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The relative contribution of fleshy epiphytic macroalgae to the
production of temperate maerl (rhodolith) beds

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Running page head: Epiphytic macroalgal production in maerl beds

ABSTRACT

Maerl beds are composed of unattached red calcareous coralline algae. When located in shallow ecosystems, these calcareous macroalgae provide substrates for the development of fleshy epiphytic macroalgae, which contribute to the productivity of maerl beds. To assess the importance of their contribution, we estimated the primary production of the main taxa of fleshy epiphytic macroalgae (*Solieria chordalis* or Rhodomelaceae), growing in two distinct *Lithothamnion corallioides* maerl beds of the Bay of Brest (Brittany, France) characterized by different depths and incident irradiances. We estimated epiphytic algal photosynthetic parameters derived from photosynthesis-irradiance curves calculated from incubations in photo-respirometry chambers at different irradiances and in the dark. A comparison with results previously obtained in *L. corallioides* showed that, in the two studied maerl beds, there were no differences between maerl and its fleshy epiphytic macroalgae in terms of photo-acclimation to low irradiances. However, fleshy epiphytic macroalgae had higher photosynthetic efficiencies and photosynthetic rates per unit of biomass or chlorophyll *a* than the maerl species. Estimations of net primary production per surface area of maerl bed indicated that fleshy epiphytic macroalgae account for 25% of maerl bed productivity. Interactions between *L. corallioides* and its fleshy epiphytic macroalgae may affect their respective contributions. In the deepest maerl beds, shading by fleshy epiphytic macroalgae may have a detrimental impact on *L. corallioides* net primary production, whereas in the shallowest maerl beds, fleshy epiphytic macroalgae may protect maerl from photoinhibition under high irradiances.

Keywords: maerl, fleshy epiphytic macroalgae, photosynthesis, productivity, red algal physiology, *Solieria chordalis*, filamentous Rhodomelaceae

1. INTRODUCTION

Macroalgae acting as ecosystem engineers form macroalgal beds, which are among the most productive habitats in coastal marine systems (Olafsson 2016). Their contribution to the biogeochemical cycles is tightly linked to the incident irradiance they receive and their metabolic rates (Hurd et al. 2014). Among macroalgal foundation species, free-living red calcareous coralline algae (known as maerl) are long-lived species that grow worldwide at different depths, from the surface under high irradiances down to 250 m under dim-light conditions (Amado-Filho et al. 2017; Riosmena-Rodríguez et al. 2017). Although very slow-growing, maerl algae can accumulate, constituting vast beds of high density and biomass, thus significantly contributing to marine coastal primary production (Martin et al. 2007, van der Heijden & Kamenos 2015).

When located in shallow environments, maerl beds are home to a highly diverse flora (Peña et al. 2014). Maerl bed flora have been assessed in tropical ecosystems (Brazil, Amado-Filho et al. 2010), in the Mediterranean (Ustica Island, Mannino et al. 2002) and in the Northeast Atlantic, from Svalbard to Portugal (Peña et al. 2014). These studies have highlighted that maerl algae harbor higher diversity and abundance of red fleshy epiphytes than brown and green epiphytes. In the NE Atlantic, maerl beds are found from the intertidal zone down to 60 m depth (Hernández-Kantún et al. 2017). Most beds are patchily distributed and found at less than 30 m depth (Peña et al. 2014), where light conditions are also favorable for the growth of fleshy epiphytic macroalgae. NE Atlantic maerl beds harbor at least 50 fleshy epiphytic macroalgal species, mostly Rhodophyta (Peña et al. 2014). In contrast to maerl species, fleshy epiphytic macroalgae are fast-growing, short-lived organisms. Their composition and biomass depend on environmental factors favorable to their growth, such as high temperature, light, and nutrient availability (Qui-Minet et al. 2018, 2021). Habitat

stability and variations in maerl morphology also influence fleshy epiphytic macroalgal abundance and species composition (Pascelli et al. 2013). The hydrodynamic regime, including winter storm disturbances, affects the abundance of fleshy epiphytic macroalgae in maerl beds (Amado-Filho et al. 2010, Qui-Minet et al. 2018). It also determines maerl morphology and, in turn, influences its associated macroflora (Bosence 1976).

The contribution of fleshy epiphytic macroalgae to the primary production of maerl beds thus depends on various environmental factors. It also depends on the living biomass of epiphytic macroalgal taxa and on their capacity to capitalize on the incident irradiance they receive. In the Bay of Brest (Brittany, France), the seasonality of maerl bed flora likely plays a major role in community primary production (Martin et al. 2007). Epiphytic macroalgal species distribution and abundance vary with season (Grall 2002) and local environmental changes (Grall 2002, Qui-Minet et al. 2018). Their contribution to carbon budgets in temperate ecosystems can be particularly important in summer due to their higher abundance during this season (Grall 2002, Guillou et al. 2002, Qui-Minet et al. 2018).

The contribution of epiphytic red macroalgae to maerl bed productivity also depends on specific photo-physiological performance of epiphyte species (Hurd et al. 2014). Although the physiology of maerl algae has been well studied (Martin et al. 2006, Schoenrock et al. 2018, Qui-Minet et al. 2019, Sordo et al. 2020, Qui-Minet et al. 2021), no study has assessed the physiology of red fleshy macroalgae inhabiting maerl beds. Maerl algae are known to show a high capacity for acclimation or adaptation to different depths/irradiance. For instance, in the Bay of Brest (Brittany, France), where *Lithothamnion corallioides* is the dominant maerl alga, summer irradiances of saturation in this species range from 100 to 200 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, depending on its location (depth and light availability) and thallus

morphology (Martin et al. 2006, Qui-Minet et al. 2021). Maximal gross production rates in *L. corallioides* are observed in summer, ranging from 1 to 3 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$.

Some studies have assessed the physiology of red fleshy macroalgae, including Rhodophyta genera known to grow in temperate maerl beds of the NE Atlantic (Dudgeon et al. 1995, Johansson & Snoejis 2002, Michler et al. 2002, McCoy et al. 2019). A study on several species of red macroalgae from the Baltic Sea and the Skagerrak (Gullmar Fjord) highlighted a high species-dependent variability in maximal gross production rates, ranging from 70 to 500 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ in summer (Johansson & Snoejis 2002). The saturating irradiances in these species are strongly related to water depth (and irradiances), with values ranging from 100 to 300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for species typical of the upper littoral (0–5 m depth) and lower values (i.e. $<100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) for species typical of the lower littoral (below 10 m depth).

The contribution of epiphytic algae to the productivity of vegetated marine coastal ecosystems has been mainly studied in seagrass beds (Moncreiff & Sullivan 2001, Borowitzka et al. 2006), but remains relatively poorly understood in macroalgal habitats despite the potentially high biomass of fast-growing epiphytes that may contribute significantly to the total productivity of these ecosystems. The epiphytic algae of seagrasses are important primary producers that can indeed make up a significant proportion (up to 60%) of the total primary production of seagrass beds (Borowitzka et al. 2006, Berlinghof et al. 2022). In contrast, epiphytic macroalgae of the kelp species *Laminaria hyperborea* contribute little to the total productivity of the entire kelp forest, relative to the kelp itself (Pedersen et al. 2014). The contribution of fleshy epiphytic macroalgae to the primary production of maerl beds has never been assessed. The lack of knowledge on the physiology of fleshy epiphytic

macroalgae limits our ability to evaluate their contribution to the productivity of macroalgal ecosystems.

The main objective of this work was to estimate the relative contribution of fleshy epiphytic macroalgae to the maerl bed productivity as a function of bottom incident irradiance variability. For the first time, we determined photosynthetic parameters of temperate fleshy macroalgal maerl epiphytes and we estimated their rates of primary production and their contribution to carbon budgets in two distinct maerl beds of the Bay of Brest (two stations), characterized by different depths/incident irradiances, macroalgal biomasses and epiphytic taxa. Macroalgae physiological parameters were measured in summer, when fleshy epiphytic macroalgal biomass reaches its highest peak in the Bay of Brest (Grall 2002, Guillou et al. 2002, Peña et al. 2010). Macroalgal productivity per surface unit of maerl bed was estimated using previous data on *L. corallioides* and fleshy epiphytic macroalgal biomass and *L. corallioides* physiology (Qui-Minet et al. 2018, 2021). Our working hypotheses were i) physiological characteristics differ between epiphytic macroalgae according to taxon and specific environmental conditions at the two stations, and ii) fleshy epiphytic macroalgae have higher production rates than maerl (*L. corallioides*), and thereby significantly contribute to the productivity of maerl beds in summer.

2. MATERIALS AND METHODS

2.1 Study site

Epiphyte and maerl primary production rates were studied at two stations (A and B) in the Bay of Brest (Britany, France), where maerl beds cover almost one third of its bottom surface.

Mean tidal range in the bay is 4 m, and minimal and maximal tidal ranges are 0.3 and 8 m, respectively. Station A is located in the northern basin of the bay (48°21'57"N, 04°26'47"W), and Station B is located in the southern basin (48°19'58"N, 04°19'57"W). Chart datum is 2.5 m at Station A and 0.7 m at Station B.

In the Bay of Brest, bottom currents have a significant impact on macroalgal assemblages (Qui-Minet et al. 2018). Summer fleshy epiphytic macroalgal biomass (DW) ranges from 21 to 49 g m⁻² at Station A and from 13 to 23 g m⁻² at Station B, with no significant statistical differences between them (Qui-Minet et al. 2018). Filamentous Rhodomelaceae are dominant at Station A. Peña et al. (2014) identified the five filamentous Rhodomelaceae species present in Brittany (France): *Polysiphonia elongata*, *P. fibrillosa*, *P. fucoides*, *P. fucellata*, *P. nigra*, *P. stricta* and *P. subulifera*. A recent revision of the *Polysiphonia* genus (Díaz-Tapia et al. 2017) has split this group of fleshy epiphytic macroalgal species into four genera: *Polysiphonia*, *Carrodoriella*, *Leptosiphonia* and *Verebrata*. Identification to the species level at Station A was not possible in the present study; we thus refer this taxon as “filamentous Rhodomelaceae”, the main fleshy epiphytic macroalgae at this location. At Station B, the dominant species was *Solieria chordalis*. Filamentous Rhodomelaceae and *S. chordalis* differ in their morphology. Filamentous Rhodomelaceae include taxa with multiaxial morphology in which upright filaments are laterally or dichotomously branched (polysiphonous morphology), whereas *S. chordalis* grows erect from a fibrous basal system and generally has two or three orders of branching (Gabrielson & Hommersand 1982). The living biomass of *Lithothamnion corallioides* is highly variable in maerl beds of the bay, but is not significantly different between Station A (from 850 to 8550 g m⁻²) and Station B (from 3100 to 5650 g m⁻²) (Qui-Minet et al. 2018).

2.2 Incubation procedure and physiological measurements

In the Bay of Brest, September is representative of the summer period in terms of temperature and irradiance (Martin et al. 2007, Qui-Minet et al. 2021). Maximal metabolic rates are reached during this period in maerl beds of the Bay of Brest (Martin et al. 2007). Physiological measurements were carried out on 17 September 2015 under the following physico-chemical conditions: temperature, $17.8 \pm 0.2^{\circ}\text{C}$ [Station A] and $16.3 \pm 0.0^{\circ}\text{C}$ [Station B]; salinity, 35.1 ± 0.0 [A] and 35.0 ± 0.0 [B], and pH 7.92 ± 0.03 [A] and 8.03 ± 0.02 [B]. *L. corallioides* physiological measurements were taken on 16–18 September 2015 (see Qui-Minet et al. (2021) under similar physico-chemical conditions and using the same methodology as that described below for epiphytes.

Algae were collected with a Van Veen grab (5 replicates of 0.1 m^2 per station), rinsed with filtered seawater on a 5 mm mesh sieve and then carefully cleaned to remove the sediments. The most abundant fleshy epiphytic taxa of each station were identified and selected as filamentous Rhodomelaceae (Station A) or *Solieria chordalis* (Station B), both taxa being free of epiphytes.

Measurements were carried out by incubating the most abundant fleshy epiphytic algal taxon at each station. Macroalgal incubations were performed in the light and in the dark. During incubations, surface irradiance in terms of photosynthetically active radiation (PAR, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was recorded every minute using a LI-COR quantum sensor (LI 192 SA). Maximum surface irradiance ranged from 570 to $1100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Macroalgal net photosynthesis (NPP) was measured under different irradiances: maximum surface irradiance (100%), and reduced irradiance levels (65%, 47%, 27%, 13% and 6%), using clear chambers and opacifying neutral filters. Respiration (R) was measured in the dark using dark chambers. NPP and R rates were obtained by measuring the initial and final oxygen concentration with an oxygen probe (Oxymeter HQ40D, Hatch Lange, Ltd. portable LDOTM)

at the beginning and at the end of the incubations. For each level of irradiance and in the dark, five photo-respirometry chambers (220 mL) were filled with bottom seawater and fleshy epiphytic macroalgae (algal dry mass of 0.5-1 g DW). Five photo-respirometry chambers were only filled with bottom seawater and used as controls. Bottom seawater was collected at each station (approximately 1 m above the bottom) in a Niskin bottle. Incubations were performed on board the R/V *Albert Lucas* immediately after collecting the algae. Chambers were kept in a water bath with a continuous flow of water coming from the bottom at the *in situ* temperature. Incubations lasted 1 hour to avoid oxygen saturation greater than 120% during light incubations and to maintain oxygen saturation above 80% at the end of dark incubations.

2.3 Sample treatment and processing

At the end of incubations, algal samples were collected and dried (60°C, 48 h). In parallel, additional samples were rinsed with filtered autoclaved seawater to remove salts, placed in 2 mL cryotubes and frozen in liquid nitrogen. Samples were maintained at -80°C prior to lyophilization for pigment analyses. To obtain a fine powder, samples were ground in a Tissue Lyser II (QIAGEN) bead mill in plastic tubes using 0.5 cm stainless steel beads (Brammer). Chlorophyll *a* of fleshy epiphytic macroalgae was analyzed using a calibrated Turner 10-AU fluorimeter, according to the Arar & Collins (1997) equation:

$$C_{S.C.} = \frac{C_{F.C.} \times \text{extract volume (L)} \times DF}{\text{Sample volume (L)}} \quad (1)$$

where, $C_{S,c}$ is the corrected chlorophyll *a* concentration ($\mu\text{g/L}$) in the whole water sample, $C_{E.C.}$ is the uncorrected chlorophyll *a* concentration in the water sample ($\mu\text{g/L}$), DF is the dilution factor, and extract volume is the volume (L) of extract prepared before dilution.

2.4 Data processing

To obtain actual macroalgal physiological parameters, fluxes were corrected with respect to control data. NPP and R rates were calculated as a function of algal dry weight ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$) or as a function of algal chlorophyll *a* content ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$) according to the following equation:

$$\text{NPP or } R = \frac{\Delta\text{O}_2 \times V}{\text{Alg} \times \Delta t} \quad (2)$$

where ΔO_2 ($\mu\text{mol L}^{-1}$) is the variation of dissolved oxygen concentration between the beginning and the end of the incubation, V (L) is the volume occupied by the seawater in the chamber, Alg is the dry weight (g) or Chl *a* content (mg) of algae in the chamber, Δt (h) is the incubation time. The relationships between irradiance (E , $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and NPP as a function of algal dry weight or as a function of algal Chl *a* content at a given irradiance, were obtained using the Chalker (1981) equation:

$$\text{NPP} = \text{GPP}_{\text{MAX}} \times \left(1 - e^{\frac{-E}{E_k}}\right) - R \quad (3)$$

Where GPP_{MAX} is the maximal gross primary production expressed in terms of algal dry weight (in $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$) or algal Chl *a* content ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$). E_k ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) is the saturating irradiance for photosynthesis and R is the respiration rate (in $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ or $\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$).

The compensation irradiance (E_c , $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) is the irradiance at which $\text{NPP} = 0$ (or $\text{GPP} = \text{R}$). Alpha (α), the photosynthetic efficiency ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)⁻¹) was calculated using the following equations:

$$\alpha = \frac{GPP_{MAX}}{E_k} \quad (4)$$

At each station, values of bottom irradiance were calculated using chart datum, tidal height and light extinction coefficients measured at each station during the summer season (0.38 for Station A and 0.43 for Station B). Bottom incident irradiance was calculated every 20 min from surface irradiance data (SOMLIT-MAREL), tidal ranges (www.maree.info) and light extinction coefficients previously obtained for summer season at each station (Qui-Minet et al. 2018). Surface irradiance (PAR) was monitored at high frequency (every 20 min) by the autonomous COAST-HF-MAREL-Iroise buoy (MAREL-Iroise/SOMLIT-Brest scientific platform) located in the Bay of Brest. Summer is here defined as the period from 16 June to 15 September 2015. Values of NPP (mg C m^{-2}) per h (or per day) were individually estimated for *L. corallioides*, filamentous Rhodomelaceae and *S. chordalis* using photosynthesis-irradiance (P-E) parameters presented here (epiphytes) or previously published (maerl, Qui-Minet et al. 2021), algal biomass data per m^2 (Qui-Minet et al. 2018) and calculated bottom irradiance values. Data were obtained in terms of $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ or $\mu\text{mol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and converted from μmol of O_2 to mg C , using photosynthetic and respiration quotients (PQ and RQ, respectively) previously reported for *L. corallioides* (PQ:1.17 and RQ:0.97, Martin et al. 2006) and for red fleshy macroalgae (PQ:1.20, Buesa 1980; RQ:1.00, Carvalho & Eyre 2011), and the molecular weight of C. In addition to the estimations of macroalgal NPP ($\text{mg C m}^{-2} \text{ day}^{-1}$), we give the 24 h NPP rates ($\text{mg C m}^{-2} \text{ h}^{-1}$) during three specific days with

contrasting tidal ranges: low water neap tide (LWNT, “low” tidal range of 1–2 m), medium water tide (MWT, “medium” tidal range of 4 m) and high water spring tide (HWST, “high” tidal range of 6–8 m).

2.5 Statistical treatment

Statistical analyses were done using *R Statistical Software* (version 4.1.1). The significance of the fitted curves was tested using the Fisher test. Because data did not follow a normal distribution (Shapiro-Wilk test) and/or the homogeneity of variances (Bartlett test), a non-parametric test (Kruskal-Wallis test) was used to compare fleshy epiphytic macroalgae P-E parameters between stations, bottom irradiance between stations (during the early morning, late morning, afternoon and evening) and NPP rates between taxa/stations. When necessary, tests were followed by a post-hoc Wilcoxon test (pairwise Wilcoxon-test, Wp).

3. RESULTS

3.1 Comparison of photosynthesis characteristics between filamentous Rhodomelaceae and Solieria chordalis

Mean rates of respiration (R) and of maximal gross primary production (GPP_{MAX}) rates were significantly higher in filamentous Rhodomelaceae than in *S. chordalis* (Fig. 1 & Table 1). In contrast, when physiological rates were normalized to the algal chlorophyll *a* (Chl *a*) content, GPP_{MAX} was significantly lower in filamentous Rhodomelaceae than in *S. chordalis* (Fig. 2 & Table 1). Irradiance of saturation (E_k) and irradiance of compensation (E_c) were significantly higher in filamentous Rhodomelaceae than in *S. chordalis* (Table 1).

267 3.2. Comparison of photosynthesis characteristics between fleshy epiphytic macroalgae and
268 maerl within and between stations

269 The physiological rates expressed in terms of algal Chl *a* content for *Lithothamnion*
270 *corallioides* and its fleshy epiphytic macroalgae were compared within stations A and B. At
271 Station A, GPP_{MAX} in *L. corallioides* was five times lower than in filamentous
272 Rhodomelaceae. At Station B, it was 12-fold lower than in *S. chordalis* (Table 2 & Fig. 2a-
273 b). *L. corallioides* photosynthetic efficiency (α) coefficients were 6-fold and 12-fold lower
274 than those of fleshy epiphytic macroalgae at stations A and B, respectively (Table 2 & Fig.
275 2a-b). *L. corallioides* R was 3-fold and 11-fold lower than that of fleshy epiphytic macroalgae
276 at stations A and B, respectively (Table 2 & Fig. 2a-b). Within each station, no significant
277 differences in terms of Ek and Ec were observed between *L. corallioides* and its fleshy
278 epiphytic macroalgae.

280 3.3 Comparison of diel cycles in incident irradiance

281 Mean bottom irradiance during the summer season was significantly different between the
282 two stations (Fig. 3). Bottom irradiance was significantly lower at Station A than at Station
283 B during the early morning (6–9:00 h), the late morning (9–12:00 h), the afternoon (12–17:00
284 h) and the evening (17–22:00 h) (Table 3). Median values of bottom irradiance during the
285 early morning were 5 and 10 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at stations A and B, respectively. They
286 were below the Ec values for *L. corallioides* (16 and 13 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at stations A
287 and B, respectively), filamentous Rhodomelaceae (19 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, Station A) and
288 *S. chordalis* (13 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, Station B). During the late morning, median values of
289 bottom irradiance remained above Ec and below Ek for the macroalgae taxa here studied.

During the afternoon, median values of bottom irradiance were below E_k for *L. corallioides* and filamentous Rhodomelaceae at Station A, whereas at station B median values of bottom irradiance were equal to E_k for *L. corallioides* ($106 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) at Station B. During the evening, median values of bottom irradiance at Station A ($11 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) were below E_c for *L. corallioides* and filamentous Rhodomelaceae, but this was not the case at Station B, where median values of bottom irradiance ($18 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) remained above E_c for *L. corallioides* and *S. chordalis*. In addition to the variability of bottom irradiance among stations, due to surface irradiance and height of tide variability, bottom irradiance also varied significantly among days (Table 3; Fig. 3; Suppl. Figs. 1 & 2).

3.4. Contribution of fleshy epiphytic macroalgae to NPP at each station

Mean rates of net primary production (NPP), estimated from summer average bottom irradiances) at noon were $42 \text{ mg C m}^{-2} \text{h}^{-1}$ in *L. corallioides* and $10 \text{ mg C m}^{-2} \text{h}^{-1}$ in filamentous Rhodomelaceae at Station A, and $55 \text{ mg C m}^{-2} \text{h}^{-1}$ in *L. corallioides* and $16 \text{ mg C m}^{-2} \text{h}^{-1}$ in *S. chordalis* at Station B (Fig. 5). Comparison of *L. corallioides* and its fleshy epiphytic macroalgae NPP ($\text{mg C m}^{-2} \text{h}^{-1}$) at both stations during the early morning, late morning, afternoon and evening, showed that NPP $\text{m}^{-2} \text{h}^{-1}$ varied significantly with tidal rhythms (LWNT, MWT and HWST), being higher in *L. coralloides* than in its fleshy epiphytic macroalgae and at Station B than at Station A. (Table 4; Figs. 4 & 5).

Throughout the summer period, diel (24 h) NPP rates ranged from -78 to $178 \text{ mg C m}^{-2} \text{day}^{-1}$ in filamentous Rhodomelaceae (Station A) and from -5 to $256 \text{ mg C m}^{-2} \text{day}^{-1}$ in *S. chordalis* (Station B) (Fig. 7), being significantly higher in *S. chordalis* (KW, $H = 16.2$, $p\text{-value} < 0.001$) (Fig. 7). Diel NPP in *L. corallioides* ranged from -214 to $728 \text{ mg C m}^{-2} \text{day}^{-1}$ at Station A and from 17 to $808 \text{ mg C m}^{-2} \text{day}^{-1}$ at Station B, being significantly higher at Station B than

at Station A (KW, $H = 5.5$, $p\text{-value} < 0.05$). Diel NPP was significantly higher in *L. corallioides* than in fleshy epiphytic macroalgae at both stations (KW, $H = 25.3$, $p\text{-value} < 0.001$ and $H = 79.8$, $p\text{-value} < 0.001$). Diel respiration rates were 145 and 101 $\text{mg C m}^{-2} \text{ day}^{-1}$ in filamentous Rhodomelaceae (Station A) and *S. chordalis* (Station B), respectively, being significantly higher in filamentous Rhodomelaceae (KW, $H = 154$, $p\text{-value} < 0.001$). In comparison, diel respiration rates in *L. corallioides* were 470 and of 335 $\text{mg C m}^{-2} \text{ day}^{-1}$ at Stations A and B, respectively, being significantly higher at Station A (KW, $H = 154$, $p\text{-value} < 0.001$). Diel respiration was significantly higher in *L. corallioides* than in fleshy epiphytic macroalgae at both stations (KW, $H = 160.0$, $p\text{-value} < 0.001$). Diel GPP rates ranged from 67 to 323 $\text{mg C m}^{-2} \text{ day}^{-1}$ in filamentous Rhodomelaceae (Station A) and from 96 to 357 $\text{mg C m}^{-2} \text{ day}^{-1}$ in *S. chordalis* (Station B), being significantly higher in *S. chordalis* (KW, $H = 16.2$, $p\text{-value} < 0.001$) (Fig. 6). Diel GPP in *L. corallioides* ranged from 203 to 1198 $\text{mg C m}^{-2} \text{ day}^{-1}$ at Station A, and from 352 to 1134 $\text{mg C m}^{-2} \text{ day}^{-1}$ at Station B, being significantly higher at Station B (KW, $H = 5.5$, $p\text{-value} < 0.05$) (Fig. 6). Diel GPP was significantly higher in *L. corallioides* than in fleshy epiphytic macroalgae at both stations (KW, $H = 130.0$, $p\text{-value} < 0.001$) (Fig. 6).

4. DISCUSSION

4.1 Epiphytic macroalgal physiology

Filamentous Rhodomelaceae and *Solieria chordalis* are ubiquitous, cosmopolitan and opportunistic taxa inhabiting cool temperate shallow coastal areas (Bunker et al. 2017). Filamentous Rhodomelaceae are common in brackish estuaries, in both intertidal and subtidal areas (Baweja et al. 2016). *S. chordalis* generally grows in wave-sheltered habitats, from Ireland to the south of Morocco and the Canary Islands (Guiry & Guiry 2020). Despite

knowledge on the ecology of these epiphytic macroalgae, few studies have been carried out on their photosynthesis capacities and their contribution to the primary production or to the C cycle in the coastal ecosystems where they are present remains unknown. Physiological characteristics of algae depend on their local environment. In the Bay of Brest, although light intensity varies considerably at stations A and B, incident bottom irradiance is significantly lower at Station A (deeper) than at Station B (shallower) (Qui-Minet et al. 2018). This difference in environmental conditions suggests that species may show potential photo-acclimation/adaptation to their local environment. The characteristics of photosynthetic parameters of filamentous Rhodomelaceae and *S. chordalis* are typical of shade-growing macroalgae and in agreement with the low incident irradiance they receive at both Station A ($<100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and Station B ($<150 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) during most of the day due to the turbidity in the Bay of Brest (light extinction coefficients of 0.4 at both stations, Qui-Minet et al. 2018). Accordingly, both taxa displayed low values of compensation irradiance (E_c) and saturation irradiance (E_k) and high photosynthetic efficiency (α), as previously observed in other red macroalgae acclimated to low irradiances (Dawes et al. 1999, Johansson G & Snoeijs P 2002). However, despite the distinct depths/incident irradiances at the two stations, lower values of E_c and E_k , and higher values of α and maximal gross primary production (GPP_{MAX}) were observed at the shallower location (Station B) in *S. chordalis* than at the deeper location (Station A) in filamentous Rhodomelaceae, suggesting greater photo-acclimation to low irradiances in *S. chordalis* than in filamentous Rhodomelaceae. This difference in performance is in agreement with the very shallow locations where filamentous Rhodomelaceae are found (Baweja et al. 2016), suggesting that this taxon is better adapted/acclimated to higher irradiances. To survive under a constantly changing light environment and to optimize photosynthesis activity, red macroalgae have

evolved several long- and short-term adaptation strategies, such as thallus anatomical changes at the individual level, morphological or organizational changes at the cellular level (long-term adaptation), or functional changes at the molecular level (short-term adaptation) (Talarico & Maranzana 2000).

No significant differences were observed between stations in terms of seawater temperature, salinity, pH, or nutrients during the incubations. Nevertheless, due to its shallowness and proximity to freshwater run-off, Station B is characterized by higher variability in physico-chemical parameters (particularly in temperature, salinity, nutrients, and carbonate system parameters) than Station A (Qui-Minet et al. 2018). Hence, differences in physiological parameters, E_c and E_k , between filamentous Rhodomelaceae and *S. chordalis* may be a result of long-term adaptation or short-term acclimation to the station-specific environmental conditions (Talarico & Maranzana 2000) and/or interspecific physiological differences.

Morphological differences between epiphytic species are also likely to affect their physiology. Differences in macroalgal morphology translate into differences in the surface area available for dissolved inorganic carbon and nutrient uptake, which result in differences in photosynthetic rates (Wallentinus 1984, Dudgeon et al. 1995, Hurd et al. 1996, Johansson & Snoejis 2002, Roleda & Hurd 2019). Consequently, the polysiphonous structure of filamentous Rhodomelaceae taxa provides them with a higher surface-to-volume ratio and thus higher photosynthesis capacities. Similarly, when comparing photosynthesis capacities of several species from Rhodophyta, Johansson & Snoejis (2002) also observed that species previously classified as *Polysiphonia* spp. (filamentous Rhodomelaceae) are among those with the highest photosynthetic performances: *Polysiphonia brodiaea* (m. *Leptosiphonia*

brodiei) and *Polysiphonia fucoides* (m. *Vertebrata fucoides*) (350 and 460 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$, respectively).

4.2 Epiphytic macroalgal physiology vs. maerl physiology

Red macroalgal taxa dominate the fleshy epiphytic macroalgal flora in the maerl beds of the Bay of Brest (Qui-Minet et al. 2018) and in other temperate maerl ecosystems (Peña et al. 2014). Red algae possess several physiological mechanisms to acclimate to different light intensities (Talarico & Maranzana 2000). In this study, fleshy epiphytic macroalgae also demonstrated a capacity to adapt to deeper and low irradiance environments, with low values of E_c (22 and 15 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at stations A and B, respectively) and E_k (171 and 106 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, at stations A and B, respectively). However, due to its calcareous structure, *Lithothamnion corallioides* has lower metabolic rates (per g) than its fleshy epiphytic macroalgae counterparts (GPP rates more than 50-fold higher). Even when photosynthetic rates were normalized to algal Chl *a* content, epiphytic macroalgae had higher rates of GPP and photosynthetic efficiency than *L. corallioides*. Due to their opportunistic nature, these epiphytic species perform better in shaded environments (Burnham et al. 2022). In this respect, the higher surface-to-volume ratio of the thin and filamentous thalli of epiphytic algae maximizes light harvesting (Hurd 2000).

Due to their seasonal and patchy presence, fleshy epiphytic macroalgae contribute to the temporal and spatial heterogeneity of the physico-chemical environment by increasing the seawater diel variations in pH, $p\text{O}_2$ and $p\text{CO}_2$ (Semese et al. 2009, Cornwell et al. 2013, Short et al. 2015, Guy-Haim et al. 2020). According to our estimations for the summer season, during sunny days when low tide occurs at noon, bottom irradiances can reach 300 μmol

407 photons $\text{m}^{-2} \text{s}^{-1}$ at Station A and $>500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at Station B. Nevertheless, despite
 408 its shallowness, the Bay of Brest experiences high turbidity (Qui-Minet et al. 2018) and
 409 during the summer season high irradiances are not reached on a daily basis. According to our
 410 estimations, maerl beds experience dim irradiances during the early morning and the evening,
 411 as well as during rainy/cloudy days. Consequently, fleshy epiphytic macroalgae may
 412 overshadow *L. corallioides*, thereby significantly reducing its NPP. According to our
 413 estimations, this effect may be detrimental for *L. corallioides* physiology in the early morning
 414 and in the evening. In this context, the overall impact of fleshy epiphytic macroalgae on *L.*
 415 *corallioides* physiology and survival varies among stations is a function of the patchy
 416 distribution of fleshy epiphytic macroalgae, bottom irradiance and macroalgal physiological
 417 parameters. Large areas of maerl beds are not covered by fleshy epiphytic macroalgae and,
 418 when present, the impact of fleshy epiphytic macroalgae on the incident irradiance received
 419 by maerl algae depends on their morphology, density and biomass. Furthermore, under dim
 420 irradiances, *L. corallioides* and fleshy epiphytic macroalgae have similar values of E_c (22
 421 and $19 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at Station A, and 15 and $12 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at Station B,
 422 respectively), and compete for light. In our study, incident irradiance differed significantly
 423 between stations A and B. At Station A, incident irradiance remained lower than E_k values
 424 measured in *L. corallioides* ($171 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, Qui-Minet et al. 2021) and
 425 filamentous Rhodomelaceae ($185 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), because during most part of the day,
 426 the highest irradiance value remained lower than E_k , reaching $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$.
 427 Therefore, if fleshy epiphytic macroalgae overshadow *L. corallioides*, they may have a
 428 negative impact on maerl primary production and subsequently its growth and survival. At
 429 Station B, macroalgae experience irradiances higher than E_k (> 150 and up to $600 \mu\text{mol}$
 430 $\text{photons m}^{-2} \text{s}^{-1}$) allowing them to reach photosynthetic saturation. Therefore, at least during

the afternoon, when irradiances are maximal, fleshy epiphytic macroalgae may here protect *L. corallioides* from photoinhibition and from any potential photodamage. Interactions with other biotic and abiotic parameters may diminish or enhance these predicted effects. For instance, reduced turbidity due to water renewal from tides and bottom currents or a reduction in fleshy epiphytic macroalgae due to herbivorous grazing can maintain a favorable physico-chemical environment for maerl under low irradiances. Nevertheless, our study highlights the ambivalent relationship between maerl and its fleshy epiphytic macroalgae inhabiting highly turbid and shallow temperate ecosystems such as the Bay of Brest.

4.3 Heterogeneity of primary production in the Bay of Brest

The comparison of macroalgal primary production (NPP) between the two maerl beds studied here demonstrated that maerl bed primary production has heterogeneous spatio-temporal patterns. In the Bay of Brest, variability in depth among stations translated into higher bottom irradiances at Station B, and therefore higher algal NPP for both *L. corallioides* and its fleshy epiphytic macroalgae. In this context, due to the lower irradiance required by algae to reach photosynthetic saturation at Station B (i.e. E_k of $100 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ for both *L. corallioides* and *S. chordalis*), maximal productivity can be reached, at least around noon, but also during the morning and afternoon, depending on tidal height. However, at Station A, maximal macroalgal productivity may only be reached when low tide occurs around noon during high water spring tides. Due to the higher spatial heterogeneity of living *L. corallioides* biomass in the maerl bed at Station A (1 to 9 kg DW m^{-2}) than at Station B ($3\text{--}6 \text{ kg m}^{-2}$) (Qui-Minet et al. 2018), maerl NPP showed higher variability at this location. The contribution of fleshy epiphytic macroalgae to the NPP also varies with bottom irradiance.

454 Filamentous Rhodomelaceae have a significantly higher GPP_{MAX} than *S. chordalis*, but their
 455 productivity is limited by incident light. When bottom light intensity is below 50 μmol
 456 photons $\text{m}^{-2} \text{s}^{-1}$, filamentous Rhodomelaceae and *S. chordalis* have similar NPP per m^2 . On
 457 the other hand, above 400 μmol photons $\text{m}^{-2} \text{s}^{-1}$, filamentous Rhodomelaceae can exceed the
 458 value of *S. chordalis* NPP by two-fold. Nevertheless, according to our estimations for
 459 summer 2015, maximal bottom irradiance at Station A was 300 μmol photons $\text{m}^{-2} \text{s}^{-1}$ (around
 460 noon and under a HWST) and thus, *L. corallioides* and its fleshy epiphytic macroalgal NPP
 461 values were higher at Station B.

462 The impact of fleshy epiphytic macroalgae on maerl bed primary production depends on their
 463 biomass and taxon composition, fleshy epiphytic algal biomass being similar between *S.*
 464 *chordalis* (Station B) and filamentous Rhodomelaceae (Station A) (Qui Minet et al. 2018).
 465 The differences in NPP between these epiphytic algae were mainly correlated with bottom
 466 irradiance and their physiological rates. Despite significantly higher biomass of *L.*
 467 *corallioides* relative to epiphyte biomass on maerl beds (fleshy epiphytic biomass was less
 468 than 50 g DW m^{-2} at both stations, whereas maerl biomasses ranged from 0.85 to 8.5 kg DW
 469 m^{-2} at Station A and from 3.1 to 5.6 kg m^{-2} at Station B, Qui-Minet et al. 2018), fleshy
 470 epiphytic macroalgae had higher photosynthetic rates, and accounted for one fourth of maerl
 471 bed NPP ($22 \pm 13\%$ and $24 \pm 0.02\%$ of NPP at stations A and B, respectively), independently
 472 of tidal height and incident surface irradiance. Species interactions were not considered here,
 473 but may affect these macroalgal productivity estimations. The relative contribution of *L.*
 474 *corallioides* to the estimated NPP can be effectively overestimated due fleshy epiphytic
 475 macroalgae shading the host *L. corallioides*. Consequently, fleshy epiphytic macroalgae may
 476 actually have a relatively higher contribution to maerl bed productivity than estimated here.
 477 Nevertheless, the shading effect of fleshy epiphytic macroalgae may also protect *L.*

corallioides from photo-inhibition under high irradiances, as occurs at Station B when bottom irradiance is greater than the irradiance of photosynthetic saturation of *L. corallioides* and *S. chordalis* ($> 100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) at Station B.

Due to the highly variable irradiance and tidal rhythms, significant daily changes in macroalgal diel (24 h) NPP can be observed at each station through the summer season. When the tide is high, summer days with low light intensity can lead to a negative macroalgal NPP ($R > GPP$). This situation is more accentuated at the deepest station (Station A) and correlated with the lower bottom irradiances at this location, which rarely reach saturating irradiances for *L. corallioides* and filamentous Rhodomelaceae. Previous studies have defined maerl beds in the Bay of Brest as heterotrophic communities, and maximal community respiration measured during summer has been estimated at $2 \text{ g C m}^{-2} \text{ day}^{-1}$ (Martin et al. 2007), including fleshy epiphytic macroalgae, the epiphytic microbiome (bacteria and microflora), the benthic fauna and the microphytobenthos associated with the sediment (Martin et al. 2007). Although this value may vary among maerl beds, according to our data, macroalgal (maerl and epiphytes) contributions to the maerl bed community respiration are 29–31% at Station A (21–24% for *L. corallioides* and 7% for filamentous Rhodomelaceae) and 22% at Station B (17% for *L. corallioides* and 5% for *S. chordalis*). On the other hand, mean community GPP in the Bay of Brest in summer has been estimated to be $1.3 \text{ g C m}^{-2} \text{ day}^{-1}$ (Martin et al. 2007). According to our estimations, summer algal GPP represents 21% (Station A) and 35% (Station B) of this value during low irradiance days, but would exceed this value by 15% during high irradiance days ($1.5 \text{ g C m}^{-2} \text{ day}^{-1}$ at both stations A and B).

5. CONCLUSIONS

The impact of fleshy epiphytic macroalgae on maerl physiology is equivocal and it depends on bottom incident irradiance, and therefore on the location of maerl beds and their specific water depths and turbidity. Under low irradiances, fleshy epiphytic macroalgae will compete with maerl for light, and under high irradiances they will protect maerl. The overall impact of fleshy epiphytic macroalgae on maerl physiology not only depends on their abundance, but on taxon composition and morphology (i.e. shading effect). In addition to the interaction between coralline algae and their epiphytes, future research should also address other biotic interactions such as grazing or interactions with local abiotic conditions, such as hydrodynamic regimes, because they may preserve maerl algae from any potential negative impact of their epiphytes.

At the ecosystem scale, bottom incident irradiance in coastal ecosystems is affected by anthropogenic activities, including nutrients and organic matter, that may increase the seawater turbidity and sedimentation rates. Our results highlight the importance of monitoring the incident irradiance received by macroalgal species acting as ecosystems engineers, because they play fundamental roles in biodiversity preservation and biogeochemical cycles. Assessing maerl bed health and applying ecosystem management policies to define threshold values of physico-chemical parameters (incident irradiance, turbidity, nutrients release, etc.) thus requires better knowledge on the physiology of maerl algae as well as of their fleshy epiphytes.

This is the first study to compare the physiological parameters of *Lithothamnion corallioides* and its fleshy macroalgal epiphytes. This is also the first assessment of the contribution (~ 25%) of fleshy epiphytic macroalgae to maerl bed C budgets. Although physiological rates of maerl are significantly lower than those of fleshy epiphytic macroalgae, due to their high living biomass in the Bay of Brest, their contribution to the C cycles is very high (~ 75% of

the total NPP). A more accurate estimation of the fleshy epiphytic macroalgae contribution to maerl bed productivity requires studying their physiology under different environmental conditions, such as temperature, irradiance or nutrient concentrations, throughout their period of occurrence. Finally, this study is also among the first to assess the contribution of fleshy epiphytic macroalgae to the primary production of coastal ecosystems dominated by foundation macroalgal species.

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TABLES.

Table 1.

Summary of the mean (\pm S.D.) parameters of photosynthesis-irradiance (P-E) curves for filamentous Rhodomelaceae and *Solieria chordalis* ($n = 5$) and of Kruskal-Wallis tests (H) to compare physiological parameters among taxa. GPP_{MAX} and R are the maximal gross primary production and respiration rates, respectively, E_k is the irradiance of saturation, E_c is the irradiance of compensation, R is the respiration rate, α (α) is the photosynthetic efficiency. Bold values indicate statistical significance at $p < 0.05$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Parameter	Filamentous Rhodomelaceae	<i>Solieria chordalis</i>	Comparison among species	
			H	p-value
GPP_{MAX} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$)	245 \pm 54	144 \pm 8	4.8	<0.05*
R ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$)	24 \pm 2	15 \pm 3	6.8	<0.01**

Ek ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	185 ± 90	115 ± 26	6.6	<0.01**
Ec ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	19 ± 4	12 ± 3	11.5	<0.01**
α $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$	1.0 ± 0.3	1.4 ± 0.4	8.2	<0.05*
GPP _{MAX} ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$)	114 ± 58	206 ± 11	12.5	<0.01**
α ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$) ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) ⁻¹)	0.6 ± 0.3	1.9 ± 0.7	8.2	<0.05*

Table 2. Summary of Kruskal-Wallis tests used to compare the physiological parameters between non-calcareous epiphytic macroalgae and *Lithothamnion corallioides* at stations A and B (n = 5). GPP_{MAX} and R are the rates of maximal gross primary production and respiration, respectively, expressed per unit of Chl *a* ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$), Ek is the irradiance of saturation ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), Ec is the irradiance of compensation ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), and α ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$) is the photosynthetic efficiency. Bold values indicate statistical significance at $p < 0.05$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Parameters	Station A		Station B	
	H	p-value	H	p-value
NPP	6.82	0.009**	6.82	0.009**
R	6.82	0.009**	6.82	0.009**
Ek	0.27	0.602	0.53	0.465
Ec	0.53	0.465	0.53	0.465
α	6.82	0.009**	6.82	0.009**

Table 3. Summary of Kruskal Wallis tests used to compare estimated bottom irradiances between stations and within stations over the course of the summer season. Bold values indicate statistical significance at $p < 0.05$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Comparison of bottom irradiance ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) between stations								
Station A vs. B	Early morning		Late morning		Afternoon		Evening	
	H	p-value	H	p-value	H	p-value	H	p-value
	6.4	0.001***	11.5	<0.001***	77.4	<0.001***	77.4	<0.001***
Comparison between days of bottom irradiance ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)								
	Early morning		Late morning		Afternoon		Evening	
	H	p-value	H	p-value	H	p-value	H	p-value

	H	p-value	H	p-value	H	p-value	H	p-value
Station A	71.5	<0.001***	144.1	<0.001***	229.5	<0.001***	80.1	<0.001***
Station B	80.8	<0.001***	167.4	<0.001***	222.4	<0.001***	66.7	<0.001***

Table 4. Summary of Kruskal-Wallis tests used to compare the rates of net primary production (in mg C m⁻² h⁻¹) per m⁻² h⁻¹ in filamentous Rhodomelaceae (Station A), *S. chordalis* (Station B) and *L. corallioides* (stations A and B) under high water spring tide (HWST), mean water tide (MWT) and low water neap tide (LWNT), during the early morning, late morning, afternoon and evening (n> 10). Bold values indicate statistical significance at p < 0.05. *** p < 0.001; ** p < 0.01; * p < 0.05.

C (mg m ⁻² h ⁻¹)								
	Early morning		Late morning		Afternoon		Evening	
	H	p-value	H	p-value	F	p-value	F	p-value
Filamentous Rhodomelaceae Tides	11.3	<0.01**	15.8	<0.001***	22.5	<0.001***	19.3	<0.001***
	HWST > LWNT MWT = LWNT		HWST < MWT & LWNT		HWST & MWT > LWNT		LWNT & MWT > HWST	
<i>S. chordalis</i> : Tides	8.8	<0.05*	11.5	<0.01**	28.2	<0.001***	17.1	<0.001***
	Inconclusive		Inconclusive		HWST > MWT > LWNT		LWNT & MWT > HWST	
<i>L. corallioides</i> Station A: Tides	11.3	<0.01**	15.8	<0.001***	22.5	<0.001***	19.3	<0.001***
	HWST > LWNT, HWST > MWT MC = LC		HWST > MWT, HWST > LWNT, HWST = MWT		HWST & MWT > LWNT		MWT & LWNT > HWST	
<i>L. corallioides</i> Station B: Tides	12.4	<0.01**	17.1	<0.001***	23.2	<0.001***	19.7	<0.001***
	HWST = MWT LWNT & MWT > HWST		LWNT > HWST & MWT		HWST & MWT > LWNT		LWNT & MWT > HWST	

FIGURES

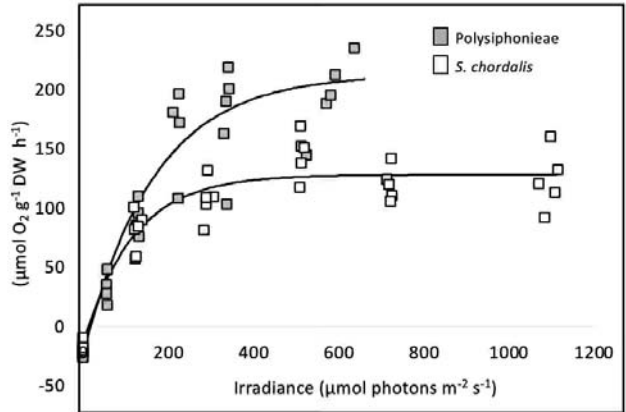


Figure 1. Relationship between net primary production (in O_2 flux per algal g DW) and irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in summer in filamentous Rhodomelaceae (dark squares) and *Solieria chordalis* (white squares).

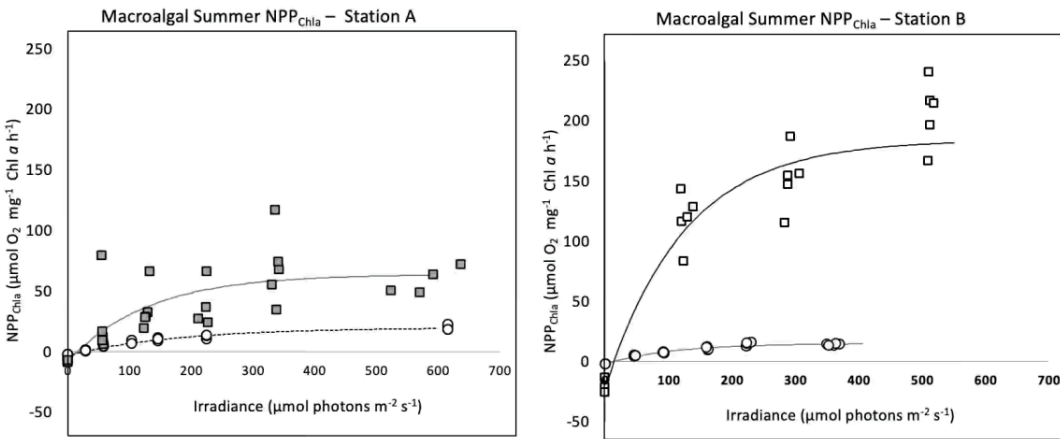


Figure 2. Relationship between net primary production per Chl *a* content (in O_2 flux per mg Chl *a*) and irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in summer in *Lithothamnion corallioides* (white dots), and filamentous Rhodomelaceae at Station A (gray squares) and *L. corallioides* (white dots) and *Solieria chordalis* (white squares) at Station B.

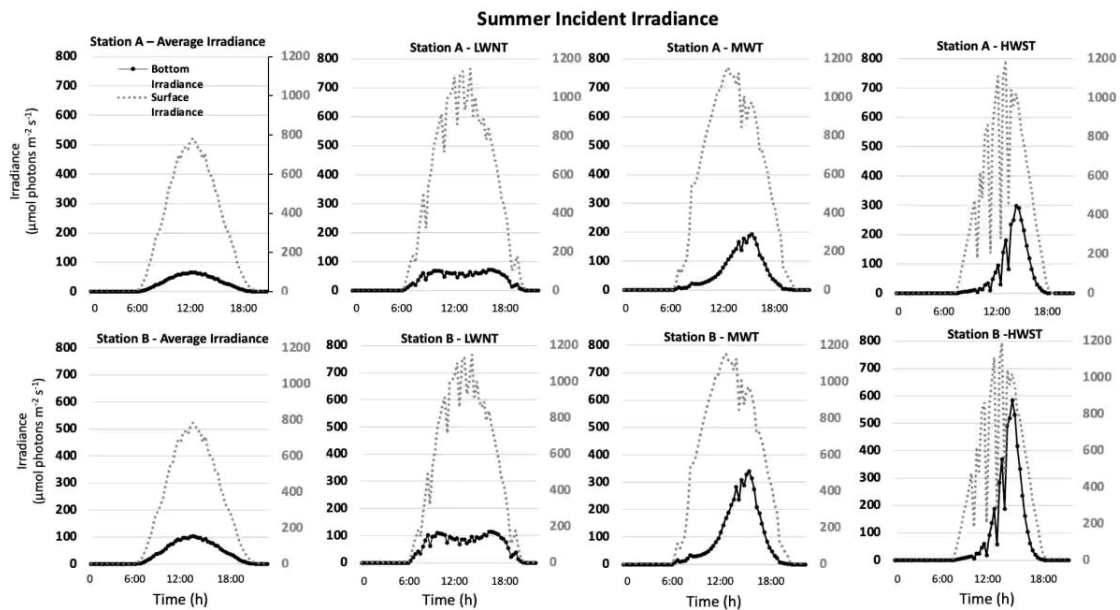


Figure 3. Estimated 24-h bottom irradiance at Station A and Station B considering average summer bottom incident irradiance and during specific summer days with low water neap tide (LWNT, 1 September 2015), medium water tide (MWT, 20 June 2015), and high water spring tide (HWSP, 25 June 2015).

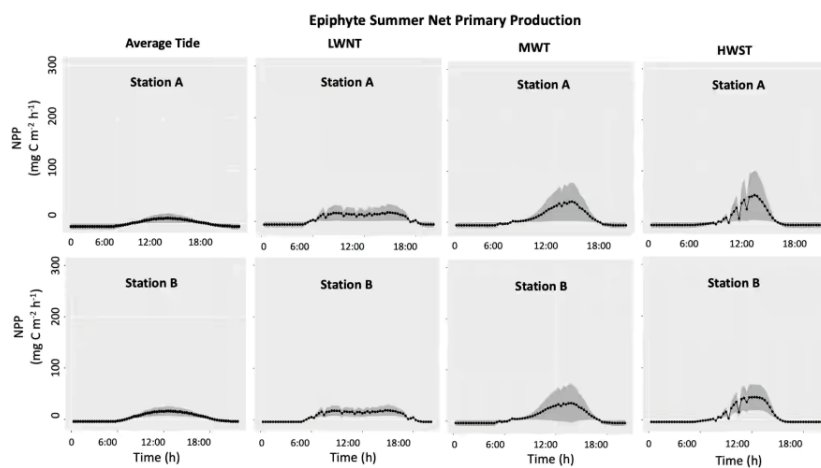


Figure 4. Estimated mean net primary production over 24 h in filamentous Rhodomelaceae at Station A and *Solieria chordalis* at Station B, from average summer bottom incident irradiance and during specific summer days with low water neap tide (LWNT, 1 September 2015), medium water tide (MWT, 20 June 2015), and high water spring tide (HWSP, 25 June 2015).

785 2015). The shaded area represents the standard deviation as a function of the heterogeneity
786 of *Lithothamnion corallioides* biomass at stations A and B, respectively ($n = 5$).
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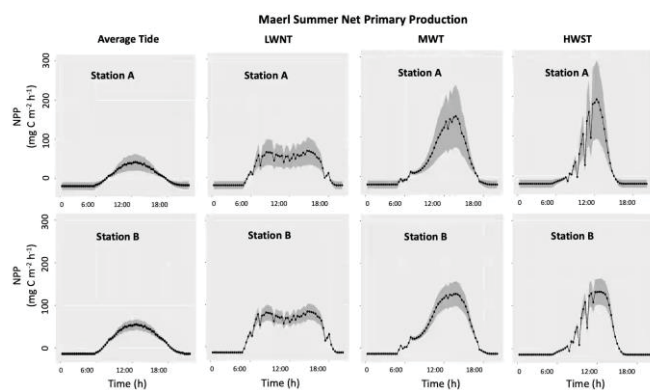


Figure 5. Estimated mean net primary production over 24 h considering average bottom irradiance during summer season in *Lithothamnion corallioides* at stations A and B, from average summer bottom incident irradiance and during specific summer days with low water neap tide (LWNT, 1 September 2015), medium water tide (MWT, 20 June 2015), and high water spring tide (HWSP, 25 June 2015). The shaded area represents the standard deviation as a function of the heterogeneity of *L. corallioides* biomass at stations A and B, respectively (n = 5).

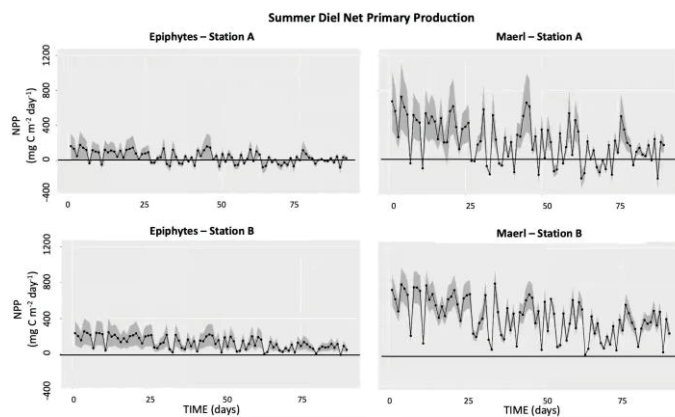


Figure 6. Estimated diel (24-h) net primary production in epiphytes (filamentous Rhodomelaceae and *Solieria chordalis*) and *Lithothamnion corallioides* at stations A and B during the summer season. The shaded area represents the standard deviation as a function of the heterogeneity of macroalgal biomass at stations A and B, respectively (n = 5).

APPENDICES/SUPPLEMENTARY FIGURES

Figure 1. Estimated daily bottom irradiance at station A during the summer season.

Figure 2. Estimated daily bottom irradiance at station B during the summer season.