

Photosynthetic activity and productivity of intertidal macroalgae: *In situ* measurements, from thallus to community scale



Aline Migné^{a,b,*}, Gaspard Delebecq^{c,d,1}, Dominique Davoult^{a,b},
Nicolas Spilmont^{c,d,e}, Dominique Menu^d, François Gévaert^{c,d}

^a Sorbonne Universités, UPMC Univ Paris 06, Station Biologique, F-29680 Roscoff, France

^b CNRS, UMR 7144 AD2M, F-29680 Roscoff, France

^c Université Lille 1, Univ Lille Nord de France, Station Marine, F-62930 Wimereux, France

^d CNRS, UMR 8187 LOG, F-62930 Wimereux, France

^e Environmental Futures Centre, Griffith University, Gold Coast Campus, QLD 4222, Australia

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ABSTRACT

The photosynthetic activity and productivity of four dominant canopy intertidal macroalgae were measured under emersion and immersion, at saturating light levels ($\text{PAR} > 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), and compared at two sites (eastern and western English Channel) in spring and summer. The photosynthetic activity of thalli was measured by the electron transport rate (ETR) using pulse-amplitude modulated (PAM) fluorescence and the productivity of individuals and of communities was measured by carbon fluxes in closed chambers. Under emersion, when thalli were still hydrated, the uppermost species *Pelvetia canaliculata* had higher photosynthetic activity (mean ETR between 327 and 460 $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) and individual gross productivity (between 60 and 212 $\mu\text{mol C g}_{\text{DW}}^{-1} \text{h}^{-1}$) than the lowermost species *Laminaria digitata* (mean ETR between 24 and 53 $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$ and gross productivity between 2 and 38 $\mu\text{mol C g}_{\text{DW}}^{-1} \text{h}^{-1}$), whatever the site and season. *P. canaliculata* had higher ETR in air than underwater (averaged 146 $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) and *L. digitata* had lower ETR in air than underwater (averaged 112 $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$), while they exhibited, respectively, 3 and 5 times higher gross productivity underwater. At the community scale, the low mid-shore zone of *Fucus serratus* had the highest mean gross productivity under emersion (47 $\text{mmol C m}^{-2} \text{h}^{-1}$) while rates were higher for the uppermost than lowermost zone at the eastern site (average 20 and 6 $\text{mmol C m}^{-2} \text{h}^{-1}$, respectively) and of the same order of magnitude for both zones at the western site (about 30 $\text{mmol C m}^{-2} \text{h}^{-1}$). Finally, the variability of under emersion primary productivity among sites and seasons was reduced when the measurements were performed on entire communities compared to isolated individuals of the dominant species.

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Abbreviations: A, absorption coefficient; DIC, dissolved inorganic carbon; DW, dry weight; Em, emersion; ETR, electron transport rate; F_m' , maximal fluorescence level; Fse, *Fucus serratus*; Fsp, *Fucus spiralis*; F_s , fluorescence steady-state level; FW, fresh weight; GCP, gross community productivity; GP, gross productivity; Im, immersion; Ld, *Laminaria digitata*; NCP, net community productivity; NP, net productivity; PAM, pulse-amplitude modulated; PAR, photosynthetically available radiation; Pc, *Pelvetia canaliculata*; R, respiration; Ro, Roscoff; Sp, spring; Su, summer; TA, total alkalinity; Wx, Wimereux; Φ_{PSII} , effective quantum yield of photosystem II.

* Corresponding author at: Sorbonne Universités, UPMC Univ Paris 06, Station Biologique, F-29680 Roscoff, France. Tel.: +33 2 98 29 23 15; fax: +33 298 29 23 80.

E-mail addresses: migne@sb-roscoff.fr (A. Migné), gasp.delebecq@hotmail.fr (G. Delebecq), davoult@sb-roscoff.fr (D. Davoult), nicolas.spilmont@univ-lille1.fr (N. Spilmont), dominique.menu@univ-lille1.fr (D. Menu), francois.gevaert@univ-lille1.fr (F. Gévaert).

1. Introduction

Rocky shores are frequently dominated by dense populations of macroalgae that exhibit distinct patterns of vertical zonation. On northern hemisphere temperate coasts, this pattern typically consists of the succession of fucoid algae from the high to the low mid shore and of laminarians (or kelps) in the lower shore. The productivity of such seaweed populations has long been shown to be important, ranging from 1 to several $\text{kg C m}^{-2} \text{y}^{-1}$ (Mann, 1973). However, these estimations were rather raw and still need to be specified. In particular, the ecological performance of macroalgae

¹ Present address: Université de Bretagne Occidentale, Institut Universitaire Européen de la Mer, F-29280 Plouzané CNRS, UMR 6539 LEMAR, F-29280 Plouzané, France.

has to be measured *in situ* and at the multi-species community scale to take into account not only the dominating species but all the species as well as their interactions in relevant conditions. Intertidal macroalgae experience two very different environments for photosynthesis, aerial and aquatic. The capacity of species from different shore levels to maintain photosynthesis during emersion periods has long been investigated based on measurements performed on isolated thalli under controlled laboratory conditions (e.g. Johnson et al., 1974; Quadir et al., 1979; Dring and Brown, 1982). Since then, differences between some shallow-water macroalgae species have been shown to be smaller at the communities scale than experiments on single thallus pieces suggested (Binzer and Middelboe, 2005) and an increasing productivity of fucoid assemblages down a shore-height gradient has been shown (Tait and Schiel, 2011). These community-scale measurements were limited, however, to immersed conditions and trends might be different under peculiar conditions of the emersion periods. The present study compares the photosynthetic activity and productivity of thalli of the dominant canopy macroalgae (*i.e.* the zone-forming species typical of the northern hemisphere temperate shores) and the productivity of the communities, based on *in situ* measurements performed either during emersion or immersion periods. First, the photosynthetic activity of adult thalli was examined using pulse-amplitude modulated (PAM) fluorescence. This technique, which relies on the variable fluorescence of chlorophyll *a*, is not a direct measurement of photosynthesis but allows an examination of the dynamic properties of photosynthesis in response to environmental changes (Enriquez and Borowitzka, 2010) during the whole tidal cycle (emersion and immersion). Second, the productivity of single individual, or several individuals of a single species, was assessed using a closed chamber system. This monospecific approach aimed at understanding the productivity dynamic of each species in response to the environment variation (aerial versus aquatic). Third, the productivity of multi-species communities was assessed using closed chamber systems under emersion. This assemblage-based approach integrated the resource partitioning among canopy-forming macroalgae and their sub-canopy assemblages. The aim of the study was to test two hypotheses: (1) the in air versus underwater ratio of photosynthetic performance decreases down a shore-height gradient; (2) the variation in photosynthetic performance among dominant canopy species of the shore is reduced when the measurements are scaled up from thallus to community.

2. Materials and methods

2.1. Target species and study sites

The target species were the three fucoids *Pelvetia canaliculata* (the uppermost zone-forming species), *Fucus spiralis* (the immediately contiguous zone-forming species) and *Fucus serratus* (the lowermost zone-forming fucoid) and the kelp *Laminaria digitata* (the lowermost zone-forming species). Two seasons (spring and summer) and two sites, differing for the timing of the tide and for turbidity, were investigated. Measurements were performed at the rocky shore of Wimereux (50°44'48"N–1°35'54"E, eastern English Channel, France) during spring tides in September 2009 (summer) on the four seaweed communities (*P. canaliculata*, *F. spiralis*, *F. serratus* and *L. digitata*) and in April 2010 (spring) on three seaweed communities (*P. canaliculata*, *F. spiralis* and *L. digitata*) and at the rocky shore of Roscoff (48°43'53"N–3°59'16"W, western English Channel, France) during spring tides in August 2010 (summer) and in May 2011 (spring) on the uppermost and the lowermost seaweed communities (*P. canaliculata* and *L. digitata*). At Wimereux, water turbidity is high and low tides of spring tide occur in the early

morning (low tides occurred between 7:30am and 10:00am, UT+2 h, for summer measurements and between 7:00am and 8:30am, UT+2 h, for spring measurements). At Roscoff, water turbidity is low and low tides of spring tide occur in the early afternoon (low tides occurred between 2:00pm and 3:30pm, UT+2 h, for summer measurements and between 1:30pm and 2:30pm, UT+2 h, for spring measurements).

2.2. Light and temperature

Photosynthetically available radiation (PAR in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was measured in air and underwater and recorded every minute using a WinCQ flat sensor (Alec Electronics). Temperature was measured in air and underwater and recorded every minute using a MDS MkV-T sensor (Alec Electronics). Average temperature during the periods of selected measurements was 18°C underwater and 20°C in the air in summer and 11°C underwater and 14°C in the air in spring, at Wimereux. It was 17°C underwater and 27°C in the air in summer and 14°C underwater and 22°C in the air in spring, at Roscoff.

2.3. Fluorescence

In vivo chlorophyll fluorescence properties were measured *in situ* using a submersible PAM fluorometer (Diving PAM, Walz). The fluorescence signal was always taken from the middle of the frond in the same place for three haphazardly-selected and marked individuals of the target species. The effective quantum yield of photosystem II (Φ_{PSII}) was measured under ambient light at different stages of the tidal cycle. The fiber optic was mounted in a home-made transparent Plexiglas holder applied to one side of the thallus in such a way that the distance between the fiber optic and the algal tissue was constant and standard. The fiber optic forms a 60° angle with the sample, avoiding shading or darkening. Φ_{PSII} was calculated as $(F_m' - F_t)/F_m'$ (Genty et al., 1989), where F_m' is the maximal fluorescence level measured during a single saturating light pulse (0.8 s) for light-adapted samples, and F_t is the fluorescence steady-state level immediately prior to the flash. Then, the electron transport rate (ETR in $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$, here after referred to as $\mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$) was estimated using the following equation:

$$\text{ETR} = \Phi_{\text{PSII}} \times \text{PAR} \times 0.5 \times A \quad (1)$$

where PAR is the photosynthetically available radiation (in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), 0.5 is a correction factor based on the assumption that the incident photons are absorbed equally by the pigments of the two photosystems, and A is the absorption coefficient determined in the laboratory using an integrating sphere (ISR-240A, Shimadzu). The absorption coefficient varied between 0.93 and 0.97 according to the species and season.

2.4. Carbon fluxes

Productivity of single or several individuals (depending on the size of the species) was measured using a benthic chamber placed on the shore at the target species level. The system was made of a transparent closed perspex dome tightly sealed on the polyvinylchloride (PVC) base of the chamber and enclosed a volume of 35.3 l. During immersion periods, an electronic management system controlled three external pumps; two pumps ensured the rapid and constant homogenization of the media while the third one ensured the renewal of the media by flushing ambient seawater between two consecutive incubations (Cévaert et al., 2011). pH was measured with a WTW sentix 41 probe (Multi 350i, WTW) and monitored every minute during 10 min incubations. Seawater was collected from inside the benthic chamber using a 100 ml

Table 1
Light condition (mean PAR and standard deviation in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) during measurements of the highest electron transport rates (ETR) and net productivities (as carbon fluxes) at individual scale (NP) and community scale (NCP) on the different zone forming species (Pc: *Pelvetia canaliculata*, Fsp: *Fucus spiralis*, Fse: *Fucus serratus*, Ld: *Laminaria digitata*) at the two sites (Wx: Wimereux, Ro: Roscoff) and seasons (Su: summer, Sp: spring) under emersion (Em) and immersion (Im).

Species	Site	Season	ETR Em		ETR Im		NP Em		NP Im		NCP Em	
			Mean PAR	sd	Mean PAR	sd	Mean PAR	sd	Mean PAR	sd	Mean PAR	sd
Pc	Wx	Su	1650	21			1359	14	1018	85	1361	13
		Sp	2023	1	574	1	630	46	611	69	2022	12
	Ro	Su	2328	259	390	38	1995	387	466	36	1231	585
		Sp	1798	152			1276	293			1551	104
Fsp	Wx	Su	1183	43			711	446			1126	439
		Sp	740	1	597	104	898	68	347	58	1302	65
Fse	Wx	Su	476	5	970	227	434	34	327	60	431	35
Ld	Wx	Su	315	5			412	32			520	13
		Sp	655	4			389	52			702	23
	Ro	Su	1933	1002	676	83	2248	439	905	206	1942	260
		Sp	1441	0	330	23	1024	72	1269	122	1395	105

syringe, then passed through cellulose acetate membrane filters ($0.8 \mu\text{m}$) and spiked with HgCl_2 pending potentiometric laboratory determination of total alkalinity (Millero et al., 1993) on 3 subsamples of 20 ml. The dissolved inorganic carbon (DIC) concentration of seawater was calculated from the pH, total alkalinity (TA), temperature and salinity according to Strickland and Parsons (1972) and using the formula given in Oviatt et al. (1986). DIC flux ($\mu\text{mol h}^{-1}$) was calculated as the difference between the final and the initial concentrations after the linearity of the pH (corrected from temperature) change has been checked. During emersion, inorganic carbon fluxes were measured in the benthic chamber using closed air circuit for CO_2 analysis (Migné et al., 2002). Changes in air CO_2 concentration (ppm) were measured in the chamber with a CO_2 infrared gas analyser (LiCor Li-6251) and recorded with a data logger (LiCor Li-1400) at 15 s intervals during incubations of about 10 min duration. CO_2 fluxes ($\mu\text{mol h}^{-1}$) were calculated from the slope of CO_2 concentration against time assuming a molar volume of 22.41 at standard temperature and pressure. The benthic chamber was opened between two consecutive incubations to renew the ambient air, and algae were weighted to assess their water loss during the emersion period. At the end of the series of measurements, algae were rehydrated to assess their fresh weight (FW) and then dried for 48 h at 60°C to assess their dry weight (DW). Fluxes were expressed as $\mu\text{mol C g}_{\text{DW}}^{-1} \text{h}^{-1}$. The relative tissue water content at time t was calculated as the percent of total water content: $[(W_t - \text{DW}) / (\text{FW} - \text{DW})] \times 100$ (where W_t represents the weight measured at time t). Productivity was assessed at the community scale during emersion using benthic chambers as described in Crowe et al. (2013). Three chambers were haphazardly-positioned (approximately 2 m apart) to account for spatial variability in each zone. Each chamber (of a total volume of 18.9 L) was made of a transparent perspex dome with a 0.3×0.3 m transparent perspex base air-tightly sealed with neutral silicon to the substratum. Changes in CO_2 mol fraction in the air were measured by an infrared CO_2 gas analyzer (LiCor Li-800). CO_2 fluxes were estimated following the same procedure as described for single species measurements. The benthic chambers were opened between two consecutive incubations to renew the ambient air. In the Fucoïd zones, algae were collected at the end of the series of measurements, and the zone-forming algae were dried for 48 h at 60°C and weighted. In the *L. digitata* zone, there was no individual of the zone forming species inside the chambers. Incubations were performed either in ambient light conditions to assess the net productivity (NP) or in dark (after the chamber has been covered with an opaque tarp) in order to assess the respiration (R) rate. The gross productivity (GP) was then calculated by correcting NP by R.

2.5. Data analyses

To compare the photosynthetic activity and the productivity of the different species measured at the different scales at the two seasons and sites, the highest electron transport rates (ETR) and the highest carbon fluxes obtained at each occasion under emersion or immersion either in ambient light (mean PAR values given in Table 1) or in darkness were selected. Care was taken to use measurements performed in ambient light at saturating irradiance levels. A threshold of $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ was chosen 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 by

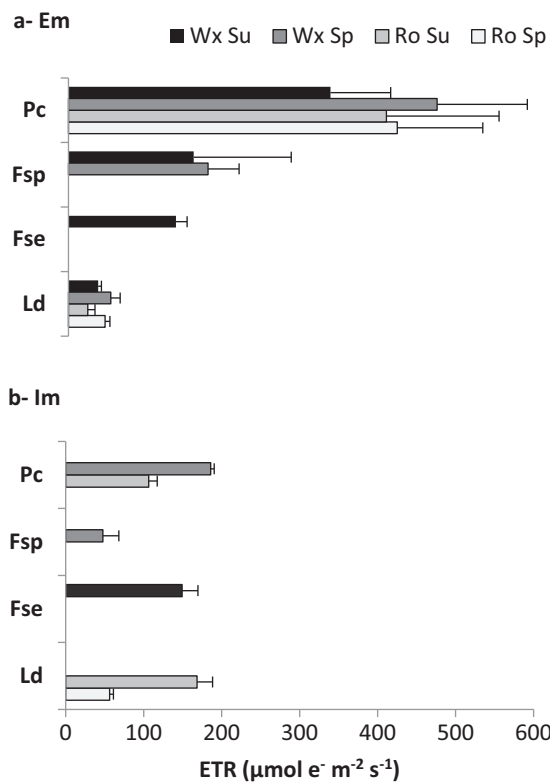


Fig. 1. Highest electron transport rate (ETR in $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$, mean \pm sd, $n=3$) measured in ambient light (PAR values given in Table 1) on thalli of the different zone-forming species (Pc: *Pelvetia canaliculata*, Fsp: *Fucus spiralis*, Fse: *Fucus serratus*, Ld: *Laminaria digitata*) at the two sites (Wx: Wimereux, Ro: Roscoff) and seasons (Su: summer, Sp: spring) under emersion (Em, A) and immersion (Im, B).

Table 2

Significance of the effect of season and site on electron transport rates (ETR) and gross community productivity (GCP) measured under emersion and on dry weight inside benthic chambers (DW) of the zone-forming species (Pc: *Pelvetia canaliculata*, Ld: *Laminaria digitata*) as tested by Scheirer–Ray–Hare *H*-test.

Variable	Zone-forming species	Factor	<i>H</i>	<i>p</i> -Value
ETR	Pc	Season	1.256	0.262
		Site	0.026	0.872
		Interaction	0.641	0.423
	Ld	Season	8.308	0.004
		Site	1.256	0.262
		Interaction	0.103	0.748
GCP	Pc	Season	0.410	0.522
		Site	2.564	0.109
		Interaction	1.256	0.262
	Ld	Season	0.026	0.872
		Site	8.308	0.004
		Interaction	0.103	0.748
DW	Pc	Season	0.923	0.337
		Site	7.410	0.006
		Interaction	0.103	0.748

Middelboe et al. (2006). For under emersion measurements, care was also taken to use measures obtained during the early stages of emersion on still hydrated algae (relative tissue water content between 72 and 97% for individual scale measurements). Some measurements could not be achieved under immersion due to the difficulty of working while diving in the backwash of the intertidal zone and some data are thus missing. The effect of site and season on the results obtained for each target species was tested when no data were missing using the Scheirer–Ray–Hare *H*-test (non-parametric 2-way ANOVA).

3. Results

3.1. Photosynthetic activity and productivity under emersion

Mean ETR was greatly higher for *P. canaliculata* than for *L. digitata* at each site and season (between 9 and 16 times higher, Fig. 1A). There was no significant difference according to the season or site for *P. canaliculata* (Table 2). For *L. digitata*, mean ETR was significantly

higher in spring than summer but there was no significant difference according to the site (Table 2).

The gross productivity rate was also higher for *P. canaliculata* than for *L. digitata* at each site and season (more than 2 times higher, Fig. 2C). For *L. digitata*, respiration rates were sometimes higher than gross productivity leading to positive carbon fluxes in the benthic chamber under light at Wimereux in summer and in both seasons at Roscoff (Fig. 2A).

The mean gross productivity rate measured at the community scale was higher for the *P. canaliculata* zone than the *L. digitata* zone at Wimereux at the two seasons (between 3 and 4 times higher) while the order of magnitude was the same for the two zones at Roscoff at the two seasons (Fig. 3C). At this scale, carbon fluxes in the benthic chambers under light were always negative, i.e. gross productivity rates were higher than respiration rates. Mean gross productivity rates measured on the *L. digitata* zone were significantly higher at Roscoff than at Wimereux but there were no significant differences according to the season (Table 2). There were no significant differences according to the season or site for *P. canaliculata* (Table 2). The mean biomass of *P. canaliculata* (Table 3) was significantly lower at Wimereux than Roscoff but there were no significant differences between seasons (Table 2).

3.2. Photosynthetic activity and productivity under immersion

The mean ETR measured during immersion was greater for *L. digitata* than for *P. canaliculata* at Roscoff in summer, the single occasion when ETR was measured underwater for both species (Fig. 1B).

At the individual scale, measurements under dark could be achieved only in three experiments (Fig. 2E), leading to only three available values of gross productivity (the highest being for *P. canaliculata* and the lowest for *L. digitata*, Fig. 2F). More experiments could be achieved under light, allowing the comparison of the net productivity rates. They were of the same order of magnitude for *P. canaliculata* than *L. digitata* at Roscoff in summer, the single occasion when NP was measured underwater for both species (Fig. 2D).

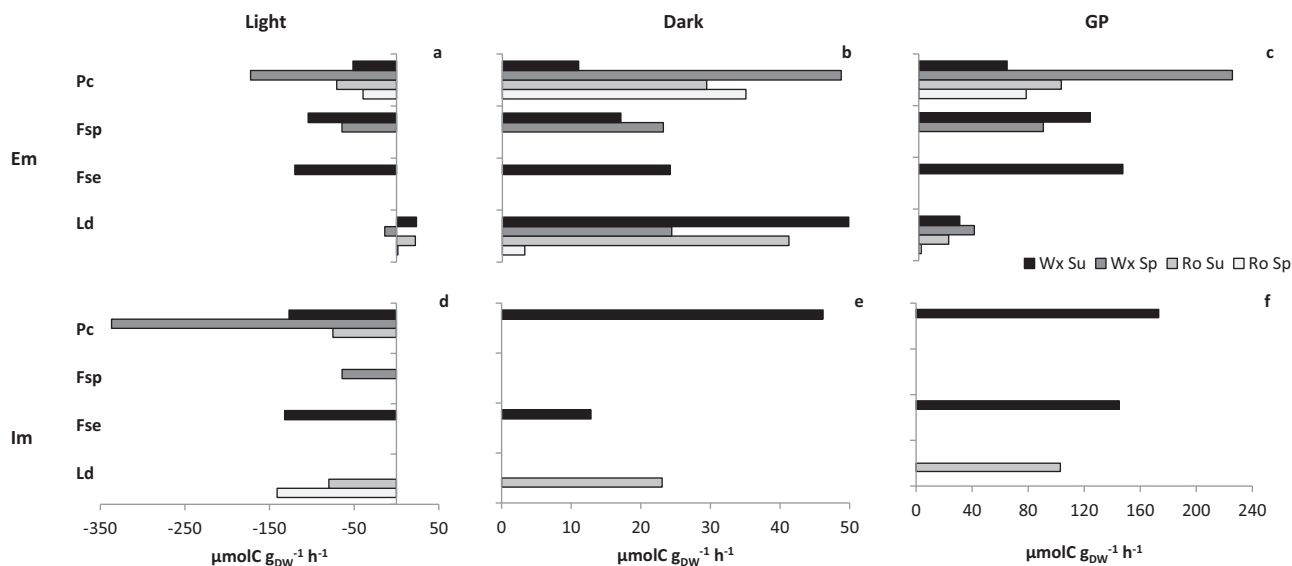


Fig. 2. Highest carbon fluxes measured in the benthic chamber at the individual scale (in $\mu\text{mol C g}_{\text{DW}}^{-1} \text{h}^{-1}$) in ambient light (A and D, PAR values given in Table 1) or in dark (B and E) on the different zone-forming species (Pc: *Pelvetia canaliculata*, Fsp: *Fucus spiralis*, Fse: *Fucus serratus*, Ld: *Laminaria digitata*) at the two sites (Wx: Wimereux, Ro: Roscoff) and seasons (Su: summer, Sp: spring) and corresponding gross productivity (GP, C and F) under emersion (Em, A–C) and immersion (Im, D–F).

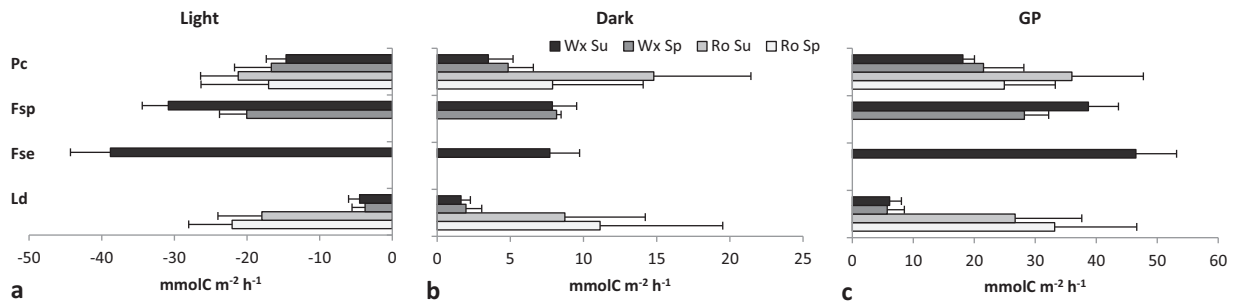


Fig. 3. Highest carbon fluxes measured under emersion in the benthic chambers at the community scale (in $\text{mmol C m}^{-2} \text{h}^{-1}$, mean \pm sd, $n=3$) in ambient light (a) PAR values given in Table 1) or in dark (b) for the different zone-forming species (Pc: *Pelvetia canaliculata*, Fsp: *Fucus spiralis*, Fse: *Fucus serratus*, Ld: *Laminaria digitata*) at the two sites (Wx: Wimereux, Ro: Roscoff) and seasons (Su: summer, Sp: spring) and corresponding gross productivity (GP, c).

3.3. Under emersion versus under immersion photosynthetic activity and productivity

The electron transport rate was higher in air than underwater for *P. canaliculata* and *F. spiralis* (the ratio reaching 3.72) but lower for *F. serratus* and *L. digitata* (the ratio reaching 0.14). For *P. canaliculata*, the higher ETR in the air was explained by the greater photon flux density in the air than underwater at Wimereux in spring (Table 1, while the effective quantum yield of photosystem II was 0.5 and 0.7 in air and water, respectively), but was also due to a greater Φ_{PSII} in the air at Roscoff in summer (0.6 versus 0.4). For *F. spiralis*, it was mainly due to a greater Φ_{PSII} in the air (0.5 versus 0.2). Particularly low values of Φ_{PSII} (<0.1) were measured for *L. digitata* under emersion at Roscoff while they were between 0.2 and 0.7 in the other cases. The ratio of individual scale net productivity in air versus water was lower than 1 at each occasion (the maximum was 0.95 for *F. spiralis*) and was even negative for *L. digitata* at Roscoff (due to respiration rates higher than gross productivity under emersion). The ratio of gross productivity in air versus water was also lower than 1 in the only three occasions it could be calculated.

4. Discussion

The present study of the photosynthetic performance of intertidal macroalgae based on *in situ* measurements emphasizes on a major result: the trends observed under emersion according to the position of the algae along the shore vary with the scale of measurements. The uppermost species *P. canaliculata* had higher photosynthetic activity and productivity under emersion than the lowermost species *L. digitata*, while the few available data showed no trend between the zone-forming species under immersion. Furthermore, the photosynthetic activity measured at the thallus scale was higher in air than underwater for the uppermost species and lower in air than underwater for the lowermost species. Dif-

ferences between zone-forming species were, however, greatly reduced when measurements were scaled up from the electron transport rate of thallus to the gross productivity of individuals and communities.

4.1. Photosynthetic performance according to the shore-level of the algae

In the present study, carbon flux measured at the individual scale, both under immersion and emersion, in ambient light conditions (with $\text{PAR} > 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) suggested that photosynthetic performance was higher underwater whatever the species was, for both sites and seasons and even if the emerged individuals were not significantly dehydrated (relative tissue water content >72%). Furthermore, a net negative productivity (respiration higher than gross productivity) was observed for *L. digitata* under emersion. However, the difference between underwater and aerial performance was lower for upper species, with a $\text{NP}_{\text{em}}/\text{NP}_{\text{im}}$ ratio as high as 0.95 for *F. spiralis*. At the thallus scale, the electron transport rate also measured both under immersion and emersion in ambient light conditions was higher in air for *P. canaliculata* and *F. spiralis* but higher underwater for *F. serratus* and *L. digitata*. Moreover, at that scale of measurement, the upper species on the shore had by far the highest photosynthetic activity under emersion and the lower species had the lowest. This obvious trend was observed independently of the season or site and could not be only explained by better light conditions during measurements for upper species.

Some previous laboratory researches, made under controlled light conditions and based on either oxygen and carbon flux (Johnson et al., 1974; Kawamitsu and Boyer, 1999) or fluorescence (Skene, 2004) measurements on thalli, also suggested that the ability of intertidal algae for sustained photosynthesis in air is enhanced for upper shore species. Johnson et al. (1974) even obtained a $\text{NP}_{\text{em}}/\text{NP}_{\text{im}}$ ratio of 6.6 for the high-shore species *Fucus distichus*. This trend might be explained by the significant ecophysiological distinctions that had been made between algae living essentially completely submersed and those spending a part of tidal cycles in the emersed state. The upper shore algae had been shown to have the potential for rapid photosynthesis in air during the short time without desiccation (Surif and Raven, 1990). Thus, the less time is available for photosynthesis, as limited by desiccation, the greater is the photosynthetic rate during the time available. The “ CO_2 concentrating mechanism”, characteristic of photosynthesis in the eulittoral Fucaeeae (Surif and Raven, 1989), may be important in increasing the efficiency of emersed photosynthesis with limited capital of water available.

Some contrasting results have, however, been obtained in laboratory studies. For example, the carbon intake in the air was higher for the lower shore *Saccharina latissima* than the uppershore *P. canaliculata* (Ni Longphuir et al., 2013), the photosynthesis rates of

Table 3

Mean dry weight (DW) and standard deviation (sd, $n=3$) of the zone-forming species (Pc: *Pelvetia canaliculata*, Fsp: *Fucus spiralis*, Fse: *Fucus serratus*) inside the benthic chambers used for the community scale fluxes measurements (surface area = 0.09 m^2) performed at the two sites (Wx: Wimereux, Ro: Roscoff) and seasons (Su: summer, Sp: spring). There was no *Laminaria digitata* inside the benthic chambers during measurements performed in the *L. digitata* zones.

Zone-forming species	Site	Season	Mean DW (g)	sd
Pc	Wx	Su	21.01	12.36
		Sp	14.86	4.03
	Ro	Su	65.25	14.56
		Sp	44.63	17.27
Fsp	Wx	Su	50.32	12.98
		Sp	42.78	16.34
Fse	Wx	Su	87.21	9.01

intertidal fucoids were always higher in water than in air (Williams and Dethier, 2005) or either higher in water or in air according to the temperature (Madsen and Maberly, 1990) and the effective PSII quantum efficiency of *L. digitata* increased after 3 h of emersion (Nitschke et al., 2011). Furthermore, the effect of short-term emersion on chl *a* fluorescence responses to irradiance has been shown to be dependent on the protocol used for the acclimation of the algae to the different light levels (Nitschke et al., 2012) and the variation of the effective PSII quantum efficiency measured *in situ* has been shown to be dependent on the meteorological conditions (Lamote et al., 2012). Different sampling, keeping and/or measuring conditions could then have influenced both laboratory and field results, leading to various conclusions among studies.

4.2. Variation in the trends of photosynthetic performance according to the scale of measurements

The trend of photosynthetic activity under emersion according to the shore-level of the algae was obvious in the present study when photosynthetic activity was measured at the thallus scale as electron transport rate. When photosynthetic activity was measured as gross productivity at the individual scale, it was also typically higher for the uppermost than the lowermost species but the trend along the shore was less obvious (even if the lack of replication prevents clear comparisons to be performed). Finally, when photosynthetic activity was measured as gross productivity at the community scale, which is a more relevant ecological unit, the highest rates were measured on the intermediate mid-shore zones and, at one of the two sites, rates were higher for the lowermost zone than for the uppermost zone. Furthermore, considering the whole set of data the coefficient of variation of net productivity under emersion was 1.15 at the individual scale and 0.55 at the community scale.

The contrasting results using either fluorescence or carbon flux measurements can suggest that thalli are not relevant ecological units but also that the photosystem II activity measured as ETR is not always a relevant measure of the rate of photosynthesis. There is a general assumption that a linear relationship between ETR and gross photosynthesis exists, as long as environmental stresses do not impose restrictions on photosynthetic carbon fixation. The linearity between ETR and photosynthesis of macroalgae has been, however, only confirmed at low light intensities (Enriquez and Borowitzka, 2010). ETR calculation is based on the assumption that light absorption is only due to photosynthetic pigments. There are, however, alternative electron sinks (e.g. the Mehler reaction, the photorespiration) which explain the deviation from linearity in the relationship between ETR and gross productivity (measured either as O₂ production or C uptake) observed at high irradiances in various primary producers (Beardall et al., 2009). This occurred as critical low values of Φ_{PSII} were reached and the irradiance at which these values were reached depended on the previous light histories undergone by the algae (Beer and Axelsson, 2004). It is the irradiance relative to the algal growth conditions rather than the irradiance during the measurement that determines the threshold. Beer and Axelsson (2004) measured critical values of Φ_{PSII} (<0.1) at lower irradiance for *Laminaria saccharina* than for *F. serratus* (250 versus 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) while both species were acclimated to 400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for 2 weeks. In the present study, critical low values of Φ_{PSII} were measured for *L. digitata* under emersion at Roscoff. Such critical values were previously measured *in situ* underwater at ebb tide around midday on the Roscoff kelps *L. saccharina* and *L. digitata*. The response of Φ_{PSII} to high irradiances was associated to an increase in the non-photochemical quenching and was explained as a down-regulation of the photosystem II (Gévaert et al., 2003; Delebecq et al., 2011).

The contrasting results measuring carbon fluxes either at the individual or at the community scale do reflect the difference in use of resources by either isolated or grouped individuals of only one species and by mixed communities allowing species to interact and supplement each other. Although individual photosynthesis must influence the community response, individual metabolism was not expected to be closely related to community metabolism, because this represents a complex integrated response of many different species exposed to a wide range of local light conditions within the canopies (Middelboe and Binzer, 2004; Binzer and Middelboe, 2005; Middelboe et al., 2006). Tait and Schiel (2011) showed that layering within macroalgal assemblages plays a major role in maintaining net photosynthesis throughout the natural range of irradiance and even enhances photosynthesis at high irradiance. Tait and Schiel (2010) measured the underwater productivity of three fucoid assemblages. The rates, on a per area basis, showed a down shore-height gradient explained by the greater biomass and number of algal species of the lower-shore assemblage. In the present study, a down shore-height gradient was also shown when measurements were performed on the three fucoid assemblages (*i.e.* at Wimereux in summer). The highest rates at the community scale were measured on the *F. serratus* zone where the biomass of the dominant canopy species and the number of species were the highest (9 species were identified inside the chambers while it was 7 for the *P. canaliculata* and 8 for the *F. spiralis* zones). The zone of *L. digitata* had also a great algal biomass (it was measured only once, at Roscoff in summer, and was $80.51 \pm 26.62 \text{ g}_{\text{DW}}/0.09 \text{ m}^2$) and had a great species richness (9 and 22 species identified inside the chambers at Wimereux and Roscoff, respectively) but lower community scale productivity under emersion, particularly at Wimereux. This certainly reflects the low efficiency in air of algae living essentially submersed. Further measurements should be performed at the community scale during immersion periods to test if the down shore-height gradient highlighted with fucoids is maintained when both fucoids and kelps are considered.

Authors contribution

AM, GD, DD, NS, FG: Conceived study, performed research, analysed data, wrote paper.

DM: Conceived benthic chamber, performed research.

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