



## Physiological responses of three temperate coralline algae from contrasting habitats to near-future ocean acidification



Fanny Noisette<sup>a,b,\*</sup>, Hronn Egilsdottir<sup>c,d</sup>, Dominique Davoult<sup>a,b</sup>, Sophie Martin<sup>a,b</sup>

<sup>a</sup> CNRS, UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, 29688 Roscoff Cedex, France

<sup>b</sup> UPMC Univ. Paris 6, UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, 29688 Roscoff Cedex, France

<sup>c</sup> Marine Research Institute, Skulagata 4, 121 Reykjavik, Iceland

<sup>d</sup> University of Iceland, Faculty of Earth Science, Askja, Sturlugata 7, 101 Reykjavik, Iceland

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### ABSTRACT

Coralline algae are major calcifiers of significant ecological importance in marine habitats but are among the most sensitive calcifying organisms to ocean acidification. The elevated pCO<sub>2</sub> effects were examined in three coralline algal species living in contrasting habitats from intertidal to subtidal zones on the north-western coast of Brittany, France: (i) *Corallina elongata*, a branched alga found in tidal rock pools, (ii) *Lithophyllum incrustans*, a crustose coralline alga from the low intertidal zone, and (iii) *Lithothamnion corallioides* (maerl), a free-living form inhabiting the subtidal zone. Metabolic rates were assessed on specimens grown for one month at varying pCO<sub>2</sub>: 380 (current pCO<sub>2</sub>), 550, 750 and 1000 μatm (elevated pCO<sub>2</sub>). There was no pCO<sub>2</sub> effect on gross production in *C. elongata* and *L. incrustans* but *L. incrustans* respiration strongly increased with elevated pCO<sub>2</sub>. *L. corallioides* gross production slightly increased at 1000 μatm, while respiration remained unaffected. Calcification rates decreased with pCO<sub>2</sub> in *L. incrustans* (both in the light and dark) and *L. corallioides* (only in the light), while *C. elongata* calcification was unaffected. This was consistent with the lower skeletal mMg/Ca ratio of *C. elongata* (0.17) relative to the two other species (0.20). *L. incrustans* had a higher occurrence of bleaching that increased with increasing pCO<sub>2</sub>. pCO<sub>2</sub> could indirectly impact this coralline species physiology making them more sensitive to other stresses such as diseases or pathogens. These results underlined that the physiological response of coralline algae to near-future ocean acidification is species-specific and that species experiencing naturally strong pH variations were not necessarily more resistant to elevated pCO<sub>2</sub> than species from more stable environment.

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### 1. Introduction

Coralline algae (Corallinaceae, Rhodophyceae) are the most dominant group of calcareous algae. They are abundant and widespread around the world from tropical to polar oceans and throughout the photic zone (Nelson, 2009). In benthic coastal areas, they are major framework builders and carbonate producers (Cabioch et al., 1992; Nelson, 2009). Corallinaceae developed different morphologies: geniculate (articulated) algae have erected, branched thalli with uncalcified joints between calcified segments; non-geniculate (non-articulated) algae are crusts attached to the substratum or occur as free-living forms called rhodoliths (Cabioch et al., 1992). In shallow waters where they develop, they have important biological and ecological roles (Foster, 2001) and are considered ecosystem engineers (Nelson, 2009). They participate in reef accretion acting as cement (Adey, 1998; Jokiel et al., 2008) or can build large habitats as coralligenous or rhodolith beds. They favor larval

recruitment and settlement of marine invertebrates (Adey, 1998), acting as nurseries for some commercial molluscs and fishes (Kamenos et al., 2004a,b). They increase benthic biodiversity, providing hard substratum to settle and microhabitats for shelter (Foster, 2001; Grall et al., 2006; Pena and Barbara, 2010).

In temperate waters, coralline algae can be found at various depths, from the intertidal to the subtidal zone. In the intertidal zone, they frequently inhabit rock pools, forming dense mats at the edges or covering the bottom of the pools (Cabioch et al., 1992). Because rock pools are disconnected from the open sea at low tide, large pH variations are common in this habitat (Morris and Taylor, 1983). Diurnal variation often exceeds one pH unit, as a result of photosynthesis and respiration (Björk et al., 2004; Morris and Taylor, 1983; Truchot and Duhameljoue, 1980). In the low intertidal zone where channels are formed in shallow waters, understory coralline algae develop on rocks and pebbles under the dense macroalgal canopy. Under the canopy, pH fluctuates according to depth, photosynthetic production, wave exposure, flow or irradiance and is likely to present strong diurnal variations of more than one unit (Middelboe and Hansen, 2007). In the subtidal zone, rhodoliths form large beds. These rhodolith beds grow in stable environments with reduced flow (Foster, 2001) and relatively low pH

\* Corresponding author at: CNRS, UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, 29688 Roscoff Cedex, France. Tel.: +33 298292333.

E-mail addresses: [fanny.noisette@sb-roscoff.fr](mailto:fanny.noisette@sb-roscoff.fr) (F. Noisette), [hronne@gmail.com](mailto:hronne@gmail.com) (H. Egilsdottir), [davoult@roscoff.fr](mailto:davoult@roscoff.fr) (D. Davoult), [sophie.martin@sb-roscoff.fr](mailto:sophie.martin@sb-roscoff.fr) (S. Martin).

variation (Teichert et al., 2012). In all these habitats, coralline algae are important contributors to the global carbon budget and carbonate production through their high community primary production and respiration and their high calcium carbonate production (Amado-Filho et al., 2012; Bensoussan and Gattuso, 2007; Martin et al., 2005, 2007).

Photosynthesis, respiration and calcification are linked metabolic processes that can influence each other (Borowitzka, 1981; De Beer and Larkum, 2001; Gao et al., 1993; Martin et al., 2013). Via  $\text{CO}_2$  uptakes and outputs, photosynthesis and respiration processes cause increase and decrease of pH respectively, in the intracellular medium and in the diffusive boundary layer (Raven and Hurd, 2012). These variations will increase the rate of calcification in the light and decrease it in the dark. Very few studies have investigated these processes all together, especially in coralline algae. Coralline species precipitate calcium carbonate ( $\text{CaCO}_3$ ) containing magnesium (i.e. high magnesian calcite, Mg-calcite) to form their thallus. This biogenic  $\text{CaCO}_3$  is more soluble than aragonite at mole percentage (mol%)  $\text{MgCO}_3$  higher than 12% (Andersson et al., 2008). In the Corallinales order, the mean mol%  $\text{MgCO}_3$  in calcite is 13% but varies depending on the taxa considered from 14% in *Corallina* genus or 25% in the *Lithothamnion* genus (Smith et al., 2012). Due to the solubility of their skeleton, coralline algae might be among the most sensitive organisms to  $\text{CO}_2$ -driven ocean acidification (Basso, 2012; Kroeker et al., 2010).

The ocean acidification phenomenon is generated by the constant increase in atmospheric  $\text{CO}_2$  partial pressure ( $p\text{CO}_2$ ) since the 1800s (Sabine et al., 2004). Surface ocean pH is predicted to decrease by 0.3–0.4 units by 2100 and by 0.7 units by the year 2300 (Caldeira and Wickett, 2003). Simultaneously, the concentration of bicarbonate ions ( $\text{HCO}_3^-$ ) is predicted to increase and carbonate ions ( $\text{CO}_3^{2-}$ ) concentration to drop by 30% by the end of the century (Orr et al., 2005). The  $\text{CaCO}_3$  saturation state ( $\Omega$ ), which is dependent on the  $\text{CO}_3^{2-}$  concentration and influences  $\text{CaCO}_3$  precipitation, is consequently expected to decrease (Feely et al., 2004). Such changes in seawater chemistry may have direct impacts on metabolic processes, particularly ones using dissolved inorganic carbon (DIC) as a substrate, and thus affect both calcifying and photosynthetic marine organisms such as coralline algae.

Responses to high  $p\text{CO}_2$  of coralline algae belonging to different morphological or taxonomical groups are variable and species-specific (see Martin et al., 2013 for a review). Most of them are negatively affected with detrimental effects on recruitment (Kuffner et al., 2008), growth (Ragazzola et al., 2012), abundance (Martin et al., 2008), photosynthetic production (Anthony et al., 2008) and calcification (Gao and Zheng, 2010). Bleaching associated to mortality (Anthony et al., 2008; Diaz-Pulido et al., 2012) has also been found to increase in response to high  $p\text{CO}_2$ . Conversely, some authors reported a positive effect on photosynthetic (Borowitzka, 1981) and calcification processes (Martin et al., 2013) or parabolic responses of calcification to increased  $p\text{CO}_2$  (Johnson and Carpenter, 2012; Ries et al., 2009). The variability of the algal responses also depends on the abiotic parameters applied during the experiments. For example, calcification of *Hydrolithon onkodes* measured under  $336 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  presented a parabolic response with the highest calcification rate under the intermediate levels of  $530 \mu\text{atm}$  (Johnson and Carpenter, 2012) whereas a constant calcification decrease was measured under  $1200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  on the same species (Diaz-Pulido et al., 2012). Hofmann et al. demonstrated with the same technique (PAM fluorometry) that photosynthesis in *Corallina officinalis* can decrease (Hofmann et al., 2012a) or remain stable (Hofmann et al., 2012b) with an increase in  $p\text{CO}_2$ . As responses of living organisms are so varying, applying the same abiotic parameters is required to compare species-specific responses.

In the present study, the metabolic processes of photosynthesis, respiration and calcification were investigated simultaneously in different algal species from contrasting habitats in response to elevated  $p\text{CO}_2$ . Assuming that organisms inhabiting highly variable environments are

likely to be more robust to ocean acidification (Harley et al., 2012; Raven et al., 2012) and able to tolerate high pH/ $p\text{CO}_2$  fluctuations, we hypothesized that coralline algae living in fluctuating habitats (intertidal rock pools and channels) will be less affected by elevated  $p\text{CO}_2$  than algae from more stable subtidal environments. We investigated the physiological responses of three different algal species: *Corallina elongata*, an erected coralline alga from rock pools; *Lithophyllum incrustans*, a pink thick crustose coralline alga (CCA) which covers the pebbles in tidal channels and *Lithothamnion corallioides*, also called “maeri”, a key species forming rhodolith beds in the subtidal zone.

## 2. Methods

### 2.1. Biological material

Three coralline algal species living in contrasting environments from the intertidal to the subtidal zone on the north-western coast of Brittany were selected for this experiment.

- (1) *C. elongata* Ellis and Solander, 1786, is a geniculate alga erected from a basal crust, composed of numerous articulated calcareous branches. It is a perennial species from the intertidal zone, abundant on exposed shores, which forms a continuous mat at rock pool edges along Atlantic and Mediterranean coasts (Cabioch et al., 1992). Specimens of *C. elongata* were sampled on October 11th, 2010 in a shaded rock pool on the low intertidal shore of “Les Amiets”, Cléder ( $48^\circ 41.45' \text{N}$ ,  $4^\circ 7.26' \text{W}$ ). Algal fronds free of epiphytic organisms were selected for the experiment and carefully separated from their substrate to obtain their encrusting base. In October 2012, under sunny conditions, temperature fluctuated by about  $1^\circ \text{C}$ , from  $16.4^\circ \text{C}$  just after disconnection from the sea (pool emersion) to  $17.5^\circ \text{C}$  just before immersion at rising tide. Changes in temperature between the night and day can reach  $4^\circ \text{C}$  in such low intertidal shaded rock pools (see Egilsdottir et al., 2013). The pH on the total scale ( $\text{pH}_T$ ) in such a rock pool can vary locally according to the depth of the pool and the presence of other macroalgae between 8.61 and 7.82, corresponding to 70 and  $1000 \mu\text{atm } p\text{CO}_2$ , respectively (see Egilsdottir et al., 2013). The photosynthetic active radiations (PAR) measured using a flat quantum sensor (LiCor®, LI-192 SA) at midday under sunny conditions at the surface of the pool was around  $30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ . This low light was due to a large rock overhanging the pool and shading the pool area along the day.
- (2) *L. incrustans* Philippi, 1837, is a non-geniculate coralline alga forming thick pink/grey crusts covering the substrate. The thallus surface is variable in terms of color, thickness and shape, the oldest ones forming thick, rippled and peeled off margins (Steneck, 1986). This species is usually immersed (Littler, 1972) and can be found in rock pools and in the sub-canopy in the low intertidal. Small pebbles entirely covered by *L. incrustans* were collected on October 13th, 2010 in the middle of the Green Island channel, front of the *Station Biologique de Roscoff* ( $48^\circ 43.73' \text{N}$ ,  $3^\circ 59.22' \text{W}$ ). Selected thalli were completely pink (without white patches), characteristic of healthy crusts. In this channel, depth can vary between a few centimetres to meters between high and low tides and spring and neap tides. Abiotic parameters were measured in October 2012 at low water mean spring tide (similar environmental conditions as during the algal collection). Temperature varied from  $17.5^\circ \text{C}$  at midday on a sunny day to  $16.2^\circ \text{C}$  during the night. Under the dense *Sargassum muticum* canopy,  $\text{pH}_T$  at low tide fluctuated between 7.83 ( $p\text{CO}_2 \approx 700 \mu\text{atm}$ ) during the night and 8.74 ( $p\text{CO}_2 \approx 50 \mu\text{atm}$ ) during the day, under sunny

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