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MORPHOLOGY OF THE CRUSTOSE CORALLINE ALGA *PSEUDOLITHOPHYLLUM MURICATUM* (CORALLINALES, RHODOPHYTA) RESPONDS TO 30 YEARS OF OCEAN ACIDIFICATION IN THE NORTHEAST PACIFIC[1]

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As the process of ocean acidification alters seawater carbon chemistry, physiological processes such as skeletal accretion are expected to become more difficult for calcifying organisms. The crustose coralline red algae (Corallinales, Rhodophyta) form an important guild of calcifying primary producers in the temperate Northeast Pacific. The morphology of important ecological traits, namely, skeletal density and thallus thickness near the growing edge, was evaluated in *Pseudolithophyllum muricatum* (Foslie) Steneck & R.T. Paine, the competitively dominant alga within this guild. *P. muricatum* shows a morphological response to increased ocean acidification in the temperate Northeast Pacific. Comparing historical (1981–1997) and modern (2012) samples from the field, crust thickness near the growing edge was approximately half as thick in modern samples compared with historical samples, while crust calcite density showed no significant change between the two sample groups. Morphological changes at the growing edge have important consequences for mediating competitive interactions within this guild of algae, and may affect the role of crustose coralline algal beds as hosts to infaunal communities and facilitators of recruitment in many invertebrate and macroalgal species.

Key index words: **calcite density; CCA; crustose coralline algae; morphology; ocean acidification; *Pseudolithophyllum muricatum*; SEM; thallus thickness**

***Abbreviations*: CCA, crustose coralline algae; DIC, dissolved inorganic carbon; pCO_2, partial pressure of CO_2 gas; PDO, Pacific Decadal Oscillation; SST, sea surface temperature**

The ongoing process of ocean acidification, caused by oceanic uptake of anthropogenic CO_2 emissions, will impact a wide range of marine organisms and ecosystems (Doney et al. 2009, Kroeker et al. 2010, Garrard et al. 2012). By changing seawater carbon chemistry, and thereby lowering the pH and carbonate saturation of seawater, continued release of CO_2 to the atmosphere could lead to greater change in ocean pH than any change during the past 300 million years (Caldeira and Wickett 2003, Hönisch et al. 2012).

Much recent attention has focused on coralline algae as a group of potentially highly susceptible organisms to the threat of ocean acidification. Indeed, as organisms that both photosynthesize and calcify, they may reveal a conflicted response to changes in seawater carbon chemistry caused by ocean acidification (Ries et al. 2009). The process of ocean acidification is engendered by the buffer dynamics of DIC in seawater. As excess atmospheric CO_2 dissolves in seawater, it combines with water molecules to form carbonic acid ($H_2CO_{3\ (aq)}$) and deprotonates to form first bicarbonate ($HCO_3^-{}_{(aq)}$) and then carbonate ($CO_3^{2-}{}_{(aq)}$) in a pH-dependent process. This trade-off in DIC forms is ecologically meaningful; macroautotrophs use bicarbonate as a carbon source for underwater photosynthesis, while calcifying organisms use carbonate to make calcium carbonate skeletal material. Because coralline algae use both bicarbonate, for algal photosynthesis, and carbonate, for skeletal accretion (Smith and Roth 1979), they represent an ideal group in which to determine the net effect of ocean acidification on the photosynthesis–calcification trade-off.

Crustose coralline red algae (Corallinaceae, Rhodophyta), a group of nongeniculate calcified algae with skeletal tissue composed of high-Mg calcite, form an important guild of primary producers in the rocky intertidal and are some of the most abundant organisms living on rocky substrates throughout the marine photic zone (Steneck and Martone 2007). Within this guild, species compete for space via overgrowth interactions. These interactions do not involve allelopathic interactions, but rather depend on physical and morphological traits of species. Competitive relationships have been extensively described in the field (Paine 1980, 1984, Steneck and Paine 1986, Steneck et al. 1991, Dethier 1994, Dethier and Steneck 2001) and reveal a hierarchical dominance structure mediated by herbivory (Paine 1984, Steneck et al. 1991).

Historically, the crustose coralline *Pseudolithophyllum muricatum* (Foslie) Steneck & R.T. Paine (*Pseudolithophyllum lichenare* or *Lithophyllum lichenare* prior to 1986; Steneck and Paine 1986) was shown

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to always outcompete all other species during overgrowth competition both in the presence and absence of grazers (Paine 1984). This species grows slowly (~11 mm per year growth in diameter in the absence of competition; R.T. Paine, unpublished data), and is relatively thick throughout the thallus, and has a raised, nonadherent growing edge (Steneck and Paine 1986). Thallus thickness is a trait that enables *P. muricatum* to withstand deeper and greater rates of grazing than its competitors. Its thick, raised growing edge forces competitors to initiate competitive interactions further away from an interaction boundary, and thus demands greater competitive investment on the part of its competitors (Paine 1984, Steneck et al. 1991). Thus, the traits that confer a competitive advantage to *P. muricatum*, thallus thickness and edge morphology, are also traits that require a greater amount of calcified tissue.

Over the relevant pH range for near-shore waters of the temperate Northeast Pacific Ocean, as measured from 2000 to 2012 at Tatoosh Island, WA (Wootton et al. 2008, Wootton and Pfister 2012), the carbonate buffer system shifts from a carbonate- to a bicarbonate-dominated system as pH decreases (Fig. 1 and Fig. S1 in the Supporting Information). Prior studies of coralline algal growth show evidence for decreased growth rates in articulated coralline algae as pH declines (Borowitzka 1979, Smith and Roth 1979), weakened structural integrity of coralline algal skeletal tissue with increasing pCO_2 (Ragazzola et al. 2012) and epithelial damage (Burdett et al. 2012). Given the context of observed pH decline in coastal waters near Tatoosh Island, it was

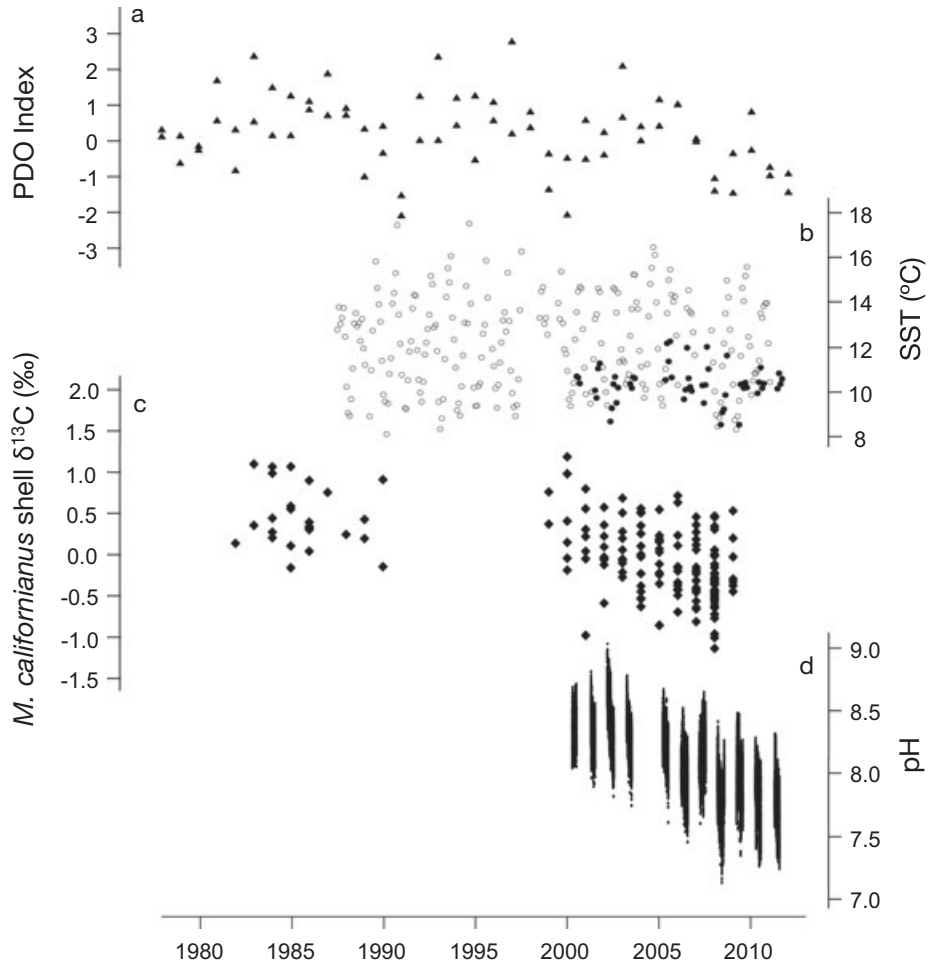

FIG. 1. (a) monthly averaged Pacific Decadal Oscillation for both June and January. (b) mean monthly sea surface temperature (SST) in °C. Hollow gray circles show mean monthly SST measured at Cape Elizabeth 1987–2012 (NOAA Buoy 46041, 47.4°N, 124.5°W; ndbc.noaa.gov), and filled black circles show mean monthly SST measured from April to September at Tatoosh Island 2000–2012 (48.4°N, 128.7°W). There was no trend in SST over time. Cape Elizabeth consistently experiences daily temperatures 2°C–3°C higher than Tatoosh Island, and is located ~50 km to the southeast (Pfister et al. 2007). (c) stable isotopic composition of carbon ($\delta^{13}C$) measured in *Mytilus californianus* shells from Tatoosh Island. Data from Pfister et al. (2011). (d) pH time series measured at Tatoosh Island, WA, USA (48.4°N, 128.7°W) exhibiting seasonal variation and year-to-year trends (pH decline −0.00017 units per year). Data points show measurements every 30 min at high tide from April to September. Updated from Wootton et al. (2008), Wootton and Pfister (2012).

hypothesized that there would be observable morphological differences between historical and modern *P. muricatum* individuals at that site.

Archival samples provide an opportunity to directly compare morphological features of historical and modern individuals of *P. muricatum*. By assessing traits of individuals belonging to the same population in the same location over time, the comparison captures natural processes corresponding to changing environmental conditions over that period. A major advantage of a comparative study in a natural setting is the ability to include processes that are impossible to simulate in the laboratory such as, for example, potential for phenotypic changes due to the acclimation of individuals, or populations changes attributable to simultaneous responses of interacting members of the ecological community. However, the use of archival material can be limited in sample size and the number of locales from which archival material is available.

Given the marked decline in seawater pH over the last decade at Tatoosh Island (Wootton et al. 2008, Wootton and Pfister 2012), this study aims to quantify whether the quantity and quality of calcified tissue in *P. muricatum* at this site reveals a response to ocean acidification. Thallus morphology was assessed in archival samples from 1981 to 1997 and modern samples from 2010 to 2012 collected at Tatoosh Island. It was hypothesized that *P. muricatum*, as a thick coralline algal crust, should reduce either its quantity or quality of calcium carbonate skeletal tissue in response to acidification.

MATERIALS AND METHODS

Sample collection. *P. muricatum* was grown and transplanted in the field at Hedophyllum Cove on Tatoosh Island, WA (48.4°N, 128.7°W). Modern samples were transplanted onto a smooth artificial surface of Sea Goin' Poxy Putty (Permalite Plastics Inc., Rancho Dominguez, CA, USA) by chiseling a piece >1.5 cm^2 from the rock and embedding the sample in a flattened patty of epoxy putty (sensu Paine 1980) in June 2010. These samples were collected in June 2012 and dried in the shade to avoid crust bleaching. These experimental methods are identical to those used from 1981 to 1997 by R.T. Paine at exactly the same location (Paine 1984). Archival specimens were collected in the spring (April–June of 1981, 1982, 1993, 1994, and 1997) and preserved as dry specimens at the University of Washington by R.T. Paine. All modern and archival samples used in this study were transplanted into grazer removal plots (removed individuals >2 mm of *Acmaea mitra*, *Katharina tunicata*, *Lottia* spp., *Mopalia* spp., *Strongylocentrotus droebachiensis*, *S. purpuratus*, and *Tonicella* spp.).

It is extremely difficult to estimate the age of CCA given that individual size is not correlated with age due to grazing, physical disturbance, and overgrowth processes that can cause cleaving of an individual thallus repeatedly over time. Furthermore, it does not necessarily follow that the center of an individual always corresponds to the oldest portion of the thallus due to the potential for asymmetric thallus growth. Crustose coralline individuals were sampled at random from the same local community in both modern and archival transplants, and chiseled pieces were not systematically taken from the same part of each crust (i.e., center versus edge). This sampling scheme for modern and archival transplants should therefore obtain an unbiased, representative subset of ontogenetic ages in the local community.

Scanning electron microscope analysis. Six modern (2012) and five archival (1981, 1982, 1993, 1994, and 1997) transplants were selected at random for tissue analysis on the scanning electron microscope (SEM). Dried algal thalli were fractured at the growing edge perpendicular to the direction of maximum growth using tweezers, mounted in cross-section, and coated in 8 nm of palladium (Pd) for SEM analysis. All samples were analyzed on an FEI Nova NanoSEM 230 at the NSF Chicago Materials Research Center at the University of Chicago (Chicago, IL, USA).

SEM micrographs were analyzed using ImageJ (US National Institutes of Health) photo analysis software. Calcite density, or the fractional area within a digital quadrat composed of calcite-bearing structures (sensu Kamenos and Law 2010), was determined by transforming cross-sectional SEM photos taken at high magnification (2,500×) into black and white images to measure relative surface areas of calcified tissue and interstitial cellular space of the cross-section. Calcite density is expressed as fractional area occupied by calcite structures, obtained by subtracting the cumulative surface area of pore spaces from total surface area of the cross-section (Fig. 2). Variation within each sample was

FIG. 2. Image conversion for determination of fraction calcified tissue. (a) Original scanning electron microscope photograph, (b) black and white threshold image, and (c) cartoon with pore spaces outlined. A cross-sectional view of sample A5 is shown in this example.

quantified by dividing each digital micrograph into four quadrants. Calcite density was compared between archival and modern samples using a two-way ANOVA in the statistical program R.

Thallus thickness was measured along a cross-sectional SEM photo taken at low magnification (75×), starting at the growing edge. Because thallus thickness can vary over the extent of the individual, thickness was measured every 33 μm along a transect perpendicular to the growth axis for all samples, starting at the growing edge. A sampling resolution of 33 μm was chosen to allow for an accurate representation of variation in thallus thickness along the transect without emphasizing any small-scale irregularities. Mean thickness at each sampling point along the transect was compared between archival and modern samples using a two-way ANOVA.

Comparison to environmental data. *P. muricatum* samples were analyzed as a time series to test for trends over time and with environmental variables (Fig. 1) by calculating the correlation coefficient (Pearson's r). SST data were obtained from Cape Elizabeth, WA (NOAA Buoy 46041, 47.4°N, 124.5°W, measured daily 1987–2012 from the National Data Buoy Center; ndbc.noaa.gov) as well as measured at Tatoosh Island, WA since 2000 (Wootton et al. 2008, Pfister et al. 2011). SST at Tatoosh Island was measured every 30 min from April to September using a Hach Hydrolab instrument (Hach Hydroment, Loveland, CO, USA). Temperature data from Cape Elizabeth (~50 km to the southwest of Tatoosh Island) extend the availability of local SST data to 1987; however, it is important to note that Cape Elizabeth SST is consistently 2°C–3°C warmer than at Tatoosh despite positive correlations between data sets (Pfister et al. 2007). The effect of the PDO index (NOAA National Data Buoy Center; ndbc.noaa.gov) was also considered independently from that of temperature.

Seawater pH was measured every 30 min at Tatoosh Island, WA from April to September of 2000–2012 (Wootton et al. 2008, Wootton and Pfister 2012). pH was measured on the total scale using a Hach Hydrolab instrument (Hach Hydroment) and periodically checked spectrophotometrically (Wootton and Pfister 2012). As there are no pH records for the NE Pacific prior to 2000, mussel shell (*Mytilus californianus*) $\delta^{13}C$ was used to reconstruct historical changes in inorganic carbon cycling at Tatoosh Island since 660 AD (Pfister et al. 2011).

RESULTS

Environmental trends. No temporal trends were identified in either SST or PDO (Fig. 1; Wootton et al. 2008, Pfister et al. 2011). pH measured at Tatoosh Island showed a rapid decline since 2000 (Fig. 1; Wootton et al. 2008, Wootton and Pfister 2012), matching regional trends (Feely et al. 2008, 2010). $\delta^{13}C$ measured in mussel shells from Tatoosh Island revealed rapid and recent changes in the seawater organic carbon cycle (Fig. 1); data from Pfister et al. (2011) showed a decline in shell $\delta^{13}C$ between historical (~660–1,100 AD) and archival (~1960–1990) of 0.36‰ and a decline between archival and modern (1999–2009) of 0.53‰. Furthermore, the temporal trend within modern samples corroborates pH decline from 2000 to present, with a decline in shell $\delta^{13}C$ of 0.071‰ per year between 1999 and 2009. These data indicated that large changes in the inorganic carbon cycle have occurred locally since the 1980s, and predominantly since 1999.

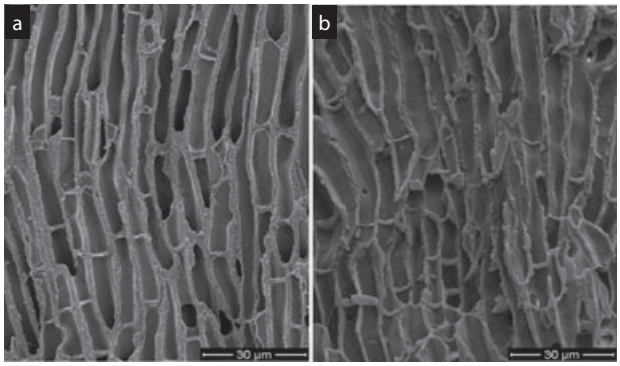

FIG. 3. Archival (a, sample A1) and modern (b, sample M4) cross-sectional scanning electron microscope photographs of representative samples (2000× magnification).

Calcite density. Calcite density, or proportion of calcite structures by surface area, did not differ between archival and modern samples of *P. muricatum* (ANOVA, $F_{1,9} = 0.276$, $P = 0.612$; Fig. 3; Table S1 in the supporting information). Archival samples had a mean calcite proportional density of 0.606 ± 0.026 (mean ± SE, $n = 5$) and ranged from 0.524 to 0.681, with variation within individual archival samples from 0.0057 to 0.010 (SE, $n = 4$). Modern samples had a mean calcite proportional density of 0.592 ± 0.009 (mean ± SE, $n = 6$) and ranged from 0.567 to 0.627. Variation within individual modern samples ranged from 0.003 to 0.017 (SE, $n = 4$); thus, modern individuals varied more than their archival counterparts. However, archival samples showed a greater range and variance in calcite density between samples, i.e., exhibited both higher and lower fractions of calcium carbonate per unit area, than did modern samples, presumably because they were sampled over multiple years. Despite the large temporal spread in archival specimens, there was no trend in calcite density over time among archival samples. No significant correlations were found between calcite density and either temperature (max $r^2 = 0.010$) or PDO index (max $r^2 = 0.006$).

Thallus thickness. Along a transect running perpendicular to the axis of maximum growth from the margin toward the center of the crust, archival *P. muricatum* samples were consistently approximately twice as thick as modern samples (Figs. 4 and 5; Table S2 in the Supporting Information). Despite large variance in both archival and modern sample groups at all distances along the transect, an archival thallus was more than twice that of a modern thallus (ANOVA, $F_{1,9} = 6.8237$, $P = 0.031$). As with the fraction of calcified tissue, archival specimens exhibited greater variation among samples than modern specimens and no significant correlations were found between crust

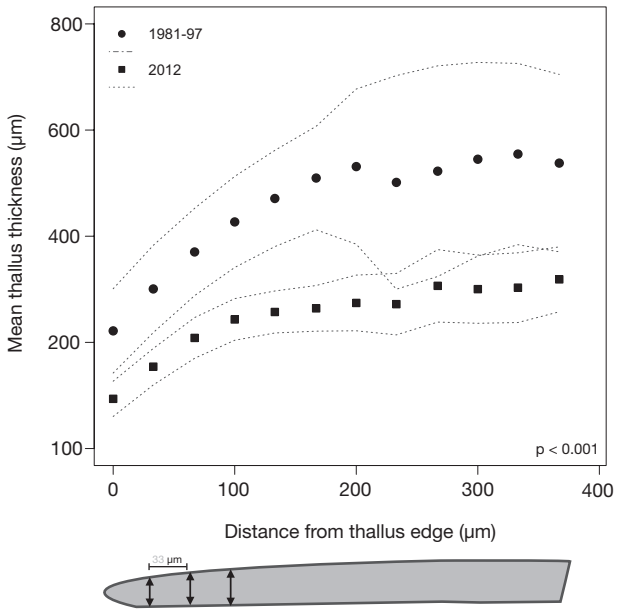

FIG. 4. Archival (a, sample A1) and modern (b, sample M1) cross-sectional scanning electron microscope photographs (75× magnification) showing thallus thickness near the growing edge.

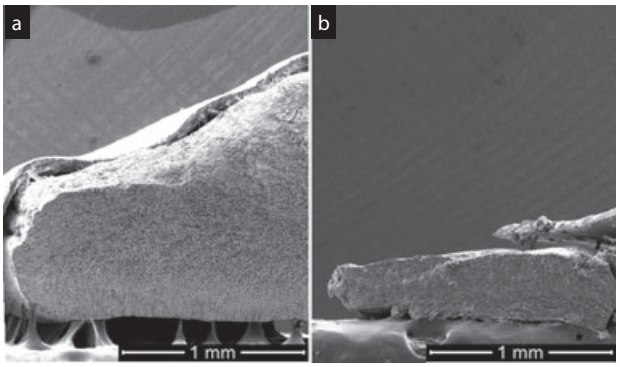

FIG. 5. Profile of mean thallus thickness from the edge toward the center (shown left to right, sampling scheme illustrated by cartoon) in archival *Pseudolithophyllum muricatum* samples (1981–1997, $n = 5$), shown with circles, and modern (2012, $n = 6$) samples, shown with squares. Dashed lines indicate SE. Mean thicknesses at all distances from the edge were significantly greater in archival samples ($P < 0.001$).

thicknesses at any point along the measured transect and either temperature (max $r^2 = 0.284$) or PDO index (max $r^2 = 0.333$). Similarly, there were no significant correlations between crust thickness and calcite density ($r^2 = 0.013$). Among archival samples, crust thickness showed no trend over time.

DISCUSSION

The crustose coralline alga *P. muricatum* appears to show a morphological response to recent ocean acidification in the Northeast Pacific Ocean. Although *P. muricatum* has maintained its density of carbonate material through time, it appears to have done so by reducing the total amount of calcified thallus via production of a thinner thallus. Thicker *P. muricatum* crusts in the past indicate that lowered pH in this region is already a negative affection calcification in CCA.

Temperature has been found to be a particularly important environmental parameter affecting thallus morphology of coralline algae. The calcite density of the subtidal rhodolith *Lithothamnion glaciale* Kjellman decreased with increasing laboratory seawater temperature and seasonally in the field, a result attributed to faster growth in branch tips that resulted in decreased calcite density (Kamenos and Law 2010). However, the correlation between calcite density and temperature and PDO index in *P. muricatum* revealed no significant relationship among any of these parameters, perhaps due to a lack of temporal trend in temperature or PDO index at Tatoosh Island (Pfister et al. 2007, 2011). This suggests an environmental variable other than temperature must be driving the observed changes in thallus morphology at this site. Given observed rapid declines in pH and changes in seawater carbon cycling at Tatoosh Island (Wootton et al. 2008, Pfister et al. 2011, Wootton and Pfister 2012), it is likely that ocean acidification has engendered morphological change in *P. muricatum*.

Because the carbonate buffer system in the vicinity of Tatoosh has shifted from a carbonate- to a bicarbonate-dominated one as pH has declined, calcifying species are expected to have a more difficult time accruing skeletal tissue as pH and carbonate concentrations drop. While most algae use bicarbonate for photosynthesis and may thus benefit from decreased seawater pH, coralline algal growth and calcification rates have been shown experimentally to be restricted in low-pH conditions due to lowered carbonate ion concentrations (Smith and Roth 1979).

Although there was no difference in mean calcite density of *P. muricatum* between historical and modern samples from the field (Fig. 3), thallus thickness at the growing edge in modern samples was generally half of what it was in archival samples (Figs. 4 and 5). Thus, although these algae have maintained their density of carbonate material through time, they appear to have done so by reducing the total amount of calcified thallus through production of a thinner thallus. Given the recorded decline in pH in this region and the expected associated decline in the availability of carbonate ions, the morphology of these corallines suggests that *P. muricatum* is responding to lowered pH conditions via maintaining carbonate density while producing less tissue.

Such a reduction in edge thickness is likely to have competitive effects for this species based on the

demonstrated competitive advantage conferred on *P. muricatum* due to a thicker growing edge relative to its competitors (Paine 1984). Decreased edge thickness in a high-CO_2 ocean will compromise the competitive dominance of *P. muricatum* within the kelp understory algal community. Because *P. muricatum* is a slow-growing alga when compared to its competitors (Paine 1984), loss of its competitive morphological overgrowth advantage may lead to decreased abundance via reduced competitive dominance.

The effects of ocean acidification on competitive responses among calcifiers might be more difficult to predict than those between calcifying and noncalcifying species because it will depend on the relative negative effects of decreasing carbonate with the possible benefits of increasing carbon for photosynthesis. While there is evidence that noncalcified algae will outcompete calcified algae as pH declines (Kuffner et al. 2008, Kroeker et al. 2012), there are to date no published studies of competition between calcified algae under conditions of acidification. Merely because both competitors should be affected by acidification, it does not necessarily follow that all calcifiers will exhibit the same magnitude of response. In this system of CCA, where species exhibit differential potential for growth and competitive ability (Paine 1984, Steneck et al. 1991), it is plausible that some species may respond to acidification sooner than others and thus disrupt documented competitive hierarchies.

Grazing pressure is known to have major effects on crust thickness and morphology of protuberances (Steneck and Adey 1976, Maneveldt and Keats 2008), and it is conceivable that similar morphological changes could be due to increased local grazer abundances. The effect of grazers on crust morphology cannot explain the results of this study, as all transplants were grown in the absence of grazers. It is nonetheless an important mechanism to consider in the context of these results. Increased grazing can cause crust thickness and textural heterogeneity either to increase (Steneck and Adey 1976) or to decrease (Maneveldt and Keats 2008), and may thus confound predictions of altered grazer abundances on CCA morphology. Furthermore, as most grazers of CCA are molluscan, it is therefore expected that they too should respond to ocean acidification stress.

Decreased resistance to grazing could be a consequence of a thinner crust. In previous grazing experiments within coralline algae of the Northeastern Pacific, both thinner crusts and those consisting of weaker $CaCO_3$ skeletal construction show poor survival in both grazing treatments and stressful environmental conditions (Dethier 1994). As *P. muricatum* becomes thinner, it may suffer from reduced abundance in the presence of high grazer densities, as well as reduced tolerance to forthcoming environmental stressors.

The potential for decreased abundance of *P. muricatum* holds ecological repercussions for the continued roles crustose corallines play in invertebrate and macroalgal settlement and creating habitat, as well as species dynamics within the CCA, as discussed above. Across global ecosystems, coralline algal carpet creates settlement habitat for juvenile invertebrates and macroalgae (Steneck 1986, Foster 2001, Kamenos et al. 2004). Competitive overgrowth interactions, in particular, create habitat heterogeneity and texture for recruit attachment of invertebrates. Disruption of the dominance hierarchy among the CCA may result in altered frequency of competitive bouts, and a change in the surface area of overgrowth boundaries available as recruitment substrate for other organisms.

Among this guild, *P. muricatum* is the only species that harbors an extensive infaunal community. Common invaders include the nestling clam, *Hiatella arctica*, the peanut worm, *Phascolosomo agassizii*, and dense aggregations of the worm, *Dodecaceria fewkesi* (Steneck and Paine 1986). As *D. fewkesi* and *P. agassizii* are noncalcifying organisms and the clam *H. arctica* has an extremely thin shell that is not directly exposed to the water column, these organisms are not necessarily expected to be directly affected by ocean acidification themselves. While it is possible that this infaunal community confers some benefits, perhaps as a source of nitrogen, the primary effect of these burrowing associates is to reduce photosynthetic algal surface area and structurally weaken the algal thallus (Steneck and Paine 1986). The effects of this infaunal community may thereby exacerbate the effects of reduced thallus thickness as seawater pH decreases.

Because CCA share similar traits across different oceans (such as thickness or growth rates, reviewed in Steneck and Dethier 1994), it follows that they may play the same ecological functions across those ecosystems (i.e., within the temperate Atlantic or tropical reef coralline algal communities). If the traits of crustose corallines in other communities respond similar to declining pH, acidification effects across systems should have similar implications for ecological function related to the local crustose coralline algal guild. In this context, it would be valuable to determine whether the morphological results of this study extrapolate to other habitats, where crustose corallines also play major roles in structuring intertidal or subtidal communities. In tropical reef habitats, for example, crustose corallines release important settlement cues for crown-of-thorns starfish and abalone larvae (Johnson and Sutton 1994, Daume et al. 1999), as well as contribute structurally to reef frameworks (Bosence 1983).

In conclusion, morphological response in the crustose coralline alga *P. muricatum* appears to be related to increased ocean acidification in the

temperate Northeast Pacific. Crust thickness near the growing edge is approximately half as thick in modern samples as in historical samples. This morphological change may have important consequences for the dynamics of competitive interactions within this guild of algae and affect the role of crustose coralline algal beds as hosts to infaunal communities and facilitators of recruitment in many invertebrate and macroalgal species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Bjerrum plot showing the concentrations of different chemical species of dissolved inorganic carbon as a function of pH. Carbonic acid (equal to concentration of dissolved CO_2) is drawn with a solid line, HCO_3^- with the large dashed line, and CO_3^{2-} with the small dashed line.

Table S1. Measured fraction of calcified tissue.

Table S2. Transect of thallus thickness from edge of crust.