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REGULAR PAPER

# Photophysiology and daily primary production of a temperate symbiotic gorgonian

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**Abstract** Gorgonians are one of the most important benthic components of tropical and temperate areas, and play a fundamental role as ecosystem engineers. Although global warming and pollution increasingly threaten them, the acquisition of nutrients, which is a key process in fitness and stress resistance, has been poorly investigated in such species. This study has thus used an advanced in situ incubation chamber for the first time with gorgonians, to assess the daily acquisition of nutrients and the photophysiology of the Mediterranean symbiotic species, *Eunicella singularis*. The xanthophyll cycle was assessed in parallel. This work has revealed that *E. singularis* presents a different functioning than the Mediterranean symbiotic corals. This gorgonian indeed relies on both autotrophy and heterotrophy in summer to optimize its energetic budget, while corals mainly shift to autotrophy for their respiratory needs and tissue growth. In addition, although *E. singularis* lives in the same depths/locations, and harbours the same symbiont genotype than the corals, the photosynthetic performances of their respective symbionts are significantly different. Indeed, *E. singularis* acquired 2–3 times less autotrophic carbon from its symbionts than corals, but maintained a positive carbon budget by reducing respiration rates, and by presenting maximal photosynthetic rates throughout the day, suggesting a very efficient light utilization. Almost no photoinhibition was observed under very high light levels, because of the induction of a xanthophyll photoprotection process. These results help understanding why gorgonians often dominate many benthic ecosystems.

**Keywords** Temperate gorgonians · Symbionts · Photosynthesis · Carbon budget · Xanthophyll cycle · Photoacclimation

## Introduction

Octocorals and particularly gorgonians spread from intertidal to abyssal waters of the world's oceans (Bayer 1961). They are one of the most important benthic components of many tropical reefs and temperate benthic ecosystems such as those from the Mediterranean Sea, often occupying 50 % or more of the available substrate (Fabricius and Alderslade 2001; Harmelin and Garrabou 2005; Tentori and Allemand 2006). They play a fundamental role as ecosystem engineer (Jones et al. 1994), because they build three-dimensional structures, which provide habitats for hundreds of associated organisms. They are thus key species for the maintenance of the biodiversity of these benthic communities. In addition, by releasing organic matter in the form of mucus, and capturing plankton and dissolved organic matter, they play a key role in the transfer of energy and nutrients between the pelagic and benthic systems (Gili and Coma 1998). Their conservation is thus essential to maintain the biodiversity of the communities they inhabit.

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Gorgonians are, however, long-lived structural species with slow growth, late maturing and low fecundity, which render them particularly fragile to environmental disturbances (Coma et al. 2006; Garrabou et al. 2009). Since the last decades, many disturbances occurred at increasing frequencies, both in the tropics and temperate areas, leading either to mass bleaching or mass mortality events of these octocorals (Cerrano et al. 2000; Linares et al. 2008; Garrabou et al. 2009; Sammarco and Strychar 2013). Growing concern about the global degradation of these benthic communities of the world's oceans has underscored the need to develop reliable conservation strategies.

Despite the abundance and ecological importance of gorgonians, their physiology has been poorly studied, and the acquisition of autotrophic carbon in species living in symbiosis with dinoflagellates of the genus *Symbiodinium* has attracted very little attention (Lasker et al. 1983). In scleractinian corals, it is generally admitted that autotrophic carbon can supply most of the host's respiratory needs (Muscatine et al. 1981, 1984), except in deep or turbid environments (Falkowski et al. 1984; Palardy et al. 2008). Corals, thus, generally strongly depend on the symbiont's photosynthetic activity for growth and survival can acclimate to different light levels by changing the symbiont's physiology or population in favour of better-adapted clades (Rowan et al. 1997). Gorgonians, however, differ from corals with respect to their reliance on autotrophy, because they have different light scattering patterns and morphologies (fan, plume), which are better adapted to prey capture and heterotrophy (Lasker 1981; Ferrier-Pagès et al. 2013), and they often host a single symbiont clade within the same species (Goulet 2007), with a facultative symbiosis (Gori et al. 2012a). The main questions are thus to know whether gorgonians that can acquire large amounts of particulate food, have the same reliance on autotrophy than scleractinian corals, or whether the two modes of nutrition are largely dependent on each other. Also, how do specific and unique gorgonian symbionts cope with environmental changes? These questions are timely because the amount of nutrients acquired, and allocated to the different animal compartments, is a key determinant of gorgonian performance (i.e. growth, propagation, resilience to stress, survival…), and also influences ecosystem processes (Madin et al. 2012). Moreover, understanding the functioning of the gorgonian symbiodinium symbiosis will aid in deciphering why gorgonians dominate many coastal ecosystems. In temperate regions, such as the Mediterranean Sea, the role of symbionts in the nutritional needs of gorgonians is even more puzzling as light is rapidly attenuated with depth, and is very low in winter due to high seawater turbidity and short day length (Muller-Parker and Davy 2001). Rates of photosynthesis in such symbioses are thus highly variable during the year, but even vary from one day to another, or within the same day, depending on the irradiance received (Muller-Parker and Davy 2001). Symbionts can thus turn to be more parasitic than symbiotic (Ferrier-Pagès et al. 2013).

Amongst the 20 gorgonian species of the Mediterranean, *E. singularis* is the only one living in symbiosis with unicellular dinoflagellates of the genus *Symbiodinium* sp, belonging only to the temperate clade A (Forcioli et al. 2011). It is also found aposymbiotic in deep waters (Gori et al. 2012a), as this gorgonian spreads from the surface down to the edge of the continental shelf (Gili et al. 1989, 2011). Although its reproduction patterns (Gori et al. 2007; Ribes et al. 2007; Gori et al. 2012b) and spatial distribution before or after a stress event (Coma et al. 2006; Forcioli et al. 2011; Gori et al. 2011) have been investigated, the role of symbionts in the acquisition of nutrients has never been assessed. Two previous studies (Gori et al. 2012b; Cocito et al. 2013), based on the analysis of $\delta^{13}$C and $\delta^{15}$N of the gorgonian tissue, have however found a strong heterotrophic signature, even in summer during high light levels. To assess the summer primary production of the symbionts of *E. singularis*, we thus continuously monitored the rates of respiration and photosynthesis of the symbiotic association over several days, using an in situ chamber (Gevaert et al. 2011) equipped with sensors for temperature, salinity, photosynthetically active radiation (PAR), and an innovative oxygen sensor based on lifetime optical fluorescence technology. We also assessed, at different time points of the daily cycle, photoacclimation, by measuring the pigment profile, xanthophyll cycling and photosynthetic performance of the symbionts. Although such measurements are common in algae (Gevaert et al. 2011; Nitschke et al. 2012), and were performed few times with scleractinian corals (Patterson et al. 1991; Ferrier-Pagès et al. 2013), they have never been applied on gorgonians or octocorals in general. The final aims of this experiment were to (i) monitor for the first time the photosynthetic capacities and respiratory needs of the temperate symbionts associated to *E. singularis* over a daily cycle; (ii) assess whether these symbionts, in summer, can provide gorgonians with sufficient autotrophic carbon to contribute to the respiratory needs of the animal, and (iii) estimate whether they are able to photo-acclimate to the high irradiance levels that might occur in summer in this temperate area. The response of *E. singularis* symbionts to changes in irradiance levels will be compared to the response of those living in symbiosis with other Mediterranean scleractinian corals. As gorgonian symbionts belong to the same temperate clade A as most of the other Mediterranean symbionts, we hypothesize that they have the same photophysiological performances. A better knowledge of the functioning of the symbiosis in these animals will enable to better predict their distribution, their dominance in many coastal areas, as well as their response to thermal stress.

## Materials and methods

### Experimental set up

Experiments were performed in June in the coastal area of the Ligurian Sea (northwest Mediterranean Sea), where gorgonians are abundant. Summer conditions were selected to get saturating irradiance, long daylight periods and maximal production, especially in this temperate region where irradiance is particularly low in winter. Six large parent colonies of the symbiotic gorgonian *E. singularis* (Esper 1791) were randomly sampled by SCUBA diving (43°42′18″N, 7°18′45″E), and each divided into one large and one small colony. An automated closed-chamber, as described in Gevaert et al. (2011), was deployed on the bottom at 7 m depth during several cycles of two continuous days. The system was composed of a transparent Plexiglas incubation chamber, containing 3 of the large gorgonian colonies at each deployment, and connected to sealed PVC boxes containing batteries and the electronic system. The detector system was composed of an underwater quantum sensor (Ultra-miniature Light Intensity Recorder MDS MKV/L, JFE Advantech) to continuously monitor PAR, and a conductivity probe (TetraCon® 325, WTW®) to record salinity, connected to a Multi 350i WTW® logger. It also contained an oxygen sensor (Rugged Dissolved Oxygen for Multi-Parameter TROLL® 9000, In-Situ), which measured optically, every 10 s, the dissolved oxygen concentration in the chamber and the seawater temperature. The Perpex of the chamber does not alter the light properties in the visible area of the solar spectrum, but it absorbs ultra-violet radiations (UVR). UVR might affect organism's photosynthetic performances by inducing photoinhibition (Hoegh-Guldberg and Jones 1999). However, in the Mediterranean Sea, the penetration depth of UVR is of few metres (Häder 1997; Piazena and Häder 2009; Durrieu de Madron et al. 2011), so that at 7–10 m depth, UVR are not a major component of the irradiance wavelengths. Inside the chamber, two pumps (Aussenpumpe Extra, Comet-Pumpen Systemtechnik, Kommanditgesellschaft) ensured continuous water mixing, with a constant flow of 12 L $\mathrm{min}^{-1}$ and the chamber was automatically and periodically flushed every 20 min and during the 20 min the incubation medium was renewed. A total of 36 renewals and 36 experimental measurements were thus achieved per 24 h cycle. The water was directly pumped from the surrounding water and automatically filtered on a 500 µm nylon membrane to exclude actively metabolizing organisms. Oxygen concentration measurements (µmol $\mathrm{L}^{-1}$) were transformed into net production or net consumption (during the night) using the volume of the chamber corrected by the volume of the gorgonians (measured by water displacement).

In parallel to each in situ deployment of the chamber, the three small colonies, duplicated from the large colonies incubated inside the chamber, were positioned outside but near the chamber. The effective quantum yield ($\Delta F{:}F'_{\mathrm{m}}$) of the photosystem II (PSII) was assessed on these small colonies, at regular intervals during the day, using a diving PAM (Waltz, ®). After this measurement, colonies were enclosed with a black plastic cover for 10–15 min, after which the maximal quantum yield ($\mathrm{F_v{:}F_m}$) was measured by applying a saturation pulse (2500 µmol photons $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$, 0.8 s). The black plastic was then removed, so that colonies remained in the ambient light until the next measurement. The relative electron transport rate (rETR) was calculated by multiplying $\Delta F{:}F'_{\mathrm{m}}$ by PAR and 0.5, and the non-photochemical quenching (NPQ) was calculated according to: $\mathrm{NPQ = (F_m - F_m')/F_m'}$. After each PSII measurements, few polyps of the above colonies were sampled and immediately frozen in liquid nitrogen, for pigment determination according to the protocol used in Ferrier-Pagès et al. (2013). After pigment extraction, 20 µL from each sample was injected into a high-performance liquid chromatography (HPLC, 32 Karat Gold system equipped with a diode array detector, Beckman Coulter) with a reverse phase column (C18 Allure, Restek) and was separated following the method of Arsalane et al. (1994). Pigments were detected and quantified close to their absorption maxima by peak area calculations using the integrator of the photodiode array detector. A preliminary calibration of the apparatus was made by injecting known amounts of standards, estimated with the molar extinction coefficient cited by Berkaloff et al. (1990). The de-epoxidation ratio (DR), i.e. de-epoxidation of diadinoxanthin to diatoxanthin, pigments of the xanthophyll cycle (Hoegh-Guldberg and Jones 1999; Lavaud et al. 2004) was calculated as in Warner and Berry-Lowe (2006):

$$\mathrm{DR} = \mathrm{Dt} / (\mathrm{Dt} + \mathrm{Dd} + \mathrm{cisDd}), \qquad (1)$$

where Dt diatoxanthin, Dd diadinoxanthin and cisDd cis-diadinoxanthin amounts.

### Characteristics of the gorgonian colonies

The total surface area of the colonies was determined by measuring the length of each gorgonian branch and the width using a calliper. For each colony, three samples were collected to assess chlorophyll, zooxanthellae and protein concentrations as described below. For zooxanthellae and chlorophyll concentrations, tissue was separated from the main axis using an air-pick, homogenized using a Potter tissue grinder, and the zooxanthellae collected by centrifugation at 2000*g* for 5 min. They were re-suspended in 5 mL filtered seawater. One mL was sampled for the determination of the zooxanthellae density using an inverse microscope (Leica®) and an improved version of the Histolab 5.2.3 image analysis software (Microvision®). Chlorophyll *a* (Chl *a*) concentration was determined according to the equations of Jeffrey and Humphrey (1975) using a spectrophotometer, after extraction in acetone. Protein concentrations were measured using a bicinchonic acid protein assay (Uptima®, Interchim, Montluçon), after extraction in a sodium hydroxide solution (1 mol $L^{-1}$) for 30 min at 90 °C. Protein standards across a concentration range from 0 to 2000 mg $mL^{-1}$ were also prepared using bovine serum albumin (BSA, Interchim®). Absorbance of each sample was measured at 560 nm, and protein content was determined using the GENESIS® programme (Kontron Instruments, Bletchley) with reference to the standards. Results were used to express daily carbon production per protein content, to be compared with literature data.

### Daily autotrophic carbon acquisition

Rates of gross photosynthesis ($P_g$), calculated by adding respiration rates ($R$) measured during the night to net photosynthetic rates ($P_n$) measured during the day (*ca.* 20 to 24 measurements) were used to calculate the total daily autotrophic acquisition of carbon ($P_C$). For this purpose, Pg (in µmol $O_2$ $cm^{-2}$ $h^{-1}$) was transformed into carbon equivalents according to Muscatine et al. (1981):

$$P_C = \mu\text{mol}O_2 \text{ produced } \times PQ, \tag{2}$$

$$R_C = \mu\text{mol } O_2 \text{ consumed } \times RQ, \tag{3}$$

where $PQ$ is the photosynthetic quotient equal to 1.1 mol $O_2$:mol C and $RQ$ is the respiratory quotient equal to 0.8 mol C:mol $O_2$.

## Results

Temperature in the chamber ranged from 18 to 21 °C depending on the time of the day and salinity remained constant at 37.6 ± 0.1. During the incubations, oxygen concentration varied from 220 to 250 µmoles $O_2$ $L^{-1}$, depending on the activity of the gorgonian colonies, but the chamber was never oversaturated. Colonies contained between 17.1 and 20.2 µg Chl *a* $cm^{-2}$ for a zooxanthellae density of $3.5 \pm 0.52 \times 10^6$ cells $cm^{-2}$, and a protein content of *ca.* 1.02 ± 0.20 mg $cm^{-2}$. The day length in summer ran from 6:00 am to 9:00 pm.

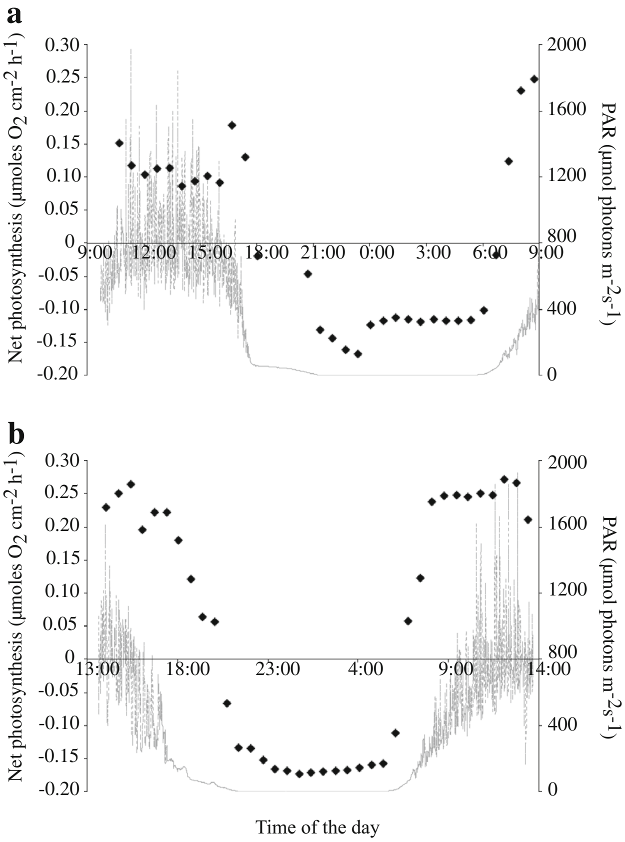

**Fig. 1** Changes in rates of net photosynthesis (*black* lozenges, µmole $O_2$ $cm^{-2}$ $h^{-1}$) and photosynthetically active radiation level (PAR, *dashed lines* and µmole photons $m^{-2}$ $s^{-1}$) during two different cycles (**a and b**), with 3 different gorgonians for each cycle

Figure 1 is an example of net oxygen production and consumption cycles obtained for *E. singularis* on three consecutive days. Irradiance at 7 m depth in summer days was high and, in these conditions, net photosynthesis ($P_n$) followed irradiance levels. On the first day, $P_n$ rapidly increased to 0.15 µmoles $O_2$ $cm^{-2}$ $h^{-1}$ around 10:30 am, then decreased to 0.09 µmole $O_2$ $cm^{-2}$ $h^{-1}$ at noon due to a slight photoinhibition, before re-increasing and reaching a maximal value of 0.18 µmole $O_2$ $cm^{-2}$ $h^{-1}$ at the end of the afternoon. The same pattern was observed the day after, with a high $P_n$ (0.25 µmole $O_2$ $cm^{-2}$ $h^{-1}$) at the beginning of the morning and a maximal value (0.26 µmole $O_2$ $cm^{-2}$ $h^{-1}$) at the end of the afternoon. It has to be noticed that $P_n$ was positive and high from the early morning to late in the afternoon. The mean (over the two cycles) daily autotrophic carbon production was equal to 48.4 ± 0.5 µg C $cm^{-2}$ $d^{-1}$ or 44.0 ± 0.4 µg C (mg protein)$^{-1}$ $d^{-1}$. During the night, gorgonian colonies respired at a constant rate varying between 0.12 and 0.17 µmoles $O_2$ $cm^{-2}$ $h^{-1}$. Mean daily respiration thus consumed between 34.5 ± 1.2 and 45.0 ± 2.3 µg C $cm^{-2}$ $d^{-1}$ (or 31.4–41.0 µg C (mg protein)$^{-1}$ $d^{-1}$). Overall, P:R ratio was always above 1 during the length of the experiment. The relationship between gross production ($P_g$) and PAR followed a least square fit model as described in Eilers and

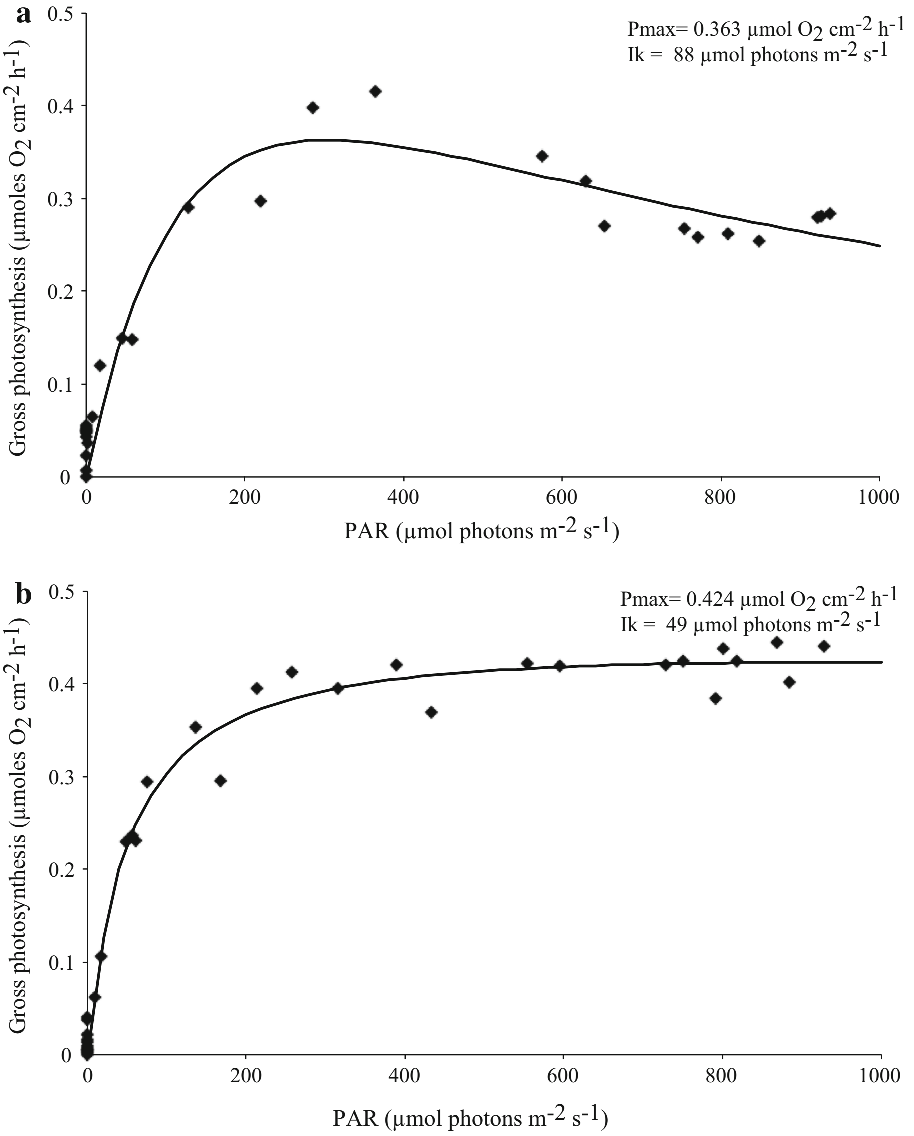

**Fig. 2** Relationship between rates of gross photosynthesis (µmole $O_2$ $cm^{-2}$ $h^{-1}$) and PAR (µmole photons $m^{-2}$ $s^{-1}$). This relationship was performed with data obtained during two (**a** and **b**) cycles

Peeters (1988), with an adjustment coefficient $R^2 > 0.95$ (Fig. 2). In some of the experiments, there was no photoinhibition, even at 1000 µmole photons $m^{-2}$ $s^{-1}$ whereas in some other days, a slight photoinhibition occurred above 600 µmole photons $m^{-2}$ $s^{-1}$. Maximal $P_g$ varied between 0.36 and 0.42 µmol $O_2$ $cm^{-2}$ $h^{-1}$ and the sub-saturation irradiance ($I_k$) was low, at *ca*. 50–90 µmoles photons $m^{-2}$ $s^{-1}$ depending on the day considered. Finally, the initial slope of the curve (α) was also low, between 0.004 and 0.009, suggesting an efficient light utilization.

Concerning the photosynthetic efficiency of the PSII of zooxanthellae *in hospite*, ($F_v$:$F_m$) measured in situ, it remained low during the whole day (Fig. 3a, b), for the two cycles. In the first cycle, there was a slight photoinhibition around 15 h (Wilkoxon test, $p = 0.001$), which corresponded to the concurrent decrease in oxygen production. The relative electron transport rate presented large variations over the two cycles and no real tendency with the irradiance could be observed (Fig. 3c, d). The non-photochemical quenching (NPQ, not shown) followed the irradiance level, with increasing values during the morning up to 3.4 between 11:00 am and 03:00 pm and a rapid decrease in the afternoon, down to 0.1–0.2 at 18:00 pm. The de-epoxidation ratio of diadinoxanthin into diathoxanthin (DR) followed the irradiance level (Fig. 4) and reached values of 0.20 ± 0.04 to 0.22 ± 0.08 for the first and second day, respectively. Moreover, the total amount of diatoxanthin + diadinoxanthin remained stable during the incubations, with 35–44 mol per 100 mol of chl *a* (and 3–10 mol per 100 mol chl a of diatoxanthin). This result suggests that

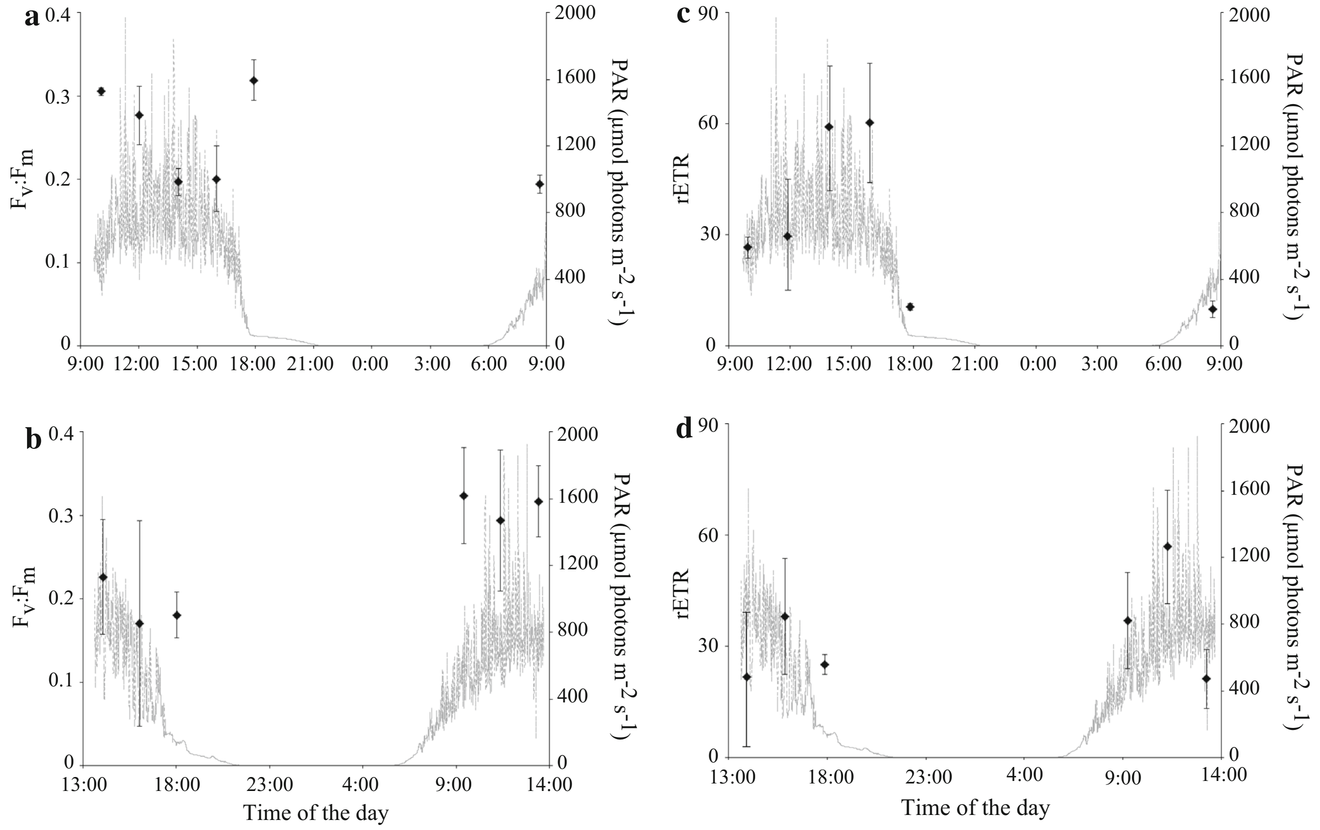

**Fig. 3** Changes in (**a**, **b**) the maximal quantum yield ($Fv$:$F_m$, *dark* lozenges) and (**c**, **d**) the relative electron transport rate (rETR, *dark* lozenges) following changes in PAR (*dashed lines*, and µmol photons m$^{-2}$ s$^{-1}$) during two cycles, represented by real hours on the *x*-axi*s*. These data are mean ± standard deviations of 3 replicates

there isn't any synthesis of pigments during the day, but rather a conversion from one pigment to the other one.

## Discussion

In situ diel fluctuations in photosynthesis, PSII photochemistry and carbon acquisition have mostly been investigated in tropical scleractinian corals (Brown et al. 1999; Gorbunov et al. 2001; Lesser and Gorbunov 2001; Warner et al. 2002), but only once, to our knowledge, in temperate corals (Ferrier-Pagès et al. 2013) and never in octocorals such as gorgonians. This work has revealed significant differences between temperate scleractinian corals and gorgonians such as *E. singularis* regarding nutrient acquisition, although the two groups host the same symbiont clade and live in the same locations. Contrary to corals, which shifted in summer from heterotrophy to autotrophy, *E. singularis* kept the two nutrition modes in parallel to optimize its nutrient input. In addition, it presented lower rates of photosynthesis compared to corals, but maintained a positive autotrophic carbon budget, by achieving maximal rates of photosynthesis throughout the day and down-regulating respiration rates, which were 2–3 times lower than those measured in corals. Finally, very few photoinhibition was observed at high irradiances, thanks to the induction of an active xanthophyll photoprotection.

Previous measurements of the carbon and nitrogen isotopic signature of the tissue of *E. singularis* sampled in the North Mediterranean Sea clearly showed that zooplankton capture contributed for a large share of the diet of this temperate gorgonian species in summer (Cocito et al. 2013). The $\delta^{13}$C signature of the gorgonian tissue was indeed very negative and close to the zooplankton signature, suggesting both a very limited autotrophic input and symbiont behaviour closer to parasitism than to symbiosis regarding carbon acquisition. The results obtained in this study challenge the above hypothesis by showing that gorgonian symbionts actually achieved high rates of photosynthesis and carbon acquisition in summer, in the same range as many temperate symbiotic anemones (Muller-Parker 1987; Davy et al. 1996; Verde and McCloskey 1996; 2007), although the animal kept high rates of heterotrophic feeding. It spreads the light on the functioning of this symbiotic association, in which the autotrophically acquired carbon is not fixed in the tissue, but mainly covers

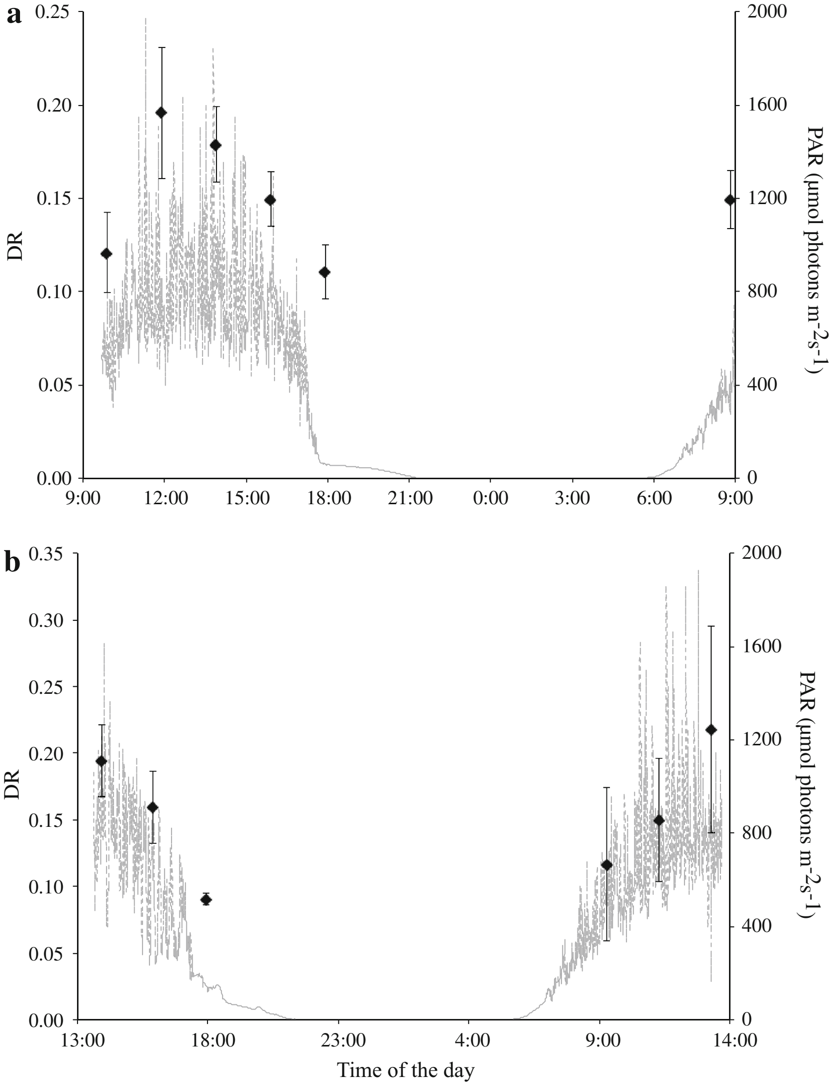

**Fig. 4** Changes in de-epoxidation ratio (DR, *black lozenges*) and PAR, (µmol photons $m^{-2}$ $s^{-1}$, *dashed lines*) during two cycles (**a** and **b**), represented by real hours on the x-axis. These data are mean ± standard deviations of 3 replicates

the immediate respiratory needs of the gorgonian, whilst carbon acquired through heterotrophic feeding is used to build tissue biomass. Such carbon partitioning explains the very low $\delta^{13}$C signature of the gorgonian tissue in summer. *E. singularis* thus presents a different functioning than the one observed in temperate corals. Indeed, corals shift from a dominance of heterotrophy in winter to autotrophy in summer, and mainly rely on the autotrophically acquired carbon for both respiration and tissue growth under high irradiances (Ferrier-Pagès et al. 2011). Conversely, *E. singularis* presents two independent and complementary nutrition modes, certainly because it has a facultative symbiosis and can be found asymbiotic in deep waters (Gori et al. 2012a). The same pattern was observed in the facultative symbiotic coral *Oculina arbuscula* (Piniak 2002), in which per-polyp capture rate and feeding efficiency were independent of the symbiotic condition. Combining autotrophy to heterotrophy is a way to maximize nutrient acquisition and ecological success, in environments where light, but not plankton concentration, is often limiting (Muller-Parker and Davy 2001).

Although *E. singularis* lives in the same depths/locations, and harbours the same symbiont genotype (temperate clade A) than the other Mediterranean corals such as *Cladocora caespitosa* (Visram et al. 2006), the photosynthetic performances of their respective symbionts are significantly different. Such difference might be due to fine level genetic variability within this clade A that has never been investigated yet. It has been demonstrated with tropical corals that the use of broad cladal designations may not be suitable to describe differences in clade physiology, only detectable at the sub-cladal level (Sampayo et al. 2008; LaJeunesse et al. 2014). On the other side, the host can also change the photosynthetic performances of its symbionts (Mieog et al. 2009), thus more studies are needed to better understand, which, from the host or the symbionts, are responsible for the differences observed. Thus, compared to Mediterranean corals, *E. singularis* presented photosynthetic rates much lower than *C. caespitosa* or *O. patagonica* (Rodolpho-Metalpa et al. 2006, 2008, 2014), but it implemented several processes for a better maximization of the capture of low irradiance levels, such as a value of the light limited photosynthesis ($\alpha = 0.0064$–$0.009$), and the onset of light saturation ($E_k = 50$–$90$ µmole photons $m^{-2}$ $s^{-1}$) in the lowest ranges reported (Enriquez et al. 1995; Anthony and Hoegh-Guldberg, 2003a, b). The maintenance of high rates of photosynthesis throughout the day, even in the early mornings or late afternoons, together with almost no decrease at high irradiances, allowed *E. singularis* to optimize its autotrophic nutrient acquisition. *E. singularis*, limited photoinhibition via the induction of photoprotective pigments (increase in the DR ratio) and non-photochemical quenching (Brown et al. 1999; Warner and Berry-Lowe 2006; Middlebrook et al. 2008). Such quenching is initiated by a proton gradient across the thylakoid membrane, leading to the acidification of the thylakoid lumen, and the catalysis of the de-epoxidation of diadinoxanthin to diatoxanthin, pigments of the xanthophyll cycle (Hoegh-Guldberg and Jones 1999; Lavaud et al. 2004). Overall, the de-epoxidation ratio was comparable to those measured for tropical (Brown et al. 1999; Warner and Berry-Lowe 2006) and temperate corals (Ferrier-Pagès et al. 2013). The maintenance of high photosynthetic rates at midday was previously observed in the coral *C. caespitosa* (Ferrier-Pagès et al. 2013), and highlights the great plasticity of the temperate clade A symbionts towards the large range of irradiance levels occurring in their environment. Conversely, tropical corals change their symbiont genotypes according to the environmental conditions (Berkelmans and van Oppen 2006; Frade et al. 2008) and can experience a large photoinhibition at midday, with a significant drop in rates of photosynthesis (Brown et al. 1999; Hoegh-Guldberg and Jones 1999; Gorbunov et al. 2001; Lesser and Gorbunov 2001).

Reduced dark respiration rate was the last adaptation of *E. singularis* to optimize its energetic budget (Enriquez et al. 1995; Anthony and Hoegh-Guldberg 2003a, b). Indeed, although autotrophic carbon acquisition in *E. singularis* (48 µg C $cm^{-2}$ $d^{-1}$) was much lower than those measured for the Mediterranean coral *C. caespitosa* (150 µg C $cm^{-2}$ $d^{-1}$, Ferrier-Pagès et al. 2013), and other tropical corals (>150 µg C $cm^{-2}$ $d^{-1}$, Atkinson and Grigg 1984; Anthony and Hoegh-Guldberg 2003b; Yakovleva and Hidaka 2004), its expenditure through respiration was also very limited. *E. singularis* consumed only 34 µg C $cm^{-2}$ $d^{-1}$, against 2–3 times more in scleractinian corals (Anthony and Hoegh-Guldberg 2003a; Ferrier-Pagès et al. 2013). The strategy used by gorgonians to optimize their energetic budget, i.e. photosynthetic efficiency maximization and down-regulation of respiration, was thus fundamentally different to the one used by most scleractinian corals, i.e. maximization of photosynthetic and respiration rates, these latter representing more than 80 % of the photosynthetically-acquired carbon (Tremblay et al. 2012). Factors that might explain the lower respiration rates in gorgonians compared to corals include their low growth rates, their lack of hard skeleton, and a possibly different respiratory substrate, but this last point remains to be investigated. CZAR (contribution of symbiont translocated carbon to animal respiration, Muscatine et al., 1981) values for *E. singularis* at 7 m depth were thus always above 100 %. Although these CZAR values have to be interpreted with caution as a result of several assumptions, in summer, with ideal sunny days, *E. singularis* can survive autotrophically, despite its high heterotrophic capacity.

All together, these results reveal that symbionts associated to *E. singularis* presented different photophysiological performances than those associated to Mediterranean scleractinian corals, although they both belong to the temperate clade A. In addition, in summer, *E. singularis* relied on autotrophy to sustain its energetic needs and on heterotrophy to build its tissue biomass. This dual nutrition mode allows gorgonians to optimize their acquisition of nutrients, especially in summer when particulate food is rare in the surrounding waters, due to water-column stratification. This dual nutrition also helps understanding why gorgonians dominate many coastal ecosystems.

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**Conflict of interest** The authors declare no competing interests

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