

Carbonate production by calcareous red algae and global change

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ABSTRACT

The most important groups of modern red calcareous algae are the Mg-calcite secreting Corallinales and Sporolithales, and the aragonitic Peyssonneliales and Nematiales. They are common on the world's shelves and are vulnerable to the global warming and the lowering of pH of sea water, caused by the ongoing increase in anthropogenic CO₂. Among them, coralline algae are ecosystem engineers and major producers of carbonate sediment, of particular importance in temperate and cold seas. Corallines respond to marine acidification and rising temperature showing decreased net calcification, decreased growth and reproduction, as well as reduced abundance and diversity, leading to death and ecological shift to dominant non-calcifying algae. Despite their key ecological and sedimentological role, and because of their vulnerability to marine warming and acidification, our knowledge of the distribution of coralline-dominated habitats and the quantification of their carbonate production is not adequate to allow proper environmental management and confident modelling of a global carbon budget. Locating the algal carbonate factories around the world, then describing them, e.g., evaluating their extent and their production, are a priority for future research.

KEY WORDS

marine acidification,
carbonate sediment,
carbonate production,
Rhodophyta,
coralline algae,
habitat mapping.

RÉSUMÉ

Production carbonatée par les algues rouges calcaires et changement climatique global. Les groupes les plus importants d'algues rouges calcaires actuelles sont, d'une part, les Corallinales et les Sporolithales, qui sécrètent de la calcite magnésienne, et d'autre part, les Peyssonneliales et les Nématiales, qui produisent de l'aragonite. Abondantes sur les plates-formes actuelles, elles y jouent un rôle majeur

non seulement pour leur contribution à la production de sédiments carbonatés, notamment en ce qui concerne les mers tempérées ou froides, mais également dans le façonnage des morphologies sous-marines. Vulnérables à l'abaissement du pH des eaux marines qui est généralement corrélé avec l'augmentation anthropique du CO₂ atmosphérique, elles sont affectées négativement par l'acidification des océans et la hausse de température: ceci peut se traduire par une diminution visible de leur calcification, affecter leur croissance ou leur reproduction. La diminution de l'abondance et de la diversité peut conduire à un remplacement par des communautés dominées par des algues non calcifiées, voire aller localement jusqu'à leur complète disparition. Malgré leur importance écologique et sédimentologique majeure, et en raison de leur vulnérabilité au réchauffement et à l'acidification des océans, notre connaissance de la distribution des habitats dominés par les corallines et la quantification de leur production n'est pas suffisante pour permettre une gestion adéquate de l'environnement et une modélisation fiable du bilan carbone global. Identifier, partout dans le monde, les zones de production de carbonates d'origine alguaire, puis les caractériser, notamment en évaluant leurs étendues et productivités respectives, constituent la priorité pour les recherches à venir.

MOTS CLÉS

acidification océanique,
sédiments carbonatés,
production carbonatée,
Rhodophytes,
algues corallines,
cartographie des habitats.

INTRODUCTION

The industrial revolution of the mid-18th century was driven by a rising exploitation of fossil fuels and produced an increasing atmospheric partial pressure of carbon dioxide (pCO₂) from a pre-industrial level of 280 to 370 ppm in 2000. A concentration of about 560 ppm, double the pre-industrial level, is expected by 2070 (Meehl *et al.* 2007).

Model predictions for atmospheric [CO₂] between AD 2100 and 2300 provide a wide range of values (450-8110 ppm; Caldeira & Wickert 2005), depending on variable assumptions and uncertainties about the future emission pathways (Sundquist 1993; Wigley *et al.* 1996; Caldeira & Wickert 2005). Among the possible scenarios, an intermediate [CO₂] ranging from 1500 to 2100 ppm would be comparable to the Eocene atmosphere (Pearson *et al.* 2009). During the past 24 million years, atmospheric [CO₂] has remained more or less stable, below 500 ppm (Pearson & Palmer 2000; Lüthi *et al.* 2008), with the glacial-interglacial fluctuations over the past 800 kyr corresponding to a 172-300 ppm oscillation of atmospheric [CO₂] (Lüthi *et al.* 2008; Hönlisch *et al.* 2009).

Atmospheric carbon dioxide is a greenhouse gas, which is warming the atmosphere and the surface ocean. Models estimate a mean global temperature in the late 21st century of about 2 to 3°C above pre-industrial temperatures. The mid-Pliocene is the most recent interval of geological time when the Earth experienced such temperature (Haywood *et al.* 2000; Jansen *et al.* 2007), although it seems that the current climate change will be much more rapid, thus decreasing the possibility of the biota's adaptation to the new conditions.

About half of the anthropogenic CO₂ emission remains in the atmosphere and contribute to the enhancement of the greenhouse effect and climate change. The increase in atmospheric [CO₂] is accompanied by increased gas transfer into the ocean surface waters (Houghton *et al.* 1992; Keeling & Whorf 1994; Takahashi *et al.* 1997). Since the beginning of the industrial era, the ocean has absorbed about 48% of the anthropogenic CO₂ (Sabine *et al.* 2004) thus acting as a sink and reducing the pace of global warming. The current ocean uptake is about 25% of the total of anthropogenic CO₂ emissions (Le Quéré *et al.* 2009).

As CO_2 dissolves at the ocean surface it reacts with water to form protons (H^+) and inorganic carbon (DIC), which is the sum of the concentrations of carbonic acid (H_2CO_3), bicarbonate (HCO_3^-), and carbonate ions (CO_3^{2-}) stored in the ocean. With increasing atmospheric pCO_2 , DIC will increase and the equilibrium of the carbonate system will shift to higher CO_2 and bicarbonate ion-levels, lower carbonate ion concentration and lower pH (Wolf-Gladrow *et al.* 1999; Feely *et al.* 2009).

These changes in carbonate chemistry are already occurring, and often referred to as “ocean acidification” (OA), although pH will not shift below the neutral value of 7. Records of ocean carbon chemistry for the last 25 years show clear trends of increasing carbon and decreasing pH that follow increasing atmospheric CO_2 , in agreement with estimates from basic marine chemistry (Bates 2007; Caldeira *et al.* 2007). The surface ocean has been acidified by 0.1 pH unit since 1800 (Orr *et al.* 2005). Current models predict that the pH of surface seawater will drop by an additional 0.2–0.4 pH units by the year 2100 (Caldeira & Wickett 2005; Sabine & Feely 2007; Feely *et al.* 2009).

Ocean warming and acidification are likely to have a large impact on marine life and biogeochemical processes, such as the dissolution of carbonate mineral and reduced production and accumulation of marine biogenic carbonates. Seawater acidification reduces the calcium carbonate (CaCO_3) saturation state (Kleypas *et al.* 2006), thus creating conditions less favourable to biogenic calcification (Raven *et al.* 2005; Atkinson & Cuet 2008; Hall-Spencer *et al.* 2008).

Saturation state has been shown to affect growth in calcifying green algae, crustose coralline algae, and corals (Gattuso *et al.* 1998; Seibel & Fabry 2003; Kleypas & Langdon 2006; Kleypas *et al.* 2006; Tyrrell 2008), which are among the key carbonate producers in coastal waters. Because the solubility of CaCO_3 increases at lower temperature and higher pressure, cold and deep ocean waters are naturally low in saturation or even undersaturated with respect to CaCO_3 , becoming corrosive and dissolving carbonate minerals (Broecker 2003). Surface ocean waters at present are supersaturated with both aragonite and calcite, but the aragonite

and calcite saturation horizons of the world’s oceans are shoaling at a rate of 1–2 m per year (Guinotte & Fabry 2008) due to the influx of anthropogenic CO_2 to the oceans. High-latitude surface waters like the southern Ocean will be undersaturated with respect to aragonite by 2050 (Orr *et al.* 2005), with calcite expected to follow 50–100 years later (Feely *et al.* 2004, 2008, 2009; Doney *et al.* 2009).

The anthropogenic increase of CO_2 has already shifted the saturation horizons for CaCO_3 towards the surface by 50–200 m above its position before the industrial revolution. So undersaturated deep waters is growing in extent upward and, by 2050, the saturated surface zone will begin to disappear in some areas (Feely *et al.* 2004, 2009).

The precipitation of calcium carbonate is a source of CO_2 , whereas carbonate dissolution acts as a sink of CO_2 (Frankignoulle *et al.* 1994). Ultimately, carbonate dissolution is expected to buffer OA and play an important role in global change, but the natural process of carbonate dissolution is too slow to neutralize the fossil fuel CO_2 for it requires decades to centuries (Andersson *et al.* 2003). The lowered carbonate saturation state may cause a selective dissolution of metastable carbonate minerals in accordance with their relative solubilities. Current evidence suggests that a metastable equilibrium is maintained between the pore water and the most soluble carbonate mineral phase present in the sediments. Thus, dissolution could buffer the acidity of the pore waters in carbonate sediments, but overlying surface waters in coastal environments will not accumulate enough alkalinity to produce a significant buffer effect (Langdon 2000; Andersson *et al.* 2003, 2005; Andersson & Mackenzie 2011).

In addition to the process of calcification, respiration from aerobic biota is a major source of CO_2 . On the other hand, photosynthesis removes CO_2 to produce new organic matter in plants, algae, and cyanobacteria. Therefore, calcifying photosynthetic organisms are at the same time sink and source of CO_2 but the algebraic result of these antithetic functions in calcareous-algae dominated environments is largely unexplored (Frankignoulle *et al.* 1994; Suzuki 1998).

BIOGENIC CARBONATE MINERALOGY AND MARINE ACIDIFICATION

Calcium carbonate occurs in invertebrate skeletons and algal thalli as aragonite or calcite. Magnesium (Mg^{2+}) can replace some of the Ca^{2+} in the calcite lattice, and calcite containing > 4% wt of $MgCO_3$ is conventionally defined as high Mg-calcite (HMC; Tucker & Wright 1990; Ries *et al.* 2009), although the 4% boundary is arbitrary and not universally recognized (Rucker & Carver 1969; Smith *et al.* 2006; Andersson & Mackenzie 2011). The extent to which a biogenic carbonate particle is prone to dissolution in seawater depends on several factors, among which the leading ones are mineralogy and the calcium carbonate saturation state, which is dependent on the carbonate ion concentration (Mucci 1983; Gehlen *et al.* 2005).

Of the two major biologically secreted forms of $CaCO_3$ in modern calcifiers, aragonite has twice the solubility of pure calcite (Zeebe & Wolf-Gladrow 2001; Politi *et al.* 2004). However, natural biogenic HMC containing > 8-12 mol% $MgCO_3$ is more soluble than aragonite, so is the most sensitive responder to acidification (Morse *et al.* 2006; Andersson *et al.* 2008, 2011).

Shelf sedimentary facies of the temperate and cold zones are enriched in calcite and HMC, derived from bryozoans, foraminifers, coccolithophores, coralline algae and echinoderms, with red coralline algae as the most important contributor of HMC. In contrast, aragonite dominates the sediments of the tropical oceans, derived from scleractinian corals and green algae (a review of sedimentary facies is provided by Mutti & Hallock 2003).

Cool-water carbonate-rich sediments will be the first to suffer the impact of a decrease of the carbonate saturation of seawater (Morse *et al.* 2006; Andersson *et al.* 2008). Consequently, existing deposits of highly soluble HMC in the medium and high latitudes are likely to be the first to undergo dissolution caused by the ongoing OA. In order to assess the role of the medium and high-latitude HMC deposits on the total carbonate budget, and their possible buffer effect in a scenario of increasing acidification, their identification and quantification is strongly needed (Guinotte & Fabry 2008; Le

Quéré *et al.* 2009). Field and laboratory experiments are needed to assess their rate of dissolution, because the observed solubility of biogenic carbonates shows a more or less pronounced offset from the theoretical behaviour described from synthetic, pure and compact minerals (Bischoff *et al.* 1983; Morse *et al.* 2006). Moreover, marine carbonate assemblages are multi-phase systems that are heterogeneous at the level of individual carbonate shell structure and composition, and at the level of particle characteristics (compactness, thickness, geometry, volume/surface ratio, etc.) (Walter & Morse 1984; Agegian & Mackenzie 1989). In this context, the focus will be on calcareous red algae.

THALLUS CALCIFICATION IN MODERN CALCAREOUS RHODOPHYTA

The largest group of present-day calcareous red algae (Rhodophyta) are corallines, of the orders Corallinales and Sporolithales (taxonomic reference in Guiry & Guiry 2011) (Figs 1; 2). The thallus of these calcified algae develops from a thin crust, is composed of cell filaments that are connected together, and grows by division of the filaments and by addition of one new cell at the tip of each filament (Fig. 1A-C) (Johansen 1981; Cabioch 1988; Woelkerling 1988 for general reference to morphogenesis and anatomy).

The cell walls of the coralline thallus are completely calcified, with two exceptions: the reproductive cells and the superficial wall of the outermost epithallial cells in contact with seawater (Fig. 1B). The precipitation of calcite in live, functional cells takes place in two steps: 1) deposition of the "primary layer" of elongate crystals of Mg-calcite oriented parallel to the wall surface, following the cell wall polysaccharide matrix; and 2) deposition of the "secondary layer" of elongate crystals with orientation perpendicular to the cell surface (Borowitzka *et al.* 1974; Flajs 1977; Cabioch & Giraud 1986) (Fig. 1B).

The cell-walls of coralline algae are composed of Mg-calcite, with [Mg] increasing in the calcite lattice as the temperature increases, in seawater with present-day Mg/Ca mole ratio (Chave 1954; Basso 1992; Halfar *et al.* 2000; Stanley *et al.* 2002; Basso

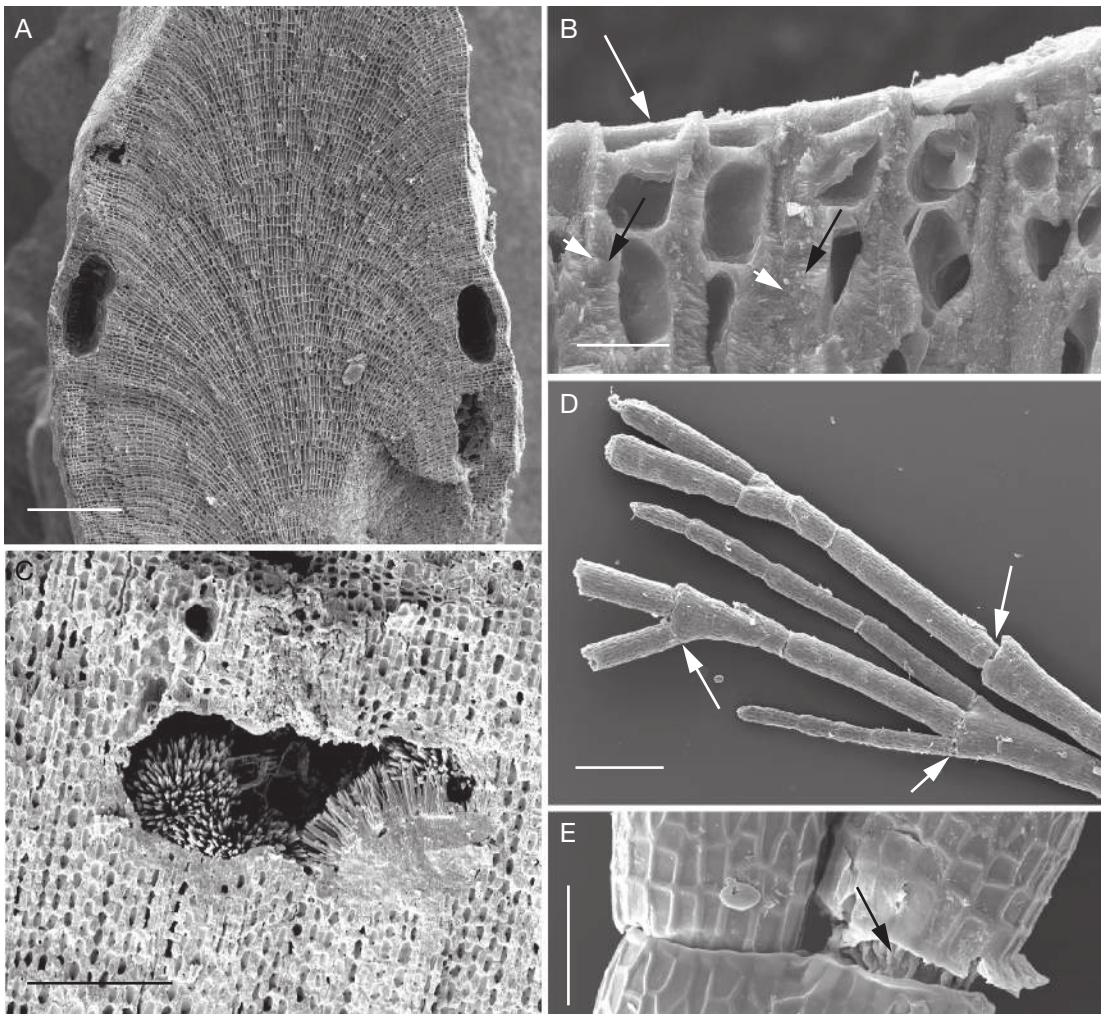


FIG. 1. — SEM photographs of the calcified thallus of coralline algae: **A**, calcified cell filaments in a protuberance of a non-geniculate plant. The empty conceptacle chambers on the border contained the non-calcified spores; **B**, a coralline growing margin showing the outermost non-calcified epithelial cell wall (white arrow). Below are the completely calcified perithalial cell walls with the primary (white arrowhead) and secondary (black arrow) Mg-calcite layers; **C**, chemical precipitation of carbonate druse inside an empty conceptacle chamber; **D**, a geniculate coralline alga with the articles (intergenicula) connected by flexible joints (genicula) made of uncalcified filaments (arrows); **E**, a close-up of a geniculum showing the non-calcified filaments (arrow). Scale bars: A, D, 250 µm; B, 10 µm; C, 100 µm; E, 50 µm.

et al. 2006; Kamenos *et al.* 2008, 2009). The [Mg] of the thallus increases with increasing temperature and calcite saturation (Agegian 1985). Temperature is negatively correlated to calcite density of thin-walled cells, within annual or subannual banding patterns (Cabioch 1966; Adey & McKibbin 1970; Giraud & Cabioch 1979; Freiwald & Henrich 1994;

Basso 1994, 1995; Halfar *et al.* 2000; Blake & Maggs 2003; Rivera *et al.* 2004; Basso *et al.* 2006; Kamenos & Law 2010). Growth rates increase with temperature, as evinced by a six-fold faster growth of *Lithophyllum margaritae* (Harriot) Heydrich incubated at 25°C than at 10°C (Steller *et al.* 2007b), although a large variability of response and adaptation

is expected in other species from different climatic belts (Adey 1970). The growth rate of *Porolithon gardineri* (Foslie) Foslie dramatically decreased with temperature above 29–30°C, but it increased linearly as function of calcite saturation, and was only slightly influenced by light intensity (Agegian 1985). In agreement with Martin & Gattuso (2009) growth and calcification of coralline algae increase with increasing temperature, within the range in the natural habitat. Above these levels, warming is detrimental and causes necrosis and death.

After the release of spores, prismatic or acicular crystals of calcite or aragonite may form in the empty conceptacles or in other microcavities (Alexandersson 1974; Harney *et al.* 2000) (Fig. 1C). Moreover, brucite was detected in some corallines under XRD analysis (Moberly 1968), although this finding has been not confirmed in recent literature.

Corallines are separated into two morpho-functional groups of no taxonomic value (Cabioch 1988): the geniculate (= articulate), with uncalcified flexible genicula alternating with rigid calcareous intergenicula, and the completely rigid non-geniculate, also referred to as crustose coralline algae or CCA (Figs 1; 2). Most genicula decompose after death, so geniculate corallines disarticulate into sand-sized particles and can accumulate *in situ* or be easily transported away from the original habitat. On the contrary, non-geniculate corallines inhabiting hard and soft substrates may enter the geologic record more or less in their original shape or produce fragments of any size: boulders derived from algal build-ups, rhodoliths several centimetres long, millimetric detached protuberances or crusts, and heavily abraded fine sand-sized fragments (Agegian & Mackenzie 1989; Tsuji 1993; Harney *et al.* 2000; Gherardi & Bosence 2001; Toscano & Sorgente 2002; Fornos & Ahr 2006; Hetzinger *et al.* 2006; Brandano & Civitelli 2007) (Fig. 2).

Geniculate and non-geniculate coralline algae are one of the most prolific carbonate producers among seagrass epiphytes worldwide (Land 1970; Nelsen & Ginsburg 1986; Walker & Woelkerling 1988; Perry & Beavington-Penney 2005). Together they are about 38–80% of the total of epiphyte-produced carbonate on seagrass leaves in southern Australia (James *et al.* 2009; Table 1). Encrusting epiphyte corallines

are very thin and disintegrate rapidly when seagrass blades are broken or decomposed, becoming carbonate mud (Nelsen & Ginsburg 1986; Perry & Beavington-Penney 2005; James *et al.* 2009).

Other orders of red algae include calcified species, namely the aragonite precipitating Peyssonneliales and Nemaliales (taxonomic reference in Guiry & Guiry 2011; Chave 1984; Nelson 2009).

Peyssonneliales are a diverse group of platy, orbicular algae with a variable but species-specific degree of calcification (Fig. 3). Some Peyssonneliales possess only scattered calcified cells and a hypobasal, extracellular calcification, while a few species of *Peyssonnelia* Decaisne such as *P. rosa-marina* Boudouresque & Denizot (Mediterranean, temperate) and some genera such as *Polystrata* Heydrich (warm temperate to tropical) are fully calcified (Fig. 3) (Denizot 1968; James *et al.* 1988; Basso 1990; Ballantine *et al.* 2000; Kato *et al.* 2006). The aragonite laid down within the cell wall is organized in layers of various thickness in which crystals are either spherulites or prisms oriented normal to the cell surface (Flajs 1977; James *et al.* 1988) (Fig. 3G). The hypobasal calcification appears as an aragonite crust 80–200 µm thick, projecting downward from the lower thallus surface and crossed by rhizoids (Fig. 3C, D). The post-mortem fate of Peyssonneliales is largely dependent on their habit and growth-form (single crust on solid substrate; layered crusts, appanate or globose forming rhodoliths on soft substrate, foliose frameworks). However, as most of them do not form thick encrustations, they easily undergo fragmentation before final burial. Those Peyssonneliales possessing only the hypobasal calcification may also enter the sedimentary record as aragonite chip-like structures, which may be distinguished from simple layers of cement as long as the traces of rhizoids are preserved (James *et al.* 1988). Based on data from Ballesteros (1994), a western Mediterranean *Peyssonnelia* bed, dominated by the completely calcified *P. rosa-marina*, contains 1477 to 2169 g m⁻² of algal carbonate, equivalent of a carbonate production of about 123–181 g m⁻² y⁻¹.

The calcareous species of Nemaliales occur in the genera *Galaxaura* Lamouroux, *Liagora* Lamouroux, *Izziella* Doty and *Titanophycus* Huisman, Saunders & Sherwood. The aragonite calcification and

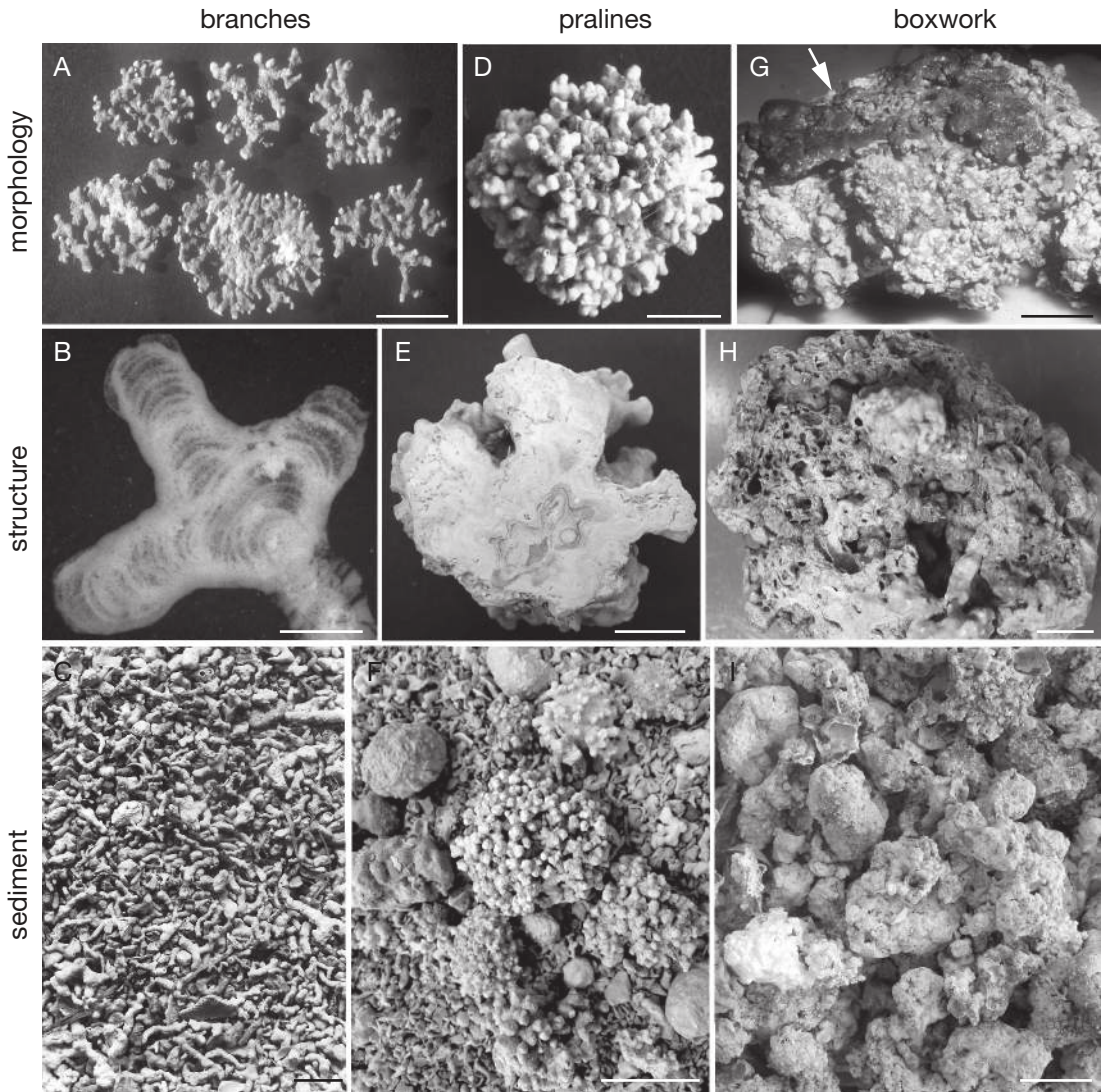


FIG. 2. — Unattached branches, pralines and boxwork rhodoliths, the three end-points of the morphological variability of non-geniculate coralline rhodoliths (Basso 1998; Basso *et al.* 2009) with relevant structure (B, E, H) and typical sediment production (C, F, I). A–C, unattached branches: A, unattached branches are the most common growth form of maerl forming species; B, unattached branches are usually monospecific and lack a nucleus; C, maerl-related sediment typically composed of branch fragments. D–F, pralines: D, a fruticose growth-form (*sensu* Woelkerling *et al.* 1993) of a praline rhodolith; E, pralines have compact internal structure and are commonly nucleated; F, rhodolith beds normally produce pebble-size sediments in a matrix of protuberance fragments and other accompanying biogenic remains. G–I, boxwork rhodoliths: G, deep rhodoliths are typically irregular in shape since growth can be asymmetric (arrow on live thallus); H, macroscopic voids and irregular internal structure of a boxwork rhodolith, usually multispecific; I, cobble-sized boxwork rhodoliths of the outer shelf. Scale bars: A, 1.5 cm; B, 1.5 mm; C–E, H, 1 cm; F, 2 cm; G, I, 4 cm.

the thallus are very variable, even within the same genus (Guiry & Guiry 2011; Lin *et al.* 2011). *Galaxaura* is found mainly in the tropics. *Liagora* is the

largest genus in the family Liagoraceae and widely distributed in warm-water and temperate regions (Guiry & Guiry 2011; Lin *et al.* 2011).

The calcareous Nematiales possess an articulated or inarticulated thallus, mostly erect, that after death is easily fragmented and transported.

The skeletal ultrastructure of *Galaxaura* was investigated by Okazaki *et al.* (1982) and Mu & Riding (1999), who found aragonite: 1) in the intercellular spaces of the algal cortex; 2) in the cell wall mostly in the form of granules; and 3) on the inner surface of the cortex as elongate crystals. The quantification of the carbonate production of Nematiales has never been addressed, though it is not expected to be significant on global scale.

RED CALCAREOUS ALGAE, GLOBAL CHANGE AND CARBONATE BUDGET OF NON-TROPICAL SHELVES

The scientific literature started to re-evaluate the geologic role of coralline algae in the seventies (Adey & McIntyre 1973; Adey & Vassar 1975) and subsequently, the common occurrence of algal carbonates in non-tropical sediments started to be a shared knowledge among geologists. More recently, some comprehensive books, reviews and a number of scientific papers on non-tropical carbonates pointed out the importance of calcareous red algae as carbonate producer (among others: Nelson 1988; Canals & Ballesteros 1997; James & Clarke 1997; Foster 2001; Pedley & Carannante 2006).

Coralline algae are common from tropical to polar oceans at all depths within the photic zone and, contrary to the other groups of calcareous red algae (Peyssonneliales and Nematiales), they are major framework builders and carbonate producers especially in temperate and cold water benthic ecosystems (Pérès 1982; Bosence 1983a; Nelson 1988; Freiwald & Henrich 1994; Fornos & Ahr 1997; James & Clarke 1997; Basso 1998; Foster 2001; Bressan *et al.* 2001; Toscano & Sorgente 2002; Gherardi 2004; Ballesteros 2006; Toscano *et al.* 2006; Bracchi & Basso 2012; Savini *et al.* 2012). For this reason the following discussion will focus on corallines.

Corallines first appeared in the Early Cretaceous and progressively diversified up to a peak in the Early Miocene, with diversification stabilizing during the

Neogene (Aguirre *et al.* 2000). From the Burdigalian to Tortonian, rhodalgal facies reached peak abundances on a global scale (Halfar & Mutti 2005). Thus, corallines are a key element of carbon and carbonate cycles in shallow-water since the Cenozoic.

Coralline algae are considered ecosystem engineers (Jones *et al.* 1994; Nelson 2009): entire subtidal seascapes of high ecological and economical value (i.e. coralligenous formations) are shaped or literally produced by concretions of coralline algae (Adey & Burke 1976; Steneck & Adey 1976; Bosence 1983a, 1984; Freiwald & Henrich 1994; Kikuchi & Leão 1997; Bressan *et al.* 2001; Ballesteros 2006). The coralligenous habitat is an outstanding example of the role of carbonate bioconstruction (Bosence 1983a; Ballesteros 2006; Nalin *et al.* 2006; Basso *et al.* 2007).

Small concretions and nodules (rhodoliths) formed by unattached growth-forms of coralline algae and calcareous Peyssonneliaceae are widespread in many subtidal environments and considered a major component of coastal ecosystem structure and functioning (Bosellini & Ginsburg 1971; Milliman 1977; Bosence 1980, 1983b, 1985; Prager & Ginsburg 1989; Littler *et al.* 1991; Laborel *et al.* 1994; Steller & Foster 1995; Piller & Rasser 1996; Basso 1998; Freiwald 1998; Foster 2001; Bressan *et al.* 2001; Gherardi 2004; Bassi *et al.* 2009; Basso *et al.* 2009).

The scientific literature on the relationship between coralline algae and the anticipated consequences of climate change, particularly global warming and OA, has been centred on three different levels: 1) the response of the individual organism; 2) the impact on the biological cycle of coralline species; and 3) the feed-back to marine acidification from habitats dominated by coralline algae, i.e. their role as source or sink of atmospheric CO₂.

The investigations by field work and pH and T manipulation experiments have been aimed to test the following hypotheses (Kroeker *et al.* 2010; Table 1): 1) calcifying plants are more sensitive to ocean acidification than non calcified plants; 2) coralline algae are more sensitive than other organisms to OA because their HMC thallus is more soluble than pure calcite and can be the most soluble mineral phase when Mg > 8-12 mol% MgCO₃; and 3) some stages in their life history are more sensitive than other.

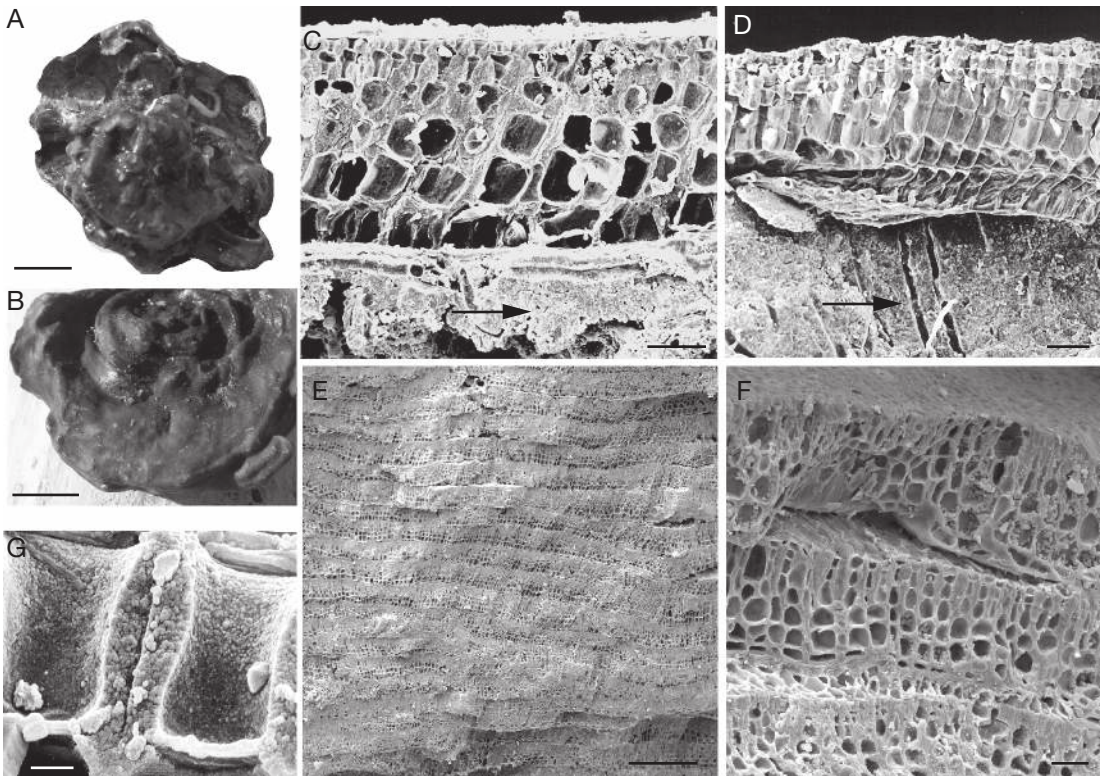


FIG. 3. — The calcified thallus of Peyssonneliales: **A**, *Peyssonnelia rosa-marina* Boudouresque & Denizot rhodolith from the Mediterranean sea; **B**, *Peyssonnelia* sp. crustose growth-form from Mediterranean hard substrates; **C**, the calcified thallus of the aragonitic *Peyssonnelia* Decaisne and the hypobasal calcification (arrow); **D**, a non calcified *Peyssonnelia* with rhizoid traces across the hypobasal calcification (arrow); **E**, a thick rhodolith-forming *Polystrata* Heydrich; **F**, detail of *Polystrata* thalli; **G**, close-up of calcified cell-walls of *Polystrata*. Note spherulitic crystals; **C-G**, SEM photographs. Scale bars: A, B, 2 cm; C, 50 μ m; D, 40 μ m; E, 250 μ m; F, 20 μ m; G, 2 μ m.

RESPONSE OF CALCIFYING VS NON-CALCIFYING ALGAE

Photosynthesis by most macroalgae appears to be limited by inorganic carbon sources in natural seawater, although some results are contradictory (among others: Surif & Raven 1989; Mercado *et al.* 2001), and the ongoing rise in the atmospheric CO_2 is expected to have a positive effect in the growth of fleshy algae (Gao *et al.* 1993b; Hendriks *et al.* 2010; Kroeker *et al.* 2010).

Along a natural pH gradient from 8.1 to 6.7 caused by volcanic vents, macroalgal associations change at both taxonomic and morphological levels (Hall-Spencer *et al.* 2008; Porzio *et al.* 2011). The majority of the macroalgae grew with only a

5% decrease in species richness as the mean pH dropped from 8.1 to 7.8. However, at pH 7.8 the species richness declined 72%, and was associated with a marked decrease of cover by turf algae. Of the twenty species of calcareous algae occurring at normal pH, none was recovered at pH 6.7, and an overall reduced cover was observed at pH 7.8, with the exception of the non-geniculate coralline *Hydrolithon cruciatum* (Bressan) Chamberlain (Porzio *et al.* 2011). Unfavourable conditions for calcification in calcifying algae apparently give an advantage to the non-calcified algae that outcompete them for space and light (Porzio *et al.* 2011), although Langdon *et al.* (2003) saw an eight-fold decrease in the calcification of a coral reef com-

munity dominated by macroalgae in response to a doubled $p\text{CO}_2$, accompanied by enhanced turnover of organic carbon and absence of effect on net organic production.

Mesocosm experiments exposing CCA to elevated $p\text{CO}_2$ ($2 \times$ present day) indicate up to a 92% reduction in total area covered by CCA and a 52% increase in soft-bodied algae (Guinotte & Fabry 2008; Kuffner *et al.* 2008).

CORALLINE ALGAE CALCIFICATION IN RESPONSE TO OA AND RISEN TEMPERATURE

A long-term experiment in a coral reef mesocosm showed that a $p\text{CO}_2$ double than present results in an 86% decrease of the total coralline cover on hard surfaces, and 250% decrease in the calcification of rhodoliths (Jokiel *et al.* 2008). Combined field work observations along natural gradient of acidification (volcanic venting) and pH manipulation in aquaria show that coralline epiphytes on *Posidonia* leaves decrease from 18-69% cover in normal seawater to nil at pH 7.7, with complete dissolution at pH 7 (Martin *et al.* 2008). However, an investigation of the response of *Neogoniolithon* Setchell & Mason to $p\text{CO}_2$ values of modern concentration, 2, 3 and 10 times the pre-industrial levels, gave a complex response: net calcification appears to increase from pre-industrial to present-day $[\text{CO}_2]$, remains more or less stable with doubled $[\text{CO}_2]$, and decreases under the highest $p\text{CO}_2$ (Ries *et al.* 2009).

Under experimental conditions of elevated temperature (ambient + 3°C) and elevated $p\text{CO}_2$ (700 ppm), the percentage of CCA deaths doubled or tripled, and was accompanied by a rate of dissolution of dead algal thalli two to four times higher (Martin & Gattuso 2009). Net calcification is reduced by half under elevated temperature and $p\text{CO}_2$ (Martin & Gattuso 2009). High CO_2 and warming at 28-29°C are bleaching agents for CCA under high irradiance (Anthony *et al.* 2008), with calcification reduced by 50% at pH 7.8 and net dissolution occurring at pH 7.6 (Anthony *et al.* 2008).

SENSITIVITY TO OA AND RISEN TEMPERATURE DURING LIFE CYCLE

The recruitment rate and growth of coralline algae is severely inhibited under elevated $p\text{CO}_2$, although

the reduced coralline cover along a natural gradient of increased CO_2 is associated with relative increase of the reproductive structures at pH 7.8 in the non geniculate genera *Neogoniolithon* and *Mesophyllum* Lemoine, and a decrease in the geniculate *Jania* Lamouroux (Porzio *et al.* 2011). Agegian (1985) also reported a reduction in recruitment when CCA are exposed to elevated $p\text{CO}_2$ in aquarium experiments (Guinotte & Fabry 2008). Mesocosm experiments exposing CCA to $p\text{CO}_2$ double than present indicate up to a 40% reduction in growth rates and 78% decrease in recruitment (Buddemeier 2007; Kuffner *et al.* 2008).

A study on the effect of marine acidification on Corallinales spores in an artificial controlled culture showed inhibition of coralline spore production and growth, and increase in the mortality of germination disks (Cumani *et al.* 2010).

QUANTIFICATION OF CORALLINE CARBONATES

During the last decades, ongoing global change became one of the biggest scientific challenges of our time, demanding an improved knowledge and quantification of the C pathways between lithosphere, hydrosphere, atmosphere, and biosphere, and of the response of each component of the system to variations in physical and chemical parameters. One piece in the puzzle is the calcifying marine biota, and an increasing number of investigations appeared, aimed at understanding the sensitivity of organisms and biomes to global change (among others: Gao *et al.* 1993a, b; Gattuso *et al.* 1996, 1999; Riebesell *et al.* 2000; Orr *et al.* 2005; CIESM 2008; Doney *et al.* 2009; Ries *et al.* 2009; Gao & Zheng 2010). Modelling the response of the oceans to increasing $[\text{CO}_2]$ requires also a quantification of the total carbonate and its mineralogy on a global scale (Milliman 1995; Kleypas *et al.* 2006; Morse *et al.* 2006; Andersson *et al.* 2008).

Under favourable oceanographic conditions, the carbonate mass produced by coralline algae is dependent on their morphology (e.g., geniculate or non-geniculate, thick excrecent crusts or thin superposed foliose thalli; Woelkerling *et al.* 1993) and

TABLE 1. — Literature compilation of results from manipulation of corallines by simulating OA and rising temperature. Abbreviations: **decr.**, decrease; **inc.**, increase.

Reference	Species	Manipulation	Results (relative to present/normal conditions)
Borowitzka 1981	<i>Amphiroa</i> spp. (geniculate), Cape Ferguson, Australia	pH manipulation in outdoor seawater aquaria	calcification: no effect at pH 7.2-8.3
Agegian 1985 reported by Kleypas <i>et al.</i> 2006	<i>Porolithon gardineri</i> (non geniculate), Hawaii	acidified mesocosm [CO ₂] = present ×2	calcification: 25% decrease; linear growth: 16% decrease
Gao <i>et al.</i> 1993a	<i>Corallina pilulifera</i> (geniculate), Japan	acidified cultures [CO ₂] = present ×4	inhibition of calcification
Langdon <i>et al.</i> 2003	<i>Halpilton cubense</i> and <i>Amphiroa fragillissima</i> (geniculate corallines), <i>Chondria dasyphylla</i> , <i>Gelidiopsis intricata</i>	acidified mesocosm [CO ₂] = present ×2	doubled carbon turnover; calcification: 85% decr.; no net increase in net primary production
Hall-Spencer <i>et al.</i> 2008	<i>Amphiroa rigida</i> , <i>Corallina</i> spp., <i>Jania</i> spp., <i>Mesophyllum lichenoides</i> , <i>Lithophyllum incrustans</i>	naturally acidified seawater, Mediterranean	Shift from dominant corallines to fleshy algae with pH 7.8; corallines absent at pH 7.2 or lower; no coralline epiphytes on <i>Posidonia</i> leaves at pH 7.6
Anthony <i>et al.</i> 2008	<i>Porolithon onkodes</i>	acidified mesocosm [CO ₂] = present ×2 and ×3; temp. = 25-26°C; high natural irradiance	bleaching: 10% and 20% inc.; productivity: 50% and 100% decrease; calcification: 0% and 130% decrease (2× and 3× [CO ₂] respectively)
Anthony <i>et al.</i> 2008	<i>Porolithon onkodes</i>	acidified mesocosm [CO ₂] = present ×2 and ×3; temp. = 28-29°C; high natural irradiance	bleaching: 10% and 30% inc.; productivity: negative values; calcification: 50% and 190% decrease (2× and 3× [CO ₂] respectively)
Kuffner <i>et al.</i> 2008	crustose coralline algae (non-geniculate), Hawaii	acidified mesocosm [CO ₂] = present ×2	recruitment: 78% decr.; percentage cover: 92% decr.
Martin <i>et al.</i> 2008	<i>Hydrolithon</i> spp., <i>Pneophyllum</i> spp. (non-geniculate epiphytes)	naturally acidified seawater, Mediterranean	epiphytic coralline cover decreased with pH, absent at pH 7.7
Jokiel <i>et al.</i> 2008	encrusting CCA and rhodoliths of <i>Lithophyllum cf. pallens</i> , <i>Hydrolithon</i> sp., <i>Porolithon</i> sp.	continuous flow acidified coral reef mesocosm, Hawaii, [CO ₂] = present ×2	cover on hard surface: 86% decrease; calcification: 250% decrease
Martin & Gattuso 2009	<i>Lithophyllum cabiochae</i>	acidified and warmed aquaria, Mediterranean [CO ₂] = 700 ppm; T = ambient + 3°C	calcification: 50% decrease; death from elevated T, increasing with [CO ₂]
Ries <i>et al.</i> 2009	<i>Neogoniolithon</i> sp.	acidified aquaria at 25°C and [CO ₂] = 409; 606; 903; 2856 ppm	net calcification increase up to [CO ₂] = 606 ppm; decreasing with higher concentrations
Cumani <i>et al.</i> 2010	<i>Lithophyllum incrustans</i>	acidified mesocosm [CO ₂] = 550 and 760 ppm	inhibition of spore production and growth; increase of mortality
Porzio <i>et al.</i> 2011	encrusting and geniculate CCA in a macroalgal community	naturally acidified seawater, Mediterranean	coralline species richness: 25% decrease and change of dominant species at pH 7.8; absent at pH 6.7

growth rate. Literature on growth-rate of coralline algae has been reviewed recently by Foster (2001).

On a global scale, few studies have focused on the quantitative contribution of biogenic carbonate and particularly on carbonate production and accumulation by coralline algae. A compilation of existing data shows that carbonate production by coralline algae spans four orders of magnitude, with the highest rates in tropical reefs, in the Mediterranean infaunal community dominated by the geniculate *Corallina elongata* Ellis & Solander and in the maerl beds of the French Atlantic. The lowest values of carbonate production are from temperate seagrass epiphyte and deep soft-bottom assemblages (Table 2). Interestingly, these three first order carbonate producers among corallines are all shallow-water dwellers and include geniculate and non-geniculate, hard-substrate and free-living growth forms in a wide latitudinal belt.

Modelling the response of the benthic system of entire basins to environmental perturbations requires the identification of more or less homogeneous sea-floor areas and knowledge of their specific contribution to the carbonate budget in terms of carbonate production and sedimentation rate, mineralogy, and susceptibility to dissolution (Milliman 1993). Literature data on carbonate component distribution over large areas frequently has no sufficient detail to allow biogeochemical quantification. Furthermore, contributions dealing with sediment geochemistry either do not consider the biogenic components or are very detailed but their scale is too small for calculation of budgets.

Direct habitat mapping and sampling by SCUBA diving is currently considered the method most adequate and appropriate for shallow-water habitat characterization and the quantification of benthic components (among others: Coggan *et al.* 2007; Steller *et al.* 2007a; Peña & Barbara 2009). Deep-water benthic habitats can be mapped at the meso-scale by bathymetric data and seismic profiles integrated with point-based information (sea-bed samples) for “ground-truthing” of the substrate and biota (Kenny *et al.* 2003; Coggan *et al.* 2007; Savini *et al.* 2012).

These methods not only allow qualitative identification and mapping of benthic habitats, but also quantification of the carbonate contribution of

biogenic components and specific mineral phases over large areas, provided that sediment analysis of representative samples is coupled with X-Ray diffractometry (Bracchi & Basso 2012).

DISCUSSION AND CONCLUSIONS

Although some recent investigations and meta-analysis of available literature pointed out the variable effects of OA on marine biota (e.g., Ries *et al.* 2009; Hendriks *et al.* 2010; Kroeker *et al.* 2010), a considerable body of evidence indicates that crustose coralline algae are one of the most vulnerable benthic element to the negative biological and chemical effects of OA and global warming (Table 1).

Since by the end of this century net dissolution is likely to exceed net calcification in coralline algae, we expect dramatic consequences in terms of changes in biodiversity and biogeochemistry, especially in those habitats dominated or literally built by these algae, outside the tropical belt (Ballesteros 2006; Martin & Gattuso 2009).

The susceptibility of coralline algae calcification to marine acidification has been confirmed and related to the solubility of their Mg-calcite thalli (Kuffner *et al.* 2007; Hall-Spencer *et al.* 2008; Martin & Gattuso 2009). So an important question requiring further investigation is assessment of the solubility of natural coralline-rich build-ups and sediments, that will vary considerably as function of the mean Mg content of their thalli.

Available estimates of the total biogenic carbonate volume in the world oceans are affected by large uncertainties, mainly due to the lack of trustworthy data on carbonate mass accumulation rates (Milliman 1993). On a world basis the coastal benthic habitats already characterized and mapped at sufficient detail are far from representative of the whole (Hetzinger *et al.* 2006; Nelson 2009).

Even in the relatively well-studied Mediterranean Sea the distribution of important benthic facies, such as those dominated by corallines on both hard and soft bottoms, is largely unknown (Ambilas *et al.* 2004), thus introducing a bias in predicting the response of the shelves to global change. About 5% of the Mediterranean Sea is shallower

TABLE 2. — Carbonate production of coralline algae at ecosystem scale. *, Data calculated on the base of coralline growth rate and % live cover provided by the authors, with a mean rhodolith density of 1.56 g cm⁻³.

Species	Location	Depth	Carbonate production (g m ⁻² y ⁻¹)	Source of data
<i>Hydrolithon</i> spp. + <i>Neogoniolithon</i> spp.	Lizard Island, Australia	windward reef	1500-10300 (100% cover)	Chisholm 2000
<i>Porolithon onkodes</i>	Rangiroa, Polynesia	CCA-dominated reef flat	7400	Pichon 1985; Payri 2000
<i>Corallina elongata</i>	Marseille, NW Mediterranean	0.5-1 m	5037	El Haïkali <i>et al.</i> 2004
<i>coralline pavement</i>	One Tree Island, Australia	0-1 m surf zone	4000	Kinsey 1985
<i>Lithothamnion corallioides</i>	Bay of Brest, France	1-10 m	145-3100	Martin <i>et al.</i> 2006
<i>Porolithon</i>	Barbados	fringing reef	2378	Stearn <i>et al.</i> 1977*
<i>Neogoniolithon</i>			1225	
<i>Lithophyllum</i>			1355	
<i>Mesophyllum</i>			167	
<i>Porolithon onkodes</i>	Penguin Bank, Hawaii	40-100 m	2100	Agegian <i>et al.</i> 1988
<i>Hydrolithon onkodes</i>	Ishigaki Is (Ryukyu Is)	upper fore reef	2044 (mean)	Matsuda 1989
<i>Lithothamnion cf. glaciale</i>	Troms, Norway	7 m	895-1432	Freiwald & Henrich 1994
		18 m	420-630	
<i>Lithothamnion corallioides</i>	maerl of Brittany, France	0-10 m	876	Potin <i>et al.</i> 1990
epiphyte corallines on seagrass	Shark Bay, western Australia		500	Walker & Woelkerling 1988
<i>Lithothamnion corallioides</i>	maerl of Galway, Ireland		88-164	Bosence 1980
<i>Phymatolithon calcareum</i>			79-422	
<i>Lithophyllum incrustans</i>	South West Wales, UK	intertidal pools	379	Edyvean & Ford 1987
crustose coralline algae	Warraber Island, Australia	reef flat	299.34	Hart & Kench 2007
<i>Lithophyllum cabiochae</i>	NW Mediterranean	25 m aquarium simulation	292	Martin & Gattuso 2009
<i>Neogoniolithon brassica-florida</i> (as <i>Spongites notarisii</i>) + geniculate	Mallorca-Menorca shelf, NW Mediterranean	0-10 m	289.4	Canals & Ballesteros 1997
<i>Lithothamnion corallioides</i>	maerl of Mannin Bay, NE Atlantic	0-10 m	29-164	Bosence & Wilson 2003
<i>Phymatolithon calcareum</i>			79-249	
maerl, several coralline species + <i>Peyssonnelia</i> spp.	Mallorca-Menorca shelf, NW Mediterranean	40-85 m	210	Canals & Ballesteros 1997
crustose coralline algae	Uva Island, Panama	reef flat	190.4	Eakin 1996
epiphyte corallines on seagrass	Southern Australia	10 m	79-168	James <i>et al.</i> 2009
coralligenous build-ups, several coralline species	Mallorca-Menorca shelf, NW Mediterranean	70-90 m	169.6	Canals & Ballesteros 1997
<i>Lithothamnion corallioides</i>	maerl of Cilento shelf, W Mediterranean	47 m	90.8	Savini <i>et al.</i> 2012
epiphyte corallines on seagrass	Mallorca-Menorca shelf, NW Mediterranean	0-35 m	68.2	Canals & Ballesteros 1997
mainly <i>Lithothamnion</i> spp. + lithophylloids	Pontian Islands shelf, W Mediterranean	40-70 m 70-100 m	31.64 (mean) 7.91 (mean)	Bracchi & Basso 2012

than 100 m. Given the lack of reliable data on the distribution of highly productive (coralline) habitats, in a conservative hypothesis of 5 g m⁻² y⁻¹ produced on average by coralline algae across the shelf < 100 m, we obtain a Mediterranean coralline

carbonate production of 0.65 × 10⁶ t y⁻¹, with large local variation (Table 2).

Locating and describing the algal carbonate factories, and the evaluation of their extent and production are a priority for future research, as a tool for

the environmental management of these hot-spots of biodiversity and to obtain a reliable carbonate budget for the world shelves.

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