

Population Characteristics of *Balanophyllia elegans* in the San Juan Archipelago

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ABSTRACT: Though reef corals are heavily studied, little is known about temperate, solitary corals. We studied the distribution, size and abundance of *Balanophyllia elegans* in the San Juan Islands at 11 sites. Our methods consisted of analyzing photos from Madrona Tree and White Sign to determine the distributions of size and abundance at these two sites. We also looked at the effect of flow on coral size and density. We found that the distributions of *B. elegans* vary by site and depth and year. Corals have the highest density at high flow sites and the highest biomass at very high flow sites. Average coral size and biomass increased over time. Our findings call for future research on this San Juan species.

INTRODUCTION

As anthropogenic effects continue to change the earth, the oceans are also experiencing some drastic changes. The Pacific Northwest coast regions have experienced an increase in acidification, hypoxia and undersaturation of aragonite in the past couple of decades (Capone and Hutchins 2013). These values are projected to continue their rapid change, resulting in a decrease in productivity and biodiversity (Capone and Hutchins 2013). In the San Juan Islands off the coast of Washington, certain changes in the diversity and composition of epilithic communities on vertical surface have been observed (Elahi *et al.* 2013). Contrary to findings in other regions, analyses showed an increase in biodiversity over 40 years (Elahi *et al.* 2013). This may be due to the vertical nature of subtidal rock walls that make them less vulnerable to invasions and natural and human disturbances. Though general diversity went up, results showed a decrease in cover of the cup coral *Balanophyllia elegans* (Elahi *et al.* 2013).

Though reef corals are heavily studied, much less is known about temperate, solitary corals. We were interested in exploring some of the basic characteristics of *B. elegans* in the San Juan Islands. How do depth, angle of rock and site flow affect the distribution and size? Have these characteristics changed over time? How has biomass changed over the years? Caroselli *et al.* (2012) studied another solitary temperate coral *Leptopsammia pruvoti*, which they found to be more tolerant of different water temperatures than *Balanophyllia europaea*, a solitary zooxanthallate scleratinian from the same area. Corals without zooxanthallae may survive better under certain changing conditions, since they do not depend on these symbionts (Caroselli *et al.* 2012). Therefore, we expect to see some small changes in the distribution and biomass of *B. elegans* over time.

The changes observed also depend on some of the life history traits of *B. elegans*. The distribution of this coral is affected by the dispersal methods of the larvae. *B. elegans* larvae

primarily disperse by crawling, not swimming (Gerrodette 1981). Therefore, the density of young corals decreases as a function of distance from the center of adults, and the population is estimated to have a dispersal rate of 7.5 cm/year (Gerrodette 1981). However, *B. elegans* larvae can survive for multiple days and could be carried farther away by currents (Gerrodette 1981). Settling area is determined by the interactive effects of water movement and substrate (Altieri 2003). These environmental factors may affect the patchy settlement of *B. elegans* more than its limited dispersal methods (Altieri 2003). Water movement also plays a part in the survival of coral recruits. Growth rate is positively correlated with water flow in another scleratinian coral, *Galaxea fascicularis* (Schutter *et al.* 2010). It is possible that at sites with higher water flow, corals have better access to nutrients and are less disturbed by competitors (Schutter *et al.* 2010). Based on these studies, we expect to find the majority of corals at sites with high flow and vertical substrates where their larvae will be stimulated to attach and the topography will protect them from competition.

Once the larvae settle and grow, the survival of *B. elegans* depends on a variety of environmental factors. The temperate corals in Southern California, *B. elegans* included, have zonation on the rocks which could be due to vertical gradients in physical and biological factors (Chadwick 1991). In these regions, *B. elegans* competes with *Corynactis californica* by polyp contact (Chadwick 1991). This coral also competes with *Trididemnum opacum*, a colonial ascidian, in the San Juan Islands, Washington (Bruno and Witman 1996). In general, colonial animals are much better at outcompeting solitary ones in limited space settings due to differences in reproductive and growth patterns and the nature of their skeletons (Jackson 1977).

In the San Juans, though, *B. elegans* is able to prosper. Skeletal height and aggregation do not protect *B. elegans* from overgrowth by *T. opacum* (Bruno and Witman 1996). However, *Balanophyllia* is able to damage *Trididemnum*'s tissue through polyp contact (Bruno and Witman 1996). This, combined with height and aggregation, may affect competitive interactions (Bruno and Witman 1996). Though *B. elegans* is not a strong competitor compared to other anthozoans, colonial species like *T. opacum* are more sensitive to physical and biological disturbances than solitary ones (Jackson 1977). Point Caution on San Juan Island has only been a marine preserve since 1990, possibly resulting in a decrease in disturbance in the area. Therefore, we may see decreases in *B. elegans* numbers and distribution as *T. opacum* is able to survive better.

Balanophyllia's survival is also affected by macroalgae and sea urchins. Areas with high densities of urchins had low densities of algae and high density of *B. elegans* (Coyer *et al.* 1993). When urchin levels are low, the coral is overgrown by kelp (Coyer *et al.* 1993). The physical contact of kelp with the coral also causes it to retract its polyps and stop feeding (Coyer *et al.* 1993). In the San Juan Islands, urchin grazing opens up space on the rocks and indirectly facilitates chitons that help recruit large sessile species (Elahi and Sebens 2012). Indirect interactions with these other species can affect *B. elegans* distribution. Therefore, we expect to find more corals at depths where kelp and other competitors for rock space are scarce and urchins and chitons are abundant.

Average survival for *B. elegans* in California ranges from 6.5 to 11 years (Fadlallah 1983). This is a shorter lifespan than most corals and gorgonians (Fadlallah 1983). However, *B. elegans* maintains a high intrinsic rate of growth due to early onset of reproduction and high larval survivorship (Fadlallah 1983). Variable juvenile and adult mortality, due to sand scour

from storms or other disturbances, check the population growth (Fadlallah 1983). The juvenile stage of *B. elegans* is the most vulnerable (Gerodette 1979). Though adult corals are able to survive in shallow water (<10 m), they are not found there due to high juvenile mortality (Gerodette 1979). This may be due to large temperature fluctuations and food scarcity (Gerodette 1979). We expect the *B. elegans* in the San Juans to have a similar distribution: becoming more abundant at great depths.

We also anticipate that abundance, size, and biomass distribution will vary over depth and time. Growth rate of the oral diameter is constant throughout the growth of the coral (Fadlallah 1983), but Fadlallah (1983) warns that oral diameter does not necessarily produce consistent or accurate estimates of coral age or size. The oral diameter of *B. elegans* grows slower than height in the early stages of growth but grows faster than height during the later stages (Fadlallah 1983). However, in order to estimate biomass from photographs, we will use live corals to search for a relationship between *B. elegans* surface area and biomass.

There are a variety of ways to determine scleratinian biomass. *B. elegans* is composed of tissue that is intertwined with a complex outer skeleton. Johannes and Wiebe (1970) used a Water-Pik, a dental tool, to separate the tissue from the skeleton. This method is not very effective at removing all the biomass for certain species and significant amounts of mesoglea are left behind (Johannes and Wiebe 1970). Schutter *et al.* (2010) used CN analysis to determine biomass of *Galaxea fascicularis*. Because of *B. elegans*' body make up, we will use CN analysis to determine biomass as well. Finding a relationship between surface area and biomass may be unsuccessful, though, as coral biomass varies with area of skeleton and body depth (Edmunds and Gates 2002).

In our research, we will explore some of the basic ecological patterns of *Balanophyllia elegans* distributions in the San Juan Islands, Washington. We will look at the effects of depth, angle of rock and site flow regime on coral biomass and distribution. We will also look at any changes in these characteristics over time. Based on previous research, we expect to find higher densities, numbers, sizes, and biomasses of *B. elegans* at deeper sites with vertical walls and high flow rates.

METHODS

Photos were taken at multiple sites and depths in the San Juan Islands over four years (2008-2011) by K. Sebens and other collaborators at Friday Harbor Labs. A 10 m transect was laid out and photos were taken along the transect using randomly predetermined numbers. Divers recorded the depth and orientation of the rock surface. We analyzed only photos with a vertical orientation from the sites Madrona Tree and White Sign in ImageJ by circling and numbering each coral in the photos. We measured largest diameter and the diameter perpendicular to it, and calculated the surface area based on the equation of an ellipse. Corals that were angled or obscured were marked and used in density and abundance analyses but not biomass or size analyses. Any photos without coral were recorded with a 0 for population density.

We used CHN analysis to calculate biomass. In this process, the specimen to be analyzed is dried for multiple days between 60 and 70°C, and the percent of carbon, hydrogen and nitrogen in the specimen is recorded. To test how accurately this process measures carbon and

nitrogen, we combined tissue from *Metridium giganteum*, an anemone without a calcium carbonate skeleton, and increasing amounts of pure calcium carbonate at different ratios (100% tissue, 1 tissue:1 CaCO₃, 1:2...1:10). The only source of nitrogen is from the tissue so using the sample of 100 % tissue, we calculated the N% in each sample. We compared our calculations to the results from the CHN analysis to find the error. Also using the 100% tissue sample, we calculated and compared the true tissue C% in the samples to the results from the CHN analysis.

Coral biomass was determined from photos through a correlation between coral surface area and mass. To establish this correlation, we took top-down and sideways photos, measured the two diameters and calculated the surface area for 10 live corals. Corals were cleaned of any diatoms or rock chips, ground up using a mortar and pestle and dried completely at temperatures between 60 and 70° C. Specimens were dried until the scale read a constant weight after a few days of drying. We placed the coral samples in test tubes and then used CHN analysis to determine the biomass of the corals from the total nitrogen reported. We assumed the same N% in coral tissue as in *M. giganteum* tissue and that any nitrogen in the calcium carbonate skeleton was negligible. With these 10 data points, we were able to determine a linear correlation between biomass and largest diameter and surface area. We used the better correlation to determine biomass in our other photos.

To compare the effect of flow rate on coral growth, we used data from 11 different sites that were split into four categories: very high, high, medium and low flow sites (Figure 1). Madrona Tree and White Sign are high. Photos from Turn (18 and 21 m. depth) and Reid (15 m) were used for the very high flow sites. Director’s House, Pump House and Three Toes were the medium flow sites. We used data previously collected by Robin Elahi from Rosario Wall, Humphrey Head, Frost Island and Willow Island for the low flow areas (Elahi *et al.* Unpublished). Flow rate was previously measured at all depths using alabaster block dissolution. For each photo between the depths of 50 and 70 feet, we counted the number of corals and measured only the 10 largest ones. We compared average surface area and average biomass of the corals at each site with flow rate data.

Site	Latitude	Longitude
White Sign	48° 33' 7.959" N	123° 0' 21.658" W
Director's House	48° 32' 48.886" N	123° 0' 25.520" W
Frost Island	48° 32' 25.616" N	122° 50' 35.225" W
Humphrey Head	48° 33' 53.183" N	122° 52' 11.805" W
Madrona Tree	48° 33' 11.386" N	123° 0' 25.210" W
Pump House	48° 32' 45.820" N	123° 0' 27.450" W
Reid Rock	48° 32' 55.852" N	122° 59' 31.704" W
Rosario Wall	48° 38' 36.628" N	122° 52' 25.669" W
Three Toes	48° 32' 58.960" N	123° 0' 20.498" W
Turn Island	48° 32' 2.702" N	122° 58' 9.577" W
Willow Island	48° 32' 25.130" N	122° 49' 24.758" W

Table 1. Coordinates for all the sites analyzed.

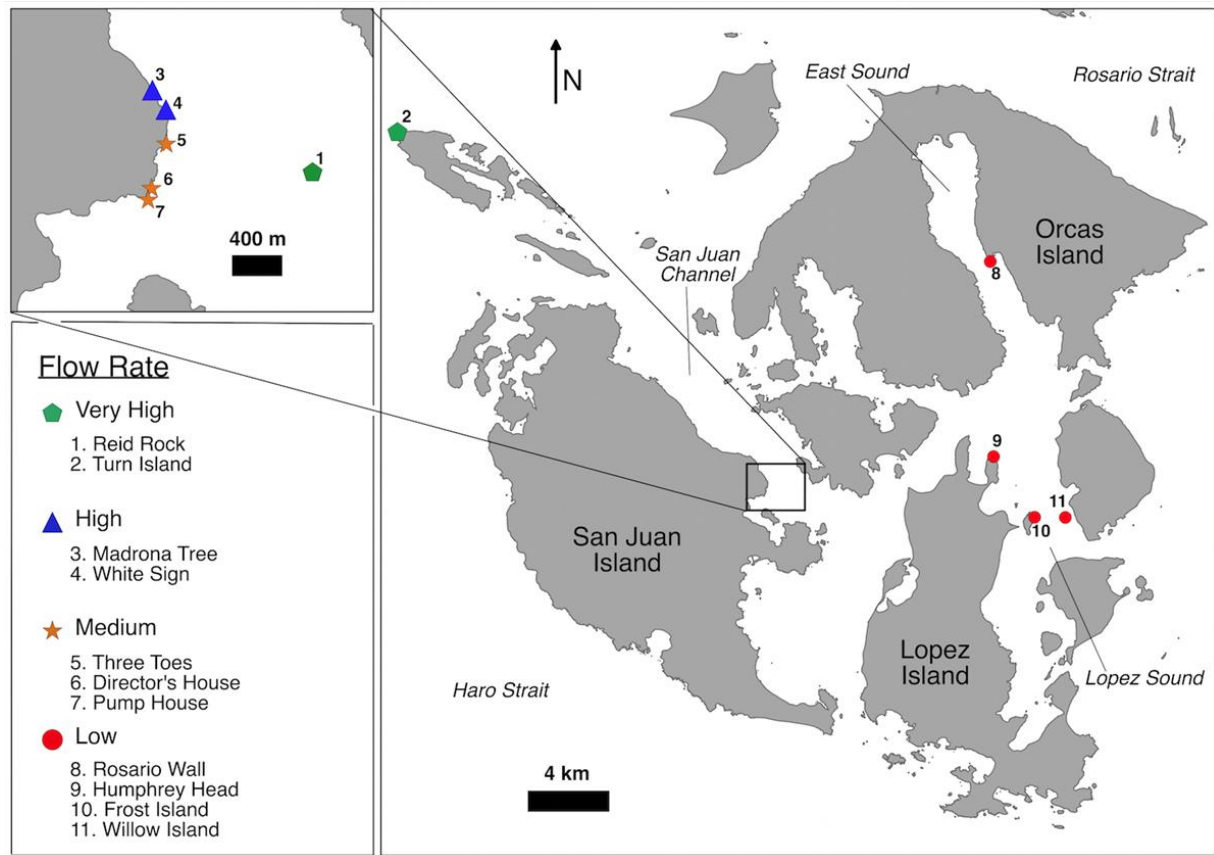


Figure 1. A map of the sites we used during our study.

Data Analysis

For our analyses, we used Excel 2010 and RStudio. At each site (Madrona Tree and WhiteSign), we calculated the density (number per m²) versus depth of *B. elegans* for both Madrona Tree and White Sign separately. We also looked at the distributions of coral surface area mean diameter, biomass, and largest diameter over different depths at both sites. We plotted the abundances of largest diameter, mean diameter (average of two diameters), biomass, and surface area at each site. We also plotted these four variables versus depth at each site.

We fitted general linear models to the data and used ANOVA tests to determine whether year, site, depth or any combinations of these variables could determine coral abundance and size. For coral size, we used both average coral size and individual coral size at each depth, year and site. To find a correlation for the flow data, we used (Spearman correlation or ANOVA?) test.

RESULTS

Analysis showed a strong linear correlation ($R^2 = 0.8803$) between actual N% and N% reported by CHN (Figure 2.A). There is also a strong linear correlation ($R^2 = 0.9157$) between the actual C% and the C% reported by CHN (Figure 2. B).

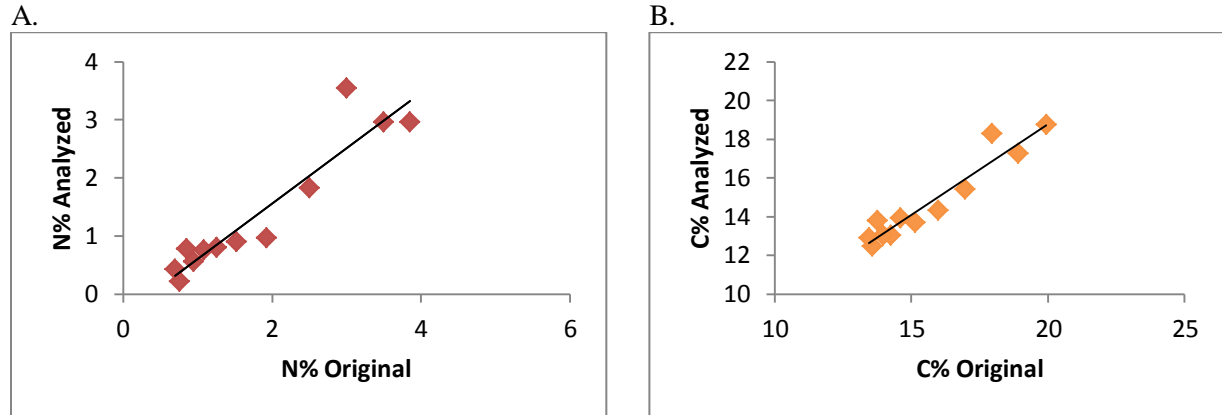


Figure 2. A) The percent nitrogen analyzed by CHN in the anemone samples versus the true percent nitrogen ($y = 0.9539x - 0.3508$, $R^2 = 0.8803$). B) The percent carbon analyzed by CHN in the anemone samples versus the true percent carbon ($y = 0.9379x + 0.0162$, $R^2 = 0.9157$).

The power correlation between largest diameter and biomass was significant ($R^2 = 0.896$, Figure 3. A). Surface area and biomass also have a significant power correlation ($R^2 = 0.8533$, Figure 3. B).

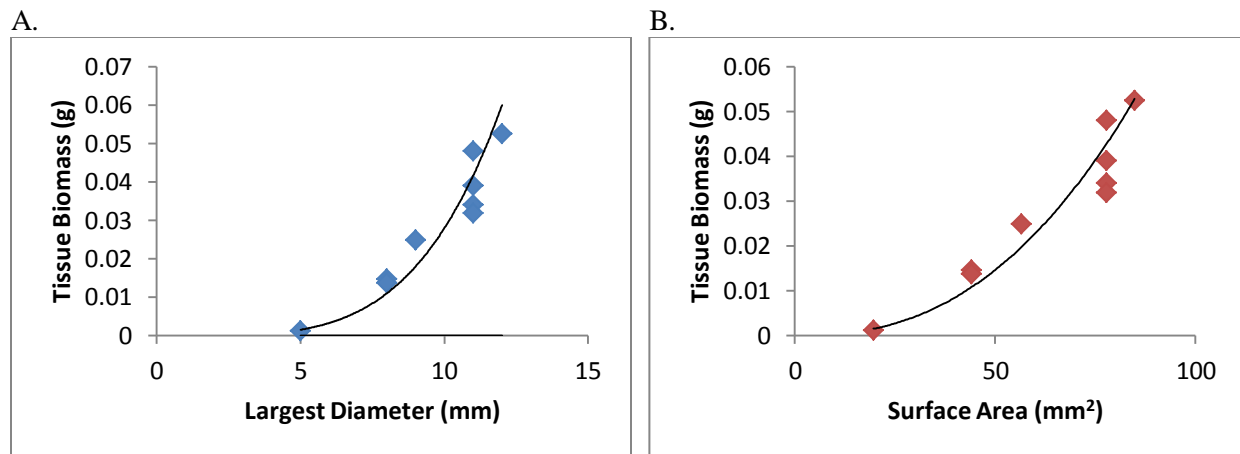


Figure 3. A) The calculated tissue biomass versus the largest diameter for the 10 corals ($y = 2E-06x^{4.1768}$, $R^2 = 0.9569$). B) The calculated tissue biomass versus the surface area for the 10 corals ($y = 1E-06x^{2.4238}$, $R^2 = 0.9595$).

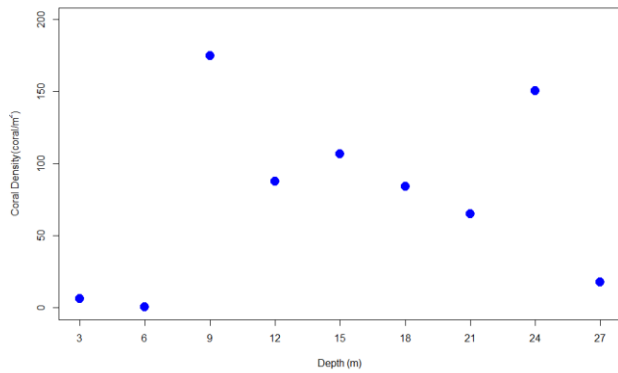


Figure 4. The coral population density (number of corals/m²) at each depth at White Sign.

At White Sign, the coral density was highest at 9 m and 24 m. (Figure 4). The abundances of largest diameter, mean diameter and surface area all have relatively normal distributions (Figure 5). The distribution of biomass is more of Poisson distribution (Figure 5). All depths have similar distributions of coral largest diameter, surface area and biomass (Figure 6). The largest corals, the ones with largest mean diameter, surface area, and biomass, are found at 6 m and 18 m (Figure 6).

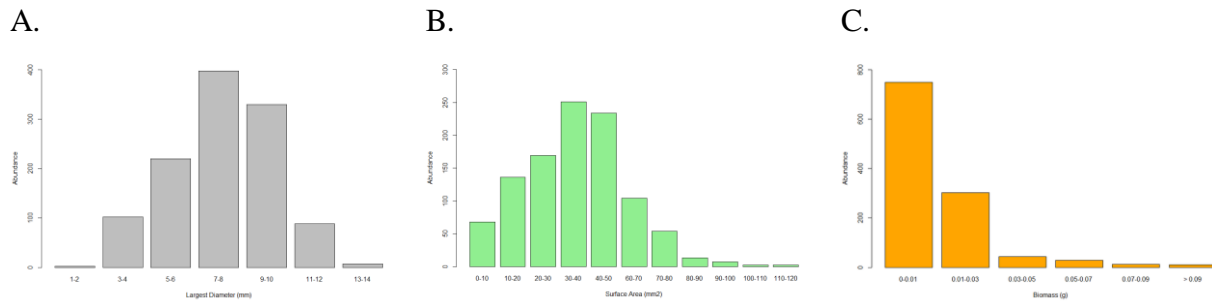


Figure 5. The abundances of A) largest diameter, B) surface area, and C) biomass at White Sign (n = 1147).

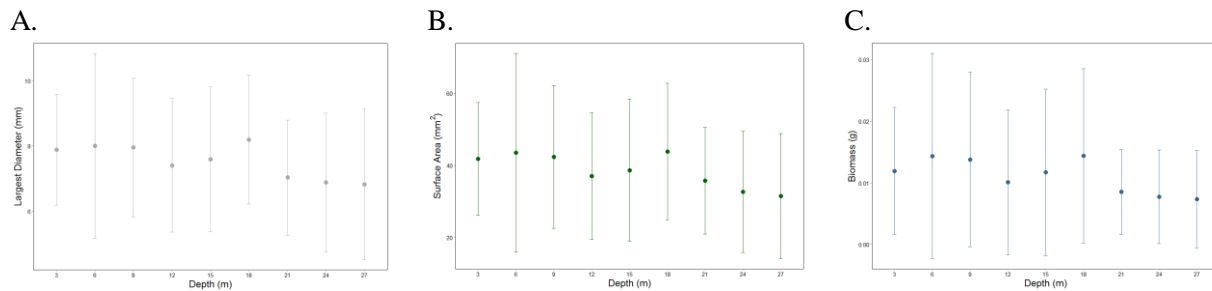
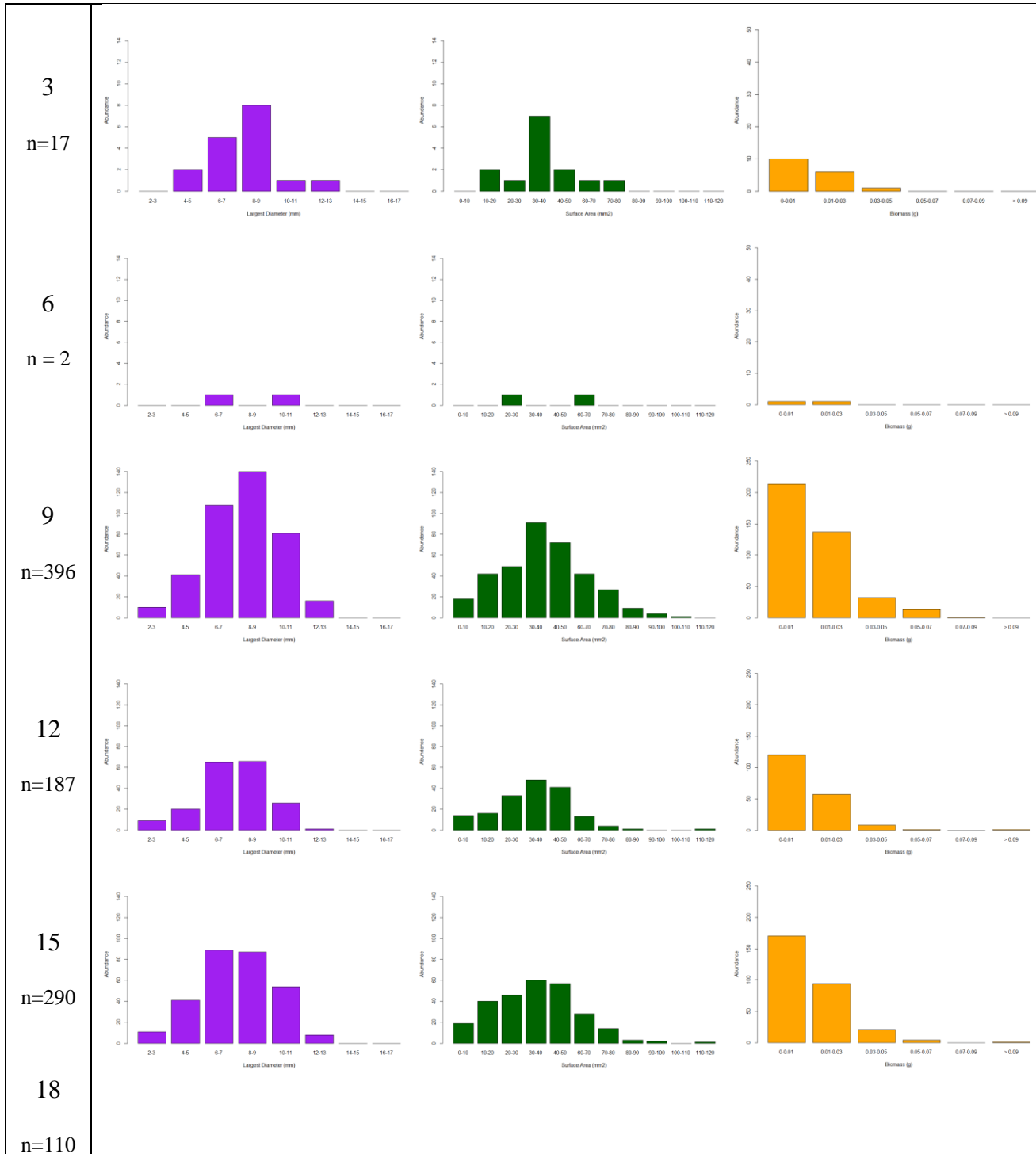


Figure 6. The means and standard deviations of A) largest diameter, B) surface area, and C) biomass over depth at White Sign (n=1147).

The abundances of largest diameter and surface follow relatively normal curves at all depths (Figure 7). Biomass has more of a Poisson curve at all depths (Figure 7).



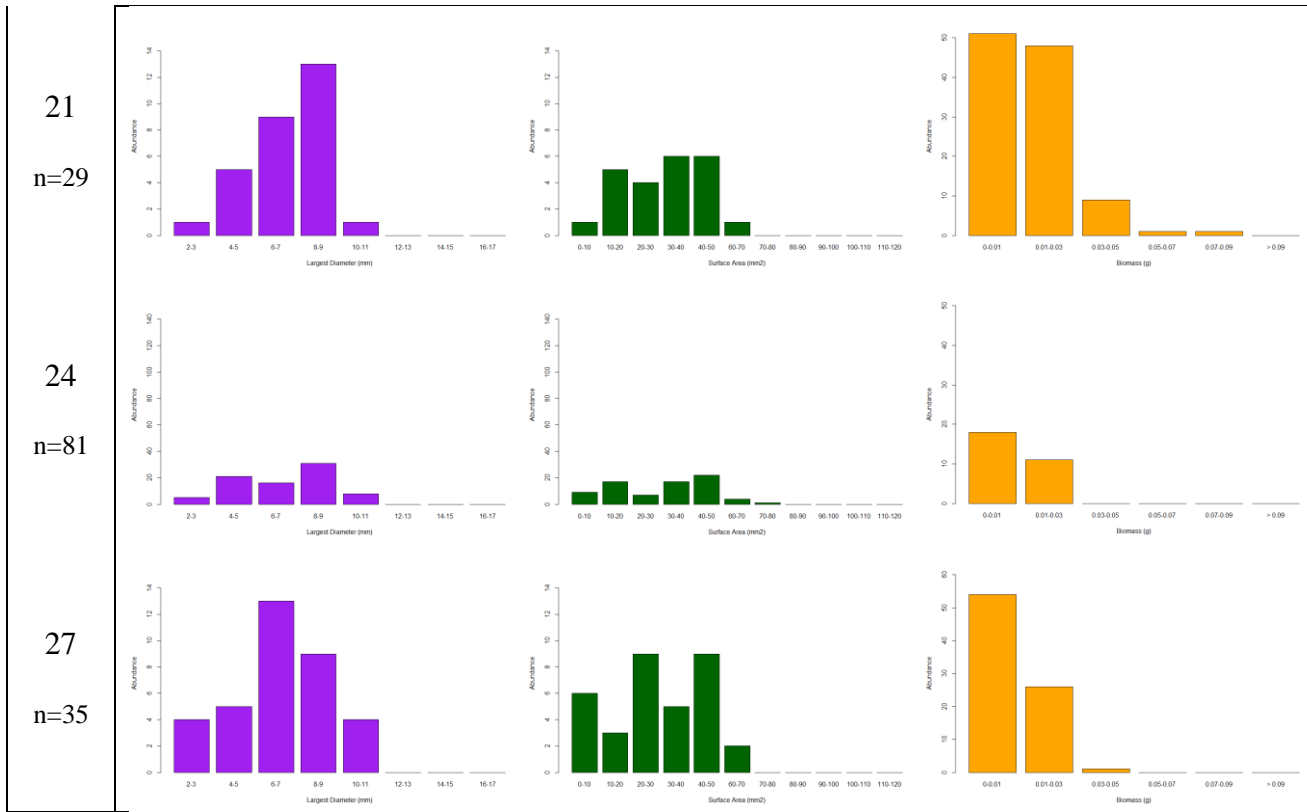


Figure 7. The abundances of largest diameter, surface area and biomass separated by depth at White Sign.

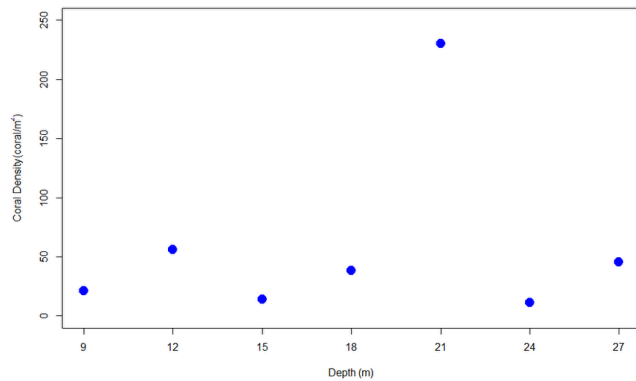


Figure 8. The coral density (number of corals/m²) at each depth at Madrona Tree.

The coral density at Madrona Tree is relatively constant and low at all depths except for 21 m (Figure 8). No corals were found at 3 and 6 m. (Figure 8). The abundances of largest diameter and surface area both have relatively normal distributions (Figure 9). The distribution of biomass is more of Poisson distribution (Figure 9). The largest corals, the ones with largest surface area and the largest biomass are found at 9 and 15 m (Figure 10).

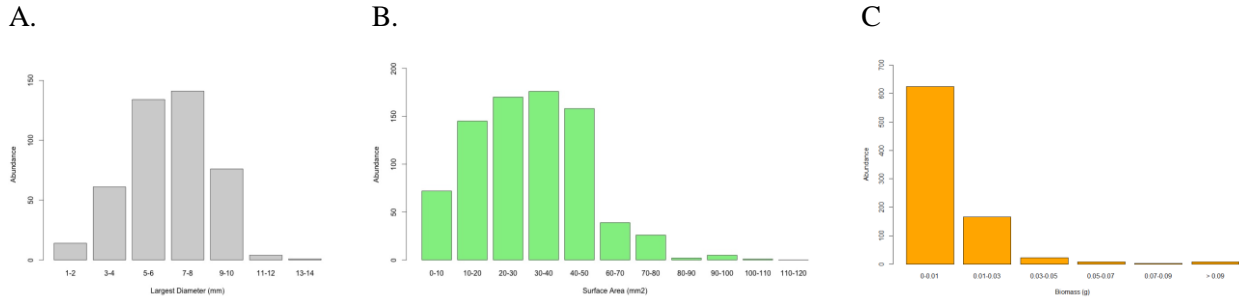


Figure 9. The abundances of A) largest diameter, B) surface area, and C) biomass at Madrona Tree (n = 831).

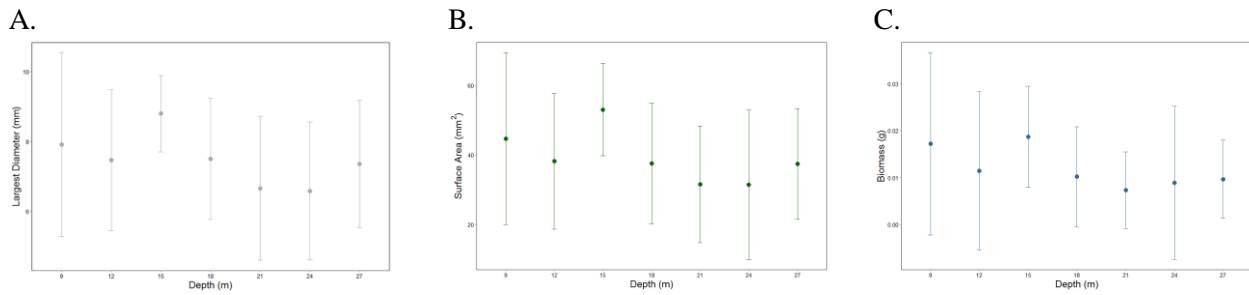
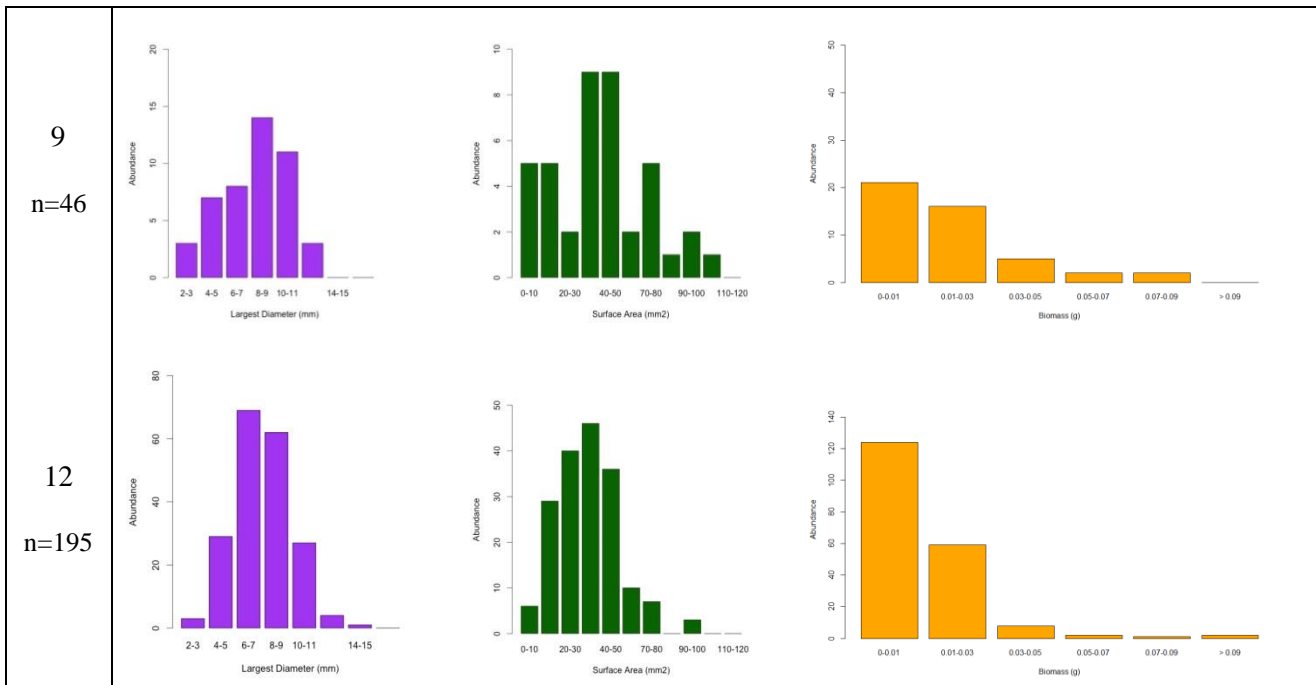


Figure 10. The means and standard deviations of A) largest diameter, B) surface area, and C) biomass over depth at Madrona Tree.

The abundances of largest diameter and surface follow relatively normal curves at all depths (Figure 11). Biomass has more of a Poisson curve at all depths (Figure 11). Very few corals were found at 15 and 24 m (Figure 11).



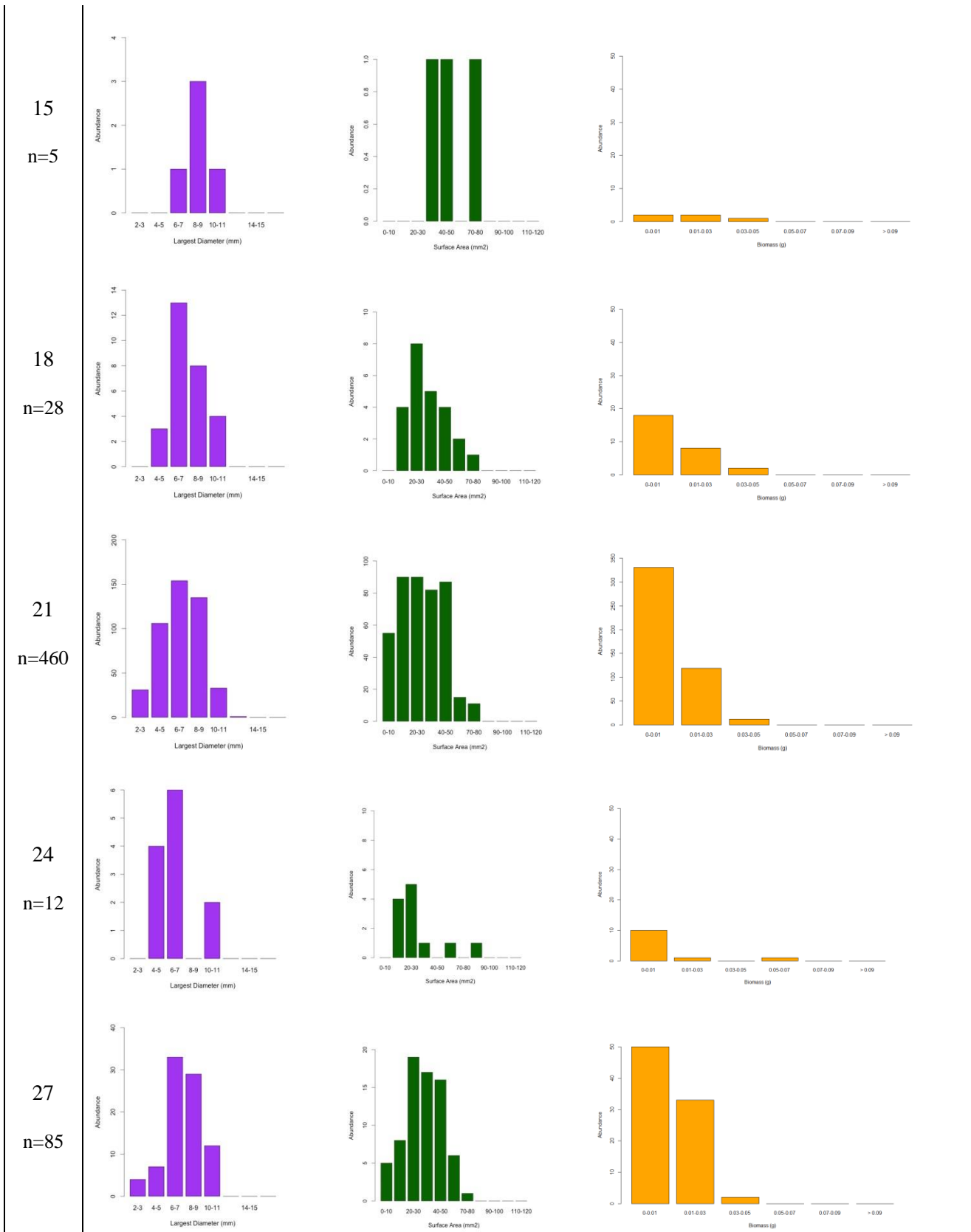


Figure 11. The abundances of largest diameter, surface area and biomass separated by depth at Madrona Tree.

The largest average coral surface areas and average biomasses, calculated at each year, depth and site, are found at 6 and 18 m. (Figure 12). Distribution of average coral surface area and average biomass is relatively similar across depths (Figure 12). The lack of data points at 3 and 6 m is due to the years at which transect photos had 0 corals in them.

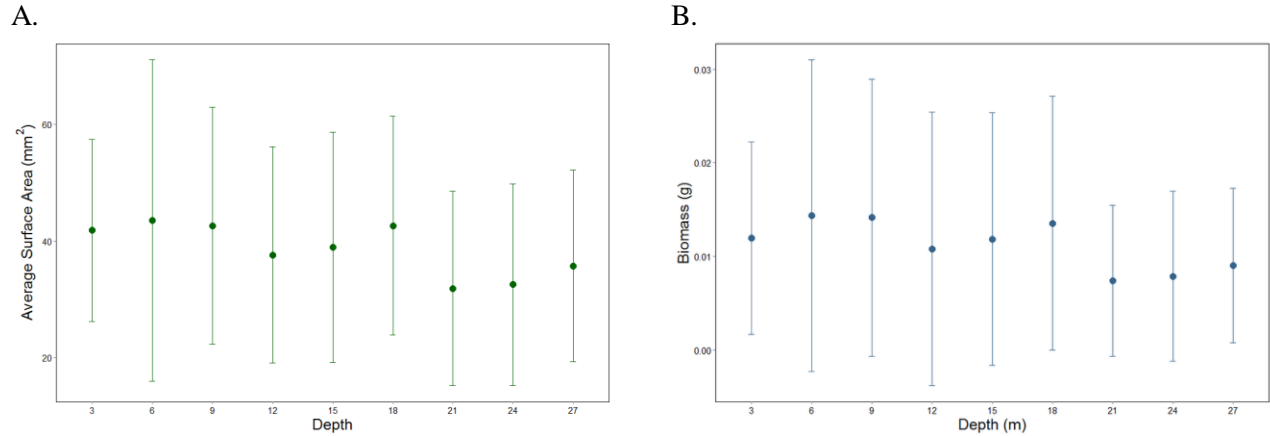


Figure 12. The A) mean coral surface area versus depth and B) average biomass versus depth for both White Sign and Madrona Tree. Each average is calculated over all years.

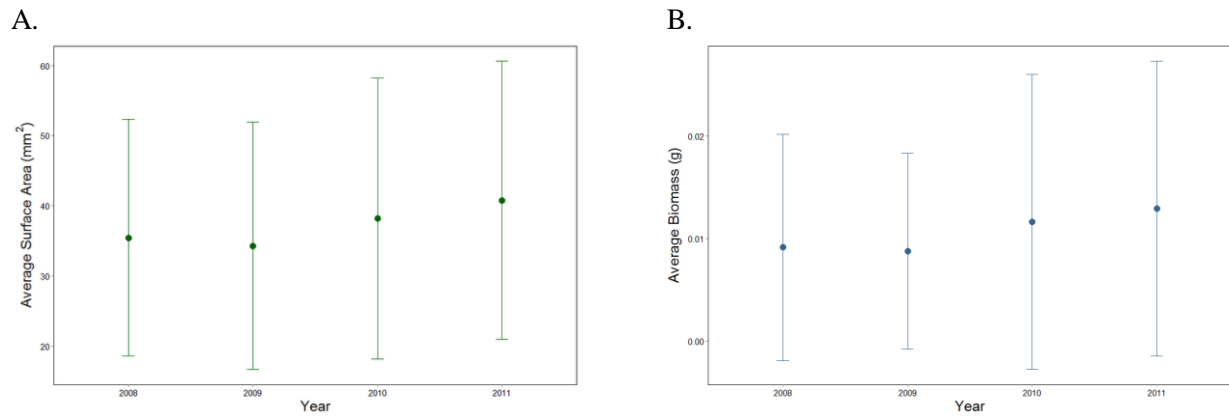
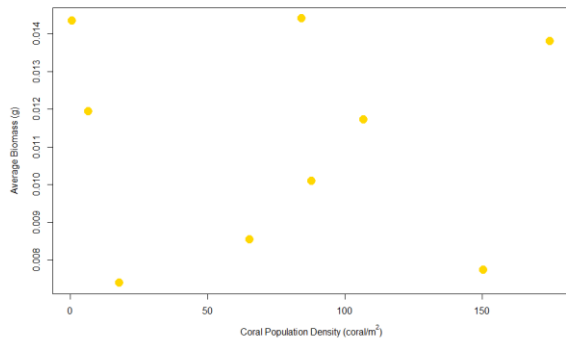


Figure 13. The A) average coral surface area versus year and B) average biomass versus year for White Sign and Madrona. Each average is calculated from a specific, year, site and corresponding depth.

The average coral surface area is relatively constant across years (Figure 13). Maximum average surface areas are found during the years 2010 and 2011 but they do not differ from the previous two years significantly (Figure 13). The years 2010 and 2011 also have the largest biomasses but not by a significant amount (Figure 13).

A.



B.

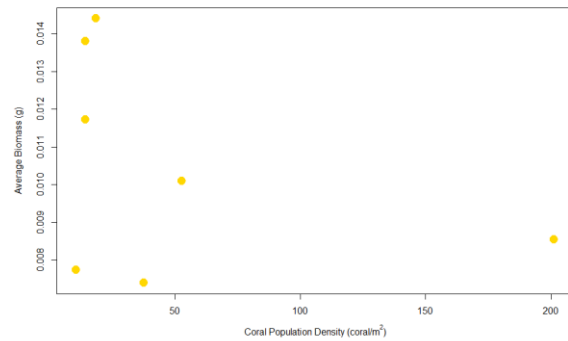
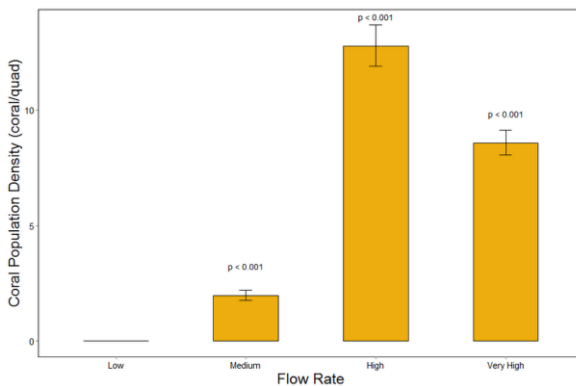


Figure 14. The average biomass plotted against the coral population density at each depth for A) White Sign and B) Madrona. There is no correlation between average biomass and coral population density.

To see if there was a correlation between average biomass and the coral population density, we plotted the two against each other at both Madrona and White Sign (Figure 14). The graphs show that there is no correlation between the biomass and density (Figure 14).

A.



B.

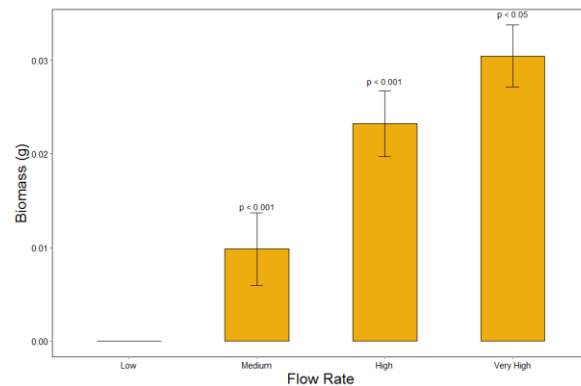


Figure 15. The A) population densities (n=170) and B) average biomasses (n=233) at different flow rates. Highest density does not correspond with highest biomass.

As previously mentioned, sites were grouped into four different flow ranks: low, medium, high and very high. Densities and biomasses were calculated from all the corals found at flow rank. Highest density is found at a high flow while the highest biomass is found at the very high flow (Figure 15).

Factor	P-Value
Year	p < 0.001
Site	p < 0.001
Depth	p < 0.001
Site * Depth	p < 0.001
Site * Year * Depth	p < 0.001

Table 2. Significance values of the Poisson general linear model on the coral abundances.

We ran a Poisson general linear model on the coral abundance, at each specific site, depth, and year. Year, site, depth and interactions between these factors are statistically significant predictors of coral abundance (Table 2).

We ran a Gaussian general linear model on the average coral surface area, at each specific site, depth, and year. Year (p < 0.001) was the only significant predictor of average coral surface area.

Factor	P-Value
Site	p < 0.001
Year	p < 0.001
Depth	p < 0.001
Site * Year	p < 0.001

Table 3. Significance values of the Gaussian general linear model on the individual coral surface areas.

We also ran a Gaussian general linear model on the individual coral surface areas. Site, year, depth and the interaction term site * year are statistically significant predictors of coral surface area (Table 3).

DISCUSSION

At White Sign, the depths 9 m and 24 m have the highest densities of corals (Figure 4). However, the largest corals are found at 6 and 18 m (Figure 6). We see this pattern at Madrona Tree as well. The highest density at Madrona Tree is at 21 m (Figure 8). The largest corals are found at 15 m though (Figure 10). Since larger corals use up more resources, intraspecific competition would cause corals to grow larger in areas where there are fewer surrounding corals (lower densities). The standard deviations overlap with each other significantly, though, which suggests that the differences in sizes between depths are not statistically significant.

Plotting the average biomasses against the population densities shows that there is no correlation between the two factors (Figure 14). At White Sign, the highest biomasses can be found at a variety of densities, suggesting that there are other factors affecting coral biomass.

We see a similar inconsistency in our flow analysis. Though the highest densities occur at high flow sites, the highest coral biomasses occur at very high flow sites (Figure 15). Again, this could be because of intraspecific competition. Also, some marine invertebrates show increased growth and survival rates in areas that are harder to settle in (Ekman and Duggins 1991). Though they may have a harder time settling at first, once they are settled, invertebrates have access to more resources (Ekman and Duggins 1991). This means that at very high flow sites, corals have difficulty settling, possibly due to the strong current or competition from other invertebrates. However, the corals that do settle have the resources to grow larger. Our flow results could be explained by the intermediate disturbance hypothesis. At high flow sites, corals experience the optimum amount of flow disturbance where they can thrive.

Our general linear models show that coral surface area and abundance can be predicted by various combinations of the factors year, site and depth (Tables 2 and 3). Because year is a significant factor, our data analysis is limited since we cannot group across years to increase our sample sizes at each depth and site. Our analyses based on abundance are most likely not representative of the true distributions at White Sign and Madrona Tree.

Because coral size and abundance can be predicted by the year, the increase in average size over the years may indicate a different phenomenon (Figure 13). The decrease in small corals could mean that the population is not reproducing very successfully. The present corals may be investing their energy in growing instead of reproducing. Another possibility is that the corals are reproducing, but the larvae are unable to settle successfully. From our data, we cannot distinguish between these two possibilities, but this question is an interesting and important area for future research.

For these analyses, we were restricted by time and sampling consistency. We could only analyze four years of data, so our analyses that look at changes over time are limited. Therefore, if we had data from more years and sites, we would be more certain of the results from our general linear models. Furthermore, divers changed their sampling method in 2009 by removing the mobile fauna (sea urchins, sea cucumbers, sea stars, etc.) before taking quadrat photos. In the photos from 2008, large sea urchins covered some of the photos, making it impossible to get an accurate count of corals in that quadrat. Also, since we took photos at random spots along the transects each year, the number of vertical photos available for analysis was not consistent each year. This would affect the distributions of density and abundance.

During our CHN analysis, we found that the extent of nitrogen masking changed with the amounts of N and C in the samples. The results from our anemone analysis were inconsistent as the C:N ratio did not increase as we added more CaCO_3 . However, we did not have enough time to correct for these data so the actual numbers for biomass are not completely correct but the distributions are what they would have been. Therefore, for analysis purposes, we can still use the graphs.

In summary, we found that we could determine coral biomass from photos. The distributions of *B. elegans* vary by site and depth and year. Though White Sign and Madrona Tree are next to each other, their distributions differ dramatically. The cause of this is still

unknown. The largest biomasses do not correlate with the highest densities, both at the site and flow levels. *B. elegans* prefers high flow sites. Average size increased over time, though not significantly. Our limited findings on the abundance, size and distribution of *Balanophyllia elegans* call for future research on this San Juan species.

Acknowledgements. We would like to thank Kenneth Sebens and Kevin Turner for their support and guidance. Thank you to Tim Dwyer, Derek Smith, Heather Denham, and Jessica Nordstrom for completing data collection. The Analytical Service Center at the University of Washington helped run our CHN analyses. Data from Robin Elahi's previous work helped us complete our flow analysis. Thanks to the University of Washington Friday Harbor Labs for providing the tools and resources for us to analyze data, as well as the Mary Gates Endowment Scholarship for providing financial support.

REFERENCES

- Altieri, Andrew H. "Settlement Cues in the Locally Dispersing Temperate Cup Coral *Balanophyllia Elegans*." *Biological Bulletin* 204.3 (2003): 241. CrossRef. Web. 27 Sept. 2013.
- Bruno, John F., and Jon D. Witman. "Defense Mechanisms of Scleractinian Cup Corals Against Overgrowth by Colonial Invertebrates." *Journal of Experimental Marine Biology and Ecology* 207.1-2 (1996): 229–241. CrossRef. Web. 20 Oct. 2013.
- Capone, Douglas G., and David A. Hutchins. "Microbial Biogeochemistry of Coastal Upwelling Regimes in a Changing Ocean." *Nature Geoscience* 6.9 (2013): 711–717. CrossRef. Web. 15 Oct. 2013.
- Carlson, David B., and Richard Randolph Olson. "Larval Dispersal Distance as an Explanation for Adult Spatial Pattern in Two Caribbean Reef Corals." *Journal of Experimental Marine Biology and Ecology* 173.2 (1993): 247–263. CrossRef. Web. 28 Sept. 2013.
- Caroselli, Erik et al. "Growth and Demography of the Solitary Scleractinian Coral *Leptopsammia Pruvoti* Along a Sea Surface Temperature Gradient in the Mediterranean Sea." Ed. Sebastian C. A. Ferse. *PLoS ONE* 7.6 (2012): e37848. CrossRef. Web. 18 Oct. 2013.
- Chadwick, Ne. "Spatial Distribution and the Effects of Competition on Some Temperate Scleractinia and Corallimorpharia." *Marine Ecology Progress Series* 70 (1991): 39–48. CrossRef. Web. 27 Sept. 2013.
- Coyer, James A. et al. "Interactions Between Corals and Algae on a Temperate Zone Rocky Reef: Mediation by Sea Urchins." *Journal of Experimental Marine Biology and Ecology* 167.1 (1993): 21–37. CrossRef. Web. 8 Oct. 2013.
- Eckman, J.E. and D.O. Duggins. "Life and Death beneath Macrophyte Canopies: Effects of Understory Kelps on Growth Rates and Survival of Marine, Benthic Suspension Feeders." *Oecologia* 87.4 (1991): 473-487. Web. 4 Dec. 2013.

- Edmunds, PJ, and RD Gates. "Normalizing Physiological Data for Scleractinian Corals." *Coral Reefs* 21.2 (2002): 193–197.
- Elahi, R, and KP Sebens. "Consumers Mediate Natural Variation Between Prey Richness and Resource Use in a Benthic Marine Community." *Marine Ecology Progress Series* 452 (2012): 131–143. CrossRef. Web. 18 Oct. 2013.
- Elahi, Robin et al. "Limited Change in the Diversity and Structure of Subtidal Communities over Four Decades." *Marine Biology* (2013): n. pag. CrossRef. Web. 1 Oct. 2013.
- Elahi, Robin, Tim Dwyer and KP Sebens. "Mesoscale variability in oceanographic retention sets the abiotic stage for subtidal benthic diversity." Unpublished.
- Fadlallah, Yusef H. "Population Dynamics and Life History of a Solitary Coral, *Balanophyllia elegans*, from Central California." *Oecologia* 58.2 (1983): 200-20.
- Gerrodette, T. "Equatorial Submergence in a Solitary Coral, *Balanophyllia Elegans*, and the Critical Life Stage Excluding the Species from Shallow Water in the South." *Marine Ecology Progress Series* 1 (1979): 227–235. CrossRef. Web. 20 Oct. 2013.
- Gerrodette, Tim. "Dispersal of the Solitary Coral *Balanophyllia Elegans* by Demersal Planular Larvae." *Ecology* 62.3 (1981): 611. CrossRef. Web. 8 Oct. 2013.
- Hurlbut, C.J. "The Effects of Larval Abundance, Settlement and Juvenile Mortality on the Depth Distribution of a Colonial Ascidian." *Journal of Experimental Marine Biology and Ecology* 150.2 (1991): 183–202. CrossRef. Web. 28 Sept. 2013.
- Jackson, J. B. C. "Competition on Marine Hard Substrata: The Adaptive Significance of Solitary and Colonial Strategies." *The American Naturalist*, 111.980 (Jul. - Aug., 1977): 743-767.
- Johannes, RE, and WJ Wiebe. "METHOD FOR DETERMINATION OF CORAL TISSUE BIOMASS AND COMPOSITION." *LIMNOLOGY AND OCEANOGRAPHY* 15.5 (1970): 822–824. Print.
- Schutter, M. et al. "The Effect of Different Flow Regimes on the Growth and Metabolic Rates of the Scleractinian Coral *Galaxea Fascicularis*." *Coral Reefs* 29.3 (2010): 737–748. CrossRef. Web. 21 Oct. 2013.