

# Field Study of Growth and Calcification Rates of Three Species of Articulated Coralline Algae in British Columbia, Canada

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**Abstract.** Ocean acidification caused by rising atmospheric CO<sub>2</sub> is predicted to negatively impact growth and calcification rates of coralline algae. Decreases in coralline abundance may have cascading effects on marine ecosystems and on carbon sequestration worldwide. In this study, we measured growth and calcification rates of three common species of articulated coralline algae (*Bossiella plumosa*, *Calliarthron tuberculosum*, and *Corallina vancouveriensis*) at an intertidal field site in British Columbia. Linear growth rates measured in the field were slow, although *Bossiella* grew significantly faster (0.22 cm mon<sup>-1</sup>) than *Calliarthron* and *Corallina* (0.17 and 0.15 cm mon<sup>-1</sup>, respectively). Growth rates in the field were generally slower than growth rates in the laboratory, suggesting that data generated in the laboratory may not be representative of natural field conditions. Growth rates did not decrease as fronds approached their maximum observed size, suggesting that maximum frond size might be determined not by intrinsic factors but by external factors such as wave-induced drag forces. Using growth data, we estimate that the largest observed *Bossiella* frond (20 cm<sup>2</sup>) and *Calliarthron* frond (40 cm<sup>2</sup>) were about 4- and 11-years-old, respectively, and had deposited approximately 1 and 6 g CaCO<sub>3</sub> in that time. Given the great abundance of coralline algae along the coast of British Columbia, deposition rates of CaCO<sub>3</sub> are expected to play a significant but poorly characterized role in carbon sequestration.

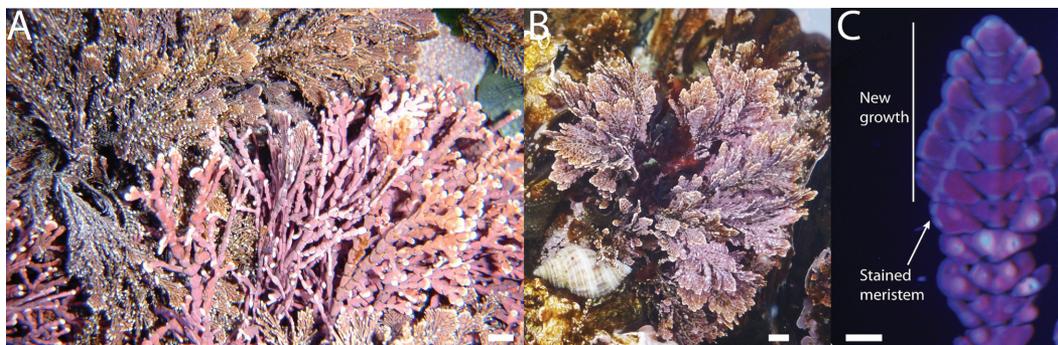
## Introduction

Coralline algae (Corallinales and Sporolithales, Rhodophyta) are important components of marine communities

worldwide, cementing coral reefs (Steneck and Adey, 1976) and quickly colonizing bare rock to provide habitat for other algae and invertebrates (Kelaher *et al.*, 2002). Corallines and their associated biofilm (Huggett *et al.*, 2006) induce settlement of a wide range of invertebrate larvae, including echinoderms (*e.g.*, Rowley, 1989; Johnson *et al.*, 1991; Swanson *et al.*, 2006), annelid worms (*e.g.*, Gee and Knight-Jones, 1962; Gee, 1965), molluscs (*e.g.*, Barnes and Gonor, 1973; Heslinga, 1981; Rumrill and Cameron, 1983; Morse and Morse, 1984), soft corals (*e.g.*, Sebens, 1983; Benayahu *et al.*, 1989; Lasker and Kim, 1996), and scleractinian corals (*e.g.*, Harrigan, 1972; Morse *et al.*, 1988; Heyward and Negri, 1999; Kitamura *et al.*, 2007). Even sponges, arguably the oldest of the extant animal phyla, have recently been found to settle and metamorphose preferentially on a species of articulated coralline algae (Avila and Carballo, 2006). Moreover, as they calcify, coralline algae precipitate calcium carbonate in their cell walls, thereby removing carbon from the biological carbon cycle and incorporating it into the geological carbon cycle (Smith, 1972; Steneck, 1986).

Coralline algae are threatened by the decline in ocean pH resulting from increasing atmospheric CO<sub>2</sub> (Nelson, 2009). Decreases in settlement, growth, and calcification of coralline algae in response to elevated CO<sub>2</sub> have already been documented in laboratory studies (Gao *et al.*, 1993; Orr *et al.*, 2005; Jokiel *et al.*, 2008; Kuffner *et al.*, 2008; Martin and Gattuso, 2009; Porzio *et al.*, 2011, 2013; Diaz-Pulido *et al.*, 2012; Ragazzola *et al.*, 2012; Noisette *et al.*, 2013a; Kroeker *et al.*, 2013) and some field studies (Kroeker *et al.*, 2012; McCoy, 2013), although responses may be species-specific (Noisette *et al.*, 2013b) and physiological adaptation may be possible (Ragazzola *et al.*, 2013). As the saturation state of calcium carbonate decreases globally

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**Figure 1.** Three species of articulated coralline algae investigated in this study: (A) *Corallina vancouveriensis* (upper left) and *Calliarthron tuberculosum* (lower right), and (B) *Bossiella plumosa*. Scale = 5 mm. (C) Meristematic branch tip of *Bossiella plumosa* viewed under black light. Calcofluor White stain indicates the position of the meristem 29 days prior. Scale = 1 mm.

with decreasing pH, calcification, growth, and competitive ability of coralline algae may be impacted (Orr *et al.*, 2005; Andersson *et al.*, 2008; Gao and Zheng, 2010; Kroeker *et al.*, 2013), potentially altering marine communities and near-shore carbon cycles. A loss of coralline algae would have wide-ranging implications for coastal ecosystems, and even a slight decline in growth, skeletal integrity, or calcification rates (Ragazzola *et al.*, 2012; McCoy, 2013) would impact marine carbon sequestration worldwide (Smith, 1972; Steneck, 1986; Daume *et al.*, 1999; Andersson *et al.*, 2008; Chung *et al.*, 2011).

Baseline studies of coralline demography are needed if we are to detect the impacts of climate change on corallines in the field, but such studies are lacking in the literature. The complexity of the intertidal zone makes replicating field conditions in a laboratory nearly impossible; field studies are necessary to gain a more complete perspective on the growth rates of organisms (Kholer, 2002; Calisi and Bently, 2009). Coralline algae are often characterized as slow-growing and long-lived, but the literature reveals large discrepancies in estimated ages and growth rates, with very few studies performed in the field (but see Johansen and Austin, 1970; Steneck, 1986; Goldberg and Foster, 2002; Blake and Maggs, 2003; Martone, 2010). For example, individual fronds of *Calliarthron*, a common genus of articulated coralline algae, have been estimated to live for 3 to 10 years (Johansen and Austin, 1970; Foster, 1975; Martone, 2010). As the ocean changes, it will become increasingly important to have accurate information about the growth of these organisms in the field in order to monitor them for changes in performance. Slow-growing species may be more vulnerable and slower to recover or adapt to changes in climate (Done, 1988; Macdonald *et al.*, 1996)

This study documents the growth and calcification rates of three species of articulated coralline algae commonly found on the coast of British Columbia (Fig. 1A, B): *Bossiella plumosa* (Manza) P.C. Silva, *Corallina vancouverien-*

*sis* Yendo, and *Calliarthron tuberculosum* (Postels and Ruprecht) E.Y. Dawson. To date, no prior studies have examined growth rates of corallines in the field along the British Columbia coast, and the goal of this study is to establish baseline data on growth and calcification rates to help characterize the vulnerability of corallines in this ecosystem and to explore the potential importance of corallines to nearshore carbon cycles.

## Materials and Methods

Coralline algae were studied at Botanical Beach, Port Renfrew, British Columbia (48.529253° N, 124.453704° W). Ten plants each of *Bossiella plumosa*, *Corallina vancouveriensis*, and *Calliarthron tuberculosum* were selected from tidepools in the upper-mid intertidal region, about 1.5 m above mean lower low water (Fig. 1A, B). Each plant consisted of about 20–50 segmented upright fronds of different sizes, emerging from a crustose base; each frond had one to several branches, each ending in an apical meristem (see Johansen, 1981). Representative voucher specimens of *Bossiella plumosa* and *Corallina vancouveriensis* were deposited into the University of British Columbia Herbarium for future taxonomic reference (A88702–A88705). All plants had signs of good health including pink color, robust shape, and few epiphytes. Plants growing on mussels or other organisms were not considered. Plants were stained *in situ* by submersion in resealable plastic bags with 500 ml of 0.04% Calcofluor white solution (Sigma-Aldrich, St. Louis, MO, Fluorescent brightener 28) for 5 to 10 min following the protocol of Martone (2010). Plants were left to grow in the field for 29 days from 9 July to 8 August 2010, after which time all fronds from each plant were harvested. Throughout the experiment, air temperatures were recorded at the Port Renfrew weather station (<http://climate.weather.gc.ca>) and sea surface water temperature and salinity were recorded at the Amphitrite Lighthouse (Fisheries and Oceans

Canada, <http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html>). Total solar irradiance and photosynthetically active radiation (PAR) were recorded at the Friday Harbor Laboratories weather tower on San Juan Island, Washington ([wx.fhl.washington.edu/vdv](http://wx.fhl.washington.edu/vdv)) using a pyranometer (LI200X, Campbell Scientific, Logan, UT) and quantum sensor (LICOR, Lincoln, Nebraska), respectively. Tide heights were estimated using Mr. Tides (ver. 3.0, Hahn Software, 2007).

Two metrics were used to calculate growth rates. The first was the change in length of each frond; the second was the change in area. We calculated both metrics for *Calliarthron* and *Bossiella*, but only the change in length for *Corallina* due to its irregular three-dimensional growth habit. For both metrics, 3–7 fronds of varying sizes were selected from each plant and photographed under a black light (330–400 nm, Peak: 365 nm; Effects by Globe Electronics, Ottawa, ON). All photographs were taken using a Canon Inc. (Tokyo, Japan) EOS Rebel XT digital SLR camera with exposure set between 5 and 30 s. ImageJ software ver. 1.43u (U. S. National Institutes of Health, Bethesda, MD) was used to measure the average length of new growth in a linear direction—the distance between the top of the stain and the edge of the meristems on each frond (Fig. 1C). To calculate the total growth over 29 days, ImageJ was used to calculate the frond area between the Calcofluor white stain and the edges of frond meristems (see Fig. 1C). Up to five random meristems were measured and averaged per frond, and three to seven fronds of varying sizes were measured per plant. The effects of plant identity ( $n = 9$ ; fixed factor) and frond area (covariate) on linear growth rate were tested using ANCOVA. Growth rates and area were log-transformed and tested for normality (Shapiro-Wilk test) and equal variances (Levene's test). For *Bossiella*, the total number of meristems was also counted to test whether larger fronds have more meristems, as previously documented for *Calliarthron* (Martone, 2010).

To estimate ages of *Bossiella* and *Calliarthron*, growth rate ( $\delta A/\delta t$ ) was plotted against total planform area of each frond ( $A$ ), and Microsoft Excel software was used to fit a power curve to the data to solve for rate constants  $K_1$  and  $K_2$ :

$$\frac{\delta A}{\delta t} = K_1 A^{K_2} \quad (1)$$

This equation was rearranged and manually integrated to determine a relationship between area and time:

$$\int K_1 \delta t = \int A^{-K_2} \delta A$$

$$K_1 t = \frac{A^{1-K_2}}{1-K_2} \quad (2)$$

Thus, it was possible to use frond size ( $A$ ) to calculate its approximate age ( $t$ ),

$$t = \frac{A^{1-K_2}}{K_1(1-K_2)} \quad (3)$$

and it was possible to predict frond size ( $A$ ) after a given amount of time,

$$A = [K_1 t(1-K_2)]^{\frac{1}{1-K_2}} \quad (4)$$

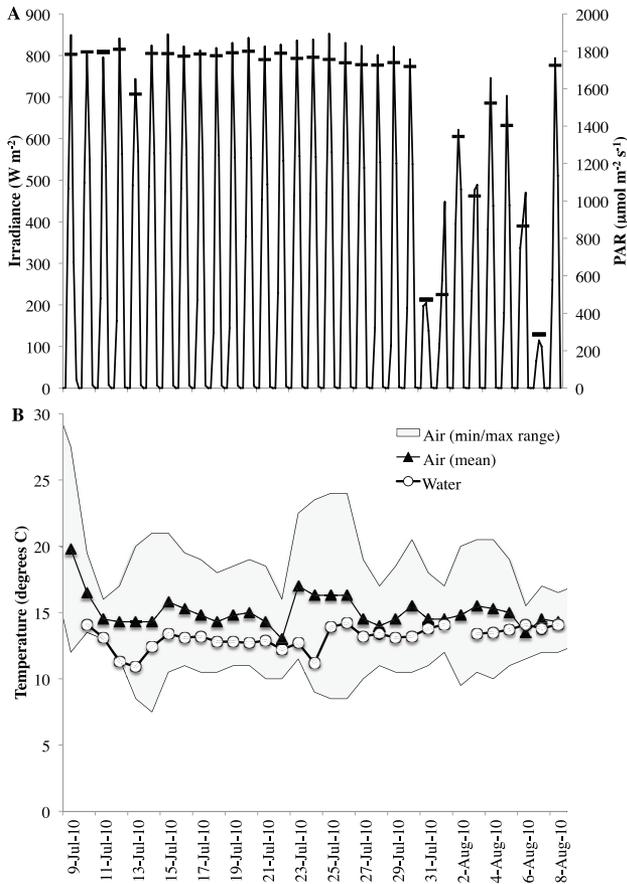
Fifteen additional, unstained plants of each species were collected from Botanical Beach. These plants were oven-dried at 40 °C overnight and weighed before being decalcified overnight in 1 mol l<sup>-1</sup> HCl to remove all CaCO<sub>3</sub>. Plants were again oven-dried at 40 °C overnight and weighed once more to determine a value for the percent mass of CaCO<sub>3</sub> for each species. Differences in calcium carbonate content were analyzed among species using ANOVA (fixed factor, three levels). To derive a relationship between area and CaCO<sub>3</sub>, mass of each experimental frond was corrected by each species-specific CaCO<sub>3</sub> percentage, and a linear regression was then fitted to frond area plotted against mass CaCO<sub>3</sub>.

## Results

From 9 July to 8 August 2010, solar irradiance often reached 400–850 W m<sup>-2</sup> daily, and PAR values often reached 900–1800 μmol m<sup>-2</sup> s<sup>-1</sup> (Fig. 2A). Average daily sea surface water temperatures were 13.1 ± 0.9 °C and air temperatures were 15.1 ± 1.3 °C (mean ± SD) (Fig. 2B). During this time period, tide heights dropped below 1.5 m only before 1310 h or after 2100 h, suggesting that tidepool temperatures may not have much exceeded water temperatures. Sea surface salinity was 30.1 ± 0.4 psu.

A wide range of frond sizes were effectively stained and monitored in each species: 0.07–20.8 cm<sup>2</sup> in *Bossiella*, 0.07–44.0 cm<sup>2</sup> in *Calliarthron*, and 0.03–13.9 cm<sup>2</sup> in *Corallina*. On average, *Bossiella* fronds grew in length by 0.22 ± 0.05 cm mon<sup>-1</sup>, *Calliarthron* fronds grew 0.17 ± 0.03 cm mon<sup>-1</sup>, and *Corallina* fronds grew 0.15 ± 0.02 cm mon<sup>-1</sup> (Figs. 3–4). Fronds of all three species followed similar growth trajectories (ANCOVA, Area × Plant, *Bossiella*:  $P = 0.24$ , *Calliarthron*:  $P = 0.10$ , *Corallina*:  $P = 0.09$ ) (Fig. 3A–C). On average, linear frond growth rate did not vary with frond size (ANCOVA, Area, *Bossiella*:  $P = 0.25$ , *Calliarthron*:  $P = 0.59$ , *Corallina*:  $P = 0.75$ ) (Fig. 3A–C), although within each species, fronds from different individual plants grew at slightly different rates (ANCOVA, Plant, *Bossiella*:  $P < 0.05$ , *Calliarthron*:  $P < 0.01$ , *Corallina*:  $P < 0.05$ ). Mean growth rates were significantly different among species (ANOVA,  $P < 0.01$ , Fig. 4). *Bossiella* fronds grew significantly faster than fronds produced by *Calliarthron* and *Corallina* (Tukey's HSD,  $P < 0.05$ ; Fig. 4).

The three coralline species do not calcify equally



**Figure 2.** (A) Solar irradiance (lines) and maximum photosynthetically active radiation (black bars) measured at Friday Harbor Laboratories, and (B) mean sea surface temperature (white circles), mean air temperature (black triangles), and maximum/minimum air temperature range (gray area) measured daily at Amphitrite Lighthouse and Port Renfrew weather station.

(ANOVA,  $P < 0.001$ ; Fig. 5). *Corallina* fronds were composed of significantly less  $\text{CaCO}_3$  ( $65.2 \pm 3.0\%$   $\text{CaCO}_3$  per dry mass) than fronds produced by *Bossiella* and *Calliarthron* ( $85.0 \pm 1.7\%$  and  $84.2 \pm 1.0\%$   $\text{CaCO}_3$  per dry mass, respectively) (Tukey's HSD,  $P < 0.05$ ; Fig. 5).

In *Bossiella*, although linear growth rate did not vary with frond size (Fig. 3), larger fronds had more meristems ( $P < 0.001$ ,  $R^2 = 0.61$ ; Fig. 6A). Because each meristem had the potential for growth, fronds with more meristems added more new frond area per month, thereby growing faster in overall size ( $P < 0.001$ ,  $R^2 = 0.76$ ; Fig. 6B).

New frond area was plotted against original frond area for *Bossiella* and *Calliarthron* (Fig. 7A, B), and power curves were fitted to calculate constants described by Eq. 1. For *Bossiella*,  $K_1 = 0.215$  and  $K_2 = 0.836$ , and for *Calliarthron*,  $K_1 = 0.080$  and  $K_2 = 0.611$  (Eq. 1). Thus, according to Eq. 4,

$$A = (1.451 \times 10_{-9})t_{6.09} \quad \text{for } Bossiella, \text{ and}$$

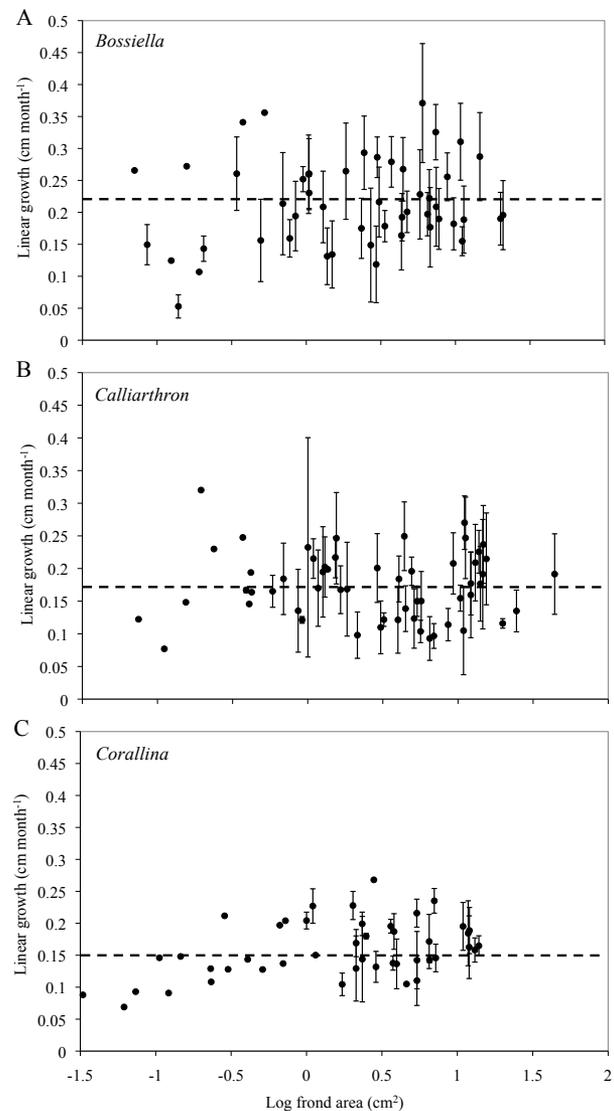
$$A = (1.344 \times 10^{-4})t^{2.57} \quad \text{for } Calliarthron. \quad (5)$$

where  $t$  is time (months) and  $A$  is total planform area ( $\text{cm}^2$ ) of a growing frond. These growth curves are plotted as Figure 7C, D. The largest observed *Bossiella* frond ( $20 \text{ cm}^2$ ) was estimated to be about 46.5-mon-old (Fig. 5C), and the largest observed *Calliarthron* frond ( $40 \text{ cm}^2$ ) was estimated to be approximately 135-mon-old (Fig. 7D).

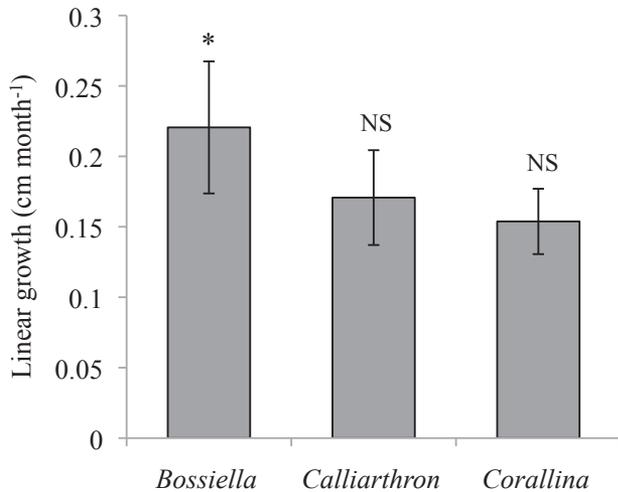
Using percent mass  $\text{CaCO}_3$  of each species (Fig. 5), the following linear correlations were made:

$$C = 49.0 A \text{ for } Bossiella \quad (R^2 = 0.89, P < 0.001), \quad (6)$$

$$C = 149.8 A \text{ for } Calliarthron \quad (R^2 = 0.88, P < 0.001),$$



**Figure 3.** Linear growth rates of (A) *Bossiella plumosa*, (B) *Calliarthron tuberculatum*, and (C) *Corallina vancouveriensis* as functions of frond size. There was no significant regression in any species.



**Figure 4.** Comparison of linear growth rates among the three experimental species. (NS = not significant, \* =  $P < 0.01$ ).

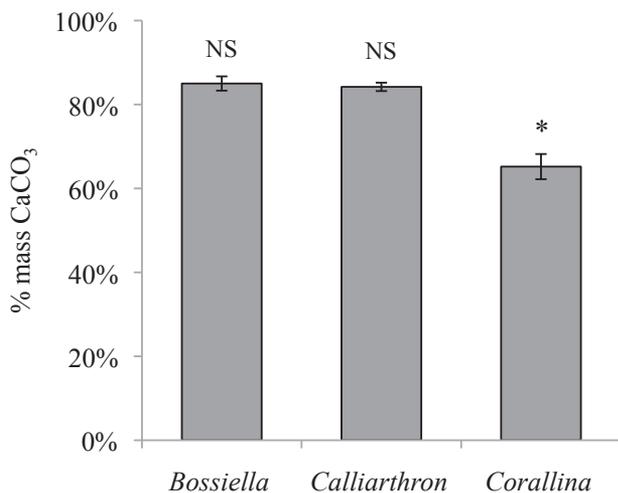
$$C = 35.0 A \text{ for } Corallina \quad (R^2 = 0.84, P < 0.001),$$

where  $C$  is the calculated mass of  $\text{CaCO}_3$  (milligrams) and  $A$  is total planform area ( $\text{cm}^2$ ) of a frond. For *Bossiella* and *Calliarthron*, combining Eq. 5 and Eq. 6 yielded mass of  $\text{CaCO}_3$  accumulated per month (Fig. 7C, D):

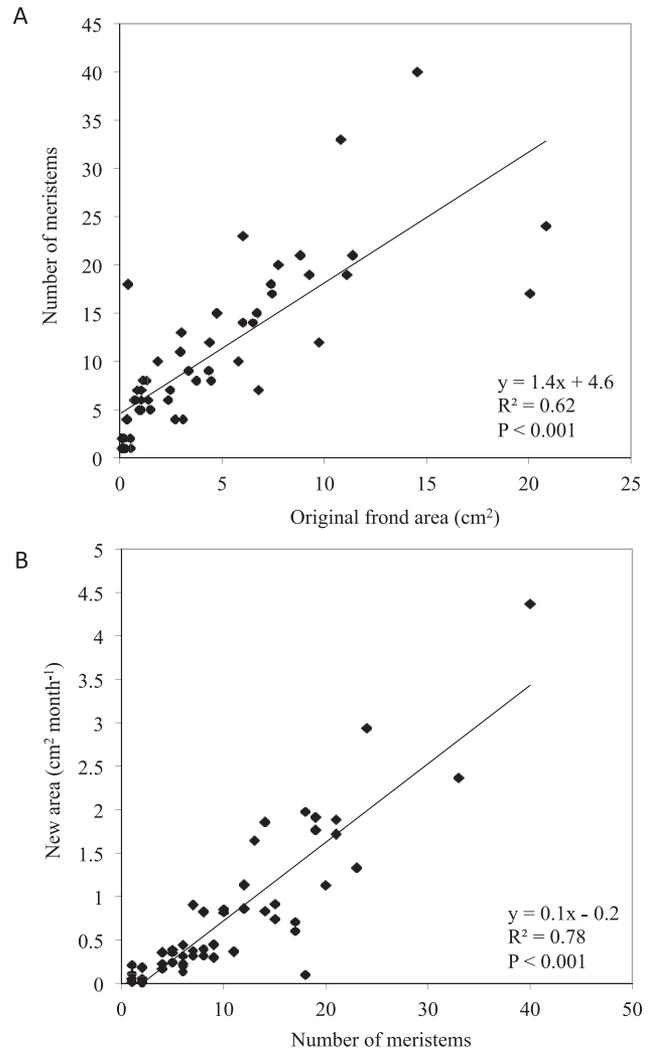
$$C = (7.11 \times 10^{-8})t^{6.09} \text{ for } Bossiella, \text{ and}$$

$$C = (2.01 \times 10^{-2})t^{2.57} \text{ for } Calliarthron. \quad (7)$$

Thus, we estimated that the largest observed *Bossiella* frond ( $20 \text{ cm}^2$ ) had accumulated 1.0 g of  $\text{CaCO}_3$  in about 4 years (Fig. 7C), whereas a growing *Calliarthron* frond accumulated 1.0 g of  $\text{CaCO}_3$  in 5.6 years (Fig. 7D). The largest



**Figure 5.** Comparison of calcium carbonate content among the three experimental species. (NS = not significant, \* =  $P < 0.001$ ).

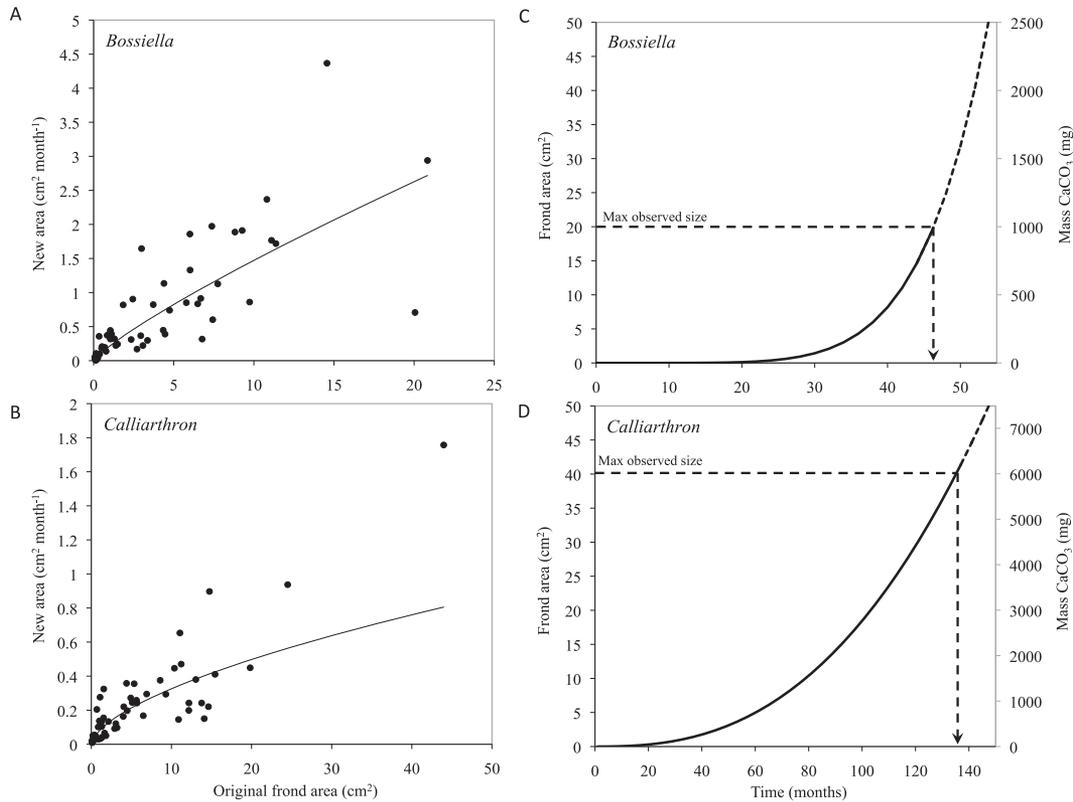


**Figure 6.** (A) Number of meristems as a function of original frond size and (B) growth rate as a function of number of meristems in *Bossiella plumosa*.

observed *Calliarthron* frond ( $40 \text{ cm}^2$ ) had accumulated approximately 6.0 g of  $\text{CaCO}_3$  in about 11 years (Fig. 7D).

## Discussion

Growth rates of articulated corallines in the field are generally slow ( $< 3 \text{ mm mon}^{-1}$ ), although still faster than most encrusting and maerl-forming corallines, which may grow less than 2.5 mm per year (Adey and McKibbin, 1970; Blake and Maggs, 2003; Rivera *et al.*, 2004; Frantz *et al.*, 2005; Schafer *et al.*, 2011). This is in contrast to other temperate algae, such as the kelps *Nereocystis luetkeana* and *Alaria marginata*, which can produce new blade tissue at rates of 4–14 cm per day (Kain, 1987; Maxell and Miller, 1996; McConnico and Foster, 2005). Growth rates of coralline species in British Columbia are similar to those in



**Figure 7.** Growth rates of (A) *Bossiella plumosa* and (B) *Calliarthron tuberculosum* as functions of original frond size. Curves fitted to these data were then used to predict frond size and CaCO<sub>3</sub> deposition as a function of time for (C) *Bossiella* and (D) *Calliarthron*. Maximum observed frond sizes suggest that individual fronds of *Bossiella* and *Calliarthron* may live to be 4- and 11-years-old, respectively.

California. For example, growth rates of *Calliarthron tuberculosum* growing subtidally off central California range from 0.125 to 0.17 cm/mon (Johansen and Austin, 1970; Goldberg and Foster, 2002), similar to rates reported for intertidal *Calliarthron* in British Columbia (0.17 cm/

mon; Table 1). Johansen and Austin (1970) noted that subtidal growth rates of *Calliarthron* were fastest in the winter when kelp forests had thinned and light levels increased. Similarly, Halfar *et al.* (2011b) reported that light availability was the primary determinant of growth in

**Table 1**

*Comparison of linear growth rates among several species of articulated coralline algae*

Genus	Species	Average growth rate (cm mon <sup>-1</sup> )	Study Site	State/Country	Reference
<i>Bossiella</i>	<i>gardneri</i>	0.33	Laboratory	CA, USA	Smith, 1972
	<i>plumosa</i>	0.22	Intertidal	BC, Canada	This study
<i>Corallina</i>	<i>officinalis</i>	0.22	Laboratory	MA, USA	Colthart and Johansen, 1973
	<i>officinalis</i>	0.20	Subtidal	N. Ireland	Blake and Maggs, 2003
	<i>officinalis</i>	0.14	Intertidal	MA, USA	Andrake and Johansen, 1980
	<i>vancouveriensis</i>	0.15	Intertidal	BC, Canada	This study
	<i>vancouveriensis</i>	0.41	Laboratory	CA, USA	Smith, 1972
<i>Calliarthron</i>	<i>cheilosporioides</i>	0.28	Intertidal	CA, USA	Martone, 2010
	<i>tuberculosum</i>	0.17	Intertidal	BC, Canada	This study
	<i>tuberculosum</i>	0.17	Subtidal	CA, USA	Johansen and Austin, 1970
	<i>tuberculosum</i>	0.41	Laboratory	CA, USA	Smith, 1972
	spp.	0.13	Intertidal	CA, USA	Goldberg and Foster, 2002

long-lived crustose coralline algae. Thus, light availability may help explain the similarity in growth rates of unshaded intertidal corallines described here and unshaded subtidal corallines in California (Johansen and Austin, 1970). Further work is needed to disentangle the individual and interactive effects of abiotic factors (such as light, temperature, and nutrients) on growth rates. In particular, the effect of temperature on coralline growth rates can vary (Kamenos and Law, 2010; Halfar *et al.* 2011a, b). Interestingly, much faster growth rates have been documented in the closely related species *Calliarthron cheilosporioides* growing in a California intertidal habitat (0.28 cm/mon; Martone, 2010), suggesting that growth rates may not be generalizable among congeneric coralline species (Table 1).

Growth rates in the field are generally slower than those documented in the laboratory. For example, linear growth rates for *Calliarthron tuberculosum* and *Corallina vancouveriensis* (0.17 and 0.15 cm/mon, respectively) are less than half that found for the same two species in the laboratory (0.41 cm/mon; Table 1). Higher growth rates in the laboratory suggest that natural conditions may limit the growth of coralline algae and that optimized laboratory conditions (*e.g.*, light, nutrients, water motion) may induce unnatural rates of growth. For example, intertidal macroalgae are often nitrogen-limited (Howarth, 1988; Bracken, 2004), so laboratory cultures enriched with nitrogen may elevate growth rates above natural levels. The large discrepancy between laboratory and field growth rates suggests that researchers should be cautious when extrapolating results from laboratory studies to ecological or physiological performance in the field.

Prior studies by Johansen and Austin (1970) and Martone (2010) found that growth rates of coralline algae decrease as frond sizes increase. This decline in growth is expected for many organisms with determinate growth—growth rate decreases as organisms approach their maximum size (Laird, 1964; Kozlowski, 1992). In our study, linear growth rate did not decrease as frond size increased for any of the three species studied. Instead, linear growth rates were constant across all frond sizes (Fig. 3), and overall frond growth rates ( $\text{cm}^2 \text{mon}^{-1}$ ) increased with increasing number of meristems (Fig. 6B). This pattern of increasing growth rate with increasing frond size seems to indicate that articulated coralline algae in British Columbia exhibit primarily indeterminate growth, and they either do not have a predetermined maximum size or are not attaining their maximum size in this habitat. Martone and Denny (2008) demonstrated that articulated corallines experience greater wave-induced drag forces as they increase in size, ultimately dislodging large plants and thereby constraining maximum size. Observed patterns of exponential growth (Fig. 7) may exist only because drag forces limit the size of plants before physiological mechanisms cause growth to decline. Furthermore, *Calliarthron* may grow larger than other coralline genera

simply because *Calliarthron* thalli (specifically, the joints or “genicula”) can resist greater forces than thalli produced by *Bossiella* or *Corallina* (Martone, 2006; Janot and Martone, unpubl.). Further testing of the biomechanical properties of coralline algae is necessary to explore these hypotheses and to detect constraints on frond strength and frond size.

Individual fronds of *Bossiella* were estimated to live 4 years, while the largest *Calliarthron* fronds were estimated to live 11 years. Since articulated corallines have perennating basal crusts that continually replenish upright fronds, it is difficult to measure the age of a plant. Ages calculated in this study represent growth of individual fronds and should not be used to estimate ages of plants, which are likely much older. Spores of *Calliarthron tuberculosum* can form a basal crust in less than 1 mon and can begin developing fronds in 2 mon under laboratory conditions (Johansen and Austin, 1970). Such rapid development from spore to first frond suggests that additional data on spore germination rates may not greatly affect age predictions.

Age estimates assume that summer growth rates are representative of growth rates year-round, an assumption that should eventually be tested. Growth rates of *Calliarthron tuberculosum* vary seasonally in subtidal habitats, increasing when light penetration is greatest (Johansen and Austin, 1970). Because light and water temperatures are greatest in the summertime, we expect that values reported here represent maximum growth rates and that age estimates are, therefore, conservative. If growth rates of intertidal articulated corallines slow down in the winter, as documented for other calcifying and noncalcifying macroalgae (Foster, 1975; Frantz *et al.*, 2005; Halfar *et al.*, 2008, 2013; Kamenos *et al.*, 2008; Dethier and Williams, 2009; Kamenos and Law, 2010), then plants may be older than calculated here, making these slow-growing organisms even slower to grow and recover from disturbance. Preliminary data collected from tidepools on San Juan Island, Washington, from 15 October to 13 November 2013 suggest that growth rates of *Calliarthron* do not slow down in autumn ( $0.18 \pm 0.04$  cm/mon), whereas growth rates of *Corallina* slow down significantly ( $0.05 \pm 0.01$  cm/mon), supporting the expected patterns proposed here (R. Guenther, University of British Columbia, pers. comm.). Further work is needed to refine the seasonality of articulated coralline growth, especially since these organisms lack the annual bands that have proven useful in determining growth periodicity of rhodolith and encrusting coralline species (Halfar *et al.*, 2008, 2013; Kamenos *et al.*, 2008).

As carbon cycle modeling becomes more advanced and integral to future climate models, accounting for the calcium carbonate ( $\text{CaCO}_3$ ) sequestered by calcifying organisms may be important in fine-tuning these models. For example, using growth rates reported here, we can estimate the amount of calcium carbonate deposited along a stretch of shoreline with large populations of *Bossiella*. After 2 years,

a single *Bossiella* frond will have deposited approximately 18 mg CaCO<sub>3</sub>, and after 3 years it will have deposited approximately 200 mg CaCO<sub>3</sub>. At our field site, we observed *Bossiella* growing in dense patches of 15 fronds/cm<sup>2</sup>, so a quick calculation shows that 1 m<sup>2</sup> of shoreline dominated by *Bossiella* may deposit up to 2.7 kg of CaCO<sub>3</sub> after 2 years and 32 kg if all plants live to be 3 years old. This estimate assumes that all fronds belong to one cohort, settling together and growing at the same rate, and does not incorporate recruitment dynamics or density dependence, which are currently unknown. Nevertheless, because large swaths of coastline in British Columbia include coralline algae, this carbon sink may be significant, and contributions of coralline algae to carbon sequestration may be non-negligible. Previous research estimated that up to 4 kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> may be deposited by calcifying seaweeds—primarily crustose corallines—in both temperate and tropical ecosystems (Smith, 1972; Freiwald and Henrich, 1994; Chisholm, 2000; Schafer *et al.*, 2011). Results from our field study suggest that CaCO<sub>3</sub> deposition rates of articulated corallines in British Columbia may exceed previous estimates. Further refining of growth and demographic rates of coralline algae could lead to a greater understanding of nearshore carbon cycling and modeling of global carbon budgets.

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