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Primary production, respiration and calcification of the temperate free-living coralline alga *Lithothamnion corallioides*

Sophie Martin *, Marie-Dorothée Castets, Jacques Clavier

LEMAR, Laboratoire des Sciences de l'Environnement Marin, UMR CNRS 6539, Institut Universitaire Européen de la Mer, Technopôle Brest-Iroise, Place Nicolas Copernic, F-29280 Plouzané, France

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Abstract

Calcification and primary production responses to irradiance in the temperate coralline alga *Lithothamnion corallioides* were measured in summer 2004 and winter 2005 in the Bay of Brest. Coralline algae were incubated in dark and clear bottles exposed to different irradiances. Net primary production reached 1.5 μmol C g^{-1} dry wt h^{-1} in August and was twice as high as in January–February. Dark respiration showed significant seasonal variations, being three-fold higher in summer. Maximum calcification varied from 0.6 μmol g^{-1} dry wt h^{-1} in summer 2004 to 0.4 μmol g^{-1} dry wt h^{-1} in winter 2005. According to *P–E* curves and the daily course of irradiance, estimated daily net production and calcification reached 131 μg C g^{-1} dry wt and 970 μg $CaCO_3$ g^{-1} dry wt in summer 2004, and 36 μg C g^{-1} dry wt and 336 μg $CaCO_3$ g^{-1} dry wt in winter 2005. The net primary production of natural *L. corallioides* populations in shallow waters was estimated at 10–600 g C m^{-2} y^{-1}, depending on depth and algal biomass. The mean annual calcification of *L. corallioides* populations varied from 300 to 3000 g $CaCO_3$ m^{-2}. These results are similar to those reported for tropical coralline algae in terms of carbon and carbonate productivity. Therefore, *L. corallioides* can be considered as a key element of carbon and carbonate cycles in the shallow coastal waters where they live.

Keywords: Primary production; Respiration; Carbon budget; Calcification; Coralline algae; *Lithothamnion corallioides*

1. Introduction

Coralline algae (Rhodophyta, Corallinacea) are abundant and widespread in coastal areas throughout the world, from polar regions to the tropics (Johansen, 1981; Steneck, 1986). Maerl develops when coralline red algae, which have a hard calcium carbonate skeleton, become free-living due to fragmentation (Birkett et al., 1998). In temperate systems, accumulation of unattached living or dead coralline algae forms large maerl beds (Martin et al., 2005). They are particularly abundant in the Mediterranean Sea and the Gulf of California, patchily distributed along the Atlantic coast, from northeastern Canada to eastern Caribbean and from Norway to the Canary Isles (Foster, 2001). According to their distribution, with kelp beds, mangroves, and seagrass meadows, maerl beds are among the Earth's ''Big-Four'' benthic communities dominated by macrophytes (Foster, 2001). Coralline algal abundance, size, shape, and species composition in maerl beds vary considerably depending on their location. On the coast of Brittany, maerl beds are mainly constructed by *Phymatholithon calcareum* (Pallas) Adey and McKibbin and *Lithothamnion corallioides* (P. and H. Crouan) P. and H. Crouan. The latter, a warm temperate alga, is the predominant species of the maerl beds in the Bay of Brest (France; Potin et al., 1990).

Several environmental factors influence coralline algal distribution. First, maerl beds are highly sensitive to desiccation (Wilson et al., 2004) and are found from the low intertidal zone to depths of 150 m only (Foster, 2001). Temperature is also a determinant factor, affecting geographical distribution and species composition of maerl beds. The northern limit of *L. corallioides* distribution is Scotland and their southern limit is the Canary Isles (Wilson et al., 2004). Furthermore, coralline species are sensitive to seasonal variations in temperature inducing changes in their physiology. *Lithothamnion* spp. growth rate increases with water temperature. Actually, the maximum growth rates in *L. corallioides* have been observed in summer (Adey and McKibbin, 1970; Potin et al., 1990). Temperature covaries with irradiance geographically and in time. These two environmental factors are tightly correlated to seasons that mainly influence the metabolism of coralline

* Corresponding author. Tel.: +33 2 98 49 86 78; fax: +33 2 98 49 86 45.
E-mail address: Sophie.Martin@univ-brest.fr (S. Martin).

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algae (Payri, 2000). Coralline algae develops where light is high enough for growth and their survival depends on irradiance availability, with drastic effects of screening by burial and silt deposits (Grall and Hall-Spencer, 2003; Hall-Spencer and Moore, 2000), but the production and calcification response to irradiance is still poorly documented (Wilson et al., 2004). Despite their ecological importance in temperate systems, primary production and calcification of coralline algae has been mainly investigated in tropical areas (Chisholm, 2000, 2003; Payri, 2000; Payri et al., 2001).

The objective of the present study is to quantify the seasonal changes of *L. corallioides* primary production, respiration and calcification in ambient conditions. We describe production and calcification responses to irradiance in summer 2004 and winter 2005 in order to estimate carbon and carbonate budgets for this temperate coralline and provide first estimates of the natural population of *L. corallioides*.

2. Materials and methods

2.1. Experimental algae

L. corallioides were collected manually by snorkeling from natural populations at the Squiffiec site (48°19′35″N, 4°23′50″W) in the Bay of Brest (Western Brittany, France). Water depth at the Squiffiec site varied according to the tide between 1 and 8 m. Only live coralline algae known for their pink color were harvested in the size range of between 1 and 3 cm diameter. Algae were thoroughly cleaned in the laboratory to remove epiphytic organisms without thalli damage. Only a few days after collection and approximately a week before conducting the tests, algae were immersed to a depth of 5 m at the experimental site (Sainte-Anne du Portzic; 48°21′10″N, 4°34′30″W).

2.2. Incubation procedure

Approximately 120 g wet weight of algae was placed into 1.5 L plastic bottles filled with natural filtered seawater. Series of bottles were incubated horizontally for a period of 3–4 h along a line fastened to a buoy to keep constant depths regardless of tidal conditions. Each series of bottles included one opaque bottle and four clear bottles incubated at four different depths from subsurface to 6 m to obtain different irradiance exposures. Measurements were carried out between 11 a.m. and 4 p.m. during sunny days in summer 2004 and winter 2005. One series of bottles was incubated in 3 August 2004, three series in 5 August 2004, three series in 26 January 2005, and three series in 8 February 2005.

Clear bottles were used to measure net algal production and calcification in light conditions, and opaque bottles to estimate respiration and calcification in dark conditions. Reference incubations without algae were performed in dark and light conditions.

Depth, temperature, salinity (in Practical Salinity Units) and incident irradiance were measured using a CTD probe equipped with an underwater quantum sensor (Sea-Bird-Electronics—QSP 2300). Profiles were performed every 30 min during the incubations and data were recorded every second. Mean irradiances at the incubation depths were calculated from surface irradiance using attenuation coefficients. Surface irradiance data (PAR, μmol m^{-2} s^{-1}) were provided by a LI COR quantum sensor (L1 192 SA) set on the automated MAREL Iroise Station (IUEM-UBO, Observatoire du Domaine Côtier), located near the sampling station. The attenuation coefficients for irradiance (K) were calculated from irradiance profiles during the incubations according to Kirk (1983).

2.3. Production, respiration and calcification measurements

Water samples for O_2, pH and total alkalinity (TA) measurements were taken at the beginning and at the end of the incubations. pH (in total scale) was measured immediately with a precision of 0.003 pH unit on a pH meter standardized with Tris–HCl and 2-amminopyridine/HCl buffer solutions (DOE, 1994). O_2 concentrations (mg L^{-1}) were determined by Winkler's titration. Water samples were transferred into 100-mL glass flasks fitted with ground glass stoppers; reagents were added immediately. Flasks were shaken and stored immersed in water in the dark pending analysis. O_2 concentrations were determined by iodometric titration using an automatic titrator with a precision of 0.1 mg L^{-1}. TA samples were passed through GF/F filters, poisoned with mercuric chloride (DOE, 1994) and stored in 250-mL bottles in a cool dark place. TA was determined in the laboratory on 20-mL sub-samples by the automatic potentiometric method using Gran titration. Reproducibility was higher than 0.02 mequiv L^{-1}. The concentration of dissolved inorganic carbon (DIC) was calculated from pH, TA, temperature and salinity, according to Lewis and Wallace (1998).

2.4. Data treatment

At the end of the incubations, algal dry wt in each bottle was measured with a precision of 1 mg, after drying at 60 °C until weight was constant.

To obtain actual algal primary production, respiration and calcification, fluxes were corrected considering control data (light and dark bottles). Calcification and primary production (in CO_2 fluxes) were estimated using the alkalinity anomaly technique (Smith and Key, 1975). Calcification is calculated by using the relationship: $Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$, for which total alkalinity decrease by 2 equiv for each mol of $CaCO_3$ precipitated. Net production and net calcification per unit dry wt were calculated using the following formula:

$$P_{\text{net}}(O_2) = \frac{\Delta O_2 v}{\text{DW}\,\Delta t}, \qquad P_{\text{net}}(CO_2) = \frac{\Delta \text{DIC}\, v}{\text{DW}\,\Delta t} - G,$$

$$G_{\text{net}}(CaCO_3) = \frac{\Delta \text{TA}\, v}{2\text{DW}\,\Delta t}$$