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

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ABSTRACT

Semi-sheltered rocky shores are characterized by a typical succession of Phaeophyceae-dominated communities where canopy-forming algae are assumed to be very productive. However, metabolic activity of whole communities, integrating the main interactions that occur in these assemblages, still needs to be investigated more deeply, especially when communities are emerged. Thus, the metabolism of the mid-intertidal *Fucus vesiculosus* and *Fucus serratus* communities was surveyed once a month throughout a year in the Bay of

Morlaix (France). *In situ* measurements of primary production and respiration were carried out at the onset of emersion periods, using benthic chambers coupled to CO₂-infrared gas analysers. Benthic measurements were performed successively on whole communities and after canopy removal, to assess the contribution of the canopies to the communities' carbon fluxes. Concurrently, nitrogen and organic carbon contents of the two *Fucus* species were evaluated monthly. Both communities exhibited high metabolic activity year-round (community gross primary production: 400-1 000 mgC m⁻² h⁻¹; community respiration: 100-500 mgC m⁻² h⁻¹), with canopies accounting for 77-97% of the global CO₂ fluxes. However, this relative canopies' contribution to global CO₂ fluxes did not follow seasonal fluctuations, whereas both metabolic activities and nitrogen and carbon contents did, confirming the importance of light and temperature in the regulation of metabolic processes. A nutrient limitation was also suggested to occur in summer, when seawater was nutrient-depleted. Finally, the *Fucus vesiculosus* community, located upper on the shore, exhibited lower photosynthetic activity than the *Fucus serratus* community, being consistent with the vertical zonation rules of intertidal habitats.

INTRODUCTION

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

51 primary producers. They must for instance synthesize 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

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

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

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

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

MATERIALS & METHODS

Study site

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

Environmental conditions

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

means seawater nutrient concentrations (NH_4^+ , NO_3^{2-} , NO_2^- and PO_4^{3-} , in $\mu\text{mol L}^{-1}$) datasets (October 2012 – December 2013).

Benthic metabolism measurements and sampling

Measurements of benthic metabolism of *F. vesiculosus* and *F. serratus* communities were performed once a month from October 2012 to December 2013, with the exception of December 2012. They were always done at the onset of emersion of a spring tide (around midday) to avoid a desiccation effect on metabolic rates. At each occasion, three intra-site replicates (2 to 5 m distance between each) of a 0.09 m² rock area were haphazardly selected for both communities (only two replicates in November 2013 for *F. serratus* community). A replicate included one to several *Fucus* thalli (> 25 cm long) with the associated community, which was essentially made-up of *Fucus* epibionts (i.e. algae and sessile invertebrates directly attached to the *Fucus*, see Wahl 2009) and biofilms, as well as sub-canopy and encrusting macroalgae, rocky and sedimentary microphytobenthos and invertebrates, including the mobile ones on *Fucus* fronds. Each area was then enclosed in a custom-built incubation chamber (17.7 L) made of clear Plexiglas, connected to an infrared CO₂ gas analyzer (LiCor Li-820) in closed air circuit. Air motion of 1 L min⁻¹ was ensured by a pump in this closed circuit. CO₂ fluxes measurements were performed at the rock-air interface, as described by Migné et al. (2002), at ambient light and in darkness by covering up the chambers. These measurements allowed estimating the total community net primary production (NPP_t) and the total community respiration (CR_t), respectively, assuming that CO₂ fluxes measured in darkness after abrupt transition from ambient light reflected the respiration activity of the communities (del Giorgio and Williams 2005). Incubations were sufficiently short (i.e. 5 - 10 min) to avoid feedback of temperature and gas concentration changes on metabolic rates. Total community gross primary production (GPP_t) was calculated as $\text{GPP}_t = \text{NPP}_t + \text{CR}_t$. CO₂

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

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

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

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

Carbon and nitrogen content

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

Statistical analysis

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

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

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

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

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

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

monthly maximal instantaneous irradiance, monthly means of air and seawater temperature and of nutrients seawater concentrations (NO_3^- , NO_2^- , NH_4^+ and PO_4^{2-}), and canopy dry mass. Predictor variables of CR_t consisted of monthly means of air and seawater temperature, and canopy dry mass.

RESULTS

Environmental conditions

Monthly maximal instantaneous irradiance followed seasonal trend, with values ranging from 311 W m^{-2} in December 2012 to 1000 W m^{-2} in May 2013 (Fig 1). Our records of incident photosynthetically available radiation during light incubations (data not shown) were significantly correlated with these values ($r = 0.885$, $p < 0.001$ for the *F. vesiculosus* community and $r = 0.784$, $p < 0.001$ for the *F. serratus* community). Monthly mean air and seawater temperatures also followed seasonal trends, with values ranging respectively from 5.8 °C in February 2013 to 18.2 °C in July 2013 and from 9.3 °C in March 2013 to 16.5 °C in August 2013 (Fig 1). Nitrates (NO_3^-) dominated the seawater N-nutrient pool throughout the year, with concentration ranging from 0.19 $\mu\text{mol L}^{-1}$ at the end of July 2013 to 12.45 $\mu\text{mol L}^{-1}$ at the beginning of February 2013 (Fig 2a). Ammonium (NH_4^+), nitrites (NO_2^-) and phosphates (PO_4^{2-}) seawater concentrations also fluctuated throughout the year, but remained lower than 0.75 $\mu\text{mol L}^{-1}$ (Fig 2b).

Benthic metabolism

Fucus vesiculosus community exhibited a gross primary production (GPP_t , mean $\pm$ SE) 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 2013 and respiration (CR_t , mean $\pm$ SE) ranging from $102.8 \pm 27.1 \text{ mgC m}^{-2} \text{ h}^{-1}$ in February 2013 to $562.7 \pm 117.1 \text{ mgC m}^{-2} \text{ h}^{-1}$ in August 2013. GPP_t of the *Fucus serratus* community

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

The variability of GPP_t was best explained by NO_3^- seawater concentration and DM_{can} taken together for the *F. vesiculosus* community whereas it was best explained by Max_{irr} , T_{air} and all seawater nutrient concentrations for the *F. serratus* community (Table 3). The variability of CR_t was best explained by the three predictor variables taken together (T_{air} , T_{seawater} and DM_{can}) for the *F. vesiculosus* community whereas it was best explained by T_{air} alone for the *F. serratus* community (Table 3).

The metabolism of these two communities was consistently dominated by the canopies (i.e. the dominant species and their epibionts) since they accounted for the huge majority of the global CO_2 fluxes (77-97% of CR_t and 83-95% of GPP_t). Nevertheless, no seasonal pattern

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

Carbon and nitrogen contents

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

DISCUSSION

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

As expected, both GPP_t and CR_t exhibited a seasonal pattern, with minima in winter and maxima in summer, in each community. Such seasonal pattern is in agreement with the general idea that light availability and temperature act as the major drivers of community metabolism (Davison 1991; Gollty 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 (Gollty 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; Hder 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

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

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

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

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

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

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

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

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

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

Conclusion and perspectives

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

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

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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	R^2	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