nature climate change

LETTERS

PUBLISHED ONLINE: 15 JUNE 2014 | DOI: 10.1038/NCLIMATE2273

Skeletal trade-offs in coralline algae in response to ocean acidification

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Ocean acidification is changing the marine environment, with potentially serious consequences for many organisms. Much of our understanding of ocean acidification effects comes from laboratory experiments, which demonstrate physiological responses over relatively short timescales[1–10]. Observational studies and, more recently, experimental studies in natural systems suggest that ocean acidification will alter the structure of seaweed communities[11–13]. Here, we provide a mechanistic understanding of altered competitive dynamics among a group of seaweeds, the crustose coralline algae (CCA). We compare CCA from historical experiments (1981–1997) with specimens from recent, identical experiments (2012) to describe morphological changes over this time period, which coincides with acidification of seawater in the Northeastern Pacific[14–16]. Traditionally thick species decreased in thickness by a factor of 2.0–2.3, but did not experience a change in internal skeletal metrics. In contrast, traditionally thin species remained approximately the same thickness but reduced their total carbonate tissue by making thinner inter-filament cell walls. These changes represent alternative mechanisms for the reduction of calcium carbonate production in CCA and suggest energetic trade-offs related to the cost of building and maintaining a calcium carbonate skeleton as pH declines. Our classification of stress response by morphological type may be generalizable to CCA at other sites, as well as to other calcifying organisms with species-specific differences in morphological types.

Coralline algae are globally distributed seaweeds that accrete a calcified skeleton and are associated with high-disturbance habitats across global ecosystems, including areas with high grazing pressure, intense wave action, or low light[17]. Crustose coralline algae (CCA) provide settlement substrates and signals as well as nursery habitat functions for a variety of coastal organisms, including corals, starfish and fishes[18,19], and thus corallines' fates could be closely tied to those of productive coastal systems worldwide.

As both photosynthesizers and calcifiers, coralline algae may respond in multiple ways to ocean acidification and have received much attention as potential 'first indicator' species. Growth, photosynthesis and calcification initially increase with declining pH and concomitant increasing availability of bicarbonate (HCO_3^-) for photosynthesis, followed by a decline in growth and calcification associated with decreased seawater carbonate (CO_3^{2-}) availability for calcification as pH continues to fall[1,20]. The expected parabolic relationship between declining pH and coralline fitness may explain the varied responses to declining pH and pCO_2 that have been recorded to date[2–8,21].

Results from experimentally elevated pCO_2 (increased acidification) show diverse patterns, including reduced coralline algal growth and tissue integrity and increased likelihood of dissolution and tissue necrosis[2–6], no effect of pCO_2 on algal growth parameters[7], and even increased inorganic carbon fixation, photosynthesis and calcification with increased dissolved inorganic carbon DIC (ref. 8). Furthermore there is evidence that coralline algae from habitats more variable in pH seem more robust in experimentally elevated pCO_2 conditions[6,8].

Growth and morphological traits that influence ecological outcomes confer greater fitness on individuals with fast growth or thick thalli (algal individuals)[22], both of which are traits that rely on accretion of calcium carbonate. Temperate CCA compete with one another for space in the kelp understory through a series of overgrowth interactions, and the outcome depends strongly on morphology and growth strategy[22–25]. Rapid lateral growth is important for occupying bare space, thickness at the growing edge is the strongest determinant of competition, and overall thicker species are favoured in the presence of grazers[22,24]. Fast lateral growth and increased thickness seem to trade-off, as they do not co-occur in any one species[24], probably as a result of energetic constraints that incur higher maintenance costs for thick crusts and the resources needed for rapid growth.

Previous work has shown that, in the Northeast Pacific, competitive interactions and community structure among CCA have changed over 30 years, in ways predictable from pH decline[13,23]. We examine morphological change in this community by comparing individuals over time. Of four CCA species that co-occur and compete in the intertidal zone in the northeast Pacific, we show that all now maintain less skeletal material than in the past, but the specific response depends on morphological type.

We examined three metrics of the calcareous skeleton of the CCA *Lithophyllum impressum, Lithothamnion phymatodeum, Pseudolithophyllum muricatum* and *Pseudolithophyllum whidbeyense*. Individuals were collected at Tatoosh Island, Washington, USA in the Northeast Pacific from plots kept grazer-free for approximately two years before specimen collection. Specimens were photographed using scanning electron microscopy (SEM) to determine the thickness of the algal thallus and the thicknesses of inter- and intra-filament cell walls for each species.

To determine change over time, we compared the historical measurements (1981–1997) to modern specimens (2012) collected from the same populations at Tatoosh Island (historical baselines reported in Supplementary Section A). We observed changes in thallus thickness over this interval, related to morphological groupings (Fig. 1). Historical specimens of *L. impressum* and

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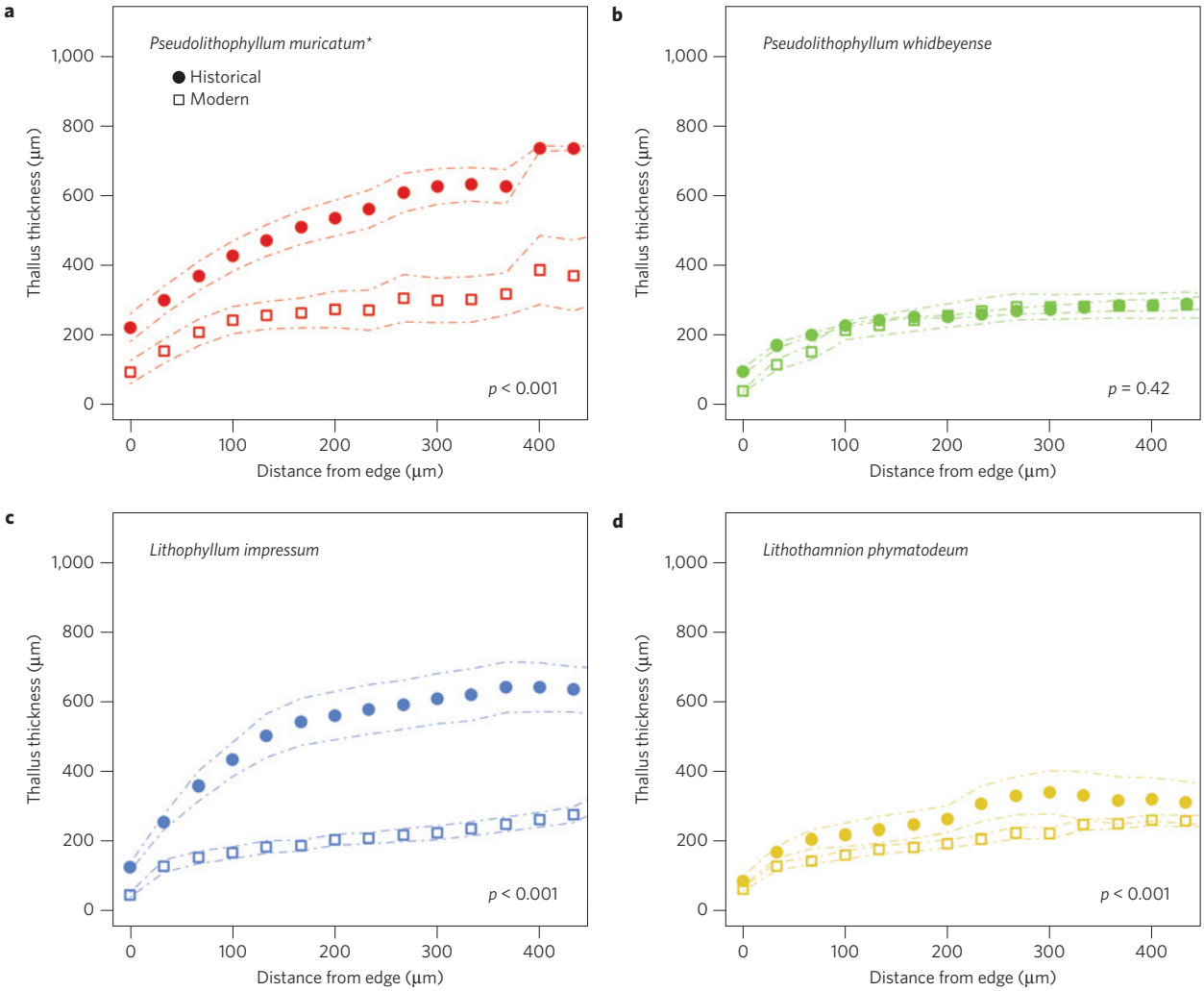

Figure 1 | Thallus thickness profiles. Thickness transects from the thallus edge towards the centre of the crust for *P. muricatum* (historical $N=4$, modern $N=6$) (**a**), *P. whidbeyense* (historical $N=6$, modern $N=6$) (**b**), *L. impressum* (historical $N=5$, modern $N=6$) (**c**) and *L. phymatodeum* (historical $N=3$, modern $N=5$) (**d**). Species means for historical specimens are shown as filled circles and averages for modern specimens as open squares. Dotted lines indicate the standard error. *Data for *P. muricatum* includes a subset of previously published data in ref. 26.

P. muricatum were 2–2.3 times thicker than modern individuals, both on average across the thallus ($p < 0.001$) and specifically at the growing margin ($p < 0.05$), the edge tissue involved in active growth and important in overgrowth interactions. *L. phymatodeum* and *P. whidbeyense*, both historically thinner than *L. impressum* and *P. muricatum*, showed mixed responses in thallus thickness. *L. phymatodeum* thinned overall, with historical specimens 1.3 times thicker than modern, but showed no response specifically at the growing edge. In contrast, *P. whidbeyense* was historically 1.8 times thicker than modern at the growing edge, but showed no change in overall thickness (details for all species reported in Supplementary Section B).

Inter-filament cell walls thinned over time in both *L. phymatodeum* (Mann–Whitney $U(67) = 327.0$, $p = 0.025$) and *P. whidbeyense* ($t(144) = 2.023$, $p = 0.025$). Changes in inter-filament cell walls were not observed in *L. impressum* ($t(144) = -1.690$, $p = 0.093$) and *P. muricatum* (Mann–Whitney $U(96) = 932.0$, $p = 0.108$). No changes were observed in the intra-filament cell walls of any species over time (Fig. 2, details in Supplementary Section C).

Coralline algae have received scientific scrutiny in the context of ocean acidification owing to their importance for maintaining local biodiversity, their influence on the coastal carbon cycle, and their potentially high susceptibility to ocean acidification. It is thus essential to understand acidification-induced changes to their skeletal morphology and its effect on ecological function. The rate at which conditions change has been shown to be important in laboratory studies of coralline algal responses to acidification[9]. Testing for responses to acidification using field-grown specimens accounts for acclimatization of individuals and populations to a stressor as it is gradually introduced over time. At our study site, a pH decline of 0.058 units yr^{-1} has been recorded since 2000 (refs 14,15) and isotopic evidence from mussel shells indicates the onset of unprecedented changes in carbonate chemistry over the past 30 years[16] in the absence of changes to other environmental parameters, including temperature and upwelling regime[14–16] (Fig. 3). Our data suggest that current field populations have already made energetic adjustments to cope with increased acidity in this region.

In response to ocean acidification and the concurrent decrease in the saturation of carbonate in seawater, a reduction in the net quantity of calcium carbonate ($CaCO_3$) skeletal material is expected. $CaCO_3$ amount could be reduced simply by changing the mineral density (quality), or also by reducing the thickness of cell walls (quantity). Both of these mechanisms reduce the structural strength of coralline tissue[3] and may have ecological implications, for example, in the case of physical disturbances, endophytic biota

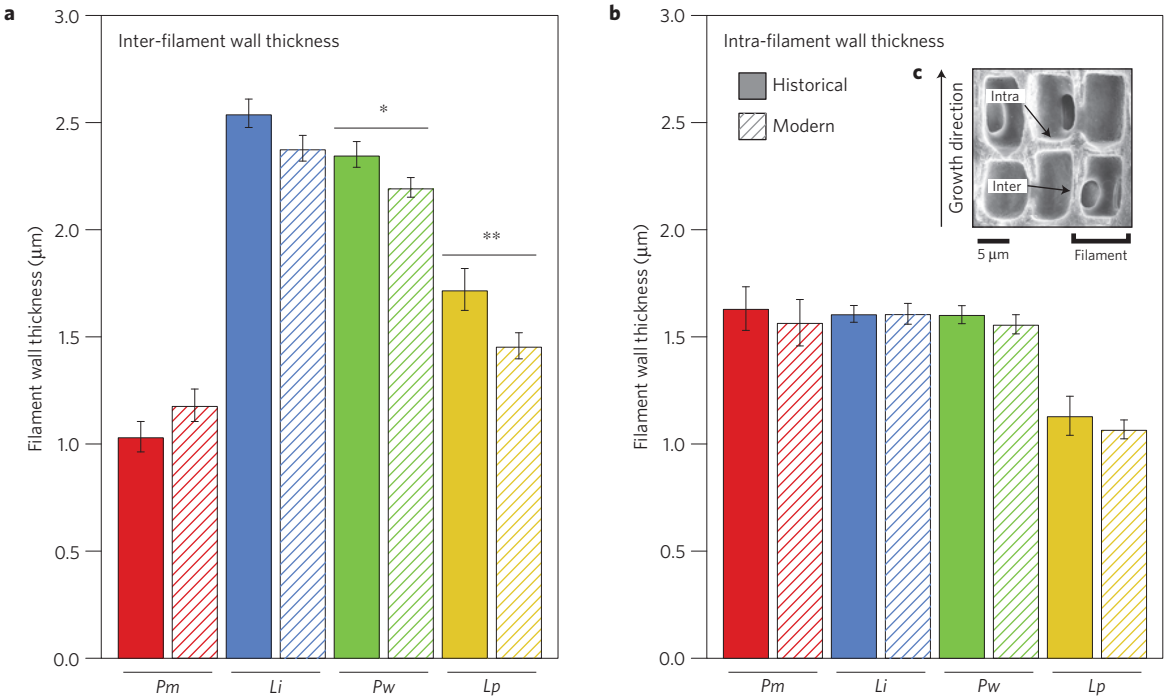

Figure 2 | Filament wall thicknesses. a,**b**, Comparison of inter-filament (**a**) and intra-filament (**b**) wall thicknesses for *P. muricatum* (historical $N=49$, modern $N=47$), *L. impressum* (historical $N=73$, modern $N=73$), *P. whidbeyense* (historical $N=73$, modern $N=73$) and *L. phymatodeum* (historical $N=22$, modern $N=45$). Data from historical specimens is shown as solid bars and modern specimens as hashed bars. Error bars indicate standard error. Significant reductions in inter-filament wall thickness were found between historical and modern specimens in *P. whidbeyense* (*, $p=0.022$) and *L. phymatodeum* (**, $p=0.025$). Inset **c** is an SEM image of *Lithothamnion glaciale* showing the positions of intra- and inter-filament walls.

or heavy grazing. In the thin, fast-growing species *L. phymatodeum* and *P. whidbeyense*, we observed a reduction in the thickness of inter-filament cell walls. These walls are arranged longitudinally within the algal individual (Fig. 2c), meaning that inter-filament cell walls form as an individual grows laterally. Therefore, decreasing the thickness of inter-filament cell walls probably reduces the cost of lateral growth in species of the thin morphological type, perhaps allowing the organism to present the same surface area for photosynthesis and maintain rapid lateral growth rates while reducing the structural cost (Supplementary Figs 1–4). On the other hand, reduced $CaCO_3$ production achieved by less total growth is concordant with the morphological changes observed in thick, slow-growing species in this study (Fig. 1), which we attribute to the larger energetic burden of maintaining a thick skeleton in lower-pH conditions.

This second mechanism may more directly affect algal ecology via competitive overgrowth interactions. In particular, decreased thickness of the growing margin will translate to a reduced competitive ability, as has been shown in the case of *P. muricatum*[13,26]. This species was formerly dominant in abundance and competitive ability in areas where grazers had been experimentally removed, and also in unmanipulated communities[23]. Modern data indicates a reversal, where *P. muricatum* now wins less than half of its competitive interactions, both with and without grazers, compared with 100% previously[13]. By testing specimens from these same competitive experiments in the 1980s–1990s (ref. 23) and 2010s (ref. 13), we have linked observed ecological change to a morphological mechanism. Changes in *P. muricatum* have been the clearest to identify thus far owing to the particular ecological importance of this species. However, we predict that *L. impressum* may be the next to show observable changes based on the morphological data we have collected here. Owing to the strong ecological dominance of a single species previously observed in this community, we hypothesize that competitive release may cause other CCA species to increase in abundance in the near term. Long-term community dynamics will ultimately depend on the severity of climate change as well as the degree of structural reduction of CCA skeletons, which could increase species' susceptibility to physical disturbances.

Recent laboratory studies of the coralline alga *Lithothamnion glaciale* revealed phased responses to elevated pCO_2 over exposure time. After three months, individuals cultured under high pCO_2 showed a reduction in cell (inter- and intra-filament) wall thickness whereas growth rate was maintained[3]. After ten months, however, there was a reduction in growth at all elevated pCO_2, but the cell wall thickness was maintained with respect to control specimens, as well as the volume-normalized amount of calcite deposited[10]. These results reveal different phases during acclimatization with a different mechanistic response in cell wall thickness and growth rate, which highlight the importance of conducting long-term studies, whether in the field or in the laboratory, and also suggest a potential sequence of trade-offs experienced as organisms begin to feel the energetic constraints of acidification stress. In the species studied here, ocean acidification seems to be more stressful to thicker species, which contain greater amounts of skeletal $CaCO_3$ per unit photosynthetic tissue (Supplementary Figs 3 and 4). Therefore, thicker species probably require an energetic response sooner than their thinner counterparts, and may thus be further along a potential trade-off sequence in present-day seawater conditions.

Recent studies have also shown the importance of including natural environmental variability in acidification due to the large diurnal variations in pH and pCO_2 experienced in kelp forest and coral reef environments[21,27]. Individuals living in a more variable habitat have been shown to be better acclimatized to changes in pCO_2 within the scope of the natural variability where an individual originated[6,21]. However, this is coupled with the finding that variable treatments exacerbate the effects of elevated pCO_2 compared to constant treatments with the same mean pCO_2 (ref. 27). Our study

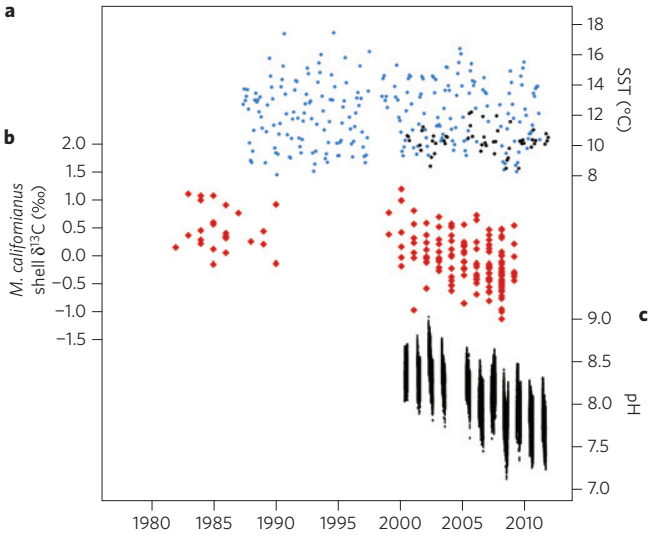

Figure 3 | Environmental context at Tatoosh Island. a, Mean monthly sea-surface temperature (SST) in °C. Blue points show data from Cape Elizabeth 1987–2012 (NOAA Buoy 46041, 47.4° N, 124.5° W; http://ndbc.noaa.gov) and black points data from Tatoosh Island 2000–2012 (48.4° N, 128.7° W). There was no trend in SST over time at either site. Cape Elizabeth consistently experiences daily temperatures 2–3 °C higher than Tatoosh Island, and is located ~50 km to the southeast[16]. **b**, Stable isotope composition of carbon ($\delta^{13}C$) measured in *M. californianus* shells from Tatoosh Island reveals a shift in carbon system chemistry over the past decade[16]. **c**, pH time series measured at Tatoosh Island exhibiting seasonal variation and year-to-year trends (pH decline −0.058 units yr^{-1}; refs 14,15). Data points show measurements every 30 min at high tide from April–September. Figure modified from ref. 13.

reports findings from a 30-year comparison of field specimens from a kelp-dominated shoreline, with large diurnal fluctuations in pH (refs 14,15), and therefore takes into account environmental variability as well as the gradual timescale of acidification in natural systems.

Although elevated water temperature has been neither observed nor predicted in the Northeastern Pacific, this phenomenon is of global concern in concert with acidification. Warmer temperatures boost growth and calcification rates in coralline algae[2,28], yet reduce the proportion of tissue that consists of $CaCO_3$ material and effectively reduce skeletal density as cells produced under elevated temperatures are less-extensively calcified[28]. Therefore, it is uncertain whether the elevated growth rates afforded by rising seawater temperatures can effectively 'rescue' observed declines in skeletal metrics engendered by ocean acidification.

In this study, we have identified a morphology-dependent response to ocean acidification in CCA, which underlies changes in the competitive abilities of these species in the field between the 1980s and 2010s (ref. 13). The mechanisms we have identified in crustose coralline algae may be applicable to other calcifying taxa with species-specific differences in morphological types dictated by skeletal thickness and growth rates. Corals are another example of 'photosynthetic' organisms that abound in morphological forms[29]. Variation in growth rates, skeletal thickness and branching alter the ratio of surface area to calcium carbonate skeletal volume, which is an energetic sink under acidification scenarios. Previous work has shown ocean acidification effects on sclerodermites, or groups of calcified fibres in the coral skeleton within septa, among coral recruits[30]. We suggest that future work looks for trade-offs between coral growth and the structure of septa, which may be analogous to intra- and interfilament cell wall structures. Owing to variations in calcification patterns, growth and structure among organisms and species, it is important to find morphological classifications to describe patterns of stress response to climate stressors such as ocean acidification. This method may be valuable as a more generalizable rule than studying individual responses at the species level.

Methods

Study site and physical data. *In situ* pH, as well as a suite of other environmental parameters, including sea-surface temperature (SST), chl *a*, salinity and dissolved oxygen[14,15] has been recorded at Tatoosh Island, Washington, USA in the Northeast Pacific (48.4° N, 128.7° W) since 2000. This data revealed a decline in pH of 0.058 units per year at Tatoosh Island[14,15]. Further, local seawater carbon chemistry near Tatoosh Island has been reconstructed from mussel shells back to 663 AD, and indicated the onset of these rapid changes in inorganic carbon chemistry occurred only over the past few decades relative to historical baselines[16]. These changes in pH and inorganic carbon cycling have occurred in the absence of other changes to the seawater environment, including changes in temperature, nutrients or upwelling[15,16]. Therefore, we have strong evidence that seawater inorganic carbon chemistry and pH have changed rapidly and in isolation over the past 30 years and intensified since 2000 at Tatoosh Island (Fig. 3).

Sample collection. At Tatoosh Island, specimens of *Lithophyllum impressum* Foslie, *Lithothamnion phymatodeum* Foslie, *Pseudolithophyllum muricatum* (Foslie) Steneck and R. T. Paine, and *Pseudolithophyllum whidbeyense* (Foslie) Steneck and R. T. Paine were transplanted onto artificial marine epoxy substrate (Sea Goin' Poxy Putty, Permalite Plastics, Rancho Dominguez, CA) by chiselling pieces $>1.5\,cm^2$ from the surrounding rock and embedding the sample into a flattened disc of wet epoxy *sensu* Paine[23]. Archival samples (*L. impressum*, $n=5$, 1981, 1981, 1993, 1994, 1997; *L. phymatodeum*, $n=3$, 1981, 1993, 1997; *P. muricatum*, $n=5$, 1981, 1982, 1993, 1994, 1997; *P. whidbeyense*, $n=6$, 1981, 1981, 1981, 1993, 1994, 1997) from previous transplants were preserved as dry specimens at the University of Washington, and were provided by R. T. Paine. Modern samples (*L. impressum*, $n=6$; *L. phymatodeum*, $n=6$; *P. muricatum*, $n=6$; *P. whidbeyense*, $n=6$) were transplanted in 2010 and collected in 2012, and were conducted with identical methods as for previous transplants, described above. Individuals were taken from the same populations and location at Hedophyllum Cove on Tatoosh Island for historical and modern transplants and collections. Individuals were collected at approximately 0 m MLLW (mean lowest low water) and all transplants were placed at exactly 0 m MLLW in historical and modern experiments. Both archival and modern specimens were dried in the shade for 48 h, and subsequently stored dry in the laboratory. All samples were grown in Hedophyllum Cove on Tatoosh Island for approximately two years, and collected during the spring (April–June). Specimens were grown in plots with grazers experimentally removed (manual removals) to control for confounding effects of grazing on thallus thickness and structure[13,23]. Growth rates were measured from digital photographs of transplants using ImageJ analysis software (http://imagej.nih.gov/ij/).

SEM measurements and analysis. For SEM analysis, archival and modern dried thalli were sectioned perpendicular to the axis of maximum growth, at the growing edge. Samples of *P. muricatum* were mounted on aluminium stubs and coated with 8 nm palladium for analysis on an FEI Nova NanoSEM 230 at the University of Chicago Materials Research Center. Samples of *L. impressum*, *L. phymatodeum*, and *P. whidbeyense* were mounted on aluminium stubs and coated with 20 nm gold for analysis on a Hitachi S-3500N SEM at the University of Bristol.

Using digital SEM photographs, we measured the intra- and inter-filament cell wall thickness (within and between cell layers, respectively; Fig. 2c; ref. 10). Measurements were made in three cells from the growth edge to avoid newly deposited material that may not be fully calcified. These measurements were performed using ImageJ analysis software. To quantify baseline species differences in historical samples, we used analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) Post-Hoc test. We used Welch's *t*-test to look for differences between treatments in for cell wall thicknesses. *L. phymatodeum* and *P. muricatum* cell wall data were non-normally distributed, so we performed a Mann–Whitney Rank Sum Test to test for differences over time in those species.

Fractional calcite density was measured using Image J analysis software (http://imagej.nih.gov/ij/). Calcite density, defined here as the fractional area within a digital quadrat composed of calcite-bearing structures[28], was determined by transforming cross-sectional SEM micrographs 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[26]. Calcite density was compared between archival and modern samples over all four species using ANOVA (Supplementary Fig. 3).

Thallus thickness along transects starting at the growing edge was also measured using digital SEM photographs[26]. The thickness of each algal thallus, or

individual, was measured at 33-μm intervals using ImageJ analysis software. To quantify baseline species differences in historical samples, we used ANOVA and Tukey's HSD Post-Hoc text, and we performed a two-tailed *t*-test to identify differences in average thallus thickness over time. All thickness and cell wall data is available in the Pangaea database (Pangaea.de), Issue #PDI-7649.

Received 13 March 2014; accepted 19 May 2014; published online 15 June 2014

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Acknowledgements

We would like to thank R. T. Paine for making his archival coralline algal specimens available for tissue analysis, Q. Guo for assistance on the SEM at the University of Chicago Materials Research Science and Engineering Center, F. B. McCoy for clerical assistance, and the Makah Tribe for access to Tatoosh Island and permission to conduct field research. R. T. Paine, C. A. Pfister, T. Price and J. T. Wootton provided helpful comments. S.J.M. would like to acknowledge research funding provided by the United States National Science Foundation Doctoral Dissertation Improvement Grant DEB-1110412 (C. A. Pfister and S.J.M.), the Achievement Rewards for College Scientists Foundation, and United States Government support under and awarded by DoD, Air Force Office of Scientific Research, National Defense Science and Engineering Graduate Fellowship, 32 CFR 168a, and by the United States National Science Foundation Graduate Research Fellowship, Grant No. 1144082. The United States National Science Foundation OCE-09-28232 (C. A. Pfister) and DEB-09-19420 (J. T. Wootton) funded Tatoosh research. F.R. would like to acknowledge the support of the Leverhulme Trust, RJ5540.

Author contributions

S.J.M. collected field specimens and designed the experiment. F.R. took SEM photos. S.J.M. and F.R. took measurements, analysed and discussed the data. S.J.M. wrote the manuscript with contributions from F.R.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to S.J.M.

Competing financial interests

The authors declare no competing financial interests.