Calculating the global contribution of coralline algae to total carbon burial

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Abstract

The ongoing increase in anthropogenic carbon dioxide (CO_2) emissions is changing the global marine environment and is causing warming and acidification of the oceans. Reduction of CO_2 to a sustainable level is required to avoid further marine change. Many studies investigate the potential of marine carbon sinks (e.g. seagrass) to mitigate anthropogenic emissions, however, information on storage by coralline algae and the beds they create is scant. Calcifying photosynthetic organisms, including coralline algae, can act as a CO_2 sink via photosynthesis and $CaCO_3$ dissolution and act as a CO_2 source during respiration and $CaCO_3$ production on short-term time scales. Long-term carbon storage potential might come from the accumulation of coralline algae deposits over geological time scales. Here, the carbon storage potential of coralline algae is assessed using meta-analysis of their global organic and inorganic carbon production and the processes involved in this metabolism. Net organic and inorganic production were estimated at 330 g C m^{-2} yr^{-1} and 900 g $CaCO_3$ m^{-2} yr^{-1} respectively giving global organic / inorganic C production of 0.7 / 1.8 * 10^9 t C yr^{-1}. Calcium carbonate production by free-living / crustose coralline algae (CCA) corresponded to a sediment accretion of 70 / 450 mm kyr^{-1}. Using this potential carbon storage for coralline algae, the global production of free-living algae / CCA was 0.4 / 1.2 * 10^9 t C yr^{-1} suggesting a total potential carbon sink of 1.6 * 10^9 tonnes per year. Coralline algae therefore have production rates similar to mangroves, saltmarshes and seagrasses representing an as yet

unquantified but significant carbon store, however, further empirical investigations are needed to determine the dynamics and stability of that store.

1. Carbon storage and coralline algae

An increase in exploitation of fossil fuels since the mid-18th century caused a rise in the partial pressure of carbon dioxide in both atmospheric (CO_2) and oceanic (pCO_2) reservoirs (Sabine et al., 2004; Meehl, 2007). Atmospheric CO_2 has risen from 280 ppm in 1750 (Denman and Brasseur, 2007) to nearly 400 ppm in 2014 (Diugokencky and Tans, 2015) at a rate unprecedented in geological history (Denman and Brasseur, 2007). The marine environment has been changing rapidly in the last few centuries too (Cubasch et al., 2013), with increasing CO_2 causing warming and acidification of the Earth's oceans (Caldeira and Wickett, 2005).

Concentrations of atmospheric CO_2 simulated by coupled climate-carbon cycle models range between 730 and 1,200 ppm by 2100 (Meehl, 2007). Therefore, a reduction of atmospheric CO_2 to a sustainable level is needed to avoid further environmental damage (Collins et al., 2013; Kirtman et al., 2013).

The oceans are a major sink of anthropogenic CO_2 emissions, accounting for ~48 % of emissions absorption since the Industrial Revolution (Sabine et al., 2004). Significantly, around 50% of the global primary production (which uses pCO_2) is by marine organisms (Beardall and Raven, 2004) with marine microalgae and bacteria being the dominant source of primary production and respiration (Duarte and Cebrian, 1996; del Giorgio and Duarte, 2002; Duarte et al., 2005). Vegetated marine habitats, including macroalgae and seagrasses, are often neglected from accounts of the global ocean carbon cycle because of their limited extent (cover < 2 % of ocean surface) (Duarte and Cebrian, 1996). However, vegetated coastal habitats have a great carbon storage capacity (Duarte et al., 2005) and the potential of marine coastal vegetation as a sink for anthropogenic carbon emissions (blue carbon) is becoming of interest (Nellemann et al., 2009). These marine macrophyte ecosystems have slow turnover rates and are therefore more effective carbon sinks than planktonic ecosystems (Smith, 1981).

Red coralline algae are present from the tropics to polar regions (Johansen, 1981; Steneck, 1986; Foster, 2001; Wilson, 2004). Coralline algae are important for ecosystems due to their role in carbon cycling, creating and maintaining habitats, and reef building / structuring roles (Nelson, 2009). They are divided in two morpho-functional groups; geniculated (articulated) and non-geniculated (non-articulated) (Johansen, 1981). The morphological states range from totally adherent to having nonadherent margins (leafy) to totally nonadherent (free-living, e.g. rhodoliths, maerls and nodules) (Steneck, 1986; Cabioch, 1988). The calcium carbonate skeleton of coralline algae prevents them from breaking down quickly compared to fleshy algae (Borowitzka, 1982; Wilson, 2004). Coralline algal species have been observed in the fossil record since the early Cretaceous (Aguirre et al., 2000) and coralline algal communities reach 500-800 years (Adey and Macintyre, 1973; Kamenos, 2010) with ~8,000 year old free-living coralline algal beds present in France (Birkett et al., 1998).

Coralline algae are important contributors to the marine calcium carbonate ($CaCO_3$) deposited in the coral reef sediments (Goreau, 1963; Adey and Macintyre, 1973) and account for approximately 25 % of $CaCO_3$ accumulation within coastal regions (Martin et al., 2007). Calcifying photosynthesisers are both a sink and a source of CO_2 (Frankignoulle, 1994). Coralline algae act as a CO_2 sink in the processes of photosynthesis and $CaCO_3$ dissolution and act as a CO_2 source in the processes of respiration and $CaCO_3$ production (Martin et al., 2005; Barron et al., 2006; Martin et al., 2006; Martin et al., 2007; Kamenos et al., 2013; Martin et al., 2013a). We aim to estimate the global distribution of coralline algae, and from that, determine their potential role in long-term total carbon burial.

2. Coralline algal succession and small-scale distribution

The distribution and abundance of coralline algae is determined by ecological processes including growth, succession and competition (Steneck, 1986; McCoy and Kamenos, 2015) as well by environmental conditions such as disturbance, temperature and irradiance (Adey and Macintyre, 1973; Kamenos et al., 2004; Gattuso et al., 2006). Coralline algae grow both laterally to increase area and vertically to increase thickness (Steneck, 1986). Coralline algal vertical accretion rates vary widely from 0.1 to 80 mm yr-1 (Adey and McKibbin, 1970; Steneck and Adey, 1976; Edyvean and Ford, 1987). Succession in coralline algae occurs when thick and/or branched crusts replace thinner unbranched crusts (Adey and Vassar, 1975; Steneck, 1986). Succession seems most rapid in the tropics, where colonization and succession takes ~1 year, compared to 6 – 7 years in the boreal North Pacific and > 10 years in the subarctic North Atlantic (Steneck, 1986; McCoy and Ragazzola, 2014). In shallow productive zones coralline algae require disturbances, mainly herbivory as well as water motion, to remain clear of fleshy algae and invertebrates (Steneck, 1986). However, towed fishing gear (e.g. trawling) can easily damage rhodoliths (maerl) (Hall-Spencer and Moore, 2000; Kamenos and Moore, 2003). Overall, coralline algal distribution is likely primarily determined by irradiance and temperature (Adey and McKibbin, 1970; Adey and Adey, 1973; Gattuso et al., 2006).

2.1 Global distribution

Coralline algae are ecosystem engineers (Nelson, 2009), major framework builders and carbonate producers, especially in temperate and cold water benthic ecosystems (Nelson, 1988; Freiwald and Henrich, 1994; Foster, 2001; Gherardi, 2004; Bracchi and Basso, 2012; Savini et al., 2012; Basso, 2012). Coralline algae are found from the low intertidal to the infralittoral and circalittoral zones (> 200 m depth) (Steneck, 1986; Basso, 1998; Foster, 2001) and have a worldwide spatial distribution (Fig. 1; Supplementary material, Table S2). While crustose coralline algae (CCA) grow exclusively on hard surfaces, free-living coralline algae are able to form rhodoliths when they settle on non-cohesive particulate substrates or are detached from existing hard substrates by fragmentation (Bosence, 1983).

2.2 Surface covered by coralline algae

The surface of the coastal zone covered by coralline algae varies spatiotemporally and differs for free-living algae, geniculate and CCA (Supplementary material, Table S1). The average coralline algal sea bed coverage from published studies is 52.5 % for CCA, 45.0 % for rhodoliths and 45.0 % for coralline algae overall. Figueiredo et al. (2008) indicate that the surface covered by CCA on the Abrolhos Bank (20,900 km^2) in Brazil ranges from 5 – 40 % on the reef flats, 30 – 80 % on the reef crests and 10 – 50 % on the reef walls with coverage varying due to differences in the abundance of turf algae and herbivory pressure. On coral reefs, CCA (e.g. *Porolithon onkodes*) can cover ~ 40 % of the reef slope (Littler and Doty, 1975; Stearn et al., 1977), 60 % of the reef flat and 5 % of lagoon sites (Atkinson and Grigg, 1984) with rhodoliths covering up 90 % of the reef crest (Sheveiko, 1981) and 90 % of the seaward shallow reef slope (Chisholm, 1988). Importantly, the area covered by coralline algae is not necessarily lower in regions dominated by other algal forms, because of their ability to occur on the primary substratum (up to 90 %) or as epiphytes on larger algae (Johansen, 1981).

3. Processes and metabolism

While coralline algae are slow growing their high abundance and spatial distribution indicates their production is likely important (Johansen, 1981) and they are major contributors to the carbon and carbonate cycles of coastal environments (Martin et al., 2013a). Organic production relates to the photosynthetic capacity of coralline algae, while inorganic production relates to the calcium carbonate production (Johansen, 1981).

3.1 Organic production

Organic production of coralline algae is low compared to other marine plants (Johansen, 1981; Steneck, 1986). However, because of their high abundance and worldwide dispersal, corallines can contribute significantly to the total marine primary production (Roberts et al., 2002). Production of 1 mole of organic material (photosynthesis) decreases dissolved inorganic carbon (DIC) by 1 mole:

$$CO_2 + H_2O \rightarrow CH_2O + O_2 \qquad \text{(R1)}$$

Primary production also decreases pCO_2, however the magnitude of these changes depends on the equilibrium constants (Johansen, 1981). Respiration increases both DIC and pCO_2 (Johansen, 1981). Coralline algal respiration is between 20 - 60 % of gross primary production (Marsh, 1970; Littler, 1973; Littler and Murray, 1974; Sournia, 1976; Wanders, 1976). Net community production for coralline algae is induced or limited by environmental parameters including light reaching the communities (Gattuso et al., 2006; Martin et al., 2006; Burdett et al., 2014), temperature (Martin et al., 2006; Kamenos and Law, 2010) and nutrient availability (Smith et al., 2001). For example, Chisholm (2003) suggested that the high rates of productivity measured in situ at Lizard Island, Australia, came from the coralline algae that derive nutrients from the underlying reef.

3.2 Inorganic production and accumulation

Photosynthesis also plays a crucial role in the production of inorganic material as it creates the environment in which calcification occurs (Johansen, 1981). The ratio of inorganic-organic production is high in coralline algae, compared to non-coralline seaweeds (Johansen, 1981). Precipitation of 1 mole $CaCO_3$ decreases DIC by 1 mole and total alkalinity by two mole:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2 \qquad (R2)$$

For calcium carbonate to be deposited an alkaline environment is required, as well as high concentrations of calcium and carbonate (Johansen, 1981). Calcification of coralline algae occurs internally, compared to external calcification in corals and other invertebrates (Chisholm, 2003). The cell-walls of coralline algae are composed of calcium carbonate, and are mainly consist of high Mg-calcite (HMC: > 4% wt of $MgCO_3$) (Moberly, 1968; Kamenos et al, 2008; Basso, 2012).

Coralligenous algal-dominated rocky bottoms and rhodolith beds are among the highest algal carbonate producers when compared with *Posidonia oceanica* meadows, sandy bottom communities, *Caulerpa-Cymodocea* meadows, coralligenous animal-dominated, photophilic algae and hemisciaphili algal communities (Canals and Ballesteros, 1997). The quantity of calcite production by coralline algae depends on their morphology (e.g., geniculate or non-geniculate, thick or thin crusts), growth rate and the environmental conditions (Basso, 2012). Coralline algal calcification is indirectly affected by temperature, often over a season cycle, as well as light limitation (Martin et al., 2006).

4. Potential global contribution of coralline algae to total carbon burial

The shallow-water ocean environment (i.e. bays, estuaries, lagoons, banks, and continental shelves) accounts for 14 – 30 % of the oceanic primary production, 80 % of organic material burial and ~50 % of $CaCO_3$ deposition (Gattuso et al., 1998). The total surface area of the coastal zone, thus the potential habitat for benthic coralline algae, is estimated between 0.45 - 49.4 * 10^{12} m^2 (Charpy-Robaud and Sournia, 1990). The coastal area, that has depths ranging between 0 and 200 m covers 7.49% of the world ocean, which correspond to 27.123 * 10^{12} m^2 (Menard and Smith, 1966). Charpy-Roubaud and Sournia (1990) suggest an area of 6.8 * 10^{12} m^2, because the average benthic photic zone of the world is shallower than 200 m. Here we will use 33 % of the coastal zone, which is the part that receives enough light for photosynthesis (Gattuso et al., 2006) and thus assuming the production mainly occurs in the top 66 m of the coastal zone. Because coralline algae usually attach to harder substrata (Bosence, 1983) the surface covered by coralline algae (Supplementary material, Table S1) has to be taken into account. However, as there are substrates (e.g. sandy substrata or other soft-bottom substrates) that are an unsuitable habitat for coralline algae, to be conservative, we have assumed only half of the estimated surface coverage percentages estimated above contain coralline algae (CCA = 26.25 %, rhodoliths = 22.5 %, coralline algae = 22.5 %). At present we have an incomplete knowledge of the real distribution of coralline algae, so we estimate a global production based on the following parameters: the production of coralline algae (median), the top 66 m global coastal zone and the surface of this coastal zone covered by coralline algae (22.5 %). We use the median in / organic C production for coralline algae due to skewed data distribution (Zar, 1999) across available studies.

4.1 Global coralline algal organic C production

Net primary production by coralline algae ranges widely from 10 g C m^{-2} yr^{-1} by *Lithothamnion coralloides* in the Bay of Brest, France (Martin et al., 2006) to 2391 g C m^{-2} yr^{-1} by *Hydrolithon onkodes* at Lizard Island, Australia (Chisholm, 2003), giving a median production of 329 g C m^{-2} yr^{-1} (n = 39) (Table 1) across depths and locations. Global C production may thus be as high as 0.7 * 10^9 t C yr^{-1}. The daily production of coralline algae corresponds with the range of production of benthic fleshy algae, turf algae, sand algae, phytoplankton, seagrasses and zooxanthellae (Table 2) and estimated yearly coralline algal production rate (329 g C m^{-2} yr^{-1}) is in the range of production by mangroves, salt marshes and seagrasses and appears more productive than coastal phytoplankton, benthic diatoms and coral reefs (Table 2). Payri (2000) observed that the annual production of a coralline algal communities corresponds to approximately one third of the production of seagrass beds, which was also observed on the west-coast of France with a production ratio of 3.12 (Martin et al., 2005). A production ratio of 1.5 – 3.7 is observed in this study when compared to seagrass production rate studies (Table 2).

The estimated production of free-living coralline algae (0.35 * 10^9 t C yr^{-1}) is in the range determined by other studies while the production for CCA (0.88 * 10^9 t C yr^{-1}) is slightly higher (Table 3). Thus, with a global oceanic production estimated at 48.5 *10^9 t C yr^{-1} (Field et al., 1998) coralline algal production represent a measurable component.

4.2 Global inorganic coralline algal C production and accumulation

Studies focusing on coralline algae and calcium carbonate indicate a production range of 8 – 7400 g $CaCO_3$ m^{-2} yr^{-1} and a median of 900 g $CaCO_3$ m^{-2} yr^{-1} (Table 4). The global net calcium carbonate production using the previously estimated surface coverage was 1.8 * 10^9 t $CaCO_3$ yr^{-1} for coralline algae. Thus $CaCO_3$ production by coralline algae of 900 g $CaCO_3$ m^{-2}

yr^{-1} lies within the range of coral reef calcite production of 75 - 4000 g $CaCO_3$ m^{-2} yr^{-1} (Canals and Ballesteros, 1997) and is comparable with the production rate in the Late Holocene ocean for coral reefs (1500 g $CaCO_3$ m^{-2} yr^{-1} (Milliman, 1993)). Basso (2012) estimated an average production rate of 5 g $CaCO_3$ m^{-2} yr^{-1} for the coralline algae in the Mediterranean sea, however this included coralline algae occurring below 100 m. Gattuso et al. (1998) suggested that communities in the coastal zone are responsible for more than 40 % (23 * 10^9 t $CaCO_3$ yr^{-1}) of the total marine calcium carbonate production. Thus the estimated calcite production by coralline algae is similar to the production of other coastal communities (e.g. coral reefs, banks and non / carbonate shelves) and might represent a large fraction of the coastal and total ocean calcite production (Gattuso et al., 1998).

Using average production rates for free-living algae and CCA a net inorganic production was estimated for these two groups. The net inorganic production for free-living algae was 22 g C-inorganic m^{-2} yr^{-1} and 150 g C-inorganic m^{-2} yr^{-1} for CCA. Thus net inorganic production by coralline algae of 108 g C-inorganic m^{-2} yr^{-1} and net organic production of 330 g C-organic m^{-2} yr^{-1} gives a PIC:POC ratio of 0.33 (PIC is the particular inorganic carbon and POC the particular organic carbon). The PIC:POC ratio for free-living algae was 0.13 and 0.40 for the CCA. Significantly, a similar PIC:POC range of ratios of 0.23-0.29 was also observed for coccolithophores (Engel et al., 2005).

4.3 Global carbon accumulation

The long-term removal of C requires the fixed carbon to remain stored for 100-1000 years (Gattuso et al., 1998). The global long-term deposition rate of free-living coralline algae is 500 mm kyr^{-1} (Table 5) and the accumulation rates range from 80 to 1400 mm kyr^{-1} for temperate (Orkney Island, Scotland) to polar (Tromsø district, Norway) systems. The calcium carbonate production by free-living algae (187 g $CaCO_3$ m^{-2} yr^{-1}) with a calcite density of 2.71 g cm^{-3} (DeFoe and Compton, 1925) corresponds to a sediment accretion of 70 mm kyr^{-1}, while for CCA this corresponds to a sediment accretion of 450 mm kyr^{-1}. Given the accretion rate of 500 mm kyr^{-1}, the preservation potential of coralline algae would be 64 %. This is consistent with the empirically calculated calcium carbonate preservation of 60 % (Milliman, 1993). However, if the preservation of CCA is excluded because of the lack of available accretion rates, and heavy grazing (Steneck, 1986), the preservation potential for this morphotype would be 14 %. As the complete preservation potential for coralline algae still requires further refining, the potential total carbon burial is estimated based on the sum of total organic production and the inorganic production. The estimated potential total burial for the free-living algae was 0.4 * 10^9 t C yr^{-1} and 1.2 * 10^9 t C yr^{-1} for CCA giving a potential total carbon burial of 1.6 * 10^9 t C yr^{-1} for coralline algae.

5. Future prospects: Ocean acidification and rising temperature

Increasing atmospheric pCO_2 will increase DIC and shift the equilibrium of the carbonate system to higher CO_2 and bicarbonate ion-levels, lower carbonate ion concentration and lower pH (Feely et al., 2009). Coralline algae may be vulnerable to the warming and lowering sea water *p*H of sea water, caused by recent increases in anthropogenic CO_2 (Kleypas et al., 2006); the sensitivity of algae is of widespread importance and it has generated several recent reviews which find coralline algae may show mixed response to global change (Nelson et al., 2009; Koch et al., 2012; Brodie et al., 2014; McCoy and Kamenos, 2015). For example, high pCO_2 conditions negatively affect community growth (Jokiel et al., 2008; Hofmann et al., 2012; Ragazzola et al., 2012), recruitment (Kuffner et al., 2008), calcification (Anthony et al., 2008; Gao and Zheng, 2010) size and abundance (Kuffner et al., 2008; Hall-Spencer et al., 2008; Porzio et al., 2011; Kroeker et al., 2013; McCoy and Ragazzola, 2014; Donnarumma et al., 2014) as well as epithelial integrity (Burdett et al., 2012). Conversely, increased atmospheric pCO_2 is expected to have a positive impact on the organic production and growth of algae due to increased pCO_2 availability (Hendriks et al., 2010). For example, Semesi et al. (2009) observed an increase in photosynthetic rates of coralline algae with a rising pCO_2 of seawater, however, whether this also translates to their accretion at longer time scales is still not clear.

The high-Mg calcite (HMC) cell-walls of coralline algae, containing 7.7-28.8 % $MgCO_3$, play a crucial role in their response to the risen temperature and acidification of seawater (Basso, 2012; Kamenos et al., 2013). Biogenic HMC cell-walls, containing > 8 – 12 % $MgCO_3$, have a high solubility and sensitive response to ocean acidification (Andersson et al., 2008). Despite this, there is evidence that they can continue to calcify in elevated pCO_2 (Kamenos et al., 2013; Martin et al., 2013b; Diaz-Pulido, 2014) but with altered skeletal integrity (Ragazzola et al., 2012; Kamenos et al., 2013; McCoy and Ragazzola, 2014). Overall it is expected that any decreasing abundance and growth of coralline algae may have knock-on consequences for worldwide coastal ecosystems (Johansen, 1981; Martin and Gattuso, 2009; Basso, 2012).

6. Conclusions

The ongoing increase of anthropogenic CO_2 is causing warming and acidification of the world's oceans. Reduction of CO_2 to a sustainable level is required to avoid further environmental damage. We calculate coralline algae to have a global average net primary production of 0.7 * 10^9 t C yr^{-1} and an estimated total global $CaCO_3$ production of 1.8 * 10^9 t $CaCO_3$ yr^{-1} which corresponds to a net inorganic production of 0.2 * 10^9 t inorganic C yr^{-1}. With their substantial preservation potential and the longevity of the deposits they create, coralline algae have a significant capacity to store carbon. However, we are still uncertain of the impact future global change is likely to have on that capacity. Given their storage potential, empirical studies are now needed to refine the calculations.

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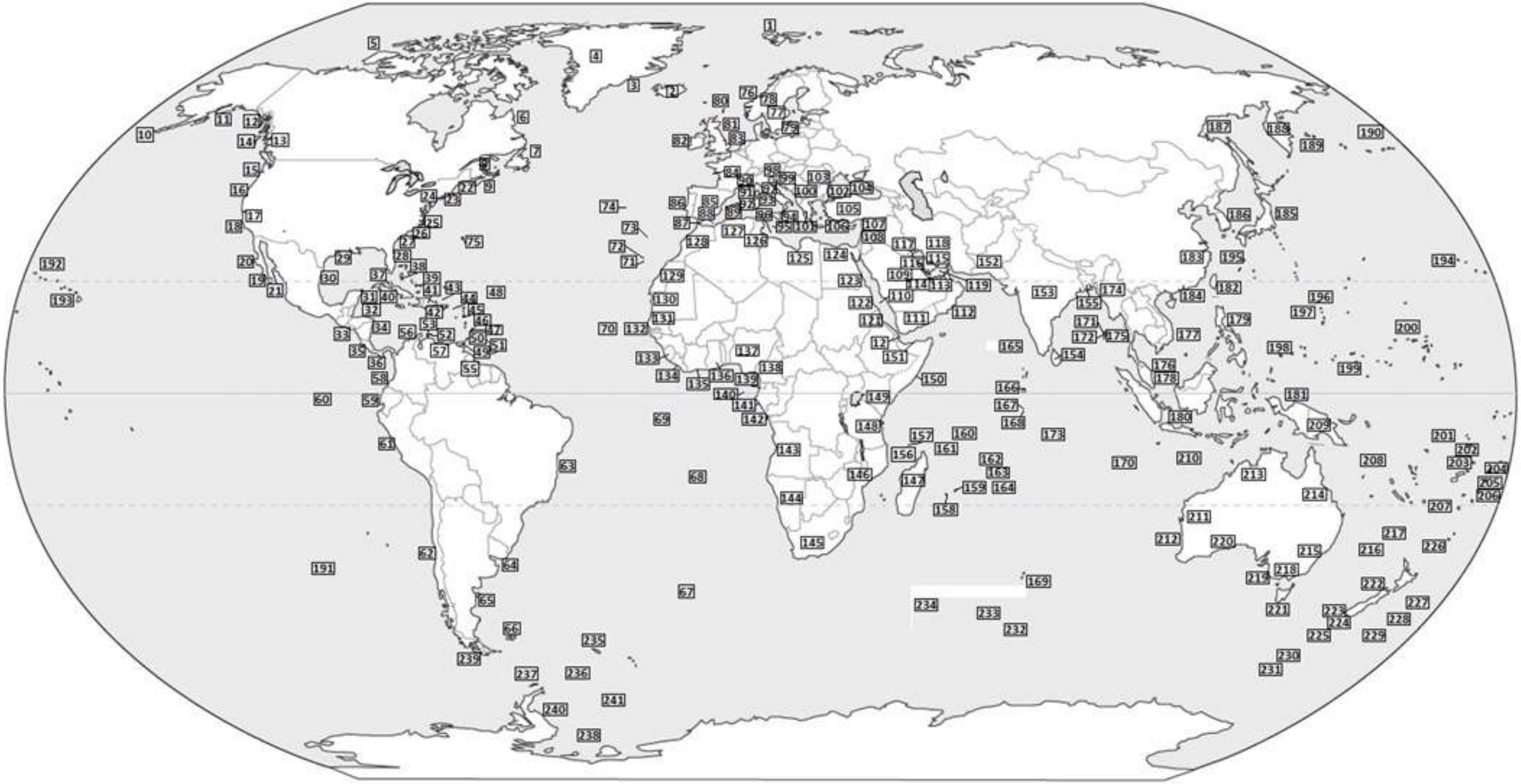

Figure 1. The global distribution of the three coralline algae Families (Corallinaceae, Hapalidiaceae and Sporolithaceae; for species list per country/region see Supplementary material, Table S2). The numbers indicate: 1. Spitsbergen, 2. Iceland, 3. Greenland, east, 4. Greenland, 5. Canada, Arctic, 6. Canada, Labrador, 7. Canada, Newfoundland, 8. Canada, New Brunswick, 9. Canada, Nova Scotia, 10. USA, Aleutian Islands, Alaska, 11. USA, Alaska, 12. Revillagigedo Islands, USA, 13. Canada, British Columbia, 14. Canada, Queen Charlotte Islands, 15. USA, Washington, 16. USA, Oregon, 17. USA, California, 18. USA, Channel Islands, California, 19. Mexico, Baja California, 20. Mexico, Isla Guadalupe, 21. USA, Gulf of California, 22. USA, Maine, 23. USA, New Hampshire, 24. USA, Connecticut, 25. USA, Virginia, 26. USA, North Carolina, 27.

USA, South Carolina, 28. USA, Florida, 29. USA, Texas, 30. Mexico, 31. Belize, 32. Honduras, 33. El Salvador, 34. Nicaragua, 35. Costa Rica, 36. Panama, 37. Cuba, 38. Bahamas, 39. Caicos Islands, 40. Jamaica, 41. Hispaniola, Dominican Republic, 42. Puerto Rico, 43. Virgin Islands, USA, 44. Saints Kitts, 45. Martinique, 46. Barbados, 47. Saint Thomas, Barbados, 48. Lesser Antilles, 49. Trinidad, 50. Tobago, 51. Trinidad and Tobago, 52. Curacao, 53. Netherlands Antilles, 54. Tropical and Subtropical Western Atlantic, 55. Guyana, 56. Aves, island of Venezuela, 57. Venezuela, 58. Colombia, 59. Ecuador, 60. Galapagos Islands, 61. Peru, 62. Chile, 63. Brazil, 64. Uruguay, 65. Argentina, 66. Falkland Islands, 67. Gough Island, 68. Saint Helena, 69. Ascension, 70. Cape Verde Islands, 71. Canary Islands, 72. Portugal, Salvage Islands, 73. Madeira, 74. Azores, 75. Bermuda, 76. Norway, 77. Sweden, 78. Scandinavia, 79. Baltic Sea, 80. Faroe Islands, 81. Great-Britain, 82. Ireland, 83. Netherlands, 84. France, 85. Spain, 86. Portugal, 87. Gibraltar, 88. Spain, Isla de Alboran, 89. Balearic Islands, Spain, 90. Monaco, 91. Corsica, 92. Sardinia, 93. Italy, 94. Sicily, 95. Malta, 96. Italy, Pelagean Islands, 97. Italy, Adriatic Sea, 98. Slovenia, 99. Croatia, 100. Albania, 101. Greece, 102. Bulgaria, 103. Romania, 104. Black Sea, 105. Turkey, 106. Cyprus, 107. Syria, 108. Israel, 109. Saudi Arabia, 110. Red Sea, 111. Yemen, 112. Oman, 113. Dubai, 114. Abu Dhabi, 115. Qatar, 116. Bahrain, 117. Kuwait, 118. Iran, 119. Persian Gulf, 120. Djibouti, 121. Eritrea, 122. Sudan, 123. Egypt, Red Sea, 124. Egypt, 125. Libya, 126. Tunisia, 127. Algeria, 128. Morocco, 129. Western Sahara, 130. Mauritania, 131. Senegal, 132. Gambia, 133. Sierra Leone, 134. Liberia, 135. Cote d'Ivoire, 136. Ghana, 137. Nigeria, 138. Cameroon, 139. Equatorial Guinea, 140. Sao Tomé and Principe, 141. Gabon, 142. Congo, 143. Angola, 144. Namibia, 145. South Africa, 146. Mozambique, 147. Madagascar, 148. Tanzania, 149. Kenya, 150. Somalia, 151. Ethiopia, 152. Pakistan, 153. India, 154. Sri Lanka, 155. Bangladesh, 156. Comores and Mayotte, 157. Aldabra Islands, 158. Réunion, 159. Mauritius, 160. Seychelles, 161. Amirante Islands, 162. Saya de Malha Bank, 163. Cargados Carajos, 164. Rodrigues Island, 165. India, Laccadive Islands, 166. Maldives, 167. Chagos Archipelago, 168. Diego Garcia Atoll, 169. Amsterdam Island, 170. Cocos (Keeling) Islands, 171. Andaman Islands, India, 172. Nicobar Islands, India, 173. Indian Ocean Islands, 174. Myanmar, 175. Thailand, 176. Malaysia, 177. Vietnam, 178. Singapore, 179. Philippines, 180. Indonesia, 181. Indonesia, New Guinea, 182. Taiwan, 183. China, 184. Hong Kong, 185. Japan, 186. Korea, 187. Russia, east, 188. Russia, Kamchatka, 189. Russia, Commander Islands, 190. Saint Paul Island, 191. Easter Island, 192. Northwestern Hawaiian Islands, USA, 193. Hawaiian Islands, USA, 194. Wake Atoll, 195. Ryukyu Islands, Japan, 196. Mariana Islands, 197. Guam, 198. Republic of Palau, 199. Federated States of Micronesia, 200. Marshall Islands, 201. Tuvalu, 202. Samoan Archipelago, 203. American Samoa, 204. Central Polynesia, 205. French Polynesia, 206. Tahiti, 207. Fiji, 208. Solomon Islands, 209. Papua New Guinea, 210. Christmas Island, Australia, 211. Australia, western , 212. Australia, Houtman Abrolhos, 213. Australia, Northern Territory, 214. Australia, Queensland, 215. Australia, New South Wales, 216. Australia, Lord Howe Island, 217. Australia, Norfolk Island, 218. Australia, Victoria, 219. Australia, Bass Strait, 220. Australia, South, 221. Tasmania, 222. New Zealand, 223. New Zealand, Stewart Islands/Rakiura, 224. New Zealand, Snares Islands/Tini Heke, 225. New Zealand, Auckland Islands, 226. New Zealand, Kermadec Islands, 227. New Zealand, Chatman Islands, 228. New Zealand, Bounty Island, 229. New Zealand, Antipodes Islands, 230. Antarctica, Campbell Islands, 231. Antarctica, Macquarie Island, 232. Antarctica, Heard Island, 233. Antarctica, Kerguelen, 234. Antarctica, Crozet Islands, 235. Antarctica, South Georgia, 236. Antarctica, South Orkney Islands, 237. Antarctica, South Shetland Islands, 238. Antarctica, Fuegia, 239. Antarctica, Tierra del Fuego, 240. Antarctica, Peninsula, and 241. Antarctica, Subantarctic Islands.

Table 1. Net primary production (daily and annual) of coralline algae (communities) from different depths and locations. Yearly primary production indicated in Italic are an estimate of the yearly production by taking a daily production and modifying this to a yearly production (x365). The median production for crustose coralline algae and free-living algae is indicated.

Structure or species	Location	Depth	Primary production (g C m^{-2} d^{-1})	Primary production (g C m^{-2} yr^{-1})	Reference
Crustose coralline algae				370	This study (n=35)
Crustose coralline algae	San Salvador Island, Bahamas	81 m	0.07	*26*	(Littler et al., 1986)
Hydrolithon spp.	Klein Piscadera, Curacao	25 m	0.21	77	(Vooren, 1981)
Sporolithon ptychoides	Klein Piscadera, Curacao	25 m	0.21	78	(Vooren, 1981)
Pseudolithoderma nigrum	Wilson Cove, California, USA		0.40	146	(Littler and Murray, 1974)
Sporolithon erythraeum	Waikiki reef, Hawaii, USA		0.50	*183*	(Littler, 1973)
Porolithon onkodes	Waikiki reef, Hawaii, USA		0.50	*183*	(Littler,1973)
Porolithon gardeneri	Waikiki reef, Hawaii, USA		0.50	*183*	(Littler, 1973)
Hydrolithon decipiens	Wilson Cove, California, USA		0.50	183	(Littler and Murray, 1974)
Phymatolithon foecundum + P. Tenue	Young Sound, NE Greenland	17 – 36 m		70 – 300	(Roberts et al., 2002)
Reef building coralline algae	Eniwetok Atoll, Hawaii, USA	2 m	0.66	240	(Marsh, 1970)
Porolithon conicum	Lizard Island, Australia	0 – 18 m	0.18 – 1.16	66 – 423	(Chisholm, 1988)
Lithophyllum sp.	Coral reef, Curacao	0.5 – 3 m	0.70	*256*	(Wanders, 1976)
Neogoniolithon fosliei	Lizard Island, Australia	0 – 6 m	0.46 – 0.95	168 – 347	(Chisholm, 1988)
Porolithon onkodes	Lizard Island, Australia	0 – 6 m	0.37 – 1.35	135 – 493	(Chisholm, 1988)
Hydrolithon reinboldii	Lizard Island, Australia	3 – 6 m	0.86 – 0.90	314 – 329	(Chisholm, 1988)
Lithophyllum intermedium	Coral reef, Curacao	0.5 – 3 m	0.90	*329*	(Wanders, 1976)
Lithophyllum congestum	Coral reef, Curacao	0.5 – 3 m	1.00	*365*	(Wanders, 1976)

Crustose coralline algae	Coral reef, Curacao	0.5 – 3 m	1.00	370	(Wanders, 1976)
Porolithon pachydermum	Coral reef, Curacao	0.5 – 3 m	1.10	*402*	(Wanders, 1976)
Lithophyllum sp.	Coral reef, Curacao	0.5 – 3 m	1.10	*402*	(Wanders, 1976)
Neogoniolithon solubile	Coral reef, Curacao	0.5 – 3 m	1.40	*511*	(Wanders, 1976)
Melobesioid species	Waikiki reef, Hawaii, USA		1.50	*548*	(Littler, 1973)
Mainly *Neogoniolithon frutescens*	Coral reef, Mooria, Tahiti	0.75 m	2.00	730	(Sournia, 1976)
Porolithon onkodes	Hawaiian Reef, USA	5 m	2.20	803	(Littler and Doty, 1975)
Porolithon gardineri	Hawaiian Reef, USA	5 m	2.40	876	(Littler and Doty, 1975)
Corallina elongata	Marseille, France	5 m	2.50	*912*	(El Haïkali et al., 2004)
Hydrolithon reinboldii	Waikiki reef, Hawaii, USA		2.60	*949*	(Littler, 1973)
Neogoniolithon conicum Lab.	Lizard Island, Australia	0 – 18 m	0.6 – 4.65	*219 – 1697*	(Chisholm, 2003)
Hydrolithon reinboldii Lab.	Lizard Island, Australia	0 – 6 m	1.6 – 3.8	*584 – 1387*	(Chisholm, 2003)
Neogoniolithon brassica-florida Lab.	Lizard Island, Australia	0 – 6 m	2.45 – 3.35	*894 – 1223*	(Chisholm, 2003)
Neogoniolithon conicum In situ	Lizard Island, Australia	0 – 18 m	0.85 – 5.9	*310 – 2154*	(Chisholm, 2003)
Neogoniolithon brassica-florida In situ	Lizard Island, Australia	0 – 6 m	2.15 – 4.7	*785 – 1716*	(Chisholm, 2003)
Hydrolithon onkodes In situ	Lizard Island, Australia	0 – 3 m	1.75 – 6.55	*639 – 2391*	(Chisholm, 2003)
Hydrolithon reinboldii In situ	Lizard Island, Australia	3 – 6 m	4.15 – 4.35	*1515 – 1588*	(Chisholm, 2003)
Hydrolithon onkodes Lab.	Lizard Island, Australia	0 – 3 m	4.01 – 6.05	*1464 – 2208*	(Chisholm, 2003)
Free-living algae				173	This study (n=4)
Nongeniculate corallines	San Salvador Island, Bahamas	76 m	0.15	55	(Littler et al., 1991)
Maerl beds	Bay of Brest, France	0.3 - 7.9 m	0.38	*138*	(Martin et al., 2005)
Lithophyllum sp.	San Salvador Island, Bahamas	76 m	0.57	208	(Littler et al., 1991)

Lithothamnion coralliodes	Bay of Brest, France	1 - 10 m	10 - 600	(Martin et al., 2006)

Table 2. The global average production rates of autotrophic coastal communities. Macroalgae in Gattuso et al., (1998) were macrophyte-dominated. Macrophytobenthic communities in Charpy-Roubaud and Sournia (1990) included brown algae, seagrasses, mangroves and salt marshes.

Community	Production rate		References
	(g C m^{-2} d^{-1})	(g C m^{-2} yr^{-1})	
Coralline algae (average)	0.9	329	This study (n=39)
Free-living algae	0.15 - 0.83	173	This study (n=4)
Crustose coralline algae	0.07 - 5	370	This study (n=35)
	0.9 – 5		(Chisholm, 2003)
Benthic fleshy algae	0.1 – 4		(Larkum, 1983)
Turf algae	1 – 6		(Larkum, 1983)
Mangroves		221	(Duarte et al., 2005)
		1081	(Gattuso et al., 1998)
Salt marshes		1585	(Duarte et al., 2005)
		210	(Gattuso et al., 1998)
Seagrasses	1 – 7^{L}	1211^{D}	^{L} = (Larkum, 1983) ^{D} = (Duarte et al., 2005)
		502	(Ranwell, 1966; Kirby and Gosselink, 1976; Odum, 1974; Turner, 1976; Thayer and Adams, 1975; Nienhuis and Bree, 1977; Zieman, 1975)
Macroalgae		1587	(Duarte et al., 2005)
		222	(Gattuso et al., 1998)
Benthic diatoms		123	(Cadee and Hegeman, 1974)

Coastal phytoplankton	0.1 – 0.5^{L}	196^{W}	^{L} = (Larkum, 1983) ^{W} = (Woodwell et al., 1973; Cadee and Hegeman, 1974; Gieskes and Kraay, 1975)
Coral reefs		148	(Duarte et al., 2005)
		120	(Gattuso et al., 1998)
Macrophytobenthos		375	(Charpy-Roubaud and Sournia, 1990)

Table 3. The total global production of different coastal communities compared to the total marine oceanic production. The macrophytobenthic community in Charpy-Roubaud and Sournia (1990) included brown algae, seagrasses, mangroves and salt marshes.

Community	Total global production (in 10^9 t C yr^{-1})	References
Coralline algae	0.7	This study (n=39)
Microphytobenthic community	0.34	(Charpy-Roubaud and Sournia, 1990)
Algal beds and reefs community	1.2	(Whittaker and Likens, 1973)
Macrophytobenthic community	2.55	(Charpy-Roubaud and Sournia, 1990)
Phytoplankton community	≥ 30	(Charpy-Roubaud and Sournia, 1990)
Marine community	48.5	(Field et al.,1998)

Table 4. Median net calcium carbonate production by coralline algae. Bracchi and Basso (2012) includes Lithophylloids, Canals and Ballesteros (1997) includes *Peysonellia*.

Species	Location	Depth	$CaCO_3$ production (g $CaCO_3$ m^{-2} yr^{-1})	Reference
Crustose coralline algae			1225	This study (n=25)
Epiphyte corallines on seagrass	Mallorca-Menorca shelf, Mediterran.	0 - 35 m	68	(Canals and Ballesteros, 1997)
Mesophyllum	Barbados	fringing reef	167	(Stearn et al., 1977)
Coralligenous build-ups + coralline species	Mallorca-Menorca shelf, Mediterran.	70 - 90 m	170	(Canals and Ballesteros, 1997)
Crustose coralline algae	Uva Island, Panama	reef flat	190	(Eakin, 1996)
Neogoniolithon brassica-florida + geniculate	Mallorca-Menorca shelf, Mediterran.	0 - 10 m	289	(Canals and Ballesteros, 1997)
Lithophyllum cabiochae	NW Mediterranean	25 m	292	(Martin and Gattuso, 2009)
Lithophyllum incrustans	South West Wales, United Kingdom	intertidal pools	379	(Edyvean and Ford, 1987)
Epiphyte corallines on seagrass	Shark Bay, western Australia	10 m	500	(Walker and Woelkerling, 1988)
Neogoniolithon conicum	Lizard Island, Australia	0 - 18 m	300 - 1550	(Chisholm, 2000)
Hydrolithon reinboldii	Lizard Island, Australia	3 - 6 m	910 - 1240	(Chisholm, 2000)
Porolithon conicum	Lizard Island, Australia	0 - 18 m	318 - 1862	(Chisholm, 1988)
Neogoniolithon	Barbados	fringing reef	1225	(Stearn et al., 1977)
Hydrolithon reinboldii	Lizard Island, Australia	3 - 6 m	1035 - 1512	(Chisholm, 1988)
Lithophyllum	Barbados	fringing reef	1355	(Stearn et al., 1977)
Neogoniolithon brassica-florida	Lizard Island, Australia	0 - 6 m	1200 - 2070	(Chisholm, 2000)
Hydrolithon onkodes	Ishigaki Is (Ryukyu Is)	upper fore reef	2044	(Matsuda, 1989)
Hydrolithon onkodes	Lizard Island, Australia	0 - 3 m	820 - 3310	(Chisholm, 2000)
Porolithon onkodes	Penguin Bank, Hawaii	40 - 100 m	2100	(Agegian et al., 1988)

Neogoniolithon fosliei	Lizard Island, Australia	0 - 6 m	1542 - 2815	(Chisholm, 1988)
Porolithon onkodes	Lizard Island, Australia	0 - 6 m	947 - 3599	(Chisholm, 1988)
Porolithon	Barbados	fringing reef	2378	(Stearn et al., 1977)
Coralline pavement	One Tree Island, Australia	0 - 1 m	4000	(Kinsey, 1985)
Corallina elongata	Marseille, France	0.5 - 1 m	5037	(El Haïkali et al., 2004)
Porolithon onkodes	Rangiroa, Polynesia	reef flat	7400	(Payri, 2000)
Free-living algae			187	This study (n=14)
mainly *Lithothamnion* spp.	Pontian Islands shelf, west Meditte.	70 - 100 m	8	(Bracchi and Basso, 2012)
mainly *Lithothamnion* spp.	Pontian Islands shelf, west Meditte.	40 - 70 m	32	(Bracchi and Basso, 2012)
Lithothamnion coralliodes	Cilento shelf, west Mediterranean	47 m	91	(Savini et al., 2012)
Rhodolith bed	Arvoredo Island, southern Brazil	7 - 20 m	55 - 136	(Gherardi, 2004)
Lithothamnion coralliodes	Mannin Bay, Ireland	0 - 10 m	29 - 164	(Bosence and Wilson, 2003)
Lithothamnion coralliodes	Galway, Ireland	< 10 m	88 - 164	(Bosence, 1980)
Phymatolithon calcareum	Mannin Bay, Ireland	0 - 10 m	79 - 249	(Bosence and Wilson, 2003)
Phymalithon calcareum maerl	Mallorca-Menorca shelf, Mediterran.	40 - 85 m	210	(Canals and Ballesteros, 1997)
Phymatolithon calcareum	Galway, Ireland	< 10 m	79 - 422	(Bosence, 1980)
Lithothamnion glaciale	Troms, Norway	18 m	420 - 630	(Freiwald and Henrich, 1994)
Lithothamnion coralliodes	Bay of Brest, France	0 - 10 m	876	(Potin et al., 1990)
Rhodolith bed	Abrolhos shelf, Brazil	20 - 110 m	1000	(Amado-Filho et al., 2012)
Lithothamnion glaciale	Troms, Norway	7 m	895 - 1432	(Freiwald and Henrich, 1994)
Lithothamnion coralliodes	Bay of Brest, France	1 - 10 m	145 - 3100	(Martin et al., 2006)

Table 5. Accumulation rates of free-living coralline algae. Coralline algae in Bosence (1985) were predominantly *Neogoniolithon* species.

Species	Location	$CaCO_3$ accumulation (mm kyr^{-1})	Reference
Rhodolith (maerl)	Troms district, Norway	1400	(Freiwald, 1998)
Mixed coralline algae	Troms district, Norway	900	(Freiwald, 1998)
Coralline algae	Orkney Islands, Scotland	80	(Farrow et al., 1984)
Branched coralline algae	Tavernier Key, Florida, USA	450	(Bosence, 1985)
Rhodolith (maerl)	St Mawes Bank, Falmouth, UK	500	(Bosence, 1980)