

LETTER

Historical comparisons reveal altered competitive interactions in a guild of crustose coralline algae

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Abstract

As the ocean environment changes over time, a paucity of long-term data sets and historical comparisons limits the exploration of community dynamics over time in natural systems. Here, we used a long-term experimental data set to present evidence for a reversal of competitive dominance within a group of crustose coralline algae (CCA) from the 1980s to present time in the northeast Pacific Ocean. CCA are cosmopolitan species distributed globally, and dominant space holders in intertidal and subtidal systems. Competition experiments showed a markedly lower competitive ability of the previous competitively dominant species and a decreased response of competitive dynamics to grazer presence. Competitive networks obtained from survey data showed concordance between the 1980s and 2013, yet also revealed reductions in interaction strengths across the assemblage. We discuss the potential role of environmental change, including ocean acidification, in altered ecological dynamics in this system.

Keywords

CCA, climate change, competitive dominance, competitive networks, Coralline algae, historical comparison, intertidal community ecology, ocean acidification.

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INTRODUCTION

Climate is known to be a key driver of species distributions and life histories, both through its effects on physical resources and its interaction with organism physiology. Indeed, much recent work across ecology has focused on determining how changes to climate, in various forms, could affect population dynamics or species composition of ecological communities. We expect that changes to climate over time will alter the interplay between organisms and physical resources, including temperature or nutrient availability, and thus alter ecological dynamics (Voigt *et al.* 2003).

An often cited concern is the effect that climate change will have on species richness or biodiversity (reviewed in Kappelle *et al.* 1999). This stems not only from a long-standing disciplinary interest concerning drivers of species coexistence (Paine 1984), but also from the idea that less diverse communities may be less resilient to stressors (originally posited by May 1973; reviewed in McCann 2000). In this study, we compare baseline competitive networks of crustose coralline algae (CCA) over 30 years in the intertidal Northeast Pacific to ask whether competitive dynamics have changed over time.

Coralline algae are widespread over many latitudes and environments (Adey & MacIntyre 1973; Littler *et al.* 1991), both during the modern day and over geologic time (Aguirre *et al.* 2000). Within the crustose coralline algae, competitive interactions are generally hierarchical with herbivore-mediated reversals that increase the level of competitive intransitivity (Dethier 1984; Paine 1984; Steneck *et al.* 1991; Dethier & Steneck 2001). Competition occurs as two-dimensional (planar) overgrowth, and a species' position in the hierarchy depends on its growth morphology (Steneck

et al. 1991). Traditionally, competitive dominants grow slowly with thick thalli and elevated growing edges, which enable them to overgrow subordinates. Conversely, subordinates grow faster and can more readily occupy bare space (Dethier 1994).

These interactions are further modified by the presence of grazers, as resistance to grazing damage depends on thallus thickness. With increasing presence of grazers, typically large-bodied chitons, limpets and urchins, the competitive networks among CCA become less deterministic, or in other words, contain increasing intransitivity of competitive outcomes (Paine 1984). Competitive intransitivity occurs when competitors cannot be ranked in a perfect competitive hierarchy (Rojas-Echenique & Allesina 2011). 'Rock-paper-scissor' dynamics, for example, are the most famously studied case of competitive intransitivity (Gilpin 1975; May & Leonard 1975). Importantly, intransitivity is a mechanism for the maintenance of biodiversity, as it can prevent or delay the establishment of a competitively dominant species (Buss & Jackson 1979; Kerr *et al.* 2002). While complete intransitivity is not documented in this guild of CCA, the natural presence of grazers promotes an intransitive competitive network below a slow-growing competitive dominant (Paine 1984).

As the ocean climate has changed over time, we may expect to see responses in this guild of important primary producers. Specifically, changes in global climate stressors such as sea surface temperature, ocean acidification or even the population dynamics of co-occurring species (including grazers) may have led to altered competitive dynamics. The degree to which network intransitivity has changed may have resonating consequences for community function, stability and species richness (Rojas-Echenique & Allesina 2011).

MATERIALS AND METHODS

Competition experiments

To set up competition experiments, we recreated the methodology of experiments conducted from 1980 to 1984 at Tatoosh Island, WA, USA, 48.4° N and 128.7° W (Paine 1980, 1984). Four species of crustose coralline algae, *Lithophyllum impressum* Foslie, *Lithothamnion phymatodeum* Foslie, *Pseudolithophyllum muricatum* (Foslie) Steneck & R.T. Paine and *Pseudolithophyllum whidbeyense* (Foslie) Steneck & R.T. Paine, were transplanted onto synthetic arenas in experimental plots. Transplants were conducted at two sites on Tatoosh Island where extensive horizontal benches at a tidal height of 0 m MLLW (mean lower low water) promote nearly 100% cover of CCA: Hedophyllum Cove (HC) on the north-eastern side of the island, and Simon's Landing (SL) on the eastern side. These sites are roughly 425 m apart and are assumed not to differ in water temperature and chemistry, although Simon's Landing experiences greater wave exposure. At each site, we established three replicate plots consisting of paired grazer removals (GR) and grazer controls (GC) at the 0 m MLLW tidal height. At Hedophyllum Cove, two of these plots are the locations of RT Paine's original experiments, with one added plot at Hedophyllum Cove and three at Simon's Landing for increased experimental replication (Fig. S1). Within each grazer treatment subplot, we placed

four 4-species transplants and six 2-species transplants, each containing one healthy individual of each species (Fig. S2). Species position within the 4-way transplants was determined at random and replicated exactly in all plots. Each plot also contained every pairwise species combination. Transplants at Hedophyllum Cove were initiated in June 2010 and terminated in June 2012. Transplants at Simon's Landing were initiated in May 2011 and terminated in August 2012.

Healthy crustose coralline individuals were sampled using a chisel to remove pieces 2 cm² or larger. These individuals were transplanted onto synthetic arenas using Sea Goin' Pox Putty (Permalite Plastics, Inc., Rancho Dominguez, CA, USA), a marine epoxy compound, following the protocol of Paine (1980). At each site, transplanted individuals originated no more than 10 m from the transplanted location, and are therefore assumed to belong to the same population within a site. Individuals were transplanted such that growth over the following year would result in a competitive interaction between species as the individuals grew laterally on the epoxy substrate. Articulated coralline species (*Bossiella* and *Corallina* spp.) were not transplanted into experimental plots, but instead grew onto epoxy arenas laterally from mature individuals on the surrounding natural substrate. Articulated corallines also colonised epoxy arenas, but colonists were small individuals that were largely ephemeral in our experiments. Articulated colonists therefore did not contribute to

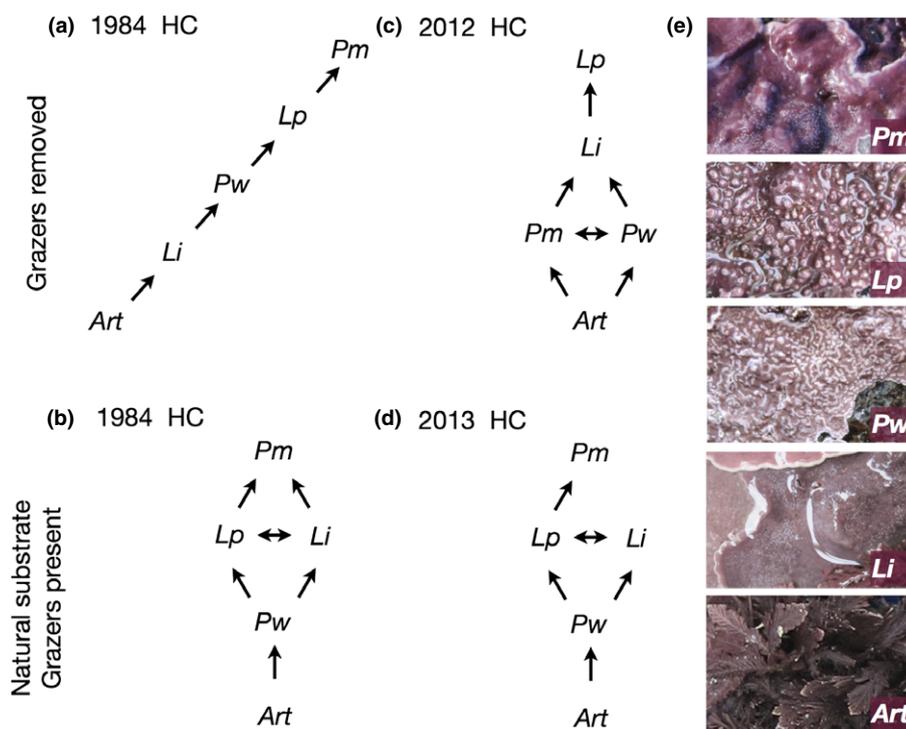


Figure 1 Competitive network diagrams among crustose coralline algae at Hedophyllum Cove. (a) Historical results based on experimental arenas without grazers. (b) Historical results from natural substrate with grazers. (c) Modern results based on experimental arenas without grazers. (d) Modern results from natural substrate with grazers. (d) Li and Pm have no connecting arrow because we did not see this interaction in 2012–2013. Arrows point to winners in grazer-free treatments, determined by a pairwise winning frequency > 0.6. Double-headed arrows indicate a pairwise winning frequency between 0.4 and 0.6. Although the topology of interactions on natural substrates is nearly identical over the study (b vs. d), the quantitative descriptions of interactions have changed significantly through time (Fig 2b). (e) Shows photographs of each species.

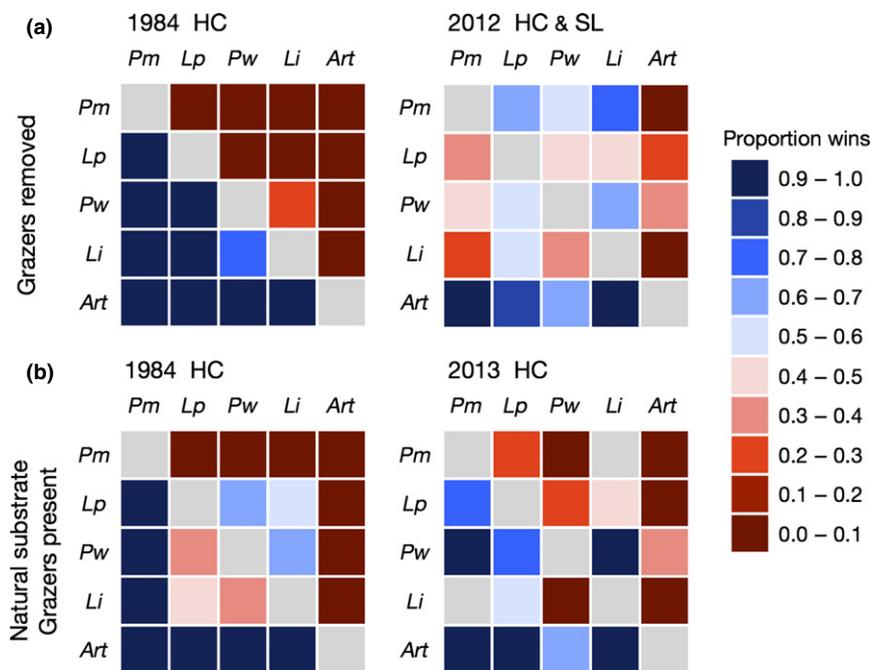


Figure 2 Pairwise winning probabilities for each crustose coralline algal species. Heat map shows the probability of a given species (labelled by column) to win a competitive bout against each other species (labelled by row), based on (a) experimental data where grazers were removed and (b) natural substrate with grazers was present. Darker blue indicates a winning probability closer to 1.0, whereas darker red indicates a winning probability closer to 0.0. Grey squares indicate no data.

final competitive outcomes, in contrast to mature individuals growing in from the edges of the arenas.

During the experiment, transplants were photographed every 10–14 days. These photographs were analysed to measure growth using both surface area and perimeter with ImageJ software (rsb.info.nih.gov/ij/) and to document overgrowth competition patterns over time. All transplants were photographed prior to their removal from the field at the end of the experiment. Transplants were fully dried and photographed again. The metric of overgrowth ability was calculated as total wins over total contests for each species, determined by planar overgrowth of one species by the other. Statistical significance of changes in competitive abilities was determined using a chi-squared test comparing observed total frequency of competitive wins to the expected based on historical data. Historical outcomes were chosen as the baseline to test for changes in the frequencies of winning between historical and modern competitive data. Competitive topologies (Fig. 1) were based on pairwise competitive frequencies (Fig. 2, Tables S1 and S2). An arrow indicates a winner defined as $\geq 60\%$ wins and a double-headed arrow indicates no clear winner defined as 40–60% wins, as per Paine (1984).

Growth rates

Growth rates are reported as change in individual surface area over initial surface area to account for size-dependent growth. A two-way analysis of variance (ANOVA) was performed for each species as a function of site and grazer treatment.

Grazer removals

Grazer removals were maintained approximately every 10–14 days during April–August of each year. Species removed included the chitons *Katharina tunicata*, *Mopalia* spp. and *Tonicella* spp.; the limpets *Acmea mitra*, *Lottia* spp. and *Tectura scutum*; and the urchins *Strongylocentrotus droebachiensis* and *Strongylocentrotus purpuratus*. All grazers within reduced grazer plots (three subplots per site, each $\sim 1.5 \text{ m}^2$, Figs S1 and S2) were recorded, measured and removed at low tide. Grazers were not removed during winter months due to restricted accessibility of Tatoosh Island during winter weather conditions. To account for this, we estimated a range of grazer removal efficiencies concordant with that used previously in this system (Paine 1980, 1984). To place an upper bound on grazer removal efficiency, grazers found in a removal plot during maintenance were assumed to have entered the plot during the mid-point of the time interval between maintenance removals, including winter intervals. To place a lower bound on grazer removal efficiency, we treated grazers found in the plot during frequent summer removals differently than those found after the winter interval. In this method, grazers found in a removal plot during summer months were treated as above and assumed to have entered the plot halfway between maintenance removals, while grazers were assumed to have entered the plot immediately during the winter interval (i.e. assumed to have been in the plot for the entire winter rather than having entered at the mid-point of the winter interval). In each case, mean abundance of each grazer species in the removal plot was calculated over 1 year and compared with ambient grazer abundances at that site to

obtain a percentage of natural grazer abundance, referred to as removal efficiency.

Abundance of grazers and coralline algae on natural substrates

Ambient abundances of grazers were obtained by 0.1-m² quadrats sampled at random at Hedophyllum Cove (2010–2013, $n = 9$ –20 quadrats per year) and Simon's Landing (2011–2013, $n = 9$ –31 quadrats per year). Trends in ambient grazer abundance over time were tested using repeated-measures analysis of variance (ANOVA) separated by site to compare historical and modern data.

Crustose coralline algal species abundances were measured at Hedophyllum Cove and at Simon's Landing by random point samples, taken by repeated, haphazard tosses of a metre stick in the kelp bed and surveying the understory beneath six randomly placed markings on the metre stick. Results are expressed as percentage of total point samples in April 2013 (Hedophyllum Cove, $n = 153$; Simon's Landing, $n = 51$). The number of all competitive bouts was determined by surveying the entire length of the randomly tossed metre stick for overgrowth interactions, defined as planar overgrowth of one coralline algal species by another. As in the historical surveys and in the interest of simplifying the competitive ability index, infrequent occurrences of stalemates or ties were noted but not counted. In addition to being rarely observed, stalemates occur only between evenly matched competitors (40–60% pairwise winning probability), so the addition of stalemate data would have no effect on pairwise overgrowth probabilities or network topologies.

RESULTS

Competitive interactions

Changes in total fraction of competitive wins for each species from the 1980s (measured at Hedophyllum Cove) to 2012 (at both Hedophyllum Cove and Simon's Landing) revealed a reversal in the dominance structure of this competitive hierarchy (Fig. 3). In these experiments, the competitive ability of the former competitive dominant, *P. muricatum*, decreased from 1.0 in 1984 to < 0.25 in 2012 at Hedophyllum Cove and < 0.50 in 2012 at Simon's Landing (Fig. 3a, f and Table S3). Pairwise win frequencies demonstrated decreased intensity of hierarchical interactions over time, marked in particular by reduced dominance of *P. muricatum* in pairwise interactions and increased competitiveness of articulated species (Fig. 2a and Table S1). It is important to note that 1984 data in the presence of grazers were obtained by observing the outcomes of coralline algal competition on the natural rock substrate, whereas 2012 data in the presence of grazers were generated from transplant experiments to an artificial substrate. We thus focus our inferences for grazer-reduced interactions occurring on synthetic competitive arenas and on survey data from natural rock substrate for interactions with grazers, each of which were included in both historical and modern data sets. Competitive network diagrams summarise data from pairwise competitive outcomes on experimental arenas in the absence of grazers, again showing increasing intransitivity over time (Fig. 1a vs. c).

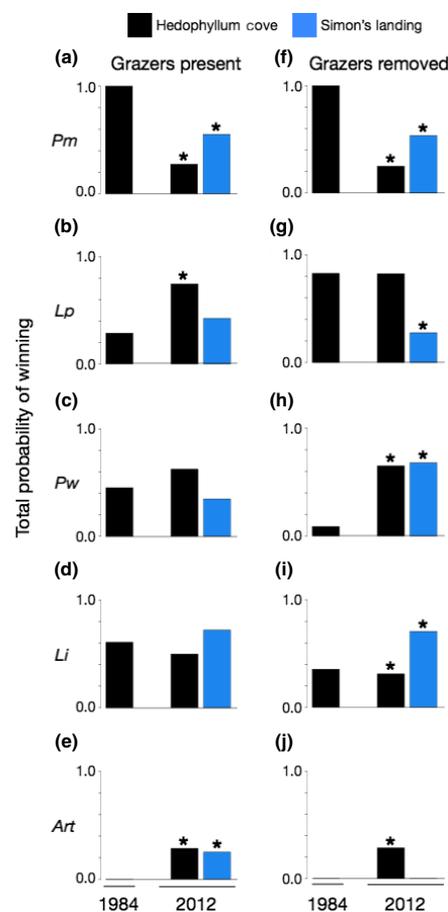


Figure 3 Competitive ability index of each crustose coralline algal species under different treatments. Total fraction wins ranges from 0.0 to 1.0 and is calculated as total number of wins over total wins and losses. Black bars indicate data from Hedophyllum Cove, and blue bars indicate data from Simon's Landing. Year is shown on the x-axis. A star (*) indicates a significant difference between 1984 Hedophyllum Cove and 2012 conditions at either Hedophyllum Cove or Simon's Landing, defined as $P < 0.001$ from a χ^2 test. (a–e) Left-hand panels show competitive ability determined with grazers present. (f–j) Right-hand panels show competitive ability determined in grazer-free treatments.

Surveys of natural rock substrate surrounding experimental transplant sites also revealed a statistically significant decline in the overall competitive ability of *P. muricatum* at both sites from 1.0 in 1984 at Hedophyllum Cove to 0.88 and 0.87 in 2013 at Hedophyllum Cove and Simon's Landing respectively (χ^2 test, $P < 0.001$; Table S2). Competitive network diagrams summarise data from pairwise competitive outcomes on natural rock substrate in the presence of grazers, showing no overall change in topology of the competitive hierarchy since 1984 (Fig. 1b vs. d). However, the hierarchical strength of interactions has declined over time even in the unmanipulated community (Fig. 2b); although *P. muricatum* still emerges as the competitive dominant under these conditions, it is observed losing to *L. phymatodeum* 28% of the time (Fig. 2b, Tables S2 and S4). Furthermore, point samples of species abundance on natural rock substrate near transplants reveal no statistical change in the abundance of *P. muricatum* over time (Table 1 and Fig. S3; linear regression, $r^2 = 0.396$, $P = 0.107$).

Table 1 Abundance of the crustose coralline alga *Pseudolithophyllum muricatum* at Tatoosh Island

Year	Month	% <i>P. muricatum</i>	Point samples (N)
1983	6	25.5	255
1986	6	17.7	85
1992	4	17.4	213
2008	5	20.3	79
2011	7	12.8	78
2013	4	6.0	84

Per cent of *P. muricatum* abundance of total point samples of crustose coralline algae taken in the kelp understory near the 0-m mean tidal height at Hedophyllum Cove, Tatoosh Island. See also Fig. S5.

Grazer abundances

Between 1984 and 2013, the density of the largest grazer has declined at Hedophyllum Cove (Fig. S4). Grazer density data at Simon's Landing are available since 1995, and grazer density at that site shows no trend over time in any species and is currently similar to what it was at Hedophyllum Cove in 1984 (Fig. S4). Abundances of all species who graze on crustose coralline algae were measured, namely the chitons *Katharina tunicata*, *Mopalia* spp. and *Tonicella* spp.; the limpets *Acmea mitra*, *Lottia* spp. and *Tectura scutum*; and the urchins *Strongylocentrotus droebachiensis* and *Strongylocentrotus purpuratus*, regardless of size (Fig. S4). The grazers who inflict the greatest damage on corallines are the black chiton, *K. tunicata*, the dunce cap limpet, *A. mitra* and the urchins *S. droebachiensis* and *S. purpuratus*. The density of the chiton *K. tunicata*, the most common large-bodied (>5 cm length) grazer, was lower in 2010–2013 than in the 1980s at Hedophyllum Cove (ANOVA, $F_{1,10} = 56.519$, $P < 0.001$), but not compared to the 1990s at Simon's Landing (ANOVA, $F_{1,10} = 2.611$, $P = 0.137$). The abundance of the chiton *Mopalia* was significantly lower at both Hedophyllum Cove and Simon's Landing in 2010–2013 (ANOVA, $F_{1,10} = 11.471$, $P = 0.007$ and $F_{1,10} = 9.219$, $P = 0.013$ respectively). The density of the limpets *Lottia* and *Tectura* was pooled due to their ecological similarity. There was no observed difference in their abundance at Hedophyllum Cove. On the other hand, the density of the dunce cap limpet *A. mitra* declined significantly at Hedophyllum Cove ($F_{1,10} = 21.135$, $P < 0.001$). We do not report differences over time at Simon's Landing for any limpet species, as their abundances were not measured previously at this site. The abundances of the chiton *Tonicella* and the urchins *S. droebachiensis* and *S. purpuratus* were not significantly different over time at either site.

Although we were unable to access experimental sites in fall and winter and we expect mobile molluscan grazers to enter the sites during this time, grazer removal treatments were highly effective when we quantified the mean number of grazers entering each plot between removals. Abundance of the grazer *K. tunicata* was reduced from 57.8 to 100.0% at Hedophyllum Cove in both years, and remained nearly completely removed at 100% (both minimum and maximum efficiency) at Simon's Landing (Table S5). Our only instance of low grazer removal efficiency was the chiton *Mopalia*, where we estimate 1–2 individuals per m² in removal plots on average each year,

whereas ambient density of *Mopalia* was around 0.5 individuals per m² (Fig. S4 and Table S5). A further indication that our grazer removals were efficient was based on the absence of grazing marks on coralline crusts in removal plots. Grazer removal efficiency in historical data is estimated at 90%, and was calculated using methods similar to our estimates of maximum removal efficiency (Paine 1984).

Growth rates

To test for trends between grazer abundances and algal growth, we examined growth rates separately by grazer treatment and site, defined as change in surface area per year, and normalised by the initial size of each individual. Growth rates did not differ as a function of grazer abundance or site (two-way ANOVA by grazer treatment and site; *L. impressum* $F_{1,90} = 0.110$, $P = 0.741$ (grazer), $F_{1,90} = 0.066$, $P = 0.798$ (site); *L. phymatodeum* $F_{1,94} = 2.637$, $P = 0.108$ (grazer), $F_{1,94} = 0.5456$, $P = 0.462$ (site); *P. muricatum* $F_{1,41} = 0.449$, $P = 0.506$ (grazer), $F_{1,94} = 0.093$, $P = 0.762$ (site); *P. whidbeyense* $F_{1,96} = 0.608$, $P = 0.437$ (grazer), $F_{1,96} = 1.001$, $P = 0.320$ (site)). Our results indicate no evidence for a growth response to grazer abundance in any of these species, whether between experimental plots with grazers removed or present, or between sites with different ambient grazer densities. When we tested the effect of grazer presence on growth rates using data only from April to August 2011, during which time grazer removals were performed most regularly and with the highest removal efficiency (Table S5), we similarly observed no effect of grazers on growth rates (ANOVA by grazer treatment due to reduced sample size: GR pooled at both sites, HC GA and SL GA in order of increasing grazers; *L. impressum* $F_{2,42} = 0.040$, $P = 0.843$; *L. phymatodeum* $F_{2,42} = 0.108$, $P = 0.744$; *P. muricatum* $F_{2,36} = 0.076$, $P = 0.785$; *P. whidbeyense* $F_{2,35} = 0.088$, $P = 0.768$).

DISCUSSION

In experimental treatments, the competitive hierarchy within this guild of crustose coralline algae has weakened, and the intransitivity of competitive interactions within coralline algae has increased between the 1980s and 2010s (Fig. 1a vs. c). Modern data on competitive interactions (2010–2012) are available from two sites on Tatoosh Island, Hedophyllum Cove and Simon's Landing, whereas corresponding data from the 1980s is available only from Hedophyllum Cove (Table 2). We therefore focus our discussion primarily on data from Hedophyllum Cove, which offers a within-site historical comparison, and use data from Simon's Landing to corroborate the directional changes in competitive interactions we found at Hedophyllum Cove. Similarly, pairwise competitive experimental bouts indicated that the dominance structure within this guild has become less deterministic between 1984 and 2012 either with or without grazers (Fig. 2a, b).

While experimental competitive abilities of all coralline species in this study changed between the 1980s and present, the former competitive dominant, *P. muricatum*, and the former group of subordinate species, articulated corallines, showed the greatest changes. *P. muricatum* has gone from winning

Table 2 Availability of historical (1980s) and modern (2010s) experimental and survey data

	1980s		2010s			
	Hedophyllum Cove		Hedophyllum Cove		Simon's Landing	
	Grazers	No grazers	Grazers	No grazers	Grazers	No grazers
Experimental arenas		X	X	X	X	X
Competition						
Growth rates			X	X	X	X
Grazer abundance	X		X	X	X	X
Natural rock surveys	X		X		X	
Competition						
Species abundance	X		X		X	
Grazer abundance	X		X		X	

1980s data are available from only Hedophyllum Cove, whereas 2010s data are available both from Hedophyllum Cove and Simon's Landing (sites on Tatoosh Island, WA, USA).

100% of experimental competitive bouts at Hedophyllum Cove between 1980 and 1984, both in the presence and absence of grazers, to winning less than 25% of the time, both with and without grazers (Fig. 3a, f). Although historical data do not exist for Simon's Landing, the decline in *P. muricatum*'s competitive ability is corroborated by results from that site, where *P. muricatum* wins less than 50% of its competitive bouts in the presence and absence of grazers (Fig. 3a, f). Slight differences between experimental outcomes at Hedophyllum Cove and Simon's Landing may be attributed to the different experimental lengths at these sites; Hedophyllum Cove experiments ran an additional 8 months, spanning the winter period during which grazer removals are less efficient.

We also find changes at the base of the experimental competitive network. Articulated corallines have gone from being truly fugitive species, which coexist with superior competitors due to greater dispersal and colonisation rates, to being viable competitors on artificial surfaces in this system (Fig. 3e, j). Alone, these changes represent a significant alteration of competitive interactions within this guild. Pairwise win frequencies led to an appreciable difference in experimental competitive network diagrams, which also indicate increased intransitivity within this guild (Figs 1 and 2a). In contrast to historical data at Hedophyllum Cove, modern competitive networks at both Hedophyllum Cove and Simon's Landing are no longer purely hierarchical in the absence of grazers (Fig. 1a vs. c). Reduced competitive ability in *P. muricatum* has already led to changes in its interactions with other species in its functional guild, and the resulting altered dominance structure will likely affect the populations of competing species. Especially in a system where complex networks of intransitive pairwise or subgroup outcomes lead to the coexistence of the members of the system as a whole (Paine 1984), alterations to ecological interactions may be important to local community structure (Kerr *et al.* 2002; Rojas-Echenique & Allesina 2011).

The experimental removal of grazers during both study periods allowed us to isolate and compare grazer-reduced performance in competitive outcome, even while grazer abundance was declining at Hedophyllum Cove between 1984 and 2013. On artificial experimental arenas, competitive networks differed in both topology (Fig. 1a, c) and in hierarchical

strengths (Fig. 2a), whereas census data from competition on natural substrate indicated reduced hierarchical strength (Fig. 2b) despite similar network topology (Fig. 1b, d). We suggest that decreased strengths of interactions and therefore increased intransitivity have not translated to a decline in the competitive dominance or local abundance of *P. muricatum* in the natural community, a result perhaps due to memory effects in slow-growing, long-lived populations.

Whereas experimental arenas effectively allow for a resetting of interactions, whether in the presence or absence of grazer effects, natural communities are subject to continuous competitive interactions with substantial carry-over effects from previous competitive bouts, potentially resulting in a slower rate of ecological change. On natural substrate, for example, there exists little to no bare space, and experimental transplants of CCA individuals onto bare substrate force the initiation of new overgrowth interactions. Interaction strengths have decreased even on natural substrate (Fig. 2), although this is not reflected in the interaction topologies. Interaction topologies can account only for the direction of interactions and do not represent their strengths, and thus remain unchanged (Fig. 1). Similarly, pairwise interaction outcomes have not changed, and survey data show little evidence for decline in the competitive dominance of *P. muricatum* (Figs 1, 2b, Tables S2 and S4). This subtle difference in competitive dynamics in the survey data may be indicative of changes underway in the natural community.

The lag time or memory effect inherent in ongoing natural community interactions may be responsible for a seemingly similar interaction topology between the 1980s and 2010s in our survey of the natural substrate when compared with experiments on artificial arenas. Lags in response may also result in a delayed decline in abundance of *P. muricatum* (Fig. 1). Because changes in abundance of long-lived species may not be detectable for decades, even when vital rates are in decline (Doak 1995), it follows that declines in long-lived temperate intertidal crustose coralline algae may be difficult to detect for years or decades. Although ages of such algae are difficult to obtain, *P. muricatum* has been observed at Tatoosh Island in circular patches of up to 0.4 m in diameter (Steneck & Paine 1986), which would take between 35 years

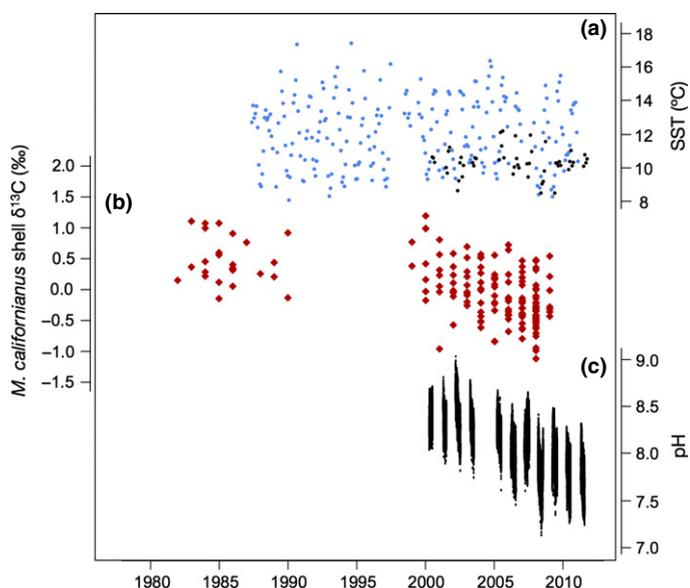


Figure 4 Environmental context at Tatoosh Island, WA. (a) Blue circles: mean monthly temperature from Cape Elizabeth, WA, USA (NOAA Buoy 46041, 47.4° N, 124.5° W, measured 1987–2012), ranges 7.5–16.9°C year-round and shows no trend over time. Black circles: mean monthly temperature from April to September measured at Tatoosh, ranges 7.9–11.6°C and shows no trend over time from 2000 to 2011 (Pfister *et al.* 2007, 2011). (b) Red diamonds: $\delta^{13}\text{C}$ from the shell carbonate of *Mytilus californianus* (data from Pfister *et al.* 2011) shows the timing of shifts in seawater carbonate chemistry at Tatoosh. (c) In black: time series of in situ pH (total scale) measured every 30 min from April to September at Tatoosh (data updated from Wootton & Pfister 2012). Within-year variance is explained by diurnal and seasonal variation in algal photosynthesis and respiration along the coast (Wootton *et al.* 2008; Pfister *et al.* 2011).

(given a maximum lateral growth rate of 5.5 mm year⁻¹, Steneck 1985) and 200 years (given a mean growth rate of 2.0 mm year⁻¹ measured for *P. muricatum* in this study) to accrue. Subtidal rhodoliths, free-living coralline algae, have been aged to several hundred years using growth bands (Hal-far *et al.* 2007). Therefore, we might not expect to see an immediate statistically detectable decline in the abundance of *P. muricatum* on the scale of this study, and the direct measurements of altered competitive dominance we observe experimentally may be the first indications of pervasive ecological change in this system (Edwards & Schreiber 2010).

Given the evidence for ecological change in this system over time and the evidence that changes were not due to grazer effects, we queried whether there were correlates with ocean climate data from the northeast Pacific. A time series of *in situ* pH measurements at Tatoosh Island reveals sustained pH decline from 2001 to 2012 unaccompanied by changes in seawater temperature (Fig. 4a, b and Figs S5, S6; Wootton *et al.* 2008; Wootton & Pfister 2012). The observed rate of pH decline at Tatoosh Island is an order of magnitude larger than has been predicted and measured at open ocean and low-latitude sites (−0.058 units year⁻¹, discussed in Wootton & Pfister 2012), and similarly low pH levels are recorded nearby in the California Current (Feely *et al.* 2008) and within Puget Sound, also in the absence of seawater

temperature change (Feely *et al.* 2010). These changes in pH are corroborated by recent, unprecedented shifts in seawater inorganic carbon chemistry over the last two decades at Tatoosh Island (Fig. 4c; Wootton *et al.* 2008; Wootton & Pfister 2012). Carbon isotope data ($\delta^{13}\text{C}$) from the shells of the mussel *Mytilus californianus* provide additional historical background for these major changes in carbonate chemistry back to 663 AD, and reveal a significant change in local carbon chemistry between archival (663–1990) and modern (1997–2010) samples (Fig. 4b; Pfister *et al.* 2011). Therefore, although our study did not expressly test the effects of ocean acidification or ocean climate drivers directly on CCA community dynamics, the altered ecological dynamics documented here are concurrent with the onset of ocean acidification at this site, and consistent with the physiological responses of coralline algae to ocean acidification reported in previous studies.

Recent studies of crustose coralline red algae have shown evidence for physiological response to ocean acidification that may explain altered competitive interactions (Martin & Gattuso 2009; Ragazzola *et al.* 2012; McCoy 2013; Noisette *et al.* 2013). At Tatoosh Island, *P. muricatum* has become thinner at its growing edge over the same 30-year interval, which aligns with the hypothesis that acidification may increase the cost of calcified tissue production and therefore favour a reduction in tissue accretion in calcifying organisms (McCoy 2013). Historically, *P. muricatum* was known to be much thicker than the other species in this guild: up to 10× thicker than its congener, *P. whidbeyense* (Steneck & Paine 1986). Edge thickness is a trait that confers an important competitive advantage within this guild (Steneck *et al.* 1991), and has enabled *P. muricatum* to previously win the majority of its competitive bouts with other species in this guild (Dethier 1994). Observed differences in its edge thickness may thus provide a logical link between effects of ocean acidification on organism physiology to changes in ecological traits described in this study.

Although we observed differences in competitive networks at Hedophyllum Cove between the 1980s and the 2010s, we did not find evidence that altered competitive interactions have resulted from a decline in the grazer community. If the observed changes in species interactions were due to grazer effects, no difference between historical and modern grazer removal data would be expected. Indeed, because we find concordant competitive reversals in both experimental arenas with grazers present and removed (quantitative topology) as well as reduced hierarchical strength on natural substrate (qualitative topology) across two sites with different ambient grazer abundances (Fig. 3), we conclude that competitive interactions are likely responding to environmental factors.

Based on the decreasing role of grazers in controlling CCA competitive network topology, we make the case here that changes induced by environmental stress, including ocean acidification, could supplant strong trophic control historically demonstrated in benthic algae (Paine 1984, 2002). As has been shown in cases of aquatic systems, trophic context is required to fully understand the effects of environmental changes to the system (Schindler 1990). Given our observations that trophic interactions have had a reduced effect on competitive dynamics among crustose coralline algae, we argue that

climate change studies should include the trophic context of a given species to test whether trophic control is central to the fate of future communities.

We constructed these experiments to be concordant in methodology and composition to those in the 1980s. However, there are two additional species that are part of this guild: *Chiharaea bodegensis* and *Mesophyllum vancouveriense*. *C. bodegensis* is competitively inferior (RT Paine, personal communication) and comprised only 1% of all coralline algae at Hedophyllum Cove in 2013, and is thus unlikely to alter the hierarchy we present. In contrast, previous studies from the 1980s to 1990s have found *M. vancouveriense* to be competitively superior to *P. muricatum* in the absence of grazers (RT Paine, personal communication). However, *M. vancouveriense* is a thin crust, and was historically competitively subordinate to *P. muricatum* with grazers present (RT Paine, personal communication). As with *C. bodegensis*, *M. vancouveriense* was absent from our censuses in 2013, which may be attributed to the occurrence of both of these species at a slightly lower tidal height (< 0 m MLLW) than the other species studied here. Thus, it remains to be seen whether the changed fate of *P. muricatum* will be exacerbated by the success of the thinner *M. vancouveriense*, which has the potential to benefit in the context of our observed decline in grazer abundance. Given the potential links between morphological traits and competitive response to ocean acidification in this guild, and the potential for sea level rise to alter fine-scale species zonation patterns within the intertidal, *M. vancouveriense* may emerge as an important competitor and contribute to the declining abundance of *P. muricatum*.

Our experimental data reveal major changes in the competitive abilities of CCA, whereas survey data indicate a slower rate of ecological change in non-experimental plots. Experimental transplants eliminate carry-over effects from previous or ongoing competition, and therefore effectively test ecological interactions. In contrast, natural communities are comprised of various stages of competition among species and individuals, and may conceal rapid ecological changes. In such cases, it is important to assay immediate species interactions as well as topologies of existing networks. As near-shore communities respond to changes in the ocean environment, altered competitive and trophic relationships will interact to shape new communities. It is important to conduct ecologically motivated experiments in natural systems and to make use of available historical experimental and observational data sets to fully comprehend the cumulative effects of such relationships on trophic control and community structure.

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AUTHORSHIP

S.J.M. and C.A.P. designed experiments, S.J.M. performed field experiments and collected census data and S.J.M. analysed the data and wrote the manuscript with contributions from C.A.P.

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