

Title:

**Depth distribution of canopy-forming algae of the order Fucales is related to their photosynthetic features.**

Running title: Photosynthesis and depth patterns in Fucales

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#### DATA AVAILABILITY STATEMENT

The data that support the results of this study are available from the corresponding author upon request.

#### ABSTRACT

Photosynthetic features and dark respiration of different species of dominant canopy-forming algae of the Order Fucales (Phaeophyceae) consistently change with depth. Photosynthetic efficiency ( $\alpha$ ) and light at compensation ( $I_c$ ) change according to the amount of light available at each depth,  $\alpha$  increasing and  $I_c$  decreasing with depth. However, the values of light at saturation ( $I_k$ ) do not show any depth pattern. Deep-water species show higher photosynthesis at saturation ( $P_{max}$ ) and lower dark respiration ( $R_d$ ) than shallow water ones. This result contrasts with the expected reduction of  $P_{max}$  in low light environments shown by terrestrial plants but is consistent with other studies

performed in macroalgae, suggesting that  $P_{\max}$  and  $\alpha$  show the same trend of variation in the marine environment. The positive correlation between  $P_{\max}$  and  $\alpha$  cannot be explained by differences in thickness as all tested species show an extremely high morphological similarity. The increase in  $P_{\max}$  with depth is also coupled to an increase of N and P content in branches, which points to nutrient-limited photosynthesis in shallow water species.

Keywords: macroalgae, photosynthesis, Fucales, *Cystoseira*, depth, light

## INTRODUCTION

The distribution of aquatic macrophytes depends on some environmental factors that are depth-dependent such as light intensity, hydrodynamism, nutrient availability and biological interactions (Zabala & Ballesteros, 1989; Witman & Dayton, 2001; Vergés et al., 2009). In particular, light intensity shows a sharp decrease with depth (Ballesteros & Zabala, 1993), which is critical for the growth of photosynthetic organisms and controls the deepest limit of aquatic macrophytes (Dennison, 1987; Kirk, 1994). Therefore, the capacity of water to absorb photosynthetic active radiation (PAR) determines the maximum depth of macrophyte growth in a water body (Kirk, 1994). At the species level, both physiological and morphological features control the performance of the individuals at different light intensities (Sant & Ballesteros, 2020).

Although well studied and well known for the littoral and intertidal zone (Ballesteros & Romero, 1988; Martins et al., 2008; Chappuis et al., 2014), vertical zonation is also present in the subtidal zone (Logan et al., 1984; Dring, 1986; Kirk, 1994), where the abundance of a certain macrophyte at a certain depth depends on the balance between biomass production and loss, together with the ability to outcompete or tolerate other species (Airoldi, 2000). Henley & Ramus (1989) suggested that the species dominating at a certain depth are the ones that make the better use of the light environment. Sant & Ballesteros (2020) collected different species distributed across a depth gradient and found that photosynthetic efficiency depended on the light level (higher efficiency at lower light levels) but that oxygen production at saturation and respiration did not directly respond to the light level but to other factors such as thallus thickness or nutrient availability, as already shown by Arnold & Murray (1980), Littler (1980) and Lüning & Dring (1985). Thus, when transferred to the marine realm, the features

characteristic of sun and shade terrestrial plants (Boardman, 1977; Field, 1988) seem to agree in the response to low light levels (high photosynthetic efficiency of plants at low light levels and low photosynthetic efficiency of plants at high light levels) but not to high light levels (lack of a negative correlation between maximum photosynthetic rates and light levels) (Sant & Ballesteros, 2020).

Species of canopy-forming brown algae of the order Fucales can be abundant in shallow Mediterranean environments subjected to low anthropogenic pressures (Sauvageau, 1912; Feldmann, 1937; Giaccone & Bruni, 1973; Sales & Ballesteros, 2009). They provide refuge and food for several fish and invertebrates, maintain complex food webs and support a high biodiversity (Chemello & Milazzo, 2002; Cheminée et al., 2013; Gianni et al., 2013). Most Mediterranean representatives of the order Fucales belong to the genera *Cystoseira* C. Agardh, *Gongolaria* Boehmer and *Ericaria* Stackhouse (Molinari-Novoa & Guiry, 2020). Even if there is a large amount of studies dealing with the taxonomy of these Mediterranean species (e.g. Sauvageau, 1912; Ercegovic, 1952; Giaccone & Bruni, 1973; Roberts, 1978; Amico et al., 1985; Cormaci et al., 2012), the communities they constitute (e.g. Boudouresque, 1969, 1971a, 1972; Verlaque, 1987; Ballesteros, 1988, 1990a, b; Ballesteros et al., 1998; Sales & Ballesteros, 2010, 2012; Sales et al., 2012), their dynamics and phenology (Hoffmann et al., 1992; Serio 1995a, b; Pizzuto, 1999; Falace et al., 2005; Falace & Bressan, 2006; Ballesteros et al., 2009; a et al., 2014, 2016a; Capdevila et al., 2016; Savonitto et al., 2019; Blanfuné et al., 2019), their decline (e.g. Cormaci & Furnari, 1999; Thibaut et al., 2005, 2015; Bianchi et al., 2014; Catra et al., 2019; Mariani et al., 2019), their vulnerability to pollution (e.g. Munda, 1993; Soltan et al., 2001; Arévalo et al., 2007; Sales et al., 2011; Pinedo et al., 2013; Ivesa et al., 2016), grazing (Vergés et al., 2009; Bonaviri et al., 2011; Sala et al., 2011; Vergés et al., 2014; Agnetta et al., 2015) or warming (Celis-Plá et al., 2017a; Capdevila et al., 2019), as well as on information about measures to improve their conservation (Verdura et al., 2018; De la Fuente et al., 2019; Medrano et al., 2020), very few studies have been devoted to their photosynthetic features (Coudret & Jupin, 1985; Tremblin et al., 1986; Delgado et al., 1995; Celis-Plá et al., 2017b) and none has addressed the light-related ecophysiological features that explain their bathymetric distribution.

In this study we aim at explaining the depth distribution of several, morphologically similar, canopy-forming species of the order Fucales (genera *Ericaria*, *Cystoseira* and *Gongolaria*) living across a bathymetric gradient by looking at their photosynthetic features when experimentally subjected to different light environments. In particular, we want to assess if those species living in shallow waters display low photosynthetic efficiencies but high photosynthetic rates at light saturation levels as expected in “terrestrial sun plants”, and if species living in deep waters show high photosynthetic efficiencies and low photosynthetic rates at light saturation levels as expected in “terrestrial shade plants”. Because dissolved nutrients in seawater increase with depth in coastal Mediterranean shallow waters and nutrients have been claimed as a limiting factor for photosynthesis and growth in Mediterranean macroalgae (Ballesteros, 1992; Delgado et al., 1994), we also measure carbon, nitrogen and phosphorus content in tissue samples.

## MATERIALS AND METHODS

Sampling site was situated in Garganellu (42°21'53''N, 8°32'23''E), a small islet within the Scandola Marine Protected Area (Parc Naturel Régional de Corse, Corsica, western Mediterranean). The southern rocky slope of the Garganellu islet smoothly descends to 50 meters, where it is replaced into a rhodolith bed. Canopy-forming algae of the order Fucales dominate the seascape from 0 to 45 meters depth, with different species replacing each other along the bathymetric gradient (Ballesteros et al. 1998, 2002, 2009). Water temperature in surface waters ranges from 12-13°C in winter to 23-25°C in summer, with constant salinity values around 38 ppt (Verlaque, 1987). A light attenuation curve from +0 to -50 m depth was measured using a spherical quantum sensor Li-1000 SPQA deployed at the southern site of Garganellu islet at 12:00 am of a sunny day at the beginning of May. The light attenuation coefficient obtained was 0.078. Thus, the light gradient through which the different species are distributed range from 90% (at -0.1 m) to 2.71% (at -45 m) of the light reaching the surface (Fig. 1).

Methods mostly follow those described in Sant & Ballesteros (2020). Sampling was performed between 30<sup>th</sup> April and 15<sup>th</sup> May, when the Mediterranean members of the order Fucales show their maximum development and growth (Sauvageau, 1912; Feldmann, 1937; Ballesteros, 1992). The distribution of the canopy-forming Fucales along depth was quantified by means of 25 cm x 25 cm quadrats divided into 25

subquadrats of 5 cm x 5 cm. Twenty quadrats were positioned haphazardly at five meters depth intervals, from 0 to 45 meters using SCUBA. The percentage of subquadrats in which a species appeared was recorded and used as a measure of occurrence. Only canopy-forming members of the order Fucales were considered, disregarding other macroalgae. A highly abundant species that appeared in all 25 subquadrats would produce a presence of 100%, whereas a total lack of a species would produce a presence of 0% (Sala & 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 (Sant & Ballesteros, 2020). Species showing an abundance >15% at some depth interval were selected for photosynthetic assays.

Collection of specimens was performed using SCUBA. Specimens of the selected species were collected during late afternoon every day at the depth showing their highest abundance. Specimens were maintained overnight submerged at sea inside mesh bags and protected from direct light until next morning. Specimens 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 epiphytes and introduced in the 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 Galeria Bay, nearby the sampling station, at 2 m depth. Different photon flux densities (PFDs) were obtained by covering the structure with a different number of neutral filters, using a black filter to measure dark respiration. We did not make the assays at different depths due to its logistic complexity. Waves moved the structure and the glass marbles shook the water inside the bottle, breaking diffusion gradients. Four replicates per species 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 24 assays per day. Nine different PFDs were assayed. 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 2000  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ . Incubation times ranged between 3 and 4 hours and assays were always performed between 10:00 am and 2:00 pm. Each specimen 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, 1971b; 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 have obtained the different photosynthetic parameters directly based on photosynthesis at saturation levels ( $P_{\text{max}}$ ) and variation of photosynthesis at low light levels (photosynthetic efficiency,  $\alpha$ ) (Arenas et al., 1995; Gómez et al., 1996; Gómez & Wiencke, 1997), which allows comparisons within our data (Sant & Ballesteros, 2020). The photosynthetic parameters finally obtained were dark respiration ( $R_d$  in  $\text{mg O}_2 \cdot \text{gAFDW}^{-1} \cdot \text{h}^{-1}$ ), light compensation point ( $I_c$  in  $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ), photosynthetic efficiency [ $\alpha$  in  $\text{mg O}_2 \cdot \text{m}^2 \text{ s} (\mu\text{mol photon} \cdot \text{gAFDW} \cdot \text{h})^{-1}$ ], light at saturation levels ( $I_k$  in  $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ), and photosynthesis at saturation levels ( $P_{\text{max}}$  in  $\text{mg O}_2 \cdot \text{gAFDW}^{-1} \cdot \text{h}^{-1}$ ) (Fig. 2).

Nutrient content in tissues for each species was measured 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 (Serveis 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 & Sabaté (1993).

Differences between  $P_{\max}$  and  $R_d$  between species were tested with a one-way ANOVA followed by a Tukey test. To compare the lineal part of the photosynthesis/PFD curves ( $\alpha$ ) 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.

## RESULTS

Up to ten species of Fucales were recorded in the southern rocky slope of Garganellu, although one (*Sargassum vulgare*) was not quantified because it did not form canopy. The canopy-forming taxa were identified as *Ericaria amentacea* var. *stricta* (hereinafter *E. amentacea*), *Cystoseira compressa* var. *pustulata*, *Ericaria brachycarpa* var. *balearica* (hereinafter *C. brachycarpa*), *Gongolaria jabukae*, *Cystoseira foeniculacea*, *Ericaria funkii* (*sensu* Verlaque et al., 1999), *Gongolaria usneoides*, *Ericaria montagnei* var. *compressa* (hereinafter *G. montagnei*) and *Ericaria zosteroides*. Their bathymetric distribution in the southern slope of Garganellu islet is presented in Fig. 3. Four different habitats or assemblages were distinguished according to the dominant species: the assemblage of *E. amentacea*, from 0.1 to 0.4 m depth, the assemblage of *E. brachycarpa*, from 5 to 20 m depth, the assemblage of *G. montagnei*, from 20 to 40 m depth, and the assemblage of *E. zosteroides* below 40 m depth. These four species, together with *E. funkii*, rather abundant in the assemblage of *G. montagnei*, were selected to perform the photosynthetic assays. The species of Fucales suddenly vanished at 50 m depth, where the habitat turned into a coralligenous outcrop and a rhodolith bed (Ballesteros, 2006).

Interspecific differences in the P/PFD curves were important, with *Ericaria funkii* and *Ericaria zosteroides* showing the highest production at high light levels, *Ericaria amentacea* and *Ericaria brachycarpa* displaying the lowest production at high light levels, and *Gongolaria montagnei* showing intermediate values (Fig. 4). The lineal part of the P/PFD curves is depicted in Fig. 5 and here too the species showing the highest, lowest and intermediate slopes are ranked in a similar way than in Fig. 4, with *E. zosteroides* showing the highest slope, *E. funkii* and *G. montagnei* showing intermediate values and *E. amentacea* and *E. brachycarpa* showing the lowest slope.

When comparing the photosynthetic parameters (Tables 1, 2), the shallowest species (*Ericaria amentacea*, *Ericaria brachycarpa*) showed the lowest values of  $P_{\max}$  and photosynthetic efficiency ( $P_{\max} < 6.5 \text{ mg O}_2 \text{ gAFDW}^{-1} \text{ h}^{-1}$ ;  $\alpha < 0.050 \text{ mg O}_2 \text{ m}^2 \text{ s} (\mu\text{mol photon gAFDW h}^{-1})^{-1}$ ), while *Ericaria funkii* and *Ericaria zosteroides*, showed values significantly higher both of  $P_{\max}$  ( $> 14.0 \text{ mg O}_2 \text{ gAFDW}^{-1} \text{ h}^{-1}$ ), and  $\alpha$  ( $> 0.080 \text{ mg O}_2 \text{ m}^2 \text{ s} (\mu\text{mol photon gAFDW h}^{-1})^{-1}$ ). *Gongolaria montagnei*, with a  $P_{\max}$  of 9.2 and  $\alpha$  of 0.065, showed intermediate values and significantly different from the other species (Table 3). Light at compensation ( $I_c$ ) were usually low, always below  $16.0 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$  (table 1), and changed inversely to  $P_{\max}$  and  $\alpha$ . *E. zosteroides* was the species with the lowest light requirements to reach a net positive production ( $I_c = 3.1$ ); *E. amentacea* and *E. brachycarpa* showed the highest  $I_c$  ( $> 13.0$ ). Regarding the light at saturation ( $I_k$ ), again *E. zosteroides* showed the lowest value ( $I_k = 121$ ) (Table 1). Although *E. amentacea* showed the shallowest distribution, its oxygen production reached saturation levels at  $I_k = 135$ , a light intensity that was lower than species living deeper such as *E. brachycarpa*, *G. montagnei* or *E. funkii* (with values of  $I_k$  of 217, 180 and  $153 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ , respectively).

Dark respiration ( $R_d$ ) was always low, *Ericaria zosteroides* showing again the lowest values ( $R_d = 0.46$ ) and *Ericaria amentacea* showing the highest values ( $R_d = 0.76$ ) (Table 1). However, differences were not significant (ANOVA, table 3). In general, the proportion between respiration and  $P_{\max}$  decreased from the shallowest to the deepest species (Table 1).

Carbon content in branches ranged between 26.7% (*Ericaria zosteroides*) and 36.8% (*Ericaria brachycarpa*) (Table 4). *E. zosteroides* showed the highest values of nitrogen and phosphorous (with  $N = 1.8\%$  and  $P = 0.095\%$ ), followed by *Ericaria funkii* ( $N = 1.2\%$  and  $P = 0.071\%$ ), while the lowest values corresponded to *Ericaria amentacea*, with  $N = 0.9\%$  and  $P = 0.034\%$  (table 4). *E. brachycarpa* and *Gongolaria montagnei* showed intermediate values. Atomic ratios C:N, C:P and N:P tended to decrease from the shallowest to the deepest species (Fig. 6). For instance, *E. amentacea* showed the highest ratios (C:N = 43.7; C:P = 2560; N:P = 58.7), followed by *E. brachycarpa* (C:N = 41.7; C:P = 2240; N:P = 53.7). The lowest ratios corresponded to

*E. zosteroides* (C:N = 16.9; C:P = 728; N:P = 43.0) and *C. funkii* (C:N = 30.7; C:P = 1116; N:P = 36.4).

## DISCUSSION

Depth distribution of the species of Fucales studied here follows the bathymetric distribution patterns already known from other Mediterranean localities (Feldmann, 1937; Giaccone, 1973; Giaccone & Bruni, 1973). The different species also show important differences regarding their photosynthetic performances. The response of photosynthesis to low light levels differs between species thriving in shallow and deep environments, which explains the already well known depth and light-related distribution of the species of the order Fucales in the Mediterranean (Giaccone, 1973). Deep water species -*Ericaria zosteroides*, *Ericaria funkii* and *Gongolaria montagnei*-, with high photosynthetic efficiencies and low respiration rates show features of “shade plants”, while shallow water species -*Ericaria amentacea*, *Ericaria brachycarpa*-, with low photosynthetic efficiencies and high respiration rates, show features of “sun plants”. Light at compensation is also lower in deep-water species ( $I_c < 11.0 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ) than in shallow water species ( $I_c > 13.0 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ). These features follow the same trends found in a similar study using algae with contrasting morphologies along a bathymetric gradient (Sant & Ballesteros, 2020), suggesting the existence of morphology-independent patterns of adaptation to low light intensity. In contrast, light at compensation ( $I_k$ ) does not show the same pattern -contrary to results from Sant & Ballesteros (2020)-, which could be related to the similarity in morphology and pigment content of the species studied here. Indeed, light at saturation ( $I_k$ ) is thought to indicate the transition zone between the photochemical and the enzymatic-regulated processes related with carbon assimilation (Henley, 1993). Thus, for the species studied here, this transition occurs at a similar range of light levels, and seems to be more conditioned by a similar physiological optimization rather than by the environmental light differences between habitats.

Photosynthetic responses at high light levels also depend on the light environment, with the species thriving in deep waters showing the highest photosynthetic rates at high light levels and no photoinhibition. Thus, species showing the highest efficiency rates

( $\alpha$ ) also show the highest  $P_{\max}$ , mimicking the results obtained by Sant & Ballesteros (2020). Species with a thick thallus or a high amount of organic carbon per square cm<sup>2</sup> can show a positive relationship between  $\alpha$  and  $P_{\max}$  (Arnold & Murray, 1980; Enríquez et al., 1995, 1996; Weykam et al., 1996; Collado-Vives & Robledo, 1999). Models showing positive relationships between photosynthetic rates and thallus thickness, even if they are valid when faced up to a wide range of morpho-functional features, do not explain the differences found in our case, where the studied species show similar thallus thickness and morphology. So, we show here that the photosynthetic features found in the same morpho-functional group of algae [thick-leathery morpho-functional group of Littler & Littler (1980)], even in species highly related taxonomically (order Fucales), can be very different and should be related to physiological adaptations to the light environment.

The species with higher nutrient content in tissues -*Ericaria zosteroides* and to a lower degree *Ericaria funkii*- are those showing a higher photosynthetic rate, in agreement with data provided by Sant & Ballesteros (2020). Both *Ericaria amentacea* and *Ericaria brachycarpa* show a low nutrient content and a lower photosynthetic rate, also in agreement with results from Sant & Ballesteros (2020). The highest availability of nitrogen with depth (Ballesteros, 1992) is probably an explanation for the highest photosynthetic rates of deep-water species, although transplant experiments are needed to properly test it.

*Ericaria zosteroides* is clearly adapted to live in deep waters. Besides its good nutritional state, it has a very reduced dark respiration in relation to its  $P_{\max}$ , an essential requirement to grow at light environments situated below 3% of subsurface light levels (Delgado et al., 1995). *Ericaria zosteroides* also has the possibility to remove carbohydrates from the tophules -vesicles situated at the beginning of the primary branches- to the apical parts (Combaut et al., 1976), which means that it can maintain a positive grow of the branches even in periods when light levels are around the compensation point (Ballesteros, 1990b). The tophules of *Ericaria funkii* and *Gongolaria montagnei* could probably play the same role.

Testing the robustness of the photosynthetic parameters examined here at a regional scale needs the performance of the same experiments at different localities covering the geographical extension range of every species. Here we are able to compare the

photosynthetic parameters of *Ericaria amentacea* and *Ericaria brachycarpa* between Corsica (this study) and Cabrera (Balearic Islands) (Sant & Ballesteros, 2020) that are distant 3° latitude and 5° longitude.  $P_{max}$ ,  $\alpha$ , and  $I_c$  are very similar and definitely very different from the values obtained for deep-water species like *Ericaria zosteroides* and *Ericaria funkii*. These results, together with the same variation pattern of photosynthetic parameters obtained by Sant & Ballesteros (2020) for morphologically different algae, suggest a strong relationship between the photosynthetic features of macroalgae and depth, which differ from those known from terrestrial plants, with  $P_{max}$  being positively correlated with  $\alpha$ .

At present, populations of several species of the order Fucales are seriously threatened in several Mediterranean areas (Thibaut et al., 2005; Bianchi et al., 2014; Thibaut et al., 2015, 2016b; Blanfuné et al., 2016; Gatti et al., 2017; Catra et al., 2019; Mariani et al., 2019) and restoration actions are being considered as a tool to recover both populations and their habitats (Gianni et al., 2013; Verdura et al., 2018; De la Fuente et al., 2019). Even if the main aim of this study was to explain the distribution patterns with depth of the species of Fucales, our results also provide interesting outputs regarding the selection of species in restoration actions, according to the light environment of the places to be restored.

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Species	$\alpha \pm se$		interc. $\pm se$		$R^2$	$n$	$F$	$p$
<i>E. amentacea</i> (-0 m)	0.045	0.002	-0.70	0.09	0.98	20	746.4	***
<i>E. brachycarpa</i> (-10 m)	0.031	0.003	-0.41	0.15	0.86	20	121.8	***
<i>G. montagnei</i> (-25 m)	0.065	0.005	-0.69	0.25	0.92	20	206.9	***
<i>E. funkii</i> (-25 m)	0.089	0.006	-0.82	0.31	0.93	20	245.6	***
<i>E. zosteroides</i> (-45 m)	0.121	0.004	-0.37	0.19	0.98	20	1191	***

Table 1.- Lineal fitting of the initial part of every PFD/photosynthesis curve (0 to 105  $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) where  $\alpha$  is the slope of the fitted line (=photosynthetic efficiency), and interc. is the intercept;  $p < 0.001$  (\*\*\*).

Species	$P_{max} \pm sd$		$I_k$	$I_c$	$R_d \pm sd$		$\%R_d/P_{max}$
<i>E. amentacea</i> (-0 m)	5.44	0.76	135.1	15.3	0.76	0.19	14.0
<i>E. brachycarpa</i> (-10 m)	6.30	1.78	216.5	13.3	0.55	0.12	8.7
<i>G. montagnei</i> (-25 m)	9.17	1.48	152.8	10.6	0.51	0.19	5.6
<i>E. funkii</i> (-25 m)	15.25	2.37	180.1	9.2	0.68	0.12	4.5
<i>E. zosteroides</i> (-45 m)	14.15	2.12	120.5	3.1	0.46	0.07	3.3

Table 2.- Photosynthetic parameters ( $P_{max}$ : photosynthesis at saturation, in  $\text{mg O}_2\cdot\text{g AFDW}^{-1}\cdot\text{h}^{-1}$ ,  $I_k$ : light at saturation, in  $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ,  $I_c$ : light at compensation, in  $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), dark respiration ( $R_d$ ), in  $\text{mg O}_2\cdot\text{g AFDW}^{-1}\cdot\text{h}^{-1}$  and ratio between  $R_d$  and  $P_{max}$  (in percentage).

	factor	df	MS	% var.	F	p	species	ame	bra	mon	funk
$P_{max}$	species	4	290.2	83.2	82.7	***	<i>bra</i>	ns			
	error	67	3.5	16.8			<i>mon</i>	***	**		
							<i>funk</i>	***	***	***	
							<i>zos</i>	***	***	***	ns
$\alpha$	light	4	179.9	67.1	512.6	***	species	<i>ame</i>	<i>bra</i>	<i>mon</i>	<i>funk</i>
	species	4	42.4	15.8	120.7	***	<i>bra</i>	ns			
	interaction	16	9.8	14.6	27.9	***	<i>mon</i>	***	***		
							<i>funk</i>	***	***	***	
							<i>zos</i>	***	***	***	***
$R_d$	species	4	0.063	43.9	2.93	ns					
	error	15	0.021	56.1							

Table 3.- Results of the one-way ANOVA (species) variables  $P_{max}$  and  $R_d$ , the Tukey test for the variable  $P_{max}$ , and results of the two-way ANOVA (species and light) and the Tukey test between species for the lineal part of the PFD/photosynthesis curves ( $\alpha$ ). df: degrees of freedom, MS: mean squares, %var: percentage of explained variance, p, signification level: non significant (ns),  $p < 0.05$  (\*),  $p < 0.01$  (\*\*),  $p < 0.001$  (\*\*\*). Abbreviations: *ame*: *Ericaria amentacea*, *bra*: *Ericaria brachycarpa*, *mon*: *Gongolaria montagnei*, *funk*: *Ericaria funkii*, *zos*: *Ericaria zosteroides*.

Species	%C $\pm$ sd		%N $\pm$ sd		%P $\pm$ sd	
<i>E. amentacea</i> (-0 m)	33.77	0.15	0.90	0.07	0.034	0.002
<i>E. brachycarpa</i> (-10 m)	36.76	0.18	1.03	0.02	0.042	0.002
<i>G. montagnei</i> (-25 m)	31.51	0.46	1.04	0.04	0.054	0.005
<i>E. funkii</i> (-25 m)	30.66	0.36	1.17	0.08	0.071	0.001
<i>E. zosteroides</i> (-45 m)	26.73	2.16	1.84	0.08	0.095	0.003

Table 4.- Carbon (%C), nitrogen (%N) and phosphorus (%P) contents in algal tissues (mean  $\pm$  sd).

## Figure legends

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

Fig. 2.- Light attenuation with depth in Garganellu at the period of time when experiments were performed.

Fig. 3.- Bathymetric distribution of the canopy-forming algae belonging to the Order Fucales at Garganellu islet (Scandola Marine Reserve, Corsica). Abundance values correspond to the average estimated from 20 reticulated quadrats at 5 m depth intervals. Numbers represent the abundance percentage at the depth of highest occurrence.

Fig. 4.- Photosynthesis/PFD curves for the tested algae.

Fig. 5.- Lineal fitting of the photosynthesis/PFD data for the tested algae at the lineal part of the curve.

Fig. 6.- C:N, C:P and N:P ratios in tissues for each of the studied species.

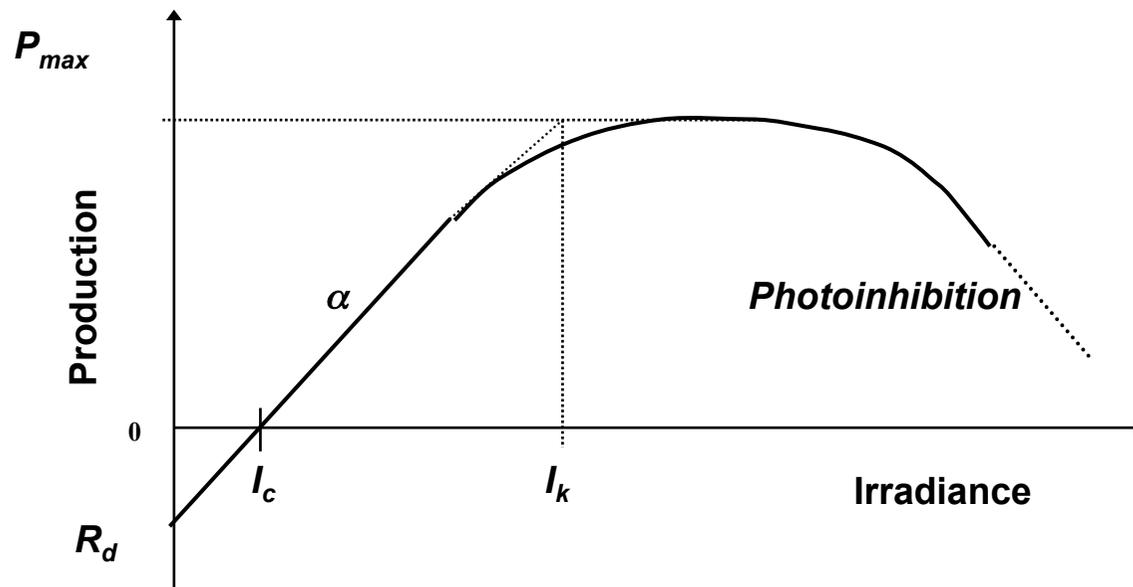


Figure 1

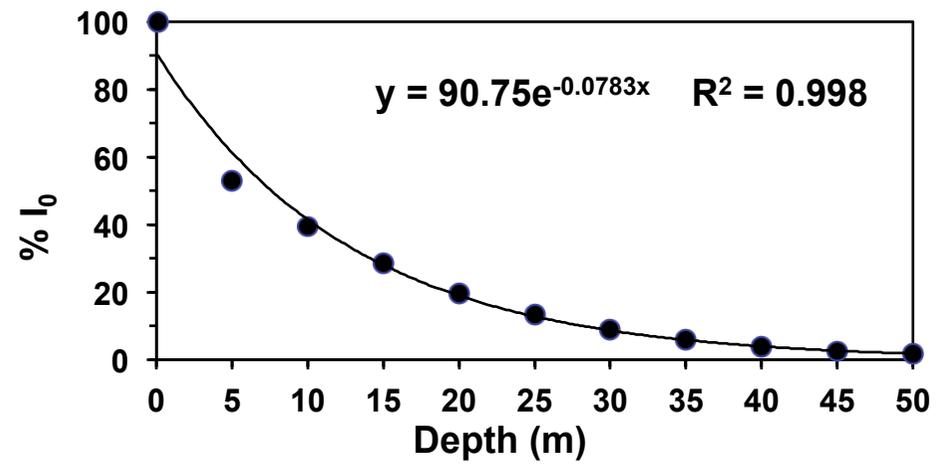


Figure 2

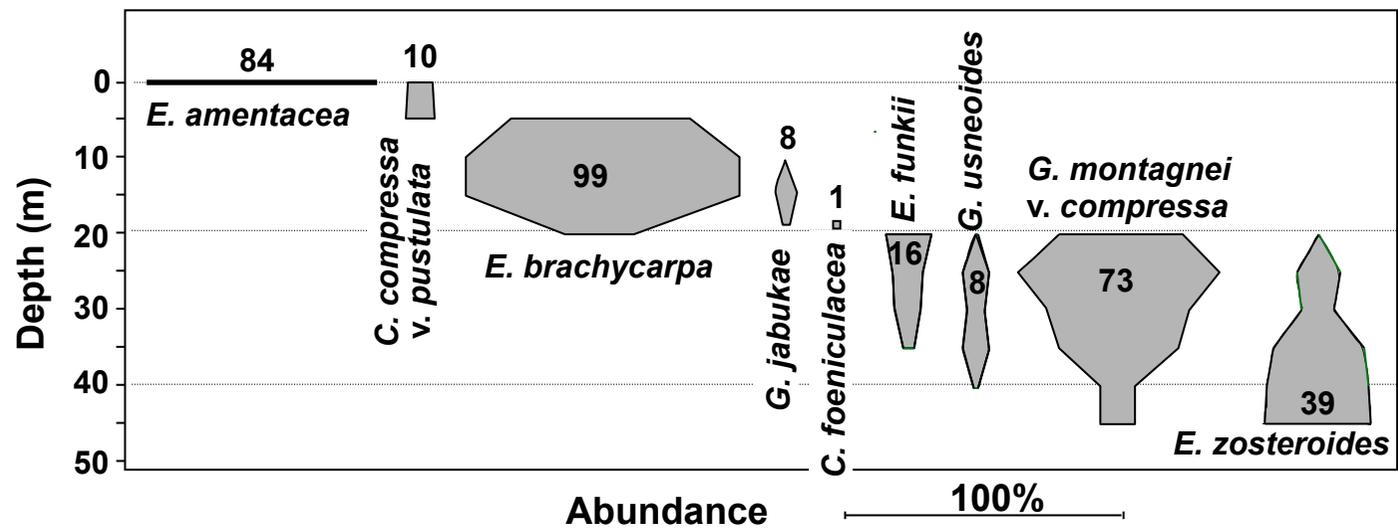


Figure 3

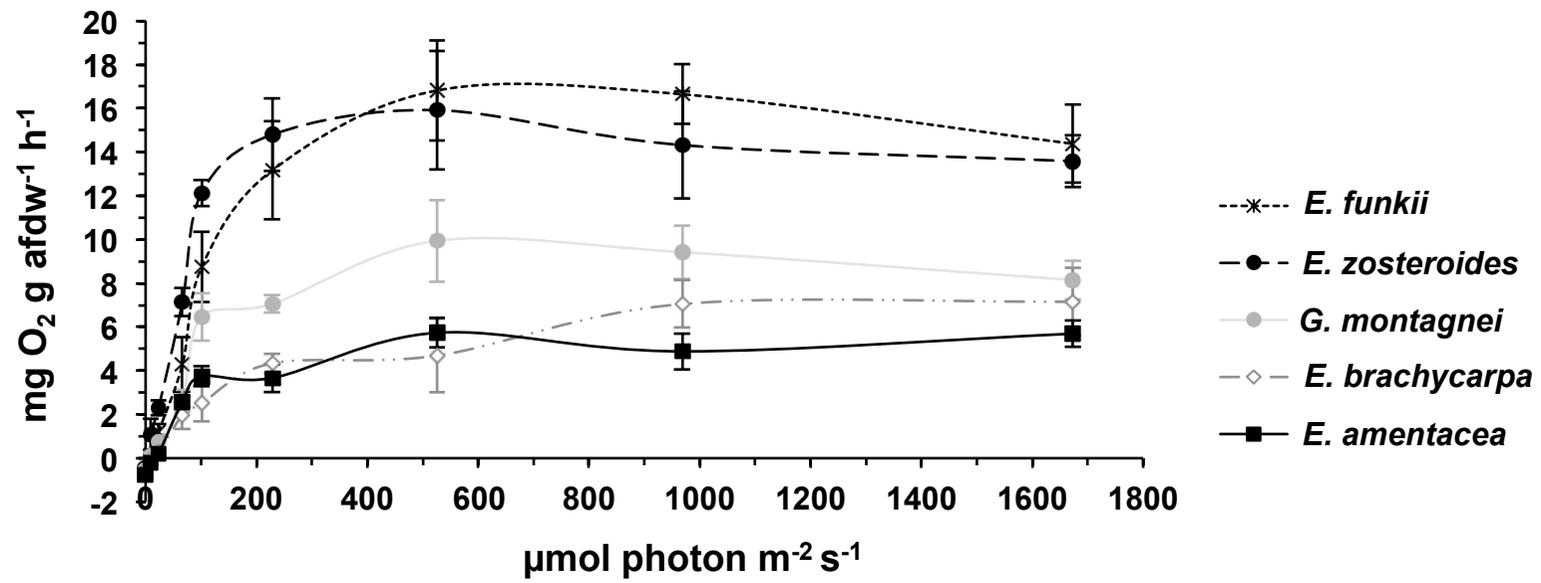


Figure 4

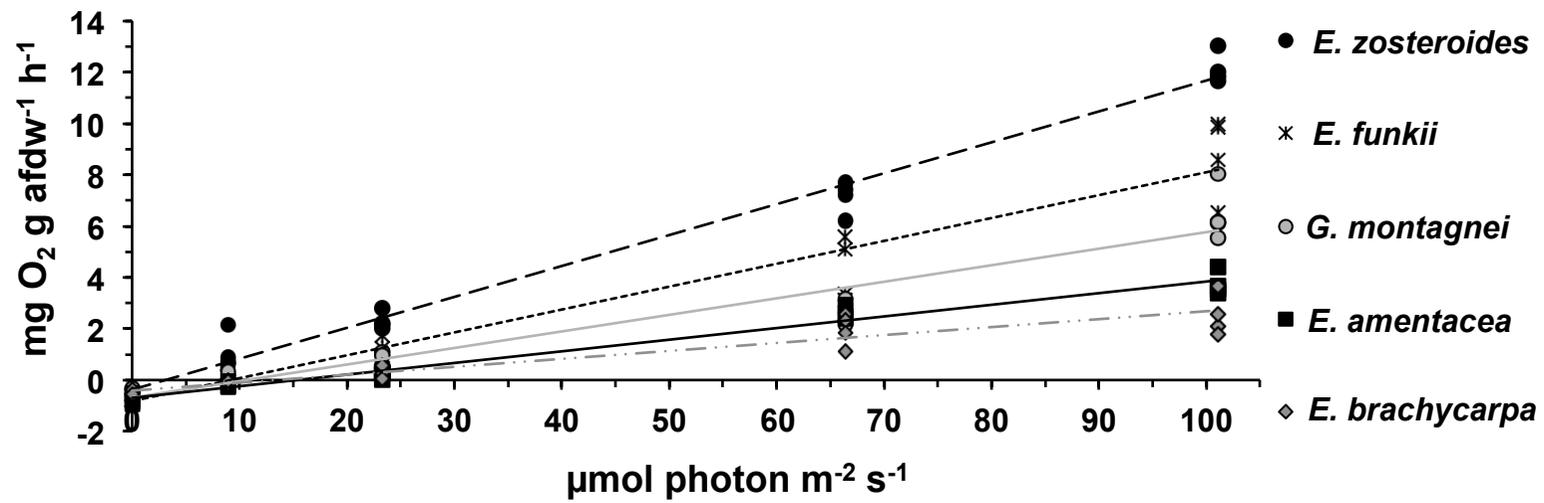


Figure 5

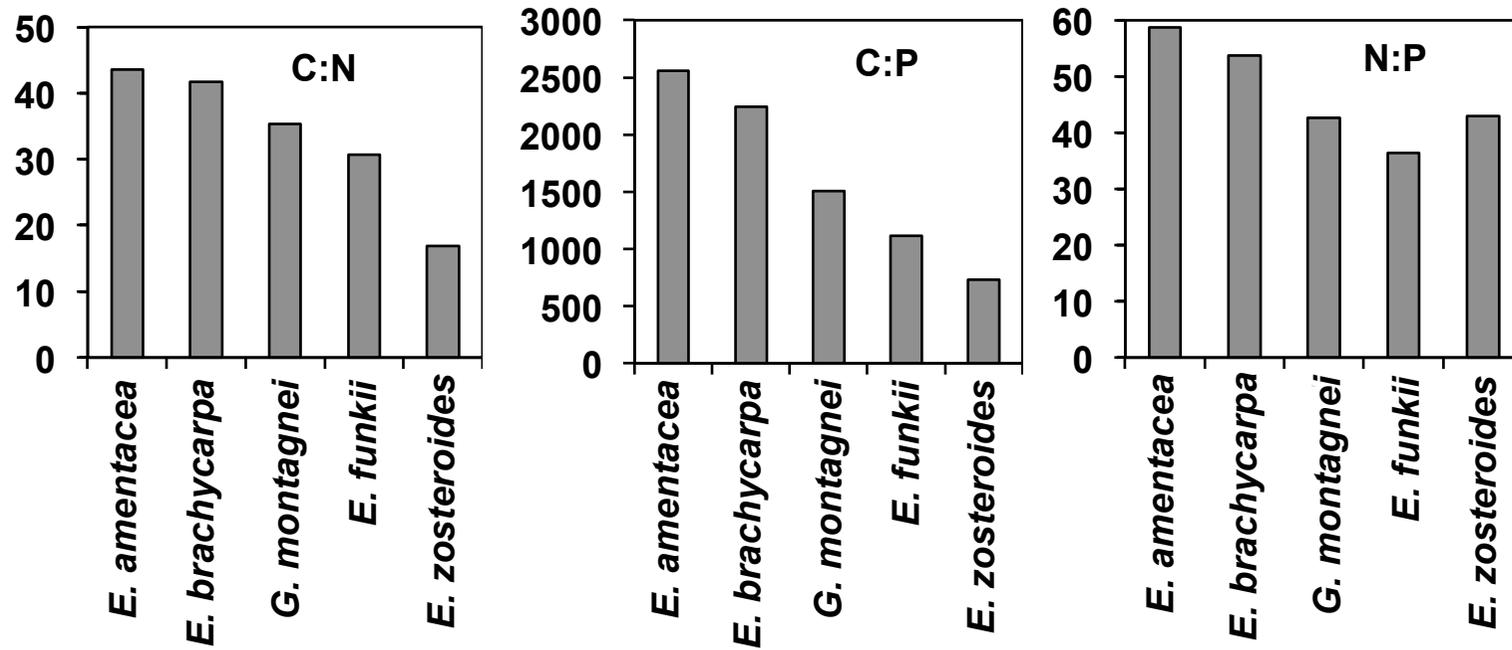


Figure 6