

Photosynthetic activity of macroalgae along a bathymetric gradient: interspecific and seasonal variability

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Summary: Marine macroalgae are unevenly distributed with depth, with substitutions of the dominant species along the bathymetric gradient. Since light shows a sharp decrease with depth and is a critical factor for algal growth, we hypothesize that species dominating at a certain depth are the best adapted to the light environment reaching that depth. To this end, we selected seven species of Mediterranean macroalgae distributed from 0 to 50 m depth and looked for their photosynthetic performances. Photosynthetic responses showed striking differences, with photosynthetic efficiencies increasing at increasing depths. However, neither oxygen production at high light levels nor respiration are related to depth but seem to respond to other factors such as thallus thickness or nutrient availability. Some species show high production values in agreement with their high productivity and fast growth, while others show low production values but high biomass and durability. Thus, the species that dominates at each light level seems to be the one that makes best use of the light environment to accomplish its life cycle.

Keywords: macroalgae; photosynthesis; depth gradients; efficiency; light.

Actividad fotosintética de macroalgas a lo largo de un gradiente batimétrico: variabilidad interespecífica y estacional

Resumen: Las macroalgas marinas se distribuyen de forma desigual en profundidad, observándose una sustitución de las especies dominantes a lo largo del eje batimétrico. Como la luz muestra una disminución muy marcada con la profundidad y es un factor crítico para el crecimiento de las algas, nuestra hipótesis es que aquellas especies que dominan a una cierta profundidad son las que están mejor adaptadas al ambiente lumínico de esa profundidad. Para comprobarlo hemos seleccionado siete especies de algas marinas mediterráneas distribuidas entre 0 y 50 m de profundidad y hemos calculado sus parámetros fotosintéticos. Las respuestas fotosintéticas muestran grandes diferencias entre especies, con las eficiencias fotosintéticas que aumentan al aumentar la profundidad donde crecen las algas. Sin embargo, tanto la producción de oxígeno a elevados niveles de luz como la respiración no están relacionadas con la profundidad, y parecen determinadas por otros factores como el grosor del talo o la disponibilidad de nutrientes. Algunas especies muestran valores de producción elevados, en sintonía con su alta productividad y rápido crecimiento, mientras que otras muestran bajos valores de producción pero una elevada biomasa y perdurabilidad. Así pues, las especies que dominan en cada ambiente lumínico parecen ser aquellas que utilizan de mejor manera la luz disponible donde crecen para completar con éxito su ciclo de vida.

Palabras clave: macroalgas; fotosíntesis; gradientes de profundidad; eficiencia; luz.

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INTRODUCTION

Bathymetric distribution of aquatic macrophytes depends on several environmental factors, including the type, slope and orientation of the substrate, light intensity, hydrodynamism, nutrient availability and

grazing pressure. Among these factors, light levels and hydrodynamism show a sharp decrease with depth (Ballesteros and Zabala 1993). Light is also a resource that is critical for algal growth and it is the main limiting factor for deep-water algal development in places where appropriate substrate is available (Spence 1976, Denni-

son 1987, Lobban and Harrison 1994). The maximum depth of most aquatic macrophytes in a specific location is inversely related to the capacity of water to absorb the photosynthetic active radiation (Kirk 1994), i.e. the clearer the water is, the deeper the algae can grow. However, the maximum depth where a macrophyte can grow also depends greatly on its physiological features. Some macrophytes (photophilic) are always found in shallow waters, where they are subjected to strong light levels, while others (sciaphilic) mainly grow in deep waters or in places with low light levels.

As a result, different species of aquatic macrophytes usually dominate at different depth intervals, a feature that is known as vertical zonation (Dring 1986, Kirk 1994). The presence/absence of a macrophyte at a certain depth depends on the equilibrium between its physiological ability to grow (which in turn depends on the available light, temperature, nutrient availability and other factors) and the ecological processes that imply biomass loss (including unsuitable environmental conditions and herbivory), together with the ability to outcompete with or tolerate other species (Airolidi 2000). In this context, we hypothesize that dominant species at a certain depth are those that outcompete others, whether because they can grow faster or because they are persistent in occupying space. Since light is a pivotal environmental factor for macrophyte growth and it decreases with depth, we expect macrophytes that dominate at different depths to show different photosynthetic performances related to light availability.

In order to provide species distribution models, it is necessary to know the physiological responses of organisms to changing environments. In terrestrial ecology one of the most accepted findings is the existence of differences in the photosynthetic performance of “sun plants” versus “shade plants” (Boardman 1977, Field 1988, Boston et al. 1989): plants living in high light environments should display a low photosynthetic efficiency at low light levels but a high photosynthetic capacity at high light levels, while those living at low light environments should display a high photosynthetic efficiency at low light levels and low photosynthetic capacity at high light levels. In benthic ecology, even if this model has been tested experimentally (Herbert and Waaland 1988, Delgado et al. 1995, Beach and Smith 1996), some studies demonstrate that the photosynthetic capacity is mainly related to thallus morphology and thickness (Arnold and Murray 1980, Littler 1980, Lüning and Dring 1985) or to the growth strategy of each species (King and Schramm 1976, Peckol and Ramus 1988).

Here we aim to test whether there is a relationship between the bathymetric distribution of several Mediterranean erect macroalgae and their photosynthetic performances. If the relationship exists, a response typical of “sun plants” would be expected in photophilic algae, while a response typical of “shade plants” would be expected in sciaphilic algae. To this end, we selected seven species of Mediterranean macroalgae that predominate at different depths, from 0 to 50 m, and compared their seasonal photosynthetic performance at different light levels. We also measured carbon,

nitrogen and phosphorus content in tissue samples as nutrients have been claimed as a limiting factor for photosynthesis and growth in Mediterranean macroalgae (Ballesteros 1992, Delgado et al. 1994).

MATERIAL AND METHODS

Samples were collected at Estell des Coll (39°07'19"N 2°56'09"E), a small islet within the Archipelago of Cabrera National Park (Balearic Islands, western Mediterranean). The water column remains very clear even in winter, with photon flux density (PFD) extinction coefficients ranging from 0.053 m⁻¹ in summer to 0.076 m⁻¹ in winter (Ballesteros and Zabala 1993). Yearly average PFD ranges between 55% (at 0.2 m) and 2% (at 50 m) of the superficial PFD. Nutrient levels are always low, corresponding to oligotrophic to ultra-oligotrophic environments, with mean dissolved phosphate values ranging from 0.04 to 0.08 µmol l⁻¹ and nitrates ranging from 0.25 to 0.80 µmol l⁻¹ (Ballesteros and Zabala 1993). Temperature ranges from 14°C to 15°C (January-March, all depths) to 27°C at surface (August-September) and 20°C to 21°C (October) at 50 m depth (Ballesteros and Zabala 1993).

The southern part of the Estell des Coll islet has an almost vertical wall that sinks down to 52 m depth, showing five different algal assemblages (Ballesteros et al. 1993, Sant et al. 2017) from the shallows to the bottom: the assemblages dominated by *Carpodesmia amentacea* v. *stricta* (0.2 m depth) (hereinafter *Carpodesmia stricta*), *Padina pavonica* and *Dictyota fasciola* (1-8 m depth), *Carpodesmia brachycarpa* v. *balearica* (10-16 m depth) (hereinafter *Carpodesmia balearica*), *Dictyopteris polypodioides* (18-40 m depth) and the coralligenous assemblage (42-52 m depth) dominated by calcareous encrusting algae (Ballesteros 2006), with *Flabellia petiolata* and *Halopteris filicina* as the main erect species at the sampling site. These seven erect algae were selected to measure their photosynthetic performance. The composition of the assemblages and their seasonality are thoroughly described in Sant et al. (2017).

Sampling was performed seasonally, in February (winter), May (spring), early September (summer) and early December (autumn). The abundance of the main species with depth was estimated by means of reticulated quadrats. Species abundance was estimated using 0.25×0.25 m quadrats divided into 25 sub-quadrats of 5×5 cm. Four quadrats were positioned haphazardly at depths of 0.2, 5, 12, 25 and 50 m in every season, making a total of 16 quadrats per year and depth. Main macroalgae within each sub-quadrat were identified and the percentage of sub-quadrats in which a species appeared was recorded and used as a measure of occurrence. A highly abundant species that appeared in all 25 sub-quadrats would produce a presence of 100%, whereas a total lack of a species would produce a presence of 0% (Sala and Ballesteros 1997, Tomas et al. 2011, Teixidó et al. 2018). The final abundance of a species within each depth was then calculated as the mean of the percentage presence values of the quadrats sampled.

In every season, specimens of the seven species were collected at their preferred depth using SCUBA diving. Diving was performed in late afternoon every day, and the algae were collected and maintained overnight, submerged at sea inside mesh bags and protected from direct light until the next morning. Specimens were sorted and prepared for photosynthesis and respiration assays in the early morning just before the experiments began. Material selection, manipulation and assays were performed according to the recommendations made by Littler (1979), Littler and Arnold (1980) and Littler and Littler (1985).

Photosynthesis assays were performed in 270 mL glass bottles. Whole blades or branches (in *Carpodesmia* spp.) were selected among the collected material, cleaned of epiphytes and introduced into 270 mL glass bottles containing seawater and a glass marble hanging inside the bottle and subjected with a nylon line. The bottles with the algal specimens were hung in a structure hanging from a buoy and placed in the sea at Cabrera harbour at 2 m depth. Waves moved the structure and the glass marbles shook the water inside the bottle, breaking diffusion gradients. Three replicates per species and three empty bottles (to account for variation not due to macroalgae) were assayed every day at a different PFD, making a total of 24 assays per day. Ten different PFDs were obtained by covering the structure with a different number of neutral filters, using a black filter to measure dark respiration. Ambient light in each assay was measured using a Li-1000 SPQA spherical sensor deployed at the same site and depth of the hanging structure. PFD attenuation inside the hanging structure with increasing number of filters was also measured ($y=100e^{-0.52x}$, $R^2=0.99$, x =number of neutral filters, y =% ambient PFD). Light intensities ranged between 0 and 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Incubation times ranged between 3 and 4 h and assays were always performed between 10:00 am and 2:00 pm. Every specimen was used only once, which made each assay independent from the others. Oxygen was measured after the assay with an Orbisphere 2607 oxygen analyser with an accuracy of 0.01 $\text{mg O}_2 \text{l}^{-1}$. Oxygen production/dark consumption was measured as the difference between the oxygen from each bottle containing a specimen and the average of the three empty bottles. Specimens used in the assays were dried at 60°C for 48 hours to obtain their dry weight (Boudouresque 1971, Romero 1981, Ballesteros 1986). The specimens were then burned in an oven for 4 h at 500°C to obtain the ash free dry weight (AFDW) (Brinkhuis 1985).

The data obtained in the assays was pooled together for every species to obtain the photosynthesis/light intensity (PFD) curves. We did not adjust any function to the curves due to the existence of different models (see Jones et al. 2014 for a discussion). Alternatively, we obtained the photosynthetic parameters directly based on photosynthesis at saturation levels (P_{max}) and variation of photosynthesis at low light levels (photosynthetic efficiency, α) (Arenas et al. 1995, Gómez et al. 1996, Gómez and Wiencke 1997), which allows comparisons within our data. The photosynthetic parameters finally obtained were (Fig. 1) dark respiration (R_d in mg O_2

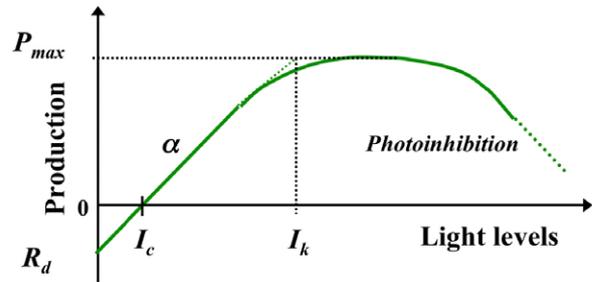


Fig. 1. – Theoretical representation of a photosynthesis/irradiance curve and the corresponding photosynthetic parameters: photosynthesis at saturation (P_{max}), light at saturation (I_k), light at compensation (I_c), photosynthetic efficiency (α) and dark respiration (R_d).

$\text{gAFDW}^{-1} \text{h}^{-1}$), light compensation point (I_c in $\mu\text{mol photon m}^{-2} \text{s}^{-1}$), photosynthetic efficiency [α in $\text{mg O}_2 \text{m}^{-2} \text{s}^{-1} (\mu\text{mol photon gAFDW h}^{-1})^{-1}$], light at saturation levels (I_k in $\mu\text{mol photon m}^{-2} \text{s}^{-1}$), and photosynthesis at saturation levels (P_{max} in $\text{mg O}_2 \text{gAFDW}^{-1} \text{h}^{-1}$).

Nutrient content in tissues for each species was measured seasonally from specimens collected at the same depths as the specimens used for the photosynthetic assays. The samples were frozen after collection and, on arrival in the laboratory, they were defrosted, dried and triturated. Carbon and nitrogen were measured with a Carlo-Erba Autoanalyzer (Servis Científico-Tècnics, University of Barcelona) and phosphorus was analysed with an inductively coupled plasma mass spectrometer (ICP) after acid digestion of the samples, following Mateo and Sabaté (1993).

Differences between P_{max} and R_d between species and between seasons were tested with a two-way ANOVA followed by a Tukey test. *P. pavonica* and *D. fasciola* were not included because they were highly seasonal. The data were log-transformed in order to accomplish the assumptions of ANOVA. Relationships between parameters were estimated using Pearson linear correlations. A principal component analysis (PCA) (ter Braak 1990) was performed using all the photosynthetic parameters obtained seasonally (P_{max} , R_d , I_c , I_k , α).

RESULTS

Distribution of the selected species with depth is presented in Figure 2. The abundances of the species followed a bathymetric pattern, as expected, with every species dominant in a particular assemblage.

Curves relating photosynthesis and light levels differed between species and sometimes between seasons (Fig. 3). *Dictyopteris polypodioides* showed the highest P_{max} and *F. petiolata* the lowest (Table 1, Fig. 4A). Specific differences in P_{max} for the five species that are present all year round were very significant (Table 2). However, *C. balearica* was the only species whose P_{max} did not differ from the others (Tukey test). Seasonal differences were also very significant globally (Table 2), with the lowest values attained in winter for deep-water species. Seasonality seemed to be much lower in deep-water species than in perennial shallow water ones, while non-perennial species (*D. fasciola*,

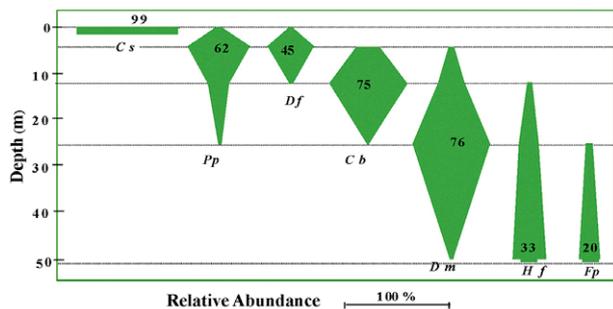


Fig. 2. – Bathymetric distribution of the main erect algal species dominating the assemblages at Estell des Coll (Cabrera, Balearic Islands). Abundance values correspond to the annual average estimated from 16 reticulated quadrats (4 quadrats per depth and season). Numbers represent the abundance percentage at the depth of highest occurrence.

P. pavonica) showed a relatively high and constant P_{max} (Table 2). Moreover, there was no relationship between P_{max} and light levels attained at the depths and seasons where a species was dominant (Table 3).

Carpodesmia stricta showed the highest light at saturation levels (I_k), followed by *C. balearica* (Table 4). Dictyotales (*P. pavonica*, *D. fasciola* and *D. polypodioides*) showed intermediate values and *H. filicina* and particularly *F. petiolata* showed the lowest ones (Fig. 4B). Species receiving more light showed the highest I_k values (Table 3). There were no clear seasonal patterns (Table 4). Inhibition of photosynthesis at high light levels (photoinhibition) was not usual in our assays and when it happened it occurred at PFDs over $850 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. This was the case of *C. balearica* ($p<0.001$) and *D. polypodioides* ($p<0.05$) in

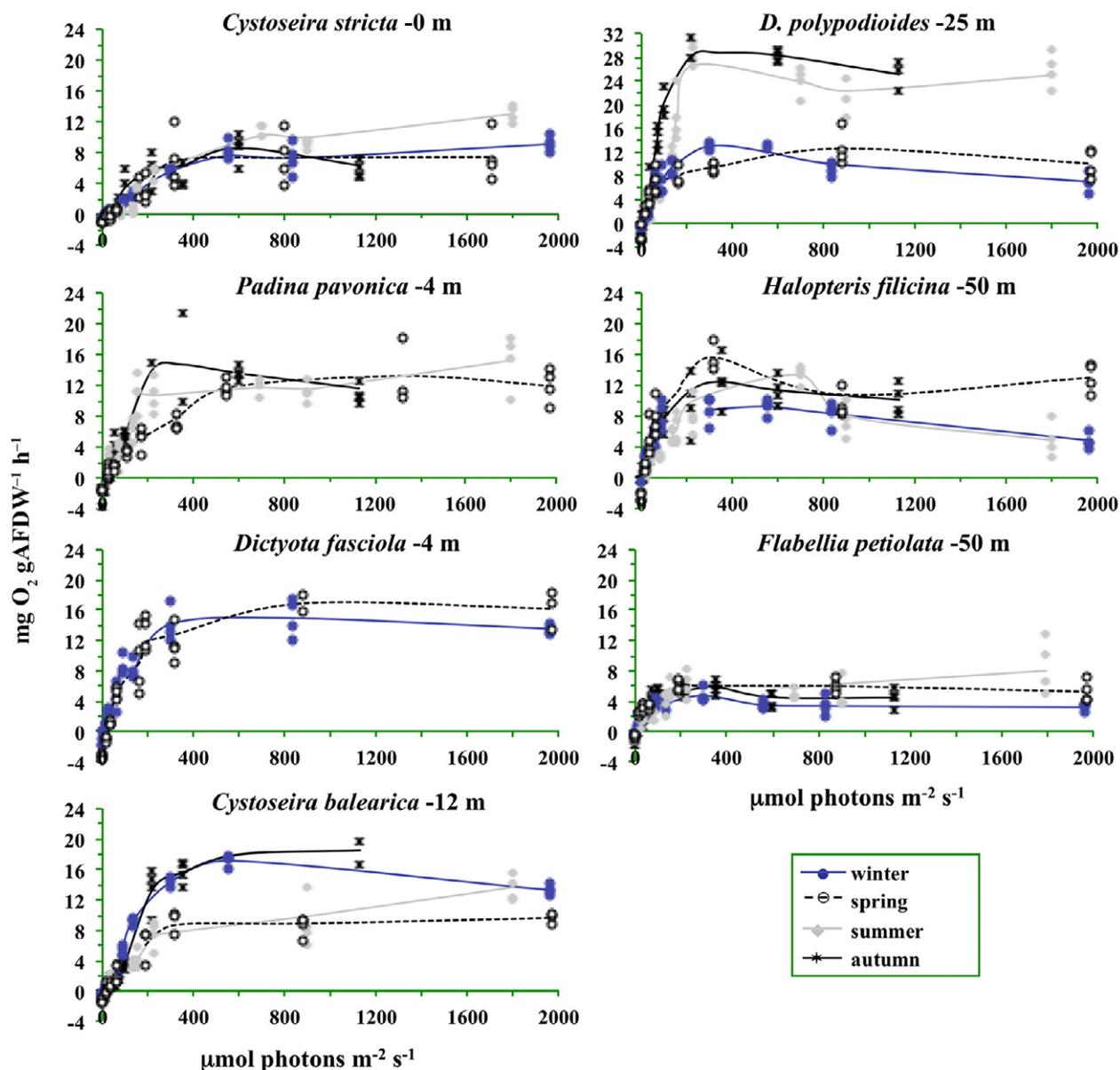


Fig. 3. – Photosynthesis/irradiance curves for the seven species in different seasons. Note that the Y scale for *Dictyopteris polypodioides* is different.

Table 1. – Photosynthesis at saturation (P_{max} , in $mg\ O_2\ gAFDW^{-1}\ h^{-1}$) for species and season.

P_{max}	winter	spring	summer	autumn	mean	sd
<i>Carpodesmia stricta</i>	8.2	5.9	13.0	6.4	8.4	3.2
<i>Dictyota fasciola</i>	14.2	13.9	-	-	14.1	0.2
<i>Padina pavonica</i>	-	12.2	11.6	13.1	12.3	0.7
<i>Carpodesmia balearica</i>	17.2	8.3	13.6	17.6	14.2	4.3
<i>Dictyopteris polypodioides</i>	13.0	10.7	26.1	27.5	19.3	8.7
<i>Flabellia petiolata</i>	3.7	5.7	6.0	4.9	5.1	1.0
<i>Halopteris filicina</i>	8.6	14.1	13.3	10.9	11.7	2.5

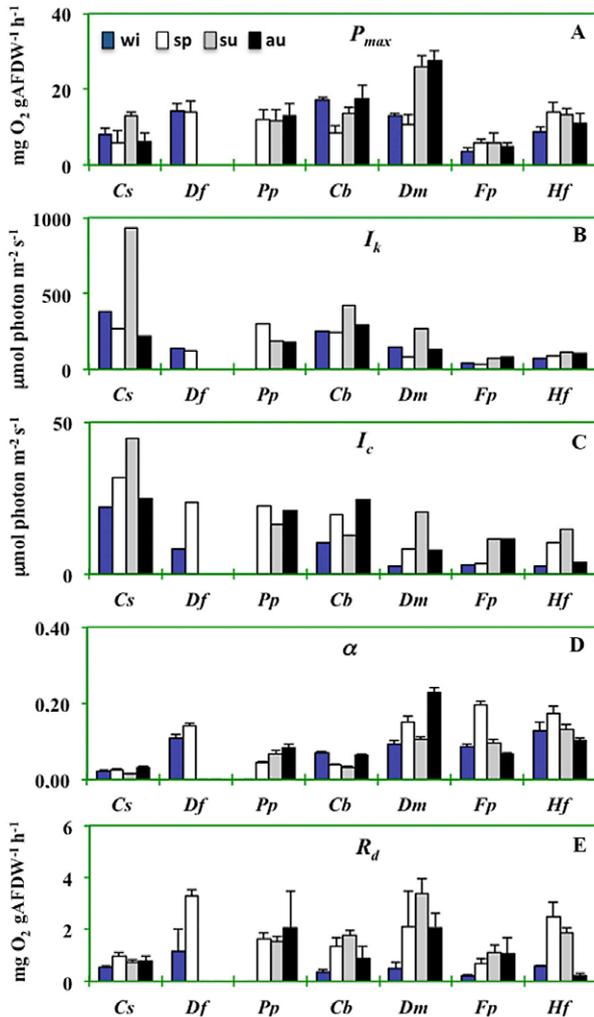


Fig. 4. – Seasonal values of the photosynthetic parameters: photosynthesis at saturation (P_{max}), light at saturation (I_k), light at compensation (I_c), photosynthetic efficiency (α) and dark respiration (R_d). Cs, *Carpodesmia stricta*; Df, *Dictyota fasciola*; Pp, *Padina pavonica*; Cb, *Carpodesmia balearica*; Dp, *Dictyopteris polypodioides*; Fp, *Flabellia petiolata*; Hf, *Halopteris filicina*.

winter and also in *H. filicina* in winter ($p < 0.01$) and summer ($p < 0.001$).

Light at compensation was lower in deep-water species than in shallow-water species (Table 5). Compensation points were always lower in winter than in other seasons, while their highest values were present in summer and autumn (Fig. 4C). Regarding photosynthetic efficiency, deep-water species were the most efficient, with the highest values for *F. petiolata* and *H. filicina* in spring and for *D. polypodioides* in autumn (Table 6, Fig. 4D). Photosynthetic efficiency was very low for *C. stricta* all year round, while *D. fasciola*

Table 2. – Results of the two-way ANOVA for P_{max} and R_d .

	factor	df	MS	% variance	F	p
P_{max}	species	4	28.21	59.8	231.5	<0.001
	season	3	5.08	8.1	41.7	<0.001
	interaction	12	2.84	18.1	23.3	<0.001
	error	216	0.12	14.0		
R_d	species	4	4.24	26.8	21.1	<0.001
	season	3	6.29	29.8	31.3	<0.001
	interaction	12	1.34	25.4	6.7	<0.001
	error	57	0.20	18.1		

showed a rather high photosynthetic efficiency when compared with the other shallow water species (*C. balearica* and *P. pavonica*) (Table 6).

Dark respiration showed a much stronger seasonality than P_{max} . The seasonal variation explained 29.8% of the total variance in the five perennial species (Table 2). Dark respiration was significantly lower for all species in winter ($p < 0.001$), and there were no differences between spring and summer. Differences between species were also noteworthy and explained almost 27% of the variance (Table 2). The interaction between species and seasons was also highly significant, which means that species-specific patterns were found in dark respiration seasonality (Table 2). The highest dark respiration values corresponded to *D. polypodioides* and *D. fasciola* (Fig. 4E, Table 7).

The variance explained by the two first axes of a PCA performed using all seasonal photosynthetic parameters for the species studied was very high (47.3% axis I, 34.3% axis II). Photosynthetic efficiency, light at saturation and light at compensation were closely associated with the first axis, while photosynthesis at saturation and dark respiration were associated with the second axis (Fig. 5). Low P_{max} values are usually associated with a low dark respiration (as occurs in winter samples) and vice versa. However, neither P_{max} nor R_d show any significant relationship with I_c and I_k , while I_c and I_k are closely related with each other and show a high positive relationship with light attenuation with depth (I_z). Deep-water species show the lowest I_k and I_c , as displayed by the inverse relationship between depth and I_k and I_c in Figure 5. I_k and P_{max} are independent, as are also P_{max} and α ($p > 0.05$). However, the only species that shows a low P_{max} and a high α

Table 3. – Correlations between the photosynthetic parameters, dark respiration and the daily highest PFD arriving at each depth. Non-significant (ns), $p < 0.05$ (*), $p < 0.001$ (***)

		P_{max}	I_k	I_c	α	R_d
Ln(I_z)	r	0.13	0.66	0.71	-0.47	0.27
	p	ns	***	***	*	ns
	n	25	24	25	25	25
Ln(I_z) « depth: $r = -0.91$ *** n=20						

Table 4. – Light at saturation (I_k , in $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) for species and season.

I_k	winter	spring	summer	autumn	mean	sd
<i>Carpodesmia stricta</i>	384.4	266.7	934.1	223.0	452.0	328.5
<i>Dictyota fasciola</i>	139.3	122.5	-	-	130.9	11.9
<i>Padina pavonica</i>	-	301.5	186.3	178.0	221.9	69.1
<i>Carpodesmia balearica</i>	253.4	242.4	423.5	295.9	303.8	83.1
<i>Dictyopterus polypodioides</i>	143.2	79.7	268.7	128.6	155.1	80.5
<i>Flabellia petiolata</i>	45.6	32.7	75.0	85.0	59.6	24.5
<i>Halopteris filicina</i>	70.1	91.4	116.7	109.2	96.8	20.8

Table 5. – Light at compensation (I_c , in $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) for species and season.

I_c	winter	spring	summer	autumn	mean	sd
<i>Carpodesmia stricta</i>	22.2	31.7	44.7	25.0	30.9	10.0
<i>Dictyota fasciola</i>	8.4	23.7	-	-	16.1	10.8
<i>Padina pavonica</i>	-	22.3	16.2	20.7	19.7	3.1
<i>Carpodesmia balearica</i>	10.5	19.8	12.7	24.5	16.9	6.5
<i>Dictyopterus polypodioides</i>	2.8	8.2	20.6	7.9	9.9	7.6
<i>Flabellia petiolata</i>	3.2	3.5	11.7	11.5	7.5	4.8
<i>Halopteris filicina</i>	2.6	10.2	14.9	3.8	7.9	5.7

Table 6. – Photosynthetic efficiency (α) for species and season.

α	winter	spring	summer	autumn	mean	sd
<i>Carpodesmia stricta</i>	0.02	0.03	0.01	0.03	0.02	0.01
<i>Dictyota fasciola</i>	0.11	0.14	-	-	0.12	0.02
<i>Padina pavonica</i>	-	0.04	0.07	0.08	0.06	0.02
<i>Carpodesmia balearica</i>	0.07	0.04	0.03	0.07	0.05	0.02
<i>Dictyopterus polypodioides</i>	0.09	0.15	0.11	0.23	0.14	0.06
<i>Flabellia petiolata</i>	0.09	0.20	0.09	0.07	0.11	0.06
<i>Halopteris filicina</i>	0.13	0.17	0.13	0.10	0.13	0.03

Table 7. – Dark respiration (R_d , in $\text{mg O}_2 \text{ gAFDW}^{-1} \text{ h}^{-1}$) for species and season.

R_d	winter	spring	summer	autumn	mean	sd
<i>Carpodesmia stricta</i>	0.53	0.96	0.75	0.78	0.76	0.18
<i>Dictyota fasciola</i>	1.16	3.28	-	-	2.22	1.50
<i>Padina pavonica</i>	-	1.65	1.55	2.07	1.76	0.28
<i>Carpodesmia balearica</i>	0.35	1.35	1.76	0.86	1.08	0.61
<i>Dictyopterus polypodioides</i>	0.49	2.11	3.37	2.08	2.01	1.18
<i>Flabellia petiolata</i>	0.19	0.68	1.12	1.06	0.76	0.43
<i>Halopteris filicina</i>	0.60	2.49	1.88	0.21	1.30	1.07

is *Flabellia petiolata*, and if we delete this species from the relationship, all the other species show a low but positive relationship between P_{max} and α ($r=0.54$, $p<0.05$, $n=21$).

Carbon (C), nitrogen (N) and phosphorus (P) content in tissue of the different species is summarized in Table 8. P content was always lower than 0.15% of dry weight. The highest values were found in winter and the lowest in late spring and summer. N content ranged between 0.5% and 2% in all the species, with the exception of the only green alga, *Flabellia petiolata*, for which it was around 4%. N content was also highest in winter and lowest in late spring. C content ranged from 19% to 42% and showed no clear seasonal pattern. The low summer P content means that C:P and N:P ratios increased in spring and summer in most species. C:N ratios showed no consistent pattern except for the increase from winter to spring (Fig. 6). N and P content in tissues was correlated with depth, but C content was not (Table 9). Thus, C:N and C:P ratios were lower in the species thriving in deep waters than in those thriving in shallow waters ($r=-0.73$ and $r=-0.62$, respectively, $p<0.001$, $n=25$). However, if *Flabellia petiolata*, which has a very high N content, was disregarded, correlation levels were lower (Table 9).

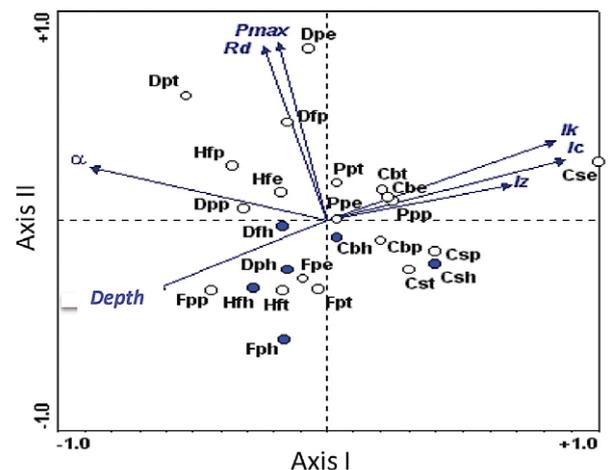


Fig. 5. – Representation of the species and seasons in a plane defined by axes I and II from a PCA made using the photosynthetic parameters as variables. Depth and I_z (irradiance at every depth and season) are not variables but have been incorporated into the representation. Full dots indicate winter samples. Every species and season is indicated by the same abbreviation as that used in Figure 4 followed by season (p, spring; e, summer; t, autumn; h, winter).

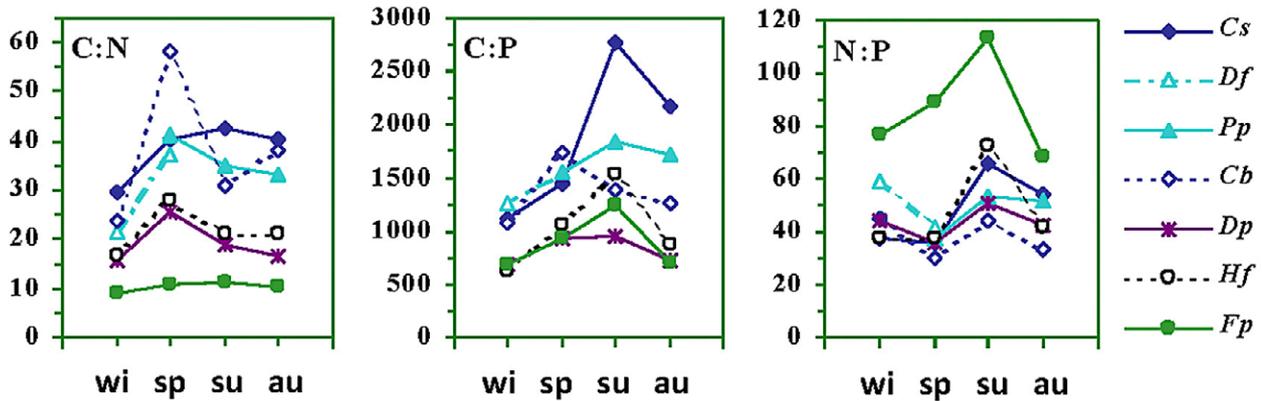


Fig. 6. – C:N, C:P and N:P ratios in tissues for each species and season. Abbreviations as in Figure 4. Cs, *Carpodesmia stricta*; Df, *Dictyota fasciola*; Pp, *Padina pavonica*; Cb, *Carpodesmia balearica*; Dp, *Dictyopterus polypodioides*; Fp, *Flabellia petiolata*; Hf, *Halopteris filicina*.

Table 8. – Carbon (%C), nitrogen (%N) and phosphorus (%P) contents in algal tissues: seasonal values and averages (mean±sd).

%C	winter	spring	summer	autumn	mean	sd
<i>C. stricta</i>	32.6	33.3	34.4	30.9	32.8	1.6
<i>D. fasciola</i>	30.2	37.1	-	-	33.7	4.0
<i>P. pavonica</i>	-	20.1	19.2	21.1	20.1	0.9
<i>C. balearica</i>	30.4	33.6	36.4	33.3	33.4	2.3
<i>D. polypodioides</i>	25.9	27.7	31.2	32.8	29.4	3.0
<i>F. petiolata</i>	37.3	42.4	38.4	35.9	38.5	2.9
<i>H. filicina</i>	25.3	27.7	28.5	23.7	26.3	2.1

%N	winter	spring	summer	autumn	mean	sd
<i>C. stricta</i>	1.29	0.98	0.95	0.90	1.03	0.18
<i>D. fasciola</i>	1.65	1.17	-	-	1.41	0.28
<i>P. pavonica</i>	-	0.57	0.65	0.75	0.65	0.09
<i>C. balearica</i>	1.49	0.67	1.36	1.02	1.14	0.34
<i>D. polypodioides</i>	1.93	1.26	1.96	2.29	1.86	0.41
<i>F. petiolata</i>	4.85	4.69	4.10	4.11	4.44	0.38
<i>H. filicina</i>	1.79	1.17	1.57	1.32	1.46	0.26

%P	winter	spring	summer	autumn	mean	sd
<i>C. stricta</i>	0.076	0.060	0.032	0.037	0.05	0.02
<i>D. fasciola</i>	0.062	0.062	-	-	0.06	0.00
<i>P. pavonica</i>	-	0.033	0.027	0.032	0.03	0.00
<i>C. balearica</i>	0.073	0.050	0.068	0.068	0.06	0.01
<i>D. polypodioides</i>	0.097	0.077	0.084	0.118	0.09	0.02
<i>F. petiolata</i>	0.140	0.116	0.080	0.134	0.12	0.02
<i>H. filicina</i>	0.106	0.069	0.048	0.070	0.07	0.02

Table 9. – Correlation (r) between C, N and P content in algal tissues with the depth at which specimens were collected, considering all the species and (inside brackets) not including the green alga *Flabellia petiolata*. ns: non-significant, * p<0.05, *** p<0.001.

	C		N		P	
depth	r	0.19 (0.24)	0.68 (0.49)	0.65 (*)	0.48 (***)	0.48 (*)
	p	ns (ns)	*** (**)	*** (**)	*** (*)	*** (*)
	n	25 (21)	25 (21)	25 (21)	25 (21)	25 (21)

DISCUSSION

The vertical distribution of the species agrees with the patterns previously described from Cabrera (Ballesteros 1993, Sant et al. 2017) and other localities from the northwestern Mediterranean (e.g. Feldmann 1937, Verlaque 1987, Ballesteros 1992). *C. stricta*, *P. pavonica*, *D. fasciola* and *C. balearica* are considered photophilic species (“sun” macroalgae), while *D. polypodioides*, *H. filicina* and *F. petiolata* show a sciaphilic to hemisciaphilic behaviour (“shade” macroalgae) (Boudouresque 1984).

Light at compensation (I_c) was the photosynthetic parameter that showed the best trend of change with depth. I_c values measured here are consistent with those found in other papers (e.g. King and Schramm 1976, Gao and Umezaki 1988). In fact, low I_c values are considered a good indicator of the capacity of surviving in a light-limited environment (Dring 1992, Kirk 1994). Here we found that “shade” macroalgae show the lowest I_c (usually <10 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$). Deep-water macroalgae also show a higher photosynthetic efficiency (α), which indicates their adaptation to capture the low light that reach the depths where they thrive. The exception here is *Dictyota fasciola*, whose α is similar to that of deep-water macroalgae. This high efficiency could be related to its short life span, since high α should provide a competitive advantage in its short growing period in comparison with other low-growing but more persistent macroalgae (in the sense of King and Schramm 1976 and Peckol and Ramus 1988). Nevertheless, the I_c of *D. fasciola* is similar to that of other species thriving in the same environment

(*P. pavonica*, *C. balearica*) and is much higher than that of the deep-water macroalgae studied here, reinforcing its shallow distribution range. A third parameter related to the depth distribution of macroalgae is I_k , which decreases with depth, as already stated (e.g. Ramus et al. 1976, Lüning 1981, Orfanidis 1992). The values obtained here are consistent with those predicted by Lüning (1981) for intertidal ($I_k=400-600$), shallow-water ($=150-200$) and deep-water macroalgae ($<100 \mu\text{mol photon m}^{-2} \text{s}^{-1}$). Moreover, the species showing I_k values higher than $200 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ also display α values lower than 0.10 in average, suggesting that macroalgae that are better adapted to thriving in low light environments attain saturation of photosynthesis at lower light levels than those thriving in a high light environment, supporting the hypothesis of the existence of “sun” and “shade” macroalgae. In short, I_c , I_k and α show a species variation trend related to the depth where macroalgae dominate the seascape and to their light environment. In general, we can hold that these three parameters are useful to discern between photophilic and sciaphilic algae, with the only exception of the already commented high α of *D. fasciola* from shallow waters.

However, the results obtained at saturation irradiances (P_{max}) and dark respiration (R_d) are not related to seaweed distribution. For instance, although the lowest P_{max} corresponds to *F. petiolata* collected at -50 m, the highest P_{max} corresponds to *D. polypodioides* at -25 m and not to a shallow water alga, as predicted. These results agree with those obtained by Ramus et al. (1976) and Peckol and Ramus (1988), who also found higher P_{max} values in deep-water than in shallow-water macroalgae. Gerard (1988) also observed higher P_{max} values in *Laminaria saccharina* thriving at intermediate depths, and Gómez (1997) also concluded that P_{max} and depth are not related. Photosynthetic activity of algae at saturation levels seems to be more related to the shape and thickness of the thallus than to the light environment, being higher in thin than in thick thalli (Ramus 1978, Littler and Littler 1980, Johansson and Snoeijs 2002), which would explain why *D. fasciola* and *D. membranacea* show the highest P_{max} . On the other hand, the thinnest algae show the highest respiration rates, in agreement with observations by King and Schramm (1976), Littler (1980) and Markager and Sand-Jensen (1992), while the thickest algae (*C. stricta* and *C. balearica*) maintain the R_d at low levels, close to the 10% of P_{max} .

P_{max} and R_d differ greatly between species and especially within seasons, as they are conditioned by temperature (Raven and Geider 1988, Davison 1991, Henley 1993). The ultraoligotrophy of the waters in Cabrera, with annual average nitrate values around $0.47 \mu\text{mol l}^{-1}$ and phosphate values around $0.05 \mu\text{mol l}^{-1}$ (Ballesteros and Zabala 1993) could also limit P_{max} , as it has been reported in tropical seas by Lapointe et al. (1987), Littler et al. (1988) and Littler and Littler (1992), and in temperate seas by Flores-Moya et al. (1995). In fact the phosphorous content in the tissues of the six brown algae are extremely low (0.05% to 0.09%), and nitrogen ranges between 1% and 1.9%. P

values are always below the critical value of 0.13 (Gerloff and Krombholz 1966), and N values are close to the critical values of 1.5% to 1.9% proposed by Fujita et al. (1989) and Hanisak (1979), pointing to a strong limitation of photosynthesis and growth caused by low nutrient availability. In general, deep-water algae are the richest in N and P, and interspecific differences are lower in winter, in agreement with a higher nutrient availability. This is why nutrient content is usually higher in deep-water algae, which are the ones that show the highest I_c , α and I_k . In brown algae, the highest P_{max} also corresponds to the algae displaying the highest N and P content and the lowest C:N, suggesting a nutrient limitation for the algae studied here.

Our results seem to support the predictions of a lack of chronic photoinhibition in the shallow water algae studied (*C. stricta*, *D. fasciola* and *P. pavonica*). *C. balearica*, *D. polypodioides* and *H. filicina* showed a significant photoinhibitory response at irradiances higher than $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, in agreement with their sciaphilic distribution. However, *F. petiolata*, collected at -50 m showed no sign of photoinhibition even at irradiances 1000 times higher than those found in its habitat. Boudouresque (1984) defines this species as antisciaphilic, i.e. a species that is sciaphilic but also able to thrive in shallow waters at high temperature and light levels, as also reported by Drew and Larkum (1967) and Larkum et al. (1967) on the Maltese coast. Thus, we believe that *F. petiolata* is confined to deep waters, not because it cannot stand high irradiances but probably because of other factors such as hydrodynamism, competition for space or herbivory. However, its behaviour as a shade plant (high photosynthetic efficiency, low I_c and low I_k) points to a very good adaptation to thriving in deep waters.

The low winter temperature seems to be responsible for the low respiration observed in all the species, in agreement with other studies (King and Schramm 1976). Seasonal variations in photosynthetic efficiency seem to be a response to seasonal changes in solar radiation. We estimated the number of hours with irradiances higher than I_c and equal to or higher than I_k from I_c , I_k , day length and light attenuation in the water column for each species (Table 10). Deep-water algae almost always have 6 hours of light higher than I_c , which means that net production occurs for at least 6 hours. Shallow water algae have between 8 and 14 hours a day, depending on the season. Saturation irradiance of shallow water algae is always lower than the days' highest irradiance, which means that photosynthesis is already saturated long before midday, and they have 6 to 12 hours of net production every day. Around the winter solstice, light could limit photosynthesis in algae found deeper than 10 m (*C. balearica*, *D. membranacea*, *F. petiolata* i *H. filicina*), since H_{sat} equals 0 (Table 10). Deep-water algae only can reach P_{max} at the end of spring and, in the case of *D. polypodioides*, also in summer. Thus, production seems to be limited by light for most of the year. In spring, though *F. petiolata* has a lower P_{max} than *H. filicina*, it is more efficient (with a much lower I_k). This clearly benefits *F. petiolata*, because its net production is positive for 10

Table 10. – Hours of daylight with irradiances higher than I_c (H_{prod}) and equal to or higher than I_k (H_{sat}).

H_{prod}	winter	spring	summer	autumn	mean	sd
<i>C. stricta</i>	10	14	12	10	11.5	1.9
<i>D. fasciola</i>	10	14	-	-	12.0	2.8
<i>P. pavonica</i>	-	14	12	8	11.3	3.1
<i>C. balearica</i>	10	14	12	8	11.0	2.6
<i>D. polypodioides</i>	10	14	12	8	11.0	2.6
<i>F. petiolata</i>	8	14	10	1	8.3	5.4
<i>H. filicina</i>	10	12	10	6	9.5	2.5
H_{sat}	winter	spring	summer	autumn	mean	sd
<i>C. stricta</i>	8	12	6	7	8.3	2.6
<i>D. fasciola</i>	8	12	-	-	10.0	2.8
<i>P. pavonica</i>	-	10	10	6	8.7	2.3
<i>C. balearica</i>	4	10	6	0	5.0	4.2
<i>D. polypodioides</i>	0	11	0	0	2.8	5.5
<i>F. petiolata</i>	0	10	0	0	2.5	5.0
<i>H. filicina</i>	0	1	0	0	0.3	0.5

hours a day, while *H. filicina* requires more light and therefore has only one hour at saturation (Table 10).

In conclusion, photosynthetic responses of the studied Mediterranean algae display striking differences. Species show either “sun” and “shade” plant behaviours at low light levels, but oxygen production at high light levels and respiration seems to respond to other factors, such as thallus thickness or other environmental factors (i.e. nutrient availability). Some species (*D. fasciola*, *D. polypodioides*) show high production values in agreement with their high productivity and fast growth, while others (*Carpodesmia* spp.) show low production values but high biomass and durability. Thus, the rule seems to be the optimization rather than the maximization of the use of the light reaching every habitat; the species that dominates at each light level is the one that makes best use of the light environment, as suggested by Henley and Ramus (1989).

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