

REVIEW

CORALLINE ALGAE (RHODOPHYTA) IN A CHANGING WORLD:
INTEGRATING ECOLOGICAL, PHYSIOLOGICAL, AND GEOCHEMICAL
RESPONSES TO GLOBAL CHANGE¹

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Coralline algae are globally distributed benthic primary producers that secrete calcium carbonate skeletons. In the context of ocean acidification, they have received much recent attention due to the potential vulnerability of their high-Mg calcite skeletons and their many important ecological roles. Herein, we summarize what is known about coralline algal ecology and physiology, providing context to understand their responses to global climate change. We review the impacts of these changes, including ocean acidification, rising temperatures, and pollution, on coralline algal growth and calcification. We also assess the ongoing use of coralline algae as marine climate proxies via calibration of skeletal morphology and geochemistry to environmental conditions. Finally, we indicate critical gaps in our understanding of coralline algal calcification and physiology and highlight key areas for future research. These include analytical areas that recently have become more accessible, such as resolving phylogenetic relationships at all taxonomic ranks, elucidating the genes regulating algal photosynthesis and calcification, and calibrating skeletal geochemical metrics, as well as research directions that are broadly applicable to global change ecology, such as the importance of community-scale and long-term experiments in stress response.

Key index words: calcification; climate change; coralline algae; crustose coralline algae; ecology; ecosystem services; ocean acidification; paleoclimate; paleoclimate proxies; photosynthesis; physiology

Abbreviations: CaCO₃, calcium carbonate; CCA, crustose coralline algae; CO₂, carbon dioxide; CO₃²⁻, carbonate; DIC, dissolved inorganic carbon; HCO₃⁻, bicarbonate; OA, ocean acidification; PAR, photosynthetically active radiation; SST, sea surface temperature

Coralline algae (Corallinales and Sporolithales, Corallinophycidae, Rhodophyta) are receiving renewed attention across the ecological and geological sciences as important organisms in the context of global environmental change, especially ocean acidification (OA). In addition to their important functional roles in ecological systems across latitudes and habitat types (e.g., reef frameworks, Adey 1998, Chisholm 2000, carbonate (CO₃²⁻) production, Bosence 1980, foundational species, Steneck and Dethier 1994, larval settlement, Daume et al. 1999, fish nurseries, Kamenos et al. 2004a), coralline algae are increasingly used as paleoecological proxies (e.g., Cabioch et al. 1999, Braga and Aguirre 2001, Perry 2001, Aguirre et al. 2007) and accurate paleoenvironmental recorders (e.g., Halfar et al. 2000, Kamenos 2010, Williams et al. 2011), thus providing a valuable mechanism for contextualizing recent oceanic changes.

Coralline diversification reveals the ability of this group to colonize a wide range of light, temperature, and energy conditions and to remain chief components of benthic marine communities through considerable fluctuations in temperature and light over geologic time (Aguirre et al. 2000). Much is known about coralline algal ecology and physiology, despite the great variety in ecological forms and cryptic diversity emerging from molecular studies. Here, we point the reader to previous reviews of the basic ecology and physiology of coralline algae (Table 1) and focus on new insights into the potential responses of coralline algae to environmental change at different scales, including responses of physiology, skeletal mineralogy, ecology, and ecosystem services.

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TABLE 1. Summary of previous reviews on the subject of coralline algae published in the last 40 years.

Discipline	Growth form				Latitude		Timescale		Reference Citation							
	Life history	Physiology	Ecology	Biogeography	Carbonate production	Calcification	Phylogenetics	Taxonomy		Sclerochronology	Geniculate	Nongeniculate	Tropical	Temperate	Modern	Paleo
x		x	x	x	x			x		x		x		x		Littler 1972
	x		x													Adey and Macintyre 1973
		x	x	x						x		x		x		Macintyre 1973
			x													Johansen 1981
			x							x		x		x		Steneck 1983
			x													Bosence 1983
			x													Littler and Littler 1984
			x													Steneck 1985
			x													Steneck 1986
			x													Woelkerling 1988
			x													Aguirre et al. 2000
			x													Foster 2001
			x													Wilson et al. 2004
			x													Nelson 2009
			x													Adey et al. 2013
			x													Foster et al. 2013

CORALLINE ALGAL ECOLOGY

Nongeniculate (crustose and rhodolith forms). Nongeniculate coralline algae, or coralline algae lacking noncalcified articulations (genicula) between calcified segments (Fig. 1, A and B), are some of the most abundant organisms throughout the hard-bottom marine photic zone (Adey and Macintyre 1973, Steneck 1986). This group includes crustose and rhodolith (or maerl) morphologies (Foster 2001). Nomenclature of free-living forms is often inconsistent in the literature, which describes “coatings,” “gravels,” “rhodolites,” and most commonly “maerl” and “rhodoliths” (Steneck 1986). This terminology can be confusing, given that several species of nongeniculate coralline algae have been observed within an individual rhodolith or coated pebble (Basso 1998, Yabur-Pacheco and Riosmena-Rodríguez 2006). We thus refer to all forms not attached to hard-bottom substratum or other macroalgae (including coralline algae) as rhodoliths, following the nomenclature of Foster (2001). Correspondingly, we define the term crustose coralline to refer to all forms that grow roughly radially on hard substrates and exhibit determinate thickness <1 cm. Many nongeniculate species are thought to exist in both rhodolith and crustose forms. However, we will occasionally separate our discussion of these two morphological groups due to some important differences in ecology and ecosystem services.

Nongeniculate coralline algae can be found on any hard substrate where light penetrates (Bosence 1983). They thrive in areas of moderate disturbance and often dominate in areas of high stress and disturbance potential where many other macrophytes are absent (Steneck 1986, Dethier 1994). This includes areas of high herbivory, wave action, sand scour, and low productivity potential such as the low photic zone, shaded understories of large macrophyte beds, and the intertidal zone (Kendrick 1991, Dethier 1994, Steneck and Dethier 1994, Dethier and Steneck 2001). Crustose forms often cover a high proportion of primary space despite a relatively flat morphology that makes them easy to overgrow (Dethier and Steneck 2001). Such areas are referred to as crustose coralline carpets (Paine 1984).

Rhodoliths are a morphologically diverse group of nongeniculate coralline algae, shaped like spheres, branching twigs, or fans and ranging from roughly 1–100 cm in size (Foster et al. 2013). Rhodolith beds tend to form on fairly level bottoms that have sufficient, but often low light, and occur in areas with moderate water motion and high bioturbation to prevent the burial of rhodoliths in sediment (Steller and Foster 1995, Connell 2003, Wilson et al. 2004, Harrington et al. 2005). Unlike crustose coralline carpets, rhodolith beds form in the absence of intense water movement, which could scatter or bury slow-growing rhodoliths (Nelson 2009, Foster et al.

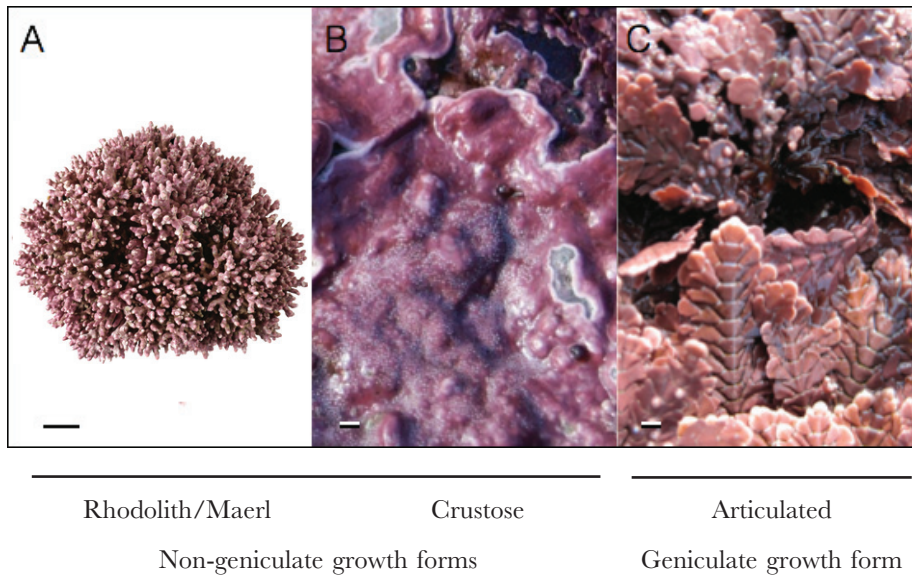


FIG. 1. Examples of (A) rhodolith (maerl), (B) crustose, and (C) geniculate growth forms of red coralline algae. Scale bars are 10 cm, 1 cm, and 5 mm, respectively. *Source.* (A) Photo by N.A. Kamenos, (B and C) photos by S.J. McCoy.

2013). Rhodolith beds can range several square kilometers in tropical and temperate settings (Foster 2001, Nelson 2009, Amado-Filho et al. 2012, Foster et al. 2013), and therefore play a significant role in calcium carbonate (CaCO_3) production on continental shelves (Amado-Filho et al. 2012).

Geniculate (articulated forms). Geniculate or articulated coralline algae consist of an algal frond growing from a basal crust. The morphology of basal crusts varies among species and individuals, and can be either extensive or appear hidden beneath the frond. Geniculate corallines are named for the noncalcified joints (genicula) that occur between the larger calcified segments (intergenicula) in an upright frond, allowing it to flex with water movement (Fig. 1C). Geniculate corallines, like nongeniculate corallines and other noncalcified macroalgae, exhibit strong patterns of zonation throughout intertidal and subtidal zones depending upon their light, desiccation, and grazing tolerances (Padilla 1984, Martone 2010, Guenther and Martone 2014).

Coralline algae illustrate ecological models of persistence. Primary substrate in the photic zone is highly contested, and thus coralline algae compete with each other as well as with fleshy and filamentous macroalgae and microalgae. Fast-growing (up to $20 \text{ mm} \cdot \text{year}^{-1}$) nongeniculate and geniculate corallines are typically early colonizers and become replaced by slow-growing, thicker, or branched crusts (Padilla 1981, Steneck 1986, Matsuda 1989) or noncalcified algal turfs (Kendrick 1991). Competitive interactions and susceptibility to herbivory among coralline algae have been well documented for many common species of both nongeniculates and geniculates, particularly in the Northeast Pacific (Paine 1980, 1984, Steneck 1986, Steneck et al. 1991, Dethier 1994, Steneck and Dethier 1994, Dethier and Steneck 2001). While the dominance

structure is generally hierarchical and dictated by thallus thickness, edge morphology, and growth rate, reversals in the competitive hierarchy are common and typically mediated by herbivores (Paine 1984, Steneck et al. 1991). A particular species' competitive ability thus depends on its growth strategy and its resistance to grazing.

Nongeniculate corallines have both competitive and positive (facilitative) relationships with macroalgae. For example, many temperate nongeniculate corallines inhabiting the intertidal or shallow subtidal depend on shading by the macro-algal canopy, while they also compete for light and holdfast space with large macrophytes (Paine 1980, 1984, Irving et al. 2004, 2005). Filamentous macroalgae may grow epiphytically on the crust surface (Figueiredo et al. 1996). Nongeniculate corallines have two primary mechanisms for the removal of epiphytic organisms from their surface: epithallial sloughing to shed surface cells and depending on herbivores to graze epiphytes off the thallus surface. During epithallial sloughing, an individual typically loses the uppermost layer of cells from its epithallus (Johnson and Mann 1986, Poeschel and Keats 1997, Figueiredo et al. 2000), though some species are "deep-layer" sloughers, shedding below the layer of actively growing (meristematic) cells (Keats et al. 1993). An alternative hypothesis for the ecological function of epithallial sloughing is that constant sloughing leads to a thin thallus, which is correlated with faster growth and stronger attachment (Keats et al. 1994).

Trophic interactions. Coralline algae can generally have both positive and negative interactions with grazers. Nongeniculate corallines benefit from low levels of herbivory (Steneck 1983, 1986), and grazer presence may even stimulate local productivity of coralline crusts (Wai and Williams 2005). In addition to sea urchins (Echinoidea), two molluscan

groups are able to graze coralline algae. Limpets (Patellacea) and chitons (Polyplacophora) have several convergent adaptations for grazing hard substrates: strong buccal muscles, unique dentition, and a heavy silicate and iron mineral coating on their teeth (Steneck 1983). In tropical areas, common grazers also include fish. In return, coralline algae are particularly well adapted to withstand grazing with calcified thalli and conceptacles (Steneck 1985).

Crustose coralline communities exhibit what is called consumer-mediated coexistence. The presence of grazers can overturn competition hierarchies by favoring grazer-resistant species over fast growers. Herbivore-mediated reversals slow the competitive exclusion of one species by another and are therefore important to the long-term persistence of nongeniculate coralline species diversity (Paine 1984, Steneck et al. 1991, Dethier and Steneck 2001). This has been best documented experimentally in temperate intertidal and shallow subtidal systems, but is likely an important process globally given the high grazing rates documented in warmer-water systems (Hay 1997). Heavy grazing can also induce morphological change in coralline algae (Maneveldt and Keats 2008), affecting algal competitive interactions, many of which are based on morphological traits such as thallus thickness and lateral growth rates (Paine 1984, Dethier and Steneck 2001, Maneveldt and Keats 2008). The basal crusts of geniculate corallines may compete for space with crustose species, but tend to be poor competitors due to their thinness (Paine 1984) and likely persist due to high colonization rates (Padilla 1981). Successional patterns in coralline algae have been well summarized by Steneck (1986) as a slow replacement of thinner, unbranched morphologies to be replaced by thicker and/or branched species.

Secondary metabolites. Marine algae produce an array of secondary compounds (also referred to as secondary metabolites). A variety of physiological and ecological functions exist even for the same compound (reviewed in Hay 1997, 2009), primarily competitive interactions (Rasher and Hay 2010, Andras et al. 2012) and grazer deterrence (Norris and Fenical 1982, Faulkner 1984, Rasher and Hay 2014). These compounds differ in mechanisms of grazer deterrence and toxicity, but are generally thought to reduce palatability, digestibility, or nutrition of algal tissue, or to be toxic through effects on the nervous system or cardiac functions (Van Alstyne 1988). Anti-grazer compounds often act as anti-fouling agents and potentially reduce microbial pathogens (Schmitt et al. 1995). Coralline algae use a variety of chemical compounds to deter epiphytes, typically fatty acids that act as algal spore lytic agents (Figueiredo et al. 1997, 2000, Kim et al. 2004, Luyen et al. 2009). The degree of allelopathy depends not only on the coralline algae but also on the identity of its epiphyte (Bôas and Figueiredo 2004).

A large proportion of research in this area has focused on the role of dimethylsulphoniopropionate (DMSP) in coralline algae. DMSP is a secondary metabolite common in many marine algae that has been identified as a cryoprotectant (Karsten et al. 1996), an antioxidant (Sunda et al. 2002), and a possible grazer defense compound (Van Alstyne and Houser 2003, Lyons et al. 2010). DMSP has been detected at high concentrations in temperate rhodolith beds comprised of primarily *Lithothamnion glaciale* and *Phymatolithon calcareum*, both in algal tissue and in the water column (Kamenos et al. 2008a), likely functioning to combat oxidative stress (Rix et al. 2012). No change in DMSP concentrations has been documented in response to stable OA scenarios in *L. glaciale*, however, DMSP concentrations increase in response to sudden pH change, leading to epithelial damage (Burdett et al. 2012a). On a coral reef flat, the lightly calcified *Amphiroa* sp. increases DMSP concentrations to maintain metabolic function during periods of low CO_3^{2-} saturation state (Burdett et al. 2013). Overall, DMSP production in coralline algae is slow process occurring at timescales of hours to days probably reflecting the energetic cost of its production (Rix et al. 2012, Burdett et al. 2013).

Interactions in a changing ocean. As the competitors of coralline algae (other coralline and fleshy algal species) and herbivores (primarily calcified echinoderms and mollusks in temperate areas) may have differential responses to OA, it is imperative that the responses of communities be assessed to disentangle direct from indirect effects of acidification. Ecologically important parameters such as growth rate and thallus thickness are directly related to CaCO_3 content and calcification rates. It is, therefore, not surprising that OA has been found to affect ecological interactions through effects on growth (Gao et al. 1993, Martin and Gattuso 2009, Ries et al. 2009, Ragazzola et al. 2012, 2013, Cornwall et al. 2013a, Egilisdottir et al. 2013, Kamenos et al. 2013, Noisette et al. 2013a,b, Kato et al. 2014) and both large- and fine-scale morphology (Ragazzola et al. 2012, 2013, McCoy 2013, Kato et al. 2014, McCoy and Ragazzola 2014) as CaCO_3 production becomes more costly. Examples of this include altered competitive interactions among coralline algae (McCoy and Pfister 2014), between coralline algae and noncalcified algae (Jokiel et al. 2008, Kuffner et al. 2008, Porzio et al. 2011, Kroeker et al. 2013), and between coralline algae and grazers (McCoy and Pfister 2014).

A high- CO_2 environment will especially affect ecological dynamics between coralline and noncalcified algae as the energetic cost of calcification increases. High acidity favors recruitment of fleshy algae over coralline algae (Kuffner et al. 2008, Kroeker et al. 2013), which will lead to an escalation of competition between coralline and nonepiphytic fleshy algae. Noncalcified or fleshy algae can benefit from

elevated HCO_3^- availability for faster photosynthetic growth without any associated negative responses of calcified tissue to lower CaCO_3 saturation states that will simultaneously affect coralline algae (Jokiel et al. 2008, Kuffner et al. 2008, Porzio et al. 2011, Hofmann et al. 2012, Kroeker et al. 2013). This mechanism will also affect interactions between coralline and epiphytic fleshy algae. The primary mechanisms of epiphyte control involve sloughing or grazing, both of which cause loss of calcified growth, and are likely to become energetically costlier as acidification continues.

ECOSYSTEM SERVICES

Tropical systems. Despite their global distribution and importance, coralline algae are perhaps most commonly recognized for their ecological services in tropical settings. Coralline algae provide calcified cement between coral heads, and can be primary reef builders (Setchell 1926, Bak 1976, Adey 1978) that provide settlement substrate for other organisms (Gherardi and Bosence 1999) and physical frameworks (Nelson 2009). In addition, coralline algae in rhodolith beds can play a physical, stabilizing role that permits coral settlement and establishment of coral reefs over geologic timescales (Tierney and Johnson 2012).

Tropical nongeniculate coralline algae promote local biodiversity. As early colonizers, nongeniculate coralline algae may either inhibit or enhance recruitment of other individuals to the community. Coralline algae are typically thought of as enhancing recruitment or triggering larval metamorphosis of other species by providing chemical cues (Morse et al. 1979, 1988, Morse and Morse 1984, Johnson et al. 1991, Johnson and Sutton 1994, Figueiredo et al. 1997, O'Leary et al. 2012) or by providing a suitable attachment substrate or sufficient structural heterogeneity. Species-specific colonization or induction cues may also, or instead, be associated with bacteria growing on the coralline algal surface, which are shed with algal cells during sloughing (Johnson et al. 1991, Johnson and Sutton 1994, Huggett et al. 2006).

These mechanisms are crucial to the diversity of tropical and temperate invertebrate communities and may be subject to change as the ocean environment changes. For example, under elevated seawater temperatures only 2°C – 4°C above mean maximum seawater temperatures, the nongeniculate coralline *Neogoniolithon fostliei* experienced a large shift in the structure of its surface microbial community as well as its ability to induce coral larval metamorphosis at the elevated temperature (Webster et al. 2011). In another example, settlement of the coral *Acropora millepora* revealed potential changes in coral recruitment in response to OA; coral larvae increasingly avoid one of their preferred

CCA substrates with rising $p\text{CO}_2$ (Doropoulos et al. 2012).

Grazing pressure plays a role in coralline algal ecosystem services, as well. The facilitative relationship between coralline algal cover and settlement of reef invertebrates is susceptible to fishing-induced trophic cascades, in which fishing increases urchin populations, which reduces cover of nongeniculate coralline algae and can thus be linked to reduced coral recruitment (O'Leary and McClanahan 2010, O'Leary et al. 2012). The reduction in coralline algal cover is exacerbated by reduced grazing by herbivorous fish in overfished regions, which favors the growth of fleshy algae over coralline algae (Belliveau and Paul 2002).

A major concern as OA intensifies has been on the impact of these reef ecosystem services as calcification becomes more difficult in coralline algae themselves. Tropical rhodolith beds are major players in the global carbon cycle through the production of CaCO_3 sediment. In shallow reefs, for example, some species produce up to $9.1 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Chisholm 2000), and 0.9 – $5 \text{ g organic carbon (net) planar} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Chisholm 2003). The most expansive rhodolith bed sits off the coast of eastern Brazil on the Abrolhos Shelf, and extends $20,900 \text{ km}^2$. In this bed, mean CaCO_3 production is $1.07 \text{ kg} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, totaling $0.025 \text{ Gt} \cdot \text{year}^{-1}$ (Amado-Filho et al. 2012).

Over geologic timescales, the saturation states of calcite and aragonite have affected sediment production in tropical regions (Ries 2006a, 2009). Experimentally, lower calcification and primary production rates and reductions in tissue mass of *Hali-medea*, *Penicillus*, and *Udotea* were observed under lower saturation states, suggesting that calcification may in fact promote photosynthesis through release of CO_2 or H^+ ions (Ries 2009). Reduced rates of primary production may have been aggravated by reduced coralline algal tissue mass or height of algal reefs (Ries 2009).

Coralline algae typically accrete high-Mg calcite, or dolomite, skeletons. The presence of dolomite ($\text{Mg}_{0.5}\text{Ca}_{0.5}\text{CO}_3$) in the nongeniculate corallines *Porolithon onkodes* and *Porolithon pachydermum* decreased the dissolution rate of coralline thalli by 6–10 times (Nash et al. 2012). Indeed, as the proportion of dolomite increases with acidity as other CO_3^{2-} minerals dissolve out, this mechanism may indicate an optimistic future for the continued role of coralline algae as reef stabilizers (Nash et al. 2012). It is important to note, however, that calcification studies on the temperate intertidal geniculate *Corallina elongata* (Egilsdottir et al. 2013) and subtidal nongeniculate *L. glaciale* (Kamenos et al. 2013) have found that individuals raised under higher $p\text{CO}_2$ incorporate a lower proportion of $\text{Mg}^{2+}/\text{Ca}^{2+}$ during calcification. This finding does not necessarily contradict the former, as dissolution over the longer



FIG. 2. Temperate, subtidal *Lithothamnion glaciale* rhodolith bed off west coast of Scotland. Photo by N. Kamenos.

term may ultimately favor the preservation of dolomite.

Temperate, Subarctic, and Arctic systems. Rhodolith beds provide important hard substrate for colonization of other marine algae and invertebrates (Fig. 2; Kamenos et al. 2004b) and sustain highly diverse communities of associated organisms (Jackson et al. 2003, Wilson et al. 2004). In a rhodolith bed, aggregations of live rhodoliths up to several cm deep can be found atop layers of dead rhodoliths and rhodolith fragments, descending into sediment (Adey 1970, Foster et al. 2013).

Many invertebrates live inside rhodoliths or burrow in surrounding sediments (Kamenos et al. 2004a,c, Hinojosa-Arango et al. 2014). Similarly, intertidal and subtidal crustose coralline algae (CCA) can play host to a variety of grazing and burrowing infauna (Adey and Hayek 2011, Chenelot et al. 2011, Adey et al. 2013). Thicker crusts host a greater diversity of infauna (Steneck and Paine 1986), including both calcifying and noncalcifying animals. The presence of an infaunal community structurally weakens the algal thallus (Steneck and Paine 1986, Adey and Hayek 2011) and may thus exacerbate potential effects of OA on structural integrity of thick coralline algal crusts. For example, thicker coralline crusts may be more vulnerable to the effects of OA (McCoy 2013, McCoy and Ragazzola 2014), and there is evidence that structural properties including cell wall thickness (Kato et al. 2014, McCoy and Ragazzola 2014) and load-bearing strength (Ragazzola et al. 2012) will be affected.

A high cover of nongeniculate coralline algae, typically found under intense grazing, such as in an urchin barren under the grazed kelp canopy (Adey 1970), may inhibit the recruitment of other organisms (Breitburg 1984). Like recruitment enhancement, recruitment deterrence is a species-specific effect. Some coralline algae inhibit barnacles and fil-

amentous diatoms from recruiting (Padilla 1981), while others inhibit different species of filamentous and fleshy algae (Masaki et al. 1981). A high-density coralline algal carpet can inhibit the recruitment of sessile space occupiers, such as polychaetes, barnacles, amphipods, bryozoans, and algae, even when grazers are excluded (Breitburg 1984). Such recruitment inhibition is closely tied to competition for space; when nongeniculate coralline algae dominate the primary substrata, recruits of other sessile organisms must recruit onto the coralline algal thallus, where it is subsequently sloughed off along with the crustose coralline's uppermost layer of cells (Masaki et al. 1981).

Both rhodolith beds and coralline carpets can be important in the coastal carbon cycle in temperate areas. Carbonate accretion rates attributable to red coralline algae can vary between 79 and 1,432 g $\text{CaCO}_3 \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ in North Atlantic rhodolith beds (Bosence 1980, Freiwald and Henrich 1994) and up to 1,350 g $\text{CaCO}_3 \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ in geniculate coralline carpets the North Pacific (Fisher and Martone 2014). Because coralline algae are such important producers of CO_3^{2-} (Adey 1965, Adey and Macintyre 1973, Basso 2011, Adey et al. 2013), the physical and chemical function of high-latitude coralline algae in response to changes in the seawater environment will be an important area of study as changes to the marine environment continue. High-latitude habitats have so far received little attention compared to warm-water beds in this context.

PHOTOSYNTHESIS AND CALCIFICATION

Growth. In coralline algae, growth characteristics depend on morphotype as well as the growth environment, specifically water motion, depth, and temperature. Among nongeniculate forms, Steneck (1985) found an inverse relationship between crust thickness and growth rate, which is hypothesized to be because thicker crusts maintain a greater quantity of living nonphotosynthetic tissue. An energetic trade-off comes into play between lateral growth and maintenance of nonphotosynthetic tissue. Some species, therefore, form only thin crusts and have determinant vertical growth (Steneck and Paine 1986), whereas many others exhibit indeterminate vertical growth and form yearly or season growth bands (e.g., *Clathromorphum* spp., Adey et al. 2013). Nongeniculate coralline algae grow relatively slowly (vertically 0.3–10 mm $\cdot \text{year}^{-1}$, Setchell 1926, Adey and Vassar 1975, horizontally 0–10 mm $\cdot \text{year}^{-1}$, McCoy and Pfister 2014).

Geniculate and branched nongeniculate coralline algae do tend to grow faster (8–30 mm $\cdot \text{year}^{-1}$; Steneck and Adey 1976, Martone 2010) with no ontogenetic effect on growth rate (Fisher and Martone 2014). This is likely because geniculate and branched nongeniculate coralline algae have a greater photosynthetic capacity derived from the

increased surface area of their branches. However, high latitude branched nongeniculate species can have growth rates as low as 200–300 $\mu\text{m} \cdot \text{year}^{-1}$ (Kamenos et al. 2008b), related to lower irradiance and colder water temperatures at high latitudes.

Photosynthetic characteristics under natural conditions. Generally, temperate nongeniculate coralline algae are low-light adapted (Burdett et al. 2012b), and exposure to higher light intensities causes a reduction in photosynthetic activity and bleaching of algal tissue, related to loss of photosynthetic pigments in surface cells (Irving et al. 2004, Martone et al. 2010a). This is not the case for tropical nongeniculate coralline algae that are found growing under high light levels on reef or algal ridge settings (Steneck and Adey 1976, Adey 1978, 1998), where they rely on dynamic photoinhibition to tolerate high photosynthetically active radiation (PAR; Burdett et al. 2014). In the temperate rhodolith *L. glaciale*, within-thallus variability in light adaptation has been documented, with branch bases less light-acclimated than the tips (Burdett et al. 2012b). This may translate to differential light availability across the thallus in rhodolith beds. In addition, there is evidence for seasonal acclimation to differing light levels in summer and winter (Burdett et al. 2012b). Geniculate coralline algae show variation in light adaptation with zonation patterns across the intertidal and subtidal zones (Guenther and Martone 2014). Patterns in light tolerance and thereby coralline algal growth may be important to coastal carbon dynamics and thus important to document further across a range of species and environments.

Calcification. Calcification rate in coralline algae is thought to be directly related to photosynthetic rate (Pentecost 1978), as well as to the ambient concentration of inorganic carbon when carbon availability is manipulated in a laboratory setting (Smith and Roth 1979, Gao et al. 1993). Evidence points to a “trans calcification” mechanism, as defined by McConnaughey and Whelan (1997) based primarily on the green freshwater alga *Chara corallina*, but documented in most biological calcification. In this mechanism, calcification is enzymatically driven; seawater HCO_3^- is taken up and converted to carbon dioxide (CO_2) for photosynthesis by an external carbonic anhydrase, which in turn produces the CO_3^{2-} used in algal calcification (McConnaughey and Whelan 1997). Digby (1977) provided a more detailed mechanism developed for *Clathromorphum* and *Corallina* spp. based on pH drift and oxygen evolution measurements in the field and in the laboratory, suggesting that diffusion of hydrogen ions of the cell (most likely at the growing tips) promotes diffusion of seawater HCO_3^- into the cell.

Although we understand some basic relationships between biological rates of growth (photosynthesis and calcification) and abiotic parameters such as temperature (e.g., Martin et al. 2007a,b, Burdett et al. 2012a,b), the ongoing foci on coralline algae

under stress from global change and on integrating additional abiotic stressors will promote our increased understanding of these physiological processes as a function of environmental parameters. Geniculate coralline algae, for example in the genera *Amphiroa*, *Bossiella*, *Calliarthron*, and *Corallina*, are often used in growth experiments due to their higher growth rates compared to nongeniculate coralline algae, and thus much of our information about calcification in coralline algae comes from geniculate species. HCO_3^- is the primary carbon species used in photosynthesis (Borowitzka 1981). In the geniculate alga *Corallina pilulifera*, calcification and photosynthesis increased in response to elevated dissolved inorganic carbon (DIC: $\text{CO}_{2(\text{aq})}$, HCO_3^- , and CO_3^{2-}), but not in response to addition of free CO_2 (Gao et al. 1993). Inhibition of calcification at high seawater pH (>9) is most likely due to release of CO_2 during respiration, which may cause localized acidification and reduced availability of DIC (Borowitzka and Larkum 1976). It is still unclear to what extent external carbonic anhydrase, an enzyme that enables algae to use HCO_3^- for photosynthesis, is used throughout the coralline algae (Koch et al. 2013).

Evidence from the nongeniculate genus *Clathromorphum* suggests that at least some coralline algae can grow in extended periods of darkness (Adey 1998, Adey et al. 2013). These observations from field specimens contribute to our understanding of dark calcification, which otherwise comes from laboratory experiments conducted on 0–24 h timescales (Ikemori 1970, Pentecost 1978, Borowitzka 1979, Borowitzka and Larkum 1976, Smith and Roth 1979, Borowitzka 1981, El Haikali et al. 2004). Dark calcification is likely sourced by an accumulation of energy during periods of light and photosynthesis, facilitated by the presence of secondary pit connections or cell fusions which are believed to allow for translocation of photosynthates within the coralline algal thallus (Pueschel and Cole 1982, Steneck 1983). This “accumulated energy” mechanism would also explain observed dissolution and restricted growth described under stressful conditions. Skeletal dissolution can occur in the dark even under ambient $p\text{CO}_2$ concentration due to reduced pH in the diffusion boundary layer between the algal surface and surrounding seawater (Hurd et al. 2011). This can be tempered by an ability to compensate for $p\text{CO}_2$ -induced nighttime dissolution by increasing their calcification rate during the day (Kamenos et al. 2013, Martin et al. 2013). Under elevated $p\text{CO}_2$, however, increased photosynthesis is restricted during the day, and this reduces the capacity for enhanced daytime calcification (Kamenos et al. 2013). We point to a great need for (i) a better understanding of the function of secondary pit connections and cell fusions, including their role in calcification and growth, and (ii) molecular studies of up- or down-regulation of enzymes used in

both calcification and photosynthesis to establish a mechanistic molecular and biochemical understanding of calcification in corallines and the energetic requirements or trade-offs associated with short- and long-term calcification in the dark.

Skeletal mineralogy and seawater conditions. All but three cell types are calcified in the coralline algae; (i) cells of reproductive structures, (ii) branch joints (genicula) of geniculate growth habits, and (iii) lesion sites of the thallus undergoing reparation (Borowitzka and Vesik 1978, Bilan and Usov 2001, Pueschel et al. 2005). CaCO_3 composition of algal tissue thus varies by species, cell type, and the age of the alga (Borowitzka 1982). Coralline red algae (Corallinales and Sporolithales) are among only two known groups of marine algae, along with the family Coccolithaceae in the phylum Haptophyta (Guiry and Guiry 2014), that precipitate primarily the calcite rather than aragonite polymorph of CaCO_3 (Bilan and Usov 2001). Coralline algae can precipitate aragonite as well as magnesium calcite, and this plasticity in skeletal composition is determined by the alga's local growth environment (Pueschel et al. 1992, Medakovic et al. 1995). Magnesium is part of the crystal lattice rather than being present in associated organics (Kamenos et al. 2009) and is thought to be incorporated secondarily into the crystal structure (Baas-Becking and Galliher 1931). Calcite is deposited within the cell wall, and polysaccharide fibrils in the cell walls serve as a structural matrix for the formation of calcite tissues (Borowitzka 1982), with species that exhibit greater mineralization having lower polysaccharide content (Bilan and Usov 2001). The only differences between the ultrastructure and morphology of coralline red algae and other noncalcified red algae that may account for mineralization in this group are found in the polysaccharide composition of coralline algal cell walls (Bilan and Usov 2001).

Geniculate coralline algae thus present insight to the process of CaCO_3 precipitation and nucleation in coralline algae. A case study of the geniculate *Calliarthron cheilosporioides* identified changes in the synthesized polysaccharides between genicula and intergenicula (Martone et al. 2010b). Specifically, xylogalactans, a type of agaran organic compound, form xylose side chains from the galactan backbone that act as nucleation points for CaCO_3 precipitation. Within the genicula of *C. cheilosporioides*, these side chains are modified or absent, thereby controlling the location of calcification within the geniculate coralline algal thallus (Martone et al. 2010b). Calcification in geniculate coralline algae may be highly specified, as evidenced by cells at the geniculum–intergeniculum interface that are half-calcified and half-uncalcified (Johansen 1981, Martone et al. 2010b). Such interesting observations further illustrate the need for molecular mechanistic studies of calcification in the coralline algae.

Corallinales and Sporolithales exhibit a high degree of mineralogical variability, though most are calcitic (Smith et al. 2012). Mineralogy is generally related to growth habit, and geniculate coralline algae typically contain no aragonite (Smith et al. 2012). Mg^{2+} content is roughly phylogenetically variable (10.5%–16.4% by weight), with the Corallinales containing more Mg^{2+} than the Sporolithales and the Hapalidiaceae (Smith et al. 2012). Latitudinal trends can be used to explore effects of temperature gradients, though latitude is also coupled with irradiance (Halfar et al. 2000, 2011). Coralline algae are rare among mineralizing organisms in that they are able to respond to ambient seawater chemistry and change their skeletal mineralogy with seawater Mg^{2+} concentrations, although whether to reduce the energetic cost of mineralizing or as a response to chemical stress remains unknown (Stanley et al. 2002, Ries 2006a,b). Different coralline algae have been found to respond differently to nonpreferred seawater chemistries. *Neogoniolithon* and *Amphiroa* sp. were able to adjust to ambient seawater Mg concentrations in the laboratory, but with a loss of skeletal organization at low $\text{Mg}^{2+}/\text{Ca}^{2+}$ (Ries 2010). In other organisms (corals), undersaturation of a preferred skeletal mineral has induced thin or no skeletons (Fine and Tchernov 2007).

Mineralogy can show fine-scale seasonal fluctuations in response to ambient water temperature (Darrenougue et al. 2013). More Mg^{2+} appears to be incorporated during faster growth (Moberly 1968, Kolesar 1978), which produces a relationship between Mg content and temperature (Chave and Wheeler 1965, Milliman et al. 1971). On the other hand, some recent studies indicate that replacement of Ca^{2+} by Mg^{2+} within the crystal lattice may be driven by temperature and not by growth rate (Kamenos et al. 2008b, 2009). Further work in this area is needed to separate the responses of temperature and growth rate and in particular to study species relationships between growth, temperature, and Mg content (sensu Adey and McKibbin 1970).

GLOBAL CHANGE IMPACTS ON PHYSIOLOGY

Elevated $p\text{CO}_2$. Many previous studies on the effects of elevated $p\text{CO}_2$ on coralline physiology and growth occurred prior to concerns over OA (e.g., Smith and Roth 1979, Borowitzka 1981, Gao et al. 1993). More recent work has extended physiological relationships with the higher $p\text{CO}_2$ levels projected for future climate scenarios, and corroborates the previous foundational work that indicated a parabolic growth response to pH and $p\text{CO}_2$ (Ries et al. 2009, Büdenbender et al. 2011). In the intertidal alga *Ellisolandia elongata*, for example, $p\text{CO}_2$ was found to have no effect on respiration, gross primary production, and calcification rates in both light and dark (Egilsdottir et al. 2013, as *Corallina elongata*).

Pollution. Effects of pollution from domestic sewage can cause increased turbidity and sedimentation of organic particles accompanied by eutrophication (Bell 1990). High levels of phosphate found in eutrophied areas have negative effects on growth and calcification in coralline algae (Björk et al. 1995). Phosphate inhibits calcite crystal growth by settling on the crystal surface, thereby preventing the formation of a crystal lattice that allows the crystals to grow (Simkiss 1964).

Herbicides have also been shown to have negative effects on photosynthesis in coralline algae. In particular, the marine herbicide diuron is used widely as an antifouling agent in marine environments and as an agricultural herbicide in the terrestrial environment (Hamilton and Haydon 1996, Martinez et al. 2001). The use of diuron in coastal tropical sugar plantations poses a real threat to coralline algae, which experience decreased photosynthetic activity in its presence (Harrington et al. 2005). This stress is exacerbated by sedimentation stress, which is also elevated in coastal agricultural areas (Harrington et al. 2005).

Multiple stressors. Overall, in the face of multiple pressures from changes in climate and community reshuffling expected from range shifts of other algae, coralline algae are expected to become less widespread at high latitudes by the end of the current century, as illustrated by recent case studies in the North Atlantic (Brodie et al. 2014). Elevated temperature has been shown to act synergistically with elevated $p\text{CO}_2$ to reduce tissue growth, though again much variation has been observed. In a study of the Mediterranean nongeniculate coralline *Lithophyllum cabiochae*, algal necroses were observed first in high temperature and the highest CO_2 (700 ppm) treatment, followed by high temperature, 400 ppm CO_2 treatments (Martin and Gattuso 2009). In *L. cabiochae*, dissolution rates exceed calcification only when both temperature and $p\text{CO}_2$ were elevated, and dissolution rates were 2–4 times greater at elevated $p\text{CO}_2$ (Martin and Gattuso 2009). In the rhodolith *Lithothamnion corallioides*, elevated temperatures reduced photosynthetic pigment content, whereas elevated $p\text{CO}_2$ affected gross production and net calcification (Noisette et al. 2013a). These observations reveal important effects of both temperature and $p\text{CO}_2$, though not directly acting together in all cases. Similar results have been found when elevated CO_2 levels are combined with ultraviolet radiation (UVR), which can act synergistically with CO_2 to affect photosynthesis, growth, and calcification (Gao and Zheng 2010).

Canopy cover in shallow coastal areas promotes the growth of coralline algal beds in the understory (Irving et al. 2004). Experimental reductions in canopy cover in both temperate and polar regions lead to crust bleaching as a result of increased PAR and UVR (Irving et al. 2004, 2005). In coralline algae, bleaching is defined as loss or degradation of photo-

synthetic pigments in surface tissue, such that the affected area appears white. In intertidal zones, however, coralline bleaching seems to be most strongly induced by desiccation stress, which can be tightly coupled to high temperature and light stress at low tide (Martone et al. 2010a), in addition to high irradiance and low canopy cover (Irving et al. 2004). However, because light and temperature alone had only mild effects on loss of pigmentation in the intertidal *Calliarthron tuberculosum*, it has been hypothesized that desiccation is responsible for coralline algae living above the low intertidal zone occurring primarily in tide pools (Martone et al. 2010a). Anecdotally, bleaching can be reversible in some situations, typically depending on the duration and severity of environmental stress (S.J. McCoy pers. obs.). In other cases, nongeniculate coralline individuals may overgrow their own bleached tissue. For example, *Pseudolithophyllum neofarlowii* lives in the upper intertidal zone on vertical surfaces in the Northeast Pacific. This species can be recognized by the texture of its thallus, which is comprised of many small protuberances (Steneck and Paine 1986) that serve the dual function of protecting live tissue beneath and flaking off easily to allow for new growth (S.J. McCoy pers. obs., R.T. Paine personal communication). Clearly, the long-term effects of coralline algal bleaching and the different factors contributing to the reversible or irreversible nature of bleaching (e.g., pigment loss vs. pigment degradation) are areas where additional investigation is needed.

Variable conditions. Recent coastal pH data sets reveal large diurnal fluctuations in photosynthesis-dominated ecosystems that include tropical reefs as well as large expanses of temperate coastal areas where coralline algae are abundant (Wootton et al. 2008, Delille et al. 2009, Semesi et al. 2009, Anthony et al. 2011, Kleypas et al. 2011, Wootton and Pfister 2012, Cornwall et al. 2013a). *Porolithon onkodes* individuals sampled from a naturally variable environment calcified 42% more in variable $p\text{CO}_2$ conditions than individuals from a uniform environment (Johnson et al. 2014). Interestingly, individual acclimation did not reduce the detrimental effects of exposure to a high $p\text{CO}_2$ treatment (660 μatm), which decreased calcification by at least 70% in all individuals (Johnson et al. 2014). In contrast, pH manipulation to mimic diurnal fluctuations in kelp forest systems reduced growth rates of the geniculate coralline alga, *Arthrocardia corymbosa*, at lower pH. Growth was further reduced additively by pH fluctuation, though recruitment, and elemental composition of algal tissue did not change with pH (Cornwall et al. 2013b).

Generalizations across morphologies and environments. Noisette et al. (2013b) showed that the metabolic rates of coralline algae across three growth forms, rhodolith (*Lithothamnion corallioides*), nongeniculate (*Lithophyllum incrustans*), and geniculate

(*Corallina elongata*), vary in response to increasing seawater $p\text{CO}_2$. However, only one species of each growth form was studied, making it difficult to determine whether these metabolic responses represent differential responses across species or across morphotypes. Mechanisms of skeletal response to pH vary by morphological and growth type of nongeniculate species. Comeau et al. (2014) found variable, location-specific responses to elevated $p\text{CO}_2$ in the nongeniculate coralline *Porolithon onkodes* across sites that differ in environmental conditions and carbon chemistry across the tropical Pacific, showing yet another degree of response variability. In another example, thick, slow-growing species reduced their thallus thickness while keeping skeletal density and cell wall thicknesses constant (McCoy 2013, McCoy and Ragazzola 2014). In contrast, thin, fast-growing species showed no change in thallus thickness, but instead reduced the thickness of interfilament cell walls (McCoy and Ragazzola 2014). This mechanism may reduce the amount of CaCO_3 required for rapid lateral growth in species with this growth strategy.

Small physiological or morphological differences between species may therefore translate to changes in population and community ecology, as has already been shown in communities of nongeniculate coralline algae (McCoy and Pfister 2014, Ordóñez et al. 2014). Clearly, more physiological studies of responses to climate stressors are needed across growth forms, preferentially replicated across phylogenetic relationships. We note here that recent molecular advances have allowed a more precise study of coralline algal taxonomy and phylogenetics (Bailey and Chapman 1998, Le Gall and Saunders 2007, 2010, Broom et al. 2008, Bittner et al. 2011, Gabrielson et al. 2011, Kato et al. 2011, Martone et al. 2012, Hind and Saunders 2013, Hind et al. 2014), and we expect many more changes in coralline algal phylogeny as more groups are sequenced in the near future.

Long-term studies can reveal markedly different results than shorter term studies. For example, laboratory cultures of *L. glaciale* maintained growth rates while decreasing skeletal quality (intra- and intercellular wall thicknesses) after exposure to acidification for 3 months (Ragazzola et al. 2012). After exposure to acidification for 10 months, the opposite result was observed; *L. glaciale* cultures preserved skeletal quality and reduced growth rates (Ragazzola et al. 2013). This is a classic example of energetic trade-offs, where plants alter their resource allocation patterns differently to cope with short-term compared to long-term stressors (Grime 1979). More generally, documented effects of coralline algal bleaching, tissue necrosis, and reduced thallus thickness include weakened structural integrity (Ragazzola et al. 2012) that may lead to increased susceptibility of coralline algal beds to physical disturbances (Martone et al. 2010a, Egilisdottir et al. 2013, McCoy 2013).

The importance of conducting experiments in an ecological context is becoming increasingly apparent (Fisher and Martone 2014, McCoy and Pfister 2014). Recent measurements of net primary productivity of a pH gradient of 7.9–8.1 along the Oregon (USA) coast showed a reduction in coralline (*Corallina vancouveriensis*) productivity with lower pH, but a neutral effect of reduced pH on productivity of a coralline-kelp assemblage (*C. vancouveriensis* and *Saccharina sessilis*; Tait 2014). Previous work with whole-lake acidification experiments has taught us that interactions between an entire species assemblage, as well as between biological and geochemical processes, cannot be simulated in a laboratory study (Schindler 1990). Yet, they play crucial roles in ecological responses to perturbations. It is important that future ecological work exploring effects of OA, temperature, and other stressors on coralline algae take into account the natural context of those responses.

PALEOENVIRONMENTAL RECORDERS

Paleoecological proxies. Paleocological studies in shallow marine environments focus on the reconstruction of ecological communities or coastal environmental characteristics, typically by identifying species with known environmental tolerances or ecological functions in fossil assemblages or sediment cores (Adey and Steneck 2001, Perry and Hepburn 2008). In this context, coralline algae are typically used in the reconstruction of tropical CO_3^{2-} environments. Combined with sediment analyses, the development of coastal reefs or shallow marine communities (e.g., Macintyre and Glynn 1976, Martindale 1992, Webster and Davies 2003, Payri and Cabioch 2004, Tierney and Johnson 2012) and community recovery from disturbance events (e.g., Perry 2001, Toth et al. 2012) can also be studied over time. From a more geological perspective, such reconstructions can also provide climatic context in which sediments were laid down (Braga and Aguirre 2001). Species' depth distributions, for example, can be used to reconstruct changes in sea level or reef accretion at a given locality (e.g., Cabioch et al. 1999, Yamano et al. 2001). Coralline algal ridges (also termed bioherms or mounds) provide a particularly accurate estimate of sea level, as they are restricted to the wave crest zone, and can track sea level within 10 cm (Adey 1986).

Ultrastructure and growth banding. The ultrastructural and mineralogical responses of coralline algae to ambient environmental conditions enable them to act as paleoenvironmental proxies, with the longest temperature reconstruction extending over 650 years (Kamenos 2010). While growing, rhodoliths and CCA of indeterminate thickness lay down annual and subannual growth bands composed of high-Mg calcite (Fig. 3; Henrich et al. 1996, Kamenos et al. 2008b). In some species, growth bands are annual (*L. glaciale*, Kamenos et al. 2008b and

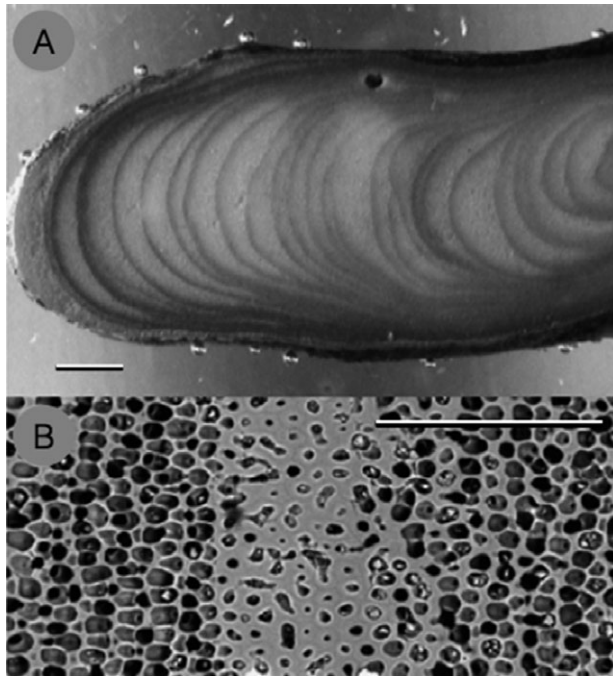


FIG. 3. (A) Transverse section through *Lithothamnion glaciale* branch tip showing seasonal banding patterns (scale bar = 500 μm). (B) SEM micrograph showing cell structure of growth banding (scale bar = 100 μm). Cells with lower calcite density (%) deposited at warmer temperatures (left and right sides of B), created seasonal banding structure observed at lower magnification in A. Modified from Kamenos et al. 2008b.

Clathromorphum compactum, Halfar et al. 2008) while in other species, for example, *Phymatolithon calcareum*, subannual banding is present (Blake and Maggs 2003). Information on past climatic regimes can be locked within such growth bands either as structural or geochemical information.

Algochronology is the use of structural metrics obtained from the growth bands of coralline algae to determine past environmental conditions (Kamenos and Law 2010). Rhodoliths lay down regular annual, and or subannual, growth bands. The frequency of the bands has been reviewed by in depth by Foster (2001). Many encrusting species do not show growth banding, likely because of high grazing pressure and a set vertical thickness in those forms. Similarly, geniculate species do not form growth bands, because they grow primarily by forming new apical segments. In rhodoliths, bands can be formed due to reduced light availability and lower temperature during winter, reduced water movement, burial, monthly/lunar growth cycles driven by tidal patterns and possible large scale climate patterns, for example, El Niño (Foster 2001). The banding patterns are created by changes in the degree of cellular calcification (Fig. 3); in *L. glaciale* a negative correlation exists between calcite density of calcified cells and temperature (Kamenos 2010) as well as temperature and light availability (Burdett et al. 2011). Growth banding patterns can therefore be

used to infer environmental processes in historical climate reconstructions.

While the width of the bands themselves do not appear to be well correlated to environmental conditions in *L. glaciale* (Kamenos and Law 2010, Burdett et al. 2011), by averaging the growth bands of multiple *Clathromorphum compactum* or *Clathromorphum nereostratum* thalli, this generated positive relationships with instrumental sea surface temperature (SST), enabling reconstruction of SST (Halfar et al. 2010, 2011). Significantly stronger relationships are present between calcite density and environmental conditions with negative relationships being present between temperature and calcite density in *L. glaciale* (Kamenos and Law 2010) as well as temperature and light (as PAR), enabling the reconstruction of both temperature and cloud cover (Burdett et al. 2011). Ultrastructural comparisons with a single environmental parameter can be characterized by noticeable variability (possibly caused by localized irradiance differences) but, by conducting calibrations using both temperature and light, that variability can be minimized (Burdett et al. 2011).

Geochemistry. The CaCO_3 skeleton of coralline algae contains multiple elements and their isotopes whose concentrations have been used in paleoenvironmental reconstruction. First insights into their geochemical elemental responses were made in the 1960s (Chave and Wheeler 1965, Moberly 1968). More recently, both elemental and isotopic deviations within their skeletons have been used as paleoclimate proxies.

Diagenetic effects and proxy development. Coralline algae are protected by the presence of a living epithallium covering the CO_3^{2-} skeleton often minimizing diagenetic effects (Alexandersson 1974). There is no evidence of unquantified vital effects, or altering of the chemical composition by the algae, in Mg/Ca temperature relationships (Kamenos et al. 2008b). Carbon and oxygen isotope ratios can be affected by the calcification process in many calcareous algae (Codiaceae, Daycladaceae, Corallinales) caused by kinetic fractionation associated with CO_2 hydroxylation during calcification (Lee and Carpenter 2001). Some studies find an offset from isotopic equilibrium ($\sim 3.5\text{‰}$; e.g., Halfar et al. 2000, Lee and Carpenter 2001, Williams et al. 2011) while in other in other studies, no evidence of isotope disequilibrium is observed (Rahimpour-Bonab et al. 1997). The calcification and fractionation process may therefore be somewhat variable within the Corallinales or perhaps from one locality to another, and therefore calibration or validation is recommended.

Before using coralline algae as proxies for new variables, it is important that a three-step process is followed to ensure the accuracy and precision of the reconstruction (Kamenos et al. 2009): (i) Calibration of a particular species to see if a relationship between the environmental variable and

within-algal proxy is present; (ii) validation of the relationship using biogeochemical analyses (e.g., molecular level characterization via synchrotron) to determine if the observed response meets the geochemical assumptions on which the proxy has been developed (e.g., Ca^{2+} substitution by Mg^{2+} ions in the calcite lattice at higher temperatures (Oomori et al. 1987, Kamenos et al. 2009); and (iii) application of that species as a calibrated and validated proxy.

Magnesium (Mg). Mg concentrations in biogenic CaCO_3 have a positive relationship with temperature and are the most commonly used proxy. Mg concentrations, as Mg/Ca or MgCO_3 , have been calibrated and validated as in situ temperature proxies in nongeniculate coralline algae (Kamenos et al. 2008b, 2009) and have been used to reconstruct marine temperature from fortnightly to decadal resolution (Fig. 4). In the northern hemisphere, these species are *L. glaciale* (Halfar et al. 2000, Kamenos et al. 2008b, Kamenos 2010, Kamenos et al. 2012), *Lithophyllum kotschyianum* (Caragnano et al. 2014), *Lithothamnion crassiusculum* (Halfar et al. 2000), *Phymatolithon calcareum* (Kamenos et al. 2008b), *Clathromorphum nereostratum* (Hetzinger et al. 2009, 2012, Williams et al. 2011), and *Clathromorphum compactum* (Gamboa et al. 2010, Hetzinger et al. 2012); in the Southern Hemisphere *Sporolithon durum* (Darrenougue et al. 2013).

Trace elements: Barium (Ba), Lithium (Li), Strontium (Sr), Uranium (U). Ba/Ca in nongeniculate coralline algae have been used to reconstruct seas surface salinity in Atlantic Canadian *Clathromorphum compactum* (Hetzinger et al. 2013), in Alaskan *Clathromorphum nereostratum* (Chan et al. 2011) and in Yemeni *Lithophyllum kotschyianum* from nutrient rich upwellings (Caragnano et al. 2014) at subannual resolutions, but all studies found no relationship with temperature. Li/Ca in Yemeni *Lithophyllum kotschy-*

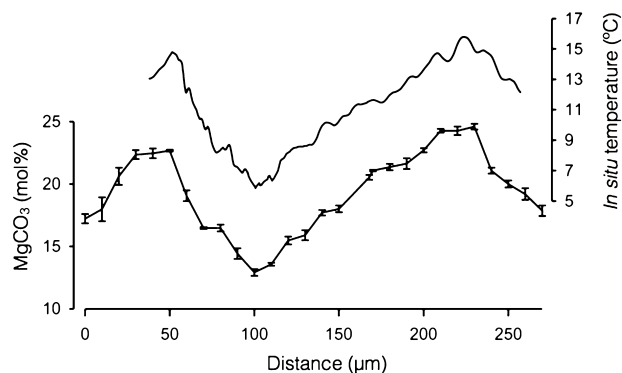


FIG. 4. Mean $\text{MgCO}_3 \pm \text{SD}$ in mol % shown by solid black line with error bars. Measurements made along transverse section (from apex to base of branch) of *Lithothamnion glaciale* by electron microprobe analysis. Solid black line with no error bars shows in situ temperature at time of skeletal deposition. Reproduced from Kamenos et al. 2008b.

num at subannual resolution has been used to reconstruct temperature (Caragnano et al. 2013).

While attempts have been made to use Sr concentrations for temperature reconstruction, they appear to be strongly influenced by vital effects or kinetic incorporation of Sr ions into the calcite lattice of *Sporolithon durum* (Darrenougue et al. 2013), *L. glaciale*, *Phymatolithon calcareum* (Kamenos et al. 2008b), and also *Clathromorphum compactum* (Hetzinger et al. 2011). Incorporation of U in *Clathromorphum compactum* was not found to be influenced by temperature (Hetzinger et al. 2011).

Isotopes. In nongeniculate coralline algae, the stable isotopic ratio of oxygen (reflecting incorporation of ^{16}O vs. ^{18}O), $\delta^{18}\text{O}$, records both temperature and salinity (Halfar et al. 2000, Kamenos et al. 2012). $\delta^{18}\text{O}$ has been used to reconstruct temperature using *L. glaciale* (Halfar et al. 2000, 2007), *Lithothamnion crassiusculum* (Halfar et al. 2000), and by subtraction of the temperature component of the signal, salinity in *L. glaciale* (Kamenos et al. 2012).

Changes in the stable isotopic ratio of carbon (incorporation of ^{12}C vs. ^{13}C), $\delta^{13}\text{C}$, have been used to reconstruct DIC concentrations in *Clathromorphum compactum* (Williams et al. 2011), and ^{14}C concentrations have been used to determine long-term growth rates of *Clathromorphum nereostratum* (Frantz et al. 2005) and to date the exact timing of climatic events recorded by *Lithothamnion crassiusculum* (Frantz et al. 2000) and *L. glaciale* (Kamenos 2010).

Associated variables, patterns, and ecosystem changes. Reconstruction of individual climatic parameters has also been used to understand changes in larger climatic phenomena. These include cloud cover via changes in cell size (Burdett et al. 2011), runoff from the Greenland Ice Sheet via changes in Mg/Ca and $\delta^{18}\text{O}$ (Kamenos et al. 2012), Aleutian Low Pressure index via changes in band width (Halfar et al. 2011), North Atlantic Oscillation index via changes in Mg/Ca (Hetzinger et al. 2012), Atlantic Multidecadal Oscillation index via changes in Mg/Ca (Kamenos 2010), and Decadal Sea Level pressure via changes in Mg/Ca (Hetzinger et al. 2012).

Environmental reconstructions from nongeniculate coralline algae have proved useful in understanding how past changes in marine productivity relate to historic environmental change. In the north Atlantic, Mg/Ca temperature reconstructions from *L. glaciale* were negatively related to abundances of the copepod *Calanus finmarchicus* allowing a projection of copepod abundance to 2040 (Kamenos 2010). In the Bering Sea, growth increments in *Clathromorphum compactum* were used to understand landings in Sockeye Salmon via reconstruction on the Aleutian Low climate pattern (Halfar et al. 2011). The novel use of coralline algal proxies combined with ecological metrics in these studies indicates the potential of coralline algae for understanding the past and future drivers of marine productivity in addition to environmental change.

Looking ahead. Research on coralline algae, particularly in the context of global climate change, has recently expanded among physiologists, ecologists, and geologists. In this review, we have summarized what is known in these areas in an effort to increase the accessibility of previous work on coralline algae for interdisciplinary researchers. In doing so, we have identified the following areas of need:

1. Molecular studies of algal calcification;
2. Resolution of the monophyly of genera and their phylogenetic relationships;
3. Potential generalization of physiological parameters to morphological or phylogenetic groups;
4. The role of multiple stressors on physiology, with an emphasis on integrating studies of pollutants;
5. Increased long-term studies focusing on acclimatization potential to OA, temperature, and UV;
6. The mechanics and long-term repercussions of coralline algal bleaching;
7. Effects of species-level stress responses on local communities;
8. Community-scale responses and field experiments;
9. Impacts of climate change on chemical cues;
10. Importance of coralline algae to reef stabilization under “future” scenarios; and
11. Refinement of coralline algae as paleorecorders with focus on the development of new proxies.

Coralline algae are a unique group of organisms in the context of global climate change. As photosynthesizers, calcifiers, ecologically important species, and paleoclimate archives, they enable us to ask diverse questions across the fields of phycology, physiology, ecology, geology, and conservation that will promote and require interdisciplinary cooperation.

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Adey, W. H. 1965. The genus *Clathromorphum* in the Gulf of Maine. *Hydrobiologia* 24:377–420.
 Adey, W. H. 1970. The crustose corallines of the northwestern North Atlantic including *Lithothamnion lemoineae* n. sp. *J. Phycol.* 6:225–9.
 Adey, W. H. 1978. Algal ridges of the Caribbean Sea and West Indies. *Phycologia* 17:361–7.
 Adey, W. H. 1986. Coralline algae as indicators of sea-level. In van de Plassche, O. [Ed.] *Sea-Level Research: A Manual for the*

Collection and Evaluation of Data. Geo Books, Norwich, pp. 229–80.
 Adey, W. H. 1998. Coral reefs: algal structured and mediated ecosystems in shallow, turbulent, and alkaline waters. *J. Phycol.* 34:393–406.
 Adey, W. H., Halfar, J. & Williams, B. 2013. The coralline genus *Clathromorphum* Foslíe emend. Adey: biological, physiological, and ecological factors controlling carbonate production in an Arctic-Subarctic climate archive. *Smithsonian Contr. Mar. Sci.* 40:1–41.
 Adey, W. H. & Hayek, L. A. C. 2011. Elucidating marine biogeography with macrophytes: quantitative analysis of the north Atlantic supports the thermogeographic model and demonstrates a distinct subarctic region in the northwest Atlantic. *Northeast. Nat.* 18:1–128.
 Adey, W. H. & Macintyre, I. G. 1973. Crustose coralline algae: a re-evaluation in the geological sciences. *GSA Bull.* 84:883–904.
 Adey, W. H. & McKibbin, D. 1970. Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnium coralloides* Crouan in the Ria de Vigo. *Bot. Mar.* 8:100–6.
 Adey, W. H. & Steneck, R. S. 2001. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *J. Phycol.* 37:677–98.
 Adey, W. H. & Vassar, M. J. 1975. Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14:55–69.
 Aguirre, J., Baceta, J. I. & Braga, J. C. 2007. Recovery of primary producers after the Cretaceous-Tertiary mass extinction: Paleocene calcareous red algae from the Iberian Peninsula. *Palaeogeogr. Palaeoclimatol.* 249:393–411.
 Aguirre, J., Riding, R. & Braga, J. C. 2000. Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. *Paleobiology* 26:651–67.
 Alexandersson, T. 1974. Carbonate cementation in coralline algal nodules in the Skagerrak, North Sea: biochemical precipitation in undersaturated waters. *J. Sediment. Petrol.* 44:7–26.
 Amado-Filho, G. M., Moura, R. L., Bastos, A. C., Salgado, L. T., Sumida, P. Y., Guth, A. Z., Francini-Filho, R. B. et al. 2012. Rhodolith beds are major CaCO₃ bio-factories in the tropical South West Atlantic. *PLoS ONE* 7:e35171.
 Andras, T. D., Alexander, T. S., Gahlen, A., Parry, R. M., Fernandez, F. M., Kubanek, J., Wang, M. D. & Hay, M. E. 2012. Seaweed allelopathy against coral: surface distribution of a seaweed secondary metabolite by imaging mass spectrometry. *J. Chem. Ecol.* 38:1203–14.
 Anthony, K. R. N., Kleypas, J. A. & Gattuso, J. P. 2011. Coral reefs modify their seawater carbon chemistry— implications for impacts of ocean acidification. *Glob. Change Biol.* 17:3655–66.
 Baas-Becking, L. G. M. & Galliher, E. W. 1931. Wall structure and mineralization in coralline algae. *J. Phys. Chem.* 35:1–13.
 Bailey, J. C. & Chapman, R. L. 1998. A phylogenetic study of the Corallinales (Rhodophyta) based on nuclear small-subunit rRNA gene sequences. *J. Phycol.* 34:692–705.
 Bak, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Neth. J. Sea Res.* 10:285–337.
 Basso, D. 1998. Deep rhodolith distribution in the Pontian Islands, Italy: a model for the paleoecology of a temperate sea. *Palaeogeogr. Palaeoclimatol.* 137:173–87.
 Basso, D. 2011. Carbonate production by calcareous red algae and global change. *Geodiversitas* 34:13–33.
 Bell, P. R. F. 1990. Status of eutrophication in the Great Barrier Reef lagoon. *Mar. Pollut. Bull.* 23:89–93.
 Belliveau, S. A. & Paul, V. J. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Mar. Ecol. Prog. Ser.* 232:105–14.
 Bilan, M. I. & Usov, A. I. 2001. Polysaccharides of calcareous algae and their effect on the calcification process. *Russ. J. Bioorg. Chem.* 27:2–16.

- Bittner, L., Payri, C. E., Maneveldt, G. W., Couloux, A., Cruaud, C., de Reviens, B. & Le Gall, L. 2011. Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochondrial genomes. *Mol. Phylogenet. Evol.* 61:697–713.
- Björk, M., Mohammed, S. M., Björklund, M. & Semesi, A. 1995. Coralline algae, important coral-reef builders threatened by pollution. *Ambio* 24:502–5.
- Blake, C. & Maggs, C. A. 2003. Comparative growth rates and internal banding periodicity of maerl species (Corallinales, Rhodophyta) from northern Europe. *Phycologia* 42:606–12.
- Bóas, A. B. V. & Figueiredo, M. A. de. O. 2004. Are anti-fouling effects in coralline algae species specific? *Braz. J. Oceanogr.* 52:11–8.
- Borowitzka, M. A. 1979. Calcium exchange and the measurement of calcification rates in the calcareous coralline red alga *Amphiroa foliacea*. *Mar. Biol.* 50:339–47.
- Borowitzka, M. A. 1981. Photosynthesis and calcification in the articulated coralline red algae *Amphiroa anceps* and *A. foliacea*. *Mar. Biol.* 62:17–23.
- Borowitzka, M. A. 1982. Mechanisms in algal calcification. In Round, F. E. & Chapman, D. J. [Eds.] *Progress in Phycological Research*, Vol. I. Elsevier Biomedical Press, New York, Amsterdam, London, pp. 137–77.
- Borowitzka, M. A. & Larkum, A. W. D. 1976. Calcification in the green alga *Halimeda*. III. The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanism of calcification. *J. Exp. Bot.* 27:879–93.
- Borowitzka, M. A. & Vesik, M. 1978. Ultrastructure of the Corallinales. I. The vegetative cells of *Corallina officinalis* and *C. cuvierii*. *Mar. Biol.* 46:295–304.
- Bosence, D. W. J. 1980. Sedimentary facies, production rates and facies models for recent coralline algal gravels. *Geol. J.* 15:91–111.
- Bosence, D. W. J. 1983. Coralline algal reef frameworks. *J. Geol. Soc. London* 140:365–76.
- Braga, J. C. & Aguirre, J. 2001. Coralline algal assemblages in upper Neogene reef and temperate carbonates in Southern Spain. *Palaeogeogr. Palaeoclimatol.* 175:27–41.
- Breitburg, D. L. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology* 65:1136–43.
- Brodie, J., Williamson, C. J., Smale, D. A., Kamenos, N. A., Mieszowska, N., Santos, R., Cunliffe, M. et al. 2014. The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecol. Evol.* 4:2787–98.
- Broom, J. E. S., Hart, D. R., Farr, T. J., Nelson, W. A., Neill, K. F., Harvey, A. S. & Woelkerling, W. J. 2008. Utility of *psbA* and *nSSU* for phylogenetic reconstruction in the Corallinales based on New Zealand taxa. *Mol. Phylogenet. Evol.* 46:958–73.
- Büdenbender, J., Riebesell, U. & Form, A. 2011. Calcification of the Arctic coralline red algae *Lithothamnion glaciale* in response to elevated CO₂. *Mar. Ecol. Prog. Ser.* 441:79–87.
- Burdett, H. L., Aloisio, E., Calosi, P., Findlay, H. S., Widdicombe, S., Hatton, A. D. & Kamenos, N. A. 2012a. The effect of chronic and acute low pH on the intracellular DMSP production and epithelial cell morphology of red coralline algae. *Mar. Biol. Res.* 8:756–63.
- Burdett, H. L., Donohue, P. J. C., Hatton, A. D., Alwany, M. A. & Kamenos, N. A. 2013. Spatiotemporal variability of dimethylsulphoniopropionate on a fringing coral reef: the role of reefal carbonate chemistry and environmental variability. *PLoS ONE* 8:e64651.
- Burdett, H. L., Hennige, S. J., Francis, F. T. Y. & Kamenos, N. A. 2012b. The photosynthetic characteristics of red coralline algae, determined using pulse amplitude modulation (PAM) fluorometry. *Bot. Mar.* 55:499–509.
- Burdett, H. L., Kamenos, N. A. & Law, A. 2011. Using coralline algae to understand historic marine cloud cover. *Palaeogeogr. Palaeoclimatol.* 302:65–70.
- Burdett, H. L., Keddie, V., MacArthur, N., McDowall, L., McLeish, J., Spielvogel, E., Hatton, A. D. & Kamenos, N. A. 2014. Dynamic photoinhibition exhibited by red coralline algae in the Red Sea. *BMC Plant Biol.* 14:139.
- Cabioch, G. M., Montaggioni, L. F., Faure, G. & Ribaud-Leurenti, A. 1999. Reef coral-algal assemblages as recorders of paleobathymetry and sea level changes in the Indo-Pacific province. *Quaternary Sci. Rev.* 18:1681–95.
- Caragnano, A., Basso, D., Jacob, D. E., Storz, D., Rodondi, G., Benzoni, F. & Detrioux, E. 2014. The coralline red alga *Lithophyllum kotschyianum* f. *affine* as proxy of climate variability in the Yemen coast, Gulf of Aden (NW Indian Ocean). *Geochim. Cosmochim. Acta* 124:1–17.
- Chan, P., Halfar, J., Williams, B., Hetzinger, S., Steneck, R., Zack, T. & Jacob, D. E. 2011. Freshening of the Alaska Coastal Current recorded by coralline algal Ba/Ca ratios. *J. Geophys. Res. Biogeosciences* 116:G01032.
- Chave, K. E. & Wheeler, B. D. Jr 1965. Mineralogic changes during growth in the red alga, *Clathromorphum compactum*. *Science* 147:621.
- Chenelot, H., Jewett, S. C. & Hoberg, M. K. 2011. Macrobenthos of the nearshore Aleutian Archipelago, with emphasis on invertebrates associated with *Clathromorphum nereostratum* (Rhodophyta, Corallinales). *Mar. Biodiv.* 41:413–24.
- Chisholm, J. R. M. 2000. Calcification by crustose coralline algae on the Northern Great Barrier Reef, Australia. *Limnol. Oceanogr.* 45:1476–84.
- Chisholm, J. R. M. 2003. Primary productivity of reef-building crustose coralline algae. *Limnol. Oceanogr.* 48:1376–87.
- Comeau, S., Carpenter, R. C., Nojiri, Y., Putnam, H. M., Sakai, K. & Edmunds, P. J. 2014. Pacific-wide contrast highlights resistance of reef calcifiers to ocean acidification. *Proc. Roy. Soc. B* 281:20141339.
- Connell, S. D. 2003. The monopolization of understory habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Mar. Biol.* 142:1065–71.
- Cornwall, C. E., Hepburn, C. D., McGraw, C. M., Currie, K. I., Pilditch, C. A., Hunter, K. A., Boyd, P. W. & Hurd, C. L. 2013a. Diurnal fluctuations in seawater pH influence the response of a calcifying macroalga to ocean acidification. *Proc. Roy. Soc. B* 280:1409–15.
- Cornwall, C. E., Hepburn, C. D., Pilditch, C. A. & Hurd, C. L. 2013b. Concentration boundary layers around complex assemblages of macroalgae: implications for the effects of ocean acidification on understory coralline algae. *Limnol. Oceanogr.* 58:121–30.
- Darrenougue, N., De Deckker, P., Payri, C., Eggins, S. & Fallon, S. 2013. Growth and chronology of the rhodolith-forming, coralline red alga *Sporolithon durum*. *Mar. Ecol. Prog. Ser.* 474:105–19.
- Daume, S., Brand-Gardner, S. & Woelkerling, W. J. 1999. Settlement of abalone larvae (*Haliotis laevigata* Donovan) in response to non-geniculate coralline red algae (Corallinales, Rhodophyta). *J. Exp. Mar. Biol. Ecol.* 234:125–43.
- Delille, B., Borges, A. V. & Delille, D. 2009. Influence of giant kelp beds (*Macrocystis pyrifera*) on diel cycles of pCO₂ and DIC in the Sub-Antarctic coastal area. *Est. Coast. Shelf Sci.* 81:114–22.
- Dethier, M. N. 1994. The ecology of intertidal algal crusts: variation within a functional group. *J. Exp. Mar. Biol. Ecol.* 177:37–71.
- Dethier, M. N. & Steneck, R. S. 2001. Growth and persistence of diverse intertidal crusts: survival of the slow in a fast-paced world. *Mar. Ecol. Prog. Ser.* 223:89–100.
- Digby, P. S. B. 1977. Photosynthesis and respiration in the coralline algae, *Clathromorphum circumscriptum* and *Corallina officinalis* and the metabolic basis of calcification. *J. Mar. Biol. Ass. U.K.* 57:1111–24.
- Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O. & Mumby, P. J. 2012. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecol. Lett.* 15:338–46.
- Egilsdottir, H., Noisette, F., Noël, L. M. L. J., Olafsson, J. & Martin, S. 2013. Effects of pCO₂ on physiology and skeletal

- mineralogy in a tidal pool coralline alga *Corallina elongata*. *Mar. Biol.* 160:2103–12.
- El Haïkali, B., Bensoussan, N., Romano, J. C. & Bousquet, V. 2004. Estimation of photosynthesis and calcification rates of *Corallina elongata* Ellis and Solander, 1786, by measurements of dissolved oxygen, pH and total alkalinity. *Sci. Mar.* 68:45–56.
- Faulkner, D. J. 1984. Marine natural products: metabolites of marine algae and herbivorous marine mollusks. *Nat. Prod. Rep.* 1:251–80.
- Figueiredo, M. A. de O., Kain Jones, J. M. & Norton, T. A. 1996. Biotic interactions in the colonization of crustose coralline algae by epiphytes. *J. Exp. Mar. Biol. Ecol.* 199:303–18.
- Figueiredo, M. A. de O., Kain Jones, J. M. & Norton, T. A. 2000. Responses of crustose corallines to epiphyte and canopy cover. *J. Phycol.* 36:17–24.
- Figueiredo, M. A. de O., Norton, T. A. & Kain Jones, J. M. 1997. Settlement and survival of epiphytes on two intertidal crustose coralline algae. *J. Exp. Mar. Biol. Ecol.* 213:247–60.
- Fine, M. & Tchernov, D. 2007. Scleractinian coral species survive and recover from decalcification. *Science* 315:1811.
- Fisher, K. & Martone, P. T. 2014. Field study of growth and calcification rates of three species of articulated coralline algae in British Columbia. *Canada. Biol. Bull.* 226:121–30.
- Foster, M. S. 2001. Rhodoliths: between rocks and soft places. *J. Phycol.* 37:659–67.
- Foster, M. S., Amado Filho, G. M., Kamenos, N. A., Risomena-Rodríguez, R. & Steller, D. L. 2013. Rhodoliths and rhodolith beds. *Smithsonian Contr. Mar. Sci.* 39:143–55.
- Frantz, B. R., Foster, M. S. & Risomena-Rodríguez, R. 2005. *Clathromorphum nereostratum* (Corallinales, Rhodophyta): the oldest alga? *J. Phycol.* 41:770–3.
- Frantz, B. R., Kashgarian, M., Coale, K. H. & Foster, M. S. 2000. Growth rate and potential climate record from a rhodolith using ¹⁴C accelerator mass spectrometry. *Limnol. Oceanogr.* 45:1773–7.
- Freiwald, A. & Henrich, R. 1994. Reefal coralline algal build-ups within the Arctic circle: morphology and sedimentary dynamics under extreme environmental seasonality. *Sedimentology* 41:963–84.
- Gabrielson, P. W., Miller, K. A. & Martone, P. T. 2011. Morphometric and molecular analyses confirm two distinct species of *Calliarthron* (Corallinales, Rhodophyta), a genus endemic to the northeast Pacific. *Phycologia* 56:298–316.
- Gamboa, G., Halfar, J., Hetzinger, S., Adey, W., Zack, T., Kunz, B. & Jacob, D. E. 2010. Mg/Ca ratios in coralline algae record northwest Atlantic temperature variations and North Atlantic Oscillation relationships. *J. Geophys. Res.* 115:C12044.
- Gao, K., Aruga, Y., Asada, K., Ishihara, T., Akano, T. & Kiyohara, M. 1993. Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to the effect of elevated CO₂ concentration. *Mar. Biol.* 117:129–32.
- Gao, K. & Zheng, Y. 2010. Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). *Glob. Change Biol.* 16:2388–98.
- Gherardi, D. F. M. & Bosence, D. W. J. 1999. Modeling of the ecological succession of encrusting organisms in recent coralline-algal frameworks from Atol das Rocas, Brazil. *Palaio* 14:145–58.
- Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK, 222 pp.
- Guenther, R. J. & Martone, P. T. 2014. Physiological performance of intertidal coralline algae during a simulated tidal cycle. *J. Phycol.* 50:310–21.
- Guiry, M. D. & Guiry, G. M. 2014. *AlgaeBase*. Available at: <http://www.algaebase.org> (last accessed June 19, 2014).
- Halfar, J., Hetzinger, S., Adey, W., Zack, T., Gamboa, G., Kunz, B., Williams, B. & Jacob, D. E. 2010. Coralline algal growth-increment widths archive North Atlantic climate variability. *Paleogeogr. Palaeoclimatol.* 302:71–80.
- Halfar, J., Steneck, R. S., Joachimski, M., Kronz, A. & Wanamaker, A. D. Jr 2008. Coralline red algae as high-resolution climate recorders. *Geology* 36:463–6.
- Halfar, J., Steneck, R. S., Schöne, B., Moore, G. W. K., Joachimski, M., Kronz, A., Fietzke, J. & Estes, J. 2007. Coralline algae reveals first marine record of subarctic North Pacific climate change. *Geophys. Res. Lett.* 34:L07702.
- Halfar, J., Williams, B., Hetzinger, S., Steneck, R. S., Lebednik, P., Winsborough, C., Omar, A., Chan, P. & Wanamaker, A. 2011. 225 Years of Bering Sea climate and ecosystem dynamics revealed by coralline algal growth-increment widths. *Geology* 39:579–82.
- Halfar, J., Zack, T., Kronz, A. & Zachos, J. C. 2000. Growth and high-resolution paleoenvironmental signals of rhodoliths (coralline red algae): a new biogenic archive. *J. Geophys. Res.* 105:22107–16.
- Hamilton, D. & Haydon, G. 1996. *Pesticides and Fertilisers in the Queensland Sugar Industry – Estimates of Usage and Likely Environmental Fate*. Department of Primary Industries, Queensland, Australia.
- Harrington, L., Fabricius, K., Eaglesham, G. & Negri, A. 2005. Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. *Mar. Poll. Bull.* 51:415–27.
- Hay, M. E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* 16:S67–76.
- Hay, M. E. 2009. Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. *Annu. Rev. Mar. Sci.* 1:193–212.
- Henrich, R., Reiwal, A., Wehrmann, A., Schafer, P., Samtleben, C. & Zankl, H. 1996. Nordic cold-water carbonates: occurrence and controls. In Reitner, J., Neuweiler, F. & Gunkel, F. [Eds.] *Global and Regional Controls on Biogenic Sedimentation*. Göttinger Arbeiten Geol. Palaeontol., Göttingen, pp. 35–53.
- Hetzinger, S., Halfar, J., Kronz, A., Steneck, R. S., Adey, W. H., Lebednik, P. A. & Schöne, B. R. 2009. High-resolution Mg/Ca ratios in a coralline red alga as a proxy for Bering Sea temperature variations from 1902 to 1967. *Palaio* 24:406–12.
- Hetzinger, S., Halfar, J., Zack, T., Gamboa, G., Jacob, D. E., Kunz, B. E., Kronz, A., Adey, W., Lebednik, P. A. & Steneck, R. S. 2011. High-resolution analysis of trace elements in crustose coralline algae from the North Atlantic and North Pacific by laser ablation ICP-MS. *Palaeoogeogr., Palaeoclimatol., Palaeoecol.* 203:81–94.
- Hetzinger, S., Halfar, J., Mecking, J. V., Keenlyside, N. S., Kronz, A., Steneck, R. S., Adey, W. H. & Lebednik, P. A. 2012. Marine proxy evidence linking decadal North Pacific and Atlantic climate. *Clim. Dynam.* 39:1447–55.
- Hetzinger, S., Halfar, J., Zack, T., Mecking, B. E., Jacob, D. E. & Adey, W. H. 2013. Coralline algal barium as indicator for 20th century northwestern North Atlantic surface ocean freshwater variability. *Sci. Rep.* 3:1761.
- Hind, K. R., Gabrielson, P. W., Lindstrom, S. C. & Martone, P. T. 2014. Misleading morphologies and the importance of sequencing type specimens for resolving coralline taxonomy (Corallinales, Rhodophyta): *Pachyarthron cretaceum* is *Corallina officinalis*. *J. Phycol.* 50:760–4.
- Hind, K. R. & Saunders, G. W. 2013. A molecular phylogenetic study of the tribe Corallineae (Corallinales, Rhodophyta) with an assessment of genus-level taxonomic features and descriptions of novel genera. *J. Phycol.* 49:103–14.
- Hinojosa-Arango, G., Rioja-Nieto, R., Suárez-Castillo, Á. N. & Risomena-Rodríguez, R. 2014. Using GIS methods to evaluate rhodolith and *Sargassum* beds as critical habitats for commercially important marine species in Bahía Concepción, B.C.S., México. *Cryptogamie, Algologie* 35:49–65.
- Hofmann, L. C., Straub, S. & Bischof, K. 2012. Competition between calcifying and noncalcifying temperate marine macroalgae under elevated CO₂ levels. *Mar. Ecol. Prog. Ser.* 464:89–105.
- Huggett, M. J., Williamson, J. E., de Nys, R., Kjelleberg, S. & Steinberg, P. D. 2006. Larval settlement of the common Australian sea urchin *Heliocidaris erythrogramma* in response to bacteria from the surface of coralline algae. *Oecologia* 149:604–19.

- Hurd, C. L., Cornwall, C. E., Currie, K., Hepburn, C. D., McGraw, C. M., Hunter, K. A. & Boyd, P. W. 2011. Metabolically induced pH fluctuations by some coastal calcifiers exceed projected 22nd Century ocean acidification: a mechanism for differential susceptibility? *Glob. Change Biol.* 17:3254–62.
- Ikemori, M. 1970. Relation of calcium uptake to photosynthetic activity as a factor controlling calcification in marine algae. *Bot. Mag. Tokyo* 83:152–62.
- Irving, A. D., Connell, S. D. & Elsdon, T. S. 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *J. Exp. Mar. Biol. Ecol.* 310:1–12.
- Irving, A. D., Connell, S. D., Johnston, E. L., Pile, A. J. & Gillanders, B. M. 2005. The response of encrusting coralline algae to canopy loss: an independent test of predictions on an Antarctic coast. *Mar. Biol.* 147:1075–83.
- Jackson, C. M., Kamenos, N. A., Moore, P. G. & Young, M. 2003. Meiofaunal bivalves in maerl and other substrata; their diversity and community structure. *Ophelia* 58:49–60.
- Johansen, H. W. 1981. *Coralline Algae, a First Synthesis*, 1st edn. CRC Press, Boca Raton, Florida, 239 pp.
- Johnson, C. R. & Mann, K. H. 1986. The crustose coralline alga, *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *J. Exp. Mar. Biol. Ecol.* 96:127–46.
- Johnson, M. D., Moriarty, V. W. & Carpenter, R. C. 2014. Acclimatization of the crustose coralline alga *Porolithon onkodes* to variable pCO₂. *PLoS ONE* 9:e87678.
- Johnson, C. R., Muir, D. G. & Reysenbach, A. L. 1991. Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* 74:281–94.
- Johnson, C. R. & Sutton, D. C. 1994. Bacteria on the surface of crustose coralline algae induce metamorphosis of the crown-of-thorns starfish *Acanthaster planci*. *Mar. Biol.* 120:305–10.
- Jokiel, P. L., Rodgers, K. S., Kuffner, I. B., Andersson, A. J., Cox, E. F. & Mackenzie, F. T. 2008. Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27:473–83.
- Kamenos, N. A. 2010. North Atlantic summers have warmed more than winters since 1353, and the response of marine zooplankton. *Proc. Natl. Acad. Sci. USA* 107:22442–7.
- Kamenos, N. A., Burdett, H. L., Alioso, E., Findlay, H. S., Martin, S., Longbone, C., Dunn, J., Widdicombe, S. & Calosi, P. 2013. Coralline algal structure is more sensitive to rate, rather than magnitude, of ocean acidification. *Glob. Change Biol.* 19:3621–8.
- Kamenos, N. A., Cusack, M., Huthwelker, T., Lagarde, P. & Scheibling, R. E. 2009. Mg-lattice associations in red coralline algae. *Geochim. Cosmochim. Acta* 73:1901–7.
- Kamenos, N. A., Cusack, M. & Moore, P. G. 2008b. Coralline algae are global palaeothermometers with bi-weekly resolution. *Geochim. Cosmochim. Acta* 72:771–9.
- Kamenos, N. A., Hoey, T. B., Nienow, P., Fallick, A. & Claverie, T. 2012. Reconstructing Greenland ice sheet runoff using coralline algae. *Geology* 40:1095–8.
- Kamenos, N. A. & Law, A. 2010. Temperature controls on coralline algal skeletal growth. *J. Phycol.* 46:331–5.
- Kamenos, N. A., Moore, P. G. & Hall-Spencer, J. M. 2004a. Nursery-area function of maerl grounds for juvenile queen scallops *Aequipecten opercularis* and other invertebrates. *Mar. Ecol. Prog. Ser.* 274:183–9.
- Kamenos, N. A., Moore, P. G. & Hall-Spencer, J. M. 2004b. Attachment of the juvenile queen scallop (*Aequipecten opercularis* (L.)) to maerl in mesocosm conditions; Juvenile habitat selection. *J. Exp. Mar. Biol. Ecol.* 306:139–55.
- Kamenos, N. A., Moore, P. G. & Hall-Spencer, J. M. 2004c. Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play?. *ICES J. Mar. Sci.* 61:422–9.
- Kamenos, N. A., Strong, S. C., Shenoy, D. M., Wilson, S. T., Hatton, A. D. & Moore, P. G. 2008a. Red coralline algae as a source of marine biogenic dimethylsulphoniopropionate. *Mar. Ecol. Prog. Ser.* 372:61–6.
- Karsten, U., Kuck, K., Vogt, C. & Kirst, G. O. 1996. Dimethylsulphoniopropionate production in phototrophic organisms and its physiological function as a cryoprotectant. In Kiene, R. P., Visscher, P. T., Keller, M. D. & Kirst, G. O. [Eds.] *Biological Chemistry of DMSP and Related Sulfonium Compounds*. Plenum Press, New York, pp. 143–3.
- Kato, A., Baba, M. & Suda, S. 2011. Revision of the Mastophoridae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *J. Phycol.* 47:662–72.
- Kato, A., Hikami, M., Kumagai, N. H., Suzuki, A., Nojiri, Y. & Sakai, K. 2014. Negative effects of ocean acidification on two crustose coralline species using genetically homogeneous samples. *Mar. Env. Res.* 94:1–6.
- Keats, D. W., Groener, A. & Chamberlain, Y. M. 1993. Cell sloughing in the littoral zone coralline alga, *Spongites yendoii* (Foslie) Chamberlain (Corallinales, Rhodophyta). *Phycologia* 32:143–50.
- Keats, D. W., Wilton, P. & Maneveldt, G. 1994. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoii* (Foslie) Chamberlain (Corallinales, Rhodophyta) in South Africa. *J. Exp. Mar. Biol. Ecol.* 175:145–54.
- Kendrick, G. A. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *J. Exp. Mar. Biol. Ecol.* 147:47–63.
- Kim, M. J., Choi, J. S., Kang, S. E., Cho, J. Y., Jin, H. J., Chun, B. S. & Hong, Y. K. 2004. Multiple allelopathic activity of the crustose coralline alga *Lithophyllum yessoense* against settlement and germination of seaweed spores. *J. Appl. Phycol.* 16:175–9.
- Kleypas, J. A., Anthony, K. R. N. & Gattuso, J. P. 2011. Coral reefs modify their seawater carbon chemistry - case study from a barrier reef (Moorea, French Polynesia). *Glob. Change Biol.* 17:3667–78.
- Koch, M., Bowes, G., Ross, C. & Zhang, X. H. 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Glob. Change Biol.* 19:103–32.
- Kolesar, P. T. 1978. Magnesium in calcite from a coralline alga. *J. Sed. Petr.* 48:815–20.
- Kroeker, K. J., Gambi, M. C. & Micheli, F. 2013. Community dynamics and ecosystem simplification in a high-CO₂ ocean. *Proc. Natl. Acad. Sci. USA* 110:12721–6.
- Kuffner, I. B., Andersson, A. J., Jokiel, P. L., Rodgers, K. S. & Mackenzie, F. T. 2008. Decreased abundance of crustose coralline algae due to ocean acidification. *Nat. Geosci.* 1:114–7.
- Le Gall, L. & Saunders, G. W. 2007. A nuclear phylogeny of the Florideophyceae (Rhodophyta) inferred from combined EF2, small subunit and large subunit ribosomal DNA: establishing the new red algal subclass Corallinophycidae. *Mol. Phylogenet. Evol.* 43:1118–30.
- Le Gall, L. & Saunders, G. W. 2010. DNA barcoding is a powerful tool to uncover algal diversity: a case study of the Phyllophoraceae (Gigartinales, Rhodophyta) in the Canadian flora. *J. Phycol.* 46:374–89.
- Lee, D. & Carpenter, S. J. 2001. Isotopic disequilibrium in marine calcareous algae. *Chem. Geol.* 172:307–29.
- Littler, M. M. 1972. The crustose Corallinales. *Oceanogr. Mar. Biol.* 10:103–20.
- Littler, M. M. & Littler, D. S. 1984. Models of tropical reef biogenesis: the contribution of algae. In Round, F. E. & Chapman, V. J. [Eds.] *Progress in Phycological Research*. Biopress, London, UK, pp. 323–64.
- Luyen, Q. H., Cho, J. Y., Kang, J. Y., Park, N. G. & Hong, Y. K. 2009. Isolation of algal spore lytic C17 fatty acid from the crustose coralline seaweed *Lithophyllum yessoense*. *J. Appl. Phycol.* 21:423–7.
- Lyons, D. A., Scheibling, R. E. & Ven Alstyne, K. L. 2010. Spatial and temporal variation in DMSP content in the invasive seaweed *Codium fragile* ssp. fragile: effects of temperature, light and grazing. *Mar. Ecol. Prog. Ser.* 417:51–61.

- Macintyre, I. G. & Glynn, P. W. 1976. Evolution of a modern Caribbean fringing reef, Galeta Point. *Panama. AAPG Bull.* 60:1054–72.
- Maneveltd, G. W. & Keats, D. W. 2008. Effects of herbivore grazing on the physiognomy of the coralline alga *Spongites yendoi* and on associated competitive interactions. *Afr. J. Mar. Sci.* 30:581–93.
- Martin, S., Charnoz, A. & Gattuso, J. P. 2013. Photosynthesis, respiration and calcification in the Mediterranean crustose coralline alga *Lithophyllum cabiochae* (Corallinales, Rhodophyta). *Eur. J. Phycol.* 48:163–72.
- Martin, S., Clavier, J., Chauvaud, L. & Thouzeau, G. 2007a. Community metabolism in temperate maerl beds. I. Carbon and carbonate fluxes. *Mar. Ecol. Prog. Ser.* 335:19–29.
- Martin, S., Clavier, J., Chauvaud, L. & Thouzeau, G. 2007b. Community metabolism in temperate maerl beds. II. Nutrient fluxes. *Mar. Ecol. Prog. Ser.* 335:31–41.
- Martin, S. & Gattuso, J. P. 2009. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Glob. Change Biol.* 15:2089–100.
- Martindale, W. 1992. Calcified epibionts as paleoecological tools: examples from the Recent and Pleistocene reefs of Barbados. *Coral Reefs* 11:167–77.
- Martinez, K., Ferrer, I., Hernando, M. D., Fernandez-Alba, A. R., Marce, R. M., Borrull, F. & Barcelo, D. 2001. Occurrence of antifouling biocides in the Spanish Mediterranean marine environment. *Environ. Technol.* 22:543–52.
- Martone, P. T. 2010. Quantifying growth and calcium carbonate deposition of *Calliarthron cheilosporioides* (Corallinales, Rhodophyta) in the field using a persistent vital stain. *J. Phycol.* 46:13–7.
- Martone, P. T., Alyono, M. & Stites, S. 2010a. Bleaching of an intertidal coralline alga: untangling the effects of light, temperature and desiccation. *Mar. Ecol. Prog. Ser.* 416:57–67.
- Martone, P. T., Lindstrom, S. C., Miller, K. A. & Gabrielson, P. W. 2012. *Chiharea* and *Yamadaia* (Corallinales, Rhodophyta) represent reduced and recently derived articulated coralline morphologies. *J. Phycol.* 48:859–68.
- Martone, P. T., Navarro, D., Stortz, C. & Estevez, J. 2010b. Differences in polysaccharide structure between calcified and uncalcified segments in the coralline *Calliarthron cheilosporioides* (Corallinales, Rhodophyta). *J. Phycol.* 46:507–15.
- Masaki, T., Fujita, D. & Akioka, H. 1981. Observation on the spore germination of *Laminaria japonica* on *Lithophyllum yessoense* (Rhodophyta, Corallinales) in culture. *Bull. Fac. Fish. Hokkaido Univ.* 32:349–56.
- Matsuda, S. 1989. Succession and growth rates of encrusting crustose coralline algae (Rhodophyta, Cryptonemiales) in the upper fore-reef environment off Ishigaki Island, Ryukyu Islands. *Coral Reefs* 7:185–95.
- McConnaughey, T. A. & Whelan, J. F. 1997. Calcification generates protons for nutrient and bicarbonate uptake. *Earth Sci. Rev.* 42:95–117.
- McCoy, S. J. 2013. Morphology of the crustose coralline alga *Pseudolithophyllum muricatum* (Rhodophyta, Corallinales) responds to 30 years of ocean acidification in the northeast Pacific. *J. Phycol.* 49:830–7.
- McCoy, S. J. & Pfister, C. A. 2014. Historical comparisons reveal altered competitive interactions in a guild of crustose coralline algae. *Ecol. Lett.* 17:475–83.
- McCoy, S. J. & Ragazzola, F. 2014. Skeletal trade-offs in response to ocean acidification. *Nat. Clim. Change* 4:719–23.
- Medakovic, D., Popovic, S., Zavodnik, N., Grzeta, B. & Plazonic, M. 1995. X-ray diffraction study of mineral components in calcareous algae (Corallinales, Rhodophyta). *Mar. Biol.* 122:479–85.
- Milliman, J. D., Gastner, M. & Müller, J. 1971. Utilization of magnesium in coralline algae. *GSA Bull.* 82:573–80.
- Moberly, R. J. 1968. Composition of magnesium calcites of algal and pelcypods by electron microprobe analysis. *Sedimentology* 11:61–82.
- Morse, D. E., Hooker, N., Duncan, H. & Jensen, L. 1979. γ -Aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. *Science* 204:407–10.
- Morse, D. E., Hooker, N., Morse, A. N. C. & Jensen, L. 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J. Exp. Mar. Biol. Ecol.* 116:193–217.
- Morse, A. N. C. & Morse, D. E. 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. *J. Exp. Mar. Biol. Ecol.* 75:191–215.
- Nash, M. C., Opdyke, B. N., Troitzsch, U., Russell, B. D., Adey, W. H., Kato, A., Diaz-Pulido, G., Brent, C., Gardner, M., Prichard, J. & Kline, D. I. 2012. Dolomite-rich coralline algae in reefs resist dissolution in acidified conditions. *Nat. Clim. Change* 2:1–5.
- Nelson, W. A. 2009. Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: a review. *Mar. Freshwater Res.* 60:787–801.
- Noisette, F., Duong, G., Six, C., Davoult, D. & Martin, S. 2013a. Effects of elevated $p\text{CO}_2$ on the metabolism of a temperate rhodolith *Lithothamnion corallioides* grown under different temperatures. *J. Phycol.* 49:746–57.
- Noisette, F., Egilsdottir, H., Davoult, D. & Martin, S. 2013b. Physiological responses of three temperate coralline algae from contrasting habitats to near-future ocean acidification. *J. Exp. Mar. Biol. Ecol.* 448:179–87.
- Norris, J. N. & Fenical, W. 1982. Chemical defense in tropical marine algae. *Smithsonian Contr. Mar. Sci.* 12:417–51.
- O’Leary, J. K. & McClanahan, T. R. 2010. Trophic cascades result in large-scale coralline algae loss through differential grazer effects. *Ecology* 91:3584–97.
- O’Leary, J. K., Potts, D. C., Braga, J. C. & McClanahan, T. R. 2012. Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance. *Coral Reefs* 31:547–59.
- Oomori, T., Kaneshima, H., Maezato, Y. & Kitano, Y. 1987. Distribution coefficient of Mg^{2+} ions between calcite and solution at 10–50 degrees C. *Mar. Chem.* 20:327–36.
- Ordoñez, A., Doropoulos, C. & Diaz-Pulido, G. 2014. Effects of ocean acidification on population dynamics and community structure of crustose coralline algae. *Biol. Bull.* 226:255–68.
- Padilla, D. 1981. Selective factors influencing the morphology of coralline algae. MS dissertation, Oregon State University, Corvallis, 80 pp.
- Padilla, D. K. 1984. The importance of form: differences in competitive ability, resistance to consumers and environmental stress in an assemblage of coralline algae. *J. Exp. Mar. Biol. Ecol.* 79:105–27.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49:667–85.
- Paine, R. T. 1984. Ecological determinism in the competition for space: the Robert H. MacArthur Award Lecture. *Ecology* 65:1339–48.
- Payri, C. E. & Cabioch, G. 2004. The systematics and significance of coralline red algae in the rhodolith sequence of the Amédée 4 drill core (Southwest New Caledonia). *Palaeogeogr. Palaeoclimatol.* 204:187–208.
- Pentecost, A. 1978. Calcification and photosynthesis in *Corallina officinalis* L. using the $^{14}\text{CO}_2$ method. *Brit. Phycol. J.* 13:383–90.
- Perry, C. T. 2001. Storm-induced coral rubble deposition: pleistocene records of natural reef disturbance and community response. *Coral Reefs* 20:171–83.
- Perry, C. T. & Hepburn, L. J. 2008. Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: taphonomic signatures of reef accretion and reef depositional events. *Earth-Sci. Rev.* 86:106–44.
- Porzio, L., Buia, M. C. & Hall-Spencer, J. M. 2011. Effects of ocean acidification on macroalgal communities. *J. Exp. Mar. Biol. Ecol.* 400:278–87.
- Pueschel, C. M. & Cole, K. M. 1982. Rhodophycean pit plugs: an ultrastructural survey with taxonomic implications. *Am. J. Bot.* 69:703–20.

- Pueschel, C. M., Eichelberger, H. H. & Trick, H. N. 1992. Specialized calciferous cells in the marine alga *Rhodogorgon carrieboensis* and their implications for models of red algal calcification. *Protoplasma* 166:89–98.
- Pueschel, C. M., Judson, B. L. & Wegeberg, S. 2005. Decalcification during epithallial cell turnover in *Jania adhaerens* (Corallinales, Rhodophyta). *Phycologia* 44:156–62.
- Pueschel, C. M. & Keats, D. W. 1997. Fine structure of deep-layer sloughing and epithallial regeneration in *Lithophyllum neoatalayense* (Corallinales, Rhodophyta). *Phycol. Res.* 45:1–8.
- Ragazzola, F., Foster, L. C., Form, A., Anderson, P. S. L., Hansteen, T. H. & Fietzke, J. 2012. Ocean acidification weakens the structural integrity of coralline algae. *Glob. Change Biol.* 18:2804–12.
- Ragazzola, F., Foster, L. C., Form, A., Büscher, J., Hansteen, T. H. & Fietzke, J. 2013. Phenotypic plasticity of coralline algae in a high CO₂ world. *Ecol. Evol.* 3:3436–46.
- Rahimpour-Bonab, H., Bone, Y., Moussavi-Harami, R. & Turnbull, K. 1997. Geochemical comparisons of modern cool-water calcareous biota, Lacepede Shelf, south Australia. *Soc. Sed. Geol.* 56:77–92.
- Rasher, D. B. & Hay, M. E. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc. Natl Acad. Sci. USA* 107:9683–8.
- Rasher, D. B. & Hay, M. E. 2014. Competition induces allelopathy but suppresses growth and anti-herbivore defence in a chemically rich seaweed. *Proc. Roy. Soc. B* 281:20132615.
- Ries, J. B. 2006a. Aragonitic algae in calcite seas: effect of seawater Mg/Ca ratio on algal sediment production. *J. Sed. Res.* 76:515–23.
- Ries, J. B. 2006b. Mg fractionation in crustose coralline algae: geochemical, biological, and sedimentological implications of secular variation in the Mg/Ca ratio of seawater. *Geochim. Cosmochim. Acta* 70:891–900.
- Ries, J. B. 2009. Effects of secular variation in seawater Mg/Ca ratio (calcite-aragonite seas) on CaCO₃ sediment production by the calcareous algae *Halimeda*, *Penicillus* and *Udotea*: evidence from recent experiments and the geological record. *Terra Nova* 21:323–39.
- Ries, J. B. 2010. Review: geological and experimental evidence for secular variation in seawater Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification. *Biogeosciences* 7:2795–849.
- Ries, J. B., Cohen, A. L. & McCorkle, D. C. 2009. Marine calcifiers exhibit mixed responses to CO₂-induced ocean acidification. *Geology* 37:1131–4.
- Rix, L. N., Burdett, H. L. & Kamenos, N. A. 2012. Irradiance-mediated dimethylsulphoniopropionate (DMSP) responses of red coralline algae. *Est. Coast. Shelf Sci.* 96:268–72.
- Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57:25–41.
- Schmitt, T. M., Hay, M. E. & Lindquist, N. 1995. Constraints on chemically mediated coevolution: multiple functions for seaweed secondary metabolites. *Ecology* 76:107–23.
- Semesi, I. S., Beer, S. & Björk, M. 2009. Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Mar. Ecol. Prog. Ser.* 382:41–7.
- Setchell, W. A. 1926. Nullipore versus coral in reef-formation. *Proc. Am. Phil. Soc.* 65:136–40.
- Simkiss, K. 1964. Phosphates as crystal poisons of calcification. *Biol. Rev.* 39:487–505.
- Smith, A. D. & Roth, A. A. 1979. Effect of carbon dioxide concentration on calcification in the red coralline alga *Bossiella orbigniana*. *Mar. Biol.* 52:217–25.
- Smith, A. M., Sutherland, J. E., Kregting, L., Farr, T. J. & Winter, D. J. 2012. Phylomineralogy of the coralline red algae: correlation of skeletal mineralogy with molecular phylogeny. *Phytochemistry* 81:97–108.
- Stanley, S. M., Ries, J. B. & Hardie, L. A. 2002. Low-magnesium calcite produced by coralline algae in seawater of Late Cretaceous composition. *Proc. Natl. Acad. Sci. USA* 99:15323–6.
- Steller, D. L. & Foster, M. S. 1995. Environmental factors influencing distribution and morphology of rhodoliths on Bahía Concepción, B.C.S., México. *J. Exp. Mar. Biol. Ecol.* 194:201–12.
- Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9:44–61.
- Steneck, R. S. 1985. Adaptations of crustose coralline algae to herbivory: patterns in space and time. In Toomey, D. F. & Nitecki, M. H. [Eds.] *Paleoalgology: Contemporary Research and Applications*. Springer-Verlag, Berlin, Germany, pp. 352–66.
- Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Ann. Rev. Ecol. Syst.* 17:273–303.
- Steneck, R. S. & Adey, W. H. 1976. The role of environment in control of morphology in *Lithophyllum congestum* a Caribbean algal ridge builder. *Bot. Mar.* 19:197–215.
- Steneck, R. S. & Dethier, M. N. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–98.
- Steneck, R. S., Hacker, S. D. & Dethier, M. D. 1991. Mechanisms of competitive dominance between crustose coralline algae: an herbivore-mediated competitive reversal. *Ecology* 72:938–50.
- Steneck, R. S. & Paine, R. T. 1986. Ecological and taxonomic studies of shallow-water encrusting Corallinales (Rhodophyta) of the boreal northeastern Pacific. *Phycologia* 25:221–40.
- Sunda, W., Kieber, D. J., Kiene, R. P. & Huntsman, S. 2002. An antioxidant function for DMSP and DMS in marine algae. *Nature* 418:317–20.
- Tait, L. W. 2014. Impacts of natural and manipulated variations in temperature, pH and light on photosynthetic parameters of coralline-kelp assemblages. *J. Exp. Mar. Biol. Ecol.* 454:1–8.
- Tierney, P. W. & Johnson, M. E. 2012. Stabilization role of crustose coralline algae during Late Pleistocene reef development on Isla Cerralvo, Baja California Sur (Mexico). *J. Coast. Res.* 279:244–54.
- Toth, L. T., Aronson, R. B., Vollmer, S. B., Hobbs, J. W., Urrego, D. H., Cheng, H., Enochs, I. C., Combosch, D. J., van Woessik, R. & Macintyre, I. G. 2012. ENSO drove 2500-year collapse of eastern Pacific coral reefs. *Science* 337:81–4.
- Van Alstyne, K. L. 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69:655–663.
- Van Alstyne, K. L. & Houser, L. T. 2003. Dimethylsulfide release during macroinvertebrate grazing and its role as an activated chemical defense. *Mar. Ecol. Prog. Ser.* 250:175–81.
- Wai, T. C. & Williams, G. A. 2005. The relative importance of herbivore-induced effects on productivity of crustose coralline algae: sea urchin grazing and nitrogen excretion. *J. Exp. Mar. Biol. Ecol.* 324:141–56.
- Webster, J. M. & Davies, P. J. 2003. Coral variation in two deep drill cores: significance for the Pleistocene development of the Great Barrier Reef. *Sed. Geol.* 159:61–80.
- Webster, N. S., Soo, R., Cobb, R. & Negri, A. P. 2011. Elevated seawater temperature causes a microbial shift on crustose coralline algae with implications for the recruitment of coral larvae. *ISME J.* 5:759–70.
- Williams, B., Halfar, J., Steneck, R. S., Wortmann, U. G., Hetzinger, S., Adey, W. H., Lebednik, P. & Joachimski, M. 2011. Twentieth century δC¹³ variability in surface water dissolved inorganic carbon recorded by coralline algae in the northern North Pacific Ocean and the Bering Sea. *Biogeosciences* 8:165–74.
- Wilson, S., Blake, C., Berges, J. A. & Maggs, C. A. 2004. Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. *Biol. Conserv.* 120:283–93.
- Woelkerling, W. J. 1988. *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinales*, 1st Edn. Oxford University Press, Oxford, UK, 268 pp.

- Wootton, J. T. & Pfister, C. A. 2012. Carbon system measurements and potential climatic drivers at a site of rapidly declining ocean pH. *PLoS ONE* 7:e53396.
- Wootton, J. T., Pfister, C. A. & Forester, J. D. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl. Acad. Sci. USA* 105:18848–53.
- Yabur-Pacheco, R. & Riosmena-Rodríguez, R. 2006. Rhodolith bed composition in the southwestern Gulf of California, Mexico. *Nagisa World Congress* 1:37–47.
- Yamano, H., Kayanne, H. & Yonekura, N. 2001. Anatomy of a modern coral reef flat: a recorder of storms and uplift in the late Holocene. *J. Sed. Res.* 71:295–304.