 François Bordeyne^{1,2}, Aline Migné^{1,2}, Dominique Davoult^{1,2}

6

7 Affiliations and addresses:

8 ¹ Sorbonne Universités, UPMC Univ. Paris 6, UMR 7144, Station Biologique de Roscoff,

9 Place Georges Teissier, 29688 Roscoff Cedex, France

10 ² CNRS, UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, 29688 Roscoff

11 Cedex, France

12

13 Corresponding author:

14 François Bordeyne

15 Email: francois.bordeyne@sb-roscoff.fr

16 Phone: 0033 298292333

17 Fax number: 0033 298292324

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 CO₂-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⁻² h⁻¹; community respiration: 100-
33 500 mgC m⁻² h⁻¹), with canopies accounting for 77-97% of the global CO₂ fluxes. However,
34 this relative canopies' contribution to global CO₂ 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 (Max_{irr} ,
123 in W m^{-2}) and monthly mean air temperature (T_{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_{seawater} , in °C) and monthly

126 means seawater nutrient concentrations (NH_4^+ , NO_3^{2-} , NO_2^- and 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 m² 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 CO₂ gas analyzer (LiCor
142 Li-820) in closed air circuit. Air motion of 1 L min⁻¹ was ensured by a pump in this closed
143 circuit. CO₂ 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_t) and the
146 total community respiration (CR_t), respectively, assuming that CO₂ 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_t) was calculated as $\text{GPP}_t = \text{NPP}_t + \text{CR}_t$. CO₂

151 fluxes were calculated from recorded data using the slope of CO₂ concentration ($\mu\text{mol}_{\text{CO}_2}$
152 $\text{mol}_{\text{air}}^{-1}$) against time (min). Therefore, GPP_t and CR_t were expressed in carbon unit (mgC m^{-2}
153 h^{-1}) assuming a molar volume of 22.4 L mol⁻¹ at standard temperature and pressure and a
154 molar mass of 12 gC mol_{CO₂}⁻¹. Finally, the community metabolic balance was calculated each
155 month for both communities as the ratio of CR_t to GPP_t.

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_r) and
161 residual community respiration (CR_r). Residual community gross primary production (GPP_r)
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 (≈ 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 (NO_3^- , NO_2^- , NH_4^+ and PO_4^{2-}), and canopy dry mass.
203 Predictor variables of 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 W m^{-2} in December 2012 to 1000 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 (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 (NH_4^+), nitrites (NO_2^-) and
218 phosphates (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 (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 (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. 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 CR_t ranged from $74.3 \pm 7.9 \text{ mgC m}^{-2} \text{ h}^{-1}$ in January 2013 to 475.9 ± 65.8
228 $\text{mgC m}^{-2} \text{ h}^{-1}$ in August 2013 (Fig 3). Both GPP_t and 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 GPP_t than *F.*
233 *serratus* community (20% lower in average) but significantly higher CR_t (25% higher in
234 average) (Table 2). The metabolic balance (i.e. CR_t/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 GPP_t and CR_t of
240 these communities.

241 The variability of GPP_t was best explained by NO_3^- seawater concentration and DM_{can} taken
242 together for the *F. vesiculosus* community whereas it was best explained by Max_{irr} , T_{air} and all
243 seawater nutrient concentrations for the *F. serratus* community (Table 3). The variability of
244 CR_t was best explained by the three predictor variables taken together (T_{air} , T_{seawater} and
245 DM_{can}) for the *F. vesiculosus* community whereas it was best explained by T_{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 CO_2 fluxes (77-97% of CR_t and 83-95% of 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 ± 0.029 mgC $g_{DM}^{-1} h^{-1}$ in November 2013 to 0.473 ± 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 ± 0.010
255 mgC $g_{DM}^{-1} h^{-1}$ February 2013 to 0.217 ± 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 ± 0.112
257 mgC $g_{DM}^{-1} h^{-1}$ in April 2013 and its respiration rate from 0.040 ± 0.008 mgC $g_{DM}^{-1} h^{-1}$ in
258 November 2012 to 0.240 ± 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⁻² h⁻¹ for GPP_t and 122–616 mgC m⁻² h⁻¹ for CR_t, 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_t (in mgC m⁻² h⁻¹) 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_t and CR_t 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 (Airoldi 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

432 ACKNOWLEDGMENTS

433 The authors thank all the EFEB team members and the students for their help on field
434 experiments. We also thank Cédric Leroux for performing the carbon and nitrogen spectral
435 analyses, and the SOMLIT network for performing seawater temperature and nutrient
436 concentrations measurements. Three anonymous reviewers are thanked for constructive
437 comments. This work benefited from the support of the French Government run by the
438 National Research Agency and with regards to the investment expenditure programme
439 IDEALG ANR-10-BTBR and was partly funded by the Brittany region.

440

441 BIBLIOGRAPHY

- 442 Airoidi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. In:
443 Gibson RN, Atkinson RJA, Gordon JDM (eds) Oceanography and Marine Biology,
444 Vol 45. Taylor & Francis Group, Boca Raton, pp 345–405
- 445 Asare SO, Harlin MM (1983) Seasonal fluctuations in tissue nitrogen for five species of
446 perennial macroalgae in Rhode Island Sound. J Phycol 19:254–257. doi:
447 10.1111/j.0022-3646.1983.00254.x
- 448 Binzer T, Sand-Jensen K (2002) Importance of structure and density of macroalgae
449 communities (*Fucus serratus*) for photosynthetic production and light utilisation. Mar
450 Ecol Prog Ser 235:53–62. doi: 10.3354/meps235053

451 Bischof K, Hanelt D, Wiencke C (2000) Effects of ultraviolet radiation on photosynthesis and
452 related enzyme reactions of marine macroalgae. *Planta* 211:555–562. doi:
453 10.1007/s004250000313

454 Bosman AL, Hockey PAR, Siegfried WR (1987) The influence of coastal upwelling on the
455 functional structure of rocky intertidal communities. *Oecologia* 72:226–232. doi:
456 10.1007/BF00379273

457 Brenchley J, Raven J, Johnston A (1998) Carbon and nitrogen allocation patterns in two
458 intertidal fucoids: *Fucus serratus* and *Himantalia elongata* (Phaeophyta). *Eur J*
459 *Phycol* 33:307–313. doi: 10.1080/09670269810001736803

460 Brinkhuis BH, Tempel NR, Jones RF (1976) Photosynthesis and respiration of exposed salt-
461 marsh fucoids. *Mar Biol* 34:349–359. doi: 10.1007/BF00398128

462 Brock E, Nylund GM, Pavia H (2007) Chemical inhibition of barnacle larval settlement by
463 the brown alga *Fucus vesiculosus*. *Mar Ecol Prog Ser* 337:165–174. doi:
464 10.3354/meps337165

465 Carlson L (1991) Seasonal variation in growth, reproduction and nitrogen content of *Fucus*
466 *vesiculosus* L. in the Öresund, Southern Sweden. *Bot Mar* 34:447–453. doi:
467 10.1515/botm.1991.34.5.447

468 Chapman ARO, Craigie JS (1977) Seasonal growth in *Laminaria longicuris*: Relations with
469 dissolved inorganic nutrients and internal reserves of nitrogen. *Mar Biol* 40:197–205.
470 doi: 10.1007/BF00390875

471 Chapman ARO, Craigie JS (1978) Seasonal growth in *Laminaria longicuris*: Relations with
472 reserve carbohydrate storage and production. *Mar Biol* 46:209–213. doi:
473 10.1007/BF00390682

474 Creis E, Delage L, Charton S, Charton S, Goullitquer S, Leblanc C, Potin P, Ar Gall E (2015)
475 Constitutive or inducible protective mechanisms against UV-B radiation in the brown

476 alga *Fucus vesiculosus*? A study of gene expression and phlorotannin content
477 responses. PLOS ONE 10:e0128003. doi: 10.1371/journal.pone.0128003

478 Davison IR (1991) Environmental effects on algal photosynthesis: Temperature. J Phycol
479 27:2–8. doi: 10.1111/j.0022-3646.1991.00002.x

480 del Giorgio PA, Williams PJ le B (2005) Respiration in aquatic ecosystems. Oxford Univ.
481 Press, Oxford

482 Duarte L, Rossi F, Docal C, Viejo R (2015) Effects of alga *Fucus serratus* decline on benthic
483 assemblages and trophic linkages at its retreating southern range edge. Mar Ecol Prog
484 Ser 527:87–103. doi: 10.3354/meps11248

485 Duarte L, Viejo RM, Martínez B, deCastro M, Gómez-Gesteira M, Gallardo T (2013) Recent
486 and historical range shifts of two canopy-forming seaweeds in North Spain and the
487 link with trends in sea surface temperature. Acta Oecologica 51:1–10. doi:
488 10.1016/j.actao.2013.05.002

489 Elser JJ, Bracken MES, Cleland EE, Bracken MES, Cleland EE, Gruner DS, Harpole WS,
490 Hillebrand H, Ngai JT, Saebloom EW, Shurin JB, Smith JE (2007) Global analysis of
491 nitrogen and phosphorus limitation of primary producers in freshwater, marine and
492 terrestrial ecosystems. Ecol Lett 10:1135–1142. doi: 10.1111/j.1461-
493 0248.2007.01113.x

494 Gagné JA, Mann KH, Chapman ARO (1982) Seasonal patterns of growth and storage in
495 *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the
496 water. Mar Biol 69:91–101. doi: 10.1007/BF00396965

497 Gevaert F, Davoult D, Creach A, Kling R, Janquin MA, Seuront L, Lemoine Y (2001) Carbon
498 and nitrogen content of *Laminaria saccharina* in the eastern English Channel:
499 biometrics and seasonal variations. J Mar Biol Assoc UK 81:727–734. doi:
500 10.1017/S0025315401004532

501 Golléty C, Crowe T (2013) Contribution of biofilm to ecosystem functioning in rock pools
502 with different macroalgal assemblages. *Mar Ecol Prog Ser* 482:69–79. doi:
503 10.3354/meps10238

504 Golléty C, Migné A, Davoult D (2008) Benthic metabolism on a sheltered rocky shore: Role
505 of the canopy in the carbon budget. *J Phycol* 44:1146–1153. doi: 10.1111/j.1529-
506 8817.2008.00569.x

507 Golléty C, Riera P, Davoult D (2010) Complexity of the food web structure of the
508 *Ascophyllum nodosum* zone evidenced by a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ study. *J Sea Res* 64:304–
509 312. doi: 10.1016/j.seares.2010.04.003

510 Gomez I, Wiencke C (1998) Seasonal changes in C, N and major organic compounds and
511 their significance to morpho-functional processes in the endemic Antarctic brown alga
512 *Ascoseira mirabilis*. *Polar Biol* 19:115–124. doi: 10.1007/s0030000050222

513 Häder D-P, Figueroa FL (1997) Photoecophysiology of marine macroalgae. *Photochem*
514 *Photobiol* 66:1–14. doi: 10.1111/j.1751-1097.1997.tb03132.x

515 Hatcher BG, Chapman ARO, Mann KH (1977) An annual carbon budget for the kelp
516 *Laminaria longicuris*. *Mar Biol* 44:85–96. doi: 10.1007/BF00386909

517 Hubas C, Davoult D, Cariou T, Artigas LF (2006) Factors controlling benthic metabolism
518 during low tide along a granulometric gradient in an intertidal bay (Roscoff Aber Bay,
519 France). *Mar Ecol Prog Ser* 316:53–68. doi: 10.3354/meps316053

520 Huppertz K, Hanelt D, Nultsch W (1990) Photoinhibition of photosynthesis in the marine
521 brown alga *Fucus serratus* as studied in field experiments. *Mar Ecol Prog Ser* 66:175–
522 182. doi: 10.3354/meps066175

523 Jacob C, Frangoudes K, Mesnildrey L, Lesueur M, Spinec F, Folliard G, Pien S, Rebours C,
524 Meland M, Gallastegi I, Inunziaga Urizarbarrena A, Marques A, Atack T, Dunningham
525 J, Maguire J, Abreu H, Walsh M (2012) Etats des lieux de la filière des macro-algues

526 en Europe. Rapport réalisé dans le cadre du projet NETALGAE - Interreg IVB. 12p.
527 (In French)

528 Jueterbock A, Kollias S, Smolina I, Fernandes JMO, Coyer JA, Olsen JL, Hoarau G (2014)
529 Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic
530 coast: acclimatization potential to climate change. *Mar Genomics* 13:27–36. doi:
531 10.1016/j.margen.2013.12.008

532 Jueterbock A, Tyberghein L, Verbruggen H, Coyer JA, Olsen JL, Hoarau G (2013) Climate
533 change impact on seaweed meadow distribution in the North Atlantic rocky intertidal.
534 *Ecol Evol* 3:1356–1373. doi: 10.1002/ece3.541

535 Kawamitsu Y, Boyer JS (1999) Photosynthesis and carbon storage between tides in a brown
536 alga, *Fucus vesiculosus*. *Mar Biol* 133:361–369. doi: 10.1007/s002270050475

537 Kemp WM, Testa JM (2011) Metabolic balance between ecosystem production and
538 consumption. In: *Treatise on estuarine and coastal science*. E. Wolanski, D.S.
539 McLusky, pp 83–118

540 Kersen P, Kotta J, Bučas M, Kolesova N, Dekere Z (2011) Epiphytes and associated fauna on
541 the brown alga *Fucus vesiculosus* in the Baltic and the North Seas in relation to
542 different abiotic and biotic variables: Epiphytes and associated fauna on brown alga.
543 *Mar Ecol* 32:87–95. doi: 10.1111/j.1439-0485.2010.00418.x

544 Knight M, Parke M (1950) A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *J*
545 *Mar Biol Assoc U K* 29:439–514.

546 Lehvo A, Bäck S, Kiirikki M (2001) Growth of *Fucus vesiculosus* L.(Phaeophyta) in the
547 northern Baltic proper: energy and nitrogen storage in seasonal environment. *Bot Mar*
548 44:345–350. doi: 10.1515/BOT.2001.044

549 Maberly SC, Madsen TV (1990) Contribution of air and water to the carbon balance of *Fucus*
550 *spiralis*. *Mar Ecol Prog Ser* 62:175–183. doi: 10.3354/meps062175

551 Middelboe AL, Sand-Jensen K, Binzer T (2006) Highly predictable photosynthetic production
552 in natural macroalgal communities from incoming and absorbed light. *Oecologia*
553 150:464–476. doi: 10.1007/s00442-006-0526-9

554 Migné A, Davoult D, Spilmont N, Menu D, Boucher G, Gattuso JP, Rybarczyk H (2002) A
555 closed-chamber CO₂-flux method for estimating intertidal primary production and
556 respiration under emersed conditions. *Mar Biol* 140:865–869. doi: 10.1007/s00227-
557 001-0741-1

558 Migné A, Delebecq G, Davoult D, Spilmont N, Menu D, Gevaert F (2015a) Photosynthetic
559 activity and productivity of intertidal macroalgae: In situ measurements, from thallus
560 to community scale. *Aquat Bot* 123:6–12. doi: 10.1016/j.aquabot.2015.01.005

561 Migné A, Golléty C, Davoult D (2015b) Effect of canopy removal on a rocky shore
562 community metabolism and structure. *Mar Biol* 162:449–457. doi: 10.1007/s00227-
563 014-2592-6

564 Migné A, Spilmont N, Davoult D (2004) In situ measurements of benthic primary production
565 during emersion: seasonal variations and annual production in the Bay of Somme
566 (eastern English Channel, France). *Cont Shelf Res* 24:1437–1449. doi:
567 10.1016/j.csr.2004.06.002

568 Moebus K, Johnson KM, Sieburth JM (1974) Rehydration of desiccated intertidal brown
569 algae: release of dissolved organic carbon and water uptake. *Mar Biol* 26:127–134.
570 doi: 10.1007/BF00388882

571 Molina-Montenegro MA, Muoz AA, Badano EI, Morales BW, Fuentes KM, Cavieres LA
572 (2005) Positive associations between macroalgal species in a rocky intertidal zone and
573 their effects on the physiological performance of *Ulva lactuca*. *Mar Ecol Prog Ser*
574 292:173–180. doi: 10.3354/meps292173

575 Oswald R, Telford N, Seed R, Happeywood C (1984) The effect of encrusting Bryozoans on
576 the photosynthetic activity of *Fucus Serratus* L. Estuar Coast Shelf Sci 19:697–702.
577 doi: 10.1016/0272-7714(84)90024-6

578 Ouisse V, Migné A, Davoult D (2010) Seasonal variations of community production,
579 respiration and biomass of different primary producers in an intertidal *Zostera noltii*
580 bed (Western English Channel, France). Hydrobiologia 649:3–11. doi:
581 10.1007/s10750-010-0254-3

582 Paine RT (2002) Trophic control of production in a rocky intertidal community. Science
583 296:736–739. doi: 10.1126/science.1069811

584 Pedersen MF, Borum J (1997) Nutrient control of estuarine macroalgae: growth strategy and
585 the balance between nitrogen requirements and uptake. Mar Ecol Prog Ser 161:155–
586 163. doi: 10.3354/meps161155

587 Quadir A, Harrison PJ, DeWreede RE (1979) The effects of emergence and submergence on
588 the photosynthesis and respiration of marine macrophytes. Phycologia 18:83–88. doi:
589 10.2216/i0031-8884-18-1-83.1

590 Raffaelli DG, Hawkins SJ (1999) Intertidal ecology. Kluwer Academic Publishers

591 Rindi F, Guiry MD (2004) Composition and spatio temporal variability of the epiphytic
592 macroalgal assemblage of *Fucus vesiculosus* Linnaeus at Clare Island, Mayo, western
593 Ireland. J Exp Mar Biol Ecol 311:233–252. doi: 10.1016/j.jembe.2004.05.009

594 Sand-Jensen K (1977) Effect of epiphytes on eelgrass photosynthesis. Aquat Bot 3:55–63.
595 doi: 10.1016/0304-3770(77)90004-3

596 Staehr PA, Testa JM, Kemp WM, Cole JJ, Sand-Jensen K, Smith SV (2012) The metabolism
597 of aquatic ecosystems: history, applications, and future challenges. Aquat Sci 74:15–
598 29. doi: 10.1007/s00027-011-0199-2

599 Tait LW, Schiel DR (2010) Primary productivity of intertidal macroalgal assemblages:
600 comparison of laboratory and in situ photorespirometry. *Mar Ecol Prog Ser* 416:115–
601 125. doi: 10.3354/meps08781

602 Tait LW, Schiel DR (2011) Dynamics of productivity in naturally structured macroalgal
603 assemblages: importance of canopy structure on light-use efficiency. *Mar Ecol Prog*
604 *Ser* 421:97–107. doi: 10.3354/meps08909

605 Thompson RC, Crowe TP, Hawkins SJ (2002) Rocky intertidal communities: past
606 environmental changes, present status and predictions for the next 25 years. *Environ*
607 *Conserv* 29:168–191. doi: 10.1017/S0376892902000115

608 Underwood AJ (2000) Experimental ecology of rocky intertidal habitats: what are we
609 learning? *J Exp Mar Biol Ecol* 250:51–76. doi: 10.1016/S0022-0981(00)00179-9

610 Viana IG, Bode A, Bartholomew M, Valiela I (2015) Experimental assessment of the
611 macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* for monitoring N sources at
612 different time-scales using stable isotope composition. *J Exp Mar Biol Ecol* 466:24–
613 33. doi: 10.1016/j.jembe.2015.01.014

614 Wahl M (2009) *Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and*
615 *Change*. Springer Science & Business Media

616 Wahl M, Jormalainen V, Eriksson BK, Coyer JA, Molis M, Schubert H, Dethier M, Karez R,
617 Kruse I, Lenz M, Pearson G, Rohde S, Wikström SA, Olsen JL (2011) Stress ecology
618 in *Fucus*: Abiotic, biotic and genetic interactions. In: *Advances in Marine Biology*.
619 Elsevier, pp 37–105

620 Williams SL, Dethier MN (2005) High and dry: Variation in net photosynthesis of the
621 intertidal seaweed *Fucus gardneri*. *Ecology* 86:2373–2379. doi: 10.2307/3451026

622 Young EB, Dring MJ, Savidge G, Birkett DA, Berges JA (2007) Seasonal variations in nitrate
623 reductase activity and internal N pools in intertidal brown algae are correlated with

624 ambient nitrate concentrations. *Plant Cell Environ* 30:764–774. doi: 10.1111/j.1365-
625 3040.2007.01666.x
626

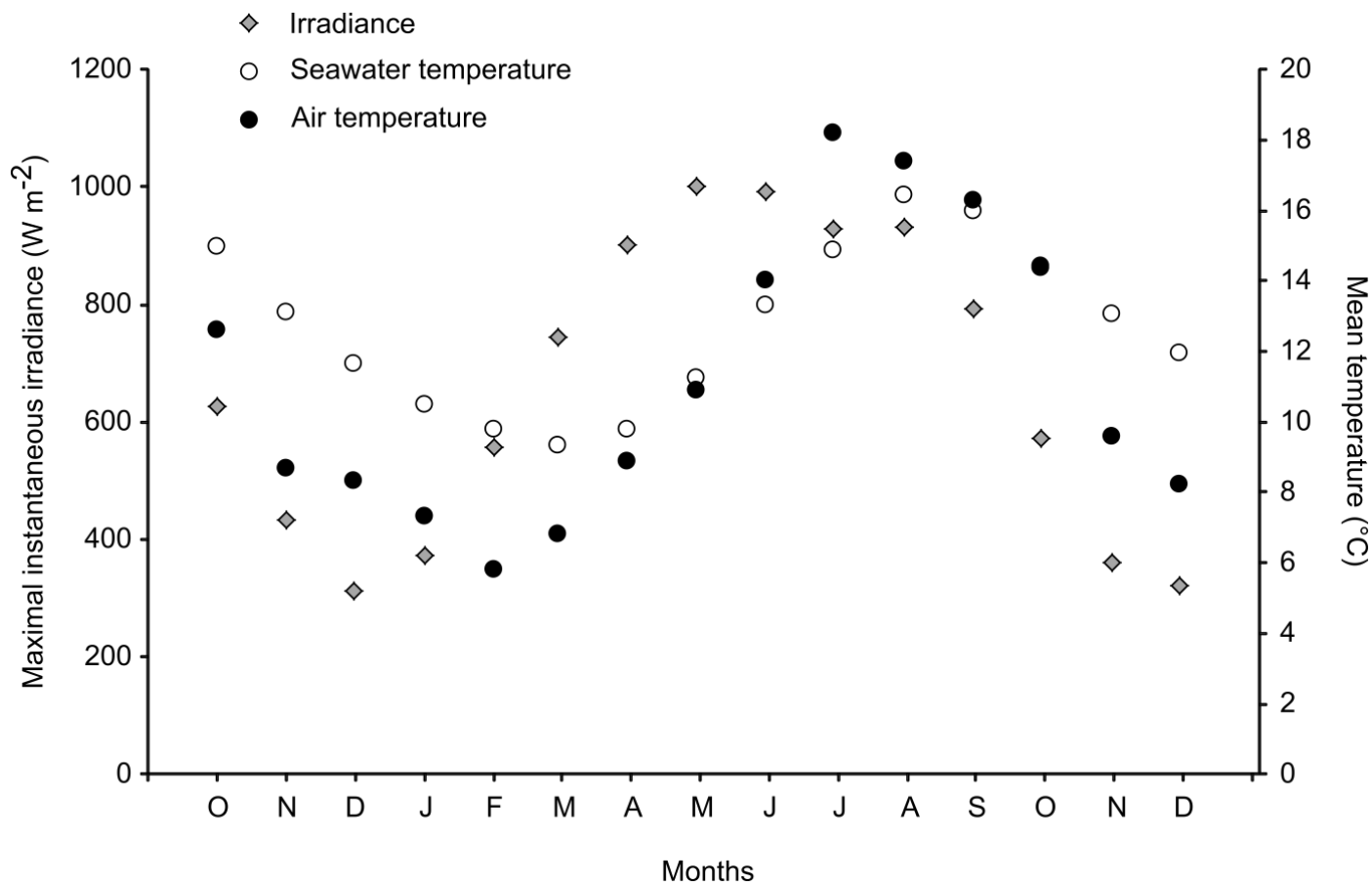


Fig. 1 Monthly maximal instantaneous irradiance, expressed in W m^{-2} , and monthly mean of seawater and air temperatures, both expressed in $^{\circ}\text{C}$, as a function of time

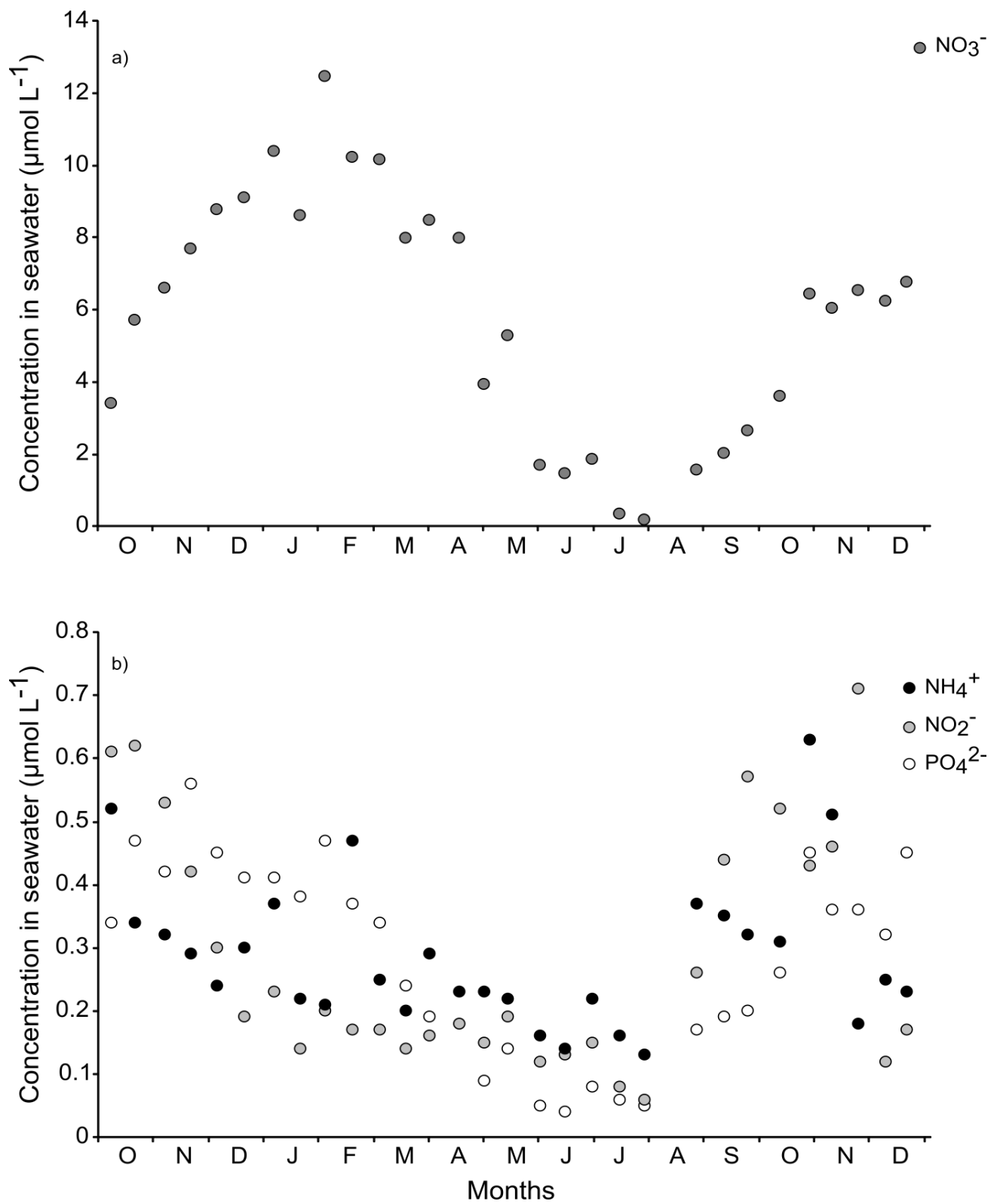


Fig. 2 Seawater concentration of (a) nitrates (NO_3^-) and (b) ammonium (NH_4^+), nitrites (NO_2^-) and phosphates (PO_4^{2-}), expressed in $\mu\text{mol L}^{-1}$, as a function of time

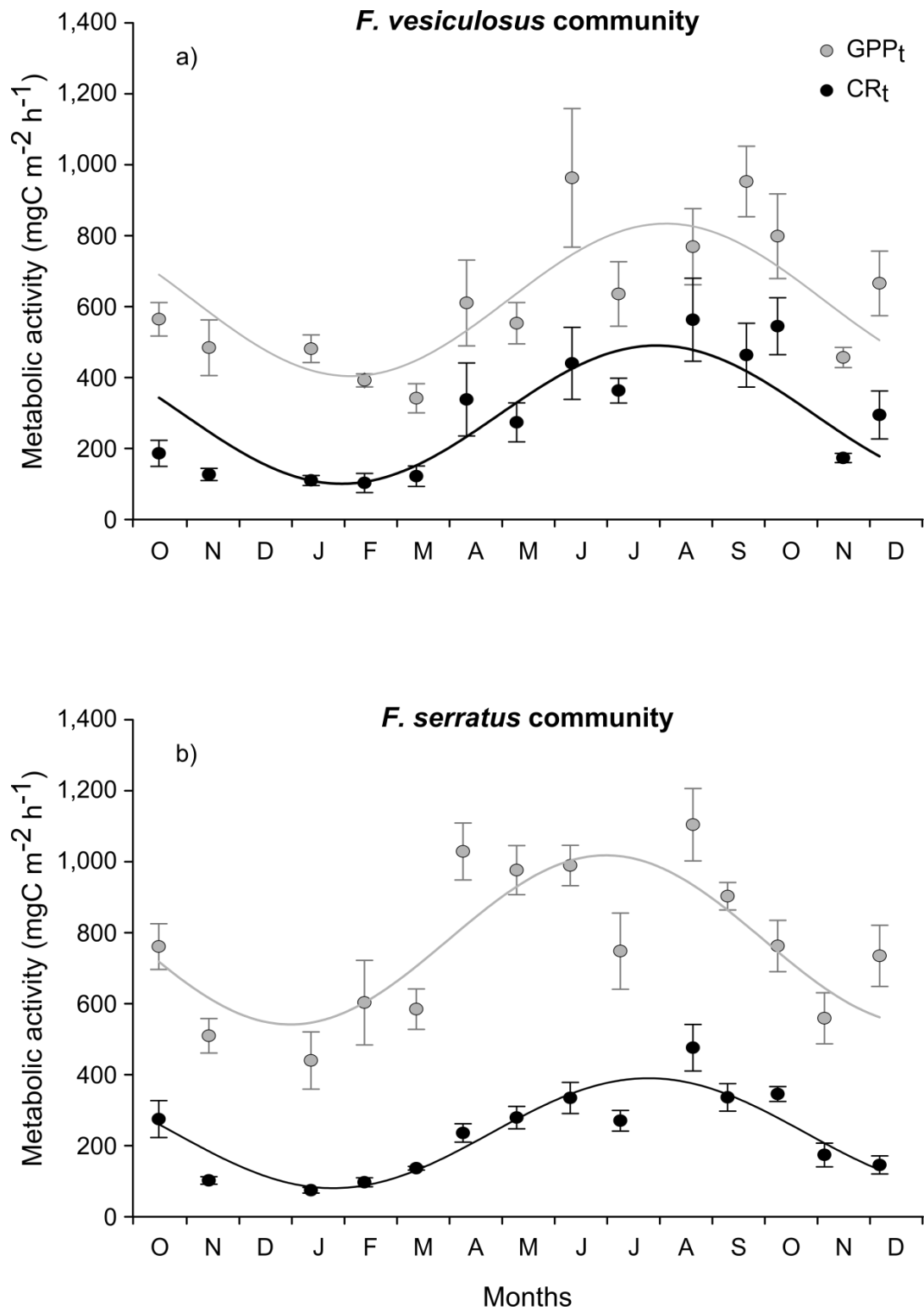


Fig. 3 Mean (\pm SE) community gross primary production (GPP_t) and respiration (CR_t), both expressed in mgC m⁻² h⁻¹, as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus* (b) communities. Grey and dark lines represent the sinusoidal curves fitted on GPP_t and CR_t data sets, respectively

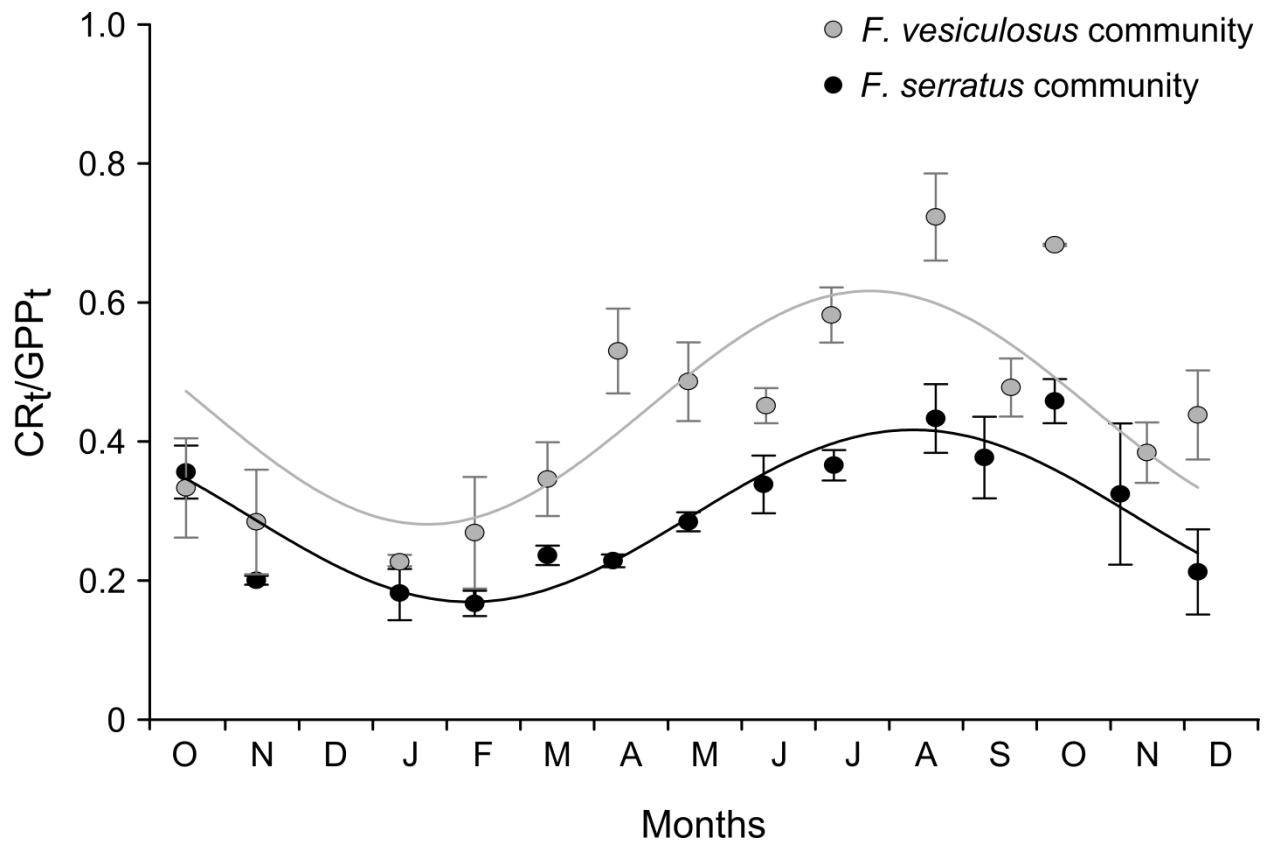


Fig. 4 Mean (\pm SE) metabolic balance, calculated as CR_t/GPP_t , as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark) communities. Grey and Dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* communities metabolic balance data sets, respectively

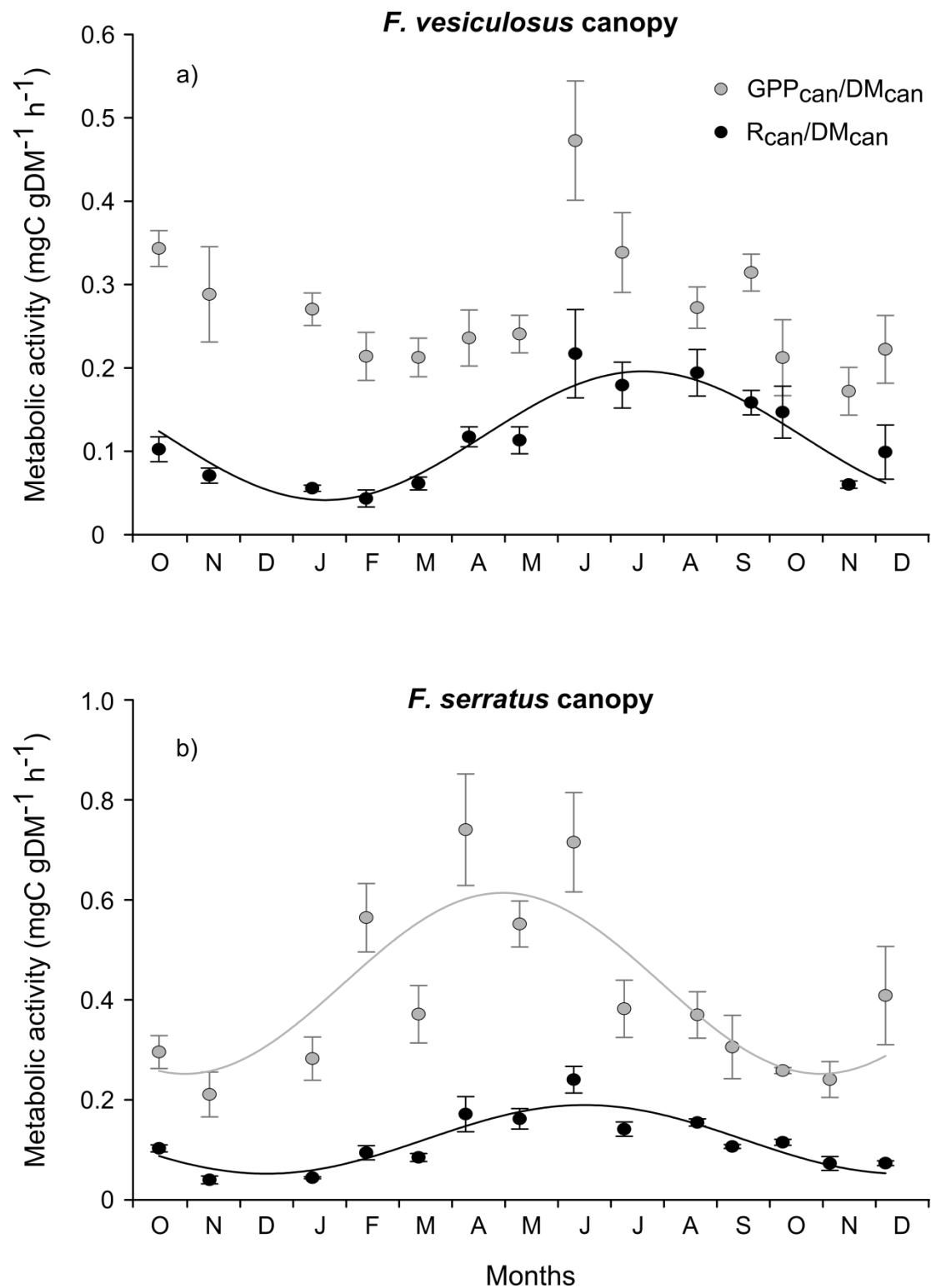


Fig. 5 Mean (\pm SE) gross canopy productivity ($\text{GPP}_{\text{can}}/\text{DM}_{\text{can}}$) and canopy respiration rate ($\text{R}_{\text{can}}/\text{DM}_{\text{can}}$), both expressed in $\text{mgC gDM}^{-1} \text{h}^{-1}$, as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus*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

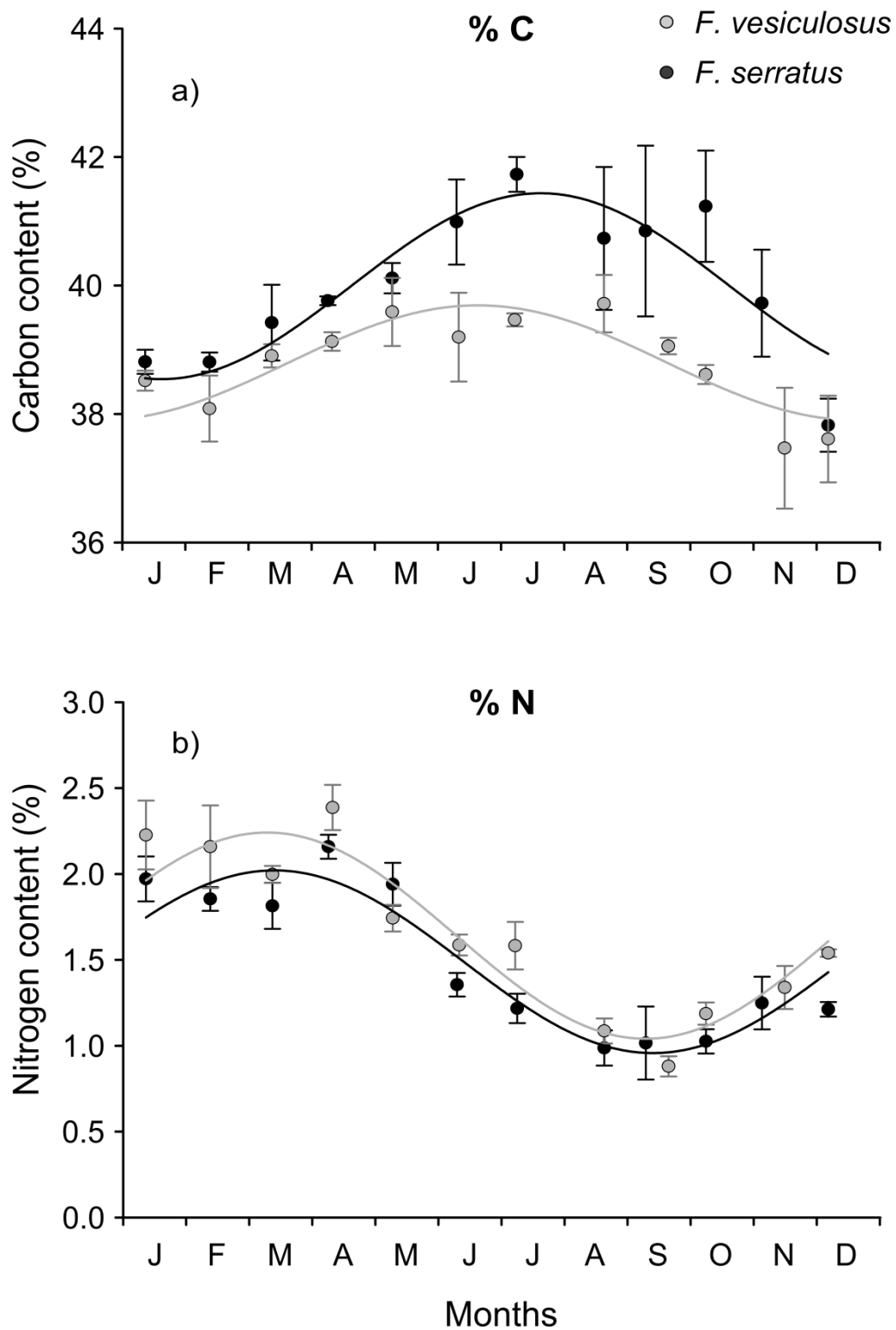


Fig. 6 Mean (\pm SE) C content (a) and N content (b), both expressed in % of DM_{can} , as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark). Grey and dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* data sets, respectively

Table 1: Sinusoidal curve parameters (n, a, b, c and R²) 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).

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

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.

	Community	Environmental variables	R²	p
GPP_t	<i>F. vesiculosus</i>	NO_3^- , DM_{can}	0.684	0.002
	<i>F. serratus</i>	Max_{irr} , T_{air} , NO_3^- , NO_2^- , NH_4^+ , PO_4^{2-}	0.840	0.016
CR_t	<i>F. vesiculosus</i>	T_{air} , $T_{seawater}$, DM_{can}	0.898	< 0.001
	<i>F. serratus</i>	T_{air}	0.749	< 0.001