Community assembly in subtidal macroalgal communities: The importance of environmental gradients

by

Valerie Mucciarelli
BSc, Western University, 2006

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in the School of Environmental Studies

Supervisory Committee

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Abstract

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As human activity along coastlines increase, degradation and destruction of coastal marine ecosystems around the globe will increase at an alarming rate. In an effort to mitigate degradation and destruction of coastal marine ecosystems, artificial reefs have been used in restoration and enhancement projects. As artificial reefs are the main method of restoring diversity to a degraded area, it is important to know the mechanisms that drive marine community assembly and diversity on those reefs. Understanding community assembly patterns of foundational species, in particular, may provide insight to community assembly patterns at higher trophic levels. Subtidal macroalgae are commonly seen as foundational species in marine environments and both deterministic and stochastic processes play a role in their assembly. Environmental gradients, which are deterministic processes, play a significant role in structuring subtidal macroalgae communities. Depth, which is negatively correlated with light, is the main driver structuring subtidal macroalgal communities, however, other gradients such as water flow, and distance to a propagule source also impact their assembly. This study sought to determine which environmental gradients play a prominent role in subtidal macroalgal community assembly. To study subtidal macroalgal community assembly, 92 artificial reef units called Reef Balls were deployed east of the Ogden Point Breakwater in Victoria, BC in June 2009. Two years passed to allow for macroalgal growth and early successional processes to occur prior to sampling the communities on thirty Reef Balls via underwater collection in July 2011. Algae were sorted by genus and dry weight was measured. To determine effects of environmental gradients on community assembly light, depth, water flow, distance to the nearest Reef Ball and distance to the breakwater

were measured at each Reef Ball. A redundancy analysis revealed that depth was the most significant environmental gradient shaping algae communities and had the greatest effect on upper canopy algae. Spatial plots reveal a depth and coastline zonation of algae genera comprising the canopy. While depth was found to significantly structure algae genera found in the canopy, there was a high degree of unexplained variation in the model. This suggests that unmeasured variables such as colonization and priority effects may be driving algal community structure in the lower canopy. Differences in community structure between upper and lower canopy reveal that multiple mechanisms are responsible for shaping subtidal algal communities. Further study is required to determine the importance of stochastic colonization events and priority effects.

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Acknowledgments

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Chapter 1 Introduction

1.1 Degradation of Marine Ecosystems

Diversity of coastal marine systems is being threatened due to anthropogenic activities causing disturbance, degradation, and stress to marine communities (Halpern et al. 2007, Hoegh-Guldberg et al. 2007, Waycott et al. 2009). As human activity along coastlines increase, degradation and destruction of coastal marine ecosystems around the globe will increase at an alarming rate (Halpern et al. 2008). Nineteen percent of the world's coral reefs have been destroyed (Wilkinson 2008), mangroves are being lost at a rate of 1-2% a year (Alongi 2002), and 29% of the global areal extent of seagrasses have been lost (Waycott et al. 2009). Pollution and excess nutrients from run-off, alterations to the natural coastline, and industrial activities all negatively impact coastal marine communities and diversity (Deysher et al. 2002, Bulleri et al. 2005, Gorman et al. 2009).

In an effort to mitigate the degradation and destruction of coastal marine ecosystems, artificial reefs have been used in restoration and enhancement projects (Deysher et al. 2002, Al-Horani and Khalaf 2013, Ngai et al. 2013). Artificial reefs have been successful at offsetting altered, damaged, or destroyed marine habitat by providing structural complexity in areas that experience low levels of negative anthropogenic stressors (Ngai et al. 2013). Their use is especially appropriate when they can be deployed within the same area in which structural complexity in the ecosystem has been reduced due to alterations in the coastline such as seawalls (Bulleri and Chapman 2004, Perkol-Finkel et al. 2006a, Chapman and Blockley 2009). In particular, artificial reef units called Reef Balls are claimed to be complex and rugose structures that are

successful at supporting a diversity of marine life in marine ecosystems all over the world (www.reefball.org). In addition to complexity, Reef Balls have a sufficiently large surface area that is able to support higher trophic level organisms such as fish and crabs (Sherman et al. 2002). Reef Balls appear to be quite successful at replicating natural substrate and supporting diverse marine communities (Sherman et al. 2002, Koenig et al. 2005).

In restoration, one of the main goals is to return biodiversity to an area (Sherman et al. 2002, Hughes et al. 2005, Campbell et al. 2014). As anthropogenic activities continue to increase, restoring biodiversity to coastal marine ecosystems will become vital (Hughes et al. 2005). As artificial reefs are the main method of restoring diversity to a degraded area, it is important to know the mechanisms that drive marine community assembly and diversity on those reefs.

1.2 Mechanisms driving community assembly in marine ecosystems

Marine communities are shaped by deterministic mechanisms as well as unpredictable mechanisms that arise from stochastic processes (Bonsdorff and Pearson 1999, Siegel et al. 2008). Stochastic processes affecting the initial stages of community assembly include immigration/dispersal and colonization, which, in turn play a role in priority effects (Kendrick and Walker 1991, Benedetti-Cecchi 2000, Cifuentes et al. 2010). Variation in these processes leads to changes in community assembly and structure (Reed et al. 1988, Benedetti-Cecchi 2000, Cifuentes et al. 2010).

Deterministic abiotic processes, such as environmental gradients, competition, and predation, also govern community assembly (Stephenson and Stephenson 1949, Bonsdorff and Pearson 1999, Fabricius et al. 2005). Competition for space and herbivory can play important roles in structuring marine communities (Kastendiek 1982, Lubchenco 1982, Breitburg 1984). Changes in competition and grazing pressures result in changes in species abundances and presence in many marine ecosystems (Kastendiek 1982, Lubchenco 1982, Breitburg 1984). Environmental gradients determine the spatial patterns in which competition and grazing occur. As environmental conditions change over an area, community composition changes as each species has a niche that governs the environmental conditions in which they are able to survive (Johansson and Snoeijs 2002). These gradients not only influence changes in community composition, and competition and grazing pressures, but also beta diversity (Eriksson et al. 2006).

Environmental gradients, such as depth, light, water flow, nutrients, and salinity, shape biotic community patterns in marine ecosystems (Sebens 1984, Vadas and Steneck 1988, Bonsdorff and Pearson 1999, Fabricius et al. 2005). One of the most influential gradient in subtidal communities is depth, which is associated with light (Bourget et al. 1994). The attenuation of light through the water column creates zonations in light-dependant organisms which in turn influences community assemblage patterns of other organisms (Friedlander and Parrish 1998, Ruitton et al. 2000, Malcolm et al. 2011).

Environmental gradients and stochastic processes impact marine communities at both large and small spatial scales (Bonsdorff and Pearson 1999, Siegel et al. 2008, Jacobucci et al. 2010, Gaylord et al. 2012). Most restoration efforts occur at relatively small spatial scales – within hundreds of metres (Perkol-Finkel et al. 2006a, Chapman

and Blockley 2009, Toft et al. 2013). Thus, it is important to understand the magnitude of impact that small variations in environmental gradients have on community assembly at small spatial scales.

When embarking upon restoration in which artificial habitat is added to an area, understanding community assembly patterns of foundational species will provide insight to community assembly patterns at higher trophic levels (Edgar et al. 2004, Ellison et al. 2005). Macroalgae are commonly observed as foundational species, thus, this study focuses on subtidal macroalgae that grew on an artificial reef.

1.3 Environmental Gradients and Abiotic Factors Affecting Algal Communities in Subtidal Marine Ecosystems

Abiotic factors that affect subtidal algae distribution and abundance within communities include salinity (Druehl 1967), nutrients (Teichberg et al. 2010), light (Connell 2005), depth (Hop et al. 2012), sedimentation (Shepherd et al. 2009), water flow (Ferrier and Carpenter 2009), and distance from a seed source (Reed et al. 1988). Light, depth, water flow, and sedimentation, can vary at small spatial scales which alters algal community composition and diversity (Reed and Foster 1984, Eckman et al. 1989, Schiel et al. 1995, Airoldi and Cinelli 1997, Ferrier and Carpenter 2009).

Light, which is associated with depth, is one of the main environmental gradients shaping algal communities (Vadas and Steneck 1988). Attenuation of wave length spectrum and intensity through the water column results in a gradation of algal communities across depths (Markager and Sand-jensen 1992, Schiel et al. 1995). Vadas and Steneck (1988) observed a concomitant gradation in functional groups in a temperate

subtidal marine system in which leathery macrophytes occupied the more shallow depths, foliose red algae at mid depths, and crustose algae occupied the deepest depths. Rarer functional groups were also dispersed at varying depths but the physically dominant macroalgae defined these zones (Vadas and Steneck 1988).

In the marine environment, water flow experienced by subtidal macroalgae can arise from tidal currents, wind-driven oscillatory flow, upwelling/downwelling water movement, density fronts, eddies, internal waves, storms, and turbulent mixing (Mann and Lazier 1991, Hurd 2000, Garland et al. 2002, Gaylord et al. 2012). These processes act at both large and small spatial scales, influencing the dispersal and growth of macroalgae (Mann and Lazier 1991, Hurd 2000, Garland et al. 2002, Gaylord et al. 2012). To maintain simplicity, hereafter, these processes will be referred to as "water flow". Water flow, often correlated with sedimentation, also influences algal community composition (Balata et al. 2007, Hansen and Reidenbach 2012). While not as influential as light, water flow does affect spore dispersal and settlement (Gaylord et al. 2006) and sedimentation (Hansen and Reidenbach 2012), and thus the dominance of sediment tolerant algal functional groups (Balata et al. 2007). Slow water velocities at the site of colonization will enhance spore settlement but it also enhances sedimentation which can suffocate spores and mature plants alike (Airoldi and Cinelli 1997, Steneck et al. 1997, Chapman and Fletcher 2002). Filamentous algae are superior in withstanding such effects compared to blade, ribbon, or encrusting forms. As a result, filamentous algae tend to dominate substrates with greater amounts of sedimentation resulting in a decrease in algal diversity (Airoldi 1998, 2003, Irving and Connell 2002b, Balata et al. 2007). High water velocities increase spore dispersal and inhibits sediment from settling and

covering algae, but it reduces the probability of spores settling (Norton and Fetter 1981, Gaylord et al. 2006, Hansen and Reidenbach 2012).

Hydrodynamics influence the distance at which algal spores are carried from a propagule source to an available patch of habitat (Gaylord et al. 2012). Algal spores have demonstrated both long and short distance dispersal capabilities resulting in variable spatial patterns associated with distance from a propagule source (Kendrick and Walker 1991, Arrontes 2005, Buchanan and Zuccarello 2012). Spores of some algal species, such as brown kelps, tend to disperse over short ranges - on the scale of metres (Kendrick and Walker 1991). This can lead to localized populations of brown kelps within an area (Schiel 1985). Long dispersal ranges, on the order of hundreds of kilometres, have also been documented for spores of many algal specimens, including some brown kelps. (Benedetti-Cecchi et al. 2001, Buchanan and Zuccarello 2012).

Determining the level of influence that environmental gradients have on subtidal macroalgal assemblages can be challenging due to heterogeneity in the natural substrate of subtidal ecosystems (Toohey et al. 2007, Zawada et al. 2010). Small changes in rugosity, shape, or area of the substrate can also significantly alter community composition (Borowitzka et al. 1990, Toohey et al. 2007, Miller and Etter 2008). Artificial reefs provide a potential solution. By deploying replicable, realistic habitats in which size, shape, and rugosity are consistent, direct comparisons of algal communities generated across the putatively seminal environmental gradients can be made (Rule and Smith 2007). Tiles or plates are the most frequently used artificial substrate in subtidal algae community studies (Dudgeon and Petraitis 2001, Wahl 2001, Coleman 2003, Korpinen et al. 2007). While minimally satisfying the role of "substrate" these physical

interventions are highly artificial (two dimensional smooth substrate of varying chemical composition) and may unintentionally facilitate or retard both plant and animal life on and around the plates. "Reef Balls" in contrast are purpose-built and designed to simulate natural hard structure however have only been rarely used in subtidal studies to date (Oritz-Prosper et al. 2001, Sherman et al. 2002, Jardeweski and de Almeida 2004, Koenig et al. 2005).

In this study Reef Balls were deployed in a physically homogenous environment parallel to a putatively significant propagule source. In so doing, this study aims to determine the relationship between small changes in environmental gradients such as light, depth, water flow, and distance to a propagule source and subtidal macroalgal community assembly and diversity. Effects of environmental gradients on genera diversity, functional groups, and community composition were explored.

Chapter 2 Methods

2.1 Overview

Environmental gradients influence marine algal community assembly and diversity (Vadas and Steneck 1988). Environmental gradients that play a dominant role in subtidal macroalgal community assemblies across small spatial scales include depth, light, water flow, and distance from a seed source (Reed et al. 1988, Connell 2005, Shepherd et al. 2009, Ferrier and Carpenter 2009, Hop et al. 2012). These abiotic factors influence community composition, diversity, and functional group composition (Ferrier and Carpenter 2009, Hop et al. 2012). In this study the relationship between macroalgal communities and depth, light, water flow, and distance from a seed source were measured. Environmental factors were measured at each sample site and the algal community was destructively sampled.

2.1 Study Site

The study was conducted in marine waters east of the Ogden Point Breakwater (48°24'47.64"N, 123°23'11.64"W) in Victoria, British Columbia, Canada (Figure 1).

Figure 1. Location of sampling site at the Ogden Point Breakwater, Victoria, BC. The rectangle outlines the sampling area. Yellow circles represent Reef Balls.

The breakwater, completed in 1917, extends 800m from shore and is constructed of concrete and granite and gravel ballast. The breakwater is located within a marine sanctuary, however angling is still permitted (Biffard, personal communication). The blocks and boulders that make up the breakwater support a marine community indicative of a late successional stage. In the subtidal area, blocks are dominated by encrusting algae and a bull kelp canopy, which is characteristic of a mature kelp forest ecosystems (Foster 1975). Scattered among the encrusting algae, erect soft bodied algae and sessile invertebrates such as anemones, tunicates, sponges, and tubeworms have also managed to

acquire space on the substrate (personal observation). The kelp canopy and the complex structure created by the blocks and boulders that make up the breakwater, support a relatively diverse marine community including vagile organisms such as crabs, fish, nudibranchs, sea stars etc. (personal observation). During the spring and summer seasons, an eel grass bed, located east of the breakwater, and the kelp canopy act as nurseries for many fish species including economically significant fish such as salmon and herring (personal observation).

The study area, located 15m east from the bottom of the breakwater, measured 120m x 100m with the long axis running parallel to the breakwater. The northeast corner of the study area is the shallowest at approximately 10m deep, while the southwest corner is the deepest at approximately 18m deep. Depth within the study area increases moving south and west from the northeast corner. The study site substratum is relatively flat, silty, with macroalgae between a 10m and 13m depth.

2.2 Reef Balls

Reef Balls (http://www.reef ball.org/index.html) are concrete, dome shaped structures of varying sizes designed to rehabilitate and restore damaged marine habitats. The concrete pH is similar to that of seawater, reducing the alkaline effects of concrete in seawater. Reef Balls were used for this study because the design, material, and structure of Reef Balls replicate natural rocky reefs found in temperate marine systems, making them effective marine habitat for this study area (http://www.reef ball.org/index.html). In addition, unlike natural rocks or boulders, each Reef Ball was constructed to have the same structure, form and rugosity. This results in rugosity and structure remaining

constant across all replicates, allowing for direct observations of algal communities responding to environmental gradients.

Reef Balls used in this study are 0.91m in diameter, 0.76m high and weigh approximately 170kg (Figure 2). The wall is twelve cm thick and each ball has six or seven holes and a hollow core.

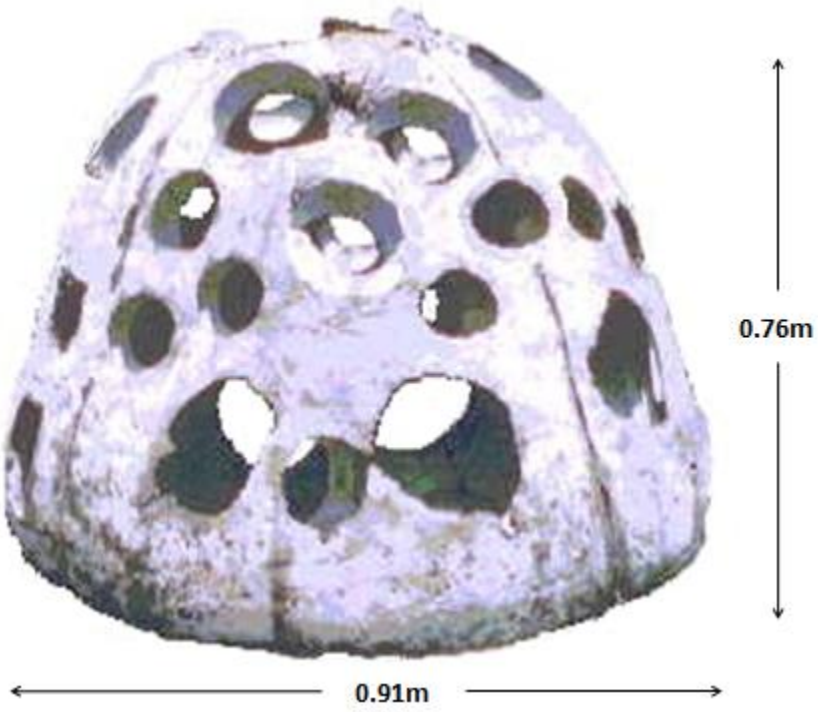

Figure 2. Reef Ball (http://www.reefball.org/)

2.3 Sampling Design

From June 27th 2009 – June 30th 2009, 92 Reef Balls were deployed in the study area, east of the Ogden Point breakwater. A landing craft with a hydraulic davit was used to transport and deploy the Reef Balls (Figure 3).

Figure 3. Photo of Reef Ball deployment method. A hydraulic davit on a landing craft was used to lower Reef Balls to ocean floor.

The hydraulic davit allowed for each Reef Ball to be lowered down to the substrate, ensuring that they would remain fully intact. During deployment, a block design layout was attempted by attaching the landing craft to a line that was anchored at both ends, and that ran perpendicular to the breakwater. Reef Balls were to be deployed along that line at equally spaced distances and on subsequent lines that ran parallel to the original anchored line. However, due to high winds and strong currents during each deployment day, the landing craft dragged the line and anchors to which it was attached and did not

deploy Reef Balls in a straight line. As a result Reef Balls were deployed in a haphazard manner (Figure 4).

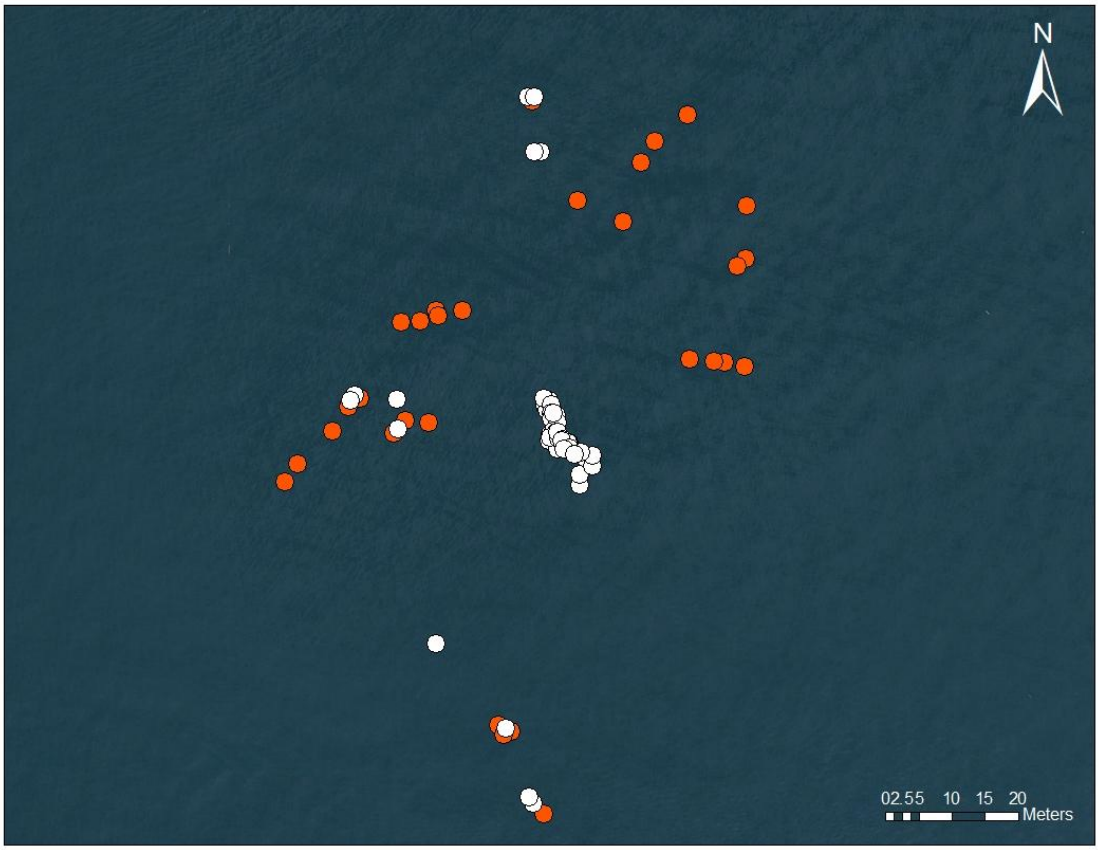

Figure 4. Aerial perspective of the Reef Balls. Orange circles are sampled Reef Balls, white circles are non-sampled Reef Balls.

Due to Reef Balls being deployed in a haphazard manner instead of a block design, there were unequal replicates at different depths, distances to breakwater and other Reef Balls and potentially different water velocities. This may have reduced the strength of detecting signals among the environmental variables due to lower replicate numbers at certain depths, distances from the breakwater and Reef Balls, and water

velocities (Krebs 1998). A high number of replicates are especially needed for macroalgae communities as they tend to be very spatially heterogeneous (Coleman 2002).

Thirty of 92 Reef Balls were sampled in this study (n=30) (Figure 4). The Reef Balls that were chosen to include in the study possessed the following criteria: a) Positioned upright b) were not part of the large cluster of 36 Reef Balls c) south facing side was exposed d) was located at a depth no greater than 18.3m. Criteria a) and c) were chosen in order to maintain consistency in the light environment across sample areas. Reef Balls that were not sitting upright had different inclinations than those that were upright. Different inclinations of substrate lead to differences in light intensity, as does differences in the direction in which the substrate faces (Brakel 1979). Criteria b) was chosen because a Reef Ball within a large cluster of Reef Balls may experience higher trophic level interactions due to the greater total surface area supporting higher trophic level species compared to Reef Balls located in isolation or in smaller groups which would have smaller total surface areas (Paddack et al. 2006). Criteria d) was chosen in order to conduct subtidal research within the limits outlined by the University of Victoria Guide for scientific diving safety.

A circular quadrat with a 30cm diameter was placed on each sampled Reef Ball. Circular quadrats were used to reduce edge effects (Krebs 1998) and to maximize the sample area which was positioned between the holes of the walls on the Reef Ball. Circular quadrats were fastened to the upper hemisphere of the south side of each Reef Ball using cable ties (Figure 5). Quadrats were only fastened to the upper half of the Reef ball to ensure light intensities were not affected by Reef Ball shape. To identify Reef Balls, each was numbered using a plastic tag and cable tie (Figure 5).

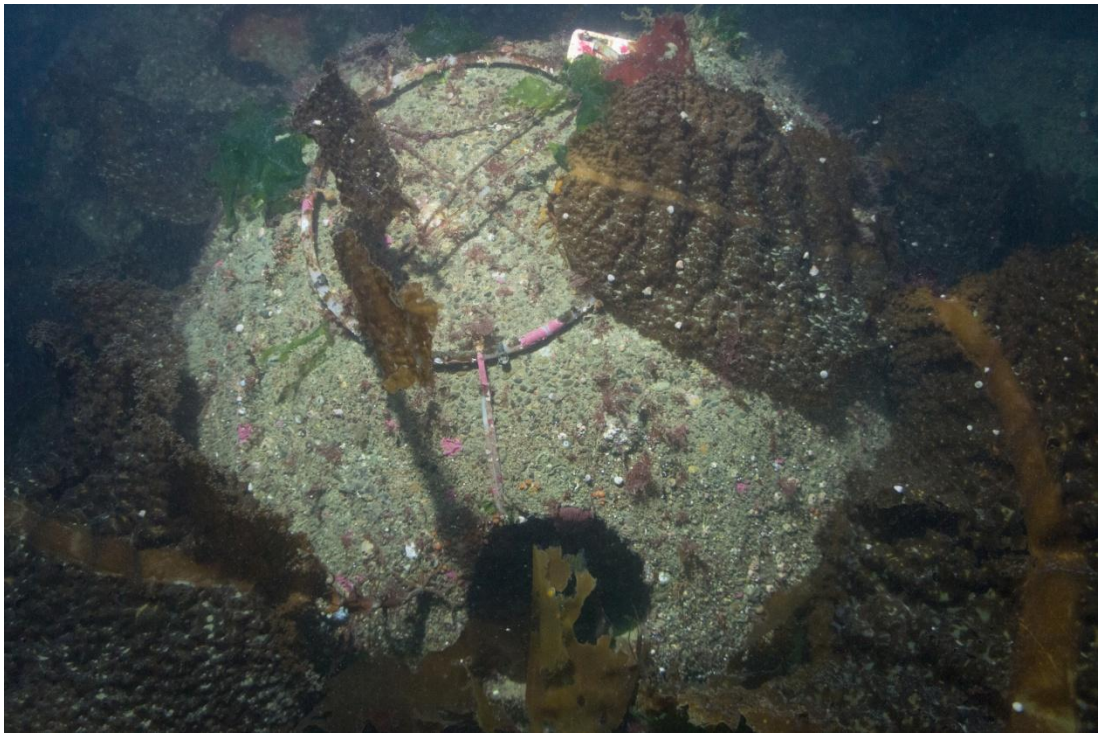

Figure 5. Photo of a circular quadrat located on the upper hemisphere of a Reef Ball. Circular quadrats are fastened to the Reef Balls using cable ties. Photo credit: Michael Blazecka

2.4 Measured Environmental Gradients

Measurements of environmental gradients occurred between August 2011 and September 2011.

2.4.1 Depth and distance

Depth of each Reef Ball was measured using an Oceanic Veo II Diving computer. Distances between Reef Balls and the breakwater were measured as the breakwater is most likely the largest source of propagules within the area. Distance between Reef Balls were measured because aside from the main source of propagules generated from the

breakwater, Reef Balls that are a short distance away from one another are the most likely source of propagules. Distance was measured from the closest edge of the top hole of the focal Reef Ball to the closest edge of the top hole of the second Reef Ball using a 100m measuring tape. Bearings from one Reef Ball to the next closest Reef Ball were measured *in situ* using a Suunto compass. A GPS coordinate was taken from the surface of the water directly above a Reef Ball using a Lowrance iFinder Expedition c(+) GPS unit. GPS coordinates for the remaining Reef Balls were calculated using trigonometric equations in Microsoft Excel 2007 using the distances and bearings measured from the Reef Ball with the measured GPS coordinate. Reef Balls were mapped in Arc GIS 10 (Figure 4).

2.4.2 Measuring Water Flow

Average water flow was measured by using modified clod cards (Thompson and Glenn 1994), or "dissolution domes". Dissolution domes, often made out of calcium sulfate, provide a relative measure of water velocity based on the proportion of the dome that dissolves in flowing water over a period of time (Thompson and Glenn 1994). The advantage of using dissolution domes over current metres is that they provide an inexpensive method of measuring average water velocity at many sample sites at the same time (Thompson and Glenn 1994, Perkol-Finkel et al. 2006b).

Dissolution domes for this study were made by pouring *Plaster of Paris* into the split half of a table tennis ball. Prior to curing, a paper clip was placed into the mold so that half of the paper clip emerged from the base of the dome. The paper clip provided a means of fastening the dome to a reef ball using a cable tie.

Water flow was measured at each Reef Ball during three 24 hour periods. Prior to deploying the dissolution domes, each dissolution dome was dried at 60°C for 24 hours and then weighed to obtain a dry weight (Howerton and Boyd 1992). Three replicates were deployed at each Reef Ball on each of the three sampling days. Dissolution domes were deployed on August 20th, August 27th, and September 17th and were retrieved 24 hours later. These dates were chosen to obtain measurements from tidal cycles with a high, medium and low average current. While hydrodynamic processes may vary throughout the year, such as an increase in surge due to winter storms, water flow was only measured during late summer due to logistics of collecting the data. In order to deploy and retrieve dissolution domes, a total of five experienced and capable volunteer divers are required for each dive. The ability to find five experienced divers that are available on particular days and times is a challenge. In addition, the ability to dive during the winter decreases as winter storms decrease accessibility to the study site. Collecting water flow measurements on additional days throughout the year may have provided additional insight on the effects of flow on macroalgae communities. However, collections were limited to three days during late summer due to the logistics of organizing volunteers as well as the decrease in accessibility to the study site during fall and winter months when the frequency of storms increases.

When dissolution domes were collected from Reef Balls, effort was made to minimize loss of material when transferring them to Ziploc© bags underwater. After retrieving the dissolution domes from the sample sites, they were placed in a drying oven for 24 hours at 60°C and then weighed to obtain a dry weight (Howerton and Boyd 1992, Thompson and Glenn 1994).

Six of the Reef Balls did not have domes affixed during the first sampling event which occurred during a tidal cycle with high average current. As a result, current was averaged over two sampling days only.

In an attempt to determine an average flow rate associated with weight loss, dissolution domes were calibrated in the lab following the procedures developed by Thompson and Glenn (1994). Experiments were carried out at the University of Victoria Aquatic Facility in a round, plastic tank with a 1.75m diameter and 61cm depth. The tank was filled with seawater to a depth of approximately 50 cm. The salinity of the seawater was the same as that found at the study site (30.5 ppm) and the water temperature was slightly lower in the tank (9.65 °C) compared to the water temperature at the study site (11 °C).

Dissolution domes were placed on a 1.02m long and 0.15cm thick Aluminum arm which was fastened to a stainless steel rod at its centre. The stainless steel rod was rotated at an average of 10 $\pm$ 0.79rpm by a 24V electric gear motor. The motor was secured to a wooden plank which lay across the tank such that the arm was positioned in the centre of the tank (Figure 6).

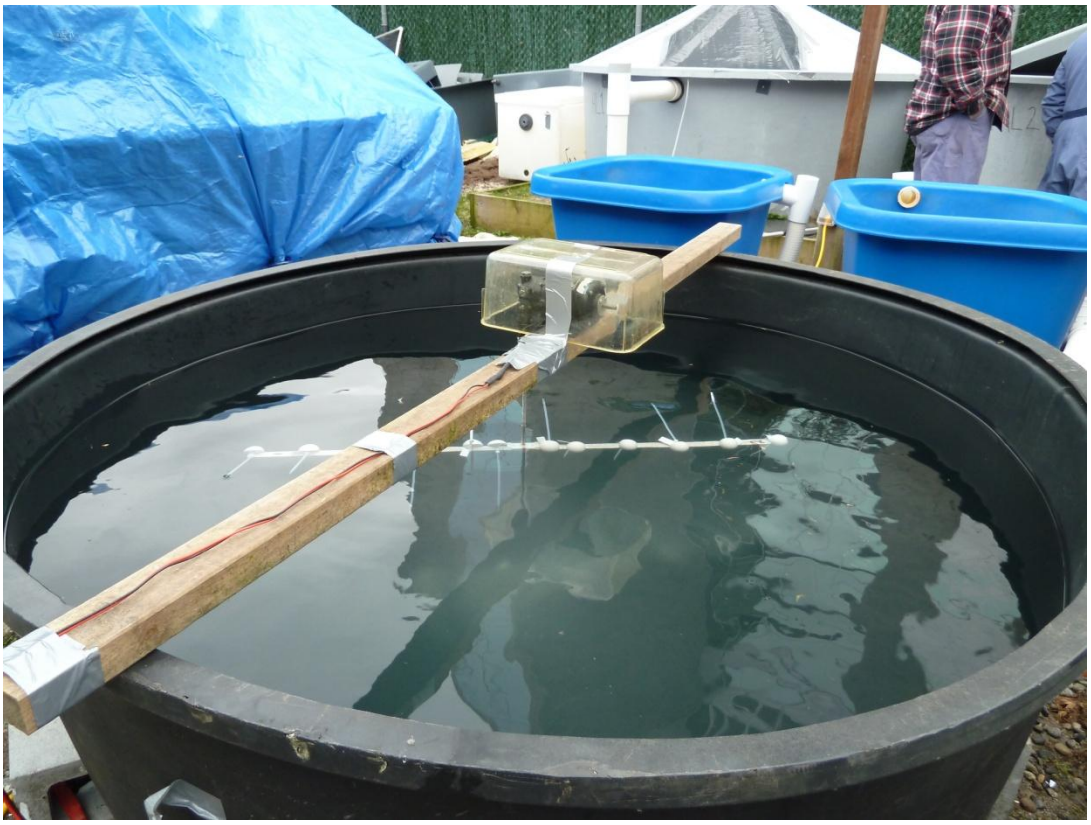

Figure 6. Dissolution dome calibration experimental set-up.

Dissolution domes were placed 5cm, 10cm, 20cm, 30cm, 40cm, or 50cm away from the centre of the arm. During each of the six trials there were 12 domes on the arm, two replicates for each position as domes were placed on either side of the rod located at the centre of the arm. As a result, each velocity treatment was duplicated for each trial (Thompson and Glenn 1994). Velocity at which the domes traveled ranged from 0.05m/s to 0.6m/s depending on the position on the arm at which the dome was placed. This velocity range was estimated to be within the range of water velocity experienced at Ogden Point based on current measurements obtained from the closest current meter – Race Passage (http://www.tides.gc.ca/eng/data/table/2011/curr_ref/1200). Five trials were run with the arm rotating and one trial was run without rotation to obtain a

dissolution rate at 0m/s. There were ten replicates for each velocity. During test trials, the experiment was run for a 24 hour period. After 24 hours, it was found that the dissolution domes experiencing higher velocities had completely dissolved. This may have been due to higher velocities in the tank compared to within the field, or due to shorter curing times for the dissolution domes used in experimental trials compared to those used in the field. Shorter curing times may have caused the domes to be less dense than those used in the field and dissolve at a faster rate (Thompson and Glenn 1994). As the rotational speed of the motor was not able to be reduced, the time of the trials were reduced to 6 hours instead of 24 hours in order to measure the weight loss of domes before they completely dissolved. Generally, dissolution rates are non-linear as they are higher when domes have a greater surface area compared to when they have a smaller surface area due to dissolution (Thompson and Glenn 1994). As minimal dissolution occurred on the domes that were placed in the field, the change in surface area was also minimal and the correction factor for changes in surface area was not needed. Thus, weight loss that occurred on dissolution domes used in experimental trials was multiplied by four to determine weight loss over a 24 hour period. Prior to and after each trial, all dissolution domes were dried for 24 hours at 60°C and weighed. Weight loss values were plotted against average water velocity to determine the equation of the line used to predict the average velocity of water that flowed past the dissolution domes in the field (Thompson and Glenn 1994) (Figure 7).

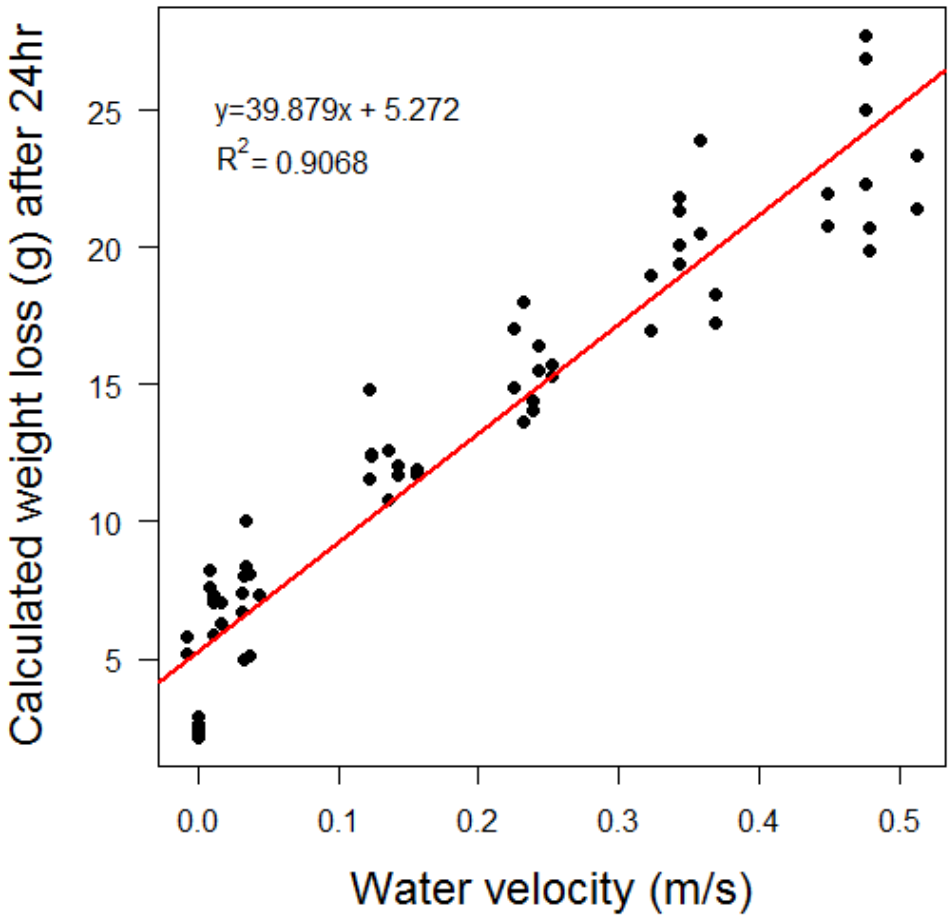

Figure 7. Calculated total weight loss (g) of dissolution domes that would occur over a 24 hour period based on measured total weight loss of dissolution domes exposed to six different water velocities (m/s) for a 6 hour period. Circles represent the calculated weight loss that would occur over a 24 hour period for each dissolution dome exposed at each of the six different water velocities. There were ten replicates measured for each water velocity and thus ten circles at each water velocity on the graph. Water velocity represented in this graph is the corrected water velocity experienced by the dissolution domes. The corrected water velocity was calculated by subtracting the velocity of the water moving in the same direction as the dissolution domes so as to obtain the true water velocity experienced by the domes (Thompson and Glenn 1994). The red line was obtained by conducting a linear regression between calculated weight loss (g) and water velocity (m/s). The equation of the slope of the regression line was used to calculate the velocity of water at each sampled Reef Ball in the study sites based on the weight loss of the dissolution domes measured at at that site.

2.4.3 Measuring Light

Downwelling light was measured at the centre of each quadrat. Although care was taken to ensure that algae canopy was not interfering with light measurements, in some instances measurements were affected. Light was measured on three consecutive sunny days. Measurements were taken on August 25, 26, and 27 2011 between 11:00 and 14:00. Light was measured using a light metre designed for underwater photography (Sekonic Marine Metre II L-164B) as this was more economical than purchasing an underwater light metre that directly measures photon flux (Jimenez et al. 1987, Vail 1987). The photo light metre was set to ASA 100, DIN 21 and shutter speed 25 and the F-stop value was recorded. To measure downwelling light, the light sensor was pointed up, resulting in the face of the metre being pointed directly towards the substrate. This made taking readings very difficult to execute underwater. To increase the ease and efficiency of reading measurements, the light metre was mounted on a PVC arm that formed a 90° angle with a mirror mounted at the bend in the arm pointing toward the face of the metre (Figure 8). Measurements could then be read by looking down the arm, which ran parallel to the substrate, to the mirror which reflected the face of the metre.

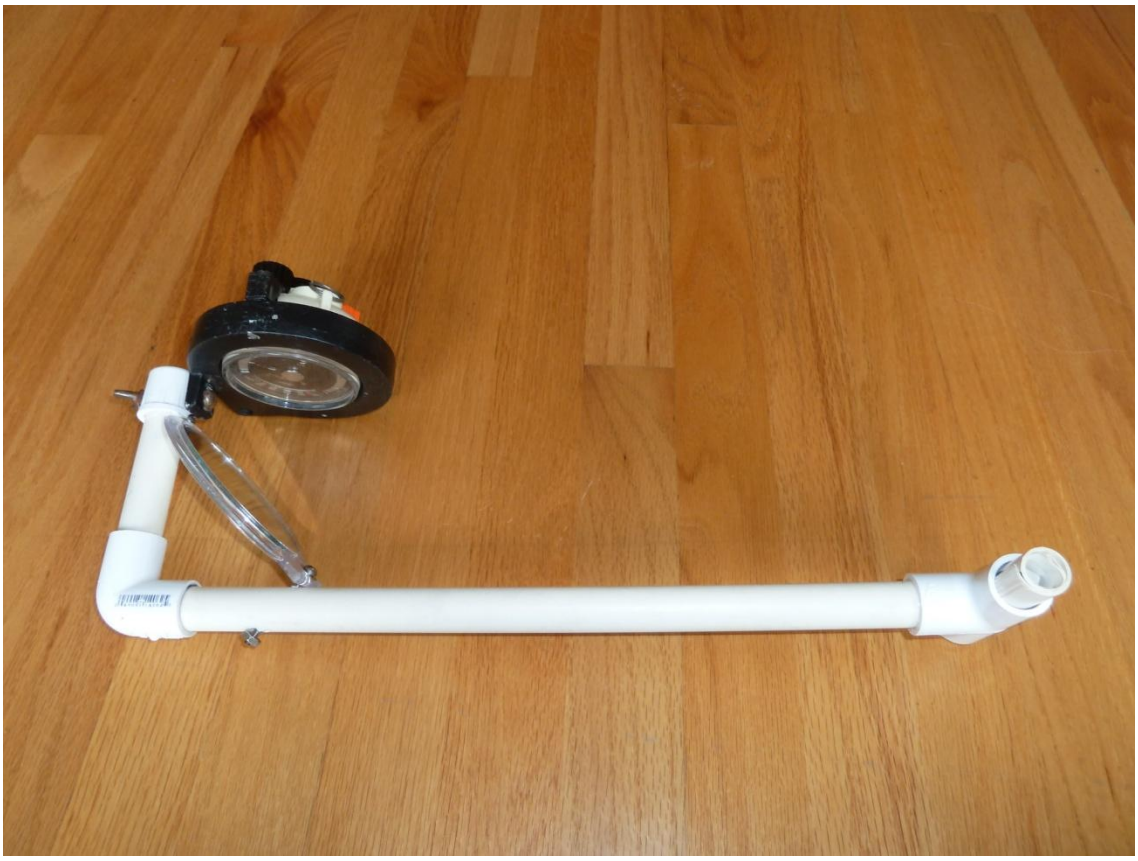

Figure 8. Mounting system for the Sekonic Marine Metre II L-164B

To associate a luminous flux per unit area with each F-stop, the Sekonic Marine Metre II was calibrated with various light sources by conducting multiple tests with each light source and for each F-stop. The calibration value (C) was calculated for each F-stop for each light source. The calibration values were averaged for each light source and again averaged to give a final calibration value. Variances in the average calibration values amongst the light sources were used to determine the $\pm$1% against the overall average. The light readings were taken on an accurate selenium based light meter (Luning and Dring 1979).

Lux was calculated using the following equation from ANSI/ISO 2720-1974:

$$\text{Lux} = \frac{[(Fstop)^2 * C]}{t * S}$$

C = Calibration value
t = shutter speed
S = ASA value

Once the calibration value was determined, F-stops recorded at each sample site were entered into the equation to obtain a Lux value.

2.5 Sampling the algae community

Underwater benthic sampling is often conducted by taking photographic samples (Airoldi 2000, Irving and Connell 2002b, Campana et al. 2009). The advantages of this method are that it increases the ease of sampling, the number of sites that can be sampled, and transfers processing time from underwater where there are physiological limits to the lab where time is unlimited (Preskitt et al. 2004). The disadvantage of photo sampling occurs when sampling a three dimensional community such as a kelp community. A photograph will capture the cover of the community at a particular point in time and may not be able to capture the entire community (Airoldi and Cinelli 1997). This presents a particular problem in the subtidal environment where algae are often in motion due to tidal or current action. A further disadvantage to the photo sampling method is that it is not possible to identify certain algae to a low taxonomic level (Preskitt et al. 2004). Many species require examination under a microscope for positive identification (Gabrielson et al. 2006). For these reasons, destructive sampling and measurement of biomass were chosen to represent subtidal algal communities. Destructive sampling

allowed for algae to be identified to a low taxonomic level, allowing for the investigation of the effects of environmental gradients on community composition and diversity.

2.5.1 Field Collection

Sampling colonized algae communities was conducted during the summer of 2011 (July 12 – July 31) using SCUBA. Within the affixed 30cm circular quadrats on the 30 experimental reef balls, the upper canopy was sampled by removing the algae, including its holdfast, using a knife. The algae was then placed in a Ziploc© bag. The lower canopy was collected by scraping the sample area using a knife and collecting the algae using a modified suction sampler (Miles and Whitlatch 1997). Each sample took between ten to fifteen minutes to sample depending on the coverage and composition of the sample. The diver would continue scraping the sample area until algae was no longer being removed from the substrate. One to three samples were collected per dive depending on the nature of the sample and site conditions. One to two dives were conducted each day depending on the timing of the tide cycles. Dives were conducted during slack tide to minimize loss of sample due to current and to follow safe dive procedures. Although these precautionary measures were taken, some algae were still lost during sampling due to water motion and low suction power of the sampler. In all cases the lost algae were small fragments that amounted to an estimated loss of less than 3% of the total biomass collected.

2.5.2 Suction Sampler

The suction sampler was based on the design of Miles and Whitlatch (1997), but modified to increase portability due to the travel required to arrive at the dive site – divers had to walk several hundred metres – and subsequently swim offshore to the sampling sites. Two modified suction samplers were fabricated, each with a 360GPH, 12V Bilge pump attached to a six centimetre diameter PVC tube. The PVC tube for one model was 41cm in length and the other 37cm in length (Figure 9).

Figure 9. Miles and Whitlatch (1997) modified suction sampler.

A mesh bag (mesh size = 2mm) was placed inside the PVC tube to collect algae that were sucked up by the sampler. A flexible hose 45 cm in length and 3.5 cm in diameter, was mounted on the top of the sampler and fastened to the PVC tube with latches. The latches allowed divers to remove the flexible hosing under water to retrieve

and replace the mesh bag after a sample had been collected. The mesh bags containing the samples were transferred to plastic Ziploc© bags for transport to the lab for processing. Samples were placed in a cooler with seawater for transportation.

2.5.3 Biomass

Samples were brought to the lab within one hour of collection and sorted to genus. Algae were identified to genus using the key of Gabrielson et al. (2006). Algae were identified to genus because in order to identify some algae to the species level, reproductive structures were required to be present and intact. This was not the case for all individuals, therefore identification was limited to genus. Identifying algae to the genus level only results in a 5% decrease in the ability to distinguish different samples (Bates et al. 2007). Sorted algae were placed into pre-weighed aluminum trays, dried at 60°C for 24 hours, and then weighed (Brokovich et al. 2010).

2.6 Statistical Analysis

2.6.1 Effects of environmental gradients on diversity

Genera richness, Shannon entropy, and Simpson diversity number were determined for each sample using the R package vegan (Oksanen et al. 2013). Each diversity measure represents a different aspect of the community and each measure has drawbacks (Magurran 1988). Genera richness indicates the number of genera found in a community, and Shannon entropy and Simpson diversity number are indices that combine richness and abundance (Magurran 1988). Shannon entropy is sensitive to rare species and

Simpson diversity number is more influenced by dominant species (Magurran 1988). Algal communities in this study are characterized by several dominant genera and many rare genera, thus it is important to determine whether environmental gradients have an effect on rare or dominant genera. By including all three diversity indices in the analysis, the effects of environmental gradients on richness of dominant and rare genera can be determined.

Shannon Entropy is defined as:

$H' = -\sum_{i=1}^{R} p_i \ln p_i$

Where p_i is the proportion of algae abundance belonging to the *i*th genera and *R* is genera richness

the Simpson diversity number is:

$\lambda = \sum_{i=1}^{R} p_i^{\,2}$

Genera richness, Shannon entropy, and Simpson diversity number were each analyzed using multiple linear regression. The explanatory variables were the same for each of the three models: water flow, light, depth, distance to breakwater, and distance to the closest Reef Ball. Backward model selection was conducted for each multiple regression test using Akaike information criteria (AIC) to determine the most parsimonious model explaining the diversity indices (Crawley 2007).

2.6.2 Effects of environmental gradients on algal community composition

To determine if depth, light, water flow, distance to breakwater, and distance to the closest Reef Ball had a significant effect on the presence and biomass of algae genera collected from 30 replicate algae communities a redundancy analysis (RDA) was conducted. RDA was chosen because unlike unconstrained methods such as PCA, that are more descriptive in nature, it determines whether explanatory variables have a significant effect on multivariate response data (Borcard et al. 2011). RDA was chosen instead of other constrained ordination methods such as Canonical Correspondence Analysis (CCA) because rare species in the data would have a biased influence by using CCA (Borcard et al. 2011). In addition, explained variation in CCA is inflated and there is no simple method to address this problem (Borcard et al. 2011) .

RDA is a method that regresses multivariate responses to explanatory variables and then runs a principal component analysis (PCA) on the fitted values obtained by the multiple linear regression (Borcard et al. 2011). RDA determines the degree to which variation in response variables is explained by explanatory variables (Borcard et al. 2011).

RDA tests were followed by a permutation test run in the R package vegan to determine if the models were significant (Oksanen et al. 2013). Permutation tests are ideal when testing for significance in ecological data because ecological data often has non-normal distributions that cannot be tested using parametric tests (Borcard et al. 2011).

Effects of abiotic factors on the presence and biomass of algal functional groups was also measured using an RDA. Functional groups included filamentous, foliose,

corticated terete, and leathery (Appendix II, Table 5) (Steneck and Dethier 1994a, Bates and DeWreede 2007). These functional groups, developed by Steneck and Dethier (1994), are based on morphological, anatomical, and as a result life-history traits that are important in responding to disturbance and productivity regimes. For example, kelps belong to the leathery functional group, which is characterized as algae that are structurally more complex, larger in size and resistant to low levels of disturbance (Steneck and Dethier 1994a). Specimens that are found within this group are better able to monopolize light due to their greater size and longer life span compared to specimens found in other functional groups (Carpenter 1990, Steneck and Dethier 1994a). Algal specimens placed in the corticated terete functional group are structurally less complex, smaller in size, and have shorter life spans compared to specimens found in the leathery functional group (Steneck and Dethier 1994a). Corticated terete specimens are also better able to monopolize light compared to other functional groups, but are outcompeted by leathery macrophytes (Steneck and Dethier 1994a). Foliose specimens are single-celled layer algae, such as *Ulva*, and filamentous algae are single-celled organisms in which cells are arranged into a single filament (Steneck and Dethier 1994a). Foliose and filamentous algal species are fast-growing, opportunistic species that tend to dominate early successional stages (Steneck and Dethier 1994a, Lotze and Schramm 2000). Due to their greater surface area, foliose specimens are better able to compete for light compared to filamentous algae (Steneck and Dethier 1994a). By organizing algae into these functional groups, factors that affect productivity, such as depth and light, and disturbance regimes, such as sediment scouring associated with different water flows, are

expected to affect the abundance and presence of functional groups (Vadas and Steneck 1988, Ferrier and Carpenter 2009).

Prior to the analysis, a Kendall Tau correlation test was run to determine whether any of the environmental variables were significantly correlated with one another. Distance to breakwater ($p < 0.0005$) and light ($p < 0.005$) were significantly correlated to depth, and thus were removed from the subsequent RDA analyses to prevent over-fitting the model. Depth was retained in the analysis rather than the other correlated abiotic factors because it is an important environmental gradient that shapes subtidal algal communities and it was the most precise measurement between depth and light (Vadas and Steneck 1988).

A Hellinger transformation was performed on genera and functional group biomass in order to reduce the influence of algae with high biomass (Borcard et al. 2011).

2.6.3 Determining whether measured abiotic factors have a significant effect in shaping subtidal algal communities

Forward selection of explanatory variables was conducted in which permutation tests are run on the F-statistic of each variable in order to identify the combination of variables yielding maximum explanatory power. Forward selection was chosen so that only variables that significantly explained variance in the model were included (Borcard et al. 2011). The most significant explanatory variable was selected to include in the model. In the case of a tie, the variable with the lowest Akaike Information Criterion (AIC) value was selected to include in the model. Additional variables were added to the model if their partial contribution to the model was significant.

2.6.4 Community assembly patterns

A Kendall's *W* coefficient of concordance was used to determine if algae formed significant genera associations that may be correlated with environmental gradients. This test incorporates a k-means partitioning which groups observations into clusters so that each observation will belong to the group with the most similar mean. The method groups observations so that the total error sums of squares (TESS) are minimized within each group. Permutation tests are then run in order to determine the significance of each group and to determine which genera are significantly associated with their group. Due to k-means partitioning being a linear calculation, a Hellinger transformation was performed on the data in order to deal with the abundance of zeros (Borcard et al. 2011). Therefore, evidence of significant clusters or algal associations would indicate some assembly rules and discount random colonization.

Spatial correlations may also be indicators of non-random colonization (Keough 1983, Kendrick and Walker 1991, Larsson and Jonsson 2006). To determine if there were any spatial correlations among algae communities a principle coordinates of neighbour matrices (PCNM) analysis was conducted using the PCNM package in R (Borcard et al. 2011). A PCNM enables modeling of non-linear trends in ecological data (Borcard et al. 2011). The analysis involves running a principle coordinate analysis (PCoA) on a distance matrix, followed by an RDA in order to detect significant spatial correlations. The method constructs a distance matrix based on the shortest distance between sites. A PCoA is then run on the distance matrix in order to reduce the number of dimensions and to obtain eigenvectors that represent the majority of the variation in the distance data. An RDA is then run using only the significant eigenvectors as spatial

explanatory variables against detrended, Hellinger transformed species data (Borcard et al. 2011). All tests were run using the statistical program R version 3.0.1 (R Development Core Team, 2013).

Chapter 3 Results

A total of 36 different genera were identified across the 30 sampled Reef Balls (Appendix II, Table 5). Genera richness (indicated as richness from here on end) per reef ball ranged from 7 to 22. The average richness across Reef Balls was 15.2 $\pm$ 3.59 genera. Shannon Entropy values ranged from 0.0785 to 2.07, Simpson Diversity number from 1.02 to 5.70, (Appendix II, **Table 6**).

3.1 Environmental Gradients and Diversity

To determine if richness, Shannon Entropy and Simpson Diversity Number changed across environmental gradients (Appendix II, Table 7), a multiple regression for each response variable was executed. Each model was reduced using AIC analysis to determine the most parsimonious model (Table 1, Table 2, Table 3)

Table 1. Results from AIC backward model selection on multiple linear regression with environmental variables as explantory variables and richness as response variable. Full model: richness ~ flow + depth + light + distance to reef ball + distance to breakwater. Df = degrees of freedom

Step	Abiotic factor removed from model	Deviance Residuals	Df	Residual Deviance	AIC
1			24	286.0439	79.64844
2	Flow	0.145733	25	286.1896	77.66372
3	Depth	0.98414	26	287.1738	75.7667
4	Distance to Reef Ball	2.212656	27	289.3864	73.99696

Table 2. Results from AIC backward model selection on multiple linear regression with environmental variables as explantory variables and Shannon Entropy as response variable. Full model: shannon entropy ~ flow + depth + light + distance to reef ball + distance to breakwater. Df = degrees of freedom

Step	Abiotic factor removed	Deviance Residuals	Df	Residual Deviance	AIC
1			24	5.486231	-38.9687
2	Light	0.02727	25	5.513502	-40.8199
3	Flow	0.147664	26	5.661166	-42.027
4	Distance to Reef Ball	0.247366	27	5.908532	-42.744

Table 3. Results from AIC backward model selection on multiple linear regression with environmental variables as explantory variables and Simpson Diversity Number as response variable. Full model: simpson diversity number ~ flow + depth + light + distance to reef ball + distance to breakwater. Df = degrees of freedom

Step	Abiotic factor removed	Deviance Residuals	Df	Residual Deviance	AIC
1			24	4.754137	-43.2655
2	Light	0.0101	25	4.764238	-45.2018
3	Flow	0.112139	26	4.876377	-46.5039

A multiple linear regression was conducted with the most parsimonious model obtained from AIC for each response variable: richness, Shannon Entropy, Simpson Diversity Number. Distance to the breakwater had a significant effect on richness ($p = 0.00996$) and the model was significant ($p = 0.03274$), but light was insignificant ($p = 0.09804$). Depth and distance to the breakwater were included in the model explaining Shannon Entropy but were insignificant (depth: $p = 0.05722$, distance to breakwater: $p = 0.05875$) and the overall model was insignificant ($p = 0.1098$). None of the environmental variables in the reduced model had a significant effect on Simpson Diversity Number (Depth: $p = 0.1706$, Distance to Reef Ball: $p = 0.1644$, Distance to breakwater: $p = 0.0941$).

3.2 Environmental Gradients and Community Composition

Redundancy analysis determines the combination of environmental variables that explain the variation in community composition (Borcard et al. 2011). The RDA revealed that the measured environmental factors explained a small proportion of variance in algal communities (22%). In an attempt to reduce the variance of residuals in the model, rare genera (total biomass < 0.020g or occurring at < 3 sites) were removed from the data (Poos and Jackson 2012). A total of 13 genera were removed leaving 23 genera that were used in a second RDA test (Table 5). Proportion of variance in algal communities explained by environmental variables did not critically increase with the removal of rare genera (23%). As a result, rare genera were retained in the data for the remainder of tests.

Biplot scores for constrained variables indicate that depth had the greatest effect on algae communities, followed by flow, and distance to the nearest reef ball (Table 4).

Table 4. Scores for genera that were most affected by extreme values of explanatory variables for each constrained axis (RDA) and the first two unconstrained axes (PC). Genera scores represent the coordinates for the vectors representing genera in the triplot. Biplot scores of explanatory variables are located below genera scores. Biplot scores represent coordinates of the explanatory variable vectors in the triplot.

	RDA1	RDA2	RDA3	PC1	PC2
Agarum	- 0.6164283	0.0248212	0.0329069	-0.3412080	0.5204491
Callophyllis	-0.1466346	-0.1803305	-0.0733324	-0.2118387	-0.2944889
Pterosiphonia	0.1557874	0.0165664	-0.0217313	-0.0722760	-0.0460207
Rhodoptilum	0.0683381	0.1338608	0.0124173	-0.2238514	-0.5029212
Saccharina	-0.0020522	0.0652297	-0.0295207	-0.0267796	-0.0343857
Ulva	0.3670149	-0.1838597	0.0556066	-0.1568278	0.2352967
Weeksia	0.2870722	0.1361335	-0.0389794	0.9301753	0.0142089
Biplot scores					

Depth	-0.9541	-0.2894	-0.07661
Flow	0.62913	-0.6999	-0.33817
Distance to reef	0.3042	0.5050	-0.80776

Depth was negatively correlated with water flow, and distance to the nearest Reef Ball along RDA1 (Figure 10). *Agarum* and *Callophyllis* were positively correlated with depth and *Weeksia*, *Rhodptilum*, *Ulva* and *Pterosiphonia* were negatively correlated with depth. *Callophyllis* was negatively correlated with distance to the nearest reef ball while *Rhodoptilum, Weeksia, Saccharina,* and *Pterosiphonia* were positively correlated. *Ulva* was positively correlated to water flow. The remaining algae genera were concentrated around the centre of the plot suggesting little effect of the measured explanatory variables. *Agarum*, and *Callophyllis* were positively correlated to one another and negatively correlated to *Ulva*, *Pterosiphonia*, *Weeksia*, *Saccharina,* and *Rhodoptilum* which were positively correlated to one another.

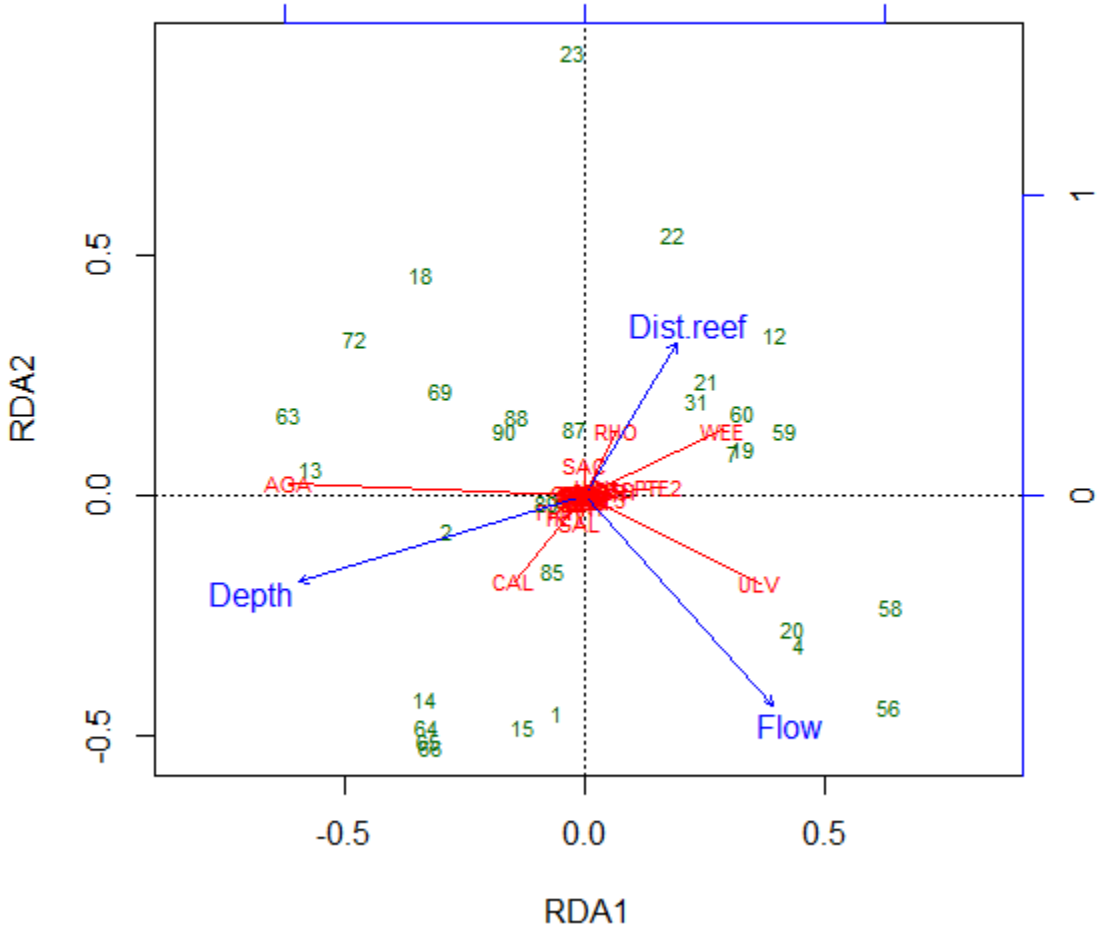

Figure 10. RDA triplot of Hellinger transformed algae genera biomass and Reef Balls constrained by environmental variables. The bottom and left hand scales are the standard deviations for standardized algae genera biomass and the right hand and top scales are standard deviations of standardized explanatory variables. Green numbers represent Reef Ball number, their location can be found in Appendix I Figure 13. Arrow length indicates the relative influence of environmental variables (blue) and the relative abundance of algae genera (red). The angle between a vector representing algae and a vector representing abiotic factors, between two algae vectors, or between two abiotic factor vectors, is a reflection of their correlation. The first two axes of the RDA triplot represent 19% and 3% of the variation in algae genera. The corresponding names of algae genera represented by codes in the plot can be found in Appendix II, Table 5.

To determine if environmental variables had a significant effect on algae community composition a global permutation test was run. The test indicated that environmental variables had a significant effect ($p= 0.003$) on algal communities. A test of canonical axes indicate that depth, the most influential variable in RDA1, significantly explained algal communities ($p= 0.001$).

In forward selection, when regressing each explanatory variable to the algae genera biomass, the test revealed that depth was the most significant explanatory variable ($p= 0.001$), followed by flow ($p= 0.042$). The first step of the forward selection test revealed that none of the remaining variables – flow, and distance to closest Reef Ball – made a significant partial contribution to the variation in the response data (flow: $p= 0.226$, distance to closest Reef Ball: $p= 0.892$). This suggests that depth is the sole explanatory variable that has a significant effect on algae community composition in this study.

Agarum, *Weeksia*, *Ulva*, or a combination of the three genera, formed an upper canopy in 21 of the 30 samples. To determine whether the three genera were driving the results in the RDA, they were removed from the data set and an RDA was run with algae genera found only in the lower canopy. The results were similar to the results obtained by the RDA run with both upper and lower canopy genera as the response variable. Explanatory variables explained a small proportion of the variation in understory algal communities (17%). Biplot scores for constraining variables indicated that depth (-0.9641) also had the greatest effect on lower canopy algae communities, followed by distance to the nearest reef ball (0.3874), and flow (0.1126). *Callophyllis* was again positively correlated with depth while *Pterosiphonia* was negatively correlated (Figure

11). *Rhodoptilum* and *Callithamnion* were positively correlated with distance to the closest Reef Ball and *Pterosiphonia* was positively correlated with water flow (Figure 11). The relationships among the environmental variables were similar to those found in the first RDA (Figure 10, Figure 11).

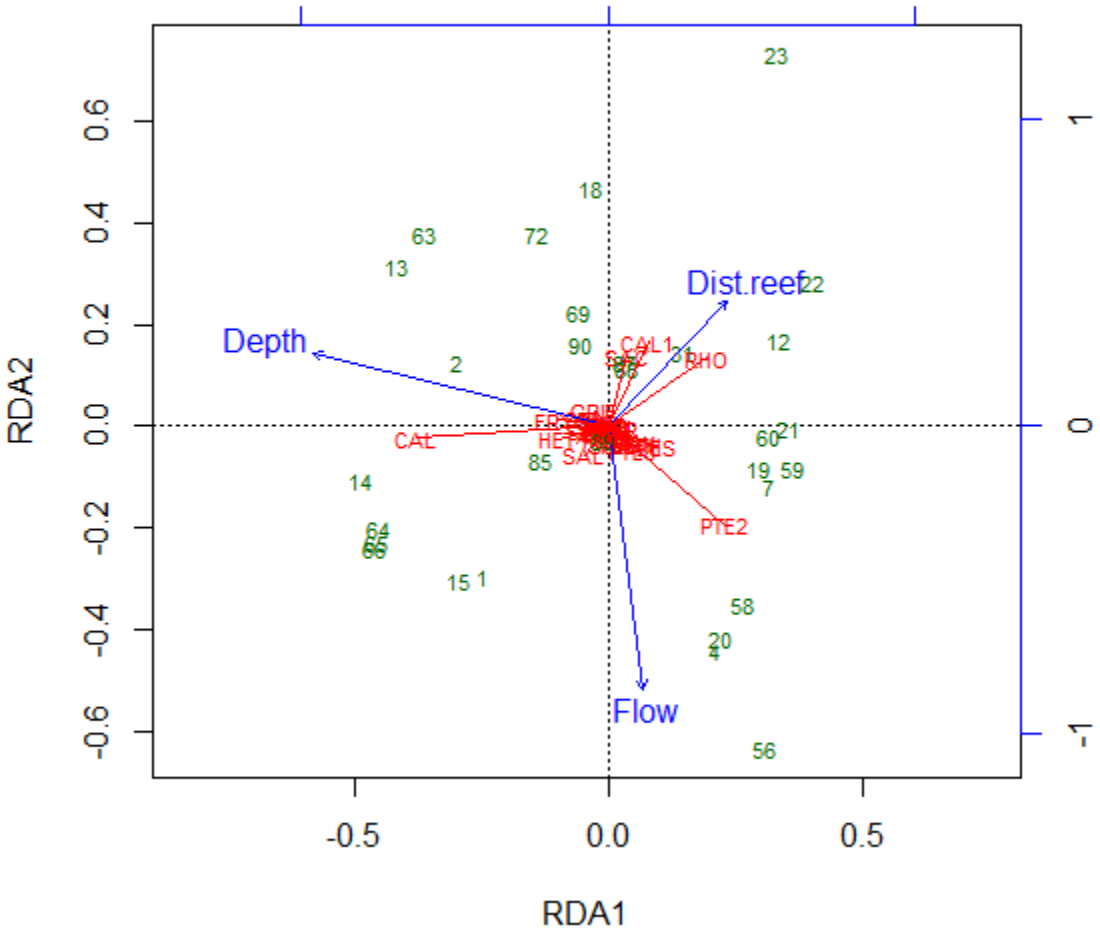

Figure 11. RDA triplot of algae genera found only in the lower canopy constrained by environmental variables**.** Algae genera biomass was Hellinger transformed prior to the RDA. The bottom and left hand scales are the standard deviations for standardized algae genera biomass and the right hand and top scales are standard deviations of standardized explanatory variables. Green numbers represent Reef Ball number, their location can be found in Appendix I Figure 13. Arrow length indicates the relative influence of environmental variables (blue) and the relative abundance of algae genera (red). The

angle between a vector representing algae and a vector representing abiotic factors, between two algae vectors, or between two abiotic factor vectors, is a reflection of their correlation. The first two axes of the RDA triplot represent 14% and 5% of the variation in algae genera. The corresponding names of algae genera represented by codes in the plot can be found in Appendix II, Table 5.

A global permutation test indicated that environmental variables had a significant effect on lower canopy algae genera ($p= 0.027$). A forward selection test indicated that depth, again, was the most significant explanatory variable ($p= 0.009$) and the only significant variable in the model (flow: $p= 0.317$, distance to closest Reef Ball: $p= 0.382$).

An RDA was run with algal functional groups as the response variable because effects of environmental gradients are often seen at coarser taxonomic resolutions (Ferrier and Carpenter 2009). The redundancy analysis run on functional groups again revealed that unmeasured variables represented a greater proportion (83%) of the variance in algal communities compared to measured environmental variables (17%). Biplot scores for environmental variables indicated that flow (0.8733) had the greatest effect on functional groups, followed by depth (-0.7670) and distance to the nearest reef ball (0.1740). Leathery functional group was highly positively correlated with depth and negatively correlated with corticated terete and foliose functional groups. Foliose algae were greatly positively correlated with flow and corticated terete algae were slightly positively correlated with distance to the nearest reef ball. Filamentous algae were located at the centre of the plot and therefore were not affected by any of the explanatory variables (Figure 12).

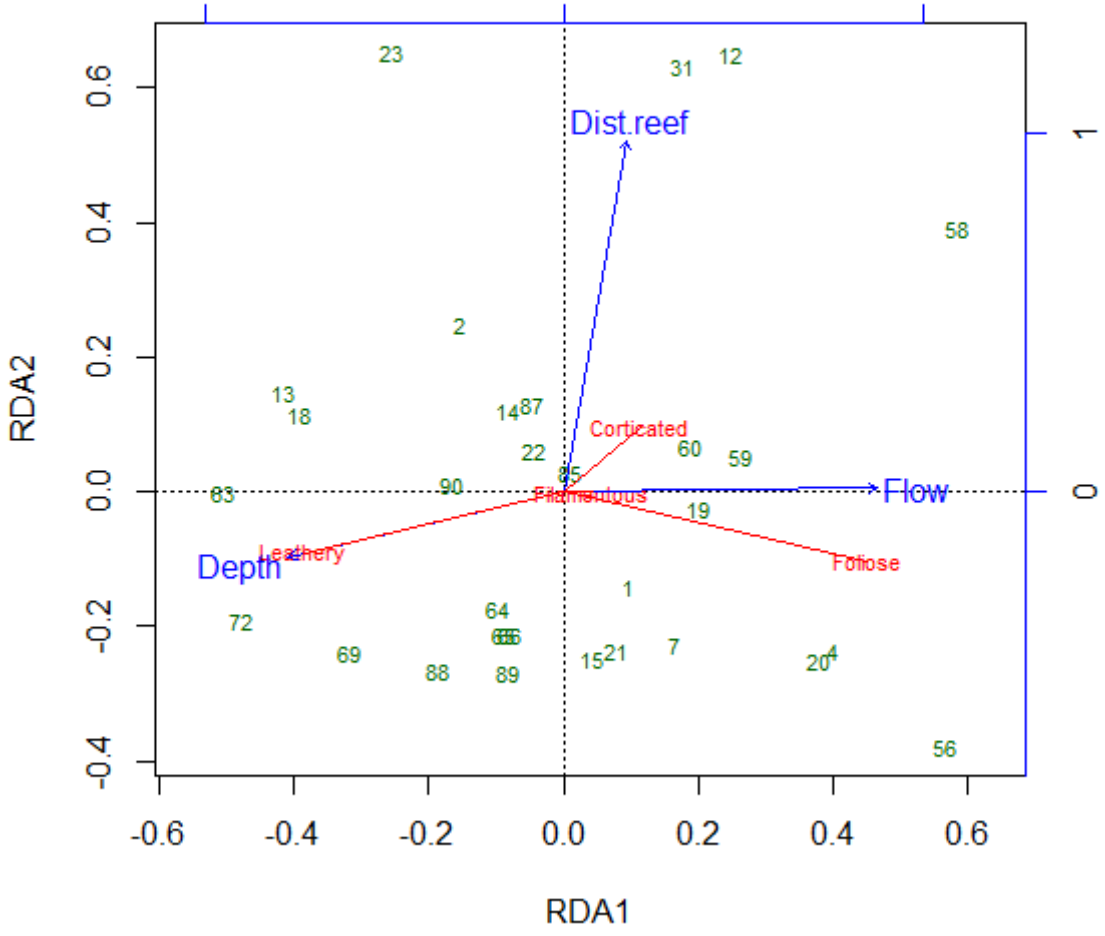

Figure 12. RDA triplot of Hellinger transformed algae functional group biomass constrained by environmental variables. The bottom and left hand scales are the standard deviations for standardized algal functional group biomass and the right hand and top scales are standard deviations of standardized explanatory variables. Green numbers represent Reef Ball number, their location can be found in Appendix I Figure 13. Arrow length indicates the relative influence of environmental variables (blue) and the relative abundance of algae genera (red). The angle between a vector representing algae and a vector representing abiotic factors, between two algae vectors, or between two abiotic factor vectors, is a reflection of their correlation. The first two axes of the RDA triplot represent 16% and 1% of the variation in algae functional groups. A list of algae belonging to each functional group can be found in Appendix II, Table 5.

A global permutation test run on algae functional groups indicated that the RDA model is not significant (p= 0.129) and that water flow, the most influential variable in RDA1, was significant (p= 0.018). A forward selection test indicated that flow was the most significant explanatory variable (p= 0.031) and the only significant variable in the model (depth: p= 0.325, distance to closest Reef Ball: p= 0.669).

3.3 Community Assembly Patterns

A K-means partitioning comparison followed by a global Kendall W test was run to find positively correlated and significantly associated algae genera groups. The Calinski criterion for the K-means partitioning comparison indicated that clustering algae genera into two groups yielded the minimum total error sums of squares (TESS). The global Kendall W test indicated that both groups are globally significant and that at least some species within the group are concordant (Group 1&2: corrected $p < 0.0001$). An *a-posteriori* test revealed that Group One is comprised of the following algae genera: *Rhodoptilum, Ulva, Desmarestia, Euthora, Pterosiphonia, Bonnemaisonia, Pterothamnium, Heterosiphonia, Sarcodiotheca, Hollenbergia, Scagelia, Griffithsia,* and *Ceramium*. Group Two is comprised of: *Weeksia, Agarum, Callophyllis, Saccharina, Sparlingia, Antithamnion, Cryptonemia, Herposiphonia, Fryella, Callithamnion, Pleonosporium,* and *Gloiocladia*. *Weeksia* and *Saccharina* had negative Spearman correlations indicating that they were incorrectly classified and that group two should be split since not all members belonged to the same group. However, upon attempting to split the genera into further groups, the groups were no longer globally significant.

A PCNM analysis demonstrated that there was no significant spatial correlation among algae communities ($p=0.46$).

Chapter 4 Discussion

4.1 Overview

This study determined that there is a significant relationship between depth and subtidal macroalgal. Results from the redundancy analysis show that only depth had a significant impact on the algae communities that grew on the Reef Balls at Ogden Point while water flow, and distance to the nearest Reef Ball played no significant role. The lack of signal in water flow and distance to the nearest Reef Ball may be due to the low variability in these environmental gradients measured across a small spatial scale (Norton 1992, Duggins et al. 2003). While depth was found to have a significant effect, the model indicated that 77% of the variation in the data is caused by factors other than the environmental variables measured. Possible explanations include grazing, sedimentation, stochastic colonization and priority effects (Benedetti-Cecchi 2000, Almany 2009).

4.2 Environmental Gradients

Environmental gradients did not significantly affect Shannon or Simpson diversity indices. Richness however did increase significantly with increasing distance from the breakwater. This result may be driven by four Reef Balls having much greater distances (~100m) from the breakwater compared to others (15m-60m) (Appendix I, Figure 14). While the four Reef Balls had relatively high richness, there were Reef Balls located closer to the breakwater with greater richness. There may be two reasons for seeing high diversity of distant Reef Balls. First, while the Reef Balls were much further than the remaining sampled Reef Balls, the distance from the breakwater is small when

considering the distance that many algal spores can travel (Norton 1992). Second, large pieces of debris such as logs, tires, etc., scattered throughout the study site may provide an alternative source of propagules.

Differences in water flow influence subtidal algal community composition and species richness (Fabricius and De'ath 2008, Palardy and Witman 2011). In this study though, effects of water flow were only seen when algae were arranged in functional groups. Foliose algae were significantly positively correlated and leathery algae were negatively correlated to water velocity. Effects of water flow may be seen at the functional group level due to water flow mainly impacting the morphology of algae and the categorization of functional groups being based on morphology (Steneck and Dethier 1994b, Kitzes and Denny 2005). Algae have been found to make morphological adaptations in high flow in order to reduce drag and the probability of becoming detached from the substrate (Kitzes and Denny 2005, Fowler-Walker et al. 2005, Martone et al. 2012).

The absence of an effect of water flow on genera community composition may also be due to low values in and a small range of water velocities (Table 7) (Ferrier and Carpenter 2009). Water velocities in this study ranged from 0.004m/s to 0.03m/s, whereas water velocities measured in other studies that examined the effects of water flow on algal community composition, such as Duggins et al. (2003) and Ferrier and Carpenter (2009), ranged from 0.1m/s to 0.9m/s and 1.89m/s to 2.98m/s respectively. Large ranges in water velocity may be required to see changes in algal genera community composition as many algae are able to develop morphological adaptations in response to water flow (Kitzes and Denny 2005, Fowler-Walker et al. 2005, Martone et al. 2012).

Distance to the nearest Reef Ball was also found to have no significant effect on genera richness, algae composition and functional group. Given that algal spores can travel tens of kilometers, or hundreds of kilometers on a dislodged plant (Norton 1992), and that the study site covers only 120m by 100m, the probability of disproportionate settlemement within the study site is unlikely. Had distance to the breakwater been retained in the redundancy analysis an effect of distance to propagule source may have been detected as distances to the breakwater from Reef Balls is much greater than distances among Reef Balls.

The small spatial scale of the study site and measuring communities across structurally similar habitats resulted in low variation in water flow and distance to propagule sources. Variation in algal community composition can occur at small spatial scales when different microhabitats, in which environmental conditions vary significantly, are measured (Connell 2005, Ferrier and Carpenter 2009). For example, encrusting coralline algae dominate the understory of canopy forming algae where light is significantly reduced, compared to areas with no canopy forming algae where turf-forming algae dominate (Connell 2005). In this study, macroalgae communities were sampled across structurally similar habitats with the same orientation, and as a result, the environmental factors measured did not vary considerably across the study site. In order to observe greater variation in factors such as water flow, distance to a propagule source, and even depth, across structurally similar habitats, much larger spatial scales must be sampled (Duggins et al. 2003). For example, to sample a larger range of water flow, or to detect an effect of distance from a propagule source, sample sites may need to be spaced kilometers apart (Norton 1992, Duggins et al. 2003).

Gradients that were not measured, such as sedimentation and grazing, may have also played a role in structuring algal communities on the Reef Balls. High levels of sedimentation often result in turf-forming algae dominating an area due to their ability to resist or tolerate smothering and scouring as well as their opportunistic life cycles (Airoldi and Cinelli 1997). Sedimentation most likely did not play a large role in this study as sedimentation is negatively correlated with water flow and thus, a significant effect from water flow would have been detected (Eckman et al. 1989, Hansen and Reidenbach 2012).

Community assembly in many marine ecosystems are governed by the top-down process of grazing, including subtidal macroalgal communities (Paine 1974, Korpinen et al. 2007, Amsler et al. 2011). Grazers are often responsible for maintaining particular algal communities, diversity, and disturbance patterns (Paine 1974, Korpinen et al. 2007, Amsler et al. 2011). Grazer composition can vary across environmental gradients such as depth and distance from a large propagule source, however these gradients tend to be quite large compared to the gradients measured in this study (Choat and Schiel 1982, Cleary et al. 2005). It is possible that small changes in grazer composition across the study site may have attributed to the significant effect of depth on macroalgae. However, explicit studies would be required in order for this to be determined.

Changes in depth not only result in changes in grazer composition but most notably result in changes in light intensity as well as light spectrum. These changes result in significant changes in algae communities found in this study and others (Vadas and Steneck 1988, Markager and Sand-jensen 1992, Johansson and Snoeijs 2002, Hop et al. 2012). In this study, the greatest difference in algae communities across depths occurred

in algae genera that form upper canopies (Figure 10). *Agarum* had the greatest correlation with deeper depths while *Ulva* and *Weeksia* were largely negatively correlated with depth (Figure 10). In this study, *Ulva* occurs mostly at shallow depths, *Weeksia* at intermediate depths and *Agarum* at the greatest depths (Appendix I, Figure 15). *Ulva* absorbs mostly red light and is therefore usually found at shallow depths where red light is available (Prescott 1968). *Agarum* maximally absorbs green light and can therefore grow at deeper depths where green light is able to penetrate (Prescott 1968).

To determine whether the upper canopy biomass versus the lower canopy was driving the results, the upper canopy was removed from analysis and again depth had a significant effect on algae genera. Most algae genera in the lower canopy belonged to the *Rhodophyta* phylum and were found across most Reef Balls. However, there were some that had greater biomass at shallow depths, such as *Pterosiphonia* and *Pleonosporium*, while others had greater biomass at deeper depths such as *Fryella* (Figure 11). Some red algae, such as *Pleonosporium*, have been found to grow larger under greater light conditions (Murray and Dixon 1975), whereas light has no significant effect on the growth rate of other red algae such as *Griffithsia* (Waaland and Cleland 1972). This is supported by the findings in this study as the biomass of *Griffithsia* was consistent across various depths and therefore various light intensities. Although lower canopy algae grow in environments with less light than upper canopy algae, lower canopy algae are still affected by depth because the presence of an upper canopy reduces only a proportion of the available light at that depth (Reed and Foster 1984, Connell 2003, Irving and Connell 2006a). In addition, the constant motion of water pushing the upper canopy in one direction or another causes the lower canopy to be exposed to full light for portions of a

tidal cycle and covered during different portions of the cycle. As a result, depth which acts as a proxy for light, still demonstrates an effect on the algae community that composes the lower canopy on Reef Balls.

Depth appears to drive the spatial patterns of the canopy genera – *Agarum*, and *Ulva* and to a lesser extent *Weeksia*. *Agarum* grows mostly at deeper depths, *Ulva* at shallow depths, and *Weeksia* appears to grow optimally at shallow to mid depths (Appendix I, Figure 15). There also appears to be a zonation of the three genera with respect to distance from shore, which is correlated with depth (Appendix I, Figure 15). Depth also appears to drive the spatial patterns of some of the understory genera such as *Pterosiphonia* and *Pleonosporium*, but the majority of understory genera occur either ubiquitously or patchily across Reef Balls. The spatial patterns observed in the upper canopy and some lower canopy algae was not detected by the PCNM analysis ($p=0.46$). This may be due to the nature of the PCNM analysis as well as the haphazard study design. A PCNM analysis creates a matrix of geographical distances among sample sites and retains distances that are equal to or greater than the greatest distance calculated between closest neighbours (Borcard et al. 2011). This would reduce testing for small scale spatial variation if there are sample sites that are located at great distances from the remaining sample sites, which is the case in my study design (Figure 4). The truncation distance in the analysis was 15m, which is much greater than the distances between Reef Balls that have similar upper and lower canopy algae (Figure 13, Table 7). Significant spatial autocorrelation may also not have been detected due to the majority of algae genera occurring ubiquitously or haphazardly across the study site.

Kendall W's coefficient of concordance test grouped the top 25 most common genera into two groups in which *Ulva* occurred in one and *Weeksia* and *Agarum* occurred in the other. *Weeksia* and *Agarum* being placed into one group by this analysis is an indication that there is a bit of overlap in the spatial distribution of the two genera and the zonation is a bit fuzzy. *Callophyllis*, which occurs in the lower canopy and was found to be positively correlated with depth in the redundancy analysis, was grouped with the deeper occurring *Weeksia* and *Agarum*. *Rhodoptilum* and *Pterosiphonia* on the other hand were placed in the same group as *Ulva* and all were found to be negatively correlated with depth. The Kendall W's coefficient of concordance, provides support that some algae can be grouped into distinct communities based on their response to depth. Less than half of the genera included in the test had significant associations with other genera indicating that a large proportion of algae genera are not significantly affected by depth.

While environmental gradients may play a small role in understory algal distribution, stochastic processes such as dispersal and colonization which influence priority effects may also be a playing a role in addition to the potential role of grazers.

4.3 Stochastic Colonization and Priority Effects

As 78% of the variation cannot be explained by any measured environmental gradients, a potential explanation for the variation observed in the data is due to stochastic processes and priority effects (Benedetti-Cecchi 2000, Almany 2009). Algal communities are often found to be patchy and variable at small spatial scales - on the order of centimetres to metres - where environmental factors do not vary significantly

(Benedetti-Cecchi et al. 2001, Coleman 2002). This spatial variability can arise at multiple stages throughout the lifehistory of a macroalga – spore dispersal, colonization, establishment, survival, and succession (Santelices 1990). Differences or stochasticity in these processes may have affected some algae genera as their occurrence and biomass was spatially variable across the study site (Appendix I, Figure 16). Other algae genera appeared to be less affected by stochastic processes as they were found to occur ubiquitously across Reef Balls with only some variation in biomass (Appendix I, Figure 17).

Random occurrence of some algae genera found in this study may be due to patchy spore distribution patterns which can arise due to differences in current direction and speed at the time of spore release, as well as interactions with variable topography (Bobadilla and Santelices 2005, Gaylord et al. 2012). As a result, several different spore distribution patterns may arise ranging from patchy spore clouds to uniform distributions that decrease in concentration with increasing distance from the source (Kendrick and Walker 1991, Bobadilla and Santelices 2005). Algae genera such as *Euthora* and *Antithamnion* that were found across all Reef Balls may have uniform spore distribution patterns compared to algae genera that were only found on a few Reef Balls such as *Fryella*. Spore distributions can also vary among species due to the physical properties of spores, such as size and density (Reed et al. 1988, Santelices 1990). Spore composition is continually changing in the water column as some spores are lost due to sinking or grazing while others are gained due to new spore releases (Santelices 1990). As a result, different compositions of spores encountering each artificial reef unit may have led to the variable spatial distribution.

Variability in algal community composition can also arise during settlement and recruitment processes. For example, while the speed of water passing the Reef Balls did not have a significant effect on the algal community, variations in direction and turbulence of flow may have influenced spore settlement (McNair et al. 1997). Reef Balls that were positioned near another Reef Ball that was in line with the main direction of current may have experienced greater water turbulence and as a result, had a greater proportion of algal spores being directed to its surface compared to Reef Balls experiencing less water turbulence.

Biotic interactions may have also led to the variable spatial distribution of algae genera. Upon reaching and attaching to the surface of the Reef Ball, spores are then exposed to grazers. By clearing a small patch on the Reef Balls, grazers allowed for new species to colonize. Grazer communities have been found to vary at small spatial scales across similar habitat patches (Olabarria and Chapman 2001). Variation in grazer abundances or composition across Reef Balls would lead to different grazing pressures on algal spore communities. Spatial variability in grazer communities occurring at the onset, as well as throughout algal community succession, would play a role in the spatial variability seen in algal communities across Reef Balls. Explicit studies examining the influence of grazers on algal community composition would determine their relative contribution to the spatial distribution of macroalgal communities found in this study.

The sequence in which algae colonized the Reef Balls likely played a large role in community formation (Benedetti-Cecchi 2000) and may have been responsible for the variation in abundance and composition for some algae genera. Algae genera that were affected by priority effects, may have been unable to colonize due to established algae

sweeping, shading, and outcompeting them (Santelices 1990). Algae genera found in the upper canopy would most likely be generating these processes since their blades or thalli are large enough to sweep spores off of, reduce the amount of light reaching and, in the case of *Agarum*, pre-empt the physical space on the substrate (Irving and Connell 2002a, 2006b).

Competition may have occurred not only when these algae genera first colonized the Reef Balls but also when disturbances, such as grazing, occurred (Reed 1990). Pressures from competition may have also stemmed from competition with sessile invertebrates, as they also compete for space (Miller and Etter 2008). The algae genera that recolonized the disturbed area would be influenced by many of the temporal and spatial processes described above. The time of disturbance and availability of spores in the area would strongly influence the community that recolonized the disturbed site (Breitburg 1985, Airoldi 2000). If algae genera that differ from the pre-existing specimens recolonize the disturbed site, the spatial variation in algal communities on Reef Balls increases.

4.4 Study Limitations

The greatest limitation to this study is that colonization and succession were not directly measured. Inferences can be made about the effects of colonization and succession on community assembly by eliminating potential effects of abiotic factors, however, specific statements cannot be made. In order to make a supported statement on the effects of colonization and succession on community assembly, specific processes

such as spore dispersal, colonization of the substrate and biotic interactions must be tested.

Conducting research in the marine environment has many challenges, especially when conducting research underwater. Challenges were faced throughout the duration of this project, beginning with the deployment of Reef Balls into the study area. As mentioned in the methods section, the original study design was to place the Reef Balls in a block design, however due to environmental conditions such as waves and wind the landing craft was not able to move in a straight line. As a result the Reef Balls were deployed in a haphazard manner affecting the study design and potentially reducing the ability to detect signals in the data due to low replicates at certain depths, light intensities, distances to propagule sources, and water velocities.

The Reef Balls were also deployed across a small area in order to increase the probability of finding them when diving. The original study design had Reef Balls placed at three distinct depths: 6m, 12m, and 18m, increasing the size of the study area to $200m^2$. By increasing the gradient in depth, distance to a propagule source, and potentially water velocity, a greater proportion of the differences in community composition and diversity across an area may have been explained. With greater differences in depth, and as a result light, changes in community composition would not only be detected in algae genera forming the upper canopy genera, but also in those that form the understory, creating a stronger signal between depth and algae community composition (Vadas and Steneck 1988).

Significantly increasing the distance from a propagule source and maintaining Reef Balls at depths that are within recreational dive limits would be challenging as the

majority of Vancouver Island's coastline is rocky and covered with macroalgae. However, if a site were found that was kilometres away from the nearest propagule source, a difference in community composition may be detected (Kendrick and Walker 1991).

The haphazard study design made it challenging to find the Reef Balls underwater. The visibility at Ogden Point varies from day to day and can range from one metre to fifteen metres at best (personal observation). On average, the visibility was between six and seven metres, making it difficult to find Reef Balls as their distance from the breakwater and from each other is much larger. In order to increase the ease of finding Reef Balls during collection periods, nylon line was laid out between Reef Balls and fastened to the substrate, providing a path between all Reef Balls. While line was laid out to improve the probability of finding Reef Balls, the lines could be difficult to find or were broken. Algae growth would cover the lines making it difficult to see them and due to the weight of algae growing on it, large detached algae becoming caught on the line, or due to other large debris getting caught during times of high current or turbulence, the line would break. As a result of not being able to see the lines, volunteer divers had a difficult time finding the Reef Balls and as a result, water velocity measurements were not collected from several Reef Balls during one collection period. This reduced sampling of water velocity from three days to two days, potentially decreasing the power of water velocity as a predictor for macroalgal communities (Krebs 1998).

One of the most limiting features of conducting underwater research is the physiological limitation that significantly reduces the amount of time that can be spent

collecting data each day. To set up the quadrats outlining the sample area and to collect algae from all 30 samples required four weeks of diving every day, sometimes twice a day. Collecting data on environmental variables took an additional two weeks. If physiological limitations did not greatly increase the number of days required to collect data, additional studies would have been conducted. The first study would have involved destructively sampling the diversity and community composition of macroalgae on the breakwater to determine the role it played in providing propagules to the Reef Balls. An additional study would be to compare the community composition and development between Reef Balls and the breakwater. By comparing community composition between Reef Balls and the breakwater, a comparison could be made between community macroalgal development between two different artificial reefs. Comparisons could also shed light on the effects that a surrounding established macroalgal community has on the recolonization of a disturbed area compared a new piece of habitat.

If I were to conduct this study again, I would have re-focused my efforts from attempting to move Reef Balls underwater into a block design to conducting studies on the effects of colonization, priority effects, and grazing on subtidal macroalgal communities.

4.5 Overall Conclusions

Determining drivers of community assembly that are predominantly responsible for community composition is a major goal in ecology. This study, in concordance with other studies, has shown that different mechanisms drive different genera of subtidal macroalgal communities in community assembly (Vadas and Steneck 1988). The genus

of macroalgae that comprises the upper canopy is determined by the main environmental gradient driving subtidal ecosystems – depth. Lower canopy algae that occur ubiquitously across the study site were not affected by environmental gradients most likely due to the low variation in environmental gradients stemming from the small spatial scale of the study site. Lower canopy algae that occur haphazardly across the study site, may be driven by a variety of mechanisms such as grazing, colonization, and priority effects. This may be due to the fact that the algae genera that made up the upper canopy have more narrow niches when it comes to light requirements compared to red algae found in the understory (Kain and Norton 1990, Pritchard et al. 2013). Red algae have a wider niche as they are able to grow at a wide range of light intensities (Kain and Norton 1990). A possible exception to this prediction is the red algae *Weeksia*, which is found in the upper canopy. While red algae tend to have the ability to grow at a wider range of light intensities, *Weeksia* may be an exception and have a more narrow range of light requirements. Intraspecific competition among upper canopy genera may also be responsible for narrowing the depth range at which *Weeskia* is found.

The different mechanisms that drive different genera of the community also create different spatial patterns. Algae genera found in the upper canopy appear to follow a depth/coastline gradient, while the lower canopy community have genera with ubiquitous and haphazard spatial patterns. Random distribution may arise due to stochastic processes such as spore dispersal, colonization, grazing etc., making it difficult to predict subtidal macroalgal community structure. This may have implications when considering restoration efforts that attempt to recreate specific communities. It brings to question whether heterogeneous macroalgal communities result in heterogeneous communities at

higher trophic levels where most restoration efforts are focused (Seaman 2007). Reef Balls are ideal structures with which to investigate this inquiry as they provide an ideal surface for macroalgae and are designed to support higher trophic levels.

Random distribution of subtidal and intertidal macroalgae has been found in other studies (Coleman 2002), however, it may be a product of the community existing at an earlier successional stage. The structure of algae communities at earlier successional stages has been found to be spatially variable and difficult to predict (Breitburg 1985, Benedetti-Cecchi et al. 2001). As succession continues, many studies have shown a convergence to a more stable and predictable community (Hirata 1986, Pacheco et al. 2011). The understory algal communities found on the Reef Balls may become more predictable at later succesional stages.

The study confirms that across small spatial scales and during early successional stages, upper canopy algae genera are structured by narrow depth gradients, while composition of understory algae may be influenced by stochastic processes, priority effects, and grazing. Further studies are required in order to determine the drivers of understory community assembly.

4.7 Future Research

This study has provided the groundwork for future research on the benthic subtidal ecosystem located on Reef Balls at Ogden Point. Through a more exploratory approach, abiotic factors that play an important role in community assembly were determined. Having established some of the important factors influencing subtidal macroalgal community structure, such as depth, future research can focus on more

experimental approaches. For example, to determine if the effects of depth on macroalgal communities is due to changes in light, experimental studies manipulating light intensity and spectrum can be conducted.

Research can also focus on directly measuring colonization and succession processes as information gathered from this study only allows for speculation. Determining spore dispersal across the study area, colonization sequence, grazing pressure, and biotic interactions such as intraspecific and interspecific competition will begin to shed light on the specific processes that are responsible for the variability so often seen in subtidal macroalgae communities found at small spatial scales (Benedetti-Cecchi et al. 2001). In addition, macroalgae communities are not distinct from sessile invertebrate communities and often compete for space on substrate (Miller and Etter 2008). Colonization and competition from sessile invertebrates influence macroalgal community structure and composition and must also be investigated to determine the role of interspecific competition on community assembly (Breitburg 1984).

The advantage of using Reef Balls for some of the future studies is that, unlike tiles, they have a large enough surface area to support higher trophic levels including algae grazers and their predators. As a result one could look at the effects that trophic interactions have on community assembly.

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Appendix I

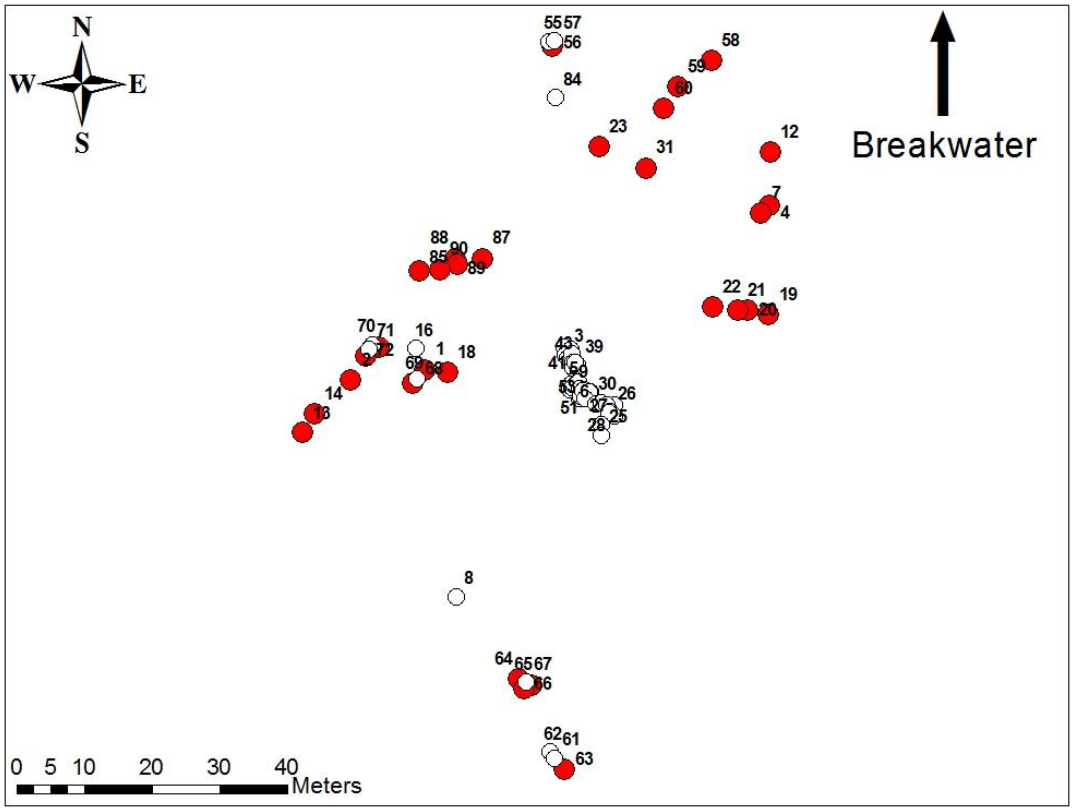

Figure 13. Aerial map of location of Reef Balls plotted in ArcMap 10.0 with UTM World Geodetic System 1984 projection. Orange circles represent sampled Reef Balls, white circles represent Reef Balls that were not sampled. Numbers on the map correspond to "Reef Ball #" found in Table 6. Arrow in top right corner points in the direction of the breakwater.

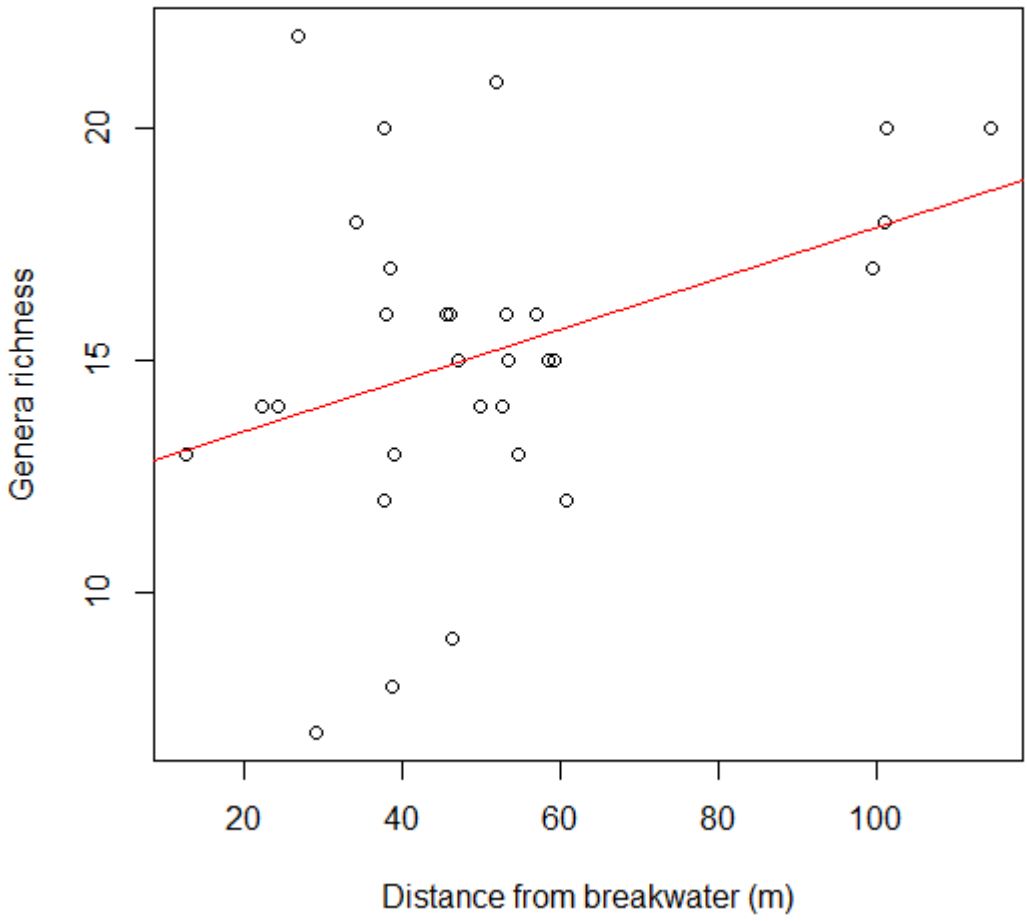

Figure 14. Scatterplot of genera richness found at each Reef Ball and distance to breakwater (m). Red line is a least squares regression line.

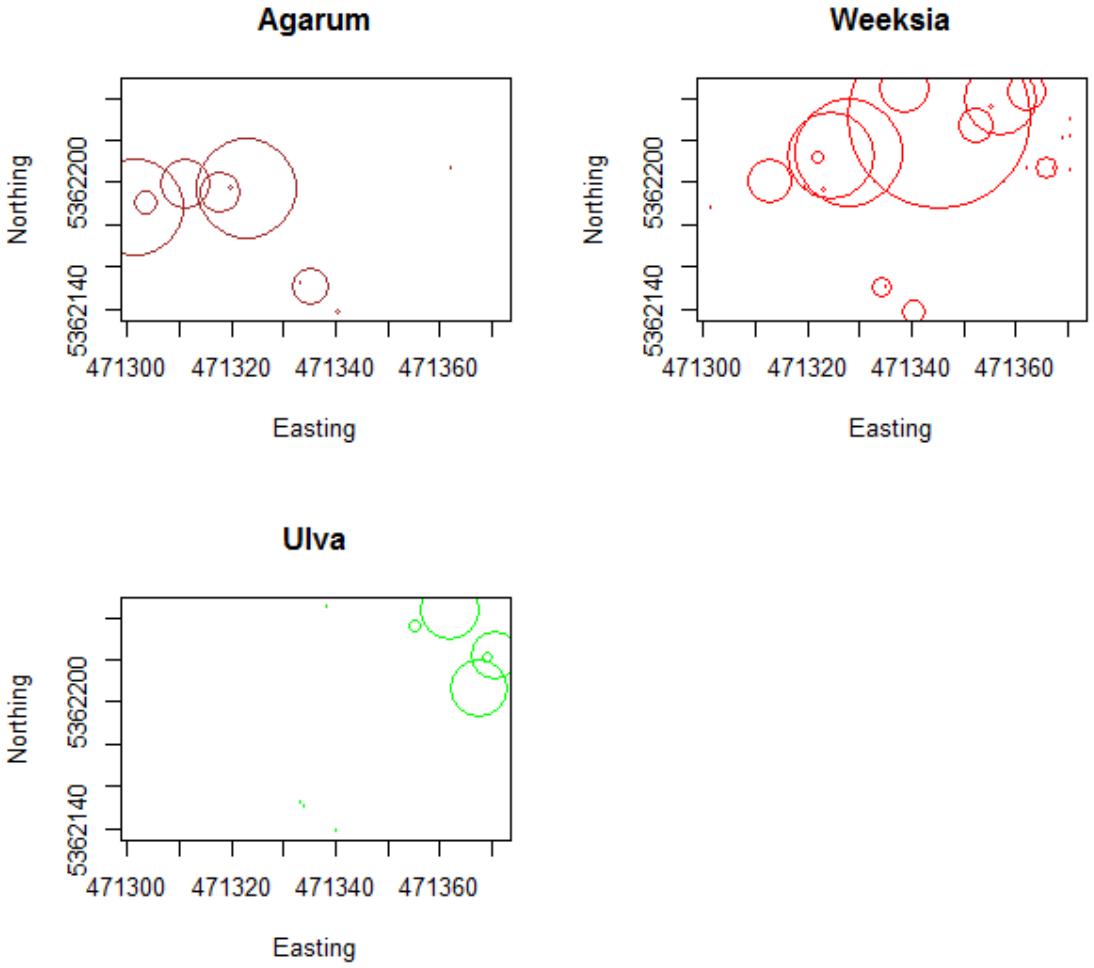

Figure 15. Distribution of dry algae biomass (g) across Reef Balls. The axes represent UTM values for a WGS-1984 projection. The breakwater would be located in the direction of increasing Northing UTMs and the shore located in the direction of increasing Easting UTMs. Name of the algae genus represented in the plot are located above the plot. Size of the circle indicates the relative biomass of algae genera found at each Reef Ball across the study site. The location of the circles represent the location of the Reef Ball at which the algae genus was found. Circles are only present if the algae genus was found on the Reef Ball. Circle sizes cannot be compared across figures as the scaling differs. Different scaling was used in order to allow algae genera with very low biomass to be seen in the figure.

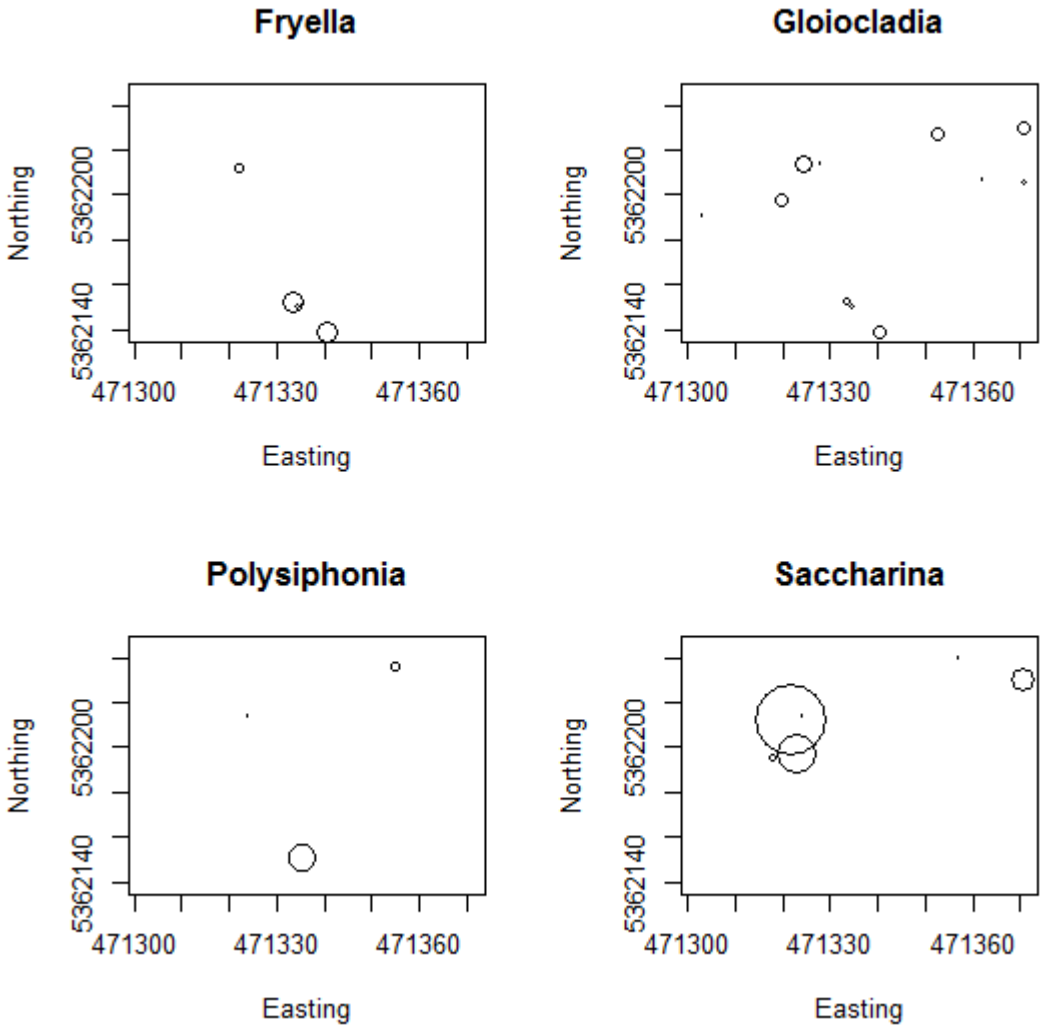

Figure 16. Distribution of dry algae biomass (g) across Reef Balls. The axes represent UTM values for a WGS-1984 projection. The breakwater would be located in the direction of increasing Northing UTMs and the shore located in the direction of increasing Easting UTMs. Name of the algae genus represented in the plot are located above the plot. Size of the circle indicates the relative biomass of algae genera found at each Reef Ball across the study site. The location of the circles represent the location of the Reef Ball at which the algae genus was found. Circles are only present if the algae genus was found on the Reef Ball. Circle sizes cannot be compared across figures as the scaling differs. Different scaling was used in order to allow algae genera with very low biomass to be seen in the figure.

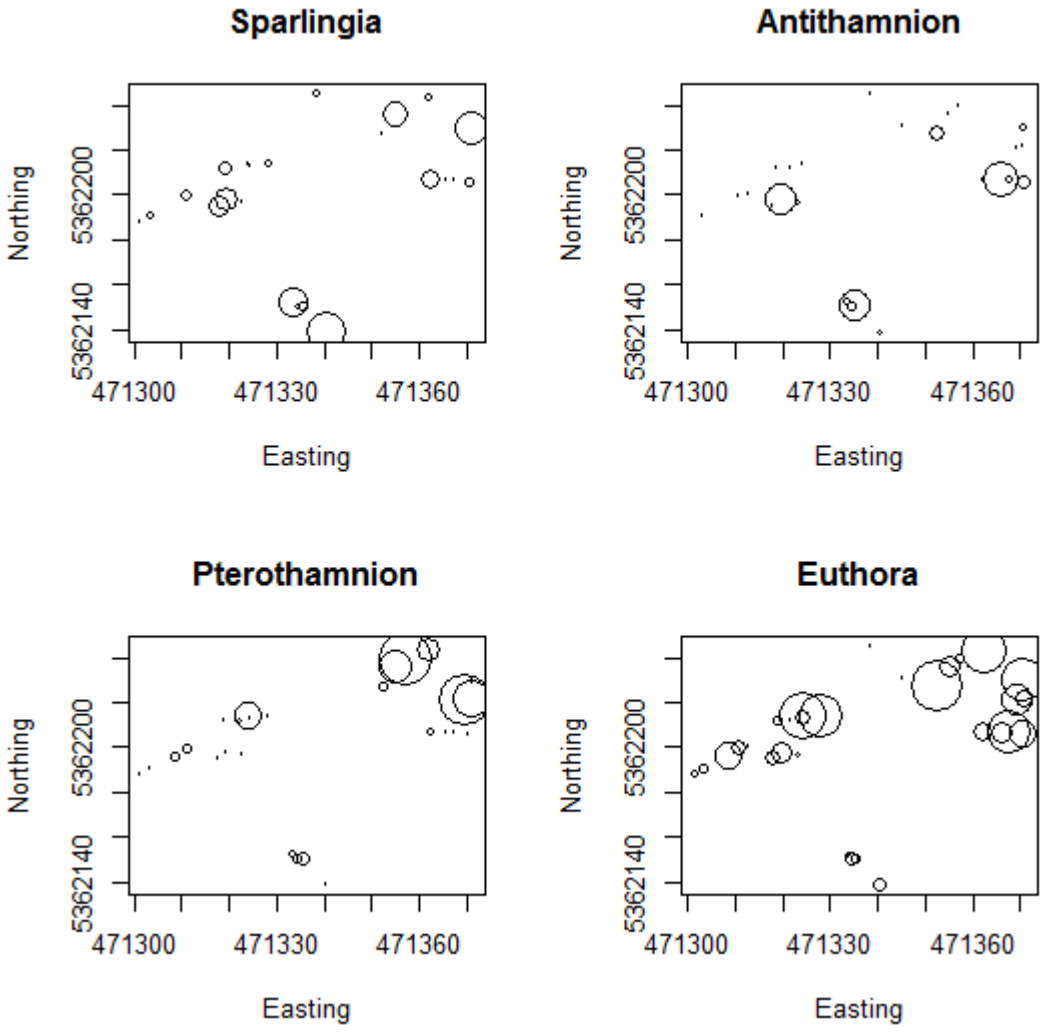

Figure 17. Distribution of dry algae biomass (g) across Reef Balls. The axes represent UTM values for a WGS-1984 projection. The breakwater would be located in the direction of increasing Northing UTMs and the shore located in the direction of increasing Easting UTMs. Name of the algae genus represented in the plot are located above the plot. Size of the circle indicates the relative biomass of algae genera found at each Reef Ball across the study site. The location of the circles represent the location of the Reef Ball at which the algae genus was found. Circles are only present if the algae genus was found on the Reef Ball. Circle sizes cannot be compared across figures as the scaling differs. Different scaling was used in order to allow algae genera with very low biomass to be seen in the figure.

Appendix II

Table 5. Algae genera collected from Reef Balls, the code name for each genera used in the RDA triplot, functional group to which they belong and the total biomass of each genera collected from all Reef Balls

Genera	Code	Functional Group	Total biomass (g)
Weeksia	WEE	Corticated terete	64.844
Agarum	AGA	Leathery	32.879
Rhodoptilum	RHO	Corticated terete	27.201
Callophyllis	CAL	Corticated terete	25.581
Ulva	ULV	Foliose	17.089
*Desmarestia**	DES	Corticated terete	3.576
Euthora	EUTH	Corticated terete	3.422
Pterosiphonia	PTE2	Corticated terete	2.658
Bonnemaisonia	BON	Corticated terete	2.249
Pterothamnion	PTE3	Filamentous	1.904
Heterosiphonia	HET	Corticated terete	1.302
Saccharina	SAC	Leathery	1.255
*Salishia**	SAL	Corticated terete	0.913
Sparlingia	SPA	Corticated terete	0.627
Antithamnion	ANT	Filamentous	0.564
Sarcodiotheca	SAR	Corticated terete	0.425
Hollenbergia	HOL	Filamentous	0.345
*Cryptonemia**	CRY	Corticated terete	0.282
Herposiphonia	HER	Corticated terete	0.281
Fryella	FRY	Corticated terete	0.262
Scagelia	SCA	Filamentous	0.207
Callithamnion	CAL1	Filamentous	0.188
Pleonosporium	PLE	Filamentous	0.184
Griffithsia	GRIF	Filamentous	0.133
Gloiocladia	GLO	Corticated terete	0.131
*Phycodrys**	PHY	Corticated terete	0.091
*Pugetia**	PUG	Corticated terete	0.043
*Polyneura**	POL1	Corticated terete	0.033
*Melanosiphon**	MEL	Corticated terete	0.026
Ceramium	CER	Filamentous	0.023
*Plocamium**	PLO	Corticated terete	0.021
*Trailiella**	TRA	Filamentous	0.018
*Polysiphonia**	POL	Corticated terete	0.012
*Odonthalia**	ODO	Corticated terete	0.008
*Pterochondria **	PTE1	Corticated terete	0.005
*Tiffaniella**	TIFF	Filamentous	0.001

* Rare genera (genera that had a total biomass < 0.020g and/or occurred at fewer than 3 sites)

Table 6. Genera richness, Shannon Entropy, and Simpson Diversity Number values across Reef Balls

Reef Ball #	Genera Richness	Shannon Entropy	Simpson Diversity Number
1	21	2.07445586	5.697535
2	14	1.49720985	3.30351
4	16	0.9750803	1.665648
7	16	1.42160107	2.590299
12	16	1.82075182	4.283512
13	13	0.46156125	1.244011
14	14	1.00444999	2.118697
15	9	0.23509135	1.091209
18	15	0.69914224	1.40617
19	12	1.45184242	2.968738
20	15	1.08767734	1.875512
21	15	1.31322934	2.840022
22	16	1.7109208	3.836598
23	7	0.07847974	1.024521
31	18	1.76263318	4.39243
56	13	0.59342752	1.336354
58	14	1.47635707	3.393048
59	14	0.86971306	1.671337
60	22	1.97398465	4.935111
63	20	1.56895763	2.944278
64	17	1.34101452	2.122218
65	18	1.12127535	2.202408
66	20	1.2805176	2.677879
69	16	1.1770504	2.730748
72	15	0.72603873	1.48266
85	12	1.09542716	2.067754
87	13	0.89131757	1.810758
88	20	1.41806483	2.663056
89	8	0.73702037	1.619067
90	17	1.38792901	2.911649

Table 7. Raw data for environmental gradients measured at each Reef Ball

Reef Ball	Average water flow(m/s)	Light(lux)	Depth(m)	Distance to closest Reef Ball(m)	Distance to breakwater(m)
1	0.023036	37.11104	12.0320	1.74	51.77
2	0.017578	44.79616	12.6116	4.26	49.65
4	0.025297	62.99776	9.7884	1.70	45.41
7	0.016897	53.05429	9.7884	1.70	46.05
12	0.022079	57.20021	9.4936	7.95	37.95
13	0.011104	29.42592	13.526	3.24	54.56
14	0.021900	32.96512	13.2212	3.24	52.61
15	0.021716	44.79616	12.3168	0.91	46.33
18	0.006353	41.25696	12.032	3.38	53.23
19	0.018941	33.57184	9.7884	3.13	60.69
20	0.024466	37.11104	9.7884	1.60	59.07
21	0.013650	33.57184	9.7884	1.60	58.50
22	0.010356	34.62517	9.7884	3.64	56.90
23	0.007109	44.79616	10.3632	7.61	28.95
31	0.022493	57.20021	10.328	7.61	34.16
56	0.028382	53.05429	9.144	0.91	12.64
58	0.032193	48.94208	9.2088	6.32	22.28
59	0.020052	44.79616	9.4236	3.78	24.33
60	0.018523	62.99776	9.7184	3.78	26.71
63	0.007201	32.96512	13.4796	2.18	114.34
64	0.020061	34.62517	13.15	1.17	99.50
65	0.020261	41.25696	13.15	0.91	101.00
66	0.020575	31.08597	13.15	0.91	101.08
69	0.007690	48.94208	12.032	0.91	53.07
72	0.004234	37.11104	12.6116	1.05	46.97
85	0.019384	37.11104	11.7372	2.97	37.60
87	0.015714	58.85184	11.1876	3.79	38.96
88	0.010152	37.11104	11.4524	0.91	37.65
89	0.013913	37.11104	11.4524	0.91	38.56
90	0.013006	37.11104	11.7372	2.78	38.42