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Calcification does not necessarily protect articulated coralline algae from urchin grazing

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ABSTRACT

Calcification is widely thought to be an adaptation that reduces the impact of herbivory. Recent work has shown that ocean acidification may negatively impact calcification of marine organisms, including coralline red algae, which could theoretically increase the susceptibility of corallines to benthic grazers. By manipulating calcium carbonate content of three articulated coralline algal species, we demonstrated that calcification has a variable and species-specific effect on urchin grazing. For two species, *Corallina vancouveriensis* and *Corallina officinalis* var. *chilensis*, reductions in calcium carbonate content did not cause a significant increase in urchin grazing, raising questions about the benefit of calcification in these species. For *Calliarthron tuberculosum*, reduced calcium carbonate content caused an increase in urchin grazing rates but only after calcium carbonate had been reduced by more than 15%, suggesting that only dramatic shifts in calcification would make *C. tuberculosum* more susceptible to urchin grazing. We hypothesize that the herbivory-reducing benefits of calcification likely depend upon coralline thallus morphology. Negative impacts of ocean acidification on calcification in coralline algae may not necessarily increase herbivory rates.

1. Introduction

Coralline algae are central players in the ecology of nearshore marine ecosystems worldwide, chemically stimulating the recruitment of invertebrates (e.g., Barner et al. 2016; Barnes and Gonor 1973; Gee 1965; Huggett et al. 2006; Swanson et al. 2006; Tebben et al. 2015) and providing important habitat that facilitates biodiversity (Akioka et al. 1999; Coull and Wells 1983; Kamenos et al. 2004; Kelaher 2002; Nelson 2009). The persistence of coralline algae in marine communities is widely believed to be due in part to their calcified thalli. Calcification is thought to increase thallus integrity and minimize the impact of herbivory (Littler and Littler 1980; Padilla 1993; Steneck 1986, 1983; Steneck and Dethier 1994; Steneck and Watling 1982). Because of the supposed protection conferred by calcification, corallines dominate areas with an overabundance of herbivores, particularly sea urchins (Filbee-Dexter and Scheibling 2014; Hind et al. 2019; Steneck 1985). Moreover, certain corallines appear to depend upon herbivory: when herbivores are experimentally removed, some corallines are outcompeted or overgrown by other algae (Johnson and Paine 2016; Paine 1984; Steneck 1982; Steneck et al. 1991).

Past research has shown that decreasing ocean pH caused by the continued dissolution of atmospheric CO_2 may compromise calcification in marine organisms, including coralline algae (Gao et al. 1993; Gao and Zheng 2010; Hofmann et al. 2012; Kamenos et al., 2016; Koch et al. 2013; Kroeker et al. 2013; Kuffner et al. 2008; Ragazzola et al. 2013, 2012; Ries et al. 2009), although some species appear to be more resilient than others (e.g., Guenther 2016; Nash et al. 2013; Noisette et al. 2013). If calcification rates decreased, coralline thalli could be weakened (Ragazzola et al. 2012) and potentially become more susceptible to grazers (Johnson and Carpenter 2012; McCoy and Kamenos 2018; McCoy and Ragazzola 2014), which could have dramatic and cascading effects on marine community composition worldwide. Unfortunately, we know surprisingly little about the importance of calcification in limiting grazing rates on coralline algae. For example, Padilla (1985) found that coralline crusts are actually easier for molluscs to graze than stretchy, fleshy algae, raising questions about the protective value of calcification. Additionally, researchers have long claimed that corallines are less nutritious than fleshy seaweeds (see Paine and Vadas

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1969). However, on a per-volume (i.e., per-mouthful) basis, coralline algae can be just as calorically-rich as fleshy algae, as both calcium carbonate and water comprise non-nutritious components of calcified and non-calcified algal thalli, respectively (Maneveldt and Keats 2008). Thallus morphology is also considered to be an important factor in grazer susceptibility (Littler and Littler 1980; Steneck and Dethier 1994; Steneck and Watling 1982), even in coralline algae (McCoy 2013; Padilla 1984; Steneck 1986; Steneck et al. 1991). Yet, the relative importance and interplay of calcification and morphology in mitigating grazer impacts is largely unknown.

In this study, we artificially and sequentially stripped calcium carbonate from the cell walls of three species of articulated coralline algae with different morphologies (*Calliarthron tuberculosum*, *Corallina officinalis* var. *chilensis*, and *Corallina vancouveriensis*) to clarify the generalized role of calcification in reducing herbivory. We selected generalist sea urchins (*Strongylocentrotus purpuratus*) to use in feeding trials, as we hoped results would reflect grazer protection rather than food preference. We hypothesized that removal of calcium carbonate would increase grazing rates on all three coralline species, but that the rate of increase would differ across species, perhaps mediated by thallus morphology. By clarifying the significance of calcification to coralline algae, we hope to better estimate the ecological impact of compromised calcification rates on coralline ecology and inform predictions about the future of marine communities as ocean conditions change.

2. Methods

Three species of articulated coralline algae with different thallus morphologies were selected for this study: *C. tuberculosum* has large calcified segments (ca. 2–4 mm diameter) and wide dichotomous branches, *C. officinalis* var. *chilensis* has smaller segments (ca. 1–2 mm diameter) and pinnate branches, and *C. vancouveriensis* has fine segments (ca. 0.5–1 mm diameter) and dense pinnate branches (Fig. 1). Experiments on *C. vancouveriensis* and *C. tuberculosum* (see representative vouchers UBC A94136 and UBC A94137, respectively) were conducted at Friday Harbor Laboratories, Washington, United States, and experiments on *C. officinalis* var. *chilensis* (see UBC A91477) were conducted at the Bamfield Marine Sciences Center, British Columbia, Canada. All three of these species have been extensively studied and DNA-barcoded previously in the Martone Lab, although specimens for this study were identified morphologically. *C. tuberculosum* (approximately 500 g) and *C. vancouveriensis* (approximately 500 g) were collected in August 2017 from Cattle Point (48.450,-122.963) and Deadman Bay (48.513, −123.147), San Juan Island, Washington USA, and *C. officinalis* var. *chilensis* (approximately 200 g) were collected from tidepools at Bluestone Point, Bamfield, British Columbia, Canada (48.819, −125.164) in November 2015. All algae were maintained in flow-through seawater tables for no longer than one week before experimentation.

Articulated fronds were divided to standardize experimental units by wet weight, while maintaining their general morphology. Samples were created for *C. tuberculosum* (*n* = 104, 2.06 ± 0.08 g, mean ± SD), *C. officinalis var. chilensis* (*n* = 75, 1.13 ± 0.08 g), and *C. vancouveriensis* (*n* = 104, 2.04 ± 0.10 g). Each sample was separately blotted dry, cleaned of visible epiphytes and epibionts, weighed, and placed into glass containers containing either seawater or acid, as described below.

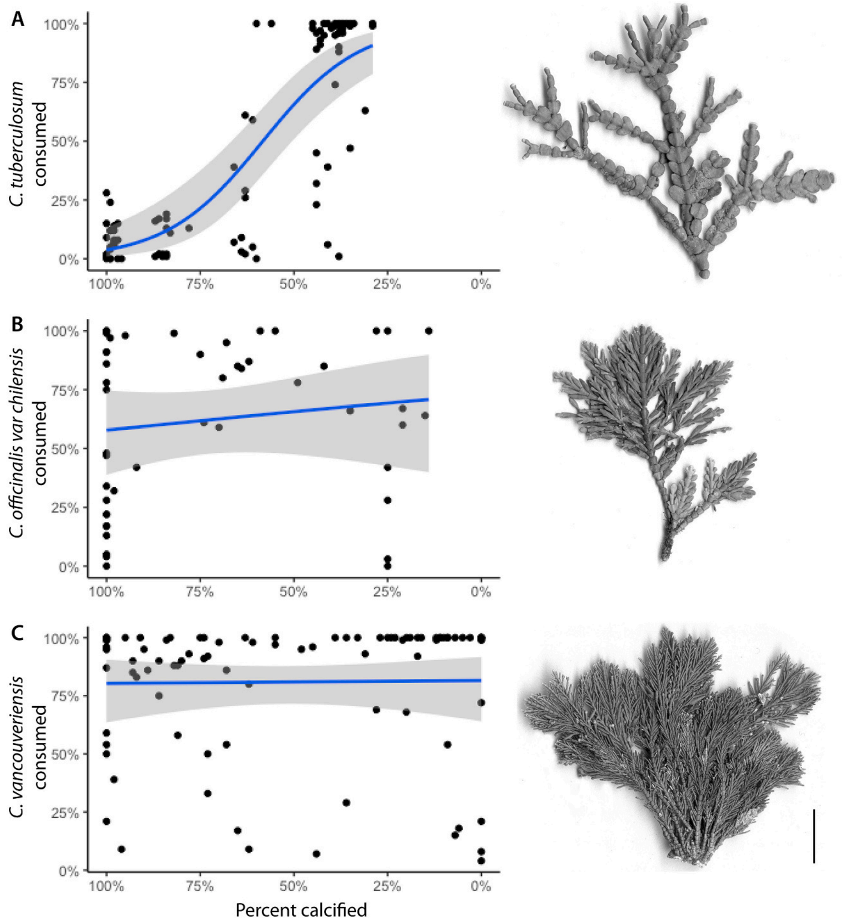

Fig. 1. Effect of calcium carbonate content on the consumption of three articulated coralline algae: (A) *Calliarthron tuberculosum*, (B) *Corallina officinalis* var. *chilensis*, and (C) *Corallina vancouveriensis*. Lines are logistic regressions with 95% confidence intervals shaded in gray. Scale bar (1 cm) applies to all images.

2.1. Manipulating calcification levels

Calcium carbonate content was manipulated by soaking samples in 1 M HCl for varying amounts of time. Soak times were adjusted slightly across species in an attempt to standardize mass loss, as thinner thalli lost proportionately more mass in acid per second than thicker species. For *C. tuberculosum*, 13 samples were assigned to each of eight treatments: unmodified (seawater control, no feeding trial), unmodified (seawater control for feeding trial), or dipped in acid for 1 s (palatability control), 2 min, 12 min, 45 min, 90 min, or 180 min. For *C. officinalis var. chilensis*, 12 samples were assigned to each of five treatments: unmodified (seawater control, no feeding trial), unmodified (seawater control for feeding trial), or dipped in acid for 1 s (palatability control), 5 min, or 30 min. For *C. vancouveriensis*, 13 samples were assigned to each of eight treatments: unmodified (seawater control, no feeding trial), unmodified (seawater control for feeding trial), or dipped in acid for 1 s (palatability control), 1 min, 5 min, 20 min, 40 min, or 90 min. All samples were immediately rinsed and transferred to seawater for several hours or overnight before feeding trials. Wet weights of samples were recorded before and after every treatment, and normal distributions were tested and verified with Shapiro-Wilk tests. Percent change in wet weight was plotted as a function of acid treatment time for each species (Fig. S1A). Changes in wet weight of unmodified samples (without feeding trial) were detected with paired *t*-tests.

Changes in percent $CaCO_3$ were subsequently calculated from the proportional change in wet weight, assuming that acid only removed calcium carbonate and did not affect water content or algal tissue. This assumption was based on standard histological methods for sectioning coralline algae that show gently decalcifying thalli with acid specifically removes calcium carbonate while preserving thallus shape, cellular arrangement, and cell wall structures (See Harvey et al. 2005; Johansen 1981). For each species, the proportion (K) of wet weight accounted for by calcium carbonate in fresh specimens was estimated as follows:

$$K = \frac{CaCO_3\ (g)}{wet\ weight\ (g)} = \frac{CaCO_3\ (g)}{dry\ weight\ (g)} \bullet \frac{dry\ weight\ (g)}{wet\ weight\ (g)} \tag{1}$$

Thereafter, the original mass of calcium carbonate (c_0) was calculated as

$$c_0 = K \bullet W_0 \tag{2}$$

where W_0 was the wet weight of a fresh specimen.

Second, assuming the wet weight (W) of any coralline sample is composed of water (w), algal tissue (a), and calcium carbonate (c), then

$$W_0 = w_0 + a_0 + c_0 \tag{3}$$

and

$$W_f = w_0 + a_0 + c_f \tag{4}$$

where W_0 is the initial wet weight of a sample and W_f is the final weight of a sample after acid treatment. Therefore, the weight change after acid treatment simply reflects the weight change of calcium carbonate,

$$W_0 - W_f = c_0 - c_f \tag{5}$$

and thus,

$$c_f = c_0 - W_0 + W_f \tag{6}$$

by substituting Eq. 2, we get

$$c_f = K \bullet W_0 - W_0 + W_f = W_0 \bullet (K - 1) + W_f \tag{7}$$

Thus, to calculate the proportion of $CaCO_3$ after any acid treatment we used the following equation:

$$\begin{aligned} Percent\ CaCO_3 &= \frac{c_f}{c_0} \bullet 100 = \left[\frac{W_0 \bullet (K-1) + W_f}{K \bullet W_0}\right] \bullet 100 \\ &= \left[1 - \frac{1}{K} + \frac{W_f}{K \bullet W_0}\right] \bullet 100 \end{aligned} \tag{8}$$

According to previously published data, the proportion of $CaCO_3$ per dry weight was 0.84 ± 0.01 (mean ± SE) for *C. tuberculosum* and 0.64 ± 0.01 for *C. vancouveriensis*, and the dry weight: wet weight ratio was 0.74 ± 0.01 for *C. tuberculosum* and 0.63 ± 0.01 for *C. vancouveriensis* (Guenther 2011; Guenther and Martone 2014). For *C. officinalis* var. *chilensis*, dry weight: wet weight ratio was calculated by comparing wet weights of samples ($n = 15$) to their respective oven-dried weights (24 h at 60 °C), and the proportion of CaCO3 per dry weight was calculated by comparing oven-dried weights of the same samples to their respective decalcified dried weight (1 M HCl overnight followed by 24 h at 60 °C). For *C. officinalis* var. *chilensis*, the proportion of $CaCO_3$ per dry weight was 0.82 ± 0.01 (mean ± SE) and the dry weight: wet weight ratio was 0.62 ± 0.01. Thus, K was calculated as follows: *C. tuberculosum* ($K = 0.62$), *C. officinalis* var. *chilensis* ($K = 0.51$), and *C. vancouveriensis* ($K = 0.40$). Calculations yielding percent calcium carbonate greater than 100%, resulting from measurement error of wet weight, were assumed to be 100%; calculations yielding percentages less than 0%, likely resulting from an overestimate of K for a particular specimen, were assumed to be 0%. Using Eq. 8, percent calcium carbonate was plotted as a function of acid treatment time for each species (Fig. S1B).

2.2. Feeding trials

Algal samples were each exposed to purple urchins, *Strongylocentrotus purpuratus*. At Friday Harbor Laboratories, urchins ($n = 91$; 159.6 ± 35.7 g; mean ± SD) had been maintained for at least 12 months and fed drift kelp biweekly in cages suspended from the laboratory breakwater, whereas at Bamfield Marine Sciences Centre, urchins ($n = 48$; 105.4 ± 47.2 g) were collected wild from Cia Rock near Bamfield, B. C., using SCUBA. Prior to experimentation, urchins were moved to seawater tables and maintained on a kelp diet, allowing them to acclimate to lab conditions (i.e. aquaria, running seawater, lighting) for approximately one week. Urchins were starved 2–3 days prior to the feeding trails. Urchins were haphazardly and uniquely paired with algal samples, placed in individual compartments, and exposed to natural light and darkness and constant seawater circulation. Feeding trials on *C. tuberculosum* and *C. vancouveriensis* lasted 24 h; feeding trials on *C. officinalis* var. *chilensis* lasted 12 h, since samples of this species were half the size. Urchins grazing on *C. officinalis* var. *chilensis* were approximately 2/3 the size of urchins grazing on the other two species, and so consumption of *C. officinalis var. chilensis* may have been underestimated. Algal samples were blotted dry and re-weighed after each feeding trial. Algal samples that appeared to gain mass in feeding trials (negative percent change), likely resulting from measurement error of wet weight, were assumed to be 0% consumed. Raw and transformed consumption datasets failed Shapiro-Wilk tests for normality. Consequently, Kruskal-Wallis non-parametric tests were used to compare the consumption of unmodified samples (seawater control), acid-dipped samples (palatability control), and samples soaked in acid for 2 min for *C. tuberculosum* and to compare the consumption of unmodified and acid-dipped samples for each of the *Corallina* species. Percent of sample mass consumed (calculated relative to wet weight after acid treatment) was plotted as a function of percent calcium carbonate for each species, and logistic regressions were fitted using generalized linear models with logit link functions followed by analysis of deviance. All statistics were conducted using R (version 4.0.3; R Core Team, 2016).

3. Results

Mass loss of unmodified samples (seawater control, no feeding trial) varied by species. Samples of *C. tuberculosum* lost 0.01 g (0.66%) on average (t = 6.61, df = 12, P < 0.001), samples of *C. officinalis* var. *chilensis* were unchanged (t = −1.21, df = 11, P = 0.25), and samples of *C. vancouveriensis* lost 0.23 g (11.1%) on average (t = 14.29, df = 12, P < 0.001). Consumption of unmodified samples (seawater controls) varied by species. Urchins ate 8.7 ± 2.6% (mean ± SE) of *C. tuberculosum* samples, 52.3 ± 9.7% of *C. officinalis var. chilensis* samples, and 81.6 ± 7.0% of *C. vancouveriensis* samples. Dipping samples in acid for 1 s (palatability control) did not significantly affect their consumption compared to seawater controls (*C. tuberculosum*: χ^2 = 0.17, df = 2, P = 0.92; *C. officinalis var. chilensis*: χ^2 = 0.01, df = 1, P = 0.99; *C. vancouveriensis*: χ^2 = 0.01, df = 1, P = 0.96); urchins ate 7.4 ± 1.5% (mean ± SE) of acid-dipped *C. tuberculosum* samples, 51.5 ± 11.5% of acid-dipped *C. officinalis* var. *chilensis* samples, and 74.7 ± 9.4% of acid-dipped *C. vancouveriensis* samples.

The effect of calcification on consumption varied by species (Fig. 1). For *C. tuberculosum*, samples with less calcium carbonate were consumed significantly more (Fig. 1A; pseudo R^2 = 0.63, G = 50.695, df = 1, P < 0.001). According to the fitted curve, 50% of *C. tuberculosum* samples would be consumed (LD_{50}) if their calcification level were reduced to 58.3 ± 3.8% (mean ± SE). However, consumption of *C. tuberculosum* samples did not increase significantly after two minutes in acid (Fig. 1A; χ^2 = 0.17, df = 2, P = 0.92), when calcium carbonate content had been reduced to 85.0 ± 1.3% (mean ± SD). For *C. officinalis var. chilensis*, there was no significant effect of calcification on consumption (Fig. 1B; G = 0.473, df = 1, P = 0.49). On average, 62% of *C. officinalis var. chilensis* samples were consumed regardless of calcification level (Fig. 1B). For *C. vancouveriensis*, there was also no significant effect of calcification on consumption (Fig. 1C; G = 0.012, df = 1, P = 0.91). On average, 81% of *C. vancouveriensis* samples were consumed regardless of calcification level (Fig. 1C).

4. Discussion

Contrary to the current paradigm, our data suggest that calcification likely plays a variable and species-specific role in protecting coralline algal thalli from herbivory. On the one hand, the consumption of *C. tuberculosum* samples increased significantly as calcium carbonate was removed, suggesting that calcification indeed protects this species from urchins. On the other hand – and contrary to our hypothesis – consumption of *C. vancouveriensis* and *C. officinalis* var. *chilensis* samples was unaffected by calcium carbonate content, suggesting that other factors besides calcification may explain in-situ observations of reduced grazing frequency of these two coralline species compared to other algal species (e.g., Johnson and Paine 2016; Paine and Vadas 1969).

Our results provide a valuable perspective on the likely interplay between calcification and thallus morphology in determining the susceptibility of coralline algal species to grazing. When fully calcified, the most finely branched coralline, *C. vancouveriensis*, was consumed most, and the most coarsely branched coralline, *C. tuberculosum*, was consumed least, entirely consistent with previous work on coralline morphology (Padilla 1984). Moreover, by manipulating thallus shape and structure, Padilla (1984) concluded that morphology was an important driver of ecological differentiation and grazing susceptibility of coralline algae. However, in this study, when calcification levels were reduced and morphology was held constant, a different story emerged. As calcium carbonate content decreased, *C. tuberculosum* was increasingly consumed, suggesting that calcification mediates the effect of morphology in protecting this coarsely branched species from herbivory. In other words, previous conclusions about the importance of coralline morphology are partially dependent upon calcification: if *C. tuberculosum* thalli were less than 50% calcified, they would likely be consumed as much as finely branched thalli of *C. vancouveriensis*.

Articulated coralline algae are often stiff due to their segmented morphology (Janot and Martone 2018; Martone and Denny 2008), and thallus stiffness generally protects articulated fronds from benthic grazers by making them difficult to hold down and manipulate (Padilla 1984). Reducing the calcium carbonate content of *C. tuberculosum* samples may have decreased their overall stiffness and thereby facilitated urchin grazing. On the other hand, samples of *C. vancouveriensis* and *C. officinalis var. chilensis* have smaller segments and are therefore naturally less stiff even when fully calcified, perhaps explaining why reductions in calcium carbonate did not increase grazer damage. Future research should clarify the tipping points in segment size and frond stiffness that mitigate benthic grazing of articulated coralline algae, and determine whether our conclusions are generalizable across other grazers, including crustaceans (e.g., amphipods, isopods), molluscs (e.g., limpets, snails, chitons), and fish.

Calcification of articulated coralline algae is an evolutionary carryover from crustose coralline ancestors (Aguirre et al. 2010; Janot and Martone 2016, 2018), in which calcium carbonate is widely considered to have been an anti-herbivore defense (Steneck 1985). But we should be cautious in assuming that calcification plays a similar role in such morphologically distinctive, articulated coralline thalli. For example, calcification may also help coralline algae resist physical damage caused by wave impact or substrate abrasion (e.g., Padilla 1993; Ragazzola et al. 2012) and may protect thalli from UV radiation (Gao and Zheng 2010). Furthermore, our basic assumption about the importance of calcification in protecting coralline crusts from grazers requires additional scrutiny. Many uncalcified crusts also excel at resisting grazers (Dethier and Steneck, 2001), and crust morphology alone (e.g., surface irregularities, thallus thickness, buried meristems) is known to mediate herbivore impacts (Steneck 1982, 1985, 1986; Steneck et al. 1991) – once again raising questions about the relative importance of morphology and calcification in reducing herbivory. Johnson and Carpenter (2012) demonstrated a modest increase in grazing susceptibility of crustose coralline thalli after calcification had been negatively impacted by acidified seawater, but whether their conclusions are generalizable remains to be demonstrated. Additional studies on the benefits of calcification in coralline crusts are needed.

While we cannot comment on the likely physiological response of these three coralline species to shifts in ocean pH, our data lend important insight into possible downstream ecological effects (or lack thereof). According to our data, negative impacts on calcification caused by ocean acidification would have variable effects on grazing susceptibility of corallines. Both *Corallina* species in this study could lose all or most of their calcium carbonate and see no change in urchin grazing rates; *C. tuberculosum* could lose 15% of its calcium carbonate and still be relatively protected. That *C. tuberculosum* appears to have more calcium carbonate than needed to resist urchins could signal alternative advantages to calcification, and perhaps reductions in calcium carbonate content would increase the likelihood of breakage under waves or UV photodamage (Padilla 1993; Ragazzola et al. 2012; Gao and Zheng 2010) or increase susceptibility to other grazer types. We hope that this study not only raises awareness of species-specific differences in ecological outcomes across coralline algae, but also helps prioritize future physiological work on species where an ecological impact is most likely.

In conclusion, our results suggest that calcification does not universally protect coralline thalli from herbivory. For two *Corallina* species, reduced calcium carbonate content had no significant effect on urchin grazing. For *C. tuberculosum*, reduced calcium carbonate content increased grazing susceptibility, but only after thalli lost more than 15% of their calcium carbonate. The benefits of calcification in mitigating herbivory on coralline thalli are species-specific and likely depend upon thallus morphology. Any negative impacts of ocean acidification on calcification are therefore expected to have variable and species-specific effects on coralline ecology.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151513.

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