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Same Stone, Different Outcomes: Marine Communities on Engineered vs. Natural Rock Shores

Lucy Anne Dando Lockwood

SAME STONE, DIFFERENT OUTCOMES:

MARINE COMMUNITIES ON ENGINEERED VS. NATURAL ROCK SHORES

A Thesis Presented

by

LUCY ANNE DANDO LOCKWOOD

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ABSTRACT

SAME STONE, DIFFERENT OUTCOMES:
MARINE COMMUNITIES ON ENGINEERED VS. NATURAL ROCK SHORES

May 2020

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The effort to protect coastal property and infrastructure from storm damage, erosion, and sea level rise has resulted in increased construction of coastal protection structures (CPS) worldwide. Researchers around the globe have found that the marine communities living on CPS differ from those living on natural rock outcroppings in the same area. We conducted a classic disturbance experiment to investigate possible differences in marine organism response and community assembly between natural and human-constructed rocky intertidal habitat along the Massachusetts coast. The one-year study used naturally occurring rock shores and human-made granite seawalls with both wave-exposed and wave-protected areas. Significant differences in both the amount of substrate utilization and the composition of the colonizing marine community on the natural and human-engineered habitats were evident one year after the clearing disturbance. The natural rock experimental plots had a higher mean proportion of macroalgal and marine invertebrate cover overall, and regrowth was dominated by red and brown algal species. Human-engineered seawalls evidenced significantly lower mean cover proportion and dominance of green algal species. Wave exposure also had a significant effect, though less than substrate type. These experimental results raise the possibility that ongoing expansion of CPS along the Gulf of Maine and New England coast could alter coastal marine ecosystems and, over time, could have far-reaching impacts on the region's marine biodiversity and ecosystem functioning.

DEDICATION AND ACKNOWLEDGEMENTS

This thesis is dedicated to my husband, Larry Constantine, who has supported my improbable journey from the onset with endless patience, love, and much coffee.

I would like to thank my advisor, Dr. Jarrett Byrnes, who introduced me to biological data analysis and re-introduced me to the world of programming, and whose blending of experimental and theoretical approaches to marine ecology has challenged me and shaped my work as an intertidal ecologist. My enduring gratitude goes to Dr. Robert Chen, for convincing me to become a student once again and to join the wonderful community that is the School for the Environment at the University of Massachusetts Boston. My appreciation and thanks also go to the many excellent UMB faculty including Dr. Ron Etter, Dr. Eugene Gallagher, and Dr. Michael Sharis, whom I have had the privilege of studying under and whose knowledge and guidance have steered my development as a scientist. I have also learned from and been supported by a wonderful group of fellow graduate students both in the School for the Environment and in the Biology Department. Finally, my heartfelt thanks and admiration go to my children, Tovah and Devan, who, along with my husband, have been relentless and unfailing cheerleaders and supporters of this effort over many years.

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CHAPTER 1

INTRODUCTION

Shorelines around the world are increasingly altered by humans to create more developable land or to protect existing human-made infrastructure and activities. Increased coastal development coupled with sea level rise and the threat of more intense or frequent storms due to global climate change is driving construction of new and ever larger coastal protection structures (CPS) such as sea walls, breakwaters, and shoreline revetments. Around the globe, marine ecologists have questioned whether these hard structures function ecologically the same as naturally-occurring rock outcropping along the shore or whether the assemblages of marine macroalgaes and invertebrates living on and around them differed from those found on natural shores. If they differ, that could have broad implications for marine ecosystem health and functioning.

Coastal lands have attracted human settlement since prehistory, offering access to food and resources, transportation and trade routes (e.g., Bailey, 2004; Bauer, 1998; Carter, 2006; Erlandson & Fitzpatrick, 2006; Gophna & Liphschitz, 1996; Ivanova, 2012; Westley & Dix, 2006). Today, population density around the world remains concentrated along the coast (Martinez et al., 2007; Neumann, 2015). Data from the 2010 US census revealed 39% of the continental U.S. population living in coastal counties even though that represents less than 10% of U.S. land area (Crossett et al., 2013) and by 2013 that population had risen to an estimated 133.2 million representing over 42% of the continental U.S. population (Fleming et al., 2018). With human settlement has come development: buildings and houses, ports and resorts, roads and refineries.

Along with increasing coastal habitation and development, climate change is now adding to the pressure on shorelines worldwide through the combination of rising sea levels and the threat of increased coastal storm frequency and intensity (Doggett, 2015; Stocker et al., 2013). In a 2014 article, *The Guardian* reported 4.2 million people in the U.S. living at four feet or less above sea level (McKie, 2014). The response has been increasing efforts to tame the effects of waves and water through the use of coastal protection structures. With projections for significantly higher sea levels in the future (Melillo et al., 2014; Rasmussen et al., 2018; Stocker et al., 2013), the push to create artificially engineered shore protection is likely to accelerate.

Collectively referred to as “hardened” or “armored” shorelines, coastal protection structures come in many forms (see Appendix A Table S1), but all aim to protect shores and shoreline property against coastal erosion and damage from waves and storm surges. In the state of Massachusetts, USA, more than 230 miles of privately-owned shoreline protection structures exist along with 140 miles of hardened publicly-owned shoreline (Fontenault et al., 2013). More than a quarter of the state’s approximately 1,500 miles of shoreline is hardened (Figure 1), with Boston Harbor the most densely at close to 60 percent. Northward, in the neighboring state of New Hampshire, approximately 70 percent of the state’s eighteen miles of Atlantic coastline is armored through the use of rocks, concrete blocks, and concrete seawalls (Blondin, 2017; Rice, 2015).

Figure 1: Map of engineered shoreline in Massachusetts in 2013.

Coastal protection structures have a disruptive effect on the marine habitats surrounding them. Jetties and groins are designed to impede shoreline sediment transport; breakwaters and seawalls are intended to dissipate wave energy. Changes to the physical conditions and the forces operating within a particular area impact the organisms inhabiting or trying to settle in that environment. Key abiotic factors are affected by CPS: sediment and organic material transport, shoreline slope, substrate, wave action, currents, and water and substrate temperature (e.g., Becchi et al., 2014; Rolet et al., 2015; Walker et al., 2008). Changes to each of these inhibit or enhance the ability of marine species to live on or around the engineered shoreline, favoring some species while creating inhospitable conditions for others.

How marine organisms respond to these anthropogenic coastal structures, and the biological underpinnings of why individual species and community assemblages respond as they do, is an area of active research worldwide. Studies have documented changes in the number, type, and diversity of species living on or around human-made coastal structures compared to those on natural coastal areas (Aguilera et al., 2014; Bulleri, 2005; Cha et al., 2013; Gacia et al., 2007; Peterson et al., 1999; Ravinesh & Bijukumar, 2013). Across studies, researchers found that, while marine life is adaptive to artificially hardened shoreline, CPSs supported decidedly different community assemblages than those found on nearby natural rocky substrate (Bulleri and Chapman, 2010; Martins, et al., 2009; Rolet, et al., 2015). The results of adding artificial hard substrate are neither equally beneficial nor equally detrimental to all littoral and nearshore organisms in a region. Some studies suggest that anthropogenic structures favor certain species over others or perhaps the converse is true and some organisms are disadvantaged under the conditions of CPSs. A common finding has been lower species richness compared to natural rocky shores or outcroppings (Morley et al., 2012). Species abundance on manmade structures also differed from that of natural hard substrate, but whether the difference in abundance was negative or positive depended on the species (Aguilera et al., 2014). The differences in species richness and species abundance translated into a general finding of lower species diversity on the artificial structures (Firth et al., 2014).

Prior to this study it was unclear whether the results seen in other parts of the world — namely that of dissimilarity between marine communities living on human-created intertidal hard substrate and those living on naturally occurring rock shores — held true in New England and the Gulf of Maine region. No published studies existed for either New England or the Gulf of Maine, and while it was likely that the same dissimilarity did hold, the validity of that assumption remained unproven. We sought to answer the question of similarity in the context of the northern Massachusetts coast within the southern Gulf of Maine in the Northwest Atlantic. Using a classic disturbance experiment on both naturally occurring rock shores and on human-made granite seawalls, we asked the question of whether the response to disturbance was the same on both types of shore in terms of level of recolonization and types of organisms recolonizing.

To investigate possible differences in community resilience and community assembly between natural and human-constructed rocky intertidal habitat within the context of the southern Gulf of Maine, we drew on an established method used by ecologists to compare intertidal communities: the disturbance experiment (*sensu* Dayton, 1971; Lubchenko & Menge, 1978; Sousa, 1979; Underwood et al., 1983). In the intertidal regions of rocky shore habitat, open space for attachment to the substrate is limited, as any bare rock is soon colonized, first by establishment of a biofilm and then by successional assemblages of foliose and encrusting macroalgae and sessile invertebrates. New patches of open space are created intermittently by storm-tossed debris and rocks, erosion, and, in a cold climate such as Massachusetts, by winter ice scour. Deliberate experimental creation of cleared, open patches of rock allows for comparison of recolonization of those patches across sites and treatments. The rate of recovery from disturbance has been experimentally connected to ecosystem productivity and biodiversity, which in turn are factors in ecosystem resiliency (Aquilino &

Stachowicz, 2012; Cardinale et al., 2011; Levin & Lubchenco, 2008; Palumbi et al., 2008; Stachowicz et al., 1999).

The study focused on two questions comparing the natural and human-made intertidal shoreline: 1) is there a difference in the amount of substrate area successfully resettled one-year after a clearing disturbance, and 2) are the newly-established assemblages of organisms the same on both natural and human-constructed rock substrate? The experiment ran for a period of one year using multiple paired sites of granite seawalls and adjacent rocky shore.

The focal questions can be stated as two experimental hypotheses that the experiment was designed to test:

H_0: After one year, the mean proportion of covered space is the same on natural rocky intertidal wall clearings as on engineered seawall clearings.

H_A: After one year, the mean proportion of covered space differs on natural rocky intertidal wall clearings from that on engineered seawall clearings.

And:

H_0: After one year, macroalgal and marine invertebrate groups found on natural rocky intertidal wall clearings are the same as those on engineered seawall clearings.

H_A: After one year, macroalgal and marine invertebrate groups found on natural rocky intertidal wall clearings differ from those on engineered seawall clearings.

Rejecting the null hypothesis on this first question would mean there was evidence of a significant response of cover proportion to the type of intertidal vertical granite habitat, natural compared to engineered. Likewise, rejecting the second null hypothesis would be evidence of a significant response of one or more macroalgal or invertebrate groups to engineered vs. natural vertical granite intertidal habitat.

A secondary line of inquiry was that of the impact of wave exposure on the one-year response to clearing. Was there was a significant difference in substrate type response due to wave exposure, i.e., did an experimentally-cleared square's wave exposure (directly exposed to waves or protected from waves) affect the one-year response to clearing? If there was an effect, was this effect greater or less than that of substrate type?

At the experiment's conclusion, the data supported rejection of both null hypotheses. The data from the intertidal assemblages on the natural and on the human-engineered habitats showed differences in both the amount of substrate utilization after the clearing disturbance and in the community profile of the colonizing marine organisms. The natural rock experimental plots exhibited a higher mean level of coverage by macroalgae and invertebrates, as measured by percent cover after one year, and had regrowth dominated by red and brown algal species as compared to the dominance of green algal species within plots on the human-engineered seawalls. Furthermore, the effect of wave exposure on the experimental plots was not significant, but the effect of substrate type was significant across both wave-exposed and wave-protected clearings.

These experimental results raise the possibility that ongoing expansion of CPS along the Gulf of Maine and New England coast could have far-reaching impacts on the region's marine biodiversity and ecosystem functioning, affecting economically and socially vital fisheries, tourism, and quality of life along the coast.

CHAPTER 2

METHODS

Study Sites

To experimentally test whether intertidal marine assemblages living on human-engineered seawalls respond differently to disturbance than those on natural rock shores, the study used both seawalls and vertical rock shores composed of the same material. Substrate material is known to affect marine community composition (Burt et al., 2009; Cha, et al., 2013; Glasby, 2000; Guidetti et al., 2004; Spagnolo et al., 2014; Tyrrell & Byers, 2007; *cf.* Bulleri, 2005), so seawalls made of blocks of local granite were specifically selected rather than seawalls made of concrete. Comparing seawalls built of local granite to naturally occurring granite shores eliminated the influence on the experiment of the numerous differences inherent in dissimilar substrate materials, such as granite and concrete (e.g., surface chemistry, roughness, pH, hardness).

Three sites in close proximity on the tip of Cape Ann along the northern Massachusetts, USA, coast were selected for the experiment (see Figure 2), as each featured a seawall constructed of local cut granite blocks with adjacent natural rock intertidal shoreline that featured vertical granite surfaces with orientations similar to that of the seawall. Keeping all the sites in the same area of the coast lessened the likelihood that any differences in the disturbance response of a seawall and that of a rock shore merely reflected large differences in larval supply rather than inherent differences between the seawalls and the natural rock shores.

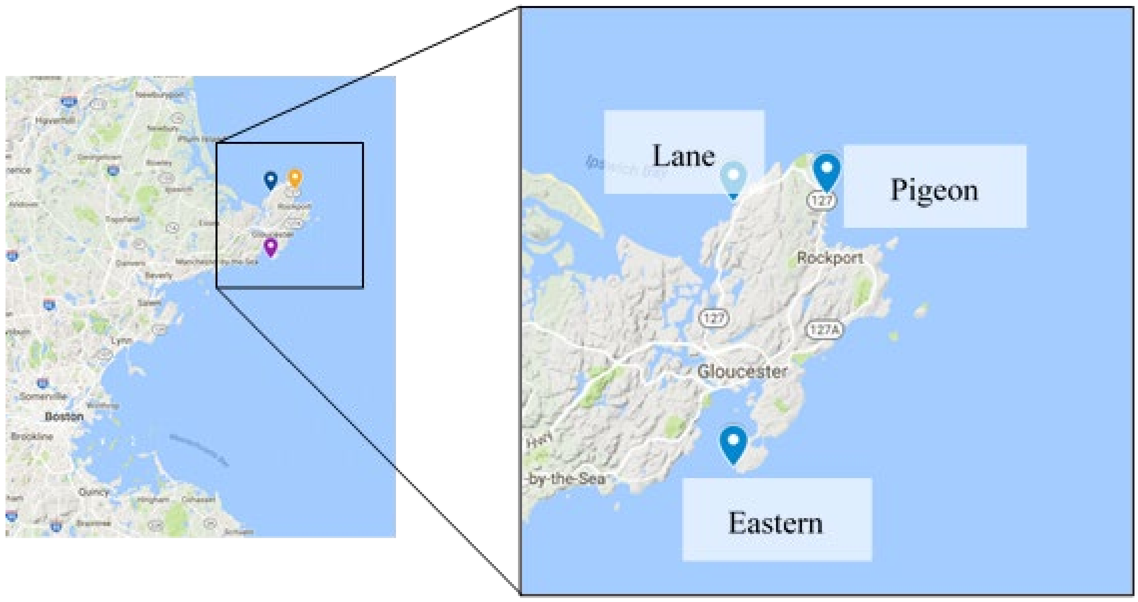


Figure 2: The three study sites on Cape Ann, Massachusetts, USA.
(Map credit: Google Maps, 2019)

The three granite seawalls selected had been built many decades ago, in one case dating back over 100 years. Winter nor'easters and blizzards had at times seriously damaged all of them, most recently in the "No Name Storm of '91", and the nor'easters of 2010 and 2013. Only seawall sections that had not been impacted by repairs in recent years were used as experimental sites, thus allowing comparison between the natural rock and the granite seawalls of mature, rather than newly formed or mid-successional, marine communities. The age of the seawalls meant that the cut granite surfaces had weathered in the marine environment for years rendering them more similar to the natural rock surfaces than would be the case with newly installed cut granite blocks (see Figure 3).

Figure 3: The protected side of the three granite seawalls used as study sites. (Clockwise from top left: Lane Cove, Pigeon Cove, and Eastern Point.)

Each of the seawall and natural rock shores sites extended vertically to at least the Mean Low Water (MLW) level. The experiment was conducted at sites where there was ample space for experimental plots in the lower intertidal region. Many seawalls in Massachusetts are constructed in the high intertidal or supratidal region of the shore where the main objective is to protect upland areas from storm wave-driven erosion. The upper half of the intertidal zone is a much harsher environment for organisms due to the longer period of emersion. The lower intertidal region, with its long immersion period, provides a more protective environment with greater access to water-borne nutrients and more watertransported propagules available for settlement, thus supporting a faster process of disturbance response and more complex climax community state.

The three sites were similar in having sufficient tidal-exchange currents along them to keep them well-flushed, even on the wave-sheltered portions of the seawalls and natural rock walls. The waters around Cape Ann have low levels of pollution thanks to strong offshore currents that supply clean water from the north and to the relative absence of heavy industry or large urban run-off that might be terrestrial sources of pollutants. Each site did experience a moderate level of motorized boat traffic. At Lane Cove and Pigeon Cove, motorized boat traffic was limited to small outboards and small to medium size lobster boats due to the shallow waters and small area of the coves, while at Eastern Point most of the boat traffic was in the main channel approximately 80 meters from the study transects. Wave energy at each location could be high during storm events – which is why the seawalls had been constructed in the first place – but was more moderate under typical conditions as observed over twelve to fourteen visits at each site during 2016 and 2017.

The existing communities of intertidal organisms at each of the study locations comprised common macroalgal and invertebrate species (see Appendix A Table S2). Photographic surveys and informal survey projects undertaken in 2016 prior to the experiment established that all the sites were dominated by macroalgal cover rather than space-occupying sessile invertebrate species, such as *Semibalanous balanoides* or *Mytilus edulis*. The brown algal species, such as *Ascophyllum nodosum* and *Fucus spp*., appeared to be most abundant, followed closely by red algal species, such as *Chondrus crispus* and *Polysiphonia lanosa,* the latter of which is hemiparasitic, found primarily on *Ascophyllum* *nodosum* and less frequently on *Fucus spp*. Green macroalgae were also present at each site, however only on the wave-protected side of the seawall at Pigeon Cove did they appear to achieve equal abundance (in the form of *Ulva spp*.) with the brown and red macroalgal species also present. Among sessile invertebrate species acorn barnacles (e.g., *Semibalanus balanoides*) were ubiquitous, found at every site on both natural and engineered substrates. Non-indigenous species of ascidian, particularly *Botrylloides violaceus*, were found at each site but not in abundance. Mobile invertebrates observed were primarily *Littorina spp.* snails and *Carcinus maenus* crabs. Overall, the communities appeared to contain the same general mix of common intertidal macroalgal and invertebrate species with no significant differences readily apparent except for the higher proportion of *Ulva spp*. on the protected side of the Pigeon Cove seawall, as noted earlier.

Experimental Design

Each study site was divided into two treatment areas: the natural rock shore and the human-made granite block seawall. Each treatment area was further sub-divided into two categories: vertical sides that were wave-exposed and vertical sides that faced away from the open ocean and thus were wave-protected (facing the opposite direction, approximately 180 degrees). Wave exposure, while not as dominant an influence as emersion time, is nonetheless an important abiotic factor affecting the distribution of intertidal organisms, particularly on hard substrate shores. Furthermore, one of the shoreline changes that coastal protection structures can introduce is creation of wave-sheltered shoreline along the "back" or landward side of seawalls, jetties, and breakwaters. It was possible, therefore, that differences in marine colonization between natural and human-made hard shorelines might be simply a result of the CPS structures having more wave-protected space. For that reason, we deliberately included in the experiment equal numbers of scraped plots that were wave-exposed and wave-sheltered for both substrate types.

The three sites had seawall faces (exposed and protected) that each featured a different directional orientation along with natural rock faces with the same or very close to the same orientations (see Appendix A Table S3). The mix of directional orientations allowed comparing the community response of the paired natural and human-constructed sites under a mix of sun exposure, prevailing wind, and prevailing wave direction conditions.

Both the seawalls and the rock shorelines extended vertically below MLW and above MHW (Mean High Water). A 30-meter transect was laid out horizontally along each vertical surface (seawall exposed, seawall protected, rock shore exposed, rock shore protected) at approximately 0.6m above MLW. Thus, each constructed seawall had two transects (exposed, protected) and each natural rock shoreline had two transects (exposed, protected) such that there were four transects total for each of the three sites.

A random number generator was used to select five whole numbers and, based on these random numbers, five locations on each 30m transect were marked. At each marked location a square area measuring 15 cm x 15 cm (225 cm^2) was cleared of all organisms. Clearings were made directly below the corresponding meter point on the transect line unless there was a crack (or in the case of the granite blocks, a crevice between blocks) in which case the clearing was shifted to the left and/or down as necessary, such that clearings were at least 5 cm from any crack or block edge and no cracks or crevices were included in the sampling area. If the initial square for clearing included any large surface anomaly such that it would be unable to be sufficiently cleared or had an area that significantly deviated from the vertical plane (e.g., an area of harder rock projecting outward from the vertical plane), the clearing area was shifted first to the left and then downward to the area closest to the original meter point that was sufficiently level with the vertical plane and capable of being scraped cleanly. Each of the squares was scraped using heavy-duty paint scrapers along with crevice tools and stiff wire brushes to remove all foliose macroalgae (including holdfasts), all invertebrates, and as much crustose algae as possible (the thin, flat, crustose algal specie *Hildenbrandia rubrum* proved difficult to remove completely as noted below). The degree of clearing was held constant across samples and sites regardless of the effort needed.

The design of the disturbance experiment at the three sites featured a factorial design with one bounded continuous dependent variable (the percentage of space-occupying macroalgal-invertebrate cover of each cleared square) and two categorical independent variables (treatments) of substrate type (engineered rock CPS or natural rock wall) and exposure (direct exposure to dominant waves or protected from dominant waves). The experimental design thus provided balanced data such that there were equal numbers of observations for each level of a factor (Table 1).

Table 1. Factorial design of the disturbance experiment

Frequency Table by Factors

Treatment	Direct-wave Exposed	Direct-wave Protected	Total
Engineered Wall	15	15	30
Natural Granite	15	15	30
Total	30	30	60

Frequency Table by Site

	Lane Cove	Pigeon Cove	Eastern Point	Total
Engineered				
Exposed	5	5	5	**15**
Protected	5	5	5	**15**
Natural				
Exposed	**5**	**5**	**5**	**15**
Protected	**5**	**5**	**5**	**15**
Total	**20**	**20**	**20**	**60**

All of the experimental clearings (20 per site, 60 clearings total) were completed over a period of six weeks in late August – early October 2016. The sites were then revisited approximately one year later over a period of six weeks in September-October 2017. Each of the sixty cleared squares was assessed to determine how much of the cleared 225 cm^2 was now covered either by attached macroalgae and invertebrates. Each scraped square was visually inspected and photographed from a distance of approximately 0.5m as measured by a hand-held length of rope. Determination of cover proportion was initially done by visual inspection at the site and then verified by photographic assessment using the open-source photo quadrat analysis software photoQuad v1.4 (Trygonis and Sini, 2012) to create a 10 x10 grid overlay on each digital photo. The cover proportion for each cleared square was recorded as a value between 0 and 100. The crustose red algae *Hildenbrandia rubrum* was not included in the percent coverage calculation owing to the fact that it grows in so thin a layer (0.2-0.5 mm thick, Guiry and Guiry, 2019) and adheres so strongly to rock surfaces that it could not be established that all such algae had been removed from the cleared squares in 2016 in the absence of more destructive clearing methods such as a blow torch or bleach wash.

In addition to the overall cover proportion calculation, each individual square was further analyzed to determine the species occupying the covered space down to the lowest taxonomic level possible with photographic analysis. The experimental squares had been photographed using a Nikon D3100 digital camera with a resolution of 14 megapixels. The resolution allowed for zooming in on a digital photo or on portion of a photo to aid in species identification. Each photographed square was processed with the open-source biological imaging software ImageJ 1.52h (Schindelin, J., et al., 2012; Schneider, C. A., et al., 2012) and with PhotoMechanic 5.0 (CameraBits, Inc., 2018) software. Each pixel region of the photograph with a visible species was individually outlined and classified by species or taxonomic group. All individual organisms (e.g., *Semibalanus balinoides*), colonies of organisms (e.g., *Botrylloides violaceus*), individual fronds of macroalgae (e.g., *Ascophyllum nodosum*), and clumps of macroalgae (e.g., *Corallina officianalis*) or invertebrates (e.g., *Eucratea loricata*) were outlined and tagged by either species name or taxonomic group for each photograph. Areas of a photograph without macroalgae or invertebrate cover remained untagged.

The analysis only assessed the top layer of organisms visible in the photograph. At the one-year point, photographed colonization and regrowth on the experimental squares were limited, with no evidence of widespread layering of marine organisms as might be found on more mature intertidal assemblages. Thus, the single-layer species analysis was not considered to have materially affected the analysis.

Data Analysis

The statistical analysis was performed using the R programming language v.3.4.2 (R Core Team, 2017) in RStudio v.1.1.423 (RStudio, Inc., 2018) using the betareg package (Cribari-Neto and Zeileis, 2010) and lmtest package (Zeileis and Hothorn, 2002) along with additional code packages written to extend R capabilities. The full list of packages and the R code used for the statistical analysis can be found in Appendix C. The initial data entry was done using Microsoft Excel for Windows version 14.0.07 (Microsoft Corporation, 2010) and the data file then read into R for the statistical analysis.

Beyond summary data statistics and initial data visualization, three separate statistical analyses of the data were performed: two analyses used the overall percent cover of the experimental square by macroalgae and sessile invertebrates after one year; one analyzed the presence and space occupancy of specific macroalgal and invertebrate groups on the experimental squares after one year.

Analysis (1)   ANOVA of the cover proportion data with two-way independent factorial design

The cover proportion data was negatively skewed (see Figure 4a), so a logit transformation was used to spread the data at the end points. Percent cover was transformed using a logit transform, ln[p/(1-p) where p is the proportion of the formerly cleared square now covered by macroalgae or invertebrates. The logit transform cannot compute values of 0 or 1, the ends of the decile range, so the R logit function adds or subtracts 0.025 to any proportions with a value of 0 or 1. To examine the effect of each of the two fixed factors (substrate type and wave exposure) on overall one-year cover proportion, we fit multiple linear regression models using additional regressor terms. The models were then compared using coefficient of variation and AIC (Akaike information criterion). The linear regression model with the best fit included an interaction term as an initial test for any interaction effects between substrate type and wave exposure, with site added as a blocking factor.

The results of the linear model were analyzed using a two-way independent Type I ANOVA to look for treatment effects with substrate type and wave exposure as fixed factors and an alpha of 0.05. The experiment had balanced data (equal numbers of observations for each level of a factor) with a continuous dependent variable: cover percent (percent of square area with macroalgal or invertebrate cover after one year) and two categorical independent variables: substrate ("engineered", i.e., human-made granite seawall or "natural", i.e., natural rock wall) and exposure ("exposed", i.e., direct wave exposure or "protected", i.e., protected from direct ocean waves). There were fifteen replicates of each treatment combination.

Assumptions of normality were assessed by visual inspection of multiple plots of the model residuals: standardized residuals vs. fitted values, histogram of residuals, quantile-quantile plot, and Cook's distance values (see Appendix B Figure S1). Plots of standardized residuals vs. fitted values showed no fitted pattern with the zero-line close to horizontal. The histogram of the model residuals, although slightly left-skewed, conforms to a rough bell curve and the Q-Q plot revealed the residuals to be not too far off from the model line and without extreme outliers. Cook's distance test was also used to assess whether any potential outliers were having undue influence on the model and none were found to do so. The three values highlighted on the Cook's distance plot (data records 25, 45, and 52) were lower percent cover values but not extreme outliers as the maximum Cook's distance for the outliers is 0.10, well below the 1.0 value considered extreme. The most extreme value identified was further examined using a Bonferroni adjusted outlier test which confirmed that no studentized residuals had a Bonferroni p-value that was significant, thus no outliers were of concern.

The Shapiro-Wilk test, which has a null hypothesis of a normal distribution, was used to check assumptions of data normality. The test returned a p-value of 0.24, thus the null hypothesis of a normal distribution was not rejected. The assumption of homoscedasticity was tested using the Non-Constant Variance score, which returned a p value of 0.703, thus the null hypothesis that the data was homoscedastic was not rejected. On the other hand, Levene's test of the data (using Brown and Forsyth variant which is less sensitive to departures from normality), revealed that exposure type and the interaction term did have unequal variances between the groups (see Appendix A Table S5). Furthermore, the results of the Studentized Breusch-Pagan test for homoscedasticity (Koenker, 1981) also indicated variances that were not purely homoscadastic. Nonetheless, ANOVA is fairly robust with data that is non-normal and has some degree of heteroscedasticity (Whitlock & Schluter, 2015), particularly with balanced data with sufficiently large sample sizes and a less than tenfold difference among variances, conditions met by our dataset.

Analysis (2) Beta regression of the cover proportion data using the R betareg() package

Using a frequentist ANOVA approach for data in which the dependent variable is bounded with values in the standard unit interval of 0 to 1 has some shortcomings even after logit transformation. As noted by Cribari-Neto and Zeileis in their 2010 paper, such data are typically heteroskedastic with more variation around the mean and less at either end of the unit interval, along with asymmetric distribution. The cover proportion data for the experiment, a bounded continuous variable, had both of those qualities, so we decided to further explore the data by conducting a second analysis, this time using an inference approach with a beta regression as developed by Ferrari and Cribari-Neto (2004). The betareg() package written by Cribari-Neto & Zeileis implements model fitting via a standard maximum likelihood approach with an additional precision parameter. The cover proportion data was not logit transformed for this second round of analysis (the betareg() package itself logit transforms the data as part of the computation), however values of 0 and 1 were adjusted to be within the required 0-1 range by the addition (or subtraction) of 0.025 to the data. Multiple models were fit, including using different link functions and additional regressor terms for the precision parameter, and models were then compared using a likelihood-ratio test and AIC. The results of the beta regression model with the best fit were tested using ANOVA (Type II mandated by the betareg() package) to assess if there were significant effects on percent cover from either of the treatments or the interaction thereof.

Analysis 3) Marine macroalgal and invertebrate group presence and cover proportion

We wanted to assess whether the macroalgal and marine invertebrate assemblages found on the natural rock sites after one year were significantly different in composition than those on the engineered seawall clearings. To do this we analyzed the one-year photographs of the experimental squares and mapped the cover proportion of seven algal and sessile invertebrate groups. We also generated count data for the two mobile invertebrate groups observed: herbivorous gastropods and carnivorous gastropods. The photographic analysis did not permit full species-level identification of all organisms in part because some species require microscopic examination to resolve to the species level. The species groups blended both functional traits and various levels of phylogenetic identification: brown structural macroalgae, red structural macroalgae, green ephemeral macroalgae, *Cirripedia* (barnacles), ascidians, bryozoans, hydroids, and two groups of gastropods: herbivores and carnivores. We generated comparative data for the species groups from 2016 start of the experiment through analysis of photo plots adjacent to the scraped plots at the time the plots were cleared.

The primary interest was in comparing the presence of locally occurring structural macroalgal species (e.g., *fucoids*, *Laminara spp*., *Ascophyllum nodosum*, *Chondrus crispus*, and *Mastocarpus stellatus*), which are perennial and provide habitat for other species, with that of the ephemeral green macroalgaes, such as *Ulva spp*., which are often speedy colonizers of cleared substrate but which do not provide lasting year-round habitat. Another group of particular interest was the acorn barnacles (*Cirripedia* phylogenic group), i.e., local species *Semibalanus balanoides*, as barnacles can be be both a pioneer species on bare intertidal substrate and a creator of habitat. Barnacles often provide a foundation for the settlement and growth of other intertidal organisms, such as *Ascophyllum nodosum* (Kordas & Dudgeon, 2009). The bryozoan category contained a single species, the habitat-forming (erect, branching) bryozoan *Eucratea loricata* which is common to the region. The hydroid category also contained a single common species, *Dynamena pumila*. The ascidian group was of interest as many of the most common ascidians in coastal Massachusetts are non-indigenous species that can have negative impacts on intertidal and subtidal communities. Researchers on both sides of the Atlantic have found that human-made substrates may support the establishment and spread of such non-native species (Airoldi et al., 2015, Tyrrell & Byers, 2007). Mobile invertebrates were represented by two gastropod groups, herbivorous (e.g., *Littorina littorea* and *Crepidula fornicata*) and carnivorous (*Nucella lapillus* and *Mitrella lunata*). Polychaetes (specifically, *Spirorbus sp.*) were present in a single experimental square and thus were not included as a grouping. As noted earlier, crustose algal species, such as *Hildenbrandia rubra*, were also excluded.

The statistical language R was used to generate summary statistics and data visualizations for both the area covered by species groups and the number of squares in which each of the species groups were found. A multivariate regression model was created using the logit-transformed percent cover of each of the seven macroalgal and sessile invertebrate groups as response (dependent) variables with fixed factors of substrate type and exposure type along with an interaction term of substrate|exposure and site as a blocking term. The model results were assessed using univariate ANOVA tests to determine whether significant differences existed in the percent cover of each of the different species groups on the two substrate types, natural rock and seawall, and on the two wave exposure regimes, protected and exposed. Each sessile species group included sixty observations with balanced data, less than tenfold difference among variances, and no extreme outliers, thus conforming to ANOVA assumptions. The mobile invertebrate groups of herbivorous and carnivorous gastropods were analyzed separately as count data (number of individuals per cleared square). We fit a multiple generalized linear models (GLM) using different distributions (Poisson, quasi-Poisson, zero-inflated Poisson, negative binomial, zero-inflated negative binomial, and hurdle) which were then compared using log-likelihood, AIC and other tests. Results from the model with the best fit – negative binomial - were then used with ANOVA (Type I) to assess the gastropod count data for significant differences across substrate type and wave exposure as fixed factors using an alpha of 0.05.

CHAPTER 3

RESULTS

One year after the 60 intertidal experimental squares had been cleared of all visible macroalgae and invertebrates, marine life had returned to all of them, in some cases almost obliterating any sign of the year-earlier disturbance. The variation in the resettlement distribution over the 60 experimental squares can be seen in the histograms in Figure 4 below.

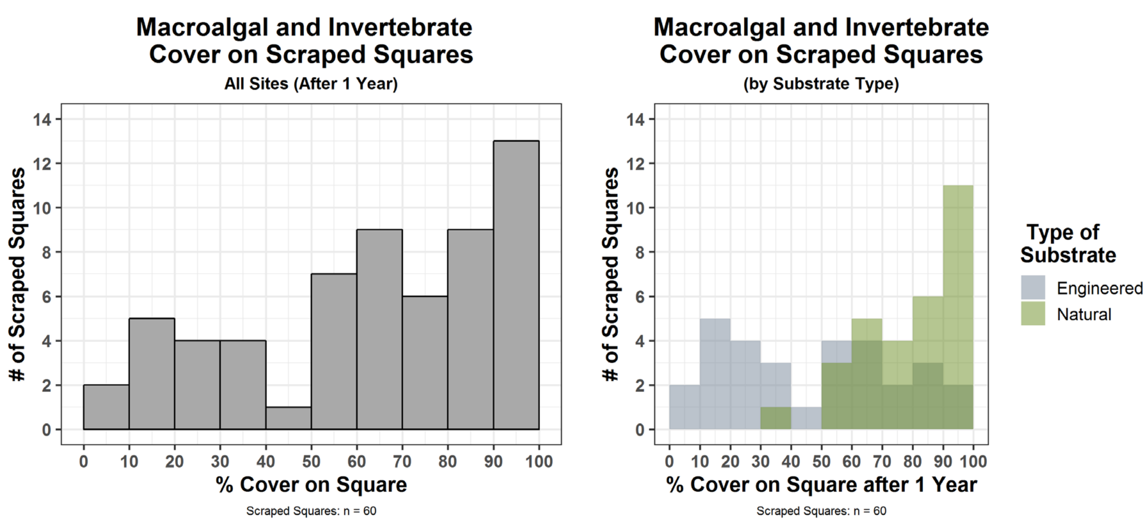


Figure 4: Histograms of % Cover on Experimental Squares.
a) showing all 60 sqares and b) square coverage by substrate type

The proportion of re-growth and colonization of marine macroalgae and sessile invertebrates ranged widely, from one plot that had only 7% cover after a year's time to five plots that were completely covered. The one-year cover proportion on the two different substrate types — engineered granite seawall and natural granite rock shoreline — (Figure 4b) is clearly left-skewed for the natural sites indicating a higher proportion of cover. Preliminary statistical analysis of the data bears out this appareant higher rate of re-colonization on the natural rock compared to that on the engineered seawalls. The mean percent cover for the 60 sites was 63.95% ± 3.71 with SD of 28.7. Engineered seawall scraped sites had mean cover of 47.17% ± 5.13 and SD of 28.11. By comparison, the subset of the observations with the smallest range in percent cover was that of scraped areas on natural granite shores which had the highest mean percent cover of 80.73% ± 3.19 after one year, the highest median cover (86% compared to 69% for all), the lowest SD of 17.5, and the least amount of sample variance (305.1 compared to 824.8 for all observations). One year later, the scraped squares on the natural granite shores had an average of 72% more cover by macroalgae and marine invertebrate species than did the squares on the granite seawalls. Summary descriptive statistics for the whole data set are provided in Table 2, with the complete set of descriptive statistics in Appendix A Table S4.

Table 2. Summary statistics for disturbance experiment: percent cover after one year

(See Appendix A Table S4 for additional descriptive statistics)

	All Plots	Engineered	Natural	Exposed	Protected
Number of Observations	60	30	30	30	30
Min (% cover)	7.00	7.00	34.00	7.00	16.00
Max (% cover)	100.00	94.00	100.00	100.00	87.00
Median (% cover)	68.50	48.00	86.00	88.50	59.00
Mean (% cover)	63.95	47.17	80.73	72.43	55.47
Std Error of the Mean	3.71	5.13	3.19	5.69	4.31
Sample Std Dev. (% cover)	28.72	28.11	17.47	31.16	23.63
95% Conf. Interval lower (% cover)	56.53	36.90	74.36	61.06	46.84
95% Conf. Interval upper (% cover)	71.37	57.43	87.11	83.81	64.10
		no CI overlap and 95% CI does not include the sample mean of the other		CI has overlap but neither includes the sample mean of the other	

The box plot in Figure 5 illustrates the difference in the cover proportion between the experimental clearings on natural granite outcroppings and the plots located on the cut granite seawalls. Note that in this boxplot based on substrate type, the 95% confidence interval upper and lower bounds have no overlap between the treatment categories, natural and engineered.

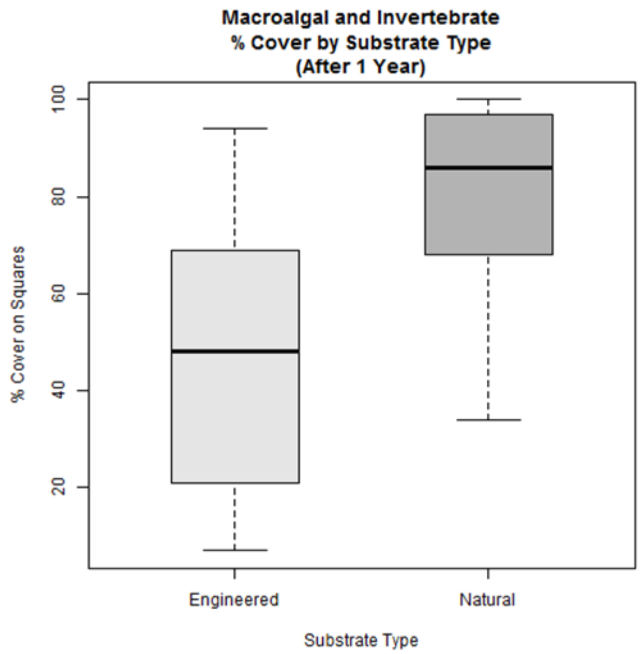


Figure 5: Box plot of % cover by substrate type.

This visualization lends support to rejecting the null hypothesis of equal means (and thus no significant difference) in the percent cover after one year between the two treatments.

Interestingly, after one year the scraped squares that were facing the open ocean (exposed) and thus subject to higher wave energies also had a higher mean cover proportion than did those that were located on the more wave-protected areas (mean 72.4% ± 5.69

exposed, 55.5% ± 4.31 protected). The difference between the means of the two levels of this factor in the experiment was smaller, however, with a greater range in the response among the exposed sites and a higher sample standard deviation (31.2 exposed, 23.6 protected), as shown in Table 2 and Appendix B Figure S2. The cross-tabulation summary statistics in Table 3 below shows that the higher mean level of re-colonization on the natural rock sites, as measured by the percent cover after one year, extended across both wave-exposed and wave-protected sites.

Table 3. Cross-factor statistics for percent cover after one year

Factor	**Exposure Type**									
	Level	Exposed			Protected					
	n= 15 for all levels	Mean	SE Mean	Std. Dev.	Mean	SE Mean	Std. Dev	Mean	SE Mean	Std. Dev.
Substrate Type	Engineered	55.47	8.73	33.81	38.87	4.8	18.6	47.17	5.13	28.11
	Natural	89.4	4.09	15.83	72.07	3.83	14.85	80.73	3.19	17.47
		72.43	5.69	31.16	55.47	4.31	23.63			

Although three separate sites around Cape Ann in Massachusetts were used for the study, site itself was not planned as an experimental factor in the study. The cover proportion means did not differ significantly among the three sites (Appendix A Table S4) but site was included as a blocking factor in the final statistical models.

Additional boxplots of the percent cover data by exposure type, site, and for the full data set may be found in Appendix B, Figure S2.

Analysis Results (1) ANOVA of cover proportion data with two-way independent factorial design

Statistical comparison of several fitted models of the cover proportion data supported using substrate and exposure as main effects, site as a blocking factor, and an interaction term. The interaction term provided an initial test for any interaction effects between substrate type and wave exposure (Equation 1).

$$Y = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \varepsilon$$

where Y = decile coverage percent, X_1 = substrate type, X_2 = wave exposure and X_3 = site.

Equation 1

The results of the linear model (Appendix A Table S5) indicated no significant interaction effect was present between substrate type and wave exposure. The absence of a significant interaction effect was confirmed by the visual interaction plot in Figure 6.

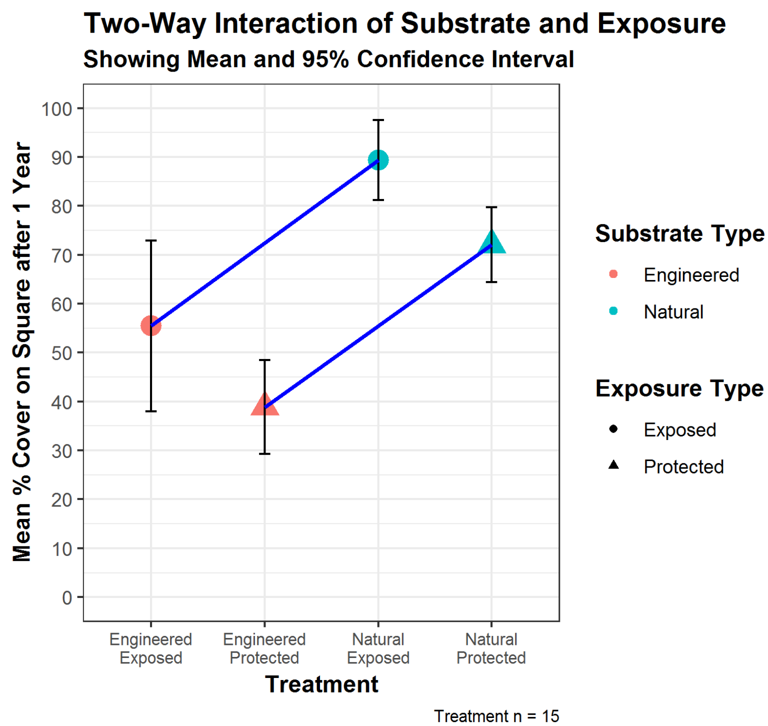


Figure 6. Visual interaction plot of substrate type and exposure type

Simpler models are generally preferable; however, omitting the interaction term from the model would mean losing some data because, while the interaction effect was not significant, some effect existed. Likewise, while site as a factor was not significant, it was included as a blocking factor in the model.

A two-way ANOVA was used as an omnibus test to assess the main effects of substrate and exposure on the mean proportion of macroalgal and sessile invertebrate cover on the scraped squares after one year. The ANOVA results (Table 4) confirmed that substrate type ($F(5, 54) = 36.961$, $p < .001$) and exposure type ($F(5,54) = 13.904$, $p < .001$) both had significant effects on the cover proportion of the squares after one year, while site ($F(5, 54) = 0.324$, $p = .724$) and the interaction term of substrate:exposure did not have a significant effect ($F(5,54) = 1.672$, $p = .202$). The study also had sufficient power (using the convention of a 0.80 threshold with $\beta = 0.20$) to detect significant effects for substrate type and wave exposure.

Welch's T-Test was computed for each of the two factors (see Appendix A Table S7), further confirming that the factors substrate type and wave exposure had a significant effect. The effect sizes, (*eta* squared and Cohen's *f* — there is ongoing debate as to which is better suited to a two-way balanced ANOVA, see Breaugh 2003, Maher et al., 2013) calculated in Table 4 confirm that substrate type had a large effect size with wave exposure having a medium-size effect on the cover proportion at one year.

Table 4. Analysis of variance table fixed-effects ANOVA using logit-transformed cover proportion as the response variable

Term	df	Sum sqrs	Mean sqrs	*F* statistic	*p*. value	*Eta* sqr η^2	Cohen's *f*	Power
Substrate Type	1	51.295	51.295	36.961	1.27e-07	0.345	0.827	1.0
Exposure Type	1	19.297	19.297	13.904	0.000463	0.130	0.507	0.962
Site	2	0.900	0.450	0.324	0.7244552	0.006	0.110	0.102
Interaction	1	2.320	2.320	1.672	0.2015076	0.016	0.176	0.253
Residuals	54	74.943	1.388					

Analysis Results (2) Beta regression of the cover proportion data using the R betareg() package

As noted earlier, an ANOVA in which the dependent variable is bounded with values in the standard unit interval (0 to 1) has some statistical shortcomings (Cribari-Neto & Zeileis, 2010) even after logit transformation, namely, the cover proportion data was typical in being heteroskedastic with more variation around the mean and less at either end of the unit interval, along with asymmetric distribution. To address this potential issue, a second analysis of the cover proportion data was completed using a beta regression model (Ferrari & Cribari-Neto, 2004), which uses maximum likelihood to fit the variate mean plus a second precision parameter.

The beta regression model providing the best fit (as determined using a likelihood-ratio test and AIC to compare models) was:

$$\text{Formula} = Y \sim X_1 + X_2 + X_3 + X_1X_2 \mid Z_1 + Z_2$$

where Y = decile coverage percent,
X_1 = substrate type, X_2 = wave exposure and X_3 = site
as the set of regressors for the main Maximum Likelihood equation using the default logit link
and Z_1 = substrate and Z_2 = exposure
are an additional set of regressors for the precision equation (phi) with the default log link.
Equation 2

The full betareg model output is found in Appendix A Table S8.

The results of the model were then tested using ANOVA , confirming the results of the earlier frequentist approach, namely, that the treatment factor substrate type had a significant effect on the cover proportion of the experimental squares, that exposure type was also significant in terms of effect, and that site and the interaction term were not significant in having an effect on the percent cover on the squares after one year, as may be seen in Table 5.

Table 5. ANOVA analysis of deviance table (Type II tests) for beta regression model using cover proportion as the response variable

Term	df	*Chi* sq	*p* value
Substrate Type	1	47.383	5.838e-12
Exposure Type	1	10.640	0.0011
Site	2	0.753	0.6864
Interaction	1	1.151	0.2833
Residuals	54		

Analysis Results (3) Marine macroalgal and invertebrate group presence and cover proportion

The third statistical analysis focused on whether the underlying substrate (natural or engineered) or different wave exposures regimes (exposed and protected) had a significant effect on the presence or cover percentage of different macroalgal and marine invertebrate groups living on the experimental squares after one year. As noted earlier, organisms had been identified to the lowest taxonomic level possible under the constraints of the photography. The cover proportion results were then binned into nine groups based on functional roles combined with taxonomic grouping (see Table 6 below).

Table 6. Macroalgae and marine invertebrate groups

Species Group	**Example**
Brown macroalgae	*Ascophyllum nodosum*
Red macroalgae	*Chondrus crispus*
Green macroalgae	*Ulva spp.*
Hydroid	*Dynamena pumila*
Bryozoan	*Eucratea loricate*
Ascidian	*Botrylloides violaceu*s
Maxillopoda	*Seminbalanus balanoides*
Gastropod – herbivorous	*Littorina littorea*
Gastropod – carnivorous	*Nucella lapillus*

The species of greatest interest were those organisms that help provide habitat for other marine organisms (e.g., perennial macroalgal species such as *Ascophyllum nodosum*) and pioneer species whose presence can help promote the establishment of additional successional species (e.g., *Semibalanus balanoides*). A secondary interest was the presence of mobile invertebrates (gastropods), both herbivores and carnivores, as they can have significant top-down pressure on macroalgae and other invertebrates, respectively. Ascidians were also a focal group, as many of the most abundant intertidal ascidian species in Massachusetts are both non-indigenous and potentially damaging as invasive fouling species.

One way to assess the distribution of species groups on the experimental squares was to count each group's presence on the experimental squares after one year. The percent cover data was analyzed by species group using a simple presence/absence approach — was an organism belonging to the group had been observed at least once somewhere on the experimental square — to produce a count of how many of the 60 squares each group had successfully colonized in a year. This was not a count of individual organisms but a count of the squares on which at least one instance each of a species groups could be seen. Using this approach macroalgal groups were the most frequently found site occupiers after one year, with brown and red macroalgae present on about an equal number of experimental squares, followed closely by the green macroalgal group. Among the marine invertebrate groups, barnacles were the most commonly found followed by ascidians and bryozoans. Herbivorus gastropods were more commonly found than carnivorous gastropods, and hydroids were the least commonly found group. The details of the count of squares on which the different species groups were observed is provided in Table 7 below and in the treemap shown in Figure 7. Additonal breakdowns of the count data by wave exposure and by site are provided in Appendix A Table S9 and Table S10 and are visualized by treemaps in Appendix B Figure S3 and Figure S4.

Table 7. Presence in experimental squares by macroalgae and invertebrate groups after one year, by substrate type

Species Group	Substrate Type			
	Engineered		Natural	
	# of Sqrs. on which present (n=30)	% of Sqrs. on which present (30 = 100%)	# of Sqrs. on which present (n=30)	% of Sqrs. on which present (30 = 100%)
Brown macroalgae	25	83%	30	100%
Red macroalgae	25	83%	28	93%
Green macroalgae	28	93%	21	70%
Hydroid	1	3%	7	23%
Bryozoan	9	30%	14	47%
Acidian	11	37%	13	43%
Maxillipoda	22	73%	20	67%
Gastropod - herb.	0	0%	17	57%
Gastropod - carn.	0	0%	11	37%

The most common algal species found growing on the cleared areas one year later were pioneer/early successional ephemeral green macroalgal species, such as *Ulva lactuca*, and re-establishment of turf or structural species already dominent on surrounding rock surfaces, e.g., *Chondrus crispus*, *Mastocarpus stellatus*, *Fucus distichus,* and *Ascophyllum nodosum*. Two invertebrate species also were common colonizers of the cleared space: the common rock barnacle *Semibalanus balanoides* and the bushy hydroid *Eucratea loricata*. All of these species had been observed in 2016 prior to the start of the experiment as being present and part of the common intertidal species community of the Cape Ann region. The one notable result from this presence/absence count analysis was the complete absence of gastropods, either herbaceous or carnivorous, from any of the engineered seawall experimental squares.

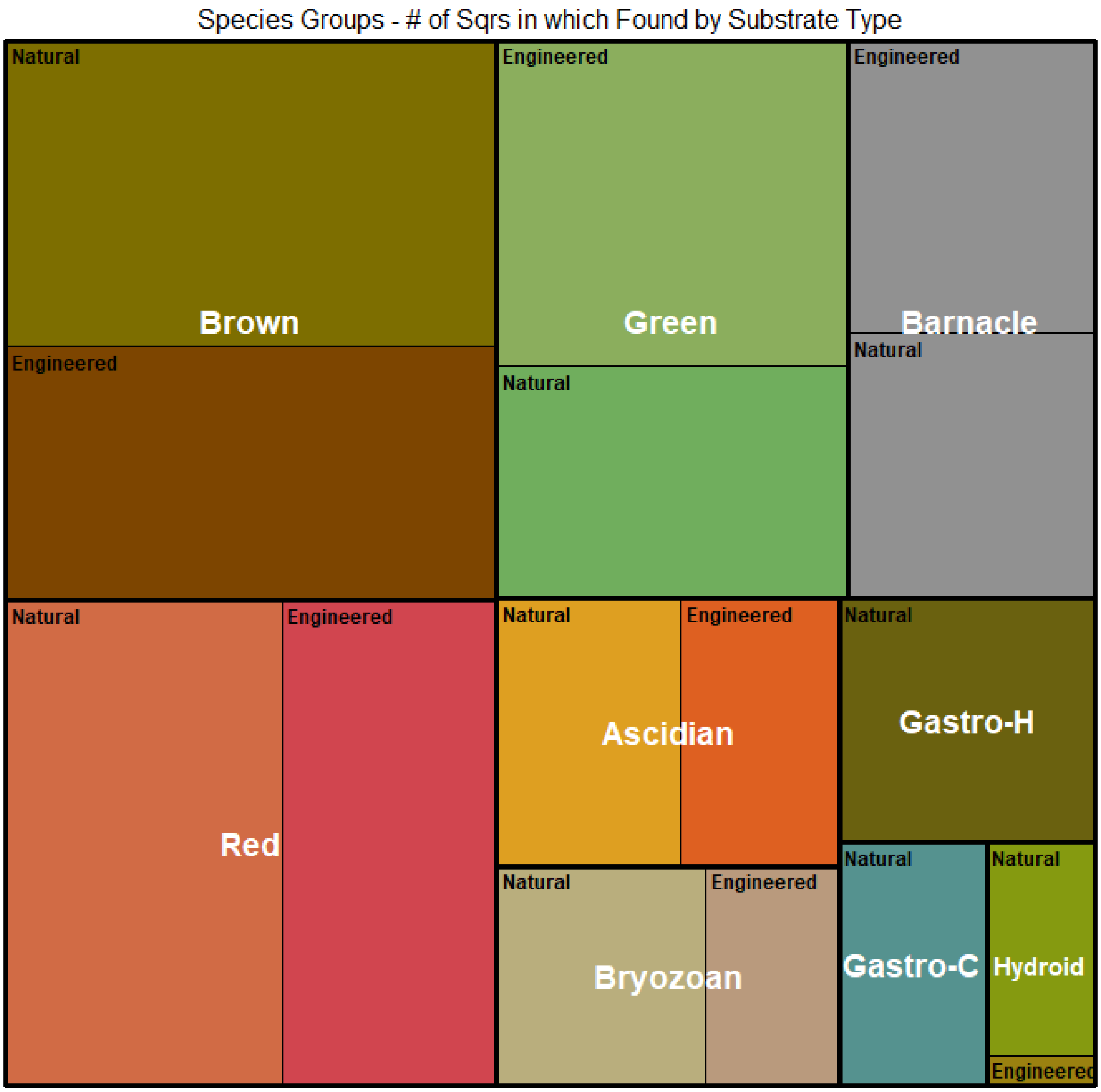


Figure 7. Treemap of 2017 macroalgae and marine invertebrate groups by the number of squares in which present, subdivided by substrate type.

Note that the Gastro_H (herbivorous gastropods) and Gastro_C (carnivorous gastropods) groups were only found on natural substrate, thus there is no subdivision for those two groups.

The second part of the species group analysis focused on the amount of physical space occupied by each of the macroalgal and sessile invertebrate groups after one year. Mobile invertebrates were not included in the spatial assessments, as they do not "cover" (take up) fixed living space on a marine surface the way that macroalgae or sessile invertebrates do. As had been observed at the sites prior to the beginning of the experiment in 2016, macroalgal groups covered the greatest amount of physical space on the experimental squares (54%) with sessile marine invertebrate groups covering 11% of the space. The remaining surface space (35% of the total 13,500 cm^2 study area, i.e., 60 squares of 225 cm^2) was either open space or covered by crustose algae or, in a single case, occupied by a species not included in one the seven groups. Determination of the actual amount of open space after one year thus cannot be accurately computed because crustose algal species, such as *Hildenbrandia rubra*, were not included in assessing cover proportion and one marine species (the *Spirorbus sp.* found on a single square) was not included in the groupings. The differences among the groups in mean percent cover after one year is visualized as boxplots in Figure 8.

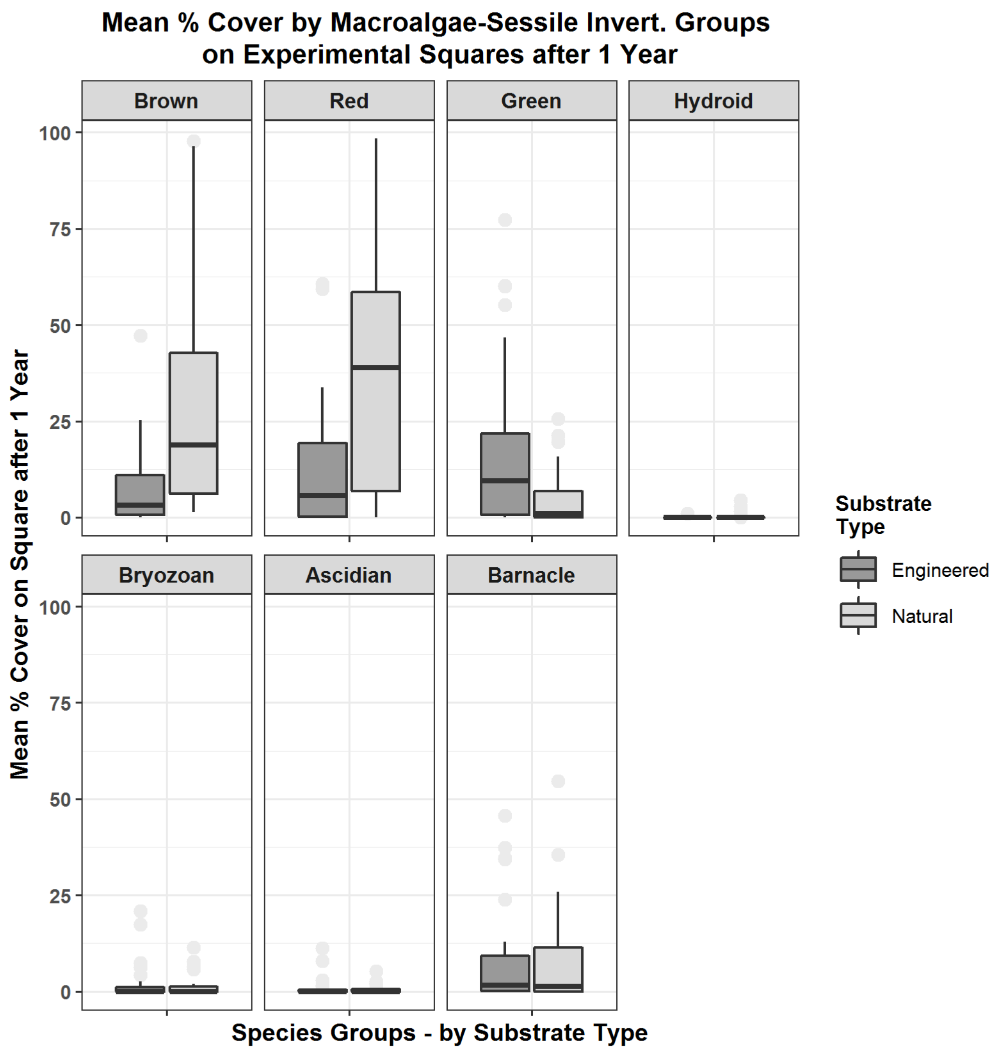


Figure 8. Macroalgae and marine sessile invertebrate groups percent cover of cleared squares after one year by substrate type

Looking only at the 65% proportion of the experimental squares that was covered at the end of one year, red macroalgae emerges as the dominant space-occupying group (38% of covered area), followed by the brown macroalgae (29% of covered area) and then the green macroalgae (17% of covered area). Barnacles occupied the greatest amount of space among the sessile marine invertebrates (12% of covered area), followed by the bryozoans (3% of covered area), the ascidians (1 % of covered area), and lastly the hydroid group which occupied the least amount of area (<1% of covered area).

The treemap in Figure 9 illustrates the covered portion of the experimental area (the 65% covered area in 2017 at the conclusion of the experiment) divided up by the seven macroalgal and sessile invertebrate groups, with each species group further subdivided by percent cover found on each of the two substrate types, engineered seawall and natural shore. What is notable from the treemap visualization is that, among the three macroalgal groups, red and brown macroalgae species dominated re-colonization of squares on the natural rock shore sites while green species dominated the regrowth on squares located on the seawall sites. The barnacle re-colonization was notable for being almost exactly equal in distribution between the natural substrate and the engineered substrate. The treemap in Figure 10 uses the same percent cover data but visualizes the species groups subdivided by exposure type, wave-exposed and wave-protected. The differences among the groups in mean percent cover after one year is visualized as boxplots in Appendix B Figure S6.

Additional summary breakdowns of the covered area after one year in terms of the percent of the space occupied by the seven macroalgal and sessile invertebrate groups are shown in Appendix A Tables S11-S13.

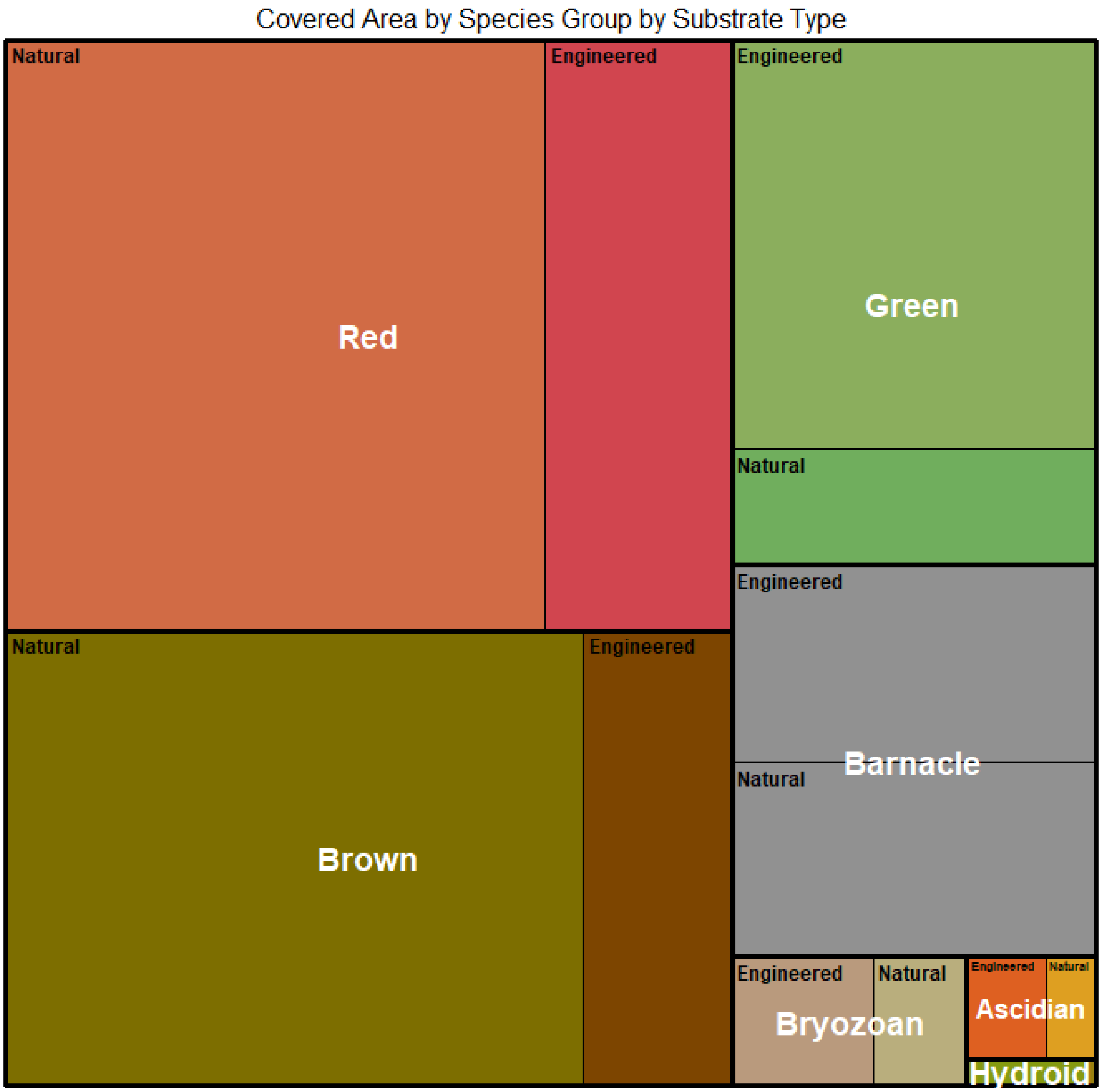


Figure 9. Treemap of 2017 macroalgae and marine invertebrate groups sized by the percentage of total experimental square area covered, subdivided by substrate type.

Note that the Gastro_H (herbivorous gastropods) and Gastro_C (carnivorous gastropods) groups are not included in the percent cover calculations as mobile species do not occupy space in the same sense as macroalgae and sessile invertebrates.

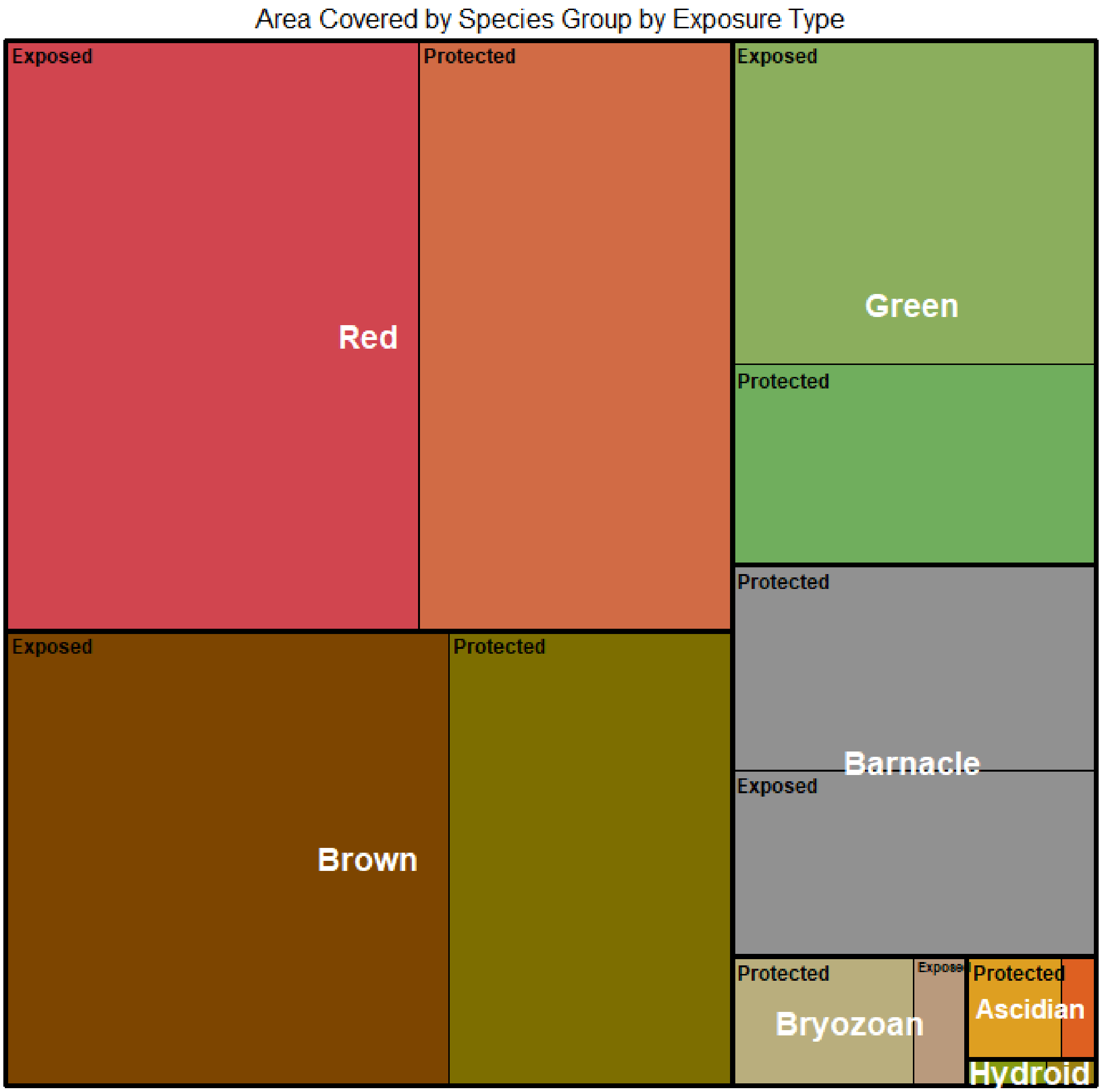


Figure 10. Treemap of 2017 macroalgae and marine invertebrate groups sized by coverage area, subdivided by exposure type.

Note that the Gastro_H (herbivorous gastropods) and Gastro_C (carnivorous gastropods) groups are not included in the percent cover calculations as mobile species do not occupy space in the same sense as macroalgae and sessile invertebrates.

To determine whether the observed differences among the amount of area re-colonized by the different species groups were significant in terms of either of the study's two experimental factors, substrate type and exposure type, regression analysis was used and univariate ANOVA tests run on the model results. The results of the regression analysis confirmed that substrate had a significant effect on each of the three of the macroalgal groups but not on any of the sessile invertebrates. Exposure was significant for the bryozoan group but for none of the other sessile invertebrate or macroalgal groups. Although site as a blocking factor was not significant overall, it was significant for the three macroalgal groups as is visualized in the treemap in Appendix B Figure S5. Lane Cove is dominated by the brown algal species while Pigeon Cove is dominated by green algal species. The full set of ANOVA results for the 2017 species data and the accompanying tests for effect sizes and power are gathered in Table 8 below. The same ANOVA analysis was also run on the assembled 2016 data, the results of which are in Table S14 in Appendix A.

Table 8. Macroalgal and sessile invertebrate percent cover analysis 2017 MANOVA Table (univariate ANOVAs)

BROWN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	0.00348	0.00348	33.382	3.87E-07	0.246	0.786	1.000
exposure	1	0.00030	0.00030	2.832	0.09817	0.021	0.229	0.391
site	2	0.00441	0.00221	21.164	1.63E-07	0.311	0.885	1.000
substrate:exposure	1	0.00035	0.00035	3.361	0.07226	0.025	0.249	0.450
Residuals	54	0.00563	0.00010					
RED	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	0.00288	0.00288	17.217	0.0001	0.178	0.565	0.986
exposure	1	0.00029	0.00029	1.708	0.1968	0.018	0.178	0.257
site	2	0.00398	0.00199	11.891	5.26E-05	0.245	0.664	0.995
substrate:exposure	1	0.00004	0.00004	0.269	0.6064	0.003	0.071	0.081
Residuals	54	0.00903	0.00017					
GREEN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	0.00110	0.00110	11.545	0.0013	0.116	0.462	0.925
exposure	1	0.00003	0.00003	0.315	0.5769	0.003	0.076	0.087
site	2	0.00307	0.00154	16.083	3.32E-06	0.324	0.772	1.000
substrate:exposure	1	0.00011	0.00011	1.104	0.2980	0.011	0.143	0.183
Residuals	54	0.00516	0.00010					
HYDROID	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	1.10E-05	1.10E-05	3.128	0.0826	0.054	0.241	0.424
exposure	1	2.08E-06	2.08E-06	0.593	0.4446	0.010	0.105	0.120
site	2	3.38E-07	1.69E-07	0.048	0.9529	0.002	0.042	0.057
substrate:exposure	1	4.17E-07	4.17E-07	0.119	0.7312	0.002	0.047	0.064
Residuals	54	1.89E-04	3.50E-06					
BRYOZOAN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	1.73E-06	1.73E-06	0.057	0.8124	0.001	0.032	0.057
exposure	1	0.00016	0.00016	5.203	0.0265	0.079	0.31	0.626
site	2	0.00015	0.00007	2.447	0.0961	0.074	0.301	0.494
substrate:exposure	1	0.00006	0.00006	2.086	0.1545	0.031	0.197	0.303
Residuals	54	0.00164	0.00003					
ASCIDIAN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	1.73E-06	1.73E-06	0.130	0.7201	0.002	0.049	0.065
exposure	1	1.81E-05	1.81E-05	1.355	0.2495	0.023	0.158	0.214
site	2	3.71E-05	1.85E-05	1.392	0.2574	0.048	0.227	0.300
substrate:exposure	1	1.10E-07	1.11E-07	0.008	0.9277	0.000	0.012	0.051
Residuals	54	7.20E-04	1.33E-05					
BARNACLE	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**	***Eta* sqr η2**	**Cohen's *f***	**Power**
substrate	1	3.00E-07	2.50E-07	0.002	0.9651	0.000	0.006	0.050
exposure	1	0.00011	0.00011	0.844	0.3622	0.015	0.125	0.151
site	2	0.00026	0.00013	1.010	0.3710	0.036	0.193	0.227
substrate:exposure	1	1.20E-06	1.23E-06	0.010	0.9226	0.000	0.013	0.051
Residuals	54	0.00699	0.00013					

The two gastropod groups were analyzed separately from the other species groups as individual count data (separate from the earlier count of number of squares in which gastropods were present), since mobile species do not occupy area on a substrate as do algal species or sessile invertebrates. The results of the negative binomial model confirmed that substrate as a factor was significant for both the herbivorous and carnivorous gastropods – not a surprise, since zero gastropods were found on the engineered seawalls. The model results were not significant for exposure type for either gastropod group but were significant for site for the carnivorous gastropod group. The results for both gastropod groups are shown in Table 9 below.

Table 9. Analysis of Deviance Tables for Gastropod Groups

HERBIVOROUS	**Df**	**Deviance**	**Residual Deviance**	**Pr(>Chi)**
			77.045	
substrate	1	42.783	34.261	6.12E-11
exposure	1	0.305	33.957	0.5809
site	2	4.340	29.617	0.1142
substrate_type:exposure_type	1	0.000	29.617	0.9997
CARNIVOROUS	**Df**	**Deviance**	**Residual Deviance**	**Pr(>Chi)**
			56.816	
substrate	1	22.110	34.706	2.575E-06
exposure	1	1.002	33.7044	0.3169
site	2	6.302	27.402	0.0428
substrate_type:exposure_type	1	0.000	27.402	0.9998

CHAPTER 4

DISCUSSION

The results of this research suggest that marine intertidal communities on natural rock walls recover more robustly from disturbance events, filling cleared areas with space-occupying organisms at a faster rate and favoring brown and red structural macroalgal species over green ephemeral ones. The overall differences in the disturbance recovery process likely stem from multiple drivers, including abiotic influences, such as substrate texture and adjacent surface regularity, and biotic factors, primarily the absence of gastropods on the human-engineered seawalls.

One year after the scraping disturbance, green macroalgal species, such as *Ulva lactuca* and *Ulva intestinalis,* known early colonizers, domintated the seawall experimental squares both in the number of squares in which they were present and in greater overall cover proportion. The green algal dominance on the seawall squares likely was driven primarily by the complete absence of herbivorous gastropods on the seawall experimental plots, specifically the locally common and abundant *Littorina* spp. Earlier studies based in Massachusetts and Maine established the preference of Littrorina spp. snails to smaller and more tender ephemeral species such as *Ulva* and *Porphyra* over tougher perennial species such as *Chondrus crispus* (Lubchenco,1978; Lubchenco, 1983, Lubchenco & Menge, 1978). Multiple studies have also shown that *Littorina* spp. plays an important role in intertidal community development and stability by reducing the presence and growth of ephemeral green species to the benefit of perennial macroalgaes such as *Chondrus cripus* (Aquilino & Stachowicz, 2012; Lubchenco & Menge,1978). The 27-month study by Aquilino and Stachowicz showed that cleared experimental patches with herbivores present had cover by ephemeral species (primarily *Ulva* spp. and diatoms) that were an order of magnitude lower than on patches where herbivores were excluded and had recovery by perennial species that were 1.5 times faster. The finding of increased perennial macroalgal density was not dependent on the surrounding species richness although experimental patches within polycultures did have faster perennial algal recovery. Thus the dominance of green macroalgal species on the engineered seawalls may reflect in part a slower progression in intertidal community recovery, with the natural shoreline squares progressing more quickly to later successional community structures while the seawall scraped sites remained dominated by assemblages of pioneer and early succession species due to the absence of herbivorous snails.

The higher proportion of covered surface on wave-exposed, ocean-facing experimental squares is notable but not surprising, as water flow is a key factor for intertidal and nearshore species, impacting larval transport, gas exchange, nutrient availability, and waste removal. The ocean-facing and the wave-protected sites were in close proximity, but the increased volume of water flowing on the wave-exposed sides would bring an increased number of propagules in proximity to the cleared squares there. Once attached, the increased water flow would aid in gas exchange, along with increasing the availability of suspended food particles and nutrients for both filter feeders (e.g., barnacles, hydroids) and macroalgaes.

Although the experiment deliberately compared sites of vertical natural granite with seawalls made of the same local granite, exposed rock often has orientations along multiple planes, with cracks and crevices in various orientations due to folding and twisting of the rock layer and more recent glacial scouring. Such natural small-scale variation has long been noted as a factor in rocky intertidal habitat (*sensu* Connell, 1972). Rock CPSs, however, are constructed from stones of similar size, shape, and texture, often with one or more straight cut edges due to their quarried origins. The seawalls used in the study used rectangular granite blocks that, although not nearly as homogenous in texture and roughness as the poured concrete used in many seawalls, nonetheless had less variation and more regular planes than the adjacent natural rock shores. While the clearings on the natural rock were only on vertical surfaces, the surrounding rock outcroppings had varied orientations and irregularities that may serve as important *refugia* for marine organisms. Increased surface homogeneity affects both settlement patterns and settlement success by planktonic larvae and algal propagules (Perkol-Finkel et al., 2012). Given the interplay with surface roughness, homogeneity, and current flow at low Reynolds numbers, the difference in surface texture has the potential to significantly affect colonization of hard substrate in the marine environment.

Coastal protection structures often change the distribution of habitat along the depth gradient, most often by introducing more steeply sloped gradients and reducing the extent of transition zones (Morley et al., 2012). The sides of the seawalls used in the experiment generally had a straight vertical plane with no slope. The Eastern Point seawall did use a ziggurat-style construction on the wave-protected side, but the experimental plots on that side were located below the first inset level. The natural rock walls, by comparison, were adjacent to rock platforms and areas with more gently sloping intertidal zones.

Beyond successful initial settlement, marine organisms have other needs if they are to survive on hard substrates. Organisms must have sufficient shelter from abiotic threats, such as being swept away by waves or currents or drying out from sun and air exposure during periods of emersion at low tide. Shelter is also needed against the biotic threats of predation and herbivory. Prior studies have linked differences between marine communities on CPS and those on natural rock to a lack of water-retaining and shaded *refugia* on the CPS (Aguilera et al., 2014; Firth et al., 2014). In this study however, that was not an obvious difference between the natural rock sites and the constructed seawalls in terms of availability such *refugia*. All three granite walls offered ample shaded, damp areas between the granite blocks. Observations made in 2016 before the start of the experiment documented use of the between block crevices by multiple species of marine invertebrates and as anchor points for macroalgae species. Furthermore, because the blocks were of varying size and were not precision-cut, there were often considerable gaps between blocks such that the seawalls were porous in places, permitting water to flow through the seawall daily at times of maximum tidal current.

The lower rate of recolonization on the engineered seawalls might reflect less diversity and abundance within the seawall communities to begin with. Certainly there are a number of marine invertebrate species which do not travel far from their source during their brief planktonic stage (Vance 1973). If the community within which the experimental clearings were made was rather depauperate, that would limit the source of new colonizers for the cleared areas. On the other hand, all of the engineered sites were in close proximity to natural rock shores which presumably would also be a source of macroalgal and invertebrate settlers. While pre-experiment observations in 2016 indicated comparable communities of common intertidal species across all sites, both engineered and natural, a more formal assessment of the undisturbed intertidal communities living on both the engineered and the natural rock sites would help clarify this issue.

Given the ongoing addition of human-engineered hard substrate over ever greater expanses of coastline, this experiment adds to concerns over potential long-term and regional impacts on marine ecosystems (Becchi et al. 2014; Dugan et al., 2008; Kohn and Blahm, 2005; Rolet et al., 2015; Vaselli et al., 2008). Based on the results from the three sets of seawall clearings, one concern would be that the assemblages on CPS may be less resilient those on natural rocky shores. While the experiment did not include an in-depth assessment of biodiversity, the complete lack of gastropods on any of the seawall squares suggests the possibility of a less biodiverse community there. Biological diversity has been shown to be a key element in an ecosystem's ability to function as a complex adaptive system (Folke, 2006; Levin, 2005) by absorbing disturbances and being able to reorganize and regenerate following a disturbance. This reduction of system volatility and dampening of the effects of perturbations makes ecosystems more effective and dependable in being able to supply vital ecosystem functions, including ecosystem services valued by humans (Stachowicz, et al., 2007). Biodiversity allows the maintenance of a highly diverse set of functional traits, which in turn is key to ecosystem health and productivity (Hillebrand and Mathiessen, 2009, Wardle, et al. 2000). Thus, changes in the composition, abundance, and productivity of the intertidal and shallow water communities over time due to CPS could have large impacts on coastal marine biodiversity and ecosystem functioning.

While the current study established that intertidal community response to disturbance differs significantly between human-engineered and natural rock walls, and between wave-exposed and wave-protected walls, it is not clear, given the one-year timescale of the study, how long such differences in cover proportion and presence/proportion of specific groups would persist. A better understanding of the temporal scope of the differences would aid in assessing broader ecosystem impacts.

In our experiment we assessed the marine biological response at only the most basic level, cover proportion after clearing and a general identification of organisms based on groupings of interest. Follow-up studies with more detailed biological assessment would help identify the drivers of differences between communities on human-engineered and natural rock shore and would provide needed detail on aspects of the intertidal assemblages not touched upon in this experiment. More detailed investigation of abiotic factors is also needed to resolve which are primary in altering the community response across the two substrate types and across the two wave regimes.

This investigation has provided useful information supporting the broader challenge of understanding the biological processes driving the establishment and succession of marine intertidal communities on artificially constructed hard substrate. The impending global rise in sea levels will necessitate the building of many more coastal protection structures.

Understanding the factors which affect the development of marine communities on such structures will aid us in designing structures that not only produce the desired coastal engineering results but also support the growth of diverse, healthy, productive marine communities.

APPENDIX A

SUPPLEMENTARY TABLES

Table S1. Common types of coastal protection structures in Massachusetts

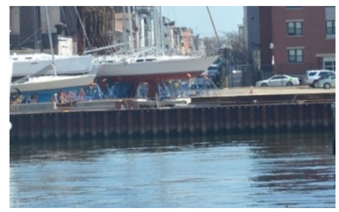
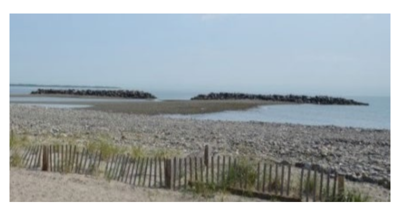
Coastal Protection Structure	Description	Example
Seawall	Concrete, concrete or stone block construction, may extend from below the low water mark to significantly above the high water mark, may be parallel to shore or extend into the coastal water. Used to prevent flooding and protect against waves.	
Bulkhead	Vertical wall directly at the water's edge, often made of steel but also concrete or treated timbers. Used to protect shoreline and allow for direct boat docking.	
Revetment	Stone rip rap or cut blocks covering a sloping shore, typically from above the high water line to below the low water mark. Used to prevent shore erosion.	
Jetty	Longer and often higher than a groin, may be made of stone or concrete blocks or solid concrete, perpendicular to shore. Used for creating protected harbor areas, stabilizing channels and river mouths, and protecting shores.	 Photo: North Jetty, Plum Island, Newburyport MA, US Army Corps of Engineers
Groin	Short, typically stone rip rap construction, perpendicular to shore. Used to change sediment transport along sandy shores.	
Breakwater	Stone rip rap, stone or concrete block construction, positioned a short distance off-shore, parallel to the shore. Used for wave attenuation and sediment transport alteration.	

Table S2. Locational details for all 12 experimental transects.

Site Details

Town	Site	Type	Exposure	Latitude	Longitude	Orientation
Gloucester	Eastern Point	Seawall	Exposed	42°34'49.8"N	70°39'55.5"W	SW
Gloucester	Eastern Point	Seawall	Protected	42°34'50.0"N	70°39'55.4"W	NE
Gloucester	Eastern Point	Rock Shore	Exposed	42°34'48.0"N	70°39'53.4"W	WSW
Gloucester	Eastern Point	Rock Shore	Protected	42°34'48.3"N	70°39'53.4"W	ENE
Gloucester	Lane Cove	Seawall	Exposed	42°40'49.0"N	70°39'35.0"W	NNW
Gloucester	Lane Cove	Seawall	Protected	42°40'48.6"N	70°39'35.0"W	SSE
Gloucester	Lane Cove	Rock Shore	Exposed	42°40'44.7"N	70°39'39.0"W	NNW
Gloucester	Lane Cove	Rock Shore	Protected	42°40'44.7"N	70°39'39.0"W	SSE
Rockport	Pigeon Cove	Seawall	Exposed	42°40'35.0"N	70°37'19.3"W	SE
Rockport	Pigeon Cove	Seawall	Protected	42°40'35.2"N	70°37'19.4"W	NW
Rockport	Pigeon Cove	Rock Shore	Exposed	42°40'35.1"N	70°37'18.5"W	SSE
Rockport	Pigeon Cove	Rock Shore	Protected	42°40'34.9"N	70°37'17.9"W	NW

Table S3. Pre-Scrape Observed Species by Site, Substrate Type and Exposure

As observed in 2016 prior to the beginning of the experiment

2016 Pre-Scrape Species Observations				
Eastern Point		**Macroalgal Species**	**Sessile Invertebrate Species**	**Mobile Invertebrate Species**
Engineered	Exposed	Fucus distichus, Ascophyllum nodosum, Chondrus crispus, Lithothamnion spp., Hildenbrandia rubra, Ulva spp.	Botrylloides violaceus, Semibalanus balanoides	Carcinus maenus
	Protected	Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Ulva spp., Lithothamnion spp., Hildenbrandia rubra	Dynamena pumila, Eucratea loricata, Semibalanus balanoides, Diadumene lineata, Metridium senile	Carcinus maenus
Natural	Exposed	Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Corallina officianalis, Ulva spp.	Semibalanus balanoides	Littorina spp., Nucella lapillus, Mitrella lunata
	Protected	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Ulva spp.	Semibalanus balanoides	Nucella lapillus, , Cancer irroratus
Lane Cove		**Macroalgal Species**	**Sessile Invertebrate Species**	**Mobile Invertebrate Species**
Engineered	Exposed	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Ulva spp.	Semibalanus balanoides, Diadumene lineata, Metridium senile	
	Protected	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Lithothamnion spp., Hildenbrandia rubra, Ulva spp.	Dynamena pumila, Eucratea loricata, Botrylloides violaceus, Didemnum vexilum, Semibalanus balanoides, Diadumene lineata, Metridium senile	Littorina spp.
Natural	Exposed	Fucus distichus, Ascophyllum nodosum, Chondrus crispus, Lithothamnion spp., Hildenbrandia rubra, Ulva spp.	Eucratea loricata, Botrylloides violaceus, Didemnum vexilus, Semibalanus balanoides	Littorina spp., Nucella lapillus
	Protected	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus	Eucratea loricata, Botrylloides violaceus, Semibalanus balanoides	
Pigeon Cove		**Macroalgal Species**	**Sessile Invertebrate Species**	**Mobile Invertebrate Species**
Engineered	Exposed	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Ulva spp.	Dynamena pumila, Euratea loricata, Botrylloides violaceus, Semibalanus balanoides	Carcinus maenus
	Protected	Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Lithothamnion spp., Ulva spp.	Eucratea loricata, Semibalanus balanoides	Carcinus maenus
Natural	Exposed	Fucus distichus, Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Hildenbrandia rubra, Corallina officianalis, Ulva spp.	Eucratea loricata, Didemnum vexilum, Semibalanus balanoides	Littorina spp.
	Protected	Ascophyllum nodosum, Polysiphonia lanosa, Chondrus crispus, Hildenbrandia rubra, Ulva spp.	Eucratea loricata, Semibalanus balanoides	

Table S4. Summary Statistics for Disturbance Experiment: Percent Cover After 1 Year

	All Plots	Engineered	Natural	Exposed	Protected	Lane Cove	Pigeon Cove	Eastern Point
Number of Observations	60	30	30	30	30	20	20	20
Min (% cover)	7.00	7.00	34.00	7.00	16.00	7.00	16.00	16.00
Max (% cover)	100.00	94.00	100.00	100.00	87.00	100.00	97.00	100.00
Range (% cover)	93.00	87.00	66.00	93.00	71.00	93.00	81.00	84.00
Median (% cover)	68.50	48.00	86.00	88.50	59.00	65.50	77.00	71.00
Mean (% cover)	63.95	47.17	80.73	72.43	55.47	59.40	67.05	65.40
Std Error of the Mean	3.71	5.13	3.19	5.69	4.31	7.22	6.02	6.16
Sample Std Dev (% cover)	28.72	28.11	17.47	31.16	23.63	32.30	26.93	27.54
Coefficient of Variation	0.45	0.60	0.22	0.43	0.43	0.54	0.40	0.42
Q1 25% (% cover)	43.75	21.25	68.50	56.00	34.50	36.25	54.75	42.75
Tukey's IQR (% cover)	44.50	46.50	27.75	40.25	40.00	46.25	33.50	45.25
Q3 75% (% cover)	88.25	67.75	96.25	96.25	74.50	82.50	88.25	88.00
Outlier lower bounds	-23.00	-48.50	26.88	-4.38	-25.50	-33.13	4.50	-25.13
Outlier upper bounds	155.00	137.50	137.88	156.63	134.50	151.88	138.50	155.88
Outliers (Tukey's boxplot rule)	0	0	0	0	0	C	C	0
95% CI lower (% cover)	56.53	36.90	74.36	61.06	46.84	44.96	55.01	53.08
95% CI upper (% cover)	71.37	57.43	87.11	83.81	64.10	73.94	79.09	77.72
Sample Variance	824.79	790.14	305.10	970.67	558.46	1043.20	725.31	758.57
Skewness	-0.52	0.21	-0.83	-1.08	-0.34	-0.36	-0.87	-0.36
Kurtosis	-0.96	-1.31	0.17	-0.16	-1.21	-1.11	-0.58	-1.21

Table S5. Percent coverage analysis linear regression model

We wanted to test whether there were any interaction effects between substrate type and wave exposure, modeled as Equation 3:

$$Y = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon$$

where Y = coverage percent, X_1 = substrate type, and X_2 = wave exposure.

Equation 3

To complete the model we also wanted to include site as a blocking factor, as shown in Equation 4:

$$Y = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \varepsilon$$

where Y = coverage percent, X_1 = substrate type, and X_2 = wave exposure and X_3 = site.

Equation 4

lm(formula = dec_cover_pct ~ (substrate_type * exposure_type) + site, data = scrape_cov)

Residuals:	Min	1Q	Median	3Q	Max
	-2. 5059	-0.7371	0.0860	0.8127	2.1141

Coefficients:	Estimate	Std. Error	t value	Pr(>|t|)	CI- Low	CI High
(Intercept)	0.8716	0.5691	1.5317	0.1314	-0.2693	2.0125
substrate_typeNatural	1.4559	0.4302	3.3846	0.0013	0.5935	2.3184
exposure_typeProtected	-1.5275	0.4302	-3.5510	0.0008	-2.3900	-0.6651
sitePigeon Cove	0.2163	0.3725	0.5807	0.5639	-0.5306	0.9632
siteEastern Point	0.2882	0.3725	0.7736	0.4426	-0.4587	1.0351
substrate:exposure	-0.7866	0.6083	-1.2930	0.2015	-2.0063	0.4331

Residual standard error: 1.178 on 54 degrees of freedom
Multiple R-squared: 0.4962, Adjusted R-squared: 0.4496
F-statistic: 10.64 on 5 and 54 DF, p-value: 3.808e-07

R-squared	Adj. R-Squared	Sigma	*F*-statistic	p.value	df
0.4962	0.4496	1.1781	10.6371	3.8078E-07	6
logLik	AIC	BIC	deviance	df.residual	
-91.8078	197.6156	212.2760	74.9430	54	

Results of linear model using:
logit-transformed decimal cover proportion as the response variable,
with substrate and exposure as explanatory factors, site as a blocking factor,
and an interaction term between substrate and exposure factors

Table S6. Additional Tests for Conformity to Assumptions of Linear Regression

Shapiro-Wilk Normality Test

A test statistic with a p-value under 0.05 means that the null hypothesis of the Shapiro-Wilk Test, that the data in the groups are normally distributed, is NOT accepted. The logit-transformed scrape data overall is normally distributed however it is left-skewed as was noted and can be seen in Figure 4.

Treatment	Statistic	p-value
All Data	0.9744	0.2382
Engineered:Exposed	0.9031	0.1060
Engineered:Protected	0.9269	0.2451
Natural:Exposed	0.8557	0.0209
Natural:Protected	0.9230	0.2139

Levene Test for Homogeneity of Variance
(HOV a.k.a homoscedasticity)
Brown and Forsyth variation using median

Levene's Test for HOV with Brown and Forsythe variation uses the group median rather than the mean and is considered more robust to data that is non-normally distributed, which the Shapiro-Wilk test and the visual historgram (Figure 4) both showed to be the case. A test statistic with a p-value under 0.05 means that the null hypothesis of the Levene Test, which is that there is equal variance among groups, is NOT accepted.

The mixed results shown in the table below (Exposure and the Interaction showing evidence of some homoscedasticity) provide evidence that the dataset is not completely normal, which is not surprising for bounded percentile data.

	Df1	Df2	F value	p-value
Substrate	1	58	0.2262	0.6360
Exposure	1	58	6.8134	0.0115
Site	2	57	0.8635	0.4271
Interaction: Substrate/Exposure	3	56	5.404	0.0023

Table S6. Tests for data normality of decile percent cover data (cont'd)

Studentized Breusch-Pagan Test for Homoscedasticity

The Breusch-Pagan test fits a linear regression model to the residuals of a linear regression model (by default the same explanatory variables are taken as in the main regression model) and rejects if too much of the variance is explained by the additional explanatory variables. The test uses a null hypothesis that the variance of the residuals is constant, thus rejecting the null hypothesis due to a result with a p-value less than the significance level of 0.05 infers that heteroscedasticity is indeed present, as is strongly the case here. The heteroscedasticity of the residuals is one the reasons to use beta regression rather than linear regression for this type of bounded percentile data.

Data: subexpsite_lm_interact (name of the model being tested)

Breusch-Pagan test statistic: 20.896 degrees of freedom: 5 p-value: 0.0008475

While some of the tests indicated heteroscedasticity of variance in the residuals, the degree of the departures was not so extreme as to preclude use of ANOVA as an analysis technique, particularly as the dataset was sufficiently large (n= 60). On the otherhand, the inclusion of two explanatory factors, one blocking factor and an interaction does put the model on the bounds of being over-fitted.

Table S7. Welch's T-Test Results
logit-transformed cover proportion as the response variable

Analysis of Variance Table (logit transformed data)

Response: dec_cover_pct

Factors	df	Sum Sq	Mean Sq	*F* value	Pr(>F)
substrate_type	1	51.295	51.295	36.9608	1.271e-07
exposure_type	1	19.297	19.297	13.9044	0.000463
site	2	0.900	0.450	0.3243	0.724455
substrate_type:exposure_type	1	2.320	2.320	1.6719	0.201508
Residuals	54	74.943	1.388		

Substrate T-Test Results: Welch Two Sample t-test (logit transformed data)

data: dec_cover_pct by substrate_type

t = -5.5251 df = 57.81 p-value = 8.212e-07

Supports alternative hypothesis: true difference in means is not equal to 0.

95 percent confidence interval:	-2.519261	-1.179221
sample estimates:	mean in group Engineered	mean in group Natural
	-0.1172576	1.7319832

Exposure T-Test Results: Welch Two Sample t-test (logit transformed data)

data: cover_pct by exposure_type

t = 2.9403 df = 45.65 p-value = 0.005132

Supports alternative hypothesis: true difference in means is not equal to 0.

95 percent confidence interval:	0.3575898	1.9108606
sample estimates:	mean in group Exposed	mean in group Protected
	1.3744754	0.2402502

Table S8. Beta regression model of percent cover

betareg(formula =
dec_cover_pct ~ substrate * exposure + site | substrate + exposure, data = scrape_cov)

Standardized weighted residuals 2:

Min	1Q	Median	3Q	Max
-2.2862	-0.8526	0.0426	0.8243	1.6277

Coefficients (mean model with logit link):

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.0560	0.2303	4.585	4.53e-06
Substrate	-1.3826	0.2470	-5.598	2.17e-08
Exposure	1.1863	0.4044	2.933	0.00336
sitePigeon Cove	-0.2025	0.2530	-0.800	0.42354
siteEastern Point	-0.1753	0.2530	-0.693	0.48851
substrate:exposure	-0.5703	0.5316	-1.073	0.28334

Phi coefficients (precision model with log link):

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.2705	0.3519	6.451	1.11e-10
Substrate	-0.1709	0.4935	-0.346	0.729
Exposure	-0.8664	0.5468	-1.584	0.113
substrate:exposure	-0.7026	0.7140	-0.984	0.325

Type of estimator: ML (maximum likelihood)
Log-likelihood: 38.45 on 10 Degrees of freedom
Pseudo R-squared: 0.495
Number of iterations: 21 (BFGS) + 2 (Fisher scoring)

Results of beta regression model
using decimal cover proportion as the response variable
including site and interaction term between substrate and exposure factors
(logit link default used) and substrate + exposure as precision parameter (log link default used)

Table S9. Presence in experimental squares by macroalgae and invertebrate groups after one year, by wave exposure

Species Group	Wave Exposure			
	Protected		Exposed	
	# of Sqrs. on which present (n=30)	% of Sqrs. on which present (30 = 100%)	# of Sqrs. on which present (n=30)	% of Sqrs. on which present (30 = 100%)
Brown macroalgae	29	97%	26	87%
Red macroalgae	26	87%	27	90%
Green macroalgae	24	80%	25	83%
Hydroid	7	23%	1	3%
Bryozoan	18	60%	5	17%
Acidian	10	33%	14	47%
Maxillipoda	24	80%	18	60%
Gastropod - herb.	10	33%	7	23%
Gastropod - carn.	7	23%	4	13%

Table S10. Presence in experimental squares by macroalgae and invertebrate groups after one year, by site

Species Group	Site					
	Eastern Point		Lane Cove		Pigeon Cove	
	# of Sqrs. on which present (n=20)	% of Sqrs. on which present (20 = 100%)	# of Sqrs. on which present (n=20)	% of Sqrs. on which present (20 = 100%)	# of Sqrs. on which present (n=20)	% of Sqrs. on which present (20 = 100%)
Brown	17	57%	20	67%	18	60%
Red	20	67%	16	53%	17	57%
Green	16	53%	14	47%	19	63%
Hydroid	4	13%	3	10%	1	3%
Bryozoan	9	30%	5	17%	9	30%
Acidian	6	20%	10	33%	8	27%
Maxillipoda	18	60%	16	53%	8	27%
Gastropod (H)	5	17%	5	17%	7	23%
Gastropod (C)	2	7%	3	10%	6	20%

Table S11. Area covered by macroalgae and sessile invertebrate species groups after one year, by substrate type

Species Group	Substrate Type	
	Engineered	Natural
	% of Total Factor Area covered by species grp. after 1 year	% of Total Factor Area covered by species grp. after 1 year
Brown macroalgae	8	30
Red macroalgae	13	36
Green macroalgae	17	5
Hydroid	< 1	< 1
Bryozoan	2	1
Acidian	1	1
Maxillipoda	8	8

Table S12. Area covered by macroalgae and sessile invertebrate species groups after one year, by wave exposure

Species Group	Wave Exposure	
	Protected	Exposed
	% of Total Factor Area covered by species grp. after 1 year	% of Total Factor Area covered by species grp. after 1 year
Brown macroalgae	15	23
Red macroalgae	21	28
Green macroalgae	8	13
Hydroid	< 1	< 1
Bryozoan	3	1
Acidian	1	< 1
Maxillipoda	8	8

Table S13. Area covered by macroalgae and sessile invertebrate species groups after one year, by site

Species Group	Site		
	Eastern Point	Lane Cove	Pigeon Cove
	% of Total Factor Area covered by species grp. after 1 year	% of Total Factor Area covered by species grp. after 1 year	% of Total Factor Area covered by species grp. after 1 year
Brown macroalgae	9	39	8
Red macroalgae	38	8	27
Green macroalgae	7	2	23
Hydroid	< 1	< 1	< 1
Bryozoan	3	1	1
Acidian	< 1	1	< 1
Maxillipoda	7	10	7

Table S14. Macroalgal and sessile invertebrate percent cover analysis 2016 MANOVA Table (univariate ANOVAs)

BROWN	Df	Sum Sq	Mean Sq	*F* statistic	p-value
substrate	1	0.00122	0.00122	4.518	0.03813
exposure	1	0.00015	0.00015	0.545	0.46360
site	2	0.00637	0.00318	11.813	5.55E-05
substrate:exposure	1	0.00005	0.00005	0.187	0.66747
Residuals	54	0.01455	0.0003		
RED	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	1E-07	1E-07	0.0003	0.9856
exposure	1	0.00070	0.00070	3.686	0.0602
site	2	0.00708	0.00354	18.503	7.58E-07
substrate:exposure	1	0.00004	0.00004	0.218	0.6422
Residuals	54	0.01034	0.00019		
GREEN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	0.00055	0.00055	9.348	0.0035
exposure	1	0.00001	0.00001	0.178	0.6752
site	2	0.00596	0.00298	50.937	3.71E-13
substrate:exposure	1	0.00003	0.00003	0.583	0.4483
Residuals	54	0.00316	0.00006		
HYDROID	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	0.00000	1.10E-11	0.000	0.9896
exposure	1	0.00001	1.29E-05	1.927	0.1708
site	2	1.19E-06	5.95E-07	0.089	0.9148
substrate:exposure	1	1E-08	9.00E-11	0.001	0.9709
Residuals	54	0.0004	6.67E-06		
BRYOZOAN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	0.00024	2.44E-04	6.299	0.0151
exposure	1	0.00023	2.28E-04	5.859	0.0189
site	2	0.00015	7.73E-05	1.991	0.1465
substrate:exposure	1	0.00016	1.64E-04	4.229	0.0446
Residuals	54	0.00210	3.88E-05		
ASCIDIAN	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	1.74E-07	1.74E-07	0.032	0.8590
exposure	1	2.27E-06	2.27E-06	0.415	0.5220
site	2	2.75E-05	1.37E-05	2.512	0.0905
substrate:exposure	1	1.12E-07	1.12E-07	0.020	0.8869
Residuals	54	2.95E-04	5.45E-06		
BARNACLE	**Df**	**Sum Sq**	**Mean Sq**	***F* statistic**	**p-value**
substrate	1	0.00001	0.00001	0.183	0.6705
exposure	1	0.00024	0.00024	3.130	0.0825
site	2	0.00111	0.00055	7.121	0.0018
substrate:exposure	1	0.00001	0.00001	0.083	0.7749
Residuals	54	0.00421	0.00008		

APPENDIX B

SUPPLEMENTARY FIGURES

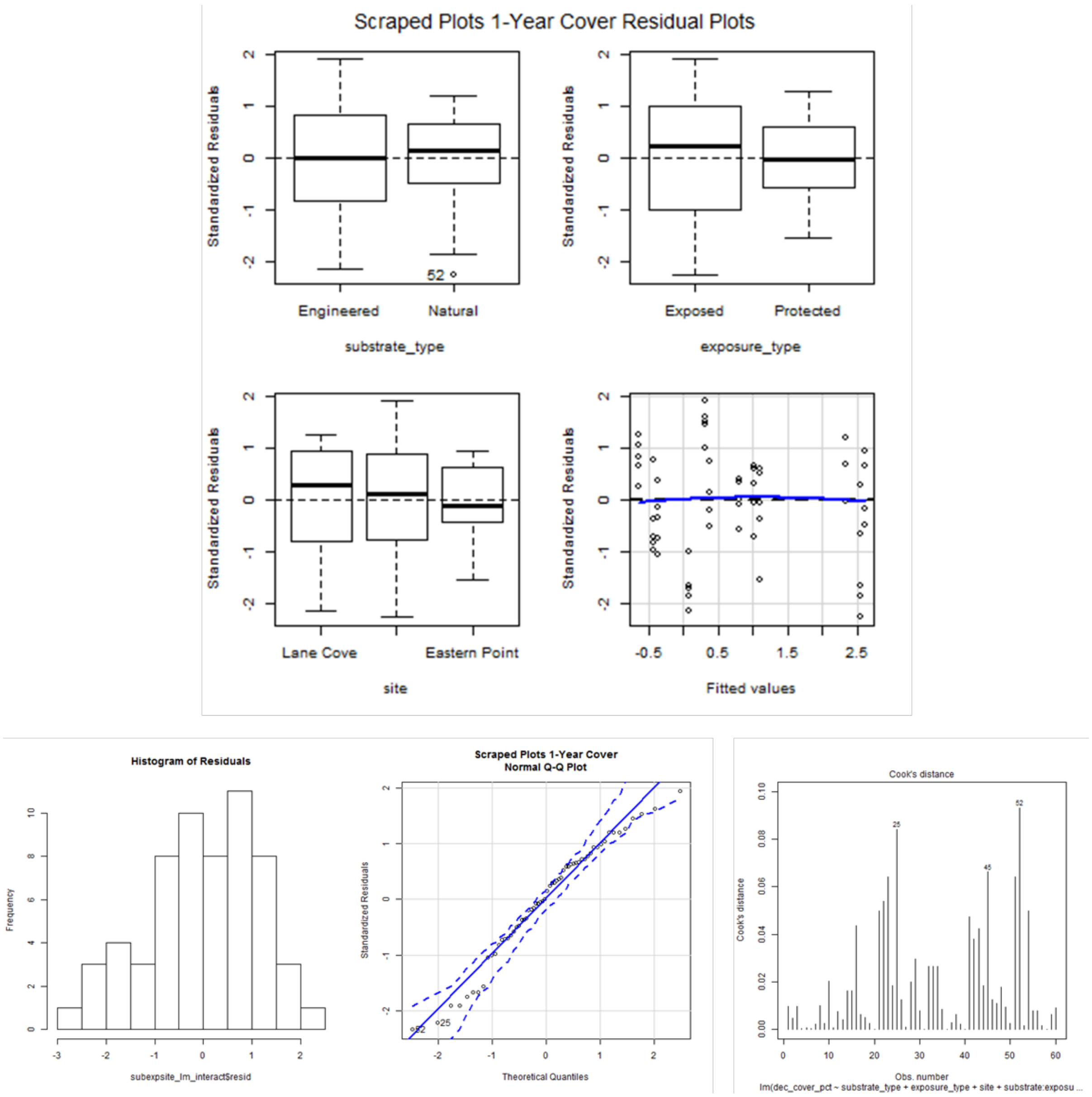


Figure S1. Model Residuals Plotted

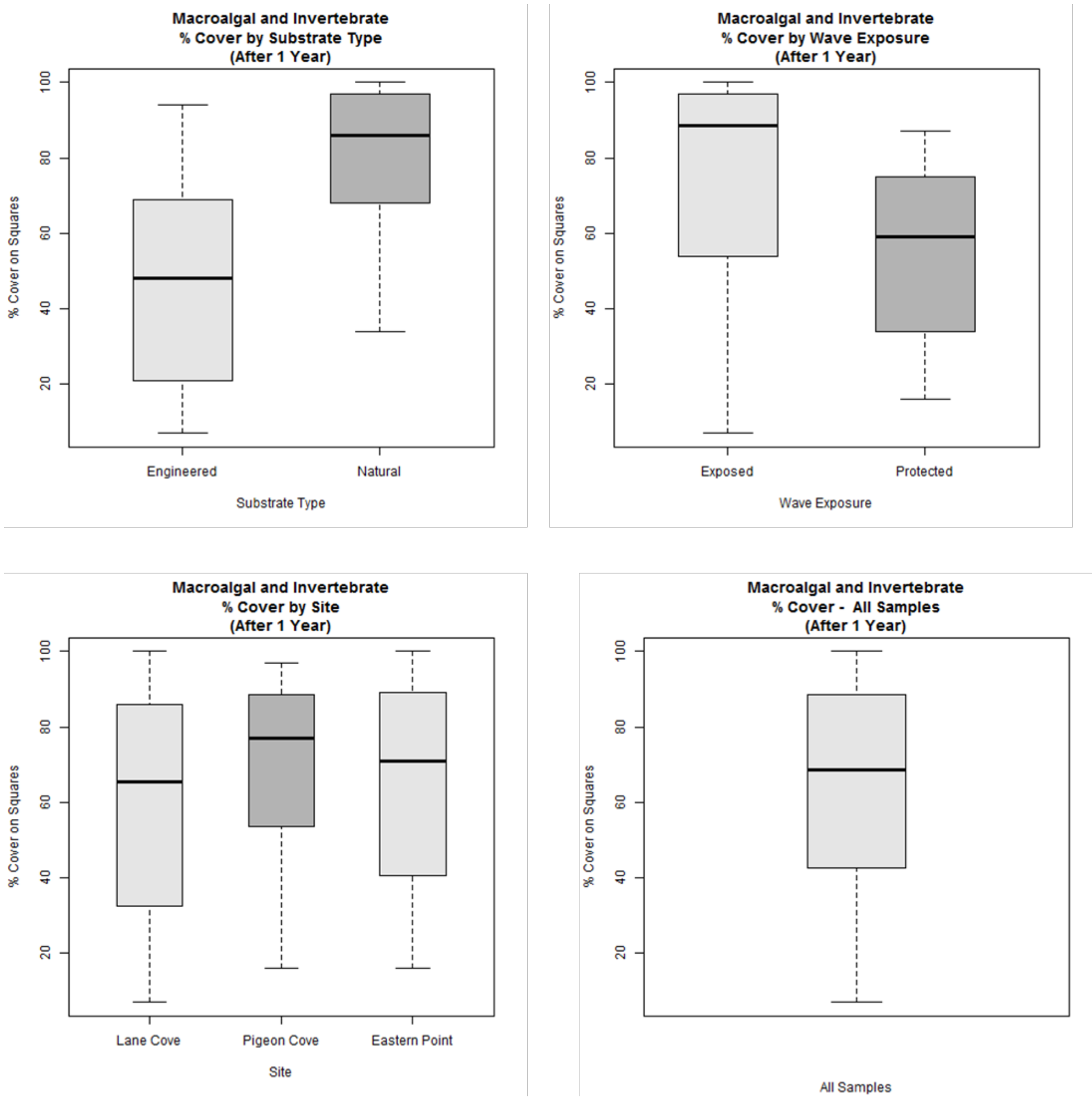


Figure S2. Boxplots of Percent Cover Data

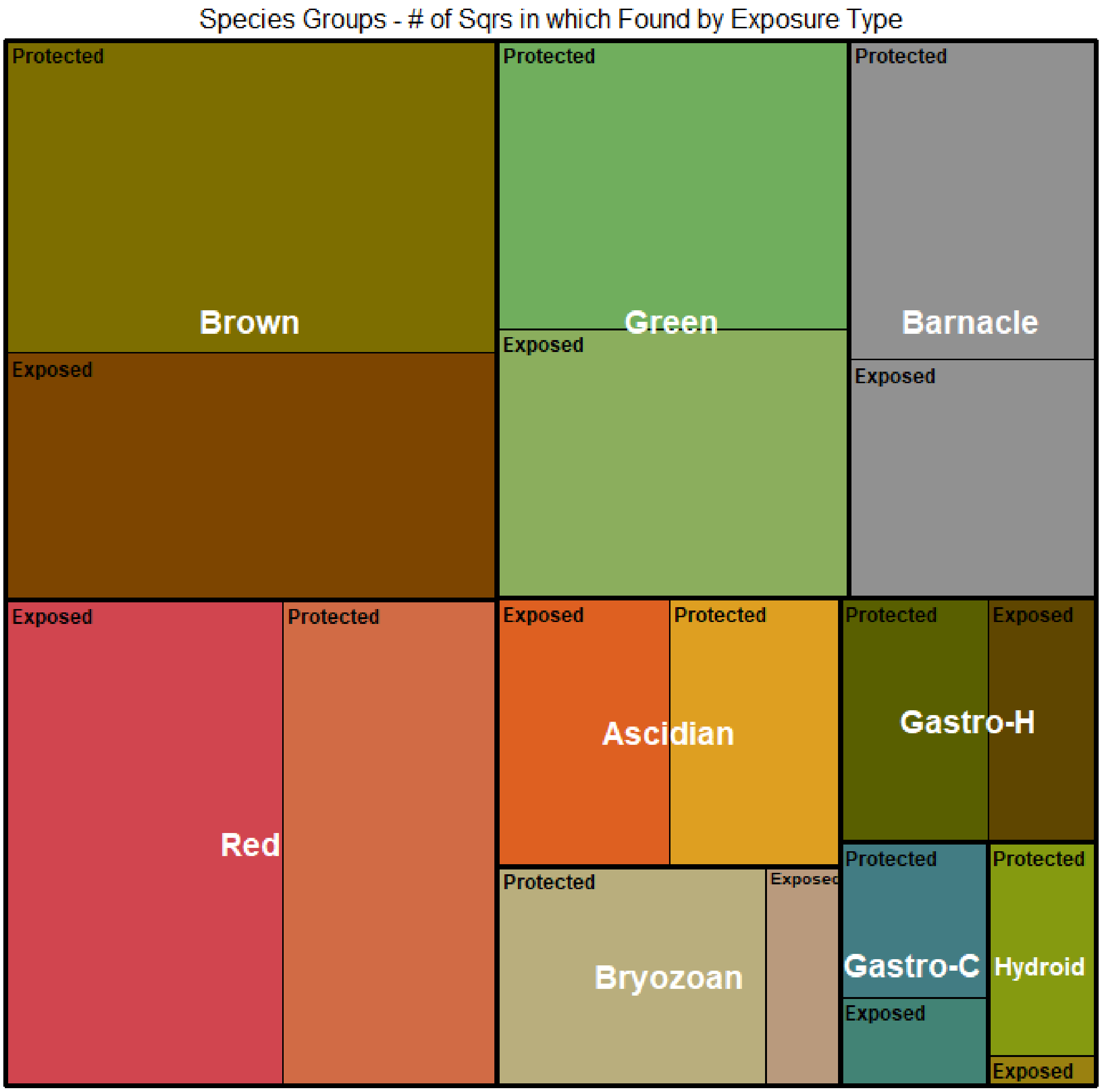


Figure S3. Treemap of 2017 macroalgae and marine invertebrate groups sized by the number of squares in which present, subdivided by exposure type.

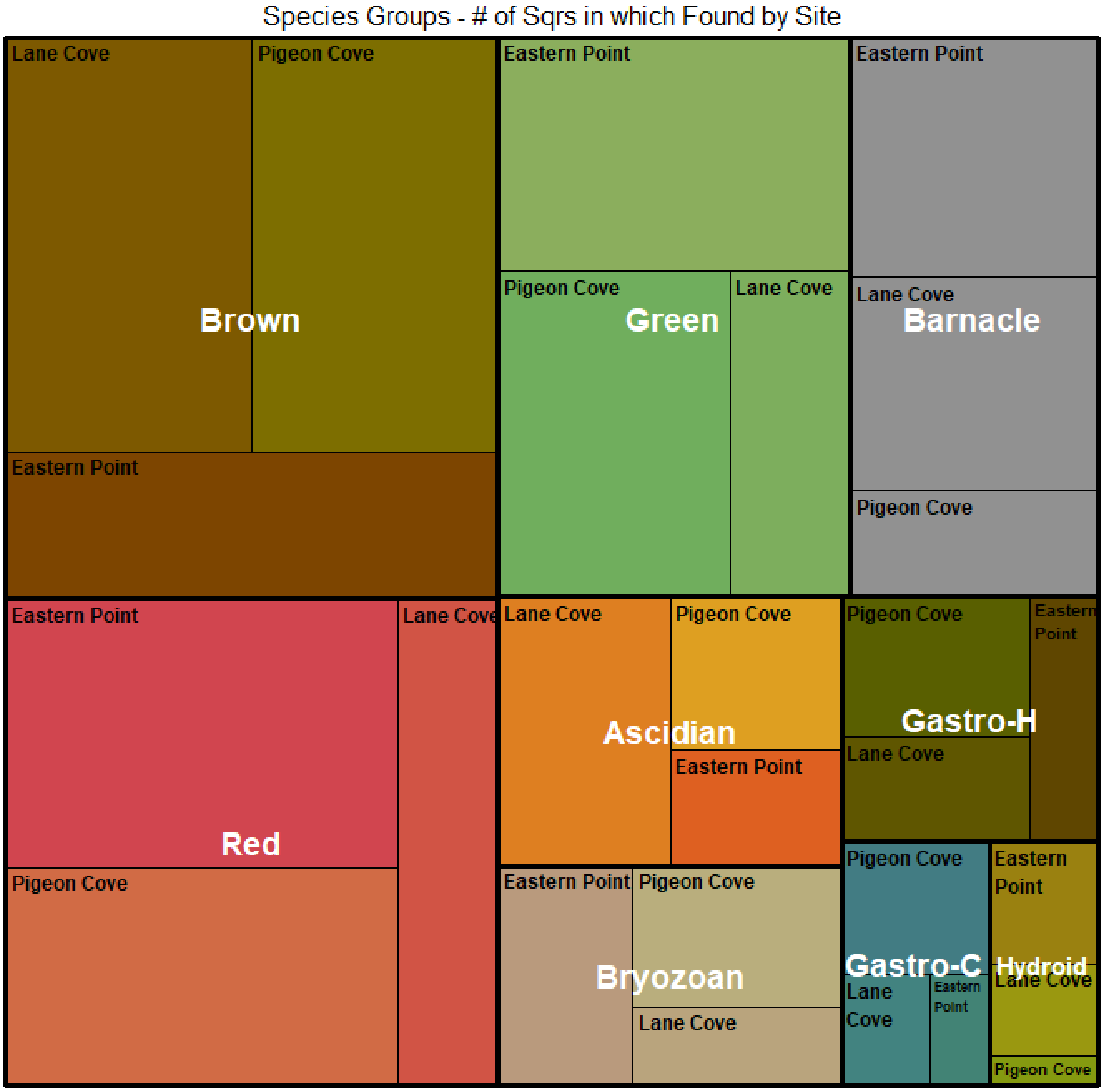


Figure S4. Treemap of 2017 macroalgae and marine invertebrate groups sized by the number of squares in which present, subdivided by site.

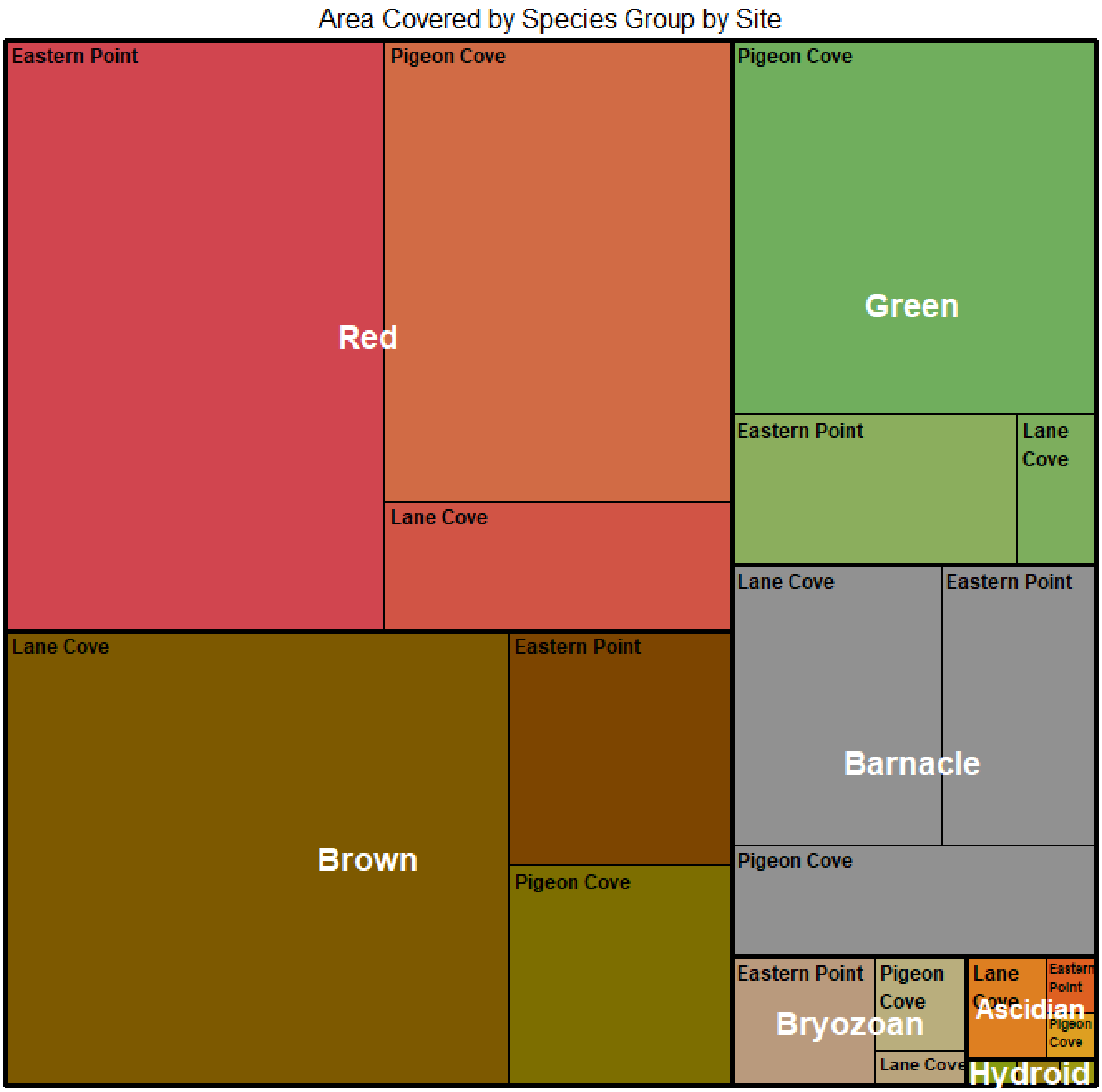


Figure S5. Treemap of 2017 macroalgae and marine invertebrate groups sized by coverage area, subdivided by site.

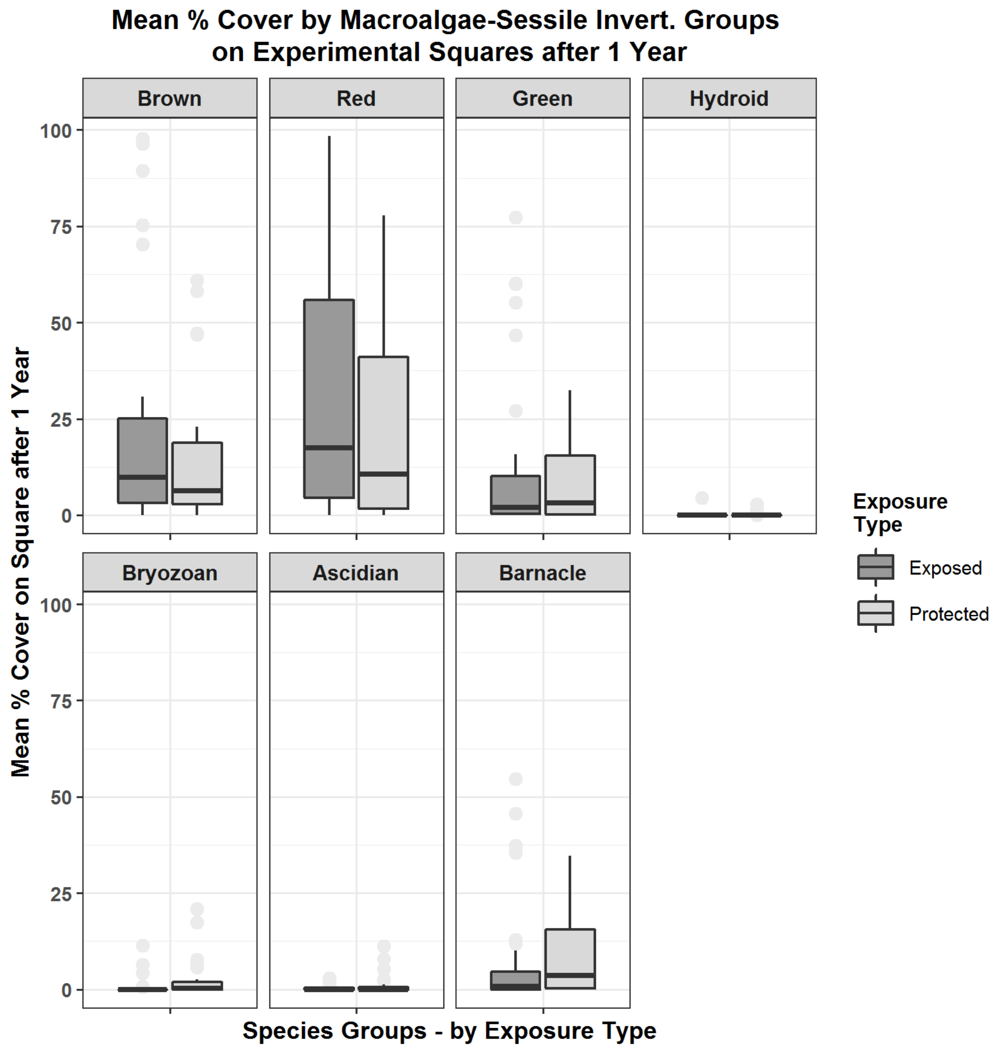


Figure S6. Macroalgae and sessile marine invertebrate groups percent cover of cleared squares after one year by wave exposure

APPENDIX C

LIST OF SOFTWARE AND R PACKAGES

Software

Git 2.23 open-source version control system, https://git-scm.com/

ImageJ 1.52h (Schindelin, J., et al., 2012; Schneider, C. A., et al., 2012)

Microsoft Excel for Windows version 14.0,7 (Microsoft Corporation, 2010)

Microsoft Word for Windows version 14.0,7 (Microsoft Corporation, 2010)

PhotoMechanic 5.0 (CameraBits, Inc., 2018

R version 3.5.3 R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio v.1.1.423 (RStudio, Inc., 2018)

R Packages

betareg
Francisco Cribari-Neto, Achim Zeileis (2010). Beta Regression in R. Journal of Statistical Software 34(2), 1-24. http://www.jstatsoft.org/v34/i02/

broom
David Robinson (2018). broom: Convert Statistical Analysis Objects into Tidy Data Frames. R package version 0.4.4. https://CRAN.R-project.org/package=broom

car
Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

dplyr
Hadley Wickham, Romain François, Lionel Henry and Kirill Müller (2018). dplyr: A Grammar of Data Manipulation. R package version 0.7.5. https://CRAN.R-project.org/package=dplyr

effsize
Torchiano M (2019). effsize: Efficient Effect Size Computation. doi: 10.5281/zenodo.1480624, R package version 0.7.6, https://CRAN.R-project.org/package=effsize.

ggplot2

Hadley Wickham (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

lmtest

Achim Zeileis, Torsten Hothorn (2002). Diagnostic Checking in Regression Relationships. R News 2(3), 7-10. URL https://CRAN.R-project.org/doc/Rnews/

MASS

Venables WN, Ripley BD (2002). *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, http://www.stats.ox.ac.uk/pub/MASS4.

msme

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openxlsx

Philipp Schauberger, Alexander Walker, Luca Braglia (2019) openxlsx() package version: 4.1.4 https://CRAN.R-project.org/package=openxlsx

pscl

Simon Jackman (2017). pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. United States Studies Centre, University of Sydney. Sydney, New South Wales, Australia. R package version 1.5.2. URL https://github.com/atahk/pscl/

Achim Zeileis, Christian Kleiber, Simon Jackman (2008). Regression Models for Count Data in R. Journal of Statistical Software 27(8). URL http://www.jstatsoft.org/v27/i08/.

readxl

Hadley Wickham and Jennifer Bryan (2018). readxl: Read Excel Files. R package version 1.1.0. https://CRAN.R-project.org/package=readxl

sjstats

Lüdecke D (2020). sjstats: Statistical Functions for Regression Models version 0.17.8. doi: 10.5281/zenodo.1284472, https://CRAN.R-project.org/package=sjstats.

tidyr

Hadley Wickham and Lionel Henry (2018). tidyr: Easily Tidy Data with 'spread()' and 'gather()' Functions.R package version 0.8.1. https://CRAN.R-project.org/package=tidyr

treemap

Martijn Tennekes, Peter Ellis (2017). Treemap() package version 2.4-2 https://CRAN.R-project.org/package=treemap

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