

The canopy-forming alga *Ericaria brachycarpa* (J.Agardh) Molinari-Nova & Guiry (Fucales, Phaeophyceae) shows seasonal and depth adaptation to the incoming light levels

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The canopy-forming alga *Ericaria brachycarpa* (J.Agardh) Molinari-Novoa & Guiry (Fucales, Phaeophyceae) shows seasonal and depth adaptation to the incoming light levels

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ABSTRACT

The shallow water canopy-forming alga *Ericaria brachycarpa* (J.Agardh) Molinari-Novoa & Guiry shows higher photosynthetic efficiency (α), maximum photosynthetic rates (P_{max}), light at compensation (I_c) and dark respiration (R_d) in individuals collected at the lower depth limit of distribution of the species (20 m) than at shallower depths (2 and 10 m). Photosynthesis at saturation light levels (P_{sat}) does not change in crossed transplants from 3 to 20 and from 20 to 3 m neither after 11 or 90 days. However, production at low light levels (P_b) increased in transplants from 3 to 20 m and decreased in transplants from 20 to 3 m after 90 days. Photosynthesis, both at high and low light levels increased from June to September. Seasonality explained most of the variance (70%) in the values of P_{sat} , whilst transplantation explained 47% of the variance for P_b and R_d . Thus, *E. brachycarpa* is able to adapt its photosynthetic performances across its depth distribution limits and easily cope with sudden variations in the light environment associated or not with seasonality.

KEY WORDS

Photosynthèse,
Ericaria brachycarpa,
depth,
adaptation,
primary productivity.

RÉSUMÉ

L'algue formant une canopée *Ericaria brachycarpa* (J.Agardh) Molinari-Novoa & Guiry (Fucales, Phaeophyceae) montre une adaptation à la profondeur et une adaptation saisonnière aux valeurs de lumière disponible. L'algue d'eau peu profonde formatrice de canopée *Ericaria brachycarpa* (J.Agardh) Molinari-Novoa & Guiry montre une majeure efficacité photosynthétique (α), photosynthèse maximale (P_{max}), lumière à la compensation (I_c) et respiration sombre (R_d) pour des individus collectés dans la limite la plus profonde de la bathymétrie de l'espèce (20 m) qu'à des profondeurs moindres (2 et 10 m). La photosynthèse en saturation (P_{sat}) ne change pas dans des transplants croisés entre 3 et 20 mètres après 11 ou 90 jours. Néanmoins, la production à une basse lumière (P_b) augmente dans les transplants de 3 à 20 m et diminue dans les transplants de 20 à 3 m 90 jours après la transplantation. La photosynthèse, tant pour les lumières hautes que pour les basses, augmente depuis juin à septembre. La variation saisonnière explique la plupart de la variance (70%) dans les données de P_{sat} tandis que la transplantation explique les 47% de la variance pour P_b and R_d . Ainsi, *E. brachycarpa* peut adapter ses performances photosynthétiques dans ses limites de distribution en profondeur et peut facilement faire face à des variations de lumière qui sont associés ou non aux conditions saisonnières.

MOTS CLÉS

Photosynthèse,
Ericaria brachycarpa,
profondeur,
adaptation,
productivité primaire.

INTRODUCTION

The photosynthetic response of aquatic macrophytes to the light intensity partially determines the habitats where they can thrive, together with other factors such as nutrient availability, hydrodynamism, environmental variability and biological interactions (Zabala & Ballesteros 1989; Witman & Dayton 2001; Vergés *et al.* 2009). Light intensity decreases with depth (Ballesteros & Zabala 1993; Kirk 1994) and determines the depth distribution limit of most aquatic macrophytes (Kirk 1994). Moreover, the depth distribution of aquatic macrophytes seems to be related to their photosynthetic features. According to Sant & Ballesteros (2020) deep-water species show higher photosynthesis at low light levels, higher photosynthesis at saturation, and lower light at compensation than shallow water species.

However, the results provided by Sant & Ballesteros (2020) are based on studies performed at the species level. No tests have been performed for specimens of the same species collected at their upper, medium and lower depth distribution ranges and thus we still do not know which is the ability of each species to adapt its photosynthetic features to its light environment. In the case that adaptation exists, a species should be able to adjust its photosynthetic system in the same way that is performed by the different species living at different depths, i.e. increasing both photosynthetic efficiency and maximum photosynthetic yields. If depth-related intraspecific differences occur, another question that remains opened is the time –days to weeks– that the photosynthetic system needs to readjust its properties according to the new light environment. This specially concerns perennial species in temperate ecosystems since the light environment not only changes with depth but also with season (Weinberg & Cortel-Breeman 1978; Ballesteros 1989).

In order to address these issues, here we 1) compare the photosynthetic features of specimens of the same species of macroalga living at different light levels; and 2) look at the adjustment of the photosynthesis/light patterns through time by transplanting specimens both from deep to shallow and from shallow to deep waters. These questions are also relevant in the frame of the rapid environmental changes that are being experienced in coastal areas subjected to different anthropogenic pressures, which reduce light transmittance in the water column.

MATERIAL AND METHODS

The selected species is *Ericaria brachycarpa* (J.Agardh) Molinari-Novoa & Guiry (Molinari-Novoa & Guiry 2020) [syn. *Cystoseira balearica* Sauvageau, *Carpodesmia brachycarpa* (J.Agardh) S. Orellana & M. Sansón], a perennial species with caespitose erect cauloids up to 15 cm long, covered by cylindric branches with some scattered spinose appendages (Cormaci *et al.* 2012; Rodríguez-Prieto *et al.* 2013). *Ericaria brachycarpa* is a species endemic to the Mediterranean, being present in the Western Mediterranean (Verlaque 1987; Hoff-

mann *et al.* 1992; Gómez-Garreta *et al.* 1994; Ribera *et al.* 1995; Sales & Ballesteros 2009; Thibaut *et al.* 2016) and the Aegean Sea (Huvé 1972; Montesanto & Panayotidis 2000; Cocito *et al.* 2000; Catra & Giardina 2009; Giakoumi *et al.* 2012; Taskin *et al.* 2012) but it seems to be absent on other Mediterranean areas like the Adriatic (Ercegovic 1952; Ivesa *et al.* 2016) or the Levantine Sea (Lakkis & Novel-Lakkis 2000; Einav & Israel 2008). *Ericaria brachycarpa* can make underwater forests which host a huge diversity of organisms (Coppejans & Boudouresque 1975; Verlaque 1987; Thiriet *et al.* 2016; Piazzzi *et al.* 2018) and have a high nursery value for some coastal fishes (Cheminée *et al.* 2013, 2017). These forests are mainly distributed in shallow environments, down to 20 m depth (Giaccone 1973; Verlaque 1987; Ballesteros *et al.* 2002; Sant 2003) and although the species is rather resistant to herbivory by fish (Vergés *et al.* 2009), it is highly consumed by the sea urchin *Paracentrotus lividus* (Lamarck, 1816) which can decrease its abundance and even create barrens (Verlaque 1987; Ballesteros *et al.* 2002; Thibaut *et al.* 2016; Piazzzi & Ceccherelli 2017). Although it is rather resilient (Piazzzi *et al.* 2017; Tamburello *et al.* 2019) the species is considered threatened by the Barcelona Convention (UNEP/MAP 2009; Verlaque *et al.* 2019).

Sampling site was located at Illa des Porros, an islet situated at the northernmost tip of Menorca (Balearic Islands, Western Mediterranean) (40°05'33"N, 4°04'39"E). The shallow area, between 2 and 15 m depth, is dominated by a forest of *E. brachycarpa*, with some specimens descending down to 22 m, where it grows mixed with other species in a community dominated by *Dictyopteris polypodioides* (A.P. De Candolle) J.V. Lamouroux.

Sampling was performed using SCUBA. Three depths were selected (3, 10 and 20 m) and the specimens collected to perform the experiments come from these depths. The abundance of *E. brachycarpa* was quantified by deploying fifty 25 cm × 25 cm quadrats divided into 25 subquadrats of 5 cm × 5 cm at each of the selected depths. The percentage of subquadrats in which *E. brachycarpa* appeared was recorded and used as a measure of occurrence (Sala & Ballesteros 1997; Tomas *et al.* 2011; Sant *et al.* 2017).

A first set of experiments was addressed to perform the photosynthesis/light intensity curves of individuals living at 3, 10 and 20 m depth, following procedures explained in Sant & Ballesteros (2020). These experiments were performed only in June. Specimens of *E. brachycarpa* were collected during late afternoon every day at each of the selected depths. Specimens were maintained overnight submerged at sea inside mesh bags and protected from direct light until next morning.

A second set of experiments involved the collection of 40 specimens of *E. brachycarpa*, 20 from 3 m and 20 from 20 m. Ten specimens of each depth were transplanted at the depth where they came from 3 to 3 (3to3) and 20 to 20 (20to20) and the other 10 were transplanted at the other depth [3 to 20 (3to20) and 20 to 3 (20to3)]. Transplantation took place at mid June. All specimens were transplanted the same day of collection and fixed again to the rock by means of a two-component non-toxic epoxy glue (IVEGOR®) (Cebrian

et al. 2006; Sales *et al.* 2011). The production of oxygen at saturation light levels (P_{sat}), production of oxygen at low light levels (P_b) and dark respiration (R_d) was measured for control specimens (non transplanted, nt3 and nt20) at the day of transplantation (0), 11 days after transplantation (11) and 90 days after transplantation (90). The same measures were performed for transplant controls and transplants at 11 (June) and 90 days after transplantation (September). Branches of the control and transplanted specimens were collected during late afternoon the day before the assays were performed, at each depth and maintained overnight submerged at sea inside mesh bags and protected from direct light until next morning.

Branches were sorted and prepared for photosynthesis and respiration assays in the early morning just before the experiments began (Sant & Ballesteros 2020). Material selection, manipulation and assays were performed according to the recommendations made by Littler (1979), Littler & Arnold (1980) and Littler & Littler (1985). Photosynthesis assays were performed in 270 mL glass bottles. Apical branches with a length of 2–3 cm were selected among the collected material, cleaned of macroepiphytes with small forceps, and introduced in the glass bottles containing seawater and a glass marble hanging inside the bottle and subjected with a nylon line. Only one to two branches were introduced at every bottle. The bottles with the algal specimens were hung in a structure hanging from a buoy and placed in the sea at Fornells Bay, nearby the sampling station, at 2 m depth. Waves moved the structure and the glass marbles shook the water inside the bottle, breaking diffusion gradients.

For the first set of experiments, four replicated bottles per depth (3, 10 and 20 m) and four empty bottles (to account for variation not due to macroalgae) were assayed every day at a different photon flux density (PFD) making a total of 16 assays per day. Nine 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 spherical sensor Li-1000 SPQA 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 2100 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$.

In the second set of experiments P_{sat} values were measured at mean PFDs of 1762 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ in June and 1243 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ in September, P_b values were estimated for mean PFDs of 119 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ in June and 106 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ in September. We also tested that the different incubation PFDs between the days of the experiment was low enough not to interfere significantly on the results (regression analysis, $p > 0.05$). R_d was measured as in the first set of experiments.

Incubation times ranged between 3 and 4 hours and assays were always performed between 10:00 am and 2:00 pm. Each branch was used only once, which made every assay independent from the others. Oxygen was measured after the assay with an Oxygen Analyzer Orbisphere 2607 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 four empty bottles. Specimens used in the assays were dried at 60°C for 48 hours to obtain their dry weight (DW) (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).

In the first set of experiments the data obtained in the assays was pooled together 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 have obtained the different 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 & Wiencke 1997), which allows comparisons within our data. The photosynthetic parameters finally obtained were dark respiration (R_d in $\text{mg O}_2 \cdot \text{gAFDW}^{-1} \cdot \text{h}^{-1}$), light at compensation (I_c in $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), photosynthetic efficiency [α in $\text{mg O}_2 \cdot \text{m}^2 \text{ s}^{-1} (\mu\text{mol photon} \cdot \text{gAFDW} \cdot \text{h})^{-1}$], light at saturation levels (I_k in $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and photosynthesis at saturation levels (P_{max} in $\text{mg O}_2 \cdot \text{gAFDW}^{-1} \cdot \text{h}^{-1}$).

Nutrient content in tissues was measured from specimens collected at the depths of 3, 10 and 20 m during the first set of experiments. 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 (Serveis Científic-Tècnics, University of Barcelona) and phosphorus was analysed with an inductively coupled plasma mass spectrometer (ICP) after acid digestion of the samples, following Mateo & Sabaté (1993).

Differences between P_{max} and R_d between depths were tested with a one-way ANOVA followed by a Tukey test. To compare the lineal part of the photosynthesis/PFD curves (α) a two-way (species and light) ANOVA followed by a Tukey test was used. Data was log-transformed in order to accomplish the assumptions of ANOVA. Relationships between parameters were estimated using Pearson lineal correlations.

Differences in P_{sat} and P_b were tested with ANOVA using factors “transplant” and “time”, where “transplant” is the kind of transplant applied and “time” is the length of the experiment in days. When there was a significant correlation between mean values and their variances, or data did not follow normality, data was transformed to accomplish ANOVA assumptions. When ANOVAs were significant ($p < 0.05$) means were compared using Tukey tests. Mean values of “transplant controls” were compared with controls (non transplanted specimens) from the same depth by means of t-Student tests. All statistical analysis were performed using SYSTAT® (SPSS Inc.).

RESULTS

The abundance of *E. brachycarpa* decreases with depth (Fig. 1), being dominant between 3 and 10 m and showing a low abundance at 20 m. The photosynthesis/PFD curves from

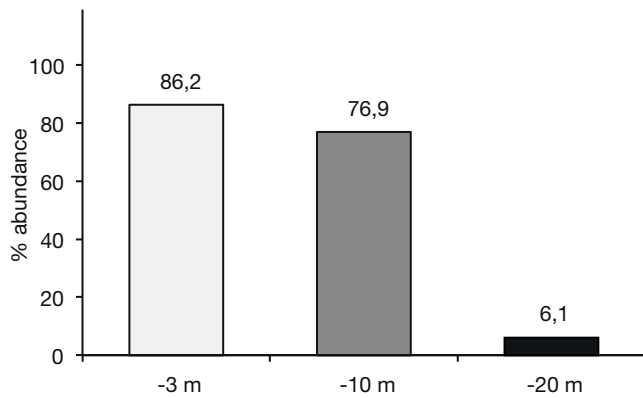


FIG. 1. — Percentage abundance of *Ericaria brachycarpa* (J. Agardh) Molinari-Novoa & Guiry at the sampling station estimated from 50 reticulated quadrats of 625 cm² per depth.

TABLE 1. — Lineal fitting of the initial part of every Photosynthesis/PFD curve (0 to 85 $\mu\text{mol photon m}^{-2}\text{s}^{-1}$) where α is the slope of the fitted line (= photosynthetic efficiency), and **interc.** is the intercept; $p < 0.001$ (***).

Depth	$\alpha \pm se$	interc. $\pm se$	R ²	n	F	p
-3 m	0.057 0.004	-0.87 0.20	0.92	20	205.4	***
-10 m	0.053 0.004	-0.74 0.17	0.92	18	183.1	***
-20 m	0.088 0.004	-1.77 0.22	0.96	20	423.7	***

TABLE 2. — Photosynthetic parameters (P_{max} : photosynthesis at saturation, in mg O₂-g AFDW⁻¹-h⁻¹, I_k : light at saturation, in $\mu\text{mol photon m}^{-2}\text{s}^{-1}$, I_c : light at compensation, in $\mu\text{mol photon m}^{-2}\text{s}^{-1}$, dark respiration (R_d), in mg O₂-g AFDW⁻¹-h⁻¹).

Depth	P_{max}	$\pm sd$	I_k	I_c	α	R_d	$\pm sd$
-3 m	6.24	1.33	124.3	15.2	0.057	0.50	0.11
-10 m	6.02	1.28	126.6	13.9	0.053	0.45	0.13
-20 m	7.65	1.50	107.2	20.1	0.088	1.00	0.14

TABLE 3. — Results of one-way ANOVAs (depth) variables P_{max} and R_d , the Tukey test for the variable P_{max} , and results of the two-way ANOVA (depth and light) and the Tukey test between species for the lineal part of the Photosynthesis/PFD curves (α). Abbreviations: **df**, degrees of freedom; **MS**, mean squares; **%var**, percentage of explained variance; **p**, signification level: non significant (ns), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

	factor	df	MS	%var.	F	p	depth	-3 m	-10 m	-20 m
P_{max}	depth	2	12.70	24.5	6.66**		-10 m	ns	-	
	error	41	1.91	75.5	-	-	-20 m	*	**	
	depth	2	0.96	77.2	5.37**		depth	-3 m	-10 m	-20 m
α	light	1	47.03	3.1	263.89***		-10 m	ns	-	
	interaction	2	1.34	4.4	7.51**		-20 m	*	*	
	error	52	0.18	15.2	-	-	-	-	-	-
R_d	depth	2	0.374	83.1	2296.00***		depth	-3 m	-10 m	-20 m
	error	9	0.016	16.9	13.40-		-10 m	ns	-	
		-	-	-	-	-	-20 m	**	***	

TABLE 4. — N:P, C:P and C:N ratios in algal (branch) tissues at different depths.

Depth	N:P	C:P	C:N
3	45.7	2533.1	55.6
10	36.2	1987.3	54.9
20	42.3	2595.2	61.4

specimens collected at 3 and 10 m are very similar and slightly different from specimens collected at 20 m (Fig. 2). The linear part of the P/PFD curves follows the same trend (Fig. 3), with a slightly steeper slope at 20 m. Photosynthetic efficiency (α) is higher in specimens living at 20 m than at 10 and 3 m (Table 1), while P_{max} , I_c and R_d are also higher (Table 2). Differences between 10 and 3 m are never significant, while differences between 20 and 10 or 3 m are always significant (Table 3). I_k is lower at 20 m than at 3 or 10 m (Table 2). N:P, C:N and C:P do not show any trend with depth (Table 4).

Regarding the transplant experiment we did not found significant differences between non-transplanted plants (controls nt3, nt20) and transplanted controls (3to3 and 20to20) ($p > 0.05$, t-Student). P_{sat} , P_b and R_d after 11 days and 90 days are presented in Fig. 4. Depth transplants (3to20 and 20to3) did not change significantly the P_{sat} after 11 days, not after 90 days (Fig. 4, Table 5). Depth transplants also did not significantly change the P_b after 11 days (Table 5) but P_b changed after 90 days, increasing for transplants from 3 to 20 and decreasing for transplants from 20 to 3 (Table 5). R_d did not change after 90 days but differences were significant between transplants 3to20 and 20to3 after 11 days (Table 5).

In general, photosynthesis (both at high and low light levels) and dark respiration increased from June to September (Fig. 4). Differences of P_{sat} between June and September were very important, explaining almost 70% of total variance for only 12.5% of variance associated to transplantation effects (Table 6). In contrast, the effect of transplantation explains 47% of total variance for P_b and R_d whilst seasonality only accounts for 11-13% (Table 6).

DISCUSSION

Specimens of *E. brachycarpa* living at 20 m show an adaptation to depth by increasing photosynthesis at saturation, light at compensation, and photosynthetic efficiency and by decreasing light at saturation. So, they are more efficient at using low light levels, require lower light levels to saturate photosynthesis, and reach higher photosynthetic rates if exposed to high light intensities. These patterns are exactly the same than those described by Sant & Ballesteros (2020) when dealing with a wide range of aquatic macrophytes distributed along a bathymetric gradient. The increase in α is typical of macrophytes adapted to survive at low light conditions (Kirk 1994; Lobban & Harrison 1994; Taiz & Zeiger 1998) but this is not the case at 20 m in the Balearic islands where there is still plenty of light (Ballesteros & Zabala 1993). The increase in P_{max} should be also related to the general positive relationship between α and P_{max} described by Sant & Ballesteros (2020) for Mediterranean macroalgae, meaning that there is a general pattern of adaptation to low light environments or decreasing light levels that spans at different taxonomical (across orders, families, genera and species) and population (within the same species) scales. This situation contrasts with results obtained when measuring photosynthetic features of blades of the same specimen of *Macrocystis pyrifera* (Linnaeus) C. Agardh distrib-

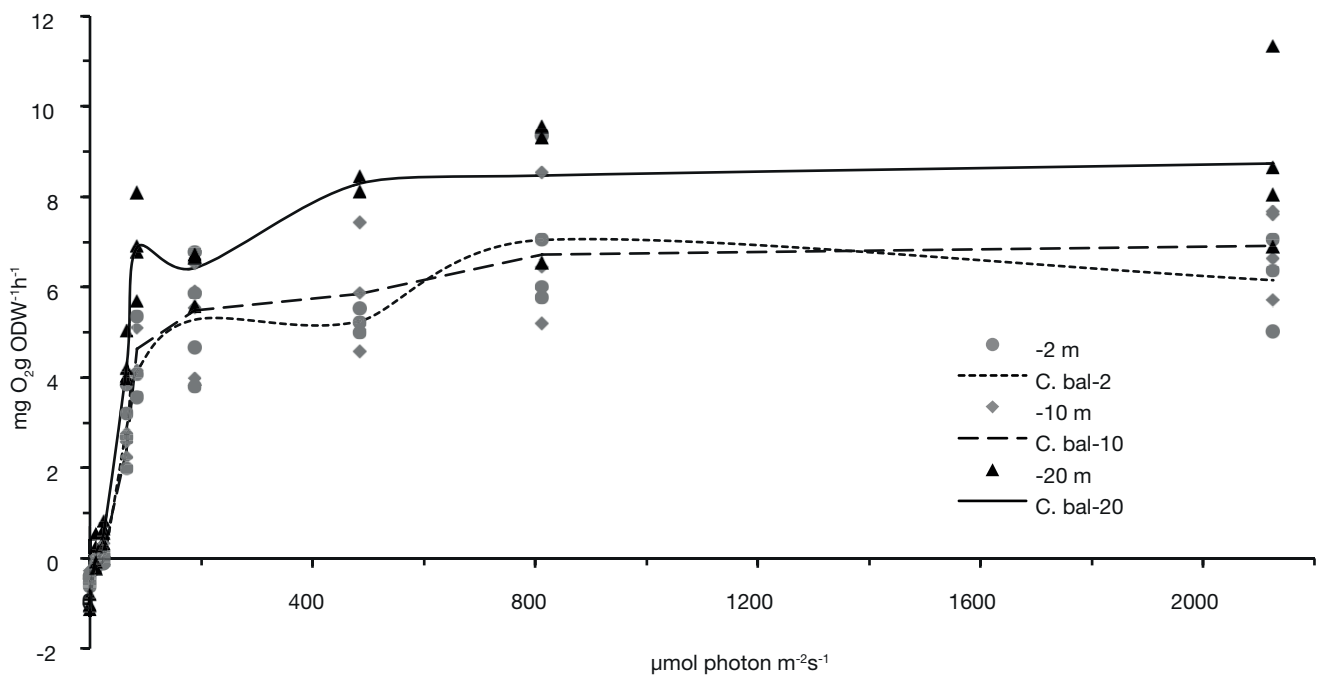


FIG. 2. — Photosynthesis/PFD curves for algal specimens collected at different depths.

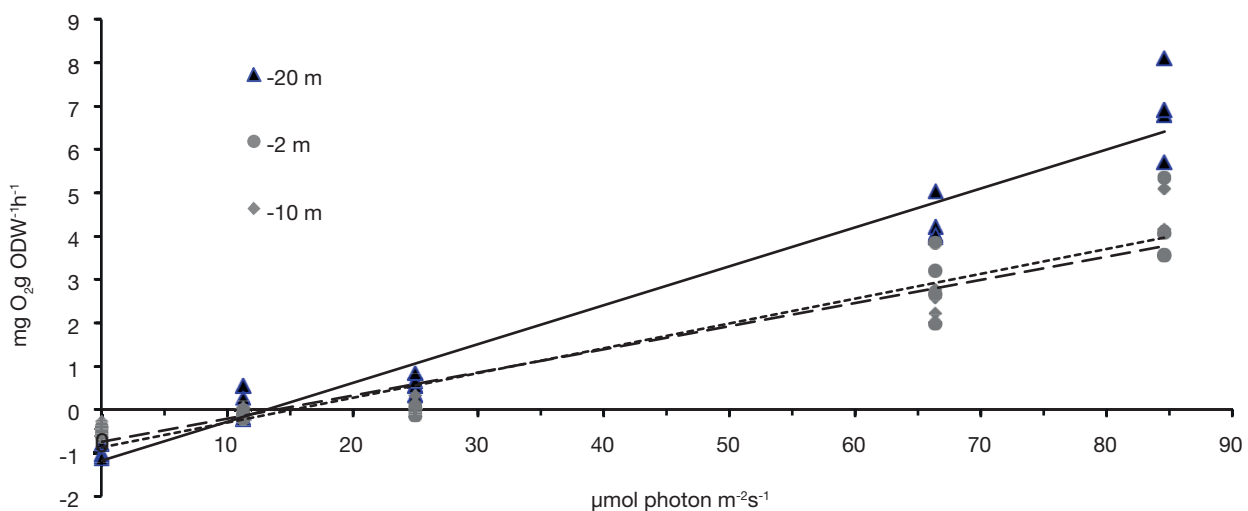


FIG. 3. — Lineal fitting of the photosynthesis/PFD data at the lineal part of the P/PFD curve for the algal specimens collected at different depths.

uted along a depth gradient (Colombo-Pallotta *et al.* 2006) where $P_{\max}$ decreases with depth but still this can be perhaps explained by the high capacity of photoassimilates translocation of this species across the same individual (Parker 1963; Fox 2013), which does not occur when dealing with different individuals. Moreover Sant & Ballesteros (2020) suggested that the higher $P_{\max}$ and α found in deep-water species could be related to a higher nutrient content in tissues but here we do not find any outstanding differences between C:N, N:P or C:P ratios between depths, meaning that nutrients should not be as important as thought. This is consistent with the

nutrient homogeneity found in waters above the thermocline, which is situated around 30 to 35 m depth in the Balearic islands (Ballesteros & Zabala 1993).

Transplant experiments show that when specimens are transplanted from shallow to deep waters there is an increase in P_b after 90 days but not in P_{sat} . Ramus *et al.* (1977) showed how *Fucus vesiculosus* Linnaeus and *Ascophyllum nodosum* (Linnaeus) Le Jolis increased both $P_{\max}$ and α when transplanted at deeper environments and suggested that the macroalgae increase photosynthetic pigments but also the number of photosynthetic units (PSU; Ramus *et al.* 1977). Since there

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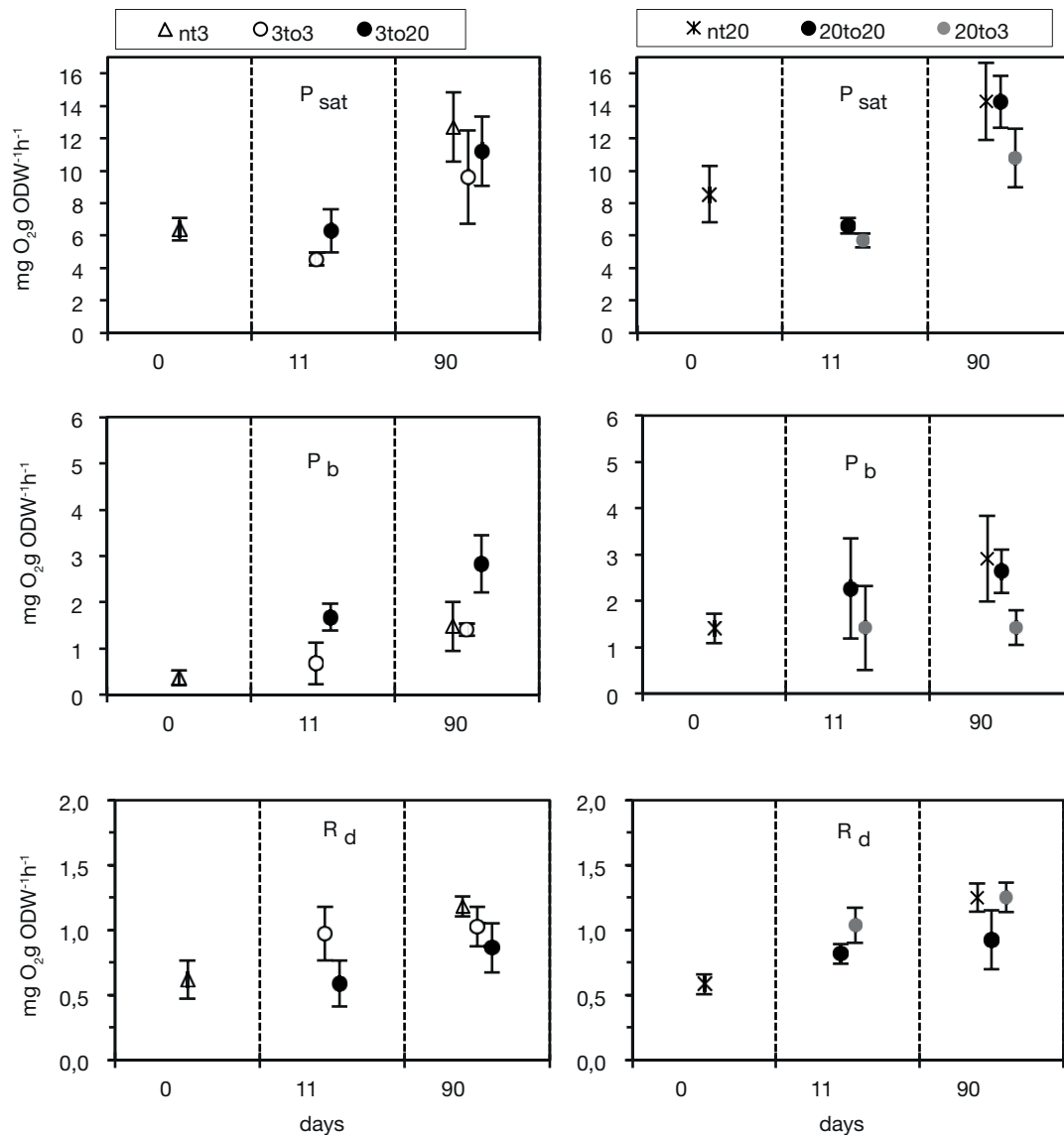


FIG. 4. — Photosynthesis at saturation (P_{sat}), photosynthesis at low light levels (P_b) and dark respiration (R_d) for specimens thriving at 3 and 20 m (not transplanted: nt3 and nt20) and for those transplanted at the same depth (3to3 and 20to20) and at different depths (3to20 and 20to3) after 11 and 90 days after transplantation.

is no increase in P_{sat} in our experiments we suggest that *E. brachycarpa* is probably only increasing pigments and no PSU, which are needed to achieve higher photosynthetic rates at high light levels. Unfortunately we did not measure pigment concentrations and thus we do not have a response for this hypothesis. In fact, the increase of P_{sat} also involves changes in enzymes related to carboxylation mechanisms (Boardman 1977; Gerard 1988; Littler & Littler 1992), which probably need longer time periods and are related to N availability (Ramus 1983; Peckol & Ramus 1988).

Regarding transplants from deep to shallow waters, there is a decrease in P_b after 90 days, which is consistent with the increase of P_b reported before, when specimens were transplanted from shallow to deep waters. This means that photo-

synthesis at low light levels, and hence α , easily responds to changes in the light environment in such a way that individuals can use more efficiently the available light.

Another interesting result of the transplant experiment is the seasonal changes observed in both P_{sat} and P_b , as well as in dark respiration, which are always higher than the changes observed in depth transplants. As in other temperate seas, the light environment changes seasonally in the Mediterranean (Ballesteros 1992; Ballesteros & Zabala 1993) and macroalgal physiology responds to this variation. In fact, Sant & Ballesteros (2020) reported a seasonal increase in P_{max} and α from spring to autumn, which is consistent with our measures and with the light intensity decrease from June to September in the Mediterranean (Weinberg & Cortel-Breeman 1978; Bal-

TABLE 5. — Above: Results of one-way ANOVAs for variables photosynthesis at saturation (P_{sat}), photosynthesis at low light levels (P_b) and dark respiration (R_d) after 11 and 90 days after transplant. Abbreviations: **df**, degrees of freedom; **MS**, mean squares; **%var.**, percentage of explained variance; **p**, signification level. Below: Comparison (Tukey test) between transplants for each of the significant ANOVAs (*, above): non significant (ns), $p < 0.05$ (*).

	11 days	df	MS	%var.	F	p		90 days	df	MS	%var.	F	p
P _{sat}	transplant	3	2.46	61.2	4.21	0.046*		transplant	3	11.75	48.5	2.51	0.132
	error	8	0.58	38.8	—	—		error	8	4.68	51.5	—	—
P _b	transplant	3	1.31	46.1	2.28	0.156		transplant	3	1.74	77.3	9.10	0.006*
	error	8	0.57	53.9	—	—		error	8	0.19	22.7	—	—
R _d	transplant	3	0.12	64.5	4.85	0.033*		transplant	3	0.09	51.5	2.83	0.106
	error	8	0.03	35.5	—	—		error	8	0.03	48.5	—	—
P _{sat}	transplant	—	3to3	3to20	20to3	—	P _b	transplant	—	3to3	3to20	20to3	—
	3to20	—	ns	—	—	—		3to20	—	*	—	—	—
	20to3	—	ns	ns	—	—		20to3	—	ns	*	—	—
	20to20	—	*	ns	ns	—		20to20	—	*	ns	*	—
R _d	transplant	—	3to3	3to20	—	—							
	3to20	—	ns	—	—	—							
	20to3	—	ns	*	20to3	—							
	20to20	—	ns	ns	ns	—							

lesteros 1992). Similar increases in maximum quantum yields in months with lower radiation levels have been found in the bull kelp, *Durvillaea antarctica* (Chamisso) Hariot (Tala *et al.* 2019). Another factor that could explain the seasonal differences in P_{max} and α is the temperature that is known to affect photosynthesis in members of the order Fucales (Stengel & Dring 1998; Murakami *et al.* 2004; Terada *et al.* 2018). In September, water temperature above the thermocline is 5°C higher than in June (Ballesteros & Zabala 1993) but there is no data in the photosynthetic response of *E. brachycarpa* to temperature and thus, no conclusion can be drawn. Nevertheless, all the data obtained in this study and that provided by Sant & Ballesteros (2020) points to the same direction: whenever there is a decrease in the amount of light -usually related to depth but also to season- Mediterranean algae respond by increasing photosynthetic efficiency and (usually) photosynthesis at saturation, as well as decreasing light at compensation. This means that the adaptation to the light environment of a population of macroalgae, in particular *E. brachycarpa*, depends both on depth and season. The plasticity of *E. brachycarpa* to adapt to the light environment suggests that the species can cope with small decreases in water transparency due to anthropogenic pressures such as sediment resuspension or chlorophyll increase in the water column related to nutrient uploads.

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TABLE 6. — Results of the two-way ANOVAs for variables P_{sat} , P_b and R_d considering factors “time” and “transplant”. Abbreviations: **df**, degrees of freedom; **MS**, mean squares; **%var.**, percentage of explained variance; **p**, signification level: non significant (ns), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). P_{sat} , P_b and R_d as in Table 5.

	factor	df	MS	%var.	F	p
P_{sat}	time	1	193.4	69.5	73.54	***
	transplant	3	11.6	12.5	4.41	*
	interaction	3	2.6	2.8	1.00	ns
	error	16	2.6	15.1	—	—
P_b	time	1	1.89	11.0	4.93	*
	transplant	3	2.69	47.0	7.03	**
	interaction	3	0.36	6.3	0.95	ns
	error	16	0.38	35.7	—	—
R_d	time	1	0.16	12.9	5.71	*
	transplant	3	0.19	47.0	6.90	**
	interaction	3	0.02	3.8	0.56	ns
	error	16	0.03	36.3	—	—

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