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Zujaila Nohemy Qui-minet, Dominique Davoult, Jacques Grall, Coralie Delaunay, Christophe Six, Thierry Cariou, Sophie Martin

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1 **PHYSIOLOGY OF MAERL ALGAE: COMPARISON OF INTER- AND**
2 **INTRASPECIES VARIATIONS**

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4 [ZUJAILA NOHEMY QUI-MINET](#)^{1, *}, [DOMINIQUE DAVOULT](#)¹, [JACQUES GRALL](#)², [CORALIE](#)
5 [DELAUNAY](#)¹, [CHRISTOPHE SIX](#)¹, [THIERRY CARIOU](#)³, [SOPHIE MARTIN](#)¹

6
7 ¹Sorbonne Université, CNRS, UMR 7144 Adaptation et Diversité en Milieu Marin, Station
8 Biologique de Roscoff, Place Georges Teissier, 29688 Roscoff Cedex, France.

9 ²Université de Bretagne Occidentale, IUEM, Place Nicolas Copernic, 29280 Plouzané,
10 France.

11 ³Sorbonne Université, CNRS, Fédération de Recherche FR2424, Station Biologique de
12 Roscoff, Place Georges Teissier, 29680, Roscoff, France.

13
14 *Corresponding author: zquiminet@sb-roscoff.fr

15 **Running head: Physiology of maerl algae.**

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28 **ABSTRACT**

29 Free-living red coralline algae play an important role in the carbon and carbonate cycles of
30 coastal environments. In this study, we examined the physiology of free-living coralline algae
31 forming maerl beds in the Bay of Brest (Brittany, France), where *Lithothamnion corallioides*
32 is the dominant maerl (i.e. rhodolith) species. *Phymatolithon calcareum* and *Lithophyllum*
33 *incrustans* are also present (in lower abundances) at a specific site in the bay. We aimed to
34 assess how maerl physiology is affected by seasonality and/or local environmental variations
35 at the inter- and intraspecific levels. Physiological measurements (respiration, photosynthetic
36 and calcification rates) were performed using incubation chambers in winter and summer to
37 compare (1) the dominant maerl species at three sites and (2) three co-existing maerl species
38 at one site. Comparison of the three co-existing maerl species suggests that *L. corallioides* is
39 the best adapted to the current environmental conditions in the Bay of Brest, because this
40 species is the most robust to dissolution in the dark in winter and has the highest calcification
41 efficiency in the light. Comparisons of *L. corallioides* metabolic rates between stations
42 showed that morphological variations within this species are the main factor affecting its
43 photosynthetic and calcification rates. Environmental factors such as freshwater inputs also
44 affect its calcification rates in the dark. In addition to interspecies variation in maerl
45 physiology, there were intraspecific variations associated with direct (water physico-
46 chemistry) or indirect (morphology) local environmental conditions. This study demonstrates
47 the plasticity of maerl physiology in response to environmental changes, which is
48 fundamental for maerl persistence.

49

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53 **Keywords:** calcification, coralline algae, environmental conditions, field experiment,
54 photosynthesis, physiology, plasticity, rhodoliths.

55

56 **Abbreviations:** Ω_{Ar} , aragonite saturation state; C, carbon; $CaCO_3$, calcium carbonate;
57 CTD probe, conductivity temperature and depth probe; DIC, dissolved inorganic
58 carbon; DW, dry weight; *E*, irradiance; *Ec*, irradiance of compensation; *Ek*, irradiance
59 of saturation; *G*, net calcification; *G_D*, calcification in the dark; *G_{MAX}*, maximal gross
60 calcification; *G_L*, calcification in the light; *GPP*, gross primary production; *GPP_{MAX}*,

61 maximal gross primary production; KW, kruskal-wallis test; MPT, montecarlo
62 permutation test; NH_4^+ , ammonium; NO_3^- , nitrate; *NPP*, net primary production; pH_T ,
63 Total scale pH; PO_4^{3-} , phosphate; *R*, respiration; R/V, research vessel; Si(OH)_4 ,
64 silicate; T_A , Total Alkalinity; v/v, volume (solute) per volume (solvent); Y_{MAX} , maximal
65 gross yield.

66

67

68 Introduction

69 Free-living non-geniculate coralline algae, also referred as maerl (or rhodoliths), are
70 distributed worldwide in coastal systems stretching from the tropics to polar regions (Foster
71 2001). They can accumulate and form large beds of live and/or dead maerl (Birkett et al.
72 1998). Individual thalli can range from 1 to 10 cm in length and take on highly branched to
73 spherical-shaped forms, depending on the species and environmental conditions (Bosence
74 1976, Steneck and Adey 1976, Birkett et al. 1998, Foster et al. 2013). Their tridimensional
75 structure bestows them with a very important role as foundation species – species that harbor
76 a diverse assemblage of flora and fauna (Cabioch 1969, Keegan 1974, Peña et al. 2014) and
77 serve as nursery habitats for many juvenile invertebrates and fish (Grall 2002; Kamenos et
78 al. 2004).

79 Coralline algae have significantly lower growth rates than non-calcareous algae and,
80 among coralline algal species, maerl growth rates are among the lowest (Heijden and
81 Kamenos 2015). Previous studies on maerl growth rates have shown variation between
82 species, thallus ages, seasons and environmental conditions. Growth rates in temperate
83 ecosystems can range from 0.01 to 2.5 mm per year (Adey and McKibbin 1970, Bosence
84 1980, Edyvean and Ford 1987, Potin et al. 1990, Fazakerley and Guiry 1998, Blacke and
85 Maggs 2003, Wilson et al. 2004, Kamenos and Law 2010).

86 Despite their slow growth rate, their high abundance and spatial distribution indicates
87 high carbon (C) and calcium carbonate (CaCO_3) production rates (Foster 2001). Due to their
88 photosynthetic and calcification capacities, maerl species are thus considered as major
89 contributors to the C and CaCO_3 cycles in coastal systems all over the world (Martin et al.
90 2005, Schwarz et al. 2005, Martin et al. 2007, Nelson 2009, Amado-Filho et al. 2012, Basso
91 and Granier 2012).

92 Recent advancements in molecular biological species identification have provided
93 important information on coralline algal diversity and distribution (Hernández-Kantún 2015,
94 Pardo et al. 2014). The distribution of the various maerl species is thought to be greatly

95 influenced by irradiance, temperature, salinity, and substratum (Adey and McKibbin 1970,
96 Birkett et al. 1998, BIOMAERL Team 1999). Although species with different geographic
97 boundaries can coexist in the same location, their abundance and survival depend greatly on
98 their environmental thresholds and plasticity to withstand variability in abiotic factors (Hurd
99 et al. 2014). For instance, algae are subject to large and non-predictable fluctuations of
100 irradiance due to cloud cover and turbidity, in addition to the predictable seasonal variations
101 in light intensity and photoperiod (Williamson et al. 2014). Species located in the shallow
102 photic zone usually use efficient mechanisms regulating light utilization to withstand
103 seasonal and daily variations in irradiance, allowing them to harvest dim light irradiances
104 (Kirk 2011) or to limit photo-inhibition and avoid photo-oxidative damage (Gomez et al.
105 2004, Burdett et al. 2014, Vasquez-Elizondo and Enriquez 2017). Algae may thus respond to
106 variation in irradiance by acclimating and/or adapting their morphology and physiology, for
107 example by modifying their pigment content and composition (Kim et al. 2013, Burdett et al.
108 2014). Interestingly, red coralline algae can occur under very high irradiance levels in the
109 tropics ($> 1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and also at the lower limit of the photic zone ($< 1 \mu\text{mol}$
110 $\text{photons m}^{-2} \text{s}^{-1}$; Burdett et al. 2014), suggesting that they have developed different adaptation
111 mechanisms to colonize various light niches.

112 Maerl species may also have to cope with different ranges and variations in
113 temperature, with a decrease towards higher latitudes and large seasonal variations at mid-
114 latitudes (Hurd et al. 2014). At a local scale, temperature variations also affect the vertical
115 distribution of maerl species (Williamson et al. 2014). Maerl beds located in mid-latitudes
116 and shallow environments, such as those found in the Bay of Brest (western France), face
117 high seasonal and daily temperature variability (Martin et al. 2006, Qui Minet et al. 2018).
118 Seawater temperature regulates chemical reaction rates and thus metabolic pathways.
119 Variation in temperature has an impact on carbon fixation, skeletal magnesium incorporation,
120 growth rates, and reproduction (Williamson et al. 2014). Comprehension of how the
121 physiology within a species is regulated by temperature variations is necessary to understand
122 their current distribution and how they will be affected by global change.

123 Salinity also affects algal physiology (King and Schramm 1982). Maerl beds located
124 in coastal systems can experience freshwater inputs and thus bursts of extremely low salinity.
125 Some maerl species such as *L. corallioides* and *P. calcareum* are known to be adapted to

126 typical marine saline environments (Birkett et al. 1998), whereas other species such as *L.*
127 *incrustans* are known to be euryhaline (Grall 2002). Extreme low salinity values have been
128 linked to negative impacts on metabolic processes, particularly calcification rates (King and
129 Schramm 1982, Schoenrock et al. 2018).

130 When located in shallow productive zones, maerl beds may require water movement
131 to avoid sedimentation and to limit the colonization of their thalli by non-calcareous epiphytic
132 algae (Steneck 1986). Furthermore, currents have been correlated with species distribution
133 and maerl morphology (Bosence 1976, Qui-Minet et al. 2018).

134 The objective of this study was to provide information on how the physiology of
135 coralline algal species forming maerl beds is affected by seasonality and/or local
136 environmental variations at the inter- and intraspecific levels. Knowledge on how temperate
137 maerl species physiology responds to current environmental conditions is essential to
138 understand their evolution under local and global change scenarios. In this study, we studied
139 variations in the physiology of *L. corallioides*, the most abundant maerl species in the Bay
140 of Brest (Britany, France) by comparing its physiological rates (i) between stations located
141 in different maerl beds of the Bay of Brest and (ii) with other co-existing maerl species:
142 *Phymatolithon calcareum* and *Lithophyllum incrustans*, also present at a specific location,
143 albeit at lower abundances (Qui-Minet et al. 2018; Fig. 1). Although the physiology of the
144 dominant species *L. corallioides* has been previously studied (Martin et al. 2006), this is the
145 first study to report *P. calcareum* and *L. incrustans* metabolic rates under *in situ* conditions.
146 We hypothesized that physiological performance of maerl species in the Bay of Brest i) varies
147 with local environmental factors and ii) affects their abundance and distribution.

148

149 **MATERIALS AND METHODS**

150 *Biological material*

151 Live maerl algae were collected in maerl beds located in the Bay of Brest (Brittany,
152 France), where mean tidal range is 4 m and maximum tidal range is 8 m. Sampling stations
153 were located in the northern basin for Station A (48°21'57"N, 04°26'47"W), and in the
154 southern basin for Stations B (48°19'58"N, 04°19'57"W) and C (48°17'304"N,
155 04°24'029"W) (Fig. 1). Chart datum depths are 2.5, 0.7, and 1.7 m at Station A, B and C,
156 respectively. Incident irradiance at the bottom, calculated from light extinction coefficients

157 in Qui-Minet *et al.* (2018), ranges at solar noon and high tide: from 10 (Station A) to 20 (C)
158 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in winter and from 50 (A) to 170 (C) $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in summer. It
159 ranges at solar noon and low tide: from 75 (A) to 190 (B) $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in winter, and
160 from 270 (A) to 570 (B) $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in summer. We collected *L. corallioides*
161 specimens at all three stations (A, B and C) and *P. calcareum* and *L. incrustans* specimens
162 at Station B, the only station of the study where the three maerl species co-exist (Fig. 2).
163 Algae were collected with a Van Veen grab (5 replicates of 0.1 m² per station). Maerl thalli
164 were carefully cleaned with seawater to remove sediments and were gently brushed when
165 needed to remove epiphytic organisms. Thalli size ranged from 1 to 2 cm, from 1.5 to 2.5
166 cm, and from 1.5 to 3 cm at stations A, B and C in *L. corallioides*; from 1.5 to 4 cm in *P.*
167 *calcareum*, and from 2 to 4 in *L. incrustans*. It is worth noting that as a result of
168 hydrodynamism (higher bottom currents), *L. corallioides* at Station C, presents a compact
169 shape relative to *L. corallioides* arbuscular shape at Stations A and B (Qui-Minet *et al.* 2018).

170

171

172 *Pigment analyses*

173 A sub-sample of the algal specimens was rinsed with filtered autoclaved seawater to remove
174 salt, stored in 2 mL cryotubes and frozen in liquid nitrogen. Samples were preserved at -80°C
175 prior to lyophilization until pigment analyses. To obtain a fine powder, samples placed in
176 plastic tubes were ground with 0.5 cm stainless steel beads (Brammer) using a Tissue Lyser
177 II (QIAGEN). Main pigments on maerl species were analyzed from 200-300 mg dry weight
178 (DW) using high-performance liquid chromatography (HPLC) according to Noisette *et al.*
179 (2013).

180

181 *Incubation procedure*

182 Maerl physiology was assessed in winter (February and March 2015) and in summer
183 (September 2015) during two light and dark incubation experiments. In the first experiment
184 (Exp. 1), *L. corallioides* specimens from Stations A, B and C were incubated under six
185 different levels of irradiance, including maximum surface irradiance (100%) and reduced
186 irradiance levels (65%, 47%, 27%, 13%, 6%). Irradiance levels were implemented by using
187 opacifying neutral filters in the dark (dark chambers), in winter (26-27 February 2015) and

188 summer (16-17 September 2015). In the second experiment (Exp. 2), the three species (*L.*
189 *corallioides*, *P. calcareum* and *L. incrustans*) from Station B were incubated in parallel under
190 surface irradiance and in the dark, in winter (16 March 2015) and summer (18 September
191 2015). Maerl thalli (corresponding to a mass of 15-30 g DW) were incubated in 220 mL in-
192 house-designed chambers filled with seawater collected ~ 1 m above the bottom of each
193 station with a Niskin bottle. Incubations lasted around 1 hour in order to avoid oxygen
194 saturation greater than 120% during light incubations and to maintain oxygen saturation
195 above 80% at the end of dark incubations.

196 Incubations were performed on board the R/V *Albert Lucas* immediately after
197 collecting the algae. Chambers were filled with bottom seawater from each station and kept
198 in a water bath with a continuous flow of water coming from the bottom to maintain algae at
199 the *in situ* temperature. For each irradiance level and in the dark, chambers without algae
200 were used as controls.

201

202 *Environmental parameters*

203 Surface irradiance (PAR, $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was measured every minute using a LI-COR
204 quantum sensor (LI 192 SA) during the incubation. In Exp. 1, incubations of *L. corallioides*
205 were done between 10:00 and 16:00. In Exp. 2, incubations of the three species at surface
206 irradiance were done between 15:00 and 17:00.

207 Seawater physico-chemical parameters were measured before each incubation at each
208 station from bottom seawater (approximately 1 m above bottom). Salinity and temperature
209 at the bottom were measured using a CTD probe (QSP-2300, Sea-Bird-Electronics).
210 Seawater samples for nutrient assays (NO_3^- , NH_4^+ , PO_4^{3-} and Si(OH)_4) and total alkalinity
211 (T_A) were filtered using 0.22 μm Sterivex cartridges (Millipore). NH_4^+ and T_A samples were
212 stored in 100 mL borosilicate glass bottles. Reagents (R1: phenol nitroprusside solution and
213 R2: complexing alkaline solution with chlorine) were added to samples intended for NH_4^+
214 analysis and then stored in the dark until further analysis. Samples for T_A measurements were
215 poisoned with mercuric chloride (0.02% v/v; Dickson et al. 2007) and then stored in a dark
216 cool place. Samples for NO_3^- , PO_4^{3-} and Si(OH)_4 analyses were stored at 4°C on board and
217 then frozen at -20°C in the lab (4-8 h later) until further analysis. NH_4^+ concentration was
218 determined using the Solorzano et al. (1969) method. NO_3^- , NH_4^+ , PO_4^{3-} and Si(OH)_4

219 concentrations in seawater were measured according to Aminot and K erouel (2007). T_A was
220 measured using HCl 0.01 N potentiometric titration with an automatic titrator (Titroline
221 alpha, Schott Si Analytics) calibrated on the National Bureau of Standards scale and by using
222 the Gran method of non-linear least-squares fit applied to pH variations from 3.5 to 3.0 mEq
223 L⁻¹ (Dickson et al. 2007). Total scale pH (pH_T) and temperature were measured using a pH
224 meter (HQ40D, Hatch Lange Ltd portable LDOTM) standardized with Tris-HCl and AMP
225 buffer solutions. Dissolved inorganic carbon (DIC) and aragonite saturation state (Ω_{Ar}) were
226 calculated from pH_T, T_A, salinity, temperature and PO₄³⁻ concentrations, using CO₂sys
227 software, version 2.1 (Lewis and Wallace 1998). Calculations were based on a set of
228 constants K1 and K2 from Mehrbach et al. (1973) refitted by Dickson and Millero (1987).
229 Dissolved oxygen (O₂) was measured using an oxygen probe (Oxymeter HQ40D, Hatch
230 Lange, Ltd portable LDOTM).

231

232 *Physiological measurements*

233 Net production (light incubation) and respiration (dark incubation) rates were determined by
234 measuring O₂ concentration at the beginning and at the end of the incubations. Dark
235 respiration referred to non-photorespiratory mitochondrial respiration. Calcification rates
236 were calculated using the alkalinity anomaly technique (Smith and Key 1975); water samples
237 were taken at the beginning and at the end of the incubations. Rates were corrected with those
238 from control chambers containing only seawater. At the end of incubations, samples of *L.*
239 *corallioides*, *P. calcareum* and *L. incrustans* were collected and dried (60°C, 48 h) for
240 biomass determination.

241 Rates of algal primary production (net primary production, *NPP* and gross primary
242 production, *GPP*), respiration (*R*) and net calcification (*G*) in the light (*G_L*) and in the dark
243 (*G_D*) were normalized to the algal biomass (g DW). To obtain the net and the gross yield
244 (efficiency of Chl *a* in *NPP* and *GPP*), the *NPP* and the *GPP* were normalized to the algal
245 Chl *a* content (mg Chl *a* g⁻¹ DW maerl). *G* was calculated using the following relationship:
246 $\text{Ca}^{2+} + 2 \text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$, for which T_A decreases by 2 equiv for each mol of
247 CaCO₃ precipitated. *NPP* (or *R*), *GPP*, *Yield_{net}* (or *gross*) and *G* were calculated according to
248 Equations (1), (2), (3) and (4):

249

250
$$NPP \text{ or } R (O_2) = \frac{\Delta O_2 \times V}{DW \times \Delta t} \quad (1)$$

251

252
$$GPP = NPP + R \quad (2)$$

253

254
$$Yield_{net \text{ (or gross)}} = \frac{NPP \text{ (or } GPP)}{Chl \ a} \quad (3)$$

255

256
$$G (CaCO_3) = \frac{\Delta T_A \times v}{2 \times DW \times \Delta t} \quad (4)$$

257

258 where NPP ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$) is the net primary production rate, R ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$)
 259 1) is the respiration rate, GPP ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$) corresponds to the sum of absolute values
 260 of NPP and R , $Yield_{net \text{ (or gross)}}$ ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$) is the NPP or GPP normalized to
 261 the chlorophyll a content ($Chl \ a$, $\text{mg Chl g}^{-1} \text{ maerl DW}$), G ($\mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ DW h}^{-1}$) is the
 262 net calcification rate in the light (G_L) or dark (G_D), ΔO_2 ($\mu\text{mol L}^{-1}$) is the variation of dissolved
 263 oxygen concentration between the beginning and the end of the incubation, v (L) is the
 264 volume occupied by the seawater in the chamber, DW (g) the dry weight of algae in the
 265 chamber, Δt (h) is the incubation time, ΔT_A ($\mu\text{mol L}^{-1}$) is the change in total alkalinity
 266 between the beginning and the end of the incubation.

267 The energy available from photosynthesis for growth was measured in the three species using
 268 the photosynthesis-to-respiration ratio ($GPP:R$). The level of interaction between
 269 photosynthesis and calcification was calculated for each species through the ratio of
 270 calcification (in the light) to photosynthesis ($G_L: GPP$). Both ratios were calculated in winter
 271 and summer under ambient irradiance for *L. corallioides*, *P. calcareum*, and *L. incrustans*
 272 (Station B).

273 The relationship between irradiance (E , $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) and NPP , $Yield_{Net}$ or G
 274 was obtained using the Chalker (1981) equation:

275
$$NPP = GPPmax \times \left(1 - e^{\frac{-E}{Ek}}\right) - R \quad (5)$$

276

277
$$Yield_{net} = Ymax \times \left(1 - e^{\frac{-E}{Ek}}\right) - R \quad (6)$$

278

279

$$280 \quad G = G_{max} \times \left(1 - e^{\frac{-E}{Ek}}\right) - G_D \quad (7)$$

281

282 where NPP ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$), $Yield_{Net}$ ($\mu\text{mol O}_2 \text{ mg}^{-1} \text{ Chl } a \text{ h}^{-1}$) and G_L ($\mu\text{mol CaCO}_3 \text{ g}^{-1}$
283 DW h^{-1}) are the net primary production, net yield, and net calcification rates at a given
284 irradiance (E , $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), GPP_{MAX} ($\mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ DW h}^{-1}$) and Y_{MAX} ($\mu\text{mol O}_2$
285 $\text{mg}^{-1} \text{ Chl } a \text{ h}^{-1}$) are the maximal gross primary production expressed in terms of total dry
286 weight and chlorophyll a content ($\text{mg Chl } a \text{ g}^{-1} \text{ DW}$), respectively. G_{MAX} ($\mu\text{mol CaCO}_3 \text{ g}^{-1}$
287 DW h^{-1}) is the rate of maximal gross calcification, Ek ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) is the half
288 saturation constant, R is the respiration term and G_D is the dark calcification term. The
289 compensation irradiance (Ec , $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) is the irradiance at which $NPP = 0$ (or
290 $GPP = R$).

291

292 *Statistical treatment*

293 Statistical analyses were done using R . Because not all the data showed a normal distribution
294 (Shapiro-Wilks test) and/or homogeneity of variances (Bartlett test), a one-way non-
295 parametric ANOVA (Kruskal-Wallis test, KW) was used to compare the physiological rates
296 (photosynthetic, respiration, and calcification in the light and in the dark) and pigment
297 content of the algae between species/stations and seasons, tests were followed by a post-hoc
298 Wilcoxon test (pairwise Wilcoxon test, Wp). Fitting of the curves was done using the Fisher
299 test of significance. A Monte Carlo permutation test (MPT) was used to compare $NPP-E$ and
300 $G-E$ parameters (GPP_{MAX} , R , G_{MAX} , G_D , Ek , and Ec) between stations and seasons.

301

302 **RESULTS**

303 The physico-chemical parameters of seawater at the beginning of the incubations at the three
304 stations in both seasons are shown in Table 1 and Table 2.

305

306 *Comparison of pigment content in Lithothamnion corallioides at the three stations (Exp. 1).*

307 Chl a content of *L. corallioides* did not vary between winter and summer at any station. In
308 winter, there was no difference in *L. corallioides* Chl a content among stations (Fig. 3a and

309 Table 3), but in summer, Chl *a* content was significantly lower at Station C than at Stations
310 A and B (Fig. 3b and Table 3). The xanthophyll content did not vary significantly between
311 winter and summer. In winter, it was heterogeneous among stations and in summer, it was
312 significantly lower at Station C relative to the other stations (Fig. 3c-d and Table 3). The
313 xanthophyll:Chl *a* ratio did not vary significantly, neither among seasons, nor among stations
314 (Fig. 3e-f and Table 3).

315

316 *Comparison of pigment content among the three maerl species at Station B (Exp. 2).*

317

318 Chl *a* content did not vary significantly between winter and summer, regardless of the maerl
319 species. In both seasons, the species with the highest Chl *a* content ($\mu\text{g g}^{-1}$ DW maerl) was *L.*
320 *incrustans* (Fig. 4a-b and Table 3). In *L. corallioides* and *P. calcareum* the major xanthophyll
321 was identified as zeaxanthin (Z), whereas *L. incrustans* contained lutein (L). The xanthophyll
322 content did not vary significantly between the two seasons in *L. corallioides* and *P.*
323 *calcareum*, but in *L. incrustans* it was higher in winter than in summer (Fig. 4c-d).
324 Comparison among species showed that *L. incrustans* had the highest xanthophyll content in
325 both seasons (Fig. 4c-d and Table 3), although in summer its content was not significantly
326 different from *P. calcareum* (Fig. 4d and Table 3). The xanthophyll : Chl *a* ratio did not vary
327 in *L. corallioides* and *P. calcareum* between seasons, whereas it increased in winter for *L.*
328 *incrustans* (Fig. 4e-f). This ratio differed among species in both seasons: in winter, the ratio
329 was higher in *L. incrustans* than in *L. corallioides* (Fig. 4e and Table 3), but in summer it
330 was higher in *P. calcareum* than in *L. incrustans* (Fig. 4f and Table 3).

331

332 *Comparison of Lithothamnion corallioides net primary production and irradiance*
333 *relationships (Exp. 1).*

334 The relationships between net primary production (*NPP*) and irradiance (*E*) were significant
335 at all three stations (Fig. 5a-b) ($R^2 > 0.95$ in winter and in summer). No photo-inhibition
336 occurred in the range of irradiance levels tested, regardless of the season (Fig. 5). Respiration
337 (*R*) was significantly higher in summer than in winter at the three stations (Tables 4 & 5). In
338 both seasons, *R* showed a heterogeneous pattern among stations (Tables 4 & 6). Maximal
339 gross primary production (GPP_{MAX}) was significantly higher in summer than in winter (Fig.
340 5 and Table 5). GPP_{MAX} was lower at Station C in both seasons (Fig. 5 and Table 6). *Ek*, the

341 irradiance at which photosynthesis saturates, did not vary significantly among seasons
342 (Tables 4 & 5) or among stations (Tables 4 & 6). Irradiance of compensation (E_c) varied
343 among seasons only at Station C, with higher values in summer than in winter (Tables 4 &
344 5). This parameter was lower at Station B than at Stations A and C in winter (Table 4 & 6).
345 Y_{MAX} was significantly higher in summer than in winter at Stations A and C, but no
346 differences between seasons were observed at Station B (Table 4 & 5). No significant
347 differences were observed between stations in winter, but a heterogeneous pattern among
348 stations was observed in winter (Tables 4 & 6).

349

350 *Comparison of Lithothamnion corallioides calcification and irradiance relationships (Exp.*
351 *1).*

352 The relationship between net calcification (G) and irradiance (E) was significant at the three
353 stations (Fig. 6) ($R^2 > 0.95$). No light-induced inhibition of calcification was demonstrated,
354 whatever the station or the season. Maximal gross calcification (G_{MAX}) was significantly
355 higher in summer than in winter at Stations A and C, but no differences among seasons were
356 recorded at Station B (Fig. 6 and Table 5). In both seasons, G_{MAX} was significantly lower at
357 Station C than at Stations A and B (Fig. 6 and Tables 4 & 6). In the dark, net dissolution was
358 observed at the three stations at both seasons. It was significantly higher in winter than in
359 summer at Station B, whereas no difference between seasons was observed at the other
360 stations (Tables 4 & 5). In winter, net dissolution in the dark was higher at Station B than at
361 Stations A and C (Table 4). In summer, no difference was observed among stations (Tables
362 4 & 6). Irradiance of saturation (E_k) was significantly higher in winter than in summer at
363 Station A (219 vs. 51 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). No significant differences between seasons were
364 observed at Stations B and C (Fig. 6 and Tables 5 & 6). No difference in E_k was observed
365 between stations regardless of the season (Fig. 6 and Table 7). Comparison between stations
366 in each season showed heterogeneity, but there were no significant differences among them
367 (Table 7).

368

369 *Comparison of gross primary production under surface irradiance and respiration rates*
370 *among the three maerl species (Exp. 2).*

371 The mean gross primary production rate (*GPP*) was significantly higher in summer (at a
372 mean irradiance of $279 \pm 186 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) than in winter ($214 \pm 65 \mu\text{mol photons}$
373 $\text{m}^{-2} \text{s}^{-1}$) in *L. corallioides* and in *L. incrustans*, whereas no difference between seasons was
374 recorded in *P. calcareum*. *GPP* was significantly higher in *L. incrustans* in both seasons
375 relative to the other species and, in winter, it was significantly higher in *P. calcareum* than in
376 *L. corallioides* (Fig. 7a-b and Table 7). The gross yield (*GPP* normalized to the Chl *a* content,
377 Y_{MAX}) in *L. corallioides* and in *L. incrustans* was significantly higher in summer than in winter
378 but it did not vary between seasons in *P. calcareum*. It ranged from 6.0 to 8.6 $\mu\text{mol mg}^{-1} \text{Chl}$
379 $a \text{ h}^{-1}$ in *L. corallioides*, from 5.4 to 7.7 $\mu\text{mol mg}^{-1} \text{Chl } a \text{ h}^{-1}$ in *L. incrustans* and from 7.9 to
380 8.1 $\mu\text{mol mg}^{-1} \text{Chl } a \text{ h}^{-1}$ in *P. calcareum*. Comparison among species showed that *P.*
381 *calcareum* had a significantly higher gross yield relative to *L. incrustans* in winter, but there
382 was no difference among species in summer (Table 7). Mean respiration rates (*R*) were higher
383 in summer than in winter in the three species (Table 7). In winter, *R* was significantly lower
384 in *L. corallioides* than in the other species (Fig. 7c and Table 7). In both seasons, it was
385 significantly higher in *L. incrustans* (Fig. 7c-d and Table 7). The ratio of gross primary
386 production to respiration (*GPP*:*R* ratio) at surface irradiance was significantly higher in winter
387 than in summer in the three species (KW, $H = 6.82$, $p = 0.009$) (Fig. 8a-b). In winter,
388 significant differences were observed with the highest value measured in *L. corallioides* and
389 the lowest in *L. incrustans* (KW, $H = 12.5$, $p = 0.002$), whereas in summer no difference was
390 observed among species (KW, $H = 4.88$, $p = 0.090$) (Fig. 8a-b).

391

392 *Comparison of calcification rates under surface irradiance among the three maerl species*
393 *(Exp. 2)*.

394 The mean net calcification rates (*G*) were higher in the light than in the dark and in summer
395 than in winter for the three species (KW, $p < 0.01$). In winter, under a mean irradiance of 214
396 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, G_L was significantly lower in *P. calcareum* than in *L. corallioides* and
397 *L. incrustans* (Table 7). In summer, under 279 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, it was lower in *P.*
398 *calcareum* than in *L. incrustans* (Fig. 9a-b and Table 7). In winter in the dark, net dissolution
399 was observed ($G_D < 0$), the highest net dissolution rate was measured in *L. incrustans* and
400 the lowest in *L. corallioides* (Fig. 9c and Table 7). In summer, G_D was positive (calcification

401 > dissolution). *L. incrustans* G_D was lower than that for *L. corallioides* and *P. calcareum*
402 (Fig. 9d and Table 7).

403 *Comparison of the calcification-to-photosynthesis ratio under surface irradiance among the*
404 *three maerl species (Exp. 1)*

405 The $G_L:GPP$ ratio was calculated under ambient light intensity in winter ($214 \pm 65 \mu\text{mol}$
406 $\text{photons m}^{-2} \text{s}^{-1}$) and in summer ($279 \pm 186 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). It was significantly higher
407 in summer than in winter in the three species (KW, $H = 6.82$, $p = 0.009$). It ranged from 0.40
408 to 0.65 in *L. corallioides*, from 0.18 to 0.47 in *P. calcareum*, and from 0.23 to 0.50 in *L.*
409 *incrustans*. In winter, the $G_r:GPP$ ratio was significantly different between the three species
410 (KW, $H = 11.58$, $p = 0.003$), the highest ratio being measured in *L. corallioides* and the lowest
411 in *L. incrustans* (Fig. 8c). In summer, differences were also observed (KW, $H = 9.62$, $p =$
412 0.008), the ratio was higher in *L. corallioides* than in *P. calcareum* (Fig. 8d).

413
414

415 **DISCUSSION**

416 By comparing maerl respiration, photosynthetic and calcification rates between species and
417 between contrasting stations in terms of physico-chemistry (salinity and carbonate chemistry)
418 and hydrodynamism (Qui-Minet et al. 2018), we shed light on the physiological plasticity in
419 maerl across species and locations.

420

421 **Respiration**

422 The seasonality of coralline algal respiration rates (R) depends on temperature (Hurd et al.
423 2014, Martin and Hall-Spencer 2017). In the present study, R was enhanced in summer
424 relative to winter in the three maerl species, regardless of their location in the Bay of Brest.
425 These results are in agreement with a previous report for *L. corallioides* (Martin et al. 2006),
426 although we found a weaker seasonal effect on R in this species: *L. corallioides* R was three-
427 fold higher, across all stations, in summer than in winter in our study compared with almost
428 five-fold higher in the previous study for similar seasons and temperature. At Station A,
429 winter R in *L. corallioides* was two times higher than the rates reported in Martin et al. (2006)
430 in the same season, whereas R was 10% (Station B) and 20% (Station C) higher in winter
431 and 10% (Stations B and C) lower in summer. Given that the Martin et al. (2006) study was
432 carried out at a different station in the Bay of Brest, such differences are most likely related
433 to local environmental parameters varying with time and/or between stations. In our study,

434 significant differences in R rates among stations were non-conclusive. Although mean values
435 of R were higher at Station A, they varied strongly between replicates, possibly indicating a
436 patchy/irregular distribution of maerl biofilm. In this context, the microflora and the bacteria
437 forming maerl biofilm have an impact on the respiration rates of the holobiont system (host-
438 microbiome) (Longphuir et al. 2007; Cavalcanti et al. 2014; Cavalcanti et al. 2018;
439 Schoenrock et al. 2018). A previous study observed that Chl a belonging to maerl epiphytic
440 microalgae varied among stations, being twice as high at Station A than at Stations B and C
441 (Qui-Minet et al. 2018). With this in mind, we hypothesize that differences in pigment
442 content may indicate differences in terms of maerl biofilm respiration rates among stations.
443 Higher biofilm and related maerl respiration rates at Station A may be due to the lower
444 abundance of grazers at this location, previously recorded by other authors (e.g. Guillou et
445 al. 2002).

446 In addition, R depends on the energy produced by photosynthesis (Hurd et al. 2014) and may
447 thus be related to algal morphology, because this parameter affects photosynthetic rates (see
448 below). Comparison among species showed that the highest R values were found in *L.*
449 *incrustans* in both seasons. This may be related to higher growth rates and thus a higher
450 metabolism for this species (Frantz and Bugbee 2005). Although algal respiration has not
451 been as studied as photosynthesis, respiration is essential for providing the ATP, NADPH
452 and C skeletons required for algal growth (Raven and Beardall 2003, Atkin et al. 2005).
453 Moreover, this higher energy demand corroborates the higher primary production and
454 calcification rates found in *L. incrustans* relative to the other maerl species.

455

456 **Photosynthesis and pigments**

457 The increase in maerl photosynthetic rates in summer is attributed to the increase in
458 temperature and irradiance levels (Martin et al. 2013, Egisildotir et al. 2016), and occurred
459 despite seawater nutrient depletion that occurs during this period in the Bay of Brest (Le Pape
460 et al. 1996, Qui-Minet et al. 2018). These results are in agreement with what Martin *et al.*
461 (2006) previously observed: summer photosynthetic rates were about two-fold higher than in
462 winter.

463 Differences in *L. corallioides* photosynthetic rates also depended on local variability. During
464 winter, physico-chemical parameters at Station B were significantly different from the other

465 stations (Qui-Minet et al. 2018): an increase in nutrients (particularly nitrates and silicates)
466 and a drop in salinity with a concomitant decrease in DIC concentration occurred. Although
467 lower salinities have been correlated with deleterious effects for *L. corallioides* (Adey and
468 McKibbin 1970), the lowest rates of maximum photosynthesis per unit mass (GPP_{MAX}) were
469 observed at Station C. This appears to be linked to the compact morphology of *L. corallioides*
470 at this location, because this morphotype has a lower surface-to-volume ratio than the
471 branched morphology observed at Stations A and B. Given that photosynthetically active
472 vegetative cells are only located in the surface layers of the thalli in coralline algae (McCoy
473 and Kamenos 2015), compact morphotypes have lower Chl *a* content per unit mass and,
474 consequently, lower photosynthetic rates. Conversely, when *L. corallioides* photosynthetic
475 rates were normalized to the Chl *a* content, no differences were observed between the three
476 stations. Therefore, differences in photosynthetic rates per unit mass between stations appear
477 to be primarily related to differences in surface-to-volume ratio between morphotypes.

478 As shown for Chl *a* content, the main xanthophyll pigment in *L. corallioides* was
479 significantly lower at Station C. The carotenoid profile of coralline algae usually includes α -
480 carotene and/or β -carotene, and one main xanthophyll: lutein, zeaxanthin, or antheraxanthin
481 (Schubert et al. 2006, Esteban et al. 2009). There is no apparent relationship between
482 phylogeny and main xanthophyll content (Schubert and García-Mendoza 2008), but
483 differences in the type of the main xanthophyll among Rhodophyte species are related to their
484 response to photo-inhibitory stress (Ursi et al. 2003). Zeaxanthin is the main xanthophyll in
485 *L. corallioides* (Noisette et al. 2013) and the main xanthophyll pigments in *L. incrustans* and
486 *P. calcareum* were described here for the first time, with *L. incrustans* being different from
487 the other species, because it contains lutein instead of zeaxanthin. Interestingly, *L. incrustans*
488 rarely occurs below 15 m (Ford et al. 1983), whereas *L. corallioides* and *P. calcareum* can
489 be found down to 20 m and 30 m, respectively (Birkett et al. 1998), where light is often
490 limiting. Given that the three species here studied are located at the same depth, higher Chl
491 *a* and xanthophyll content in *L. incrustans* may be related to its flat-branched morphology.
492 Contrary to what has been reported in *L. corallioides* and *P. calcareum*, *L. incrustans* shows
493 resistance to photo-inhibition under high light intensities and stressful conditions of pH and
494 temperature (Qui-Minet et al. 2019). Nonetheless, zeaxanthin appears to have a major role
495 against photo-inhibition, compared with lutein (Schubert and García Mendoza 2008); higher

496 photoprotective pigment content and thallus reflectance have also been correlated with higher
497 resistance to photo-inhibition (Schubert and García Mendoza 2008, Burdett et al. 2014).
498 Variations in photosynthetic rates are commonly observed among species and genotypes
499 (Pallardy 2008). They can be linked to many parameters such as differences in metabolism
500 and anatomy (Pallardy 2008, Heijden and Kamenos 2015, Hofmann and Heesch 2018).
501 Accordingly, the higher photosynthetic capacities of *L. incrustans* (it showed the highest
502 *GPP* at both seasons) seem to be enhanced by a higher surface-to-volume ratio than the other
503 species. Photosynthetic rates are also affected by environmental factors (Lee and Bazin 1991,
504 Heijden and Kamenos 2015). In the Bay of Brest, the three maerl species studied here are
505 located at a shallow depth (chart datum depth of 0.7 m and average tide of 4 m). Therefore,
506 they are subject to high light intensities, particularly in summer at low tide, when bottom
507 light intensity can reach extreme values of more than 500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Martin et al.
508 2006, Qui-Minet et al. 2018). In this context, mean ambient light intensities recorded during
509 our incubations ($\sim 200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) are consistent with mean daily bottom irradiance
510 for the summer season, but can be considered high for the winter season. Contrary to what
511 was observed for the other study species (*L. corallioides* and *L. incrustans*) and previously
512 reported for temperate coralline algae (Martin et al. 2013, Egilsdottir et al. 2015), *P.*
513 *calcareum* *GPP* did not vary significantly between winter and summer. Moreover, under the
514 environmental conditions reported in this study, it showed the highest winter Y_{MAX} relative to
515 the other species. According to its northern distribution and its presence in deeper
516 environments, of the three species, *P. calcareum* seems to be the best adapted to lower depths
517 and thus lower temperatures and irradiances (Adey and McKibbin 1970, Mendoza and
518 Cabioch 1998). Nevertheless, this species did not display any photo-inhibition at an ambient
519 light intensity of $\sim 200\text{-}300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ regardless of the season.
520 Interestingly, the season did not induce any variation in the individual pigment content within
521 a species at a given station. This suggests that they are already adapted to strong variations
522 in light availability (tides, turbidity, cloudiness variability, etc.) throughout the year in the
523 Bay of Brest. For instance, bottom irradiance at solar noon in the Bay of Brest has been
524 estimated to reach almost 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at low tide in winter, which is within the
525 order of magnitude of values found in summer at high tide (Qui-Minet et al. 2018). Similarly,
526 the absence of significant differences between stations in terms of irradiance of saturation

527 (*Ek*) for *L. corallioides* is probably due to the high variability in bottom irradiance in the Bay
528 of Brest.

529

530 **Calcification**

531 The main environmental parameters affecting CaCO₃ precipitation rates in coralline algae
532 are irradiance, temperature and CaCO₃ saturation in seawater (Martin et al. 2006, Teichert
533 and Freiwald 2014, Williamson et al. 2017). The amount of calcite produced by coralline
534 algae is also known to vary with species, their morphology, growth rates and environmental
535 conditions (Heijden and Kamenos 2015).

536 Although no dissolution was previously reported in *L. corallioides* from the Bay of Brest
537 (Martin et al. 2006), we observed net dissolution in *L. corallioides* in the dark. This is most
538 likely linked to the different environmental conditions between stations and studies. The Bay
539 of Brest is affected by freshwater inputs, which are higher at Station B. In winter, this station
540 can reach extremely low values of salinity, alkalinity and carbonate availability (Qui-Minet
541 et al. 2018), the latter being detrimental to the calcification process (King and Schramm
542 1982). Although winter pH at this station remained above 8.0, a decrease in CO₃²⁻ availability
543 at Station B during winter incubations may have been deleterious for *L. corallioides*
544 calcification. Comparison between stations consistently showed that the net dissolution rate
545 of *L. corallioides* in the dark was four- and five-fold higher at Station B than at Stations A
546 and C, respectively. However, no negative impact was observed on the calcification process
547 in the light. A similar G_{MAX} was observed at Stations A and B, which is consistent with the
548 enhancement of calcification by photosynthesis previously reported for other coralline algal
549 species (Chisholm 2000, Williamson et al. 2017, Hofmann et al. 2018). Effectively,
550 photosynthesis increases the internal pH and therefore the CO₃²⁻ at the site of calcification
551 (Borowitzka and Larkum 1987, Williamson et al. 2017). This relationship indicates that the
552 environment at the cellular level was thermodynamically favorable for inorganic CaCO₃
553 precipitation, regardless of the conditions in the surrounding water (Cyronak et al. 2016). On
554 the other hand, differences in *L. corallioides* net calcification in the light observed among
555 stations seem mostly explained by *L. corallioides* morphotypes and, as observed for GPP_{MAX} ,
556 the lowest G_{MAX} was observed at Station C in both seasons.

557 We also observed a seasonal effect on calcification rates. In summer, G_{MAX} was enhanced at
558 Stations A and C, but not at Station B. This may be related to a possible underestimation of

559 summer G_{MAX} at Station B due to the low maximal irradiance reached *in situ* during summer
560 incubation experiments. The maximum surface irradiance reached at Station B was 370 μmol
561 photons $\text{m}^{-2} \text{s}^{-2}$ compared with 450 and 600 μmol photons $\text{m}^{-2} \text{s}^{-2}$ at Stations A and C,
562 respectively.

563 At Station B, *P. calcareum* had the lowest net calcification rates among species in the light
564 in both seasons. Growth rates being higher at the tips than at the basal parts (King and
565 Schramm 1982), the more branched morphology of *L. corallioides* with many apical tips
566 compared with *P. calcareum*, may explain its higher calcification rates. More optimal
567 environmental conditions in the bay for this species may also explain its dominance at this
568 location. Various studies carried out in Northern Europe have reported higher growth rates
569 in *L. incrustans* (Edyvean and Ford 1987) compared with *L. corallioides* and *P. calcareum*
570 (Adey and McKibbin 1970, Blacke and Maggs 2003), which is in agreement with the higher
571 calcification rates observed in our study in comparison to the other species. The highest G_L
572 measured in summer in *L. incrustans* may be related to its more southern geographical
573 distribution (Hernández-Kantún et al. 2015) and preference for shallow depths (Ford et al.
574 1983). Higher summer temperatures and irradiances observed at Station B are likely
575 favorable for its development at this location. Nevertheless, in the dark in both seasons,
576 comparison between species showed that *L. incrustans* was the species with the highest net
577 dissolution, suggesting it is the most disadvantaged species in winter, when maerl beds
578 remain in the dark most of the time. In the same manner, the lower maerl biomass at Station
579 B relative to Stations A and C may be partly related to the significantly higher dissolution
580 maerl species undergo in the dark following freshwater inputs (Qui-Minet et al. 2018).

581 In agreement with previous studies on the physiology of these maerl species (Martin et al.
582 2006, Qui-Minet et al. 2019), the three species presented higher calcification rates in summer,
583 in the light they were more than two-fold higher than in winter. These results are consistent
584 with the higher growth rates previously reported for *L. corallioides* in summer (Potin et al.
585 1990).

586 In *P. calcareum*, optimal temperature for growth is between 12-13°C (Adey and McKibbin
587 1970). In this study, we observed higher calcification rates at 16°C than at 10°C (light
588 intensity being comparable in winter and summer seasons). However, *NPP* was favored in
589 winter (10 °C) relative to summer (16 °C). Therefore, our results suggest a seasonal

590 decoupling between photosynthesis and calcification for this species. Despite differences in
591 metabolic rates among species and seasons, the $GPP:R$ ratio was higher in the three species
592 in winter and the $G_L:GPP$ ratio was higher in summer. The latter relationship suggests greater
593 tissue synthesis in winter than in summer and is in agreement with their higher energy
594 demand for growth (respiration rates) in summer.

595

596 **CONCLUSION**

597 According to our results, *L. corallioides*, which is the dominant maerl species in the Bay of
598 Brest, seems to be able to cope with the variable environmental parameters prevailing
599 throughout the bay under winter and summer conditions. This species did not have the highest
600 metabolic rates, but had the highest $G_L:GPP$ ratio under ambient irradiance and the lowest
601 dissolution rates relative to the other maerl species co-existing in the Bay of Brest, across all
602 seasons.

603 Considering the light intensities of our study, a light:dark photoperiod of 8:16 h in winter,
604 and 14:10 h in summer, estimations of net calcification ranged from 3 to 12 $\mu\text{mol CaCO}_3 \text{ g}^{-1}$
605 DW day^{-1} in *L. corallioides*, from 3 to 9 $\mu\text{mol CaCO}_3 \text{ g}^{-1} \text{DW day}^{-1}$ in *P. calcareum* and
606 from 0.6 to 14 $\mu\text{mol CaCO}_3 \text{ g DW day}^{-1}$ in *L. incrustans*, in winter and in summer,
607 respectively. Nevertheless, light calcification values were calculated at irradiances that are
608 greater than average incident bottom winter values, thus, under more realistic lower winter
609 irradiances, *L. incrustans* may have had no growth or undergone dissolution.

610 In terms of local changes at small scales, freshwater inputs can negatively affect maerl
611 calcification and thus the CaCO_3 budget through the enhancement of dissolution of maerl
612 algae, notably in winter when maerl beds remain in the dark during most of the day. This is
613 especially evident at Station B, where maerl biomass per unit surface remains the lowest
614 (Qui-Minet *et al.*, 2018). Interestingly, differences in metabolic rates at the three stations do
615 not explain patterns in living maerl biomass among stations, Station C possessing the highest
616 biomass (Qui-Minet *et al.* 2018). This lack of a clear pattern at the scale of the Bay of Brest
617 highlights the importance of biotic and abiotic interactions, as well as any natural and
618 anthropogenic disturbances previously undergone.

619 On the one hand, this work emphasizes the particular ability of *L. corallioides* to maintain its
620 photosynthetic and light calcification rates in unfavorable environmental conditions due to

621 freshwater inputs. Photosynthesis seems to have a fundamental role in maintaining a
622 favorable internal environment for calcification. With this in mind, the uncoupling of these
623 processes under any future global change scenario may be detrimental for the calcification
624 process under stressful conditions, because *P. calcareum* is more vulnerable than the other
625 species. On the other hand, *L. corallioides* was not able to prevent a significant increase in
626 CaCO₃ dissolution in the dark following a drop in seawater carbonate parameters.
627 Noteworthy, maintaining photosynthetic and calcification rates in the light under stressful
628 conditions may have a metabolic cost.

629 Significant differences in production rates between different morphotypes have an impact on
630 C and CaCO₃ budgets. Contrasting morphologies within the same species may affect maerl
631 plasticity with regard to environmental changes. Morphology determines maerl
632 photosynthetic capacity, which is closely interlinked with respiration and calcification rates.
633 We verified that irradiance promotes calcification rates in the light and we speculate that low
634 GPP:R ratios favor CaCO₃ dissolution in the dark. Morphology and photo-protective
635 pigments also affect maerl ability to withstand different light intensities, which is
636 fundamental under global change scenarios. Further work regarding other biological aspects
637 at the inter- and intraspecies level, such as their photo-physiology, biofilm composition and
638 reproduction mechanisms would allow a deep understanding of their fate in rapidly changing
639 coastal systems.

640

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647

648 **ORCID Numbers:**

649 Zujaila Nohemy Qui-Minet: 0000-0001-6002-5240
650 Dominique Davoult: 0000-0001-8678-3998
651 Christophe Six: 0000-0002-8506-1149
652 Thierry Cariou: 0000-0001-6719-9876
653 Sophie Martin: 0000-0002-1256-3674

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943 FIGURES

944 **Figure 1.** Map of the Bay of Brest showing the surface covered by maerl beds and the
945 sampled stations: Station A (*Lithothamnion corallioides*), Station B (*L. corallioides*,
946 *Phymatolithon calcareum*, and *Lithophyllum incrustans*), and Station C (*L. corallioides*).

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948 **Figure 2.** Photos of *Lithothamnion corallioides* from Station A, *L. corallioides*,
949 *Phymatolithon calcareum* and *Lithophyllum incrustans* from Station B, and *L. corallioides*
950 from Station C.

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953 **Figure 3.** Experiment 1: Variations in Chlorophyll *a* (Chl *a*) content, main xanthophyll
954 content (MX) and the MX:Chl *a* ratio in *Lithothamnion corallioides* at Stations A, B and C
955 in winter (a, c, e) and in summer (b, d, f). Box plots extend from the 25% to the 75%
956 percentiles of all the data, the central horizontal line represents the median, and bars extend
957 to the 95% confidence limits.

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960 **Figure 4.** Experiment 2: Variations in Chlorophyll *a* (Chl *a*) content, main xanthophyll
961 content (MX) and the MX:Chl *a* ratio in *Lithothamnion corallioides*, *Phymatolithon*
962 *calcareum* and *Lithophyllum incrustans* at Station B, in winter (a, c, e) and in summer (b, d,
963 f). Box plots extend from the 25% to the 75% percentiles of all the data for each species, the
964 central horizontal line represents the median, and bars extend to the 95% confidence limits.

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966 **Figure 5.** Experiment 1: Relationship between net primary production (in $\mu\text{mol O}_2 \text{ g DW}^{-1}$)
967 and irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in winter (a) and in summer (b) in *Lithothamnion*
968 *corallioides* at Stations A (gray circles), B (black circles) and C (white circles).

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971 **Figure 6.** Experiment 1: Relationship between net calcification (in $\mu\text{mol CaCO}_3 \text{ g DW}^{-1}$) and
972 irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in winter (a) and in summer (b) in *Lithothamnion*
973 *corallioides* at Stations A (gray circles), B (black circles) and C (white circles).

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975 **Figure 7.** Experiment 2: Variations in *Lithothamnion corallioides*, *Phymatolithon calcareum*
976 and *Lithophyllum incrustans* gross primary production (GPP) and respiration (R) rates at
977 Station B in winter (a and c, respectively) and in summer (b and d, respectively). Box plots
978 extend from the 25% to the 75% percentiles of all the data for each species, the central
979 horizontal line represents the median, and bars extend to the 95% confidence limits.

980

981 **Figure 8.** Experiment 2: Variation in *Lithothamnion corallioides*, *Phymatolithon calcareum*
982 and *Lithophyllum incrustans* (at Station B) gross primary production:respiration (GPP:R) and
983 calcification in light:gross primary production (G_l :GPP) ratios in winter (a and c,
984 respectively) and in summer (b and d, respectively). Box plots extend from the 25% to the
985 75% percentiles of all the data for each species, the central horizontal line represents the
986 median, and bars extend to the 95% confidence limits.

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989 **Figure 9.** Experiment 2: Variations in *Lithothamnion corallioides*, *Phymatolithon calcareum*
990 and *Lithophyllum incrustans* calcification rates at Station B in the light and in the dark in
991 winter (a and c, respectively) and in summer (b and d, respectively). Box plots extend from
992 the 25% to the 75% percentiles of all the data for each species, the central horizontal line
993 represents the median, and bars extend to the 95% confidence limits.

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1004 **TABLES.**

1005

1006 **Table 1.** Mean values (\pm SD) of seawater physico-chemical parameters measured in winter
1007 and summer on the days of incubations during Experiment 1 at Stations A, B and C and
1008 Experiment 2 at Station B (n = 3). SW: seawater, Ω_{Ar} : Aragonite Saturation State, T_A :
1009 Alkalinity (mmol kg SW^{-1}), DIC: Dissolved Inorganic Carbon (mmol kg SW^{-1}).

Season	Experiment	Station	Temperature (°C)	Oxygen (mg L^{-1})	Salinity	pH _T	Ω_{Ar}	T_A (mmol kg SW^{-1})	DIC (mmol kg SW^{-1})
Winter									
27 February 2015	Exp. 1	A	9.3 \pm 0.1	8.7 \pm 0.0	34.0 \pm 0.0	8.05 \pm 0.00	1.7 \pm 0.0	2.28 \pm 0.00	2.10 \pm 0.00
27 February 2015	Exp. 1	B	8.9 \pm 0.1	8.8 \pm 0.0	23.0 \pm 0.1	8.04 \pm 0.01	1.2 \pm 0.1	1.82 \pm 0.22	1.73 \pm 0.15

27 February 2015	Exp. 1	C	9.7 ± 0.5	8.5 ± 0.0	32.0 ± 0.8	8.04 ± 0.06	1.6 ± 0.0	2.23 ± 0.01	2.07 ± 0.05
27 March 2015	Exp. 2	B	10.5 ± 0.1	9.0 ± 0.0	33.3 ± 0.6	8.14 ± 0.00	2.3 ± 0.0	2.26 ± 0.00	2.04 ± 0.00
Summer									
16 September 2015	Exp. 1	A	17.8 ± 0.2	9.8 ± 0.0	35.1 ± 0.0	7.92 ± 0.03	2.3 ± 0.1	2.37 ± 0.00	2.18 ± 0.01
16 September 2015	Exp. 1	B	16.3 ± 0.0	7.4 ± 0.0	35.0 ± 0.0	8.03 ± 0.02	2.4 ± 0.1	2.30 ± 0.00	2.42 ± 0.12
17 September 2015	Exp. 1	C	16.5 ± 0.1	7.5 ± 0.0	35.0 ± 0.0	8.01 ± 0.00	2.4 ± 0.0	2.34 ± 0.01	2.12 ± 0.01
18 September 2015	Exp. 2	B	16.4 ± 0.1	7.4 ± 0.1	35.0 ± 0.0	8.00 ± 0.01	2.4 ± 0.0	2.29 ± 0.01	2.10 ± 0.01

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1011 **Table 2.** Mean values (± SD) of nutrient concentrations and irradiance measured in winter
 1012 and summer on the days of incubations during Experiment 1 at Stations A, B and C and
 1013 Experiment 2 at Station B (n = 3).

Season	Experiment	Station	[NO ₃ ²⁻] (μmol L ⁻¹)	[NH ₄ ⁺] (μmol L ⁻¹)	[PO ₄ ⁻] (μmol L ⁻¹)	[SiO ₄ ⁻⁴] (μmol L ⁻¹)	Irradiance (μmol photons m ⁻² s ⁻¹)
Winter							
27 February 2015	Exp. 1	A	22.5 ± 2.7	0.6 ± 0.0	0.6 ± 0.1	7.2 ± 2.0	480 ± 65
27 February 2015	Exp. 1	B	111.2 ± 4.8	1.2 ± 0.2	0.6 ± 0.1	34.1 ± 9.0	291 ± 25
27 February 2015	Exp. 1	C	32.1 ± 0.8	0.7 ± 0.0	0.6 ± 0.0	13.2 ± 0.5	273 ± 102
27 March 2015	Exp. 2	B	26.9 ± 0.4	0.2 ± 0.0	0.3 ± 0.0	5.5 ± 0.2	214 ± 65
Summer							
16 September 2015	Exp. 1	A	2.0 ± 0.0	0.7 ± 0.0	0.2 ± 0.0	4.3 ± 0.0	600 ± 186
16 September 2015	Exp. 1	B	1.5 ± 0.3	1.0 ± 0.2	0.4 ± 0.0	4.8 ± 0.0	370 ± 86
17 September 2015	Exp. 1	C	1.2 ± 0.0	0.8 ± 0.1	0.4 ± 0.0	5.0 ± 0.0	446 ± 102
18 September 2015	Exp. 2	B	2.6 ± 0.3	1.5 ± 0.4	0.5 ± 0.1	4.6 ± 0.0	279 ± 186

1014 **Table 3.** Summary of the results of one-way non-parametric (Kruskal-Wallis) tests followed by
 1015 post-hoc Wilcoxon tests (shown in italics), testing differences in Chlorophyll *a* content, main
 1016 xanthophyll (zeaxanthin or lutein) content and Chlorophyll *a* : main xanthophyll ratio between
 1017 Stations A, B and C in *Lithothamnion corallioides* (Exp. 1) and between the three maerl species:
 1018 *L. corallioides* (*L.c.*), *Phymatolithon calcareum* (*P.c.*) and *Lithophyllum incrustans* (*L.i.*), at
 1019 Station B (Exp. 2) in winter and summer. Comparison of the season effect at each station and for
 1020 each species was done using a one-way non-parametric (Kruskal-Wallis) test (n=3).

	Chlorophyll <i>a</i>		Main Xanthophyll		Xanthophyll:Chlorophyll <i>a</i>	
	F	p	F	p	F	P
Exp. 1						
Station comparisons						
Winter	5.46	0.065	6.26	0.044*	0.06	0.970
Post-hoc Wilcoxon	A = B = C		A = B = C		A = B = C	
Summer	9.42	0.009**	9.42	0.009**	3.02	0.221
Post-hoc Wilcoxon	A & B > C		A & B > C		A = B = C	
Season						
Station A	2.45	0.117	0.53	0.465	0.27	0.601

Station B	0.53	0.465	0.53	0.465	0.53	0.465
Station C	0.27	0.601	0.01	0.917	0.53	0.465
Exp. 2						
Species comparisons						
Winter	8.66	0.013*	8.96	0.011*	9.38	0.009**
Post-hoc Wilcoxon	<i>L.i. > L.c. = P.c.</i>		<i>L.i. > L.c. = P.c.</i>		<i>L.c. = P.c. = L.i.</i>	
Summer	10.22	0.006**	7.46	0.024*	6.50	0.039*
Post-hoc Wilcoxon	<i>L.i. > L.c. = P.c.</i>		<i>L.i. > L.c.</i> <i>P.c. = L.i., P.c. = L.c.</i>		<i>P.c. > L.i.</i> <i>L.c. = P.c., L.c. = L.i.</i>	
Season						
<i>L. corallioides</i>	0.01	0.917	0.53	0.465	0.53	0.465
<i>P. calcareum</i>	0.27	0.601	0.88	0.347	0.53	0.465
<i>L. incrustans</i>	0.88	0.347	4.81	0.028*	6.82	0.009**

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1023 **Table 4.** Parameters of primary production-irradiance (*NPP-E*) and calcification-irradiance
1024 (*G-E*) curves for *Lithothamnion corallioides* at Stations A, B, and C in winter and summer.
1025 Results are expressed as means \pm SE (n = 5). *GPP_{MAX}* (or *G_{MAX}*): maximum rates of gross
1026 photosynthesis (or calcification) ($\mu\text{mol O}_2$ or CaCO_3 , $\text{g DW}^{-1} \text{h}^{-1}$); *Y_{MAX}*, *R* (or *G_D*): dark
1027 respiration (or calcification) rates ($\mu\text{mol O}_2$ or CaCO_3 , $\text{g DW}^{-1} \text{h}^{-1}$); *Ek*: saturating irradiance
1028 ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$); *Ec*: compensation irradiance ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$).

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Season	Station	-----Primary production-----					-----Calcification-----			
		<i>GPP_{MAX}</i>	<i>R</i>	<i>Ek</i>	<i>Ec</i>	<i>Y_{MAX}</i>	<i>G_{MAX}</i>	<i>G_D</i>	<i>Ek</i>	
Winter	A	1.59 \pm 0.61	0.13 \pm 0.02	290 \pm 157	21 \pm 2	8 \pm 3	0.64 \pm 0.13	-0.02 \pm 0.02	219 \pm 127	
	B	1.28 \pm 0.37	0.09 \pm 0.01	160 \pm 92	11 \pm 2	12 \pm 6	0.64 \pm 0.11	-0.08 \pm 0.02	162 \pm 43	
	C	0.66 \pm 0.14	0.09 \pm 0.02	136 \pm 35	19 \pm 3	10 \pm 2	0.35 \pm 0.03	-0.04 \pm 0.02	120 \pm 19	
Summer	A	3.10 \pm 0.15	0.29 \pm 0.14	171 \pm 35	22 \pm 5	22 \pm 3	0.85 \pm 0.09	-0.03 \pm 0.01	70 \pm 10	
	B	2.46 \pm 0.18	0.29 \pm 0.01	106 \pm 19	15 \pm 1	17 \pm 2	0.63 \pm 0.08	-0.02 \pm 0.02	93 \pm 39	
	C	1.10 \pm 0.26	0.23 \pm 0.03	190 \pm 70	38 \pm 10	15 \pm 4	0.35 \pm 0.06	-0.03 \pm 0.03	98 \pm 38	

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1032 **Table 5.** Summary of the results of one-way Monte Carlo permutation test (MPT) followed
1033 by a post-hoc permutation test to evaluate the effect of season on the primary production-
1034 irradiance (*NPP-E*) and calcification-irradiance (*G-E*) parameters in *Lithothamnion*
1035 *corallioides* at Stations A, B, and C (n = 5). *GPP_{MAX}* is the maximal gross primary production
1036 ($\mu\text{mol O}_2 \text{g DW}^{-1} \text{h}^{-1}$), *G_{MAX}* is the maximal gross calcification ($\mu\text{mol CaCO}_3 \text{g DW}^{-1} \text{h}^{-1}$),
1037 *Ek* is the irradiance of saturation ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$), *Ec* is the irradiance of compensation
1038 ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$), *R* is the respiration rate ($\mu\text{mol O}_2 \text{g DW}^{-1} \text{h}^{-1}$), and *G_D* is the dark
1039 calcification rate ($\mu\text{mol CaCO}_3 \text{g DW}^{-1} \text{h}^{-1}$).

Parameter	Primary production		Calcification	
	F	P	F	P

Season	GPP_{MAX}/G_{MAX}				
Station A	2.39	0.030*	2.23	0.030*	
Station B	2.61	0.010**	0.87	0.499	
Station C	2.30	0.024*	1.87	0.048*	
<i>Ek</i>					
Station A	-1.36	0.188	-1.88	0.028*	
Station B	-1.27	0.141	-1.84	0.055*	
Station C	1.43	0.136	-0.34	0.819	
<i>Ec</i>					
Station A	0.38	0.736	-0.36		
Station B	1.14	0.278	-2.88		
Station C	2.55	0.008**	1.03		
<i>R/G_d</i>					
Station A	-2.13	0.029*	-1.95	0.116	
Station B	-2.82	0.008**	2.55	0.016*	
Station C	-2.92	0.008**	-1.47	0.058	
<i>Y_{MAX}</i>					
Station A	2.51	0.032*			
Station B	1.57	0.142			
Station C	2.18	0.007**			

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Table 6. Summary of one-way Mont Carlo Permutation test followed by a post-hoc permutation test to compare the primary production-irradiance ($NPP-E$) and calcification-irradiance ($G-E$) parameters in *Lithothamnion corallioides* between Stations A, B, and C (n = 5). GPP_{MAX} is the maximal gross primary production ($\mu\text{mol O}_2 \text{ g DW}^{-1} \text{ h}^{-1}$), G_{MAX} is the maximal gross calcification ($\mu\text{mol CaCO}_3 \text{ g DW}^{-1} \text{ h}^{-1}$), Ek is the irradiance of saturation ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), Ec is the irradiance of compensation ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), R is the respiration rate ($\mu\text{mol O}_2 \text{ g DW}^{-1} \text{ h}^{-1}$), and G_d is the dark calcification rate ($\mu\text{mol CaCO}_3 \text{ g DW}^{-1} \text{ h}^{-1}$).

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Parameter	Primary production		Calcification	
	F	P	F	P
Winter				
<i>GPP_{MAX}/G_{MAX}</i>	6.75	0.011*	9.12	0.002**
	A = B > C		A = B > C	
<i>Ek</i>	4.29	0.068	3.59	0.117
	A = B = C		A = B = C	
<i>Ec</i>	9.14	0.002**	6.20	0.032*
	A = C > B		A = B = C	
<i>R/G_d</i>	5.75	0.035*	8.97	< 0.001***
	A = B = C		B > A = C	
<i>Y_{max}</i>	1.81	0.446		
	A = B = C			
Summer				
<i>GPP_{MAX}/G_{MAX}</i>	12.41	< 0.001***	11.12	< 0.001***
	A = B > C		A = B > C	
<i>Ek</i>	4.80	0.046*	2.18	0.369
	A = B = C		A = B = C	
<i>Ec</i>	10.39	< 0.001***	6.19	0.009**
	C = A > B		A = B = C	
<i>R/G_d</i>	5.35	0.001***	6.70	0.017*
	A = B = C		A = B = C	
<i>Y_{MAX}</i>	7.11	0.012*		
	A = B = C			

Table 7. Summary of the post-hoc Kruskal-Wallis and Wilcoxon tests to compare gross primary production (*GPP*), net primary production (*NPP*), respiration (*R*), calcification at light (*G_L*) and at dark (*G_D*) rates in *Lithothamnion corallioides* (*L.c.*), *Phymatolithon calcareum* (*P.c.*) and *Lithophyllum incrustans* (*L.i.*) (n = 5).

Comparison	<i>GPP</i>		<i>NPP</i>		<i>Y_{MAX}</i>		<i>R</i>		<i>G_L</i>		<i>G_D</i>	
	H	p-value	H	p-value	H	p-value	H	p-value	H	p-value	H	p-value
Winter	12.0	0.002**	9.3	0.010**	8.8	0.012*	12.5	0.002**	9.0	0.011*	12.5	0.002**

<i>Post-hoc Wilcoxon</i>												
	<i>L.i. > P.c. > L.c.</i>		<i>P.c. = L.i.</i> <i>L.i. > L.c.</i>		<i>P.c. > L.i.</i> <i>L.c. = P.c.</i> <i>L.c. = L.i.</i>		<i>L.i. > P.c. > L.c.</i>		<i>L.c. = L.i. > P.c.</i>		<i>L.c. > P.c. > L.i.</i>	
<i>Summer</i>	9.8	0.007**	9.98	0.007**	3.4	0.179	9.4	0.009**	9.7	0.008**	10.8	0.007**
<i>Post-hoc Wilcoxon</i>												
	<i>L.i. > P.c. = L.c.</i>		<i>L.i. > P.c. = L.c.</i>		<i>L.c. = P.c. = L.i.</i>		<i>L.i. > P.c. = L.c.</i>		<i>L.i. > P.c.</i> <i>L.c.=L.i.,</i> <i>L.c.=P.c.</i>		<i>L.c.>L.i.</i> <i>P.c. > L.i.</i>	
Season at Station												
B												
<i>L. corallioides</i>	4.8	0.028*	0.5	0.465	5.8	0.016*	6.8	0.009**	6.8	0.009**	6.8	0.009**
<i>P. calcareum</i>	0.0	0.916	4.8	0.028*	0.0	0.917	6.8	0.009**	6.8	0.009**	6.8	0.016*
<i>L. incrustans</i>	5.8	0.016*	0.1	0.754	6.9	0.009**	6.8	0.009**	6.8	0.009**	6.8	0.009**

