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Intertidal ecology of riprap jetties and breakwaters : marine communities inhabiting anthropogenic structures along the west coast of North America

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Intertidal Ecology of Riprap Jetties and Breakwaters: Marine Communities Inhabiting Anthropogenic Structures along the West Coast of North America

A Dissertation submitted in partial satisfaction of the requirements for the

degree

Doctor of Philosophy

in

Biology

by

Benjamin Alan Pister

Committee in charge:

Professor Kaustuv Roy, Chair
Professor Paul Dayton
Professor David Holway
Professor Walter Jetz
Professor Lisa Levin

2007

The Dissertation of Benjamin Alan Pister is approved, and it is acceptable in quality and form for publication on microfilm:

Chair

University of California, San Diego

2007

DEDICATION

I dedicate this dissertation to my parents, James and Virginia Pister. No finer human beings could a son wish for in a couple of parents. Apparently I used to sit on their backs, following them around in the intertidal, staring wide eyed at the sea stars, clams, Irish Lords, Dungeness crab, the occasional octopus, kelp, and that scary grass that makes you sink up to your ankles. Had we not spent those days at McDonald Spit, I doubt I would be who I am today.

EPIGRAPH

. . . the impulse which drives a man to poetry will send another man into the tide pools and force him to try to report what he finds there.

John Steinbeck, Sea of Cortez

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First and foremost, I wish to thank my family: my parents James and Virginia Pister; my sisters Jessica and Amanda Pister; my grandparents Ed and Adel Rozek, and Bob and Alice Pister. Your confidence in me never wavered, even when I had none. Each of you have done your very best to play a supportive and loving role in my life for which I am eternally grateful. I can only hope to live by your example. Except my sisters. I don't ever want to be someone's sister. You're going to have to continue to settle for a brother.

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with this man. Whatever quality I possess as an ecologist is due to this wonderful man.

My other committee members, Lisa Levin, Walter Jetz, and especially David Holway have always kept their doors open and have each offered a wonderful compliment of advice and expertise. David has been especially helpful in discussing the planning and analysis of my work as well as the writing. Walter has been very helpful with the labyrinth that is statistics. Lisa has provided invaluable and unique wisdom on writing and various aspects of marine ecology and careers therein.

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Thanks, also, to Art Poon for the drawing in Appendix C. The drawing is in reference to the possible facilitation of invasive species by riprap in CHAPTER 2.

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The text of Chapter 2 is in preparation for publication in Evolutionary Ecology Research. The text of Chapter 3 is in preparation for publication in Marine Biology. The text of Chapter 4 is in preparation for publication in Ecology Letters. The dissertation author is the primary author on all of them. Kaustuv Roy is a co-author on the manuscript from Chapter 4.

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ABSTRACT OF THE DISSERTATION

Intertidal Ecology of Riprap Jetties and Breakwaters: Marine Communities Inhabiting Anthropogenic Structures along the West Coast of North America

by

Benjamin Alan Pister

Doctor of Philosophy in Biology

University of California, San Diego, 2007

Professor Kaustuv Roy, Chair

Riprap is simply the rocky rubble used to construct jetties, breakwaters and armored shorelines. Riprap structures are designed to reduce wave energy, protect shorelines from erosion, and alter currents and sedimentation processes. These anthropogenic structures have become an ubiquitous form of coastal modification throughout the world. Despite the obvious abundance, habitats of anthropogenic origin are generally overlooked by marine ecologists. Nevertheless, anthropogenic structures, especially in urban areas, will play an ecological role, if only because of their abundance. Here I investigate the ecological role of riprap using rocky intertidal communities along the west coast of North America.

First, I describe the floral and faunal communities growing on four riprap structures in southern California and compare them to nearby natural rocky intertidal communities. I found the rocky intertidal communities on the riprap structures in wave exposed areas to be surprisingly lush and diverse. In general, using the tops and sides of boulders I found the community structure and overall diversity to be statistically indistinguishable between riprap and natural rocky intertidal environments. There were some differences in individual species abundance, and in the diversity of mobile organisms which appear to be caused by variation in wave forces.

To test the hypothesis that larger differences would exist between riprap and natural rock, I conducted a field experiment using tiles of sandstone and granite. These substances are the dominant rock types of the natural rock and riprap in San Diego county, respectively, and represent a possible source of variation in rocky intertidal communities. These two rock types, however, did not create a difference in settlement of rocky organisms.

Finally, I investigated the relationship of functional diversity and species diversity using riprap structures between Seward, Alaska and San Diego, California. Functional diversity increased with species diversity with a small amount of redundancy in the most speciose sites.

These results contribute to the growing knowledge of urban ecology, and help fill the tremendous knowledge gap in marine environments in urban areas. This research adds to a small handful of studies on riprap in the southern California region and represents the basis for future work on marine ecology, urban ecology, and the interaction between human activities and the marine environment.

CHAPTER 1

Introduction to the Dissertation

The study of community ecology involves investigating the variation seen in the natural world from place to place and from time to time. Throughout the past century students of the natural world have become increasingly aware that human activities have a very profound impact on the variation observed in natural marine communities (Moore 1939; McDougall 1943; Karlson 1978; Glasby & Connell 1999; Jackson *et al.* 2001; Worm *et al.* 2006). These impacts are diverse and varied and presently are among the most important and urgent areas of ecological study and management. Among these impacts are physical changes to the landscape. Humans have been physically modifying the marine landscape to facilitate their activities for thousands of years (Rouse & Ince 1957; Frost 1963). Within the past few centuries the industrious capacity of the human race along with excessive growth in coastal populations has created a series of anthropogenic structures in the ocean that rival many natural habitats in spatial and temporal scale. These anthropogenic structures have become so extensive that understanding how they affect the variation in communities, and their contributions as habitat, is necessary for understanding the variation in coastal communities in general.

A HISTORICAL EXAMPLE

Consider Caesarea Maritima. King Herod the Great built this city from scratch on the Mediterranean coast of present day Israel. He did this largely to lure the lucrative shipping trade of the time moving between Rome and her territories. In order to do this he needed a harbor, but no natural harbor existed in the vicinity. So he built one. By the time he was finished it rivaled the harbors at Athens and Alexandria. The engineering feats needed to complete this colossal artificial structure were impressive, even by today's standards. Among them was the invention of hydraulic cement that would harden underwater after being poured. The outer breakwater alone was over 500 meters long.

The ancient harbor at Caesarea Maritima is in ruins today, largely due to an earthquake in antiquity and the lack of maintenance due to several invading armies. Nevertheless, Herod's great harbor is still there, albeit mostly submerged. No longer used for mooring ships, it is still used by the benthic inhabitants of the eastern Mediterranean, as it has been for over 2000 years.

Herod's harbor was not the first anthropogenic structure of its kind, though it seems to have been the first one built without the aid of the natural shape of the land. Already there were ancient harbors when the ground was first broken at Caesarea Maritima (Frost 1963). This example illustrates that humans have had the ability to profoundly change the coastal marine landscape through the use of their own constructions for a very long time. For some reason, it is still easy to underestimate our own abilities.

RIPRAP

Riprap is simply the rocky rubble used to build jetties and breakwaters and to stabilize shorelines from erosion. It is often quarried from nearby sources, although the rock itself may not be indigenous to the local marine environment. For example, much of the riprap in southern California comes from a quarry on Catalina (Turhollow 1975). Much of it is granite. In San Diego County, most of the rocky shoreline is sandstone (Tway 1991). Because riprap is comprised of natural rock, it is still a natural substance, although synthetic structures, such as Dolos (which resemble toy jacks, but are made of concrete and weigh 40 tons), are also widely used. However, artifacts of construction set riprap structures apart from natural shorelines. Among them is a change in scale of physical complexity. At small scales (meters) riprap is extremely heterogeneous, as anyone who has spent time trying to crawl over the stones can attest. Natural boulder fields (*sensu* Sousa 1979) may or may not match this heterogeneity. But at larger scales (kilometers), they are very much homogenous, straight, and consistent. Natural shorelines, at least rocky ones, rarely exhibit that level of consistency. There are many other artifacts that may be of interest to both the wayward cyprid searching for a nice place to metamorphose and the curious scientist searching for a nice place to lay a transect. Certainly they are worthy of more than a brief introduction at the beginning of a dissertation.

Humans have used riprap in California, Oregon, and Washington for well over a century (Turhollow 1975; Komar 1998). A local example is the Zuniga jetty, at the mouth of San Diego Bay. This jetty was constructed in 1890, and is roughly 7,500 feet long (Turhollow 1975). Since then miles upon miles of shoreline in southern California have been converted to riprap. Approximately

30% of the coastline between Pt. Conception and the U.S./Mexico border has some form of riprap on it (Clark *et al.* 2002).

Harbor development in southern California began with the Spanish American war at the turn of the 20th century and the construction of the Panama Canal (Turhollow 1975). Since then, the continuing needs of the Navy, commerce, and industrial advances, such as increases in tanker size, have largely driven the construction and expansion of the harbors of the west coast.

Eventually the economics of maritime recreation led to the planning of several small boat harbors such that no more than 35 miles separated one port from the next between Morro Bay and San Diego (Turhollow 1975). This goal was obtained by the early 1970's. By 1966, there were over 345,000 pleasure craft registered in the state of California. Needless to say that number has increased since then. These vessels require safe harbors and floating docks for mooring. And harbors require riprap. All of these structures mean new hard substrate on the coast that many marine organisms are capable of colonizing.

In addition, the continuing flock of humans to the coastline over the past century has lead to the need for flood control, piers, and shoreline protection (Turhollow 1975; Forstall 1996; Komar 1998). Ironically, the need for erosion control and beach restoration was largely due to unforeseen results of harbor construction and the altered flow of many of the regions rivers (Turhollow 1975; Komar 1998). The use of riprap, along with other coastal modifications it seems, has created a positive feedback loop of increasing anthropogenic structures in marine (and freshwater) environments along the west coast of North America.

Riprap, thus, may provide an intriguing link between the economic, military, and social needs of humans and the ecology of near shore marine ecosystems. The rocky intertidal zone has been the source for a disproportionate amount of ecological study (e.g. Baker 1909; Hatton 1938; Moore & Kitching 1939; Connell 1961; Lewis 1964; Paine 1966; Dayton 1971; Lubchenco & Gaines 1981; Littler *et al.* 1983; Raimondi 1990; Helmuth *et al.* 2002; Wootton 2002; Roy *et al.* 2003, to name a few). It is somewhat surprising that very few studies have been conducted on riprap, given the fact that in some regions it rivals the spatial extent of natural habitats (Clark *et al.* 2002). Although some papers have studied marine communities that happen to inhabit riprap (Reish 1964), one of the earliest studies in California to draw attention to the ecological consequences of riprap was Davis et al. (1982). They found that the creation of an artificial riprap reef near Torrey Pines State Park, dramatically changed the structure of the soft bottom community for hundreds of yards in every direction. More recently, Davis et al. (2002) studied the communities on the vast stretches of riprap lining San Diego Bay to illustrate the role of wave exposure in structuring the intertidal communities in the area. Osborn (2005) conducted her thesis on riprap in Monterey Bay and found that the variable rock types created differences in the settlement and recruitment patterns of upper intertidal organisms. A small, but growing number of studies from other parts of the world are contributing to what we know about urban ecology in the marine environment, and about riprap in particular. They are cited throughout the dissertation.

OBJECTIVE OF THE DISSERTATION

Subsequent chapters present studies I conducted to describe the communities on riprap structures and understand some of the ecological consequences they may have. Chapter 2 is a descriptive study that documents the intertidal communities on several riprap structures in southern California and how they might differ from an analogous natural rocky intertidal community. Chapter 3 describes an experiment that tests the effect of the different rock types used for riprap and the natural rock of San Diego County. In Chapter 4 I use riprap as a tool to explore the relationship between species diversity and functional diversity over a large spatial scale. This is an urgent topic facing ecologists today. The importance of riprap to marine ecology lies not only in its abundance and ability to sustain healthy marine communities, but as a possible tool for conservation, management, and the study of broader ecological questions.

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CHAPTER 2

Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat

ABSTRACT

Riprap is the rocky rubble used to build jetties, breakwaters, and armored shorelines. Roughly 30% of the southern California shoreline supports some form of riprap, while 29% of the shoreline is natural rocky substrate. Astonishingly few studies have investigated this anthropogenic rocky habitat given that it rivals a natural habitat on a regional scale. The ability of these structures to contribute ecologically to marine environments is essential for the health of both marine ecosystems and the urban areas nearby. In this study I compare the diversity and community structure of wave-exposed rocky intertidal communities on four riprap and four natural sites in southern California. I ask the following questions: (1) on average, does diversity or community composition differ between intertidal communities on riprap and natural rocky habitats in southern California, (2) if so, which organisms contribute to those differences, (3) which physical factors are contributing to these differences, and (4) do riprap habitats support higher abundances of invasive species than natural habitats? Most variation, largely driven by wave exposure, was found to exist between sites regardless of whether they were riprap or natural. On average, riprap and natural rocky habitats in wave-exposed environments in southern California did not differ from each other in diversity or community composition. Sessile species made up the majority of species recorded, and no differences were found in diversity or community structure when they were part of the analyses. Mobile species, when considered on their own were more diverse on natural shores, largely driven by a handful of molluscan species that were relatively uncommon. The presence of invasive species was negligible on both substrates. These results are somewhat in contrast to studies from other regions which often find significant differences in diversity and community structure. The impact of riprap structures in marine environments has tremendous conservation implications and an accurate understanding of intertidal ecology in urban areas must include the vast stretches of riprap along urban shorelines.

INTRODUCTION

Riprap, the rocky rubble used to construct jetties, breakwaters and armored shorelines has been in use in southern California since the late 1800’s (Turhollow 1975). Its use and construction are widespread and riprap now rivals the extent of natural rock along southern California's shoreline (30% and 29% respectively, Clark et al. 2002). Ecologically, the southern California coastline is one of the most thoroughly investigated shorelines in the world. But we know almost nothing concerning the ecology of riprap structures in this marine ecosystem. Despite the extensive scientific literature devoted to the rocky intertidal of southern California, only a handful of ecological studies focus on riprap

(Reish 1964; Rader 1998; Davis *et al.* 2002). In other words, despite over a century of research, almost nothing is known about half of the rocky shoreline in southern California. Investigating marine communities growing on riprap is therefore important because if our understanding of the ecology of rocky intertidal communities is based solely on natural substrates we may have an inaccurate view of ecological processes in the region. Furthermore, scientists may be taking for granted that what we know about benthic ecology on (or in) natural substrates is sufficient to understand ecological processes in areas with many anthropogenic structures. Even if current ecological knowledge is sufficient to understand processes on anthropogenic structures, any large scale or biogeographic work must account for them as possible habitat.

The spatial extent of anthropogenic structures such as riprap will likely continue to increase. Indeed, riprap likely represents one of the few marine habitats that is increasing in area**.** Coastal human populations are increasing, and as they do shorelines will need additional reinforcement (Forstall 1996). In addition, environmental changes caused by climate change, such as rising sea levels and increasing storm intensity, are expected to threaten coastal urban settlements (Dean *et al.* 1987; McCarthy *et al.* 2001). The proper design of riprap structures and other coastal modifications is a popular research area in civil engineering, and is of huge economic importance (Herbich 2000;

Engineers 2002). Far less research has focused on the biological communities they support. It is clear that the effects on flora and fauna are rarely considered when designing or constructing these massive modifications (Turhollow 1975; Mulvihill *et al.* 1980). Given the extent of riprap structures and its future increase, the ability of these structures to host suitable marine communities is essential for the future of marine ecosystems along with the social and economic health of coastal urban areas.

The ecological study of urban marine ecosystems is very much in its infancy (Glasby & Connell 1999; Bulleri 2006). Several studies focus on a variety of urban structures in marine environments. For example, oil platforms (e.g. Sammarco et al. 2004), pilings (Sutherland & Karlson 1977; e.g. Karlson 1978; Cole *et al.* 2005), floating harbor pontoons(e.g. Holloway & Connell 2002), seawalls (e.g. Bulleri et al. 2005), and ship wrecks (e.g. Wendt et al. 1989), along with riprap. But these structures are not identical, and what holds for one may not hold for another. What little research has been conducted on marine riprap has revealed somewhat conflicting results and the potential for biogeographic variation certainly exists (Table1). Some studies report no differences in community structure or diversity between riprap and natural rocky habitats (Chapman 2006; Clynick 2006), while others have found clear differences for only some taxa (Bulleri & Chapman 2004; Moschella *et al.*

2005; Osborn 2005). Some studies have found that riprap supports lower diversity compared to that typical of natural rocky habitats (Moschella et al. 2005), while others suggest it supports more (Clynick 2006). Recent studies also suggest that anthropogenic structures favor invasive species over native ones (Wasson *et al.* 2005; Glasby *et al.* 2006; Tyrrell & Byers 2007). Riprap, for example, facilitates the establishment and spread of invasive species in the Mediterranean (Bulleri & Airoldi 2005; Bulleri *et al.* 2006). Given the ubiquity of riprap in southern California the potential for invasive species to gain footholds in the region could be high. There are many questions that must be addressed before we can claim an adequate understanding of the ecological roles of riprap in marine environments.

The first steps in understanding the ecological roles of riprap in urban marine environments is to document the communities present on riprap and test for differences between riprap natural rocky habitats (Niemela 1999). My goals in this study are to ask the following questions: (1) on average, does diversity differ between intertidal communities on riprap and natural rocky habitats in southern California, (2) does community composition differ between those habitats, (3) if so, which organisms contribute to those differences, (4) which physical factors are contributing to these differences, and (5) do riprap habitats support higher abundances of invasive species than natural habitats?

The answers to these questions will give ecologists a better understanding of the ecological contribution of riprap structures as valid marine habitats.

METHODS

Field Sites and Data Collection

I surveyed intertidal communities at four exposed riprap and four exposed natural rocky boulder sites in southern California, USA between December 2004 and March 2006 (Figure 2-1, Table 2-2). The sites were sampled in a haphazard order, which should eliminate any temporal bias between the two habitat types. The four riprap sites consisted of the northern jetty at the entrance to Mission Bay (MB), the outer breakwater at Dana Pt. Harbor (DBW), the northern jetty at the entrance to Newport Bay (NP), and the northern (western) breakwater at San Pedro (SP). The four natural rocky sites included the Scripps Intertidal Reserve (SIO), Dana Pt. State Reserve (DPR), Corona del Mar (CDM) and Pt. Fermin (PF). Each of these sites were chosen because they are accessible, on the open coast and exposed to ambient wave conditions, are reasonably large in area, and are in relatively close proximity to a site of the opposite rock type. In addition these natural sites are steep, uneven, and have large boulders (i.e. so that they are similar to riprap), to the extent that this is possible. A general description of these temperate rocky intertidal communities is illustrated in several classic publications (Abbott & Hollenberg 1976; Morris *et al.* 1980; Ricketts *et al.* 1985). All these sites, like almost all sites in southern California, are influenced by the direct presence of humans (e.g. trampling), and pollutants from either harbors and/or terrestrial sources (Murray *et al.* 1999; Roy *et al.* 2003; Huff 2006).

Within each site a minimum of five vertical transects were laid haphazardly in locations chosen to represent ambient wave exposure. Because the slopes of each site (and therefore the transect length) varied, I used biological boundaries to define the endpoints of transects. Each transect began in the upper intertidal at the upper limit of *Chthamalus fissus* and ended in the mid to low intertidal at the upper limit of *Eisenia arborea.* Along each transect eight .25 x .25 meter PVC quadrats were placed at evenly spaced intervals only on the tops or outward facing sides of boulders. Quadrats were moved laterally (i.e. at the same tidal height) when necessary to avoid sampling crevices or more than one face of a boulder. This sampling scheme is designed to ensure consistency between sites and to avoid a bias by sampling microhabitats present only at some sites, such as tidepools (Davis *et al.* 2002; Murray *et al.* 2006). This sampling scheme also ensures equal sample sizes at the same relative tidal heights. Note that in this scheme the entire vertical transect, rather than individual quadrats, represents a sample of the intertidal community.

Digital photos were taken using a digital camera positioned directly above each quadrat and all species above 3-5 mm that could be consistently observed were identified *in situ* (Foster et al. 1991). In addition I counted all mobile organisms. Species that could not be consistently observed were excluded from statistical analyses. For example, the frequently occurring crab *Pachygrapsis crassipes* was usually swift enough to dart away before being counted, and the cryptic isopod *Idotea spp*. was probably sufficiently camouflaged in many tufts of algae to remain unnoticed much of the time.

Each photo was analyzed in the lab using Image J (Rasband 2005). Each photo was cropped to include only the quadrat. I quantified percent cover by projecting 25 dots randomly onto each photo and assigning a value of 4% to each organism that occurred under each dot. Percent cover and counts of each species were summed for each transect.

Physical data

I obtained data on several oceanic variables from the Coastal Data Information Program (CDIP) operated by the Scripps Institution of Oceanography, which maintains an archive of data collected from buoys throughout southern California (www.cdip.ucsd.edu 2006, Table 2-2). In addition to the CDIP data I measured the dip, the distance from the upper intertidal to the lower intertidal (i.e. transect length), area of the site, the distance from shore that a wave one meter in height would break, the width of the swash zone, and latitude. Dip was measured using a protractor placed on each quadrat and averaged for each transect. Area and swash zone width were estimated from linear measurements obtained using Google Earth (www.earth.google.com). Using the rule of thumb that a wave breaks at a depth approximately equal to its height, the distance from shore of the one meter isocline at each site was estimated from NOAA navigational charts (Denny & Wethey 2001). Age was obtained from publications by the Army Corps of Engineers (Bottin 1988).

Analyses

I used two different measures of diversity: richness (i.e. number of species) and Simpson's Diversity Index (1-D) (Magurran 2004). The reciprocal form of Simpson's Diversity Index (1-D) is considered more robust, especially at smaller sample sizes, than the more popular Shannon-Weiner Index (Lande 1996; Magurran 2004). Diversity measures across sites and across the two habitat types (riprap and natural rock) were compared using a nested ANOVA with Site (MB, SIO, DBW, DPR, CDM, NP, SP, PF) nested within Habitat (Natural or Riprap). Data were log transformed as necessary to achieve equal variances.

Because my data consist of both counts and percent cover, they cannot be combined except after a presence/absence transformation. However, this removes all information about abundance. Therefore analyses are performed on occurrences of all species summed within transects and on percent cover of sessile species and counts of mobile species respectively. When comparisons are made using presence/absence data, including richness, sessile species that were observed in quadrats but that did not occur under a dot while quantifying percent cover are included. Other than in comparisons involving percent cover data, these relatively rare species were excluded.

To test for differences in community composition I used a Two-way Nested Analysis of Similarity (ANOSIM) performed on Bray-Curtis dissimilarities (Clarke 1993; McCune & Grace 2002). Except when using presence/absence, Bray-Curtis values were calculated using non-transformed and non-standardized data. I used non-Metric Multidimensional Scaling (MDS) to ordinate the data for visual comparisons.

I identified species contributing cumulatively 75% of the dissimilarities using SIMPER. SIMPER (Similarity Percentages) is a routine in the Primer package that identifies the average contribution of individual species to the dissimilarity between groups, and thus helps to identify which species may be contributing large differences between communities (Clarke 1993).

I used Analysis of Variance (as described above) to test for differences in the abundance of individual species between riprap and natural rock. Species were tested if their cover exceeded 1% cover or their count exceeded 1% of the total individuals within a transect.

To identify which environmental variables might explain community patterns I conducted a Mantel test using the BIO-ENV procedure in Primer (Clarke 1993). The biological similarity matrix was generated using Bray-Curtis dissimilarities on non-standardized presence absence data. The physical similarity matrix was generated using Normalized Euclidean Distance on untransformed data. The Spearman rank correlation is calculated and permutation is used to compare the two matrices.

Diversity and univariate statistics were computed in R and multivariate analyses conducted in Primer (Clarke 1993; Team 2005).

RESULTS

I found a total of 72 species on natural rock and 67 species on riprap (Table 2-3). Natural rock did not significantly differ from riprap in sessile species richness (53 and 57 species respectively; $F_{1,6} = 1.6811$, $P = 0.2035$). Of these 13 species were recorded only on natural rock and 17 only on riprap (Table 2-3). Natural rock harbored 18 mobile species, and riprap only ten, which was significant ($F_{1,6} = 36.5275$, P = <0.001). The ten species on riprap were shared between both habitats, whereas the other eight on natural rock did not occur on riprap (Table 2-3). Some taxa could not be identified to species in the field and were recorded at the lowest taxonomic level possible. Sessile species included the following: 49 algae, 1 plant, 2 anemones, 5 barnacles, 5 bryozoans, 4 bivalves, 1 gastropod, 2 polychaetes, and 1 sponge. Of the mobile fauna 12 species were gastropods, 5 were chitons, and 1 species was an echinoderm. These data are certainly an underestimate of the species richness in both habitats, since several taxa are extremely difficult to identify to species level (e.g. *Gelidium* spp*., Polysiphonia* spp*.,* and small juvenile limpets). To be conservative, I lumped all similar species that could not be identified consistently throughout the study (Oliver & Beattie 1996). This includes all limpets (which were generally small) with the exception of *Lottia gigantea*, which is consistently distinguished from the other limpets.

Richness did not differ between riprap and natural rock when examining all species together ($F_{1,6} = 1.0764$, P = 0.3068), or only sessile species (Figure 2-2). However, when only mobile species were examined a significant difference was found (Table 2-4). Simpson's Diversity Index yielded the same results; no significant difference between riprap and natural rock for all species together (t-test, F =0.0002, P = 0.9883), and sessile species ($F_{1,6}$ = 1.6512, P = 0.2075), but significantly greater diversity on natural rock for mobile species ($F_{1,6}$ = 9.7184, P = 0.0036). The eight mobile species found in natural rocky habitats but not on riprap account for only 33 individuals out of 7,498 counted (Appendix A).

Results were consistent for all comparisons of community structure using ANOSIM whether considering only sessile, only mobile, or all species together. Significant differences exist among sites, but not between natural rock and riprap (Table 2-4). Significant R values between sites suggest that one or more sites are different from the others regardless of whether it is riprap or not. The non-significant R values at the Habitat level suggest that at least some of the sites that are different from each other belong to the same habitat group (i.e. Riprap or Natural Rock), and that differences between the habitats are minimal in comparison. MDS ordinations support these conclusions as well (Figure 2-3). Thus, on average, rocky intertidal communities on the tops or sides of boulders in semi-exposed environments in southern California do not significantly differ from those in natural rocky habitats.

SIMPER identified four mobile taxa that contributed cumulatively to over 90% of the dissimilarity among mobile species, including the combined limpets (not including *Lottia gigantea)*, the snails *Littorina* *keenae* and *Littorina scutulata*, and *Lottia gigantea* (Table 2-5). The latter three were significantly different in abundance between riprap and natural rock (α=0.05, Table 2-6). *Lottia gigantea* was more abundant on riprap. But the Littorines occurred in greater abundance on natural rock. It should be noted that *L. keenae* generally occurred above the beginning of transects on both riprap and natural rock, and therefore its true abundance was certainly underestimated. SIMPER identified 11 sessile taxa contributing over 75% of the dissimilarity among sessile organisms (Table 2-5). Of these 11 taxa, only five were significantly different between riprap and natural rock (Table 2-6). *Caulacanthus ustulatus*, *Corallina vancouveriensis*, and *Ralfsia pacifica* were more abundant on natural rock, whereas *Balanus glandula* and *Policipes polymerus* occurred in greater abundance on riprap.

Forty-three species contributed more than 1% cover or count to at least one transect (Table 2-6). Of these, 19 were significantly different in abundance. Twelve were sessile species. Of the 12, the following were more abundant on natural rock: *Anthopleura elegantissima*, *Caulacanthus ustulatus*, *Corallina vancouveriensis*, Coralline crust, *Mastocarpus* sp., *Pseudochama exogyra*, and *Ralfsia pacifica*. The other five sessile species; *Balanus glandula*, *Endarachne binghamiae*, *Policipes polymerus*, *Prionitis lanceolata*, and *Tetraclita rubescens*, were significantly more abundant on riprap. Of the 12 mobile species found to contribute 1% or more to the count within a transect, seven were significantly different between natural rock and riprap. In addition to the snails identified by SIMPER, *Acanthinucella spirata*, *Fissurella volcano*, *Lepidochitona hartwegii*, and *Nuttallina* spp. were more abundant on natural rock. *Lottia gigantea* was the only mobile species that occurred in greater abundance on riprap.

The Mantel test identified three variables as best explaining the distribution of all species between sites (ρ=.716). A permutation test rejected the null hypothesis that ρ was equal to 0 (p=0.003). The three variables identified were mean significant wave height**,** the width of the swash zone, and the length of the transect, which is a proxy for the linear distance between high and low tide because the endpoints were determined biologically. This latter variable effectively determines the area over which the energy contained in a wave is spread when it hits the shore. All three variables suggest that greater wave forces experienced by the organisms on riprap explain their variation among sites. In this case, differences apply to mobile invertebrates.

DISCUSSION

Taken together these results suggest that the diversity and community composition of intertidal organisms are similar on open coast riprap and natural rock in southern California. These results also differ from the patterns described on many other riprap structures (but not all, Table 2-1) as well as studies in terrestrial urban areas that show differences in diversity and community structure along urban to rural gradients and other anthropogenically modified habitats (Rebele 1994; Eversham *et al.* 1996; McDonnell *et al.* 1997). While a few studies on marine riprap have found evidence that, at times, diversity and community structure can be quite similar to natural rock, the results presented here stand in stark contrast to those studies that have found differences. This suggests that there is variation in the ability of riprap to support marine communities. In turn this implies that the role of anthropogenic structures in providing habitat within marine ecosystems is not universal and may differ from region to region.

Diversity and Community Composition

The difference in mobile species richness found here was caused by a handful of mobile organism encountered relatively infrequently in both habitats. Only 33 individuals out of 7,498 make up the eight species (6.8% of all species), found exclusively on natural rock. These species may simply not be abundant on the tops or sides of boulders, preferring flat benches or tide pools. That is certainly the case for *Tegula funebralis* (Ricketts et al. 1985). But in addition, wave forces may prevent some of them from holding onto the rock in riprap sites. Most of the mobile species not found on riprap are high-spired gastropods, which are known to be more susceptible to wave forces (Vermeij 1993). This would also explain why *Lottia gigantea* is found in greater abundances on riprap while the Littorines are not. Except for the chitons *Lepidochitona hartwegii* and *Nuttallina* spp., the mobile species occurring in greater abundance on natural rock are also high-spired. Several of the species found only on natural rock in this study are quite abundant on the sheltered side of the breakwaters where wave exposure is dramatically reduced. In fact, the only species in this study, mobile or sessile, that has not been observed on both riprap and natural rock at some point in time by the author or in a published study (e.g. Rader 1998) is *Macron lividus.* Furthermore, the abundance of some gastropods, such as *Mexicanthina lugubris* is noticeably higher in cracks and crevices, and even the interstitial space within the breakwater (*personal observation*). None of these microhabitats were sampled here. Thus, the distribution of mobile species on riprap structures certainly deserves further scrutiny. Experimentation may be needed to determine what the exact causes are for different abundances.

Given that approximately 75% of the species in this study were sessile, and no differences were found among them, it is understandable why the differences between riprap and natural rock disappear when considering all the species together for diversity and community structure. Some of the sessile species were significantly different in abundance. Other than wave exposure (see below) it is not immediately clear what factors might explain the differences for individual species. As for the mobile species, experimentation may be needed to explain them. It is important to be clear about the ecological scale of interest. Despite the difference in some individual species, when considering the community as a whole there is no difference between riprap and natural rock in this study.

Chapman (2003) found a similar pattern on seawalls. In her study there were no differences between seawalls and natural rocky reefs for algae, or for all taxa considered together, although she did not quantify abundance so only richness could be evaluated. However, she did find differences in the number of animal species, and mobile animals in particular. Chapman attributes this difference to the lack of suitable micro-habitats, such as crevices or tide pools on the seawalls, although none of the alternative hypotheses, such as differences in wave exposure, are tested. Clearly there are many other micro-habitats on riprap structures which lack the smooth simplicity of seawalls. As suggested above, several micro-habitats on riprap likely contain species that also occurred in natural rocky habitats. Still, it is interesting that the same general pattern for mobile species was also found for seawalls.

There may be several reasons why riprap and natural rocky intertidal areas were found to be similar in this study but not in others

(Table 2-1). Osborn (2005) conducted her study on the *Endocladia/Balanus* communities restricted to the upper intertidal zone in central California. The upper and lower intertidal zones are defined by variation in physical and biological factors, and it is not surprising that results from the upper intertidal may differ from those from the lower intertidal. Chapman and Bulleri (2003) found a similar situation on seawalls, where intertidal communities displayed differences at high and mid-shore levels, but not at lower levels. Another reason may be age. All the riprap sites in this study were several decades old, the youngest being DBW, 38 years old at the time of sampling (Bottin 1988). In studies where age was found to influence diversity all the sites were relatively young - less than 20 years, and most less than 10 (Sammarco *et al.* 2004; Osborn 2005; Pinn *et al.* 2005). It seems reasonable that when constructing new riprap habitats that provide large amount of initial bare space there may be several years of succession (Moore 1939; Reish 1964). In some regions the amount of natural rocky habitats may be relatively diminutive in comparison to soft bottom communities and therefore dispersal to new rocky habitat may be limited (e.g. Bacchiocchi & Airoldi 2003). In contrast, southern California has a well developed and diverse rocky flora and fauna that is probably able to colonize new structures immediately and thoroughly, both intertidally and subtidally. All these possibilities suggest that regional variation in habitat distribution, species pool, history, and other physical factors may be very important for the ability of riprap to support local marine communities.

Wave Exposure

In this study, most of the variation in diversity and community composition occurs at the site level. Each site may differ greatly from other sites regardless of whether it is riprap or natural, enough so that a general comparison of the two different habitat types reveals few differences, except in the mobile species. There are many factors that could be contributing to this variation among sites, especially because the distance between sites was quite variable (Table 2-2). But even here evidence suggests much of the variation is caused by differences in wave exposure, which is known to be of profound influence on rocky intertidal communities (Ricketts *et al.* 1985; Denny & Wethey 2001; Denny *et al.* 2004).

The Mantel test identified three variables that together best explain the distribution of species observed: mean significant wave height, swash zone, and the transect length. Although the dynamics of breaking waves in the intertidal are extremely complex, all three of these factors influence the wave forces experienced by intertidal organisms (Denny & Wethey 2001; Smith 2003; Bucharth & Hughes 2006). Indeed, the importance of wave forces have been documented in several other studies on riprap and anthropogenic structures as well (Southward &

Orton 1954; Davis *et al.* 2002; Bacchiocchi & Airoldi 2003; Bulleri *et al.* 2006; Jonsson *et al.* 2006). Mean significant wave height was often measured from the same buoy for riprap and rocky intertidal sites (Table 2-2). Wave height data is simply not available on a finer spatial scale at the shoreline. Needless to say, the higher the wave height the greater the force exerted on rocky intertidal organisms. The swash zone, which was usually shorter at riprap sites, also means that waves approach much closer to shore before breaking, which in turn means more kinetic energy hits the intertidal zone. The transect length was indicative of the area of which a wave imparts its kinetic energy as it hits the shoreline. These distances were always shorter on riprap, which means more energy was imparted on a smaller area. The net result is that organisms may be experiencing greater wave energy on riprap sites than on nearby natural sites under similar conditions. This would explain the difference in mobile species, as well as the distribution of many of these species on the interior or calmer side of breakwaters.

Several artifacts of construction enhance the forces generated by waves as they collide with breakwaters (Bucharth & Hughes 2006). For example, riprap structures are generally very steep, commonly with slopes of 30 degrees or more (Bottin 1988). This means a wave will impart much more energy onto a smaller area than it would on a shallower sloping shore. Also, since jetties and breakwaters are built extending out from shore, the water in front of them is usually deeper, which allows a wave to approach much closer before friction with the bottom slows the wave down. Indeed, waves frequently break directly onto the intertidal zone on riprap structures, whereas in natural areas waves frequently break before reaching shore (*personal observation*).

Invasive Species

Only a few of the species found in either habitat were invasive (Table 2-3). *Caulacanthus ustulatus* (Rhodophyta), a species not recorded in the area before 1990, occurred in moderate abundance on natural rock but not at all on riprap (Zuccarello *et al.* 2002; Murray *et al.* 2005). The bryozoans *Bugula neritina* and *Watersipora subtorquata* occurred uncommonly only on natural rock, while *Mytilus galloprovincialis* occurred infrequently in both habitats. Some studies have found anthropogenic structures to facilitate invasions (Bulleri & Airoldi 2005; Wasson *et al.* 2005{Glasby, 2006 #1378; Bulleri *et al.* 2006; Tyrrell & Byers 2007). That is clearly not the case for the open coast southern California riprap structures. However, the rocky intertidal environment on the west coast of North America, especially in exposed conditions, is known to be sparsely invaded (Maloney et al. 2006). Furthermore, *Caulacanthus ustulatus* and *Mytilus galloprovincialis* have been observed on riprap inside protected bays (Becker et al. 2007, *personal observation*). This implies that the anthropogenic origin of many hard substrates by itself is not sufficient to explain a preponderance of invasive species in some areas, and that an interaction with wave exposure may be involved.

The only other study in southern California that investigated the communities on riprap is by Davis et al. (2002, but see Rader 1998). Davis et al. compared intertidal and fish communities inhabiting pairs of sites on exposed and sheltered sides of riprap structures in San Diego Bay. Their sites also ranged over a wave exposure gradient from the mouth to the head of San Diego Bay. They found that as wave exposure decreased, and the disparity in wave exposure between the paired sites diminished, the communities became more similar. In addition, exposed communities at the head of the bay, where wave exposure was low, differed greatly from those at the mouth of the bay where wave exposure was higher. Furthermore, they sampled natural rock outside the bay in more exposed conditions and found they were most similar to the most exposed sites inside the bay (i.e. at the mouth). In general richness and cover of organisms was greater in more exposed conditions. Wave exposure clearly plays a dominant role structuring communities in riprap habitats, just as it does in natural ones.

Future Investigations

There is much more work to be done before we have a sufficient understanding of the ecological role riprap plays in marine environments.

In this study I limit my investigation to wave-exposed sites. Riprap is used in a variety of marine environments that differ widely in many parameters, including wave exposure. Indeed, riprap may be more common in areas that already enjoy some measure of protection from waves, such as the ports and harbors of northern California, Oregon, and Washington where wave exposure on the open coast is far more extreme than southern California (Walker 1988; Lockhart & Morang 2002). Also, when riprap is used to armor shorelines (e.g. in harbors), as opposed to a free standing structures such as a jetty or breakwater, it likely differs greatly in physical factors that may affect marine organisms (e.g. wave exposure, desiccation, run-off, proximity to the bottom, etc.). The ability of riprap to support marine organisms in these different environments is essential for understanding how current and new structures might affect the environment.

Whether or not organisms living on riprap structures are contributing reproductively to local populations is also of vital interest. If they are then populations on riprap structures may be considered ecological resources and should be monitored. If not, then they likely act as demographic sinks. In southern California where much of the riprap has been constructed over soft bottoms, it probably enhances the abundances of organisms living on rocky substrates, at the expense of the soft-bottom communities (Davis et al. 1982). Furthermore, if riprap populations are propagule sources then they could heavily influence the connectivity and genetic structures of populations within the region by altering the distance between suitable habitats and facilitating migration, in addition to supporting populations in natural areas (Becker et al. 2007). This question is very important for conservation efforts since, at present, monitoring studies in southern California typically ignore riprap (J. Engle, *personal communication*).

One aspect of riprap that seems to have never been investigated ecologically is the interstitial space. When large boulders are piled on top of each other there is naturally a great volume of space in between. In fact, engineers have found this “pore” space to have a strong influence on the stability of the structure and its ability to absorb wave energy (Bucharth & Hughes 2006). It seems probable that pore space has a strong biological influence as well. All of the space on boulders *inside* the riprap structures is potential habitat. Most riprap structures are permeable to some extent and benthic organisms colonize every available centimeter of space (*personal observation*). This pore habitat, which is in essence three dimensional, is vast and likely greatly exceeds the benthic habitats measured in this and other studies so far, which has been essentially two dimensional in nature. Physical conditions are very different in this pore space and may approximate a cave environment. Such caves occur on the west coast of North America, but not to a large extent (e.g. Secord & Muller-Parker 2005). But riprap is common in the United States and thus the pore habitat is also common (Smith 2003). Preliminary observations suggest a large number of filter-feeding organisms such as barnacles, sponges, bryozoans, hydroids, tunicates, and anemones thrive in this habitat. It may also provide shelter for a variety of species as juveniles (Binns & Remmick 1994). Finally, these organisms almost certainly influence the characteristics of the water column (Wilkinson et al. 1996). All of these factors deserve further scrutiny.

The possibility that riprap structures may be ecologically beneficial in some ways should not be overlooked. Some species clearly thrive on riprap. For example, *Lottia gigantea,* a commonly harvested species that significantly modifies spatial patterns in the upper rocky intertidal (Pombo & Escofet 1996; Lindberg *et al.* 1998), was five times more abundant on riprap than on natural rock (*data not shown*). Riprap structures are also known to attract and support a variety of fish and have been reported as extremely good lobster diving and sport fishing sites (Chapman 1963; Davis *et al.* 1982; Kovach 1996). An interesting conservation application of riprap might be as marine reserves. Unlike many terrestrial habitats, humans can be excluded from riprap without compromising its intended anthropogenic purpose, that is, absorbing wave energy. There are many complex economic and social considerations to be accounted for when deciding how best to use anthropogenic structures in urban marine environments (Love *et al.* 2003; Airoldi *et al.* 2005; Moschella *et al.* 2005). While these aspects are beyond the scope of this study, they do underscore the necessity and urgency of studying the ecological importance of riprap and other anthropogenic structures in marine environments.

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Table 2-1 Summary of previous studies comparing riprap to natural rock.

Study	Location	Habitat Type	Difference in Diversity?	Difference in Community Structure?
Osborn 2005	Monterey, CA	Intertidal Riprap Shoreline	Yes, for algae only riprap higher	Yes
Bulleri & Chapman 2004	Livorno, Italy	Intertidal Riprap Breakwater	Not tested	Mixed, 3 of 9
Moschella et al. 2005	Lyme Regis, UK	Intertidal Riprap Breakwater	Yes, riprap lower[a]	Yes
Moschella et al. 2005	Gabicce, Italy	Intertidal Riprap Breakwater	Yes, riprap lower[a]	Yes
Moschella et al. 2005	Calonge, Spain	Intertidal Riprap Breakwater	Yes, riprap lower[a]	Yes
Moschella et al. 2005	Cubelles, Spain	Intertidal Riprap Breakwater	Yes, riprap lower[a]	Yes
Clynick 2006 comparisons difference	Livorno, Italy	Subtidal Riprap Breakwater	Mixed, riprap higher in 2 of 6 comparisons	Mixed, 1 of 6 found a
Chapman 2006	Sydney, Australia	Intertidal Artificial Boulder Fields[b]	No	No

[a] Note that in Moschella et al. 2005 there doesn't seem to be a statistical comparison of diversity.

[b] These boulders are left over from the construction or degradation of seawalls. While not a riprap structure per se, they are qualitatively similar.

Table 2-2 A summary of the riprap and natural rocky sites used in this study; Mission Bay (MB), Scripps Institute of Oceanography (SIO), Dana Pt. Breakwater (DBW), Dana Pt. State Reserve (DPR), Corona del Mar (CDM), Newport Harbor (NP), San Pedro (SP), and Pt. Fermin (PF). “CDIP buoy” refers to the buoy that wave data was collected from. “Ta” is the average period of a wave which is equal to 1/average frequency and average frequency is equal to the energy weighted over the wave spectrum. “1-meter isocline” refers to the distance from shore to the one meter isocline.

	MB	SIO	DBW	DPR
Latitude	32º 45.5'N	32º 52.3'N	33º 27.5'N	33º 27.6'N
Longitude	117º 15.6'W	117º 15.2'W	117º 42.3'W	117º 42.6'W
Type	Riprap	Natural	Riprap	Natural
Sampling Date	Jan-Feb 2005	Mar 2005	Dec 2005-Mar 2006	Dec 2004 - Feb 2005
CDIP Buoy	093	073	096	096
Construction Date	1949	-	1968	-
Mean Significant Wave Height (m)	1.01m	0.89m	0.88m	0.90m
Mean Wave Period (s)	13.77s	10.68s	13.91s	13.82s
Mean Ta (s)	7.83s	7.49s	7.62s	7.33s
Mean SST SST (C)	17.86º	15.80º	18.01º	18.13º
Chart	18765	18774	18746	18746
1-meter isocline (m)	3.72m	5.32m	3.34m	5.05m
Mean Dip	32.38º	13.125º	36.45º	24.06º
Mean Transect Length	7.97m	32.15m	7.28m	20.22m
Area (m^2)	5963m^2	7897m^2	16463m^2	21406m^2
Mean Swash Zone Width (m)	9.05m	55.63m	6.15m	31.89m

Table 2-2 Continued

	CDM	NP	SP	PF
Latitude	33º 35.5'N	33º 35.3'N	33º 42.3'N	33º 42.4'N
Longitude	117º 52.3'W	117º 52.8'W	118º 16.3'W	118º 17.7'W
Type	Natural	Riprap	Riprap	Natural
Sampling Date	Mar 2005	Apr 2005	Dec 2005-Jan 2006	Jan - Mar 2006
CDIP Buoy	172	172	092	092
Construction Date	-	1934	1910	-
Mean Significant Wave Height (m)	0.74m	0.74m	0.96m	0.96m
Mean Wave Period (s)	13.77s	13.77s	11.96s	11.96s
Mean Ta (s)	7.22s	7.22s	6.72s	6.72s
Mean SST (C)	16.89º	16.89º	17.09º	17.42º
Chart	18754	18754	18749	18749
1-meter wave (m)	6.37m	1.67m	2.27m	4.75m
Mean Dip	32.09º	40.33º	43.15º	28.65º
Mean Transect Length	23.62m	5.05m	4.41m	11.03m
Area (m^2)	5963m^2	4605m^2	13481m^2	6083m^2
Mean Swash Zone Width (m)	31.84m	15.54m	4.16m	29.28m

Table 2-3 Summary of Species found in Natural Rocky (NR) intertidal and Riprap (RR) intertidal habitats with the number of transects each species occurred in each habitat type. Species with an * exceeded 1% cover or 1% of the individuals in a single transect, and were thus tested individually (see text). Species marked with an ^{a} are invasive.

Sessile Species	NR	RR
Green Algae		
Chaetomorpha linum	1	4
Cladophora sp.	0	1
green crust*	4	12
Ulothrix spp.*	0	2
Ulva spp.*	19	14
Unidentified green	0	1
Brown Algae		
Cumogloia sp.	1	0
Dictyopteris undulata	0	2
Egregia menziesii*	0	3
Eisenia arborescens*	0	4
Endarachne binghamiae*	5	11
Giffordia granulosa	0	1
Halidrys dioica	1	0
Leathesia difformis	2	4
Petrospongium rugosum	5	4
Ralfsia pacifica*	21	17
Ralfsia sp.*	13	9
Scytosiphon dotyi	0	3
Selvetia fastigiata	2	0
Unidentified brown	5	6
Unidentified brown	5	6
Plants		
Phyllospadix torreyi	1	0

Sessile Species	NR	RR
Red Algae		
Bosiella orbigiana*	5	12
Calliarthron tuberculusom	0	2
Callothamnion rupicola	1	0
_Caulacanthus ustulatus_*^{a}	20	0
Chondria californica	1	0
Corallina pinnatifolia*	21	21
Corallina vancouveriensis*	11	15
Coralline crust*	20	18
Cryptopleura corallinara*	5	5
Gelidium spp.*	15	13
Hildenbrandia sp.*	4	5
Jania crassa	1	0
Laurencia pacifica*	13	2
Lithophyllum lichenare*	0	3
Lithothrix asperegillum	1	2
Mastocarpus sp.*	3	0
Mazaella affinis	1	9
Mazaella leptorhyncos	4	2
Microcladia coulteri	1	0
Nemalion helminthes	1	3
Plocamium pacificum	0	1
Plocamium violaceum	0	3
Polysiphonic spp.*	5	12
Porphyra sp.*	6	5
Prionitis lanceolata*	3	7
Pseudolithophyllum neofarlowii	0	1
Rhodymenia sp.	4	4
Unidentified Red	5	4

Table 2-3 continued.

Sessile Species	NR	RR
Anemones		
*Anthopleura elegantissima**	17	5
Anthopluera sola	1	1
Barnacles		
*Balanus glandula**	19	21
*Chthamalus fissus**	21	21
Megabalanus californicus	3	14
*Policipes polymerus**	17	21
*Tetraclita rubescens**	16	21

Sessile Species	NR	RR
Bivalves		
*Mytilus californianus**	21	21
Mytilus galloprovincialis [a]	2	8
*Pseudochama exogyra**	9	5
Septifer sp.	11	1
Sessile Gastropods		
Serpullorbis squamigerus	4	1
Polychaetes		
*Phragmatopoma californica**	19	14
Serpulids	13	14
Sponges		
Sponge	1	0
Unidentified		
Unidentified orange crust	0	2

Sessile Species	NR	RR
Bryozoans		
Bugula neritina [a]	1	0
Hippodiplosa insculpta	1	7
Schizoporella unicornis	0	3
Thallamoporella californica	0	3
Watersipora subtorquata [a]	2	0

Mobile Species	NR	RR
Gastropods		
*Acanthinucella spirata**	9	0
Combined limpets*	21	21
*Conus californicus**	1	0
*Fissurella volcano**	19	16
*Littorina keenae**	21	15
*Littorina scutulata**	20	7
*Lottia gigantea**	15	20
*Macron lividus**	3	0
*Mexicanthina lugubris**	3	1
Nucella emarginata	2	2
Roperioa poulsoni	*1*	*0*
Tegula funebralis	2	0
Polyplocophora		
Lepidochitona dentiens	1	0
*Lepidochitona hartwegii**	9	1
Mopalia muscosa	3	0
Nuttallina spp.*	21	20
Striped chiton	1	0
Echinoderms		
*Strongylocentrotus purpuratus**	2	4

Table 2-4 Results of Nested 2-Way ANOSIM tests for community differences. P-values are determined through permutation.

	Site Level		Habitat Level	
	R-values	p-values	R-Values	p-values
All Species	0.855	0.001	-0.104	0.771
Sessile Species Only	0.791	0.001	-0.354	0.943
Mobile Species Only	0.480	0.001	-0.156	0.800

Table 2-5 Species identified by SIMPER as contributing to the dissimilarities between natural rock and riprap. The average abundance per transect in riprap (RR) and natural rocky (NR) habitats are in the first two columns (counts for mobile species, percentages for sessile species). The third column indicates the average Bray-Curtis dissimilarity (D) of each species between habitats. The fourth column is the percentage each species contributes to the overall dissimilarity between habitats.

Mobile Species	RR	NR	Mean	Contributing%
Limpets	141.76	121.19	24.76	38.78
Littorina keenae	14.90	150.00	23.90	37.43
Littorina scutulata	2.62	37.71	7.45	11.66
Lottia gigantean	13.29	2.48	2.66	4.17
Sessile Species				
Mytilus californianus	1.20	1.21	10.05	16.11
Corallina pinnatifolia	0.84	1.06	7.45	11.95
Balanus glandula	0.77	0.12	6.25	10.02
Chthamalus fissus	1.17	1.21	5.68	9.11
Caulacanthus ustulatus	0.00	0.63	4.91	7.88
Corallina vancouveriensis	0.13	0.30	2.67	4.29
Policipes polymerus	0.31	0.04	2.47	3.95
Gelidium spp.	0.14	0.21	2.12	3.41
Ralfsia sp.	0.11	0.19	2.10	3.37
Ralfsia pacifica	0.10	0.27	1.89	3.03
Ulva spp.	0.19	0.09	1.82	2.93

Table 2-6 Results of nested ANOVA comparisons for individual species abundance. Only sessile species contributing greater than 1% cover and mobile species contributing 1% count within at least one transect are considered. When significant (α = 0.05) the habitat in which the greater abundance occurs is noted in the final column. NR = natural rock and RR = riprap.

Sessile Species	MS	F	p-value	Habitat
Anthopleura elegantissima	0.1070	6.4546	0.0158	NR
Balanus glandula	4.4103	42.0270	≤0.0001	RR
Bosiella orbigniana	0.0011	0.1308	0.7198	
Caulacanthus ustulatus	4.0984	37.7220	≤0.0001	NR
Chthamalus fissus	0.0130	0.0520	0.8210	
Corallina pinnatifolia	0.5282	1.3483	0.2537	
Corallina vancouveriensis	0.3260	5.4978	0.0250	NR
Coralline crust	0.2785	10.6399	0.0025	NR
Cryptopleura corallinara	0.0011	0.1308	0.7198	
Egregia menzeisii	0.0098	2.2690	0.1412	
Eisenia arborescens	0.0038	1.6865	0.2028	
Endarachne binghamiae	0.1907	6.0846	0.0188	RR
Gelidium spp.	0.0409	0.8085	0.3749	
Hildenbrandia sp.	0.0003	0.9105	0.3467	
Laurencia pacifica	0.0337	3.3856	0.0745	
Lithophyllum lichenare	0.0055	1.0119	0.3216	
Mastocarpus sp.	0.0014	4.2857	0.0461	NR
Mytilus californianus	0.0017	0.0027	0.9590	
Phragmatopoma california	0.0704	2.1858	0.1485	
Policipes polymerus	0.8093	16.1333	0.0003	RR
Polysiphonic spp.	0.0101	1.9720	0.1693	
Porphyra sp.	0.0020	1.1346	0.2943	
Prionitis lanceolata	0.1573	14.4030	0.0006	RR
Pseudochama exogyra	0.4081	20.5750	≤0.0001	NR
Pseudolithophyllum neofarlowii	0.0010	2.5298	0.1210	
Ralfsia pacifica	0.1534	7.3523	0.0106	NR
Ralfsia sp.	0.0672	0.9000	0.3495	
Tetraclita rubescens	0.3001	18.8936	0.0001	RR
Ulothrix spp.	0.0015	1.0119	0.3216	
Ulva spp.	0.1101	1.5262	0.2252	
Unidentified green crust	0.0014	0.8510	0.3628	

Mobile Species	MS	F	p-value	Habitat
Acanthinucella spirata	6.8810	8.3554	0.0067	NR
Combined limpets	4443.0000	0.5899	0.4477	
Conus californicus	0.0952	1.0119	0.3216	
Fissurella volcano	5.1137	11.4330	0.0018	NR
Lepidochitona hartwegii	4.0238	5.6378	0.0234	NR
Littorina keenae	54.8420	25.7308	≤0.0001	NR
Littorina scutulata	63.1320	58.6136	≤0.0001	NR
Lottia gigantea	20.0773	49.3518	≤0.0001	RR
Macron lividus	0.3810	3.2381	0.0808	
Mexicanthina lugubris	0.2143	2.0238	0.1640	
Nuttallina spp.	2.7188	5.8361	0.0212	NR
Strongylocentrotus purpuratus	1.5238	2.8944	0.0980	

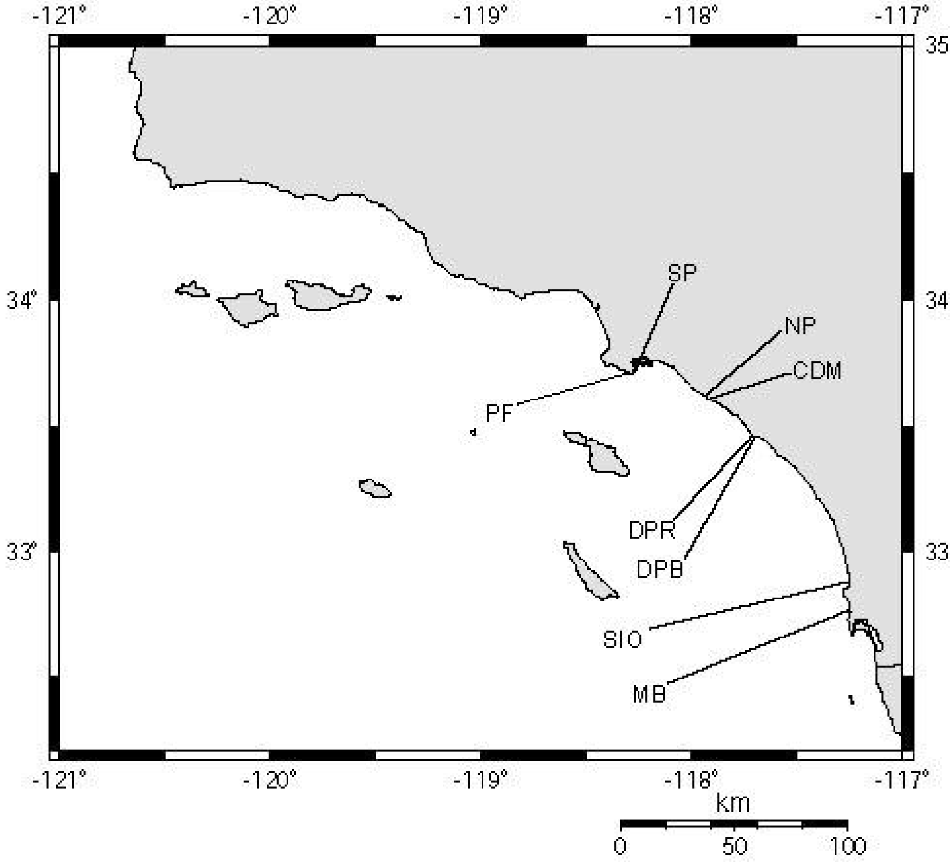
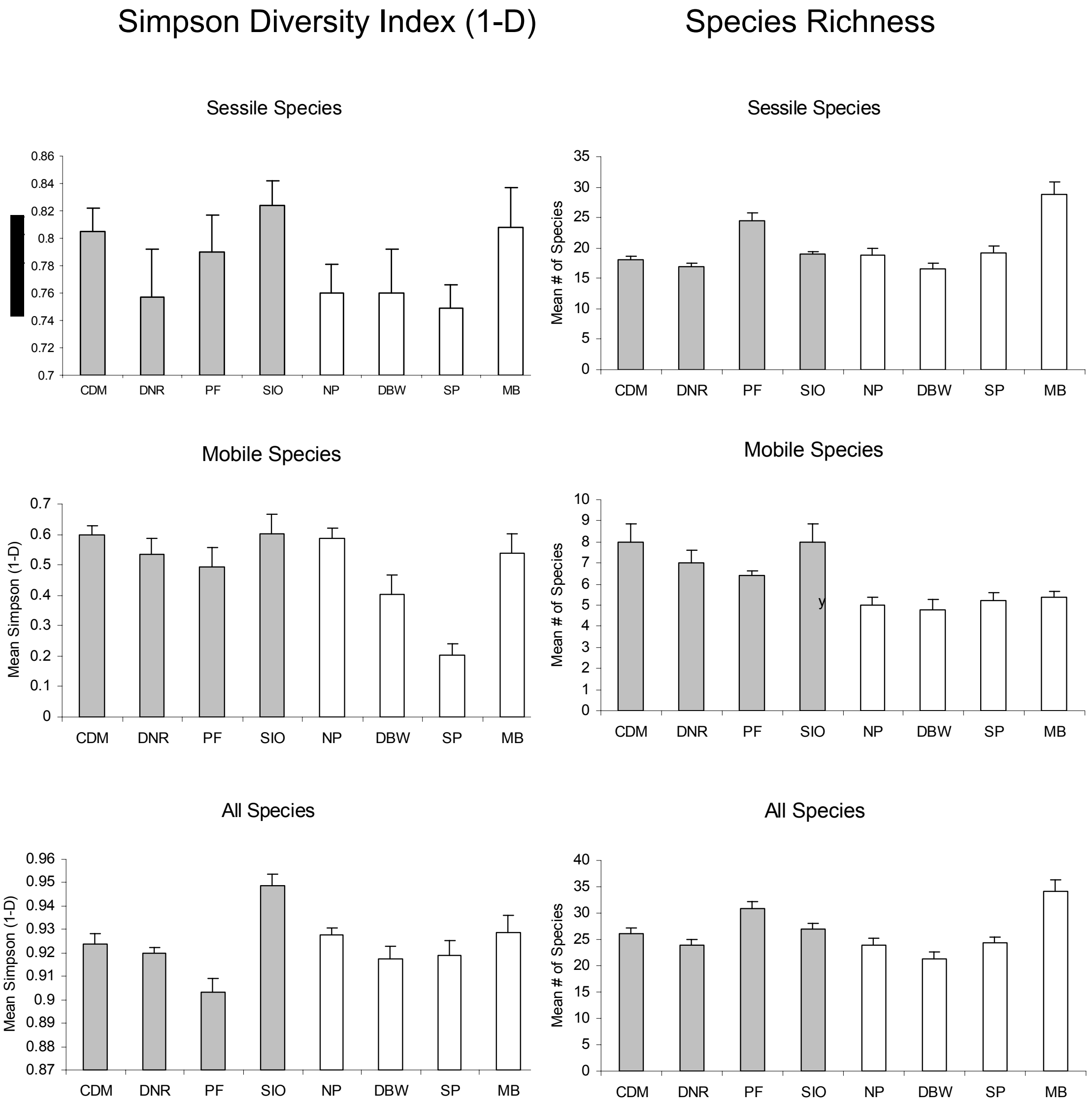


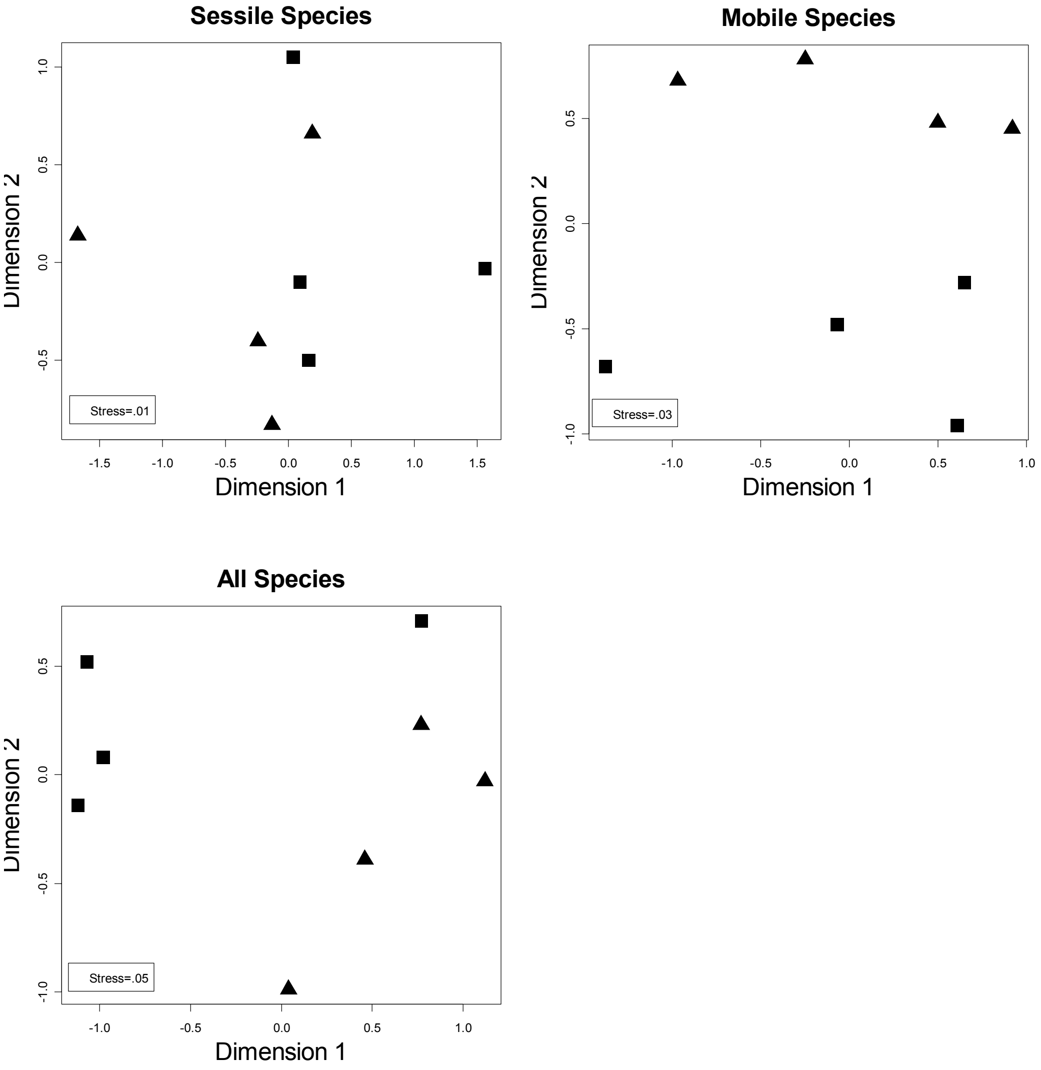
Figure 2-1 The southern California coastline with sites labeled. Riprap sites include Mission Bay (MB), Dana Pt. Breakwater (DPB), Newport (NP), and San Pedro Breakwater (SP). The natural rocky sites include Scripps Institute of Oceanography (SIO), Dana Pt. State Reserve (DPR), Corona del Mar (CDM), and Pt. Fermin (PF).

Figure 2-2 Mean Simpson and Richness values within each site. Sessile and Mobile species have been analyzed separately, and then combined and analyzed together. Solid bars indicate natural rocky sites and stippled bars indicate riprap sites. Error bars represent standard error of the mean.


Simpson Diversity Index (1-D)
Species Richness
Sessile Species
0.86
0.84
0.82
0.8
0.78
0.76
0.74
0.72
0.7
CDM
DNR
PF
SIO
NP
DBW
SP
MB
Sessile Species
Mean # of Species
35
30
25
20
15
10
5
0
Mobile Species
Mean Simpson (1-D)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Mobile Species
Mean # of Species
10
9
8
7
6
5
4
3
2
1
0
y
All Species
Mean Simpson (1-D)
0.96
0.95
0.94
0.93
0.92
0.91
0.9
0.89
0.88
0.87
All Species
Mean # of Species
40
35
30
25
20
15
10
5
0

[redacted]

Figure 2-3. MDS ordinations of riprap and natural rocky sites: sessile species only (stress = 0.01), mobile species only (stress = 0.03), and all species with a presence absence transformation (stress = 0.05). Each triangle represents the sum of all transects with each site. The distance between any two triangles represents how similar the data from each site are. The closer the triangles the more similar the data are. Triangles represent riprap sites and squares represent natural rocky sites.



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CHAPTER 3

A test of rock-type on diversity and community composition in the southern California rocky intertidal

ABSTRACT

Scientists have long recognized that substrate can have a very important influence on benthic organisms. However, tests of how natural rock composition affects diversity or community composition of benthic habitats *in situ* are rare. Understanding the effects of rock composition on marine communities are very important because humans often alter the coastline by installing riprap structures and seawalls composed of non-indigenous rock. Here, a field experiment designed to test whether granite and sandstone, the dominant rock types used in riprap or found in natural sites in San Diego County, affect the diversity and community composition of a rocky intertidal habitat in southern California yielded no differences due to rock type. Rather, differences in diversity and community composition could be explained by a change in season and the physical factors that change with it. This suggests that any effects due to the composition of rocky substrates may be negligible and/or overwhelmed by other factors, such as wave exposure. This result has implications for the construction of new structures using rocky rubble to protect the coastline, such as jetties and breakwaters. Several authors have suggested incorporating factors to enhance marine communities into the

design of such structures. This study suggests that changing the rock type, at least for southern California, may not have an effect on enhancing marine communities on artificial substrates.

INTRODUCTION

Benthic marine environments are notoriously patchy. Understanding the processes that generate and maintain patchiness in these environments has been one of the primary goals of ecologists for a long time (e.g. Baker 1909; Huntsman 1918; Hewatt 1935; Hatton 1938; Doty 1946). Scientists have long suspected that substrate plays an important role in the variation of marine communities (Zobell & Allen 1935; Hatton 1938; McDougall 1943; Pomerat & Weiss 1946; Wisely 1958). But surprisingly few studies have experimented with the effects of natural (i.e. non-synthetic) hard substrate composition on benthic marine communities in the field.

Field studies that investigated the effects of non-synthetic substrate composition on benthic marine communities have produced varied results. From a very early experiment in France, Hatton (1938) found no difference in settlement of *Semibalanus balanoides* on three types of granite and diabase. Moore and Kitching (1939), however, reported differences in abundance of *Chthamalus stellatus* on hard and soft rocks from a field survey in England. In a multi-scale experiment using shale, gabbro, mudstone, and sandstone Caffey (1982) found no effect on settlement or survival of the barnacle *Tesseropora rosea* in southeast Australia. McGuinness and Underwood (1986), also in Australia, experimented with sandstone and shale boulders and reported no effect of rock type on species diversity, although there were effects on the abundance of some individual species. Raimondi (1988) manipulated basalt and granite on shores in the Gulf of California to show that a difference in thermal capacity could cause a variation in settlement of *Chthamalus anisopoma*. In the most thorough comparison of natural substrates, Holmes et al. (1997) tested 15 different rock types on the settlement of *Semibalanus balanoides* in Scotland. They found differences for some, but not all, of the rock types. In their experiment slate, quartz, and marble had the greatest settlement while millstone grit sandstone and granitic gneiss had the fewest. Finally Osborn (2005), in a test of the rock types used to armor shorelines in Monterey Bay, used tiles of basalt, sandstone, granite, and slate to test for differences in settlement and recruitment of *Chthamalus fissus/dalli* and *Balanus glandula* in central California, U.S.A. Although she found clear differences, the results were not the same for both species and also differed between sites for *Chthamalus fissus/dalli*. Furthermore, Osborn found slate to be the least favorable for barnacle settlement, which is the direct opposite of what Holmes et al. (1997) found for *Semibalanus balanoides*. Others studies, testing a mixture of natural and synthetic materials, found variable results from place to place and from time to time (Osman 1977; McGuinness & Underwood 1986; McGuinness 1989).

The above studies indicate different results for different organisms in different places. Some have found differences, and some have not, despite well executed experiments (e.g. Caffey 1982; Osborn 2005) In addition, most of them investigate only one or a few species. Several other studies explore the effects of substrate composition on settlement of marine organisms or communities. But most are field surveys with no experimentation (e.g. Bavestrello *et al.* 2000; Cattaneo-Vietti *et al.* 2002; Guidetti *et al.* 2004), lab experiments (e.g. Crisp & Ryland 1960; Mihm *et al.* 1981; Rittschof *et al.* 1984; Bavestrello *et al.* 2000; Groppelli *et al.* 2003; Faimali *et al.* 2004), or tests of synthetic substrates such as concrete or glass (e,g, Coe 1932; Pomerat & Weiss 1946; Crisp & Barnes 1954; Meadows 1969). There is not enough evidence to predict or understand the variation in a benthic marine community caused by rock composition in an area that has not been studied carefully.

Furthermore, it seems clear that these effects may be negligible or non-existent in some places but important in others (Glasby 2000). This is a very important result. First, understanding which environmental factors do not cause variation is just as important as understanding which do. Second, if a factor causes variation in some locations, but not others, generalizations or predictions based on previous studies may be misleading when applied to unstudied locations or conditions (Glasby 2000).

The effects of substrate composition on the abundance and distribution of marine communities is of tremendous practical importance due to human modification of urban coastlines (Glasby & Connell 1999; Davis *et al.* 2002; Osborn 2005, Pister in review). Artificial structures, such as seawalls, jetties, and breakwaters, have been added to hundreds of miles of coastlines (Glasby & Connell 1999; Moschella *et al.* 2005; Moschella *et al.* 2005). In southern California alone humans have altered 30% of the coastline with riprap, the rocky rubble used to build jetties and breakwaters (Clark et al. 2002). In San Diego County, riprap covers 80.16 km of 259.36 km of coastline (personal observation). These structures are often built from non-synthetic rock types that are different from the indigenous rock of the surrounding shoreline (Davis *et al.* 2002; Osborn 2005). The effects of substrate composition used in marine urban structures have rarely been compared with the natural substrates in the same area (Glasby 2000; Osborn 2005). Given the ubiquity of anthropogenic structures, like riprap, and the likelihood of further alterations to the shoreline (Dean *et al.* 1987; McCarthy *et al.* 2001), understanding the role of urban substrate composition on benthic organisms is essential for effective management and predicting human impacts.

This study tests the effects of sandstone and granite on species diversity and community composition in the southern California rocky intertidal environment. These substrates represent the dominant indigenous and riprap rock types, respectively, in San Diego county (Tway 1991, personal observation). Osborn (2005) found that barnacles settled in greater abundance on native rocks in comparison to other non-indigenous rock types. Glasby (1999) found that the native sandstone supported different communities than nearby concrete and wood substrates of urban structures. Sandstone is also more porous than granite which makes it more likely to retain water during low tide, thus reducing dessication (Pomerat & Weiss 1946; Anderson & Underwood 1994). I tested the prediction that sandstone tiles will develop communities of different composition and greater diversity than granite tiles. Recruitment is known to vary seasonally (Coe 1932; Osman 1977; Morris *et al.* 1980; Osborn 2005). Therefore I also tested the prediction that community composition and diversity will continue to diverge through time. The null hypotheses are simply that no difference in diversity or community composition between sandstone and granite will emerge.

METHODS

Site

This experiment was conducted in the rocky intertidal zone within the Scripps Coastal Reserve at the Scripps Institution of Oceanography, located at 32º 52.3' N and 117º 15.2' W. This site consists of a broad, shallow sloping mudstone bench strewn with large mudstone boulders in a semi-exposed open coast wave environment. The lower intertidal zone, where the experiment was conducted, typically consisted of patchy beds of the mussel *Mytilus californianus* mixed with the gooseneck barnacle *Policipes polymerus*. Mussel beds were interspersed with fleshy red algal turf communities (e.g. *Gelidium* spp., and *Laurencia pacifica*) and coralline turf communities (e.g. *Corallina pinnatifolia* and *Corallina vancouveriensis*).

Tiles and Experimental Design

Tiles were made of granite or sandstone floor tiles purchased from local masonry stores, and cut with a tile saw to 10 x 10 cm. Granite and sandstone tiles measured 9.3 mm and 14.5 mm thick, respectively. A 5.3 mm (3/16") hole was drilled in the center of each tile for later attachment.

Tiles were arranged into three arrays, with each array serving as a single replicate. Each array consisted of two pieces of marine plywood, with 12 tiles anchored to each piece of wood using stainless steel bolts. Tiles were spaced 2 cm apart with four rows of three tiles each. Each piece of plywood was fastened to the rock with four stainless steel bolts set into holes filled with marine epoxy. The two pieces of plywood in each array were anchored adjacent to each other, thus forming a single unit. Tiles were attached to plywood in order to reduce the number of holes drilled into the rock. Two pieces of wood were used for each array in order to reduce the wave force endured by any one piece and to minimize tile loss should any part of the array break free.

Tiles were arranged randomly within an array with the constraint that an even number of each rock type was distributed on each piece of plywood. The intent of this was to maintain a semblance of balance should some part of an array be lost. Arrays were installed on outward facing boulders at approximately 0.0 MLLW, and spaced roughly 10 meters apart. Enough tiles were attached to each array so that one replicate of each rock type could be removed each month. Thus, there were 24 tiles in each array, 12 each of sandstone and granite.

Sampling

Each month at low tide one tile of each rock type from each array (for a total of six tiles), was removed and replaced with clean tiles of the same rock type. Removed tiles were then brought to the lab for sampling. This scheme produced a temporally independent set of tiles each month. Preliminary analysis during the first six months revealed no differences between sandstone and granite tiles. So after six months tiles were no longer sampled monthly, and simply left alone for the remainder of the experiment. The experiment began in March 2004 and terminated in February 2005.

At the termination of the experiment temporally independent sets of tiles had been recovered for 11 sequential monthly time periods, (i.e. sets of tiles had been deployed for one month, two months, three months … 11 months; Figure 3-1). After five months half of one array was lost, reducing replication for some longer time periods. Also, this design resulted in two sets of tiles deployed for five months, and two sets deployed for six months. The first set of five and six month tiles collected in August and September 2004, respectively, are hereafter referred to as the “summer” tiles. The second set for each interval started in August and September 2004, respectively, and both ended in February 2005 (Figure 3-1). These sets are hereafter referred to as the “winter” tiles.

I took digital photographs of each tile in the lab for measurement of cover using Image J (Rasband 2005). Initially I measured cover by tracing each organism precisely with the tracing tool in Image J and the software to measure the exact area. Eventually I compared this method to another that employs a macro to place 25 randomly distributed dots on each photo. I assigned 4% cover to each organism under a dot, and 0.5% to any organism occurring on the tile but not under a dot (Meese & Tomich 1992; Dethier *et al.* 1993). Using a dissecting scope to examine each tile while measuring the cover of species in the digital photograph, I was able to obtain accurate identifications and measurements for all species present. Two granite and three sandstone tiles were selected at random and both methods were conducted on each. Paired t-tests revealed no differences between cover distributions quantified by each method on all five tiles (t_{13}=0.0195, p=0.98, t_7=-.1321, p=0.89, t_4=-0.0818, p=0.93, t_{10}=-0.1150, p=0.91, t_{11}=0.3053, p=0.76, respectively). So I used the second method on the remainder of the tiles and combined the data.

Analysis

Diversity was measured using species richness (defined as the number of species) and the Simpson Diversity Index (1-D). The reciprocal form of the Simpson Diversity Index, 1-D, is considered more robust, especially at smaller sample sizes, than the more popular Shannon-Weiner Diversity Index (Lande 1996; Magurran 2004). Differences in these measures between sandstone and granite tiles deployed for the same time periods were tested using analysis of variance (ANOVA). Differences in community composition were tested using Analysis of Similarities (ANOSIM) on Bray-Curtis dissimilarities of non-transformed data (Clarke 1993; McCune & Grace 2002). Non-Metric Multidimensional Scaling (MDS) was used to ordinate these data for visual comparisons.

I tested the abundance of individual species for differences between sandstone and granite tiles deployed for 11 months (Appendix B). This time treatment had the greatest amount of replication and had been deployed the longest. Any differences that occurred should be most evident in this set of tiles. Comparisons were made using ANOVA on species that averaged ≥1% cover on tiles from at least one of the treatments.

Simpson Diversity Index values and all parametric statistical tests were calculated in R, ANOSIM and MDS were calculated in Primer (Clarke 1993; Team 2005).

RESULTS

There were no differences between the sandstone and granite in richness ($p>0.1$) or Simpson Diversity Index ($p>0.25$) for any time period. ANOSIM also revealed no differences in community composition ($p>0.05$), and MDS also supports this result.

Because replication was low (≤ 3) for time intervals other than 11 months, I used a nested anova model with time (months) nested within rock type (granite or sandstone) to test for differences in diversity between sequential pairs of months in order to increase replication. No differences were found between sequential pairs and so the time intervals were pooled in the following manner: 1 & 2 months, 3 & 4 months, summer 5 & 6 months, winter 5 & 6 months, 7 & 8 months, and 9 & 10 months. After pooling, there were still no differences between rock types in species richness, Simpson Diversity Index (Table 3-1), or community structure

(Figure 3-2). The 9 & 10 month ANOSIM p-value was 0.063, and the 11 month p-value was 0.066. However, the R values (0.256 and 0.083, respectively) were close to 0.0, indicating that any differences were very small. An MDS for the 11 month tiles supporting the result of no difference in community composition is presented in Figure 3-2.

Of the 52 species that occurred on the 11-month tiles, only 16 occurred with an average abundance ≥1% cover (Appendix B). None were significantly different between sandstone and granite ($p>0.1$).

To test for possible seasonal effects the summer 5 & 6 month tiles were compared to the winter 5 & 6 month tiles. Species richness on the summer tiles was greater than on the winter tiles (ANOVA, $F_{1,21}=6.131$; $p=0.021$). Simpson Diversity Index did not differ between seasons (ANOVA, $F_{1,21}=0.406$; $p=0.531$). But community composition did differ between summer and winter (ANOSIM, $R=0.190$; $p=0.008$; Figure 3-3). Summer tiles averaged 17 (± se 1.6) species from a total pool of 58 (Appendix B). Winter tiles averaged only 10.18 (± se 1.8) from a total pool of 35. Most of the additional species on the summer tiles were small or occurred in low abundances. Thirty-three of the 35 winter tile species also occurred in the summer, although in generally lower abundance (Appendix B). The species occurring on the summer tiles but not the winter tiles represent every major taxon reported, including green, red, and brown algae, ascidians, barnacles, bryozoans, cnidarians, mollusks, polycheates and sponges. All but six of these species (*Centrocerus clavulatum*, *Corallina* sp., *Erythrocystis saccata*, *Mazzaella leptorhyncus*, juvenile anemone, and white sponge) occur on tiles during other time periods.

DISCUSSION

In every test between sandstone and granite substrates presented here, there is no evidence that rock type has any affect on diversity or community composition (Tables 3-1, 3-2). In addition, tests of individual species abundance tiles deployed for the full 11 months, which should be the most likely tiles to reveal a difference between sandstone and granite, also revealed no significant differences. These results suggest that differences between sandstone and granite are not sufficient to cause significant variation, at least at small spatial scales, in the rocky intertidal communities of southern California.

We cannot know whether differences would have developed had the experiment run longer. However, 11 months is as long, or longer than many experiments have been conducted for in rocky intertidal environments (e.g. Dayton 1971; Menge & Lubchenco 1981; Bulleri 2005). It is certainly long enough for at least some differences for individual species to develop if they were going to (Menge 1997). Yet none did. Therefore more time should not affect the results of this experiment.

The only statistically significant difference occurred between tiles deployed for similar periods of time but over different seasons (summer and winter, Figure 3-3). The additional species occurring on summer tiles were generally in low abundance (< 1% on average), and sometimes occurred only once or twice. The winter tiles shared all but two species with the summer tiles. This explains why a significant difference was found for species richness, but not for Simpson Diversity Index which is strongly influenced by abundant species (Magurran 2004). It also explains why the ANOSIM R-value was so low (0.190), as the data were not transformed and therefore dominated by the more abundant species(Clarke 1993). There are several notable environmental changes that occur between summer and winter that could account for the change in community; mainly, the timing of low tides switches from night to day, wave exposure increases, and the water temperature decreases (www.cdip.ucsd.edu). Overall these changes result in an increase in disturbance and environmental extremes in the rocky intertidal that may have reduced diversity during the winter season. This difference between seasons is also evidence that sufficient time elapsed during the course of the experiment to observe meaningful results.

These results agree with those of other studies that found substrate composition to be of minor importance in causing variation between urban and natural habitats(Connell 1999; Glasby 1999; Glasby 2000). Instead other environmental factors are likely to influence variation in benthic communities on riprap structures. For example, Glasby (2000) demonstrates substrate orientation has an effect. Jonsson et al. (2006) and Southward and Orton (1954) found wave exposure to be a dominant factor on riprap structures. And Sousa (1979) determined that wave force and boulder size strongly influenced diversity in a boulder field very similar to the one in this experiment.

Interestingly, the results presented here differ from those found by Osborn (2005) in central California. She found that *Balanus glandula* recruited to native substrates in higher densities, and *Chthamalus dalli/fissus* would recruit in greater density to sandstone and the native mudstone than slate, basalt, or granite. Osborn’s study was also designed to test the effect of rock types used in riprap armoring, which consisted of basalt and sandstone at her sites. One explanation for the different results between these studies is the intertidal height at which they were conducted. Osborn conducted her experiment relatively high, where *Balanus* and *Chthamalus* were abundant. Mine was conducted much lower, where neither barnacle occurs in much abundance. Substrate composition may therefore have an interactive effect with tidal height. Alternatively, substrate composition may have a greater influence in central California than in southern California. A large biogeographic break exists between the two locations at Pt. Conception, and the flora and fauna consist of several different species that may respond differently (Valentine 1966; Murray & Littler 1981).

The results presented here are important for understanding the ecological influence of riprap structures in marine environments. Jetties, breakwaters, and armored shorelines are quite abundant, and the addition of more riprap to marine environments is anticipated due to climate change and the increase of human habitation near the coast (Dean *et al.* 1987; Forstall 1996; McCarthy *et al.* 2001). Some authors have suggested designing future structures differently to enhance marine communities (Airoldi *et al.* 2005; Bulleri 2005; Moschella *et al.* 2005; Chapman 2006). On exposed shorelines like those found in southern California, changing the rock composition of riprap may not matter, and other design facets could be much more important.

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Table 3-1 ANOVA table for differences in richness and Simpson Diversity Index between granite and sandstone tiles within paired months. Summer tiles were deployed in March and collected in August (five months) or September (six months). Winter tiles were deployed in August (six months) or September (five months) and collected in February.

	Richness				Simpson Diversity (1-D)		
	DF	MS	F	P	MS	F	P
1 & 2 months	1	0.333	0.131	0.724	0.014	0.201	0.662
Residuals	10	2.533			0.072		
3 & 4 months	1	0.333	0.028	0.869	0.035	0.527	0.484
Residuals	10	11.667			0.067		
Summer							
5 & 6 months	1	6.750	0.186	0.674	0.006	0.122	0.734
Residuals	10	36.15			0.051		
Winter							
5 & 6 months	1	30.30	0.838	0.383	0.043	1.675	0.227
Residuals	9	36.15			0.025		
7 & 8 months	1	14.02	0.211	0.657	0.015	0.221	0.650
Residuals	8	66.20			0.068		
9 &10 months	1	10.00	0.305	0.595	0.038	0.710	0.423
Residuals	8	32.70			0.054		
11 Months	1	19.21	0.447	0.509	0.007	0.265	0.611
Residuals	27	42.96			0.028		

Table 3-2 ANOSIM results from comparisons of community composition between granite and sandstone tiles within paired months. Summer tiles were deployed in March and collected in August (five months) or September (six months). Winter tiles were deployed in August (six months) or September (five months) and collected in February.

Paired Months	R	P
1 & 2 months	-0.083	0.797
3 & 4 months	0.009	0.353
5 & 6 months (summer)	0.013	0.366
5 & 6 months (winter)	0.129	0.160
7 & 8 months	-0.083	0.652
9 & 10 months	0.256	0.063
11 months	0.083	0.066

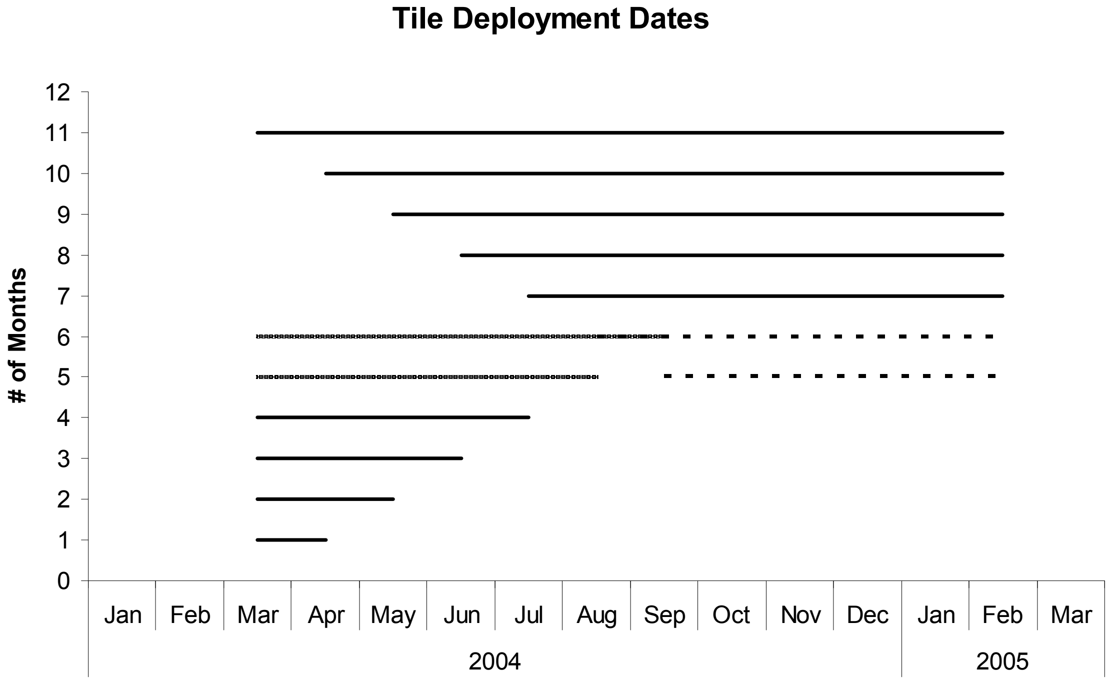

Figure 3-1 Scheme illustrating the time and dates tiles were deployed. Each line represents a set of tiles. The number of months deployed is on the ordinate, and the actual months deployed is on the abscissa. Note that tiles deployed five and six months over summer are represented by stippled lines and tiles deployed for the same amount of time but over winter are represented by dotted lines.

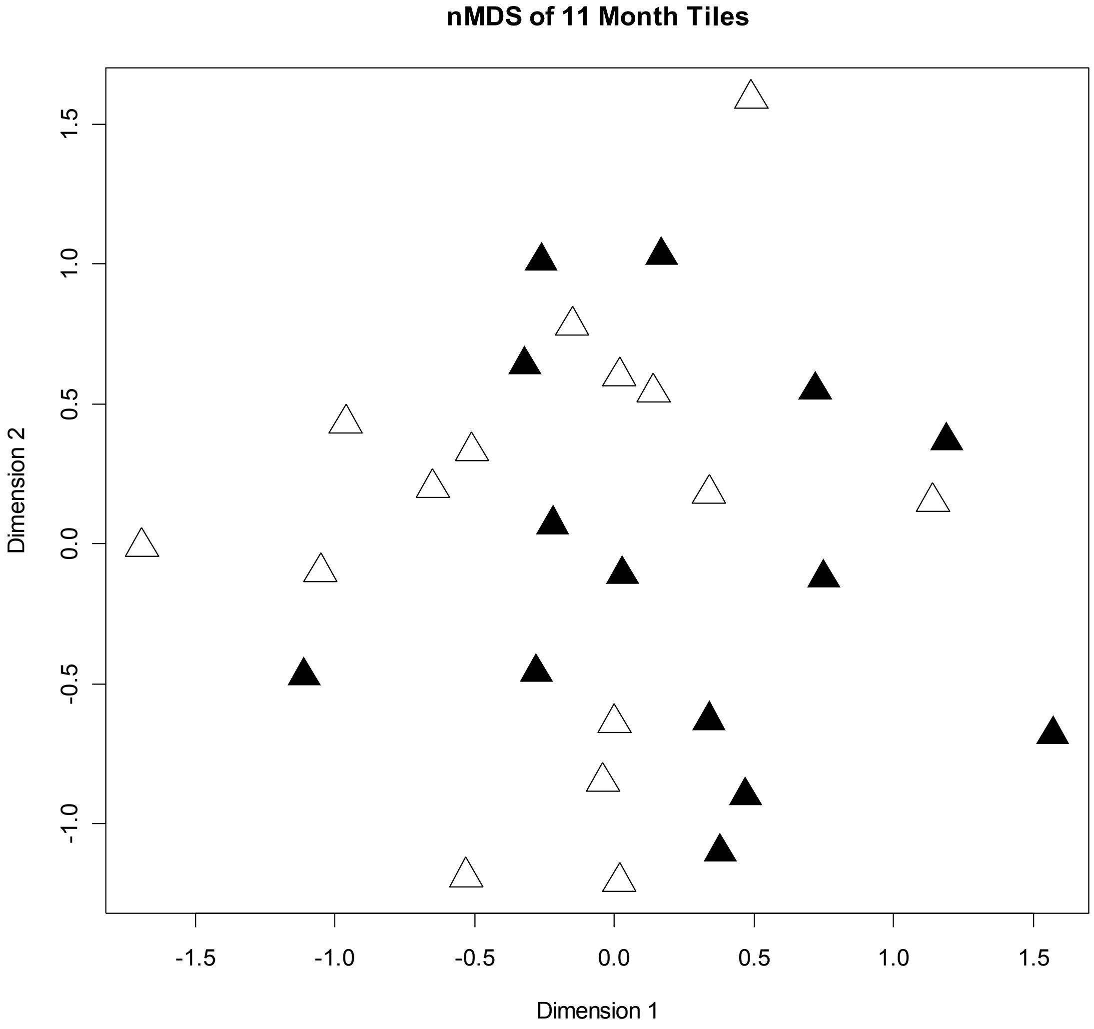

Figure 3-2 A non-Metric Multidimensional Scaling (MDS), based on non-transformed Bray-Curtis dissimilarities of all species, from tiles deployed for 11 months. Distances between symbols represent the relative differences in the community growing on the tiles. Filled triangles represent sandstone tiles and open triangles represent granite tiles. Stress = 0.23; ANOSIM R=0.083, p=0.066.

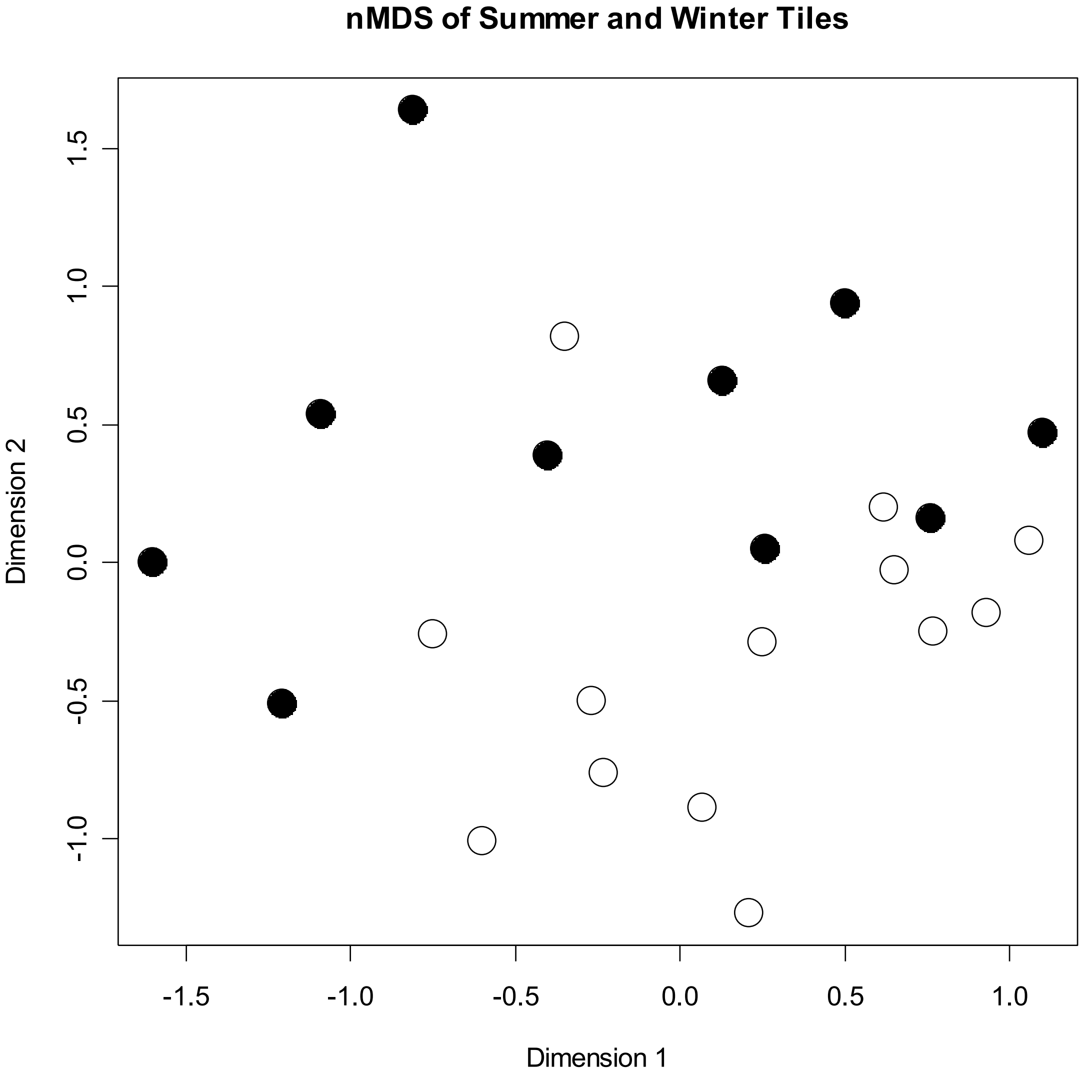

Figure 3-3 A non-Metric Multidimensional Scaling (MDS) based on non-transformed Bray-Curtis dissimilarities of all species, from tiles deployed five and six months over summer and winter. Distances between symbols represent relative differences in the community growing on the tiles. Open circles represent five or six month tiles deployed over summer. Closed circles represent five and six month tiles deployed over winter. Stress = 0.13; ANOSIM R=0.611, p=0.001.

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CHAPTER 4

On the Relationship Between Functional Diversity and Species Richness in Rocky Intertidal Assemblages on Riprap Structures

ABSTRACT

The relationship between biodiversity and ecosystem function as mediated by functional diversity is a topic of increasing importance. Human-induced changes to ecosystems have brought about a decrease in diversity, which can affect ecosystem function and in turn the health of human society and the environment. Understanding the relationship between changes in diversity and ecosystem function can help scientists understand the full ecological consequences of human activities. Ultimately, this knowledge may lead to an ability to predict these consequences in lieu of anthropogenic, or natural, disturbance. Our knowledge of biodiversity, functional diversity and ecosystem function is especially deficient in the ocean. Here I examine the relationship between species diversity and functional diversity in the rocky intertidal environment of the west coast of North America. First I ask whether this relationship is different between natural rocky intertidal habitats and riprap, the rocky rubble used to build breakwaters and jetties. Riprap is an especially abundant anthropogenic marine habitat. In southern California functional diversity increased with species diversity, and the relationship was statistically indistinguishable between riprap and natural rock. Second, I examined the

relationship on riprap sites as species diversity increases over 29 degrees of latitude from Alaska to southern California. Functional diversity increased with species diversity with a slight curve indicating a small amount of functional redundancy. This result is similar to the low functional redundancy described in the few marine studies over larger spatial scales. To date, this study is the first to examine the relationship between species diversity and functional diversity over a large latitudinal scale in a marine environment.

INTRODUCTION

Understanding the relationship between biodiversity and ecosystem function is one of the most urgent goals in ecology (Ehrlich & Wilson 1991; Diaz & Cabido 2001; Diaz *et al.* 2006). This goal and its urgency stem primarily from human-induced changes in environments and community composition across the globe (Jackson *et al.* 2001; Hooper *et al.* 2005). Biodiversity is closely linked with ecosystem function (Chapin *et al.* 1997; Tilman *et al.* 1997; Loreau *et al.* 2001; Diaz *et al.* 2006). Theoretically, the greater the biodiversity in a community the greater the ability of that community to perform a particular function, and the more likely that function will continue should anthropogenic impacts reduce or alter species composition (Tilman 2001). The loss of biodiversity, due to a myriad of anthropogenic threats, is one of the most serious environmental problems the human race currently faces (Jackson *et al.* 2001; Diaz *et al.* 2006; Worm *et al.* 2006). It follows that ecosystem functions are also being reduced or lost

(Chapin III et al. 2000). However, the relationship between biodiversity and ecosystem function is not well understood (Naeem & Wright 2003). Furthermore, evidence suggests that the relationship can be idiosyncratic depending on the environmental context, species involved, and biomass (Emmerson & Raffaelli 2000; Covich *et al.* 2004).

One way to investigate the relationship between biodiversity and ecosystem function is by using functional diversity as a proxy for ecosystem function. Functional diversity is the value and range of those species and organismal traits that influence ecosystem functioning (Tilman 2001). It provides a link between the diversity in a community and the ecosystem functions of interest. In essence, the functional diversity of a particular community is the aspect of the community that will impact or influence an ecosystem function. Ecologists use functional diversity to understand various ecological processes that occur in a particular community and how the organisms within those communities are related to, or influence those processes. In this study I investigate the relationship between biological diversity and functional diversity in a marine environment and the influence that anthropogenic structures have on that relationship. Our knowledge concerning biodiversity and ecosystem functions is especially deficient in marine ecosystems (Naeem 2006) (but see Levin *et al.* 2001; Covich *et al.* 2004). Understanding this relationship, along with how human activities can modify it, is vital to effective conservation and management of marine environments as well as the future urban development of coastlines.

Disambiguation and Definitions

The scientific literature is chock full of inconsistent and sometimes confusing jargon on the topic of ecosystem function (Hooper *et al.* 2005; Jax 2005; Petchey & Gaston 2006). Some definitions are given in order to ensure clarity. Traditional descriptions of organisms within a community or assemblage refer to what an organism is, usually in relation to its evolutionary history. For example organism X is a mussel, or *Mytilus californianus.* An organism's “function” refers to what an organism does, usually in relation to some defined ecological process (Jax 2005; Petchey & Gaston 2006). For example, organism X functions as a filter feeder, or a consumer. “Functional traits” are components of an organism’s phenotype that contribute to a particular ecosystem function. Unrelated organisms may share functional traits and are therefore considered similar or identical within the context of ecosystem functions. For example, *Mytilus californianus*, a mussel, and *Balanus glandula*, a barnacle, although distantly related both share the functional trait of filter feeding, and thus may be considered to perform the same function as consumers of plankton. An ecosystem function is broadly defined as an ecological process or ecological good or service (Tilman 2001; Jax 2005; Srivastava & Vellend 2005). Alternatively, how organisms obtain a resource or react to an environmental effect (e.g. disturbance) may be considered an ecosystem function (Naeem & Wright 2003). For example, ecosystem functions include carbon sequestration, nitrogen fixation, or pollination (Mayfield *et al.* 2005). Positions in a food web, such as primary producer, consumer, or decomposer are also examples of ecosystem functions (Tilman 2001).

It is crucial to understand that ecosystem functions and functional groups are human constructs, selected by investigators that attempt to link the identity of species within a community with what they actually do. Functional groups are not natural units and have no definitive boundary. Their definition, thus, relies heavily on the skill and expertise of the scientist investigating them. An organism may belong to any number of functional groups. Those groups, along with the ecosystem functions, will always be context dependent (Petchey & Gaston 2006). This study focuses on the relationship between species diversity and functional diversity. It does not directly investigate ecosystem function. Functional diversity is assumed to be related to the ecosystem functions mentioned in the paper, but at no time is the relationship tested, nor are the ecosystem functions actually measured. Such investigations will require significant additional effort and should certainly be conducted in the future.

Biodiversity, as it is traditionally defined, refers to the number of species (richness) or the relative abundance (evenness and dominance), phylogenetic relationships, or the spatial and temporal distributions of species or other taxa

(Norse *et al.* 1986; Webb *et al.* 2002; Magurran 2004). It also includes functional diversity. Biodiversity is a broad term and will be used as such within this paper. There are many ways to quantify biodiversity, and they will always be referred to specifically throughout this paper. Here I focus on biodiversity at the species level (hereafter referred to as 'species diversity'). Functional diversity has been defined in many ways and the precise definition is often taken for granted or assumed to be known (Jax 2005; Petchey & Gaston 2006). As mentioned above, I will follow Tilman's (2001) definition: 'the value and range of those species and organismal traits that influence ecosystem functioning.' Functional diversity will always be measured from the species assemblages in this study.

Functional Diversity in Marine Ecosystems

The potential for species extinctions and loss of biodiversity in the ocean due to human disturbance has never been higher (Jackson 1997; Jackson *et al.* 2001; Worm *et al.* 2006). The degree of functional redundancy in impacted marine ecosystems will have a strong influence on the changes in ecosystem processes, goods, and services due to human impacts. However, investigations of the relationship between species diversity and functional diversity in marine ecosystems remain few and far between, mostly due to the large scales and difficulties of working underwater. In addition, this relationship has never been examined on anthropogenic structures in marine environments. Indeed, this relationship is poorly known for most ecosystems besides grasslands (Naeem & Wright 2003). Most marine studies to date concern experimental manipulations or observational studies on small scales (Paine 2002; Duffy *et al.* 2003; Lohrer *et al.* 2004; Bruno *et al.* 2005; but see Micheli & Halpern 2005; Bracken & Stachowicz 2006).

Anthropogenic substrates, such as seawalls, jetties, pilings, piers, oil platforms, and many other types have come to dominate many marine habitats, especially near urban areas (Glasby & Connell 1999; Chapman & Bulleri 2003; Love *et al.* 2003; Sammarco *et al.* 2004; Airoldi *et al.* 2005). Riprap, the rocky rubble used to build jetties, breakwaters and armored shorelines, is especially plentiful (Clark et al. 2002, Chapter 1). Their ability to sustain healthy marine communities is vital for the environmental, economical, and even social health of both the marine ecosystem and the urban areas adjacent to them (Rosenzweig 2003). Sustaining healthy marine communities on anthropogenic structures should include maintaining functional diversity and ecosystem functions similar to a natural marine community.

In this study I examine the relationship between species diversity and functional diversity in the rocky intertidal environment on the west coast of North America. To test the hypothesis that anthropogenic structures have lower functional diversity for a given number of species I compare intertidal communities from four natural rocky sites and four riprap sites in southern California. To test how species diversity affects functional diversity as species are added to (or subtracted from) a community I used data from 15 rocky intertidal sites spanning ~28 degrees of latitude with pronounced variation in species diversity and community composition (Lubchenco & Gaines 1981; Roy *et al.* 1998; Roy & Martien 2001). The variation in oceanographic regimes and biogoegraphical provinces provides an excellent natural experiment to test the dependence of functional diversity on species diversity. There are two, non-mutually exclusive hypotheses why functional diversity should increase with species diversity along this latitudinal gradient. First, functional diversity could increase with species diversity because new species are added to the community with functional traits unlike those of species already present. In other words, the trend is due to a change in community composition (Williams 2001; Petchey & Gaston 2002). Second, functional diversity could increase with species diversity because of the increased chance of including a species with extraordinary functional attributes (i.e. increased sampling or the selection probability effect, Huston 1997; Stevens *et al.* 2003). In other words, the trend is simply due to an increase in the number of species.

In general the relationship between species diversity and functional diversity is dependent on the functional redundancy of the species within the community (Stevens *et al.* 2003; Micheli & Halpern 2005; Petchey & Gaston 2006, Figure 4-1). Functional redundancy is the degree to which different species exhibit similar functional traits. If each species is functionally unique (i.e. no functional redundancy), functional diversity will increase linearly with species diversity (A in Figure 4-1). Alternatively, species may exhibit some similarity in functional traits but the relationship remains linear, always increasing as species diversity increases (B in Figure 4-1). Another scenario is that species contribute many new functional traits not already present in the community (low functional redundancy), increasing functional diversity rapidly at low species diversity. The rate at which functional diversity increases will decline as functional traits become more redundant, and eventually reach an asymptote when no new functional traits are added (C in Figure 4-1). Whether this asymptote exists, and at what level of diversity it exists, is a critical question for ecology, conservation biology, and management (Micheli & Halpern 2005). Studies conducted in kelp forest ecosystems and on fish assemblages have found low functional redundancy, akin to B in Figure 4-1 (Bellwood *et al.* 2003; Micheli & Halpern 2005).

METHODS

Field Sites and Data Collection

I surveyed rocky intertidal communities at 15 sites between 32.75º N and 60.11º N from December 2004 to August 2006 (Figure 4-2). The eight sites in southern California are those from Chapter 1, four of which are riprap and four are natural rock. The four riprap sites consisted of the northern jetty at the entrance to Mission Bay (MB), the outer breakwater at Dana Pt. Harbor (DBW), the northern jetty at the entrance to Newport Bay (NP), and the northern (western) breakwater at San Pedro (SP). The four natural rocky sites included the Scripps Intertidal Reserve (SIO), Dana Pt. State Reserve (DPR), Corona del Mar (CDM) and Pt. Fermin (PF). Two sites are in northern California at Half Moon Bay (HMB) and Crescent City (CC). One site is Neah Bay (NB) in Washington State. Four sites exist on the Kenai Peninsula in Alaska; Seward (SEW), Seldovia (SEL), and two in Homer (H1 and H2). Table 4-2 reports the latitude and longitude of each site.

Within each site a minimum of five vertical transects were laid haphazardly in locations chosen to represent ambient wave exposure. Because the slopes of each site (and therefore the transect length) varied, I used biological boundaries to define the endpoints of transects. Each transect began in the upper intertidal at the upper limit of *Chthamalus* sp. (or *Balanus glandula* when *Chthamalus* was not present) and ended in the mid to low intertidal at the upper limit of kelps such as *Eisenia arborea.* Along each transect eight 0.25 x 0.25 meter PVC quadrats were placed at evenly spaced intervals only on the tops or outward facing sides of boulders. Quadrats were moved laterally (i.e. at the same tidal height) when necessary to avoid sampling crevices or more than one face of a boulder. This sampling scheme is designed to ensure consistency between sites and to avoid a bias by sampling microhabitats present only at some sites, such as tidepools (Davis *et al.* 2002; Murray *et al.* 2006). This sampling scheme also ensures equal sample sizes at the same relative tidal heights.

Digital photos were taken using a digital camera positioned directly above each quadrat and all species above 3-5 mm that could be consistently observed were identified *in situ* (Foster et al. 1991). In addition I counted all mobile organisms. Species that could not be consistently observed were excluded from statistical analyses. For example, the frequently occurring crab *Pachygrapsis crassipes* usually darted away before being counted, and the cryptic isopod *Idotea spp*. was probably sufficiently camouflaged in tufts of algae to remain unnoticed much of the time.

Each photo was analyzed in the lab using Image J (Rasband 2005). Photos were cropped to include only the quadrat. I quantified percent cover by projecting 25 dots randomly onto each photo and assigning a value of 4% to each organism that occurred under each dot. Organisms not occurring under a dot but recorded inside the quadrat were assigned a value of 0.5% (Meese & Tomich 1992; Dethier *et al.* 1993). Percent cover and counts of each species were summed for each transect.

Identification of Functional Traits

There is no agreed upon method for identifying functional traits, and no method is perfect (Naeem & Wright 2003). The relationship between functional diversity and species diversity may be specific to the system it's measured in, and is especially sensitive to the defined functional groups or traits and the specific ecosystem functions in question. Ideally I would use precise values for assigning functional traits and measuring functional diversity. But that type of quantitative information is simply unavailable for most marine organisms. Expert knowledge and opinion concerning how organisms interact with their environment is useful, and even essential for determining functional traits, especially in circumstances were precise values are unknown (Petchey & Gaston 2006). Given the current state of knowledge about the dynamics of biodiversity, functional diversity, and ecosystem functions, it seems wise to treat functional classifications as ‘hypotheses that need to be tested (Petchey & Gaston 2006). Here I follow the work of others as much as possible concerning functional classification of intertidal organisms. Only when I could find no precedence did I assign function traits.

Steneck and Dethier (1994) provided a useful functional classification of algae which I follow here (Table 1). They divided algae from the Puget Sound, the Gulf of Maine, and the Caribbean into seven functional groups based on morphological and physiological traits. These functional groups are microalgae, filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes, leathery macrophytes, articulated calcareous algae, and crustose algae. In general, algal species in these groups share traits that constrain them to similar levels of productivity and responses to herbivorous disturbance. Therefore these species are classified according to two ecosystem functions; primary productivity and disturbance resistance (Steneck & Dethier 1994). A marine grass, *Phyllospadix* sp., is an important and common plant found throughout west coast rocky intertidal environments, but was not accounted for by Steneck and Dethier. Because it does not share the same physiological traits used to assign algae to functional groups, I assigned it to its own functional group.

Animals were assigned to functional groups based primarily on their methods of obtaining food. Thus, the functional classification refers to the ecosystem function of secondary production. In general I followed Micheli and Halpern's (2005) classification for invertebrates in kelp forest communities. Functional groups included filter feeders, mobile grazers, mobile predators, sessile predators, and scavengers. Micheli and Halpern (2005) classified anemones as "sessile planktivorous invertebrates", a group that included filter feeders. But the anemone mode of obtaining food, along with their prey, is very different from that of the filter feeders in this community, and therefore the anemones are classified separately here as sessile predators. In addition, many of the animals in the rocky intertidal aggregate to form a kind of biogenic reef habitat that is used by other organisms (e.g. mussel beds, Lohse 1993). Animals were also classified on the basis of whether they aggregate to form such biogenic habitats.

Analyses

Functional diversity has been measured in many ways. There is no standardized or widely accepted method (Diaz & Cabido 2001; Tilman 2001; Petchey & Gaston 2002; Petchey *et al.* 2004). Here I use a hierarchical method called FD (Petchey & Gaston 2002; Petchey & Gaston 2006). In this paper FD refers specifically to Petchey and Gaston's method, and is not an acronym for the words 'functional diversity.' Some papers have used this acronym. FD is a method closely related to PD, an accepted measure of phylogenetic diversity (Faith 1994; Petchey & Gaston 2002). Briefly, FD is the sum of branch length of a functional dendrogram. It is calculated by constructing a trait matrix containing values ($x_{s,t}$) of trait *t* and species *s*. The trait matrix is converted to a distance matrix which is then clustered into a dendrogram. The branch lengths are then calculated (see Petchey & Gaston 2002; Petchey & Gaston 2006; Mouillot *et al.* 2007 for evaluations of this method). I constructed a trait matrix based on the classification described above and in Table 4-1. I computed FD in R following the procedure outlined in Petchey and Gaston (2002) and with R code provided by Owen Petchey (http://owensplace.wetpaint.com/page/Example+1). FD can be used with binary data. The abundance of the organisms are ignored and each simply possesses a functional trait (1) or it does not (0). Also, this method specifically uses functional traits. The use of the term "functional trait" is synonymous with the term "functional group" in the other analyses below.

Other authors have calculated functional diversity using functional richness and the Shannon-Wiener diversity index (e.g. Stevens *et al.* 2003; Micheli & Halpern 2005). Functional richness is defined simply as the number of functional groups (or traits) within a community. Shannon-Wiener is calculated on species abundances pooled by functional group. I include them here as a comparison to previous studies that have calculated functional diversity using richness and Shannon-Wiener. Only functional groups containing sessile species were calculated because their abundances were measured as percent cover while mobile species were measured as counts. The two types of data are not compatible without eliminating all information on abundance which would defeat the purpose of an index such as Shannon-Wiener. Sessile species represented 75% of the total species, so most of the assemblage remained after excluding mobile species. I measured species diversity as species richness (i.e. the number of species within a community) or using the Shannon-Wiener diversity index, which includes evenness (Magurran 2004). Species richness was used for comparing species diversity to FD and functional richness. Shannon-Wiener diversity of species was used to evaluate Shannon-Wiener diversity of functions (Figure 4-5). The relationship between species diversity and functional diversity was evaluated using regression models.

To test whether riprap affects the relationship between species diversity and functional diversity I calculated species richness and FD for each transect in the four riprap sites and four natural sites from southern California (Figure 4-2).

To evaluate the relationship between species diversity and functional diversity as species are added to a community I calculated species richness and FD for pooled data within each site for all 15 sites between Alaska and southern California (Figure 4-3). To determine whether the cause of the relationship is due to a change in community composition or simply the increase in species I repeated the FD analysis for simulated communities created by randomly subsampling species from the entire species pool of the data set. I repeated the simulation 1000 times for each species richness level along a range encompassing the real data (from 6 species to 60 species). The average upper and lower 95% quartiles were calculated for each level and displayed in Figure 4-3. I also repeated the analysis using the Shannon-Wiener diversity index and functional richness but without the subsampling iterations (Figure 4-4).

FD, regressions, and simulated communities were all generated in R (Team 2005). Shannon-Wiener diversity index was calculated using Ecosim (Gotelli & Entsminger 2006).

RESULTS

The relationship between FD and species richness on both riprap and natural rock in southern California was significantly positive (Figure 4-2). In both cases a log linear regression explained the most variation (riprap: F = 60.48, d.f. = 18, P = ≤0.0001, R^2 = 0.8645; natural rock: F = 32.81, d.f. = 18, P = ≤0.0001, R^2 = 0.7608). There was no significant difference between the relationships within riprap or natural rocky intertidal communities (ANCOVA slope: $F_{1,38}$ = 0.0249, P = 0.8754; intercept: $F_{1,38}$ = 1.8126, P = 0.1862). There fore, I reject the hypothesis that anthropogenic structures have lower functional diversity for a given number of species. Linear models explained similar amounts of variation for both riprap and natural rock (riprap linear R^2 = 0.8481, natural rock linear R^2 = 0.7323). Since both habitat types are indistinguishable in this relationship between species diversity and functional diversity, the natural sites were included in the analysis of all 15 sites, the remaining of which were all riprap structures.

Functional diversity for all 15 sites, calculated as FD, also showed a significantly positive relationship with species richness (Figure 4-3). A log linear model best described the variation in the data (F = 727.5, d.f. = 13, P = ≤ 0.0001, R^2 = 0.9824). A linear model also explained a similar amount of the variation (R^2 = 0.9504). However, Akaike's information criterion (AIC) is lower for the log linear model than for the linear model (-97.82 and -82.258, respectively) indicating a better fit to the data. A slight curvature in the data is visible in Figure 4-3 as FD increases more slowly at higher species diversity, illustrated by the data points occurring below the linear line of best fit at the ends of the range and above it in the middle. This can also be seen in a plot of the residuals (Figure 4-4). The slight curve in the line is indicative of a small amount of redundancy (line C in Figure 1). However, there is no evidence that an asymptote has been reached, and therefore the communities with higher species richness have not saturated with respect to FD.

The observed data fall between the 95% confidence intervals of the simulated data, indicating that FD increases as would be expected by the random addition of species. Therefore, the increase in functional diversity is due to an increase in the number of species, and not because the identity of the species within the community is changing.

Functional diversity also increased with species diversity when using the Shannon-Wiener diversity index to calculate diversity (Figure 4-5). Functional diversity increases positively with the log linear model of species diversity (F = 27.3, d.f. = 13, P = 0.0002, R^2 = 0.6774, slope = 0.6527). Again, the linear model describes a similar amount of variation (R^2 = 0.6343), but the AIC indicates the log linear model is a better fit (log linear = 6.2101, linear = 8.0906). Although the log linear model implies that some functional redundancy exists with a relationship similar to line C in Figure 4-1, there is no evidence of an asymptote or saturation.

Functional diversity as measured by functional richness showed no relationship to species richness (data not shown). Both the log linear and linear models had slopes not significantly different from 0 (F = 0.5192, d.f. = 13, P = 0.4839; F = .4603, d.f. = 13, P = 0.509). In addition, the amount of variance explained was exceedingly poor (log linear: R^2 = 0.038, linear: R^2 = 0.034).

DISCUSSION

Functional Diversity on Anthropogenic Structures

The relationship between species diversity and functional diversity is not well known for most ecosystems (Naeem 2002). Understanding this relationship is vital to understanding how species diversity affects ecosystem functions and is of immediate concern due to widespread degradation of environments due to human impacts (Ehrlich & Wilson 1991; Jackson *et al.* 2001; Diaz *et al.* 2006; Duffy & Stachowicz 2006). In this study I quantified this relationship for the first time on anthropogenic structures in the ocean. There was no statistical difference in this relationship between riprap and natural rock (Figure 4-2).

Humans can impact natural environments in a plethora of ways. Logically, functional diversity may differ between a human impacted environment and the pristine analog. For example, functional diversity has been shown to differ between pristine forests and those cleared by humans in terrestrial plant communities (Mayfield et al. 2005). Riprap is a common form of coastal modification to protect shorelines from wave exposure and erosion. In southern California, riprap has been added to a large fraction of the original shoreline (Clark 2002, CHAPTER 1). Riprap structures are also common structures in urban areas throughout the world (Walker 1988). From first principles we might expect riprap to differ in functional diversity from natural rocky habitats. However, the results presented here, suggest that the relationship between species diversity and functional diversity (and thus ecosystem function) on riprap is similar to that on natural rocky shores. I must emphasize that this relationship was only tested in southern California on relatively exposed shorelines. Whether or not the same result will be found for riprap in other environments (e.g. bays, estuaries, riparian) must be investigated further. In the other recent study of riprap communities in southern California, Davis et al. (2002) found that riprap in San Diego bay differed from natural rock outside the bay, with increasing differences as distance from the outer coast increased. In addition, there is no modern natural rock in San Diego Bay, suggesting that riprap has a profound impact on the functional diversity and ecosystem functions of the bay environment. This is an important area of further research because riprap, along with other anthropogenic structures, is likely to increase due to climate change and the increasing human populations along coastlines (Dean *et al.* 1987; Forstall 1996; McCarthy *et al.* 2001).

The results presented here for functional diversity on riprap have at least two broad implications. First, they imply that at least some widespread anthropogenic habitats may perform valuable ecosystem services. If this is true, then it may be possible to enhance these services through the design of riprap structures. How this might be accomplished is a topic worthy of further investigation, especially in light of the huge amount of riprap currently in use, and the continuing destruction of marine environments (Jackson et al. 2001).

Which ecosystem functions and services are most desirable, and whether or not humans should seek to modify coastal habitats in such ways, are questions that quickly lead away from ecology to other disciplines (Moschella et al. 2005). Nevertheless, ecology can certainly provide useful information to help answer those questions. At the very least, future investigations of ecosystem function in near shore ecosystems should include riprap.

The second implication of this study is that riprap can be quite useful for investigating natural ecological processes (Hawkins & Hartnoll 1982). In this study, riprap provided a useful habitat to study over large spatial scales because it exhibited relatively consistent intrinsic environmental properties between sites separated by long distances. Riprap structures are less likely to differ with respect to attributes such as structural complexity between sites. In addition, many riprap structures are easily accessible and can be good places to set up field experiments and other studies without damage to natural habitats.

FD and Species Richness

To examine the relationship between functional diversity and species diversity I took advantage of the change in species richness over a latitudinal gradient. The number of species in the rocky intertidal communities measured here increased from 15 in Seward, Alaska to 52 at Mission Bay in southern California. Along this latitudinal gradient species composition also changes dramatically. The 15 sites span three major biogeographic provinces; the

Aleutian, the Oregonian, and the California provinces (Valentine 1966). Both the changing identity of the species and the increase in species richness could induce an increase in FD. The simulation of communities by selecting species at random allows a test between these two alternate hypotheses. The observed data fall within the range of the simulated data indicating that the identity of the species within the communities (which changes from site to site) has very little effect on the functional diversity with regard to the functional traits used. This suggests that these traits are largely independent of one another. It also means that the increase in functional diversity was entirely due to the increase in the number of species. These results agree with the theoretical predictions of Petchey and Gaston (2002) who found that when multiple ecosystem functions are considered species richness alone will be more important for functional diversity. This is also consistent with the hypothesis that more species for more ecosystem processes because different species will be important for different processes at different times and places (Walker *et al.* 1999; Yachi & Loreau 1999).

Stevens et al. (2003) performed a similar analysis of the functional diversity of new world bat communities. Unlike the results presented here, they found that functional diversity increased faster than expected by species diversity alone. The reasons for the divergent results are not clear. However, they do mean that more broad scale studies on diversity gradients are necessary before a fundamental understanding of the relationship between species diversity and functional diversity is attained.

The shape of the relationship between FD and species diversity was slightly curved indicating that new species added to the communities were contributing at least some functional traits similar to those already present. However, the trend is slight, and any functional redundancy implied by this curve must be fairly low. These results suggest that disturbance in the rocky intertidal that results in the removal of species will also result in decreased ecosystem function, specifically primary and secondary production. They also suggest that communities with lower species richness will be contributing less to those ecosystem functions over a larger spatial area. Micheli and Halpern (2005) and Bellwood et al. (2003) also report low functional redundancy in kelp forests, marine protected areas, and coral reefs. This result has profound consequences for marine ecosystems, as they are sustaining heavy disturbance on both local and regional scales (Jackson *et al.* 2001; Roy *et al.* 2003; Huff 2006; Worm *et al.* 2006).

Other Measures of Functional Diversity

In one of the very few marine studies to examine species diversity and functional diversity, Micheli and Halpern (2005) used richness and the Shannon-Wiener diversity index to measure functional diversity in a southern California kelp forest community. They found that functional diversity increased with species diversity for both measures. Furthermore they found that the relationship was linear, and for Shannon-Wiener the slope was steep (0.97), indicating low functional redundancy. In contrast to Micheli and Halpern, I found no relationship between functional richness and species richness. This is in agreement with recent work that suggests using functional richness is a poor predictor of ecosystem function (Petchey et al. 2004).

I did find a significant relationship using the Shannon-Wiener diversity index, although it was not as steep as reported by Micheli and Halpern (2005), nor was it best described by a linear model. However, both studies provide evidence of low functional redundancy in marine ecosystems.

Different measures of functional diversity contain different kinds of information (Stevens *et al.* 2003; Petchey *et al.* 2004; Petchey & Gaston 2006). Therefore the meaning of differences in results found by FD, Shannon-Wiener, and functional richness are unclear. The use of FD, and methods like it, are perhaps more informative and may use fewer assumptions than using traditional biodiversity indices such as Shannon-Wiener or richness, to quantify functional diversity (Petchey & Gaston 2002; Botta-Dukat 2005; Petchey & Gaston 2006; Mouillot *et al.* 2007). In any case, results obtained using FD are best compared to other studies using FD. Likewise, studies using other measures, like Shannon-Wiener are most informative when compared to other studies using the same metric.

In this study I have shown that the relationship between species diversity and functional diversity may be equivalent on riprap and in natural rocky intertidal communities. For the ecosystem functions considered here the number of species is more important than species identity in rocky intertidal communities. Furthermore, the trends in both FD and Shannon-Wiener suggest that, in general, functional redundancy in this ecosystem is relatively low. Ecosystem functions in these communities are thus especially susceptible to disturbance or other processes that tend to remove species from the community.

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Table 4-1 Species recorded at all 15 sites and the functional traits/functional groups they are assigned to.

Species	Functional Trait/Group
Microalgae	
Diatoms	Microalgae
Unid green crust	Microalgae
Green Algae	
Chaetomorpha linum	Filamentous Algae
Cladophora sericea	Filamentous Algae
Cladopohra columbiana	Filamentous Algae
Rhizoclonium	Filamentous Algae
Sum *Ulothrix*	Filamentous Algae
Unid green	Filamentous Algae
Ulva spp.	Foliose Algae
Brown Algae	
Alaria marginata	Leathery Macrophytes
Analipus japonica	Corticated Macrophytes/Crustose Algae
Colpomenia peregrina	Corticated Foliose Algae
Dictyota flabellata	Corticated Foliose Algae
Egregia menzeisii	Leathery Macrophytes
Eisenia arborescens	Leathery Macrophytes
Endarachne binghamiae	Corticated Foliose Algae
Fucus gardneri	Leathery Macrophytes
Giffordia	Filamentous Algae
Halidrys dioica	Leathery Macrophytes
Hedophyllum	Leathery Macrophytes
Leathesia difformis	Corticated Foliose Algae
Melanosiphon intestinalis	Corticated Foliose Algae
Pelvetiopsis limitata	Leathery Macrophytes
Petalonia	Corticated Foliose Algae/Crustose Algae
Petrospongium rugosum	Crustose Algae
Ralfsia pacifica	Crustose Algae
Ralfsia sp.	Crustose Algae
Scytosiphon dotyi	Corticated Foliose/Crustose Algae
Scytosiphon lomentaria	Corticated Foliose/Crustose Algae
Silvetia compressa	Leathery Macrophytes
Sorantheria ulvoidea	Corticated Foliose Algae
Unid brown crust	Crustose Algae

Table 4-1 continued.

Species	Functional Trait/Group
Red Algae	
Bosiella orbigiana	Articulated Calcareous Algae
Calliarthron tuberculosum	Articulated Calcareous Algae
Callithamnion pikeanum	Corticated Macrophytes
Callithamnion rupicola	Filamentous Algae
Callophyllus sp.	Corticated Foliose Algae
Caulacanthus ustulatus	Corticated Macrophytes
Chondria sp.	Corticated Macrophytes
Corallina pinnatifolia	Articulated Calcareous Algae
Corallina vancouveriensis	Articulated Calcareous Algae
Corralline crust	Crustose Algae
Cryptopleura corallinara	Corticated Foliose Algae
Cryptopleura lobulifera	Corticated Foliose Algae
Cumogloia sp.	Corticated Macrophytes
Endocladia muricata	Corticated Macrophytes
Gastroclonium subarticulatum	Corticated Macrophytes
Gelidium and allies	Corticated Macrophytes
Gloiopeltis furcata	Corticated Macrophytes
Halosaccion glandiforme	Corticated Foliose Algae
Hildenbrandia sp.	Crustose Algae
Jania crassa	Articulated Calcareous Algae
Laurencia pacifica	Corticated Macrophytes
Lithothamnion californicum	Crustose Algae
Lithothrix aspergillum	Articulated Calcareous Algae
Mastocarpus jardinii	Corticated Foliose Algae/Crustose Algae
Mastocarpus/Petrocelis sp.	Corticated Foliose Algae/Crustose Algae
Mazzaella affinis	Corticated Foliose Algae
Mazzaella leptorhyncos	Corticated Foliose Algae
Melobesia mediocris	Crustose Algae
Microcladia borealis	Corticated Macrophytes
Microcladia coulteri	Corticated Macrophytes
Nemalion helminthes	Corticated Macrophytes
Neorhodomella sp.	Corticated Macrophytes
Osmundea sinicola	Corticated Macrophytes
Osmundea spectabilis	Corticated Macrophytes
Palmaria callophylloides	Corticated Foliose Algae
Palmaria hecatensis	Corticated Foliose Algae
Palmaria sp.	Corticated Foliose Algae
Plocamium pacificum	Corticated Macrophytes

Table 4-1 continued.

Species	Functional Trait/Group
Red Algae continued	
Plocamium violaceum	Corticated Macrophytes
Porphyra sp.	Foliose Algae
Prionitis lanceolata	Corticated Macrophytes
Pseudolithophyllum murica	Crustose Algae
Rhodymenia sp.	Corticated Macrophytes
Sum polysiphonic spp.	Corticated Macrophytes
Unid red crust	Crustose Algae
Grass	
Phyllospadix sp.	Grass
Mollusks	
Acanthinucella spirata	Mobile Predator
Anthopleura elegantissima	Sessile Predator/Reef FormingorColonial
Anthopleura sola	Sessile Predator
Anthopleura xanthogrammi	Sessile Predator
Callistochiton	Mobile Grazer
Combined limpets	Mobile Grazer
Conus californicus	Mobile Predator
Cryptochiton stelleri	Mobile Grazer
Epiactis prolifera	Sessile Predator
Fissurella volcano	Mobile Grazer
Katharina tunicata	Mobile Grazer
Lepidochitona dentiens	Mobile Grazer
Lepidochitona hartwegii	Mobile Grazer
Littorina keenae	Mobile Grazer
Littorina scutulata	Mobile Grazer
Littorina sitkana	Mobile Grazer
Lottia gigantea	Mobile Grazer
Macron lividus	Mobile Predator
Margarites helicinus	Mobile Grazer
Mexicanthina lugubris	Mobile Predator
Mopalia lignosa	Mobile Grazer
Mopalia muscosa	Mobile Grazer
Mytilus californianus	Sessile Filterfeeder/Reef Forming or Colonial
Mytilus galloprovincialis	Sessile Filterfeeder/Reef Forming or Colonial
Mytilus trossolus	Sessile Filterfeeder/Reef Forming or Colonial
Nucella canaliculata	Mobile Predator

Table 4-1 continued.

Species	Functional Trait/Group
Mollusks continued	
Nucella emarginata	Mobile Predator
Nuttallina sp.	Mobile Grazer
Onchidella borealis	Mobile Grazer
Pseudochama exogyra	Sessile Filterfeeder/Reef Forming or Colonia
Roperia poulsoni	Mobile Predator
Septifer sp.	Sessile Filterfeeder
Serpulorbis squamigerus	Sessile Filterfeeder/Reef Forming or Colonia
striped chiton	Mobile Grazer
Tonicella lineata	Mobile Grazer
unidentified chiton	Mobile Grazer
Echinodems	
Leptasterias hexactis	Mobile Predator
Pisaster ocreceaus	Mobile Predator
Strongylocentrotus purpuratus	Mobile Grazer
Arthropods	
Kelp crab	Mobile Predator
Ligia	Mobile Grazer/Scavenger
Neomolgus littoralis	Mobile Predator
Pagurus spp.	Mobile Grazer/Scavenger
Pugettia gracilis	Mobile Predator
yellow mite	Mobile Predator
Bryozoans	
Bugula neritina	Sessile Filterfeeder
Eurystomella bilabiata	Sessile Filterfeeder
Schizoporella unicornis	Sessile Filterfeeder
Thallamoporella californica	Sessile Filterfeeder
Unid bryo	Sessile Filterfeeder
Watersipora sp.	Sessile Filterfeeder
Polycheates	
Phragmatopoma californica	Sessile Filterfeeder/Reef FormingorColonial
Serpula vermicularis	Sessile Filterfeeder
Spirorbis sp.	Sessile Filterfeeder

Table 4-1 continued.

Species	Functional Trait/Group
Barnacles	
Balanus glandula	Sessile Filterfeeder
Balanus crenatus	Sessile Filterfeeder
Chthamalus fissus/dalli	Sessile Filterfeeder
Megabalanus californicus	Sessile Filterfeeder
Pollicipes polymerus	Sessile Filterfeeder/Reef Forming or Colonial
Semibalanus cariosis	Sessile Filterfeeder
Tetraclita rubescens	Sessile Filterfeeder
Sponge	Sessile Filterfeeder

Table 4-2 Latitude and Longitude for sites in CHAPTER 4. MB = Mission Bay, SIO = Scripps Institute of Oceanography, DPNR = Dana Pt. State Reserve, DPRR = Dana Pt. Breakwater, CDM = Corona del Mar, NPO = Newport, SP = San Pedro, PF = Pt. Fermin, HMB = Half Moon Bay, CC = Crescent City, NB = Neah Bay, SEL = Seldovia, H1 = Homer 1, H2 = Homer 2, SEW = Seward.

Site	Latitude	Longitude
MB	32° 45.5' N	117° 15.6' W
SIO	32° 52.3' N	117° 15.2' W
DPNR	33° 27.6' N	117° 42.6' W
DPRR	33° 27.5' N	117° 42.3' W
CDM	33° 35.5' N	117° 52.3' W
NPO	33° 35.3' N	117° 52.8' W
SP	33° 42.3' N	118° 16.3' W
PF	33° 42.4' N	118° 17.7' W
HMB	37° 29.6' N	122° 29.6' W
CC	41° 44.3' N	124° 11.7' W
NB	48° 22.7' N	124° 37.2' W
SEL	59° 26.3' N	151° 43.1' W
H1	59° 36.3' N	151° 24.9' W
H2	59° 36.6' N	151° 25.6' W
SEW	60° 6.9' N	149° 26.0' W

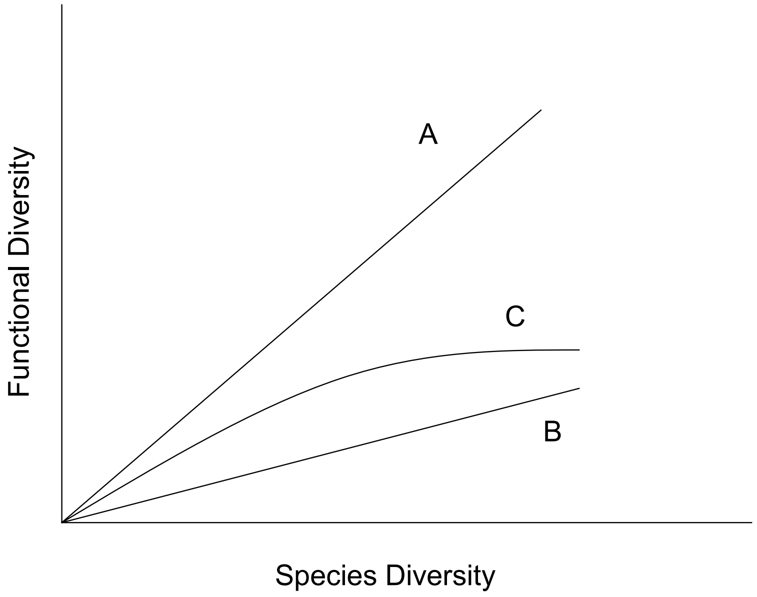
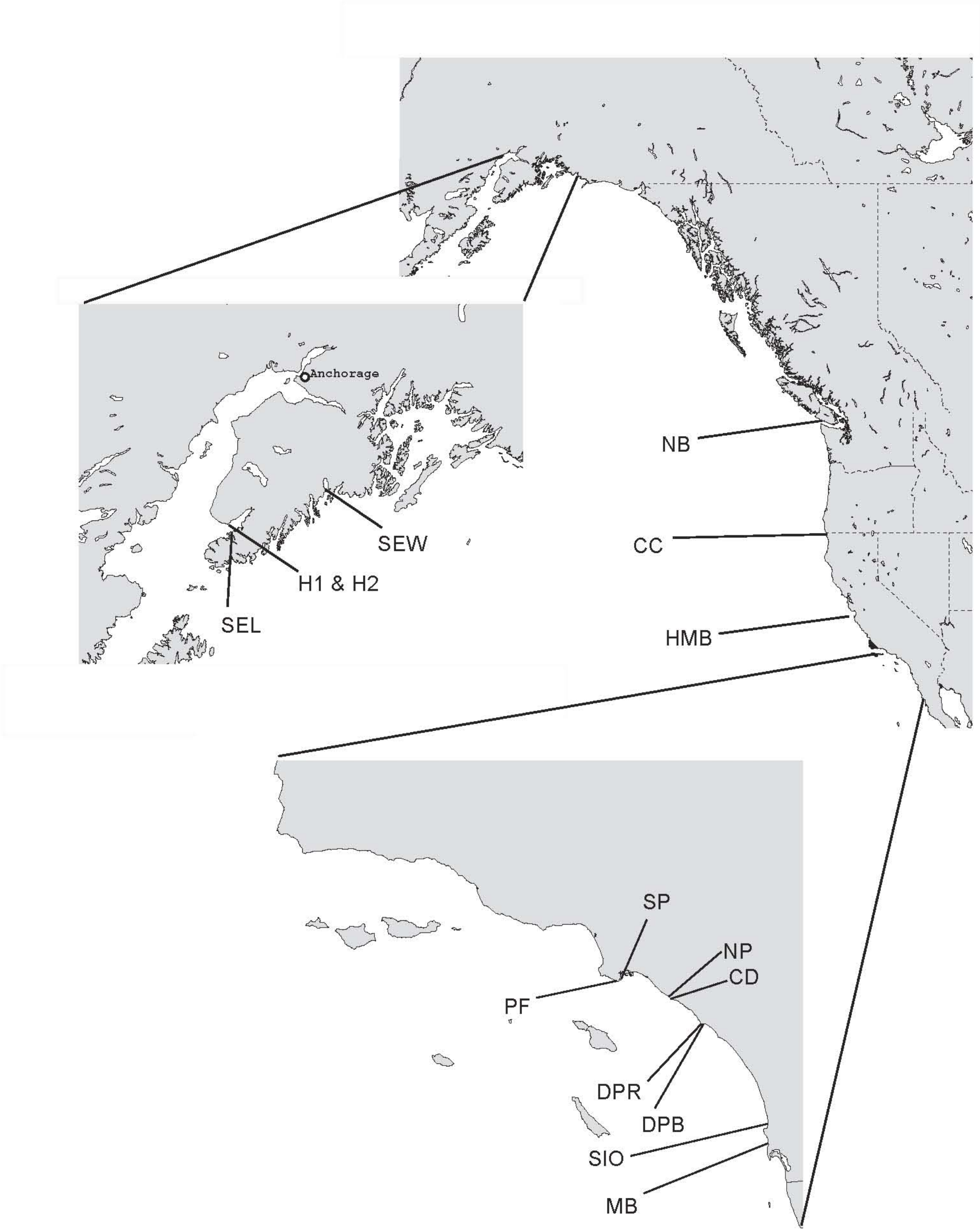


Figure 4-1 Graph of the theoretical relationships between species diversity and functional diversity.

Figure 4-2 Maps of all 15 sites. The Kenai Peninsula, Alaska, is in the upper left, with Seldovia (SEL), Homer 1 and Homer 2 (H1 & H2) and Seward (SEW). The upper right shows the west coast from San Diego to Anchorage. Note the three sites: Neah Bay (NB), Crescent City (CC), and Half Moon Bay (HMB). The bottom map of southern California shows four riprap sites: San Pedro (SP), Newport (NP), Dana Pt. Breakwater (DPB), and Mission Bay (MB); and four natural sites: Pt. Fermin (PF), Corona del Mar (CD), Dana Pt. State Reserve (DPR), and Scripps (SIO).


Anchorage
SEW
H1 & H2
SEL
NB
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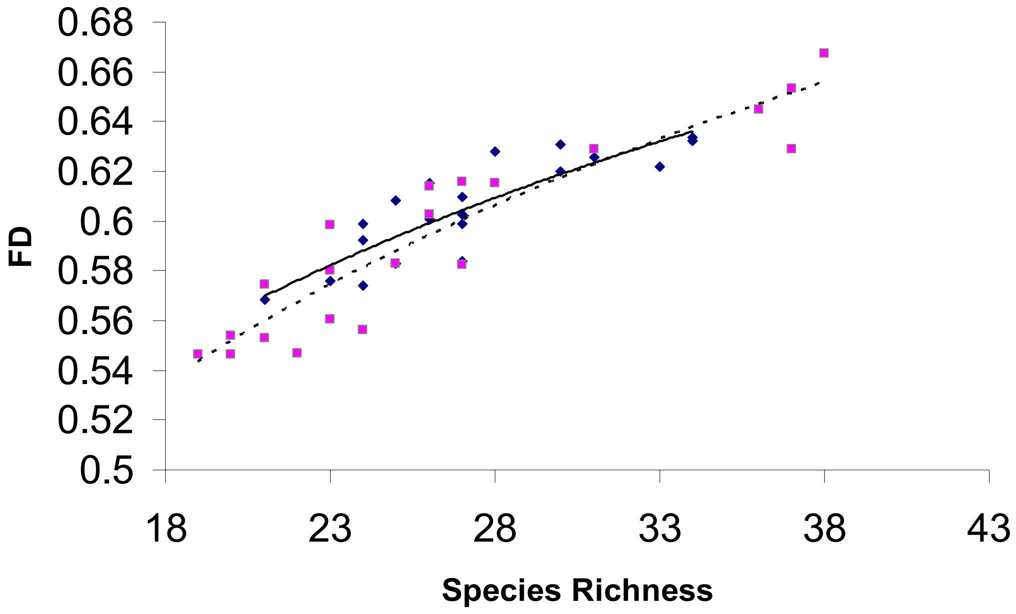

Figure 4-3 Species richness and functional diversity (FD) for riprap and natural rocky sites in southern California. Each symbol represents a transect, 21 for riprap and 21 for natural rock. Squares represent riprap and diamonds represent natural rock. Trend lines are shown for the log linear regression model. The dotted line is fitted to riprap data, the solid line to natural rock data.

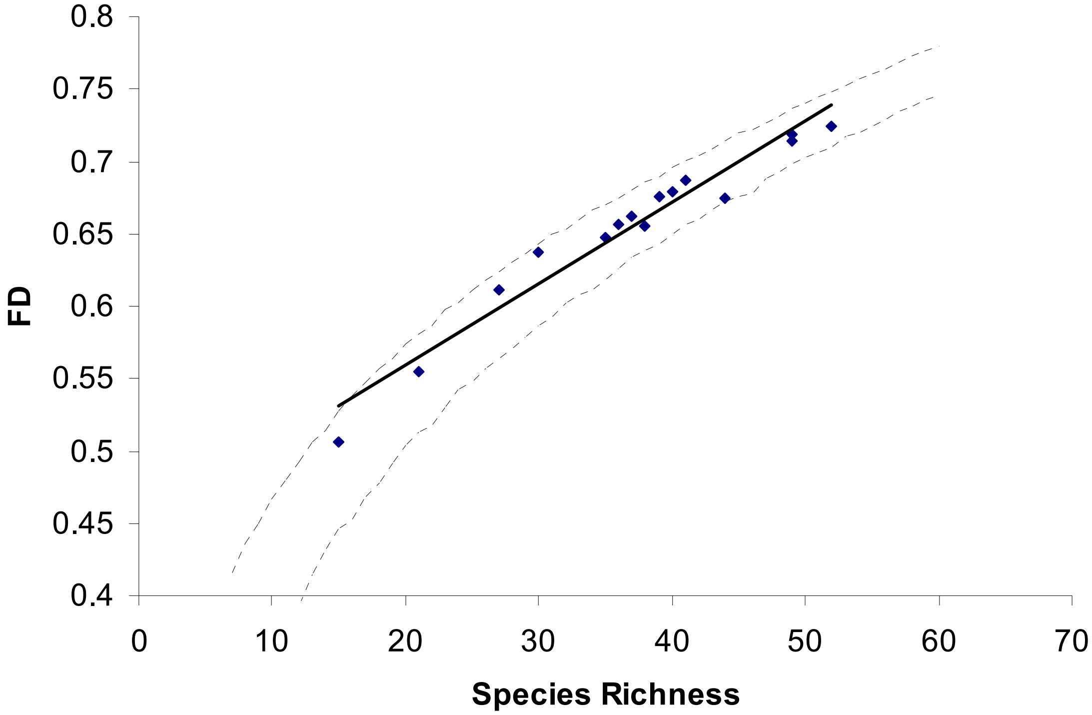

Figure 4-4 Species richness and functional diversity (FD) for all sites. Dotted lines represent upper and lower 95% confidence intervals of simulated data. Symbols represent observed data. The trend line shown is for a linear model to illustrate the slight curve in the observed data points.

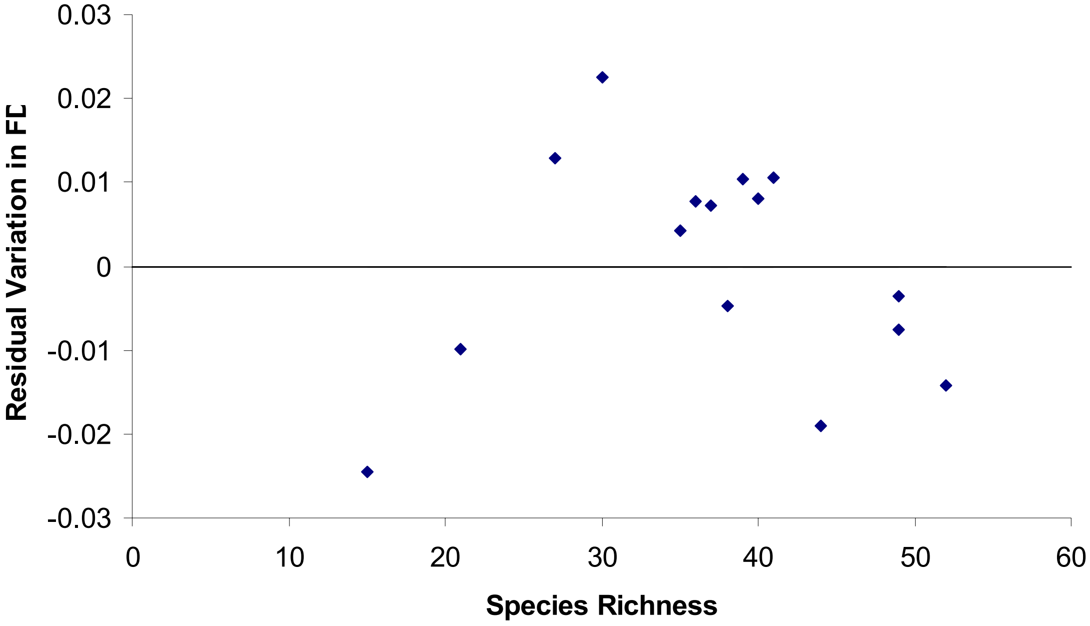

Figure 4-5 A plot of the residual variation for the linear model describing the relationship between FD and species richness for all 15 sites.

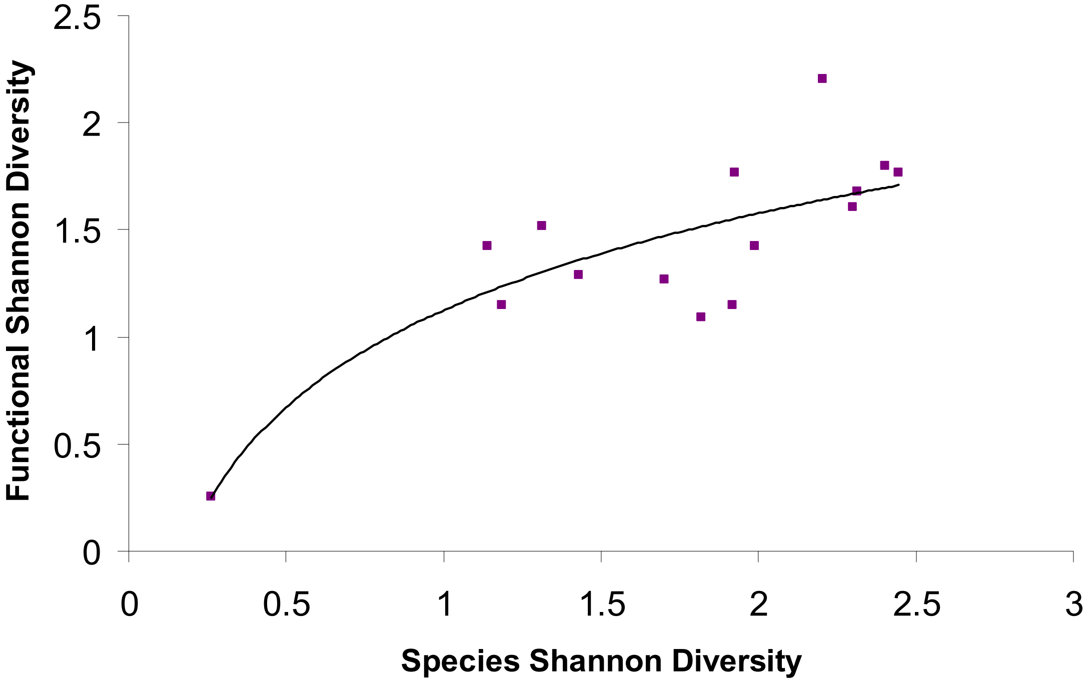

Figure 4-6 Species diversity and functional diversity as measured by the Shannon-Wiener diversity index for all sites. The trend line is described by the log linear function.

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Appendix A - Data for CHAPTER 2 and CHAPTER 4

These are the sum abundances for each organism in each transect. Sessile species are presented as percent cover, mobile species as counts. Every transect had 8 quadrats and all quadrats were summed for the total abundance within each transect. Unlike the data within Chapter 2 and Chapter 4, several species are presented individually here, that should probably be added together to remain conservative in estimating the number and abundance of species. For example, my ability to distinguish the various *Gelidium* species, along with *Pterocladiella*, and *Chondracanthus* did not develop until after several of the southern California sites had been sampled. Similarly, I recommend combining all of the polysiphonic red algae, as these are also very difficult to distinguish in the field and I don't trust all my earlier identifications. Petrocelis is the crustose form of *Mastocarpus* sp. Wherever possible, I recorded the percent cover of algal species with a crustose and upright stage during different generations separately. At the time of this writing, Enteromorpha is considered a type of *Ulva* and the genus is under considerable revision. At times, I recorded all organisms that could be considered Enteromorpha as *Ulva* sp. Transects are numbered. For example, CC1 is the first transect from Crescent City. Although, they may not be consecutive because they refer to specific transects on raw data sheets, some of which were not used due to incompleteness, or loss, etc. From north to south: SEW = Seward, Alaska, H1 = Homer, Alaska, H2 = Homer, Alaska, approximately half a kilometer from H1, SEL = Seldovia, Alaska, NB = Neah Bay, Washington, CC = Crescent City, California, HMB = Half Moon Bay, California, PF = Pt. Fermin, California, SP = San Pedro, California, NPO = Newport, Calfifornia, CDM = Corona del Mar, California, DPNR = Dana Pt. State Reserve, California, DPRR = Dana Pt. Breakwater, SIO = Scripps Institute of Oceanography in La Jolla, California, and MB = Mission Bay, California. The only natural rock sites are from southern California, and are Pt. Fermin, Corona del Mar, Dana Pt. State Reserve, and Scripps.

Transect	CC1	CC2	CC3	CC4	CC5
Analipus japonicus (crust)	0.00%	0.50%	0.00%	1.00%	0.00%
Anthopleura elegantissima	0.00%	0.50%	0.50%	0.00%	0.00%
Anthopleura xanthogrammica	0.00%	0.00%	1.00%	0.00%	1.00%
Balanus glandula	73.00%	40.50%	72.50%	49.50%	88.00%
Bare rock	104.00%	160.50%	124.00%	160.00%	168.00%
Bosiella orbigiana	0.00%	0.50%	40.50%	0.50%	57.00%
Callithamnion pikeanum	0.00%	0.00%	0.00%	0.00%	0.50%
Callophyllus sp.	0.00%	0.00%	0.00%	8.00%	0.50%
Ceramium sp.	0.50%	22.00%	12.00%	0.00%	4.50%
Chthamalus fissus	9.50%	69.50%	21.00%	18.50%	8.00%
Cladophora sericea	0.00%	0.00%	0.00%	0.00%	0.00%
Combined limpets	191	193	374	64	174
Corallina vancouveriensis	94.00%	193.00%	153.00%	89.00%	80.50%
Corralline crust	0.50%	0.50%	0.00%	0.00%	0.50%
Cryptopleura lobulifera	28.00%	16.50%	52.50%	0.50%	276.00%
Diatoms	0.00%	0.50%	0.00%	0.00%	0.00%
Endocladia muricata	172.00%	96.00%	128.00%	32.50%	81.00%
Hedophyllum sessile	0.00%	0.00%	36.00%	0.00%	0.00%
Katharina tunicata	2	8	20	3	1
Lepidochitona dentiens	0	2	0	0	1
Leptasterias hexactis	2	20	11	5	3
Littorina scutulata	128	38	30	30	54
Mastocarpus jardinii	8.50%	4.50%	0.50%	4.00%	1.00%
Mastocarpus papillatus	9.00%	8.50%	0.50%	0.50%	1.00%
Mytilus californianus	216.50%	28.00%	28.00%	296.00%	1.00%
Nucella emarginata	1	0	5	1	0
Osmundea sinicola	0.00%	0.00%	0.50%	0.00%	2.00%
Osmundea spectabilis	0.00%	0.00%	0.00%	0.00%	1.00%
Pelvetiopsis limitata	0.00%	0.00%	0.00%	68.00%	0.00%
Petrocelis sp.	17.50%	29.00%	13.50%	9.00%	5.50%
Phragmatopoma californica	0.50%	0.50%	0.50%	0.00%	0.00%
Pisaster ocreceaus	1	1	2	0	0
Plocamium pacificum	0.50%	0.50%	0.50%	0.50%	16.00%
Policipes polymerus	45.00%	56.00%	64.00%	9.50%	4.00%
Polysiphonia sp.	0.50%	0.00%	8.50%	1.00%	0.00%
Porphyra sp.	1.00%	0.00%	0.00%	0.00%	0.00%
Ralfsia pacifia	26.00%	62.00%	61.00%	69.50%	18.50%
Semibalanus carriosis	17.00%	20.50%	5.00%	25.00%	0.50%
Strongylocentrotus purpuratus	0	1	0	0	0
Ulva spp.	5.00%	1.00%	0.00%	1.00%	0.00%
Unid brown crust	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Red	1.00%	0.50%	0.50%	0.00%	0.00%

Transect	CDM1	CDM2	CDM3	CDM4	CDM5
Acanthinucella spirata	1	5	0	0	1
Anthopleura elegantissima	24.00%	21.50%	20.50%	0.00%	24.00%
Balanus glandula	6.50%	34.50%	9.50%	1.00%	18.50%
Bare rock	348.00%	168.00%	228.00%	304.00%	236.00%
Caulacanthus ustulatus	0.50%	4.00%	0.00%	0.50%	4.00%
Chondracanthus canaliculatus	0.00%	0.00%	0.50%	0.00%	0.00%
Chthamalus fissus	121.00%	328.00%	205.00%	105.00%	168.00%
Combined limpets	95	147	135	223	122
Corallina pinnatifolia	44.00%	132.50%	108.50%	100.50%	132.00%
Corallina vancouveriensis	0.00%	0.00%	0.00%	60.00%	8.00%
Corralline crust	44.50%	116.00%	33.00%	24.00%	64.00%
Endarachne binghamiae	0.00%	4.00%	0.00%	1.00%	0.00%
Fissurella volcano	3	2	3	8	0
Leathesia difformis	0.00%	0.00%	0.00%	4.00%	0.00%
Lepidochitona dentiens	0	0	0	1	0
Lepidochitona hartwegii	2	1	0	0	0
Littorina keenae	391	374	371	129	266
Littorina scutulata	26	96	55	79	135
Lottia gigantea	12	0	3	1	6
Macron lividus	0	1	0	0	0
Mopalia muscosa	1	1	1	0	0
Mytilus californianus	80.50%	97.00%	185.00%	149.00%	150.00%
Nucella emarginata	0	1	0	0	0
Nuttallina sp.	42	60	25	18	20
Pagurus spp.	0	0	2	0	0
Phragmatopoma californica	28.00%	0.00%	56.50%	0.50%	1.50%
Policipes polymerus	16.50%	0.50%	1.00%	1.00%	4.50%
Pseudochama exogyra	8.50%	0.00%	0.00%	0.00%	0.00%
Ralfsia pacifia	13.50%	7.00%	2.50%	25.50%	18.00%
Ralfsia sp.	21.00%	6.00%	25.00%	52.50%	8.50%
Septifer sp.	2.00%	1.50%	1.00%	0.50%	1.50%
Serpulids	0.50%	2.00%	1.50%	0.50%	1.00%
Serpulorbis squamigerus	1.50%	1.00%	0.50%	0.00%	0.50%
Tegula funebralis	2	0	0	0	0
Tetraclita rubescens	1.00%	5.00%	1.50%	5.50%	0.50%
Ulva spp.	2.00%	1.50%	5.50%	5.00%	0.50%
Unid green crust (microalgae)	12.50%	12.00%	0.00%	12.00%	20.00%
Unid Red	0.50%	0.00%	0.00%	0.00%	0.00%
Watersipora sp.	0.50%	0.00%	0.00%	0.00%	0.00%

Transect	DPNR10	DPNR5	DPNR6	DPNR7	DPNR8	DPNR9
Acanthinucella spirata	0	2	0	3	1	0
Anthopleura elegantissima	1.00%	17.00%	5.00%	65.00%	18.00%	9.50%
Balanus glandula	2.00%	133.00%	2.00%	14.50%	1.50%	5.00%
Bare rock	300.00%	68.00%	284.00%	144.50%	336.00%	380.00%
Caulacanthus ustulatus	24.00%	41.50%	89.00%	12.50%	92.50%	20.50%
Ceramium sp.	0.00%	0.50%	0.00%	0.00%	0.00%	0.00%
Chondracanthus canaliculatus	0.00%	0.00%	24.00%	0.00%	25.00%	8.00%
Chthamalus fissus	133.00%	0.50%	117.00%	82.00%	65.00%	24.50%
Combined limpets	54	172	107	82	79	29
Corallina pinnatifolia	48.00%	108.50%	24.00%	45.50%	76.50%	128.00%
Corallina vancouveriensis	0.00%	0.00%	80.00%	12.00%	0.00%	0.00%
Corralline crust	12.50%	20.50%	32.50%	12.50%	0.50%	4.50%
Endarachne binghamiae	0.50%	8.50%	0.00%	0.00%	0.00%	0.00%
Fissurella volcano	19	17	9	25	21	2
Gastroclonium subarticulatum	0.00%	1.00%	20.00%	0.00%	0.00%	0.00%
Gelidium sp.	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Halidrys dioica	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Laurencia pacifica	0.50%	2.00%	16.00%	0.50%	0.50%	0.50%
Lepidochitona hartwegii	0	1	0	0	1	0
Littorina keenae	75	3	1	1	419	112
Littorina scutulata	13	0	90	69	21	6
Lottia gigantea	1	5	0	4	2	3
Mazzaella leptorhyncos	0.00%	0.00%	0.00%	0.50%	0.00%	0.00%
Mazzaella leptorhyncos	0.00%	0.00%	0.00%	0.50%	0.00%	0.00%
Microcladia coulteri	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Microcladia coulteri	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Mytilus californianus	296.50%	324.50%	116.50%	380.00%	120.00%	100.50%
Nucella emarginata	0	0	0	1	0	0
Nuttallina sp.	5	15	12	6	18	12
Phragmatopoma californica	9.50%	9.50%	4.50%	13.50%	61.00%	28.50%
Policipes polymerus	1.00%	0.50%	1.00%	44.00%	1.50%	4.00%
Pseudochama exogyra	0.00%	0.00%	0.00%	0.00%	0.50%	0.00%
Ralfsia pacifia	28.00%	32.50%	17.50%	1.00%	32.50%	33.00%
Ralfsia sp.	5.00%	0.00%	0.00%	0.00%	13.00%	0.50%
Rhodymenia sp.	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Serpulids	0.50%	0.00%	0.00%	0.00%	0.50%	0.00%
Striped chiton	0	2	0	0	0	0
Tegula funebralis	0	0	0	1	0	0
Tetraclita rubescens	1.00%	1.00%	0.00%	0.50%	1.00%	1.00%
Ulva spp.	0.50%	9.00%	1.50%	0.50%	1.00%	0.00%
Unid brown	0.50%	0.00%	0.00%	0.50%	1.00%	8.00%
Unid red	0.50%	0.00%	0.00%	8.00%	0.50%	0.00%

Transect	DPRR21	DPRR6	DPRR7	DPRR8	DPRR9
Balanus glandula	21.50%	1.50%	116.00%	73.50%	3.00%
Anthopleura elegantissima	0.00%	0.50%	0.00%	0.00%	0.00%
Bare rock	304.00%	170.00%	132.00%	284.00%	248.00%
Bosiella orbigiana	0.50%	0.50%	0.00%	12.00%	0.50%
Centrocerus sp.	0.00%	0.00%	0.50%	0.00%	0.00%
Ceramium sp.	8.00%	0.00%	0.00%	4.00%	0.00%
Chondracanthus canaliculatus	0.00%	0.00%	0.00%	28.00%	0.00%
Chthamalus fissus	244.00%	188.50%	220.00%	113.50%	276.50%
Combined limpets	183	129	352	161	154
Corallina pinnatifolia	76.00%	72.50%	145.00%	50.00%	68.00%
Corallina vancouveriensis	8.00%	4.50%	9.00%	16.50%	40.50%
Corralline crust	0.00%	0.50%	2.00%	0.00%	0.50%
Eisenia arborescens	0.50%	32.00%	0.00%	8.00%	0.00%
Eurystomella bilabiata	0.50%	0.00%	0.00%	0.00%	0.00%
Fissurella volcano	7	4	0	5	4
Gelidium sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Kelp crab	1	0	0	0	0
Littorina keenae	98	0	0	0	2
Littorina scutulata	8	0	4	0	18
Lottia gigantea	7	19	35	19	44
Mazzalla affinis	0.00%	0.00%	4.00%	0.00%	0.50%
Megabalanus californicus	0.00%	2.00%	2.00%	1.50%	1.00%
Mytilus californianus	148.50%	256.00%	172.50%	104.50%	140.00%
Mytilus galloprovincialis	0.50%	0.00%	0.50%	0.00%	0.00%
Nuttallina sp.	19	10	18	9	15
Phragmatopoma californica	0.50%	2.00%	1.50%	0.50%	1.00%
Plocamium violaceum	0.00%	0.00%	0.00%	0.00%	8.00%
Policipes polymerus	13.00%	116.00%	25.00%	64.00%	9.00%
Prionitis lanceolata	12.00%	0.00%	0.00%	0.00%	0.00%
Pseudochama exogyra	0.50%	0.00%	0.00%	0.00%	0.00%
Pterosiphonia sp.	0.00%	24.50%	1.50%	1.00%	0.00%
Ralfsia pacifia	0.50%	0.50%	9.00%	16.50%	0.00%
Ralfsia sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Schizoporella unicornis	0.50%	0.00%	0.00%	0.50%	0.50%
Serpulids	0.50%	0.00%	0.00%	0.00%	0.00%
Tetraclita rubescens	17.00%	1.50%	14.50%	49.00%	25.80%
Ulva spp.	0.00%	0.00%	0.50%	0.00%	0.00%
Unid Green Crust	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Green Crust (Microalgae)	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Orange Crust	0.00%	0.00%	0.00%	0.50%	0.00%
Unid Orange Crust	0.00%	0.00%	0.00%	0.50%	0.00%
Unid Red	0.00%	0.00%	0.00%	0.00%	0.50%

Transect	H1-1	H1-2	H1-3	H1-4	H1-5
Balanus crenatus	0.00%	0.00%	0.00%	0.00%	0.00%
Balanus glandula	500.00%	588.00%	576.00%	524.00%	488.00%
Bare rock	224.50%	209.00%	225.00%	264.50%	308.00%
Cladophora sericea	4.00%	0.50%	0.50%	0.50%	0.50%
Combined limpets	455	261	142	191	235
Coralline Crust	0.00%	0.00%	0.00%	0.50%	0.00%
Diatoms	0.50%	1.00%	1.50%	0.50%	0.50%
Enteromorpha sp.	0.50%	2.00%	1.50%	5.00%	1.50%
Fucus gardneri	65.00%	4.50%	0.50%	8.50%	4.50%
Littorina scutulata	3	5	1	4	3
Littorina sitkana	80	75	43	20	35
Melanosiphon intestinalis	0.00%	0.00%	0.00%	0.50%	0.00%
Mytilus trossolus	1.50%	1.50%	1.00%	1.00%	2.00%
Neorhodomella sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Porphyra sp.	0.50%	0.50%	0.50%	0.00%	0.50%
Scytosiphon dotyi	0.50%	0.00%	0.00%	0.00%	0.50%
Semibalanus carriosis	0.50%	0.00%	0.00%	0.00%	0.50%
Ulothrix sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Ulva spp.	9.00%	8.00%	1.00%	1.00%	1.00%
Unid Algae	0.00%	0.50%	0.50%	0.00%	0.50%
Unid Brown Crust	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Green Crust (Microalgae)	0.00%	0.00%	0.50%	0.00%	0.00%
Yellow Mite	1	0	0	0	0

Transect	H2-1	H2-2	H2-3	H2-4	H2-5
Balanus crenatus	0.00%	0.00%	0.00%	0.00%	0.50%
Balanus glandula	261.50%	332.00%	428.00%	516.50%	400.00%
Bare rock	125.00%	189.00%	120.50%	77.50%	105.50%
Cladophora sericea	0.00%	5.00%	8.50%	1.50%	21.00%
Combined limpets	165	169	215	140	162
Diatoms	10.00%	1.50%	5.00%	0.50%	24.50%
Enteromorpha spp.	2.50%	1.50%	1.00%	1.50%	17.00%
Fucus gardneri	365.00%	272.50%	184.50%	201.50%	102.00%
Gloiopeltis furcata	0.50%	0.00%	0.00%	1.00%	1.50%
Halosaccion glandiforme	0.50%	0.00%	0.00%	0.00%	0.00%
Leptasterias hexactis	0	0	1	1	0
Littorina scutulata	0	0	3	4	0
Littorina sitkana	216	347	221	399	248
Melanosiphon intestinalis	1.00%	0.50%	0.00%	0.50%	0.50%
Mytilus trossolus	1.00%	1.50%	1.50%	2.50%	0.50%
Palmaria callophylloides	32.50%	8.50%	24.50%	8.50%	52.00%
Palmaria hecatensis	0.00%	0.50%	0.50%	0.50%	24.00%
Palmaria sp.	0.00%	0.00%	0.50%	0.00%	0.00%
Polysiphonia sp.	0.50%	0.50%	16.00%	0.00%	4.00%
Porphyra sp.	9.00%	1.00%	4.50%	1.50%	9.50%
Prionitis lanceolata	0.00%	0.00%	0.00%	0.00%	0.50%
Ralfsia pacifia	0.00%	0.50%	0.50%	0.50%	1.00%
Red mite	3	0	0	0	0
Scytosiphon dotyi	1.50%	1.50%	9.00%	1.00%	28.50%
Semibalanus carriosis	0.50%	0.50%	1.00%	0.50%	0.00%
Spirorbis	0.50%	0.00%	0.00%	0.00%	0.00%
Ulothrix sp.	1.00%	0.00%	0.00%	0.00%	0.00%
Ulva spp.	14.00%	0.50%	5.00%	8.50%	12.50%
Unid Brown	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Red	0.50%	0.50%	2.00%	1.00%	1.00%
Urospora sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Yellow Mite	1	0	0	0	1

Transect	HMB1	HMB2	HMB3	HMB4	HMB5
Balanus glandula	0.50%	0.00%	0.50%	0.50%	0.50%
Bare rock	232.00%	276.00%	288.00%	48.00%	208.00%
Bosiella orbigiana	0.50%	0.50%	1.00%	2.00%	0.50%
Calliarthron tuberculosum	0.00%	0.50%	12.00%	28.00%	0.00%
Ceramium sp.	12.50%	20.00%	9.50%	29.00%	32.50%
Chthamalus fissus	53.00%	25.50%	2.50%	18.00%	58.00%
Cladophora columbiana	0.00%	0.00%	0.00%	0.50%	0.50%
Combined limpets	370	523	661	447	722
Corallina pinnatifolia	252.00%	120.00%	205.00%	337.00%	172.50%
Corallina vancouveriensis	21.50%	48.00%	21.00%	10.50%	21.50%
Corralline crust	0.00%	0.00%	4.50%	0.50%	1.00%
Cryptopleura lobulifera	2.00%	28.50%	36.50%	84.00%	20.50%
Cumogloia sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Egregia menzeisii	0.00%	0.00%	4.00%	0.00%	0.00%
Endocladia muricata	4.50%	9.00%	24.50%	0.50%	64.00%
Lepidochitona dentiens	0	0	0	1	0
Lepidochitona hartwegii	0	0	0	0	2
Littorina scutulata	0	0	9	0	11
Lottia gigantea	0	0	6	1	0
Mastocarpus jardinii	16.00%	0.50%	0.00%	8.00%	48.00%
Mastocarpus sp.	24.00%	4.00%	12.50%	0.00%	0.50%
Mazzalla affinis	0.00%	4.00%	12.00%	5.00%	9.50%
Melobesia mediocris	0.00%	0.00%	0.00%	0.00%	0.50%
Microcladia borealis	0.00%	0.00%	1.00%	0.00%	12.50%
Microcladia coulteri	0.00%	0.00%	0.50%	0.50%	0.00%
Mytilus californianus	40.50%	97.00%	1.00%	112.50%	168.00%
Neorhodomella sp.	0.00%	0.00%	4.00%	0.00%	0.00%
Nuttalina californica	5	2	1	7	11
Petalonia fascia	69.00%	45.00%	82.00%	80.50%	80.00%
Petrospongium rugosum	16.00%	0.50%	13.00%	29.00%	6.00%
Phragmatopoma californica	1.00%	9.00%	1.50%	2.50%	1.00%
Phyllospadix sp.	0.00%	84.50%	0.00%	0.00%	0.00%
Plocamium violacium	0.00%	0.00%	0.00%	0.50%	0.50%
Policipes polymerus	1.00%	0.00%	1.00%	0.00%	1.00%
Porphyra sp.	1.00%	2.00%	12.50%	4.00%	1.50%
Prionitis lanceolata	4.00%	0.00%	1.00%	12.00%	12.00%
Pugettia gracilis	1	0	0	0	0
Ralfsia pacifia	24.50%	4.50%	104.00%	73.00%	58.00%
Ralfsia sp.	40.00%	92.00%	0.00%	0.00%	0.00%
Serpulids	0.00%	0.00%	0.00%	0.00%	0.50%
Sponge	0.00%	0.00%	0.00%	0.50%	0.00%
Strongylocentrotus purpuratus	0	5	0	3	0
Ulva spp.	0.50%	0.00%	0.50%	0.50%	0.00%
Unid Brown Crust	4.00%	0.00%	0.00%	0.00%	0.00%
Unid Red Crust	0.00%	0.00%	0.00%	84.00%	0.00%

Transect	MB1	MB2	MB3	MB4	MB5
Balanus glandula	6.50%	16.50%	4.50%	8.50%	9.50%
Bare rock	236.00%	264.00%	80.50%	252.00%	288.00%
Bosiella orbigiana	28.50%	25.00%	2.50%	1.00%	0.50%
Ceramium sp.	0.00%	0.00%	0.50%	16.00%	0.00%
Chaetomorpha linum	0.00%	1.00%	5.00%	1.50%	5.00%
Chondracanthus canaliculatus	40.00%	88.00%	8.50%	40.50%	0.50%
Chthamalus fissus	57.00%	85.50%	89.00%	85.00%	88.50%
Cladopohra columbiana	0.00%	4.50%	0.00%	0.00%	0.00%
Combined limpets	79	31	58	90	170
Corallina pinnatifolia	60.50%	72.00%	356.00%	260.00%	184.00%
Corallina vancouveriensis	0.00%	44.50%	53.50%	32.50%	1.00%
Corralline crust	6.00%	0.50%	8.50%	8.00%	0.00%
Cryptopleura corallinara	0.00%	24.00%	52.50%	108.00%	48.00%
Diatoms	0.50%	12.50%	0.00%	0.00%	0.00%
Endarachne binghamiae	1.00%	1.50%	25.50%	8.50%	1.00%
Eurystomella bilabiata	0.00%	0.50%	0.00%	0.50%	0.00%
Fissurella volcano	1	6	9	10	10
Gastroclonium subarticulatum	0.00%	0.00%	4.00%	0.00%	0.50%
Gelidium sp.	12.00%	5.00%	1.00%	24.50%	12.50%
Laurencia pacifica	0.00%	0.00%	8.50%	0.50%	0.00%
Lithothrix aspergillum	0.00%	1.00%	0.00%	0.50%	0.00%
Littorina keenae	0	26	10	8	6
Littorina scutulata	0	0	16	3	5
Lottia gigantea	24	7	13	8	24
Mazzalla affinis	0.50%	1.00%	1.00%	0.50%	0.00%
Megabalanus californicus	1.00%	1.50%	1.50%	2.00%	1.00%
Mexicanthina lugubris	1	0	0	0	0
Mytilus californianus	300.50%	1.00%	6.50%	9.00%	37.00%
Nuttallina sp.	14	1	12	6	0
Petrospongium rugosum	0.00%	0.50%	8.00%	1.00%	9.50%
Phragmatopoma californica	24.00%	81.00%	9.50%	2.00%	1.00%
Plocamium pacificum	0.00%	0.00%	0.00%	0.00%	0.50%
Plocamium violcaium	0.50%	0.50%	0.00%	0.00%	0.00%
Policipes polymerus	36.50%	5.00%	3.00%	1.00%	1.00%
Polysiphonia sp.	0.00%	0.00%	17.00%	1.50%	0.00%
Porphyra sp.	0.00%	0.50%	1.50%	0.00%	2.00%
Prionitis lanceolata	4.00%	0.00%	0.00%	0.00%	0.00%
Pseudochama exogyra	0.00%	0.50%	2.00%	1.50%	1.00%
Pterocladiella sp.	0.00%	0.00%	12.50%	12.50%	0.00%
Ralfsia pacifia	25.00%	52.50%	16.00%	0.50%	44.00%
Ralfsia sp.	1.50%	1.00%	96.50%	49.00%	88.00%
Rhodymenia sp.	4.50%	0.00%	0.00%	4.50%	1.00%
Schizoprella unicornis	0.00%	0.50%	0.00%	0.00%	0.00%
Scytosiphon dotyi	0.00%	0.50%	0.00%	0.50%	4.50%
Serpulids	0.50%	5.00%	2.00%	1.00%	1.00%
Serpulorbis squamigerus	0.00%	0.50%	0.00%	0.00%	0.00%
Tetraclita rubescens	6.00%	65.00%	2.00%	4.50%	16.50%
Thallamoporella californica	0.00%	0.00%	0.50%	0.50%	0.50%
Ulothrix sp.	0.00%	0.00%	0.50%	0.00%	25.00%
Ulva spp.	0.50%	36.00%	20.50%	0.50%	8.50%
Unid Brown	4.00%	0.00%	0.00%	0.00%	0.50%
Unid Brown Crust	0.00%	0.00%	0.00%	0.00%	1.00%
Unid Green Crust (Microalgae)	0.00%	0.50%	0.50%	0.50%	0.00%
Unid Red	0.00%	0.50%	0.00%	0.00%	0.00%
Urospora sp.	0.00%	0.00%	0.00%	0.00%	0.00%

Transect	NB1	NB2	NB3	NB4	NB5
Alaria marginata	144.50%	4.00%	0.00%	40.00%	16.00%
Analipus japonicus (crust)	0.00%	0.00%	0.00%	0.00%	0.50%
Analipus japonicus (upright)	0.00%	0.00%	0.50%	0.00%	0.00%
Balanus glandula	61.50%	80.00%	52.50%	105.00%	29.50%
Bare rock	8.00%	180.00%	56.00%	76.00%	64.00%
Bosiella orbigiana	8.50%	0.00%	0.00%	0.00%	0.50%
Callithamnion pikeanum	2.00%	0.00%	0.00%	0.50%	0.50%
Callophyllus sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Ceramium sp.	4.00%	0.00%	0.00%	0.00%	0.00%
Chthamalus fissus	21.00%	13.50%	8.50%	12.00%	2.00%
Cladophora sericea	0.00%	0.00%	0.00%	0.00%	4.00%
Cladopohra columbiana	20.50%	0.00%	0.50%	0.50%	1.00%
Combined limpets	19	9	12	39	81
Corallina vancouveriensis	7.00%	28.00%	44.00%	66.00%	41.00%
Corralline crust	2.00%	20.00%	16.00%	17.00%	1.50%
Cryptochiton stelleri	1	0	0	0	0
Cryptopleura corallinara	0.50%	0.50%	0.00%	0.00%	0.00%
Diatoms	0.50%	0.00%	0.00%	0.00%	0.00%
Egregia menzeisii	20.00%	0.00%	0.00%	0.00%	0.00%
Endocladia muricata	24.50%	0.00%	0.50%	0.00%	8.00%
Enteromorpha spp.	0.00%	0.00%	1.00%	0.50%	0.00%
Fucus gardneri	5.00%	0.00%	16.50%	28.00%	21.50%
Gigartina sp.	0.00%	0.00%	52.00%	0.00%	0.00%
Halosaccion glandiformis	0.50%	0.00%	24.50%	0.00%	0.00%
Hedophyllum sessile	24.00%	0.00%	0.00%	104.00%	28.00%
Hildenbrandia sp.	0.00%	0.00%	16.00%	0.00%	0.00%
Katharina tunicata	4	0	1	8	1
Leathesia nana	0.00%	0.50%	0.00%	0.00%	0.00%
Lepidochitona dentiens	0	0	1	10	1
Lepidochitona hartwegii	3	0	0	0	0
Ligia sp.	1	5	0	1	1
Littorina scutulata	39	24	9	11	1
Littorina sitkana	1	2	0	3	0
Mastocarpus jardinii	73.50%	53.50%	94.00%	1.50%	17.50%
Mastocarpus papillatus	12.50%	13.00%	8.00%	1.00%	32.50%
Mastocarpus sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Microcladia borealis	1.50%	0.00%	0.00%	0.00%	0.00%
Neorhodomella sp.	5.50%	0.00%	0.50%	0.00%	4.50%
Onchidella borealis	0	0	0	0	1
Petrocelis sp.	197.50%	324.50%	216.00%	241.00%	316.00%
Phragmatopoma californica	0.00%	0.00%	0.00%	0.50%	0.00%
Plocamium pacificum	0.00%	0.50%	0.00%	0.50%	0.00%
Polysiphonia sp.	64.50%	0.00%	0.50%	12.00%	24.50%
Porphyra sp.	4.00%	17.00%	74.00%	84.50%	144.50%
Prionitis lanceolata	0.50%	0.00%	0.00%	0.00%	0.00%
Pterosiphonia sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Ralfsia pacifia	0.00%	0.00%	0.00%	0.00%	8.00%
Red Mite	0	0	0	0	1
Rhizoclonium sp.	1.00%	0.00%	0.00%	0.00%	0.00%
Rhodymenia sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Semibalanus cariosis	0.50%	30.50%	14.50%	1.00%	0.50%
Sponge	0.50%	0.00%	0.00%	0.50%	0.50%
Tonicella lineata	2	0	1	1	1
Ulva spp.	101.00%	61.00%	117.00%	21.00%	56.50%
Unid Red	0.00%	0.00%	0.00%	0.50%	0.50%
Unid Red Crust	0.00%	12.00%	0.00%	0.00%	0.00%

Transect	NPO1	NPO2	NPO3	NPO4	NPO5	NPO6
Anthopleura sola	0.00%	0.00%	0.00%	4.00%	0.00%	0.00%
Balanus glandula	32.50%	50.00%	37.00%	14.50%	36.50%	65.50%
Bare rock	220.00%	192.00%	268.00%	264.00%	272.00%	256.00%
Bosiella orbigiana	0.00%	0.00%	0.00%	0.00%	0.50%	0.00%
Ceramium sp.	1.00%	0.00%	12.00%	0.50%	0.00%	0.50%
Chondracanthus canaliculatus	0.00%	0.00%	0.00%	0.00%	0.50%	0.00%
Chthamalus fissus	73.00%	108.50%	77.50%	50.00%	89.50%	69.00%
Combined limpets	29	41	54	59	24	41
Corallina pinnatifolia	8.00%	112.50%	60.50%	56.50%	36.00%	8.00%
Corallina pinnatifolia	6	9	4	6	2	9
Corallina vancouveriensis	0.00%	0.50%	0.00%	8.00%	0.00%	28.00%
Corralline crust	12.50%	0.50%	0.50%	40.50%	4.00%	2.00%
Diatoms	1.50%	4.50%	0.00%	1.00%	0.00%	0.00%
Egregia menzeisii	44.00%	0.00%	12.00%	0.00%	8.00%	0.00%
Eisenia arborescens	0.00%	0.00%	0.50%	0.00%	0.00%	0.00%
Endarachne binhamiae	12.50%	8.00%	56.00%	36.00%	128.00%	20.00%
Eurystomella bilabiata	0.00%	0.00%	0.00%	0.00%	0.50%	0.50%
Fissurella volcano	0	0	1	1	1	0
Gastroclonium subarticulatum	0.00%	0.00%	8.00%	0.00%	0.50%	0.00%
Hildenbrandia sp.	0.50%	1.00%	0.00%	0.00%	0.00%	0.00%
Leathesia difformis	0.00%	0.00%	0.00%	0.50%	1.50%	0.50%
Lepidochitona hartwegii	2	0	0	0	0	0
Littorina keenae	0	39	26	10	29	4
Lottia gigantea	10	12	12	6	17	6
Mazzaella leptorhyncos	0.00%	0.00%	0.00%	0.50%	0.00%	0.50%
Megabalanus californicus	0.00%	0.00%	0.00%	0.00%	2.00%	1.00%
Mytilus californianus	185.50%	276.00%	284.00%	292.00%	33.50%	256.50%
Mytilus galloprovincialis	0.00%	0.00%	0.00%	0.00%	0.50%	0.00%
Nucella emarginata	0	2	0	0	2	0
Phragmatopoma californica	0.00%	0.00%	0.00%	0.00%	0.50%	0.50%
Policipes polymerus	84.50%	24.50%	13.50%	53.00%	8.50%	33.50%
Porphyra sp.	1.00%	0.00%	0.00%	0.00%	0.50%	0.00%
Ralfsia pacifia	5.00%	12.50%	4.50%	0.50%	24.50%	4.00%
Ralfsia sp.	0.50%	0.00%	0.00%	0.50%	0.50%	0.00%
Serpulids	1.00%	0.50%	0.50%	0.50%	1.00%	0.50%
Strongylocentrotus purpuratus	0	0	0	3	0	0
Tetraclita rubescens	11.00%	13.50%	2.50%	2.50%	2.00%	6.00%
Ulva spp.	144.00%	5.00%	20.50%	4.50%	132.00%	20.00%
Unid Brown	0.00%	0.50%	4.50%	0.00%	8.00%	0.00%
Unid Brown Crust	0.50%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid Brown Crust	0.50%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid Green Crust (Microalgae)	12.50%	20.00%	0.50%	20.00%	4.00%	16.50%
Unid Orange Crust	0.00%	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Orange Crust	0.00%	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Red	0.00%	0.00%	0.00%	0.50%	1.00%	0.00%

Transect	PF1	PF2	PF3	PF4	PF5
Anthpleura elegantissima	0.50%	0.00%	0.00%	0.50%	0.00%
Balanus glandula	5.50%	1.00%	8.00%	2.50%	1.50%
Bare rock	332.00%	112.00%	208.00%	116.00%	172.00%
Bosiella orbigiana	4.00%	0.50%	0.50%	48.00%	0.50%
Callithamnion rupicola	0.00%	0.50%	0.00%	0.00%	0.00%
Caulacanthus ustulatus	0.50%	1.00%	0.50%	4.00%	4.50%
Ceramium sp.	0.00%	0.00%	0.50%	1.50%	32.00%
Chaetomorpha linum	0.50%	0.00%	0.00%	0.00%	0.00%
Chondracanthus canaliculatus	28.50%	5.00%	76.50%	0.00%	76.00%
Chondria sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Chthamalus fissus	104.50%	101.00%	65.00%	164.50%	180.50%
Combined limpets	55	143	115	432	489
Corallina pinnatifolia	116.00%	244.00%	316.00%	352.00%	156.00%
Corallina vancouveriensis	88.00%	168.00%	96.50%	56.00%	60.00%
Corralline crust	36.00%	2.50%	16.50%	5.50%	9.00%
Cryptopleura corallinara	32.50%	13.00%	88.50%	49.00%	16.50%
Cumogloia sp.	0.00%	0.00%	0.00%	0.00%	0.50%
Diatoms	0.00%	0.00%	0.00%	0.00%	1.00%
Fissurella volcano	11	20	23	13	9
Gastroclonium subarticulatum	0.50%	48.00%	0.50%	0.00%	44.50%
Gelidium coulteri	0.00%	0.00%	0.00%	0.00%	0.50%
Gelidium sp.	0.50%	4.50%	0.00%	0.50%	0.00%
Hildenbrandia sp.	1.00%	0.50%	0.00%	13.00%	1.00%
Laurencia pacifica	0.00%	0.50%	0.00%	0.50%	0.00%
Leathesia difformis	0.00%	0.00%	0.00%	0.00%	0.50%
Lepidochitona hartwegii	4	1	0	1	1
Lithothrix aspergillum	8.00%	0.00%	0.00%	0.00%	0.00%
Littorina keenae	377	109	114	58	101
Littorina scutulata	44	2	20	13	29
Lottia gigantea	2	0	0	0	0
Mastocarpus sp.	0.00%	12.00%	0.00%	8.00%	4.00%
Mazzalla affinis	0.00%	0.00%	0.00%	0.00%	4.50%
Megabalanus californicus	0.50%	0.50%	0.50%	0.00%	0.00%
Mytilus californianus	49.50%	70.00%	1.50%	5.00%	28.00%
Mytilus galloprovincialis	0.00%	0.50%	0.00%	0.00%	0.50%
Nemalion helminthes	0.00%	0.00%	0.00%	0.50%	0.00%
Nuttallina sp.	14	34	3	16	34
Petrospongium rugosum	0.50%	0.00%	0.50%	0.50%	0.50%
Phragmatopoma californica	2.00%	50.50%	5.50%	5.50%	13.00%
Phyllospadix sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Policipes polymerus	1.00%	1.50%	0.50%	0.50%	0.50%
Polysiphonia sp.	0.00%	1.00%	0.00%	0.00%	0.00%
Porphyra sp.	0.00%	0.00%	0.50%	0.00%	1.00%
Prionitis lanceolata	1.00%	8.00%	0.00%	8.00%	0.00%
Pseudochama exogyra	0.00%	1.00%	0.50%	0.00%	0.00%
Pterocladiella sp.	0.00%	0.00%	0.00%	0.50%	0.00%
Ralfsia pacifia	40.00%	1.00%	12.00%	21.00%	20.00%
Rhodymenia sp.	0.50%	1.00%	0.00%	0.00%	0.00%
Septifer sp.	0.00%	0.50%	0.00%	1.00%	0.00%
Serpulids	0.50%	1.50%	2.00%	2.00%	1.50%
Sponge	0.00%	0.00%	0.00%	0.50%	0.00%
Strongylocentrotus purpuratus	0	0	1	0	1
Tetraclita rubescens	0.00%	0.00%	0.00%	1.00%	0.50%
Ulva spp.	0.00%	1.50%	2.00%	1.50%	42.00%
Unid Algae	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Red	0.50%	0.00%	0.00%	0.00%	0.00%

Transect	SEL1	SEL2	SEL3	SEL4	SEL5
Balanus glandula	93.00%	176.00%	189.00%	93.00%	145.50%
Bare rock	221.00%	180.00%	128.50%	220.50%	284.50%
Callithamnion pikeanum	0.50%	0.00%	0.00%	0.00%	0.00%
Cladophora sericea	0.00%	13.00%	0.00%	0.00%	1.00%
Colpomenia peregrina	1.00%	0.00%	0.50%	0.50%	0.50%
Combined limpets	360	411	478	561	504
Epiactis prolifera	0.00%	0.50%	0.00%	0.00%	0.00%
Fucus gardneri	233.00%	176.50%	288.50%	248.50%	147.00%
Gigartina sp.	0.00%	0.50%	0.00%	0.00%	0.00%
Katharina tunicata	7	11	1	5	3
Leathesia nana	4.00%	0.00%	0.00%	0.00%	0.50%
Leptasterias hexactis	0	2	0	0	0
Littorina scutulata	9	20	25	9	8
Littorina sitkana	409	369	415	362	267
Margarites helicinus	0	1	0	0	0
Mastocarpus jardinii	0.00%	0.00%	0.00%	0.50%	0.00%
Melanosiphon intestinalis	0.00%	0.00%	0.50%	0.00%	0.00%
Mytilus trossolus	37.50%	5.00%	21.50%	33.50%	45.00%
Neorhodomella sp.	80.50%	61.00%	52.50%	32.50%	24.50%
Nucella canaliculata	7	0	1	2	0
Onchidella borealis	0	1	0	0	0
Polysiphonia sp.	80.00%	10.00%	44.90%	100.00%	80.50%
Porphyra sp.	0.00%	0.00%	0.50%	0.00%	0.00%
Ralfsia pacifia	13.00%	9.00%	1.00%	2.50%	1.00%
Red Mite	5	4	3	3	1
Semibalanus cariosis	45.00%	164.50%	77.00%	76.50%	56.00%
Sorantheria ulvoidea	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Bryozoan	0.00%	1.00%	0.00%	0.00%	0.00%
Urospora sp.	0.50%	0.00%	0.00%	0.00%	0.00%

Transect	SEW1	SEW2	SEW3	SEW4	SEW5
Balanus crenatus	4.50%	1.00%	0.00%	8.50%	4.00%
Balanus glandula	58.50%	142.00%	101.00%	133.00%	200.00%
Bare rock	116.00%	252.00%	184.00%	157.00%	133.50%
Cladophora sericea	0.50%	4.00%	0.00%	0.50%	0.00%
Combined limpets	37	71	36	11	17
Enteromorpha sp.	73.00%	76.50%	56.90%	33.00%	77.50%
Fucus gardneri	336.50%	253.00%	313.00%	344.00%	300.00%
Gigartina sp.	0.00%	0.50%	0.00%	0.00%	0.00%
Ligia sp.	0	0	0	0	1
Mud	4.00%	12.00%	0.00%	12.00%	0.00%
Mytilus trossolus	141.00%	105.50%	2.00%	38.00%	21.00%
Porphyra sp.	45.50%	45.50%	49.00%	18.00%	69.00%
Red Mite	10	9	4	5	1
Scytosiphon lomentaria	1.00%	0.00%	0.00%	4.50%	0.00%
Ulva spp.	96.00%	28.50%	8.50%	69.00%	36.50%
Unid Brown Crust	0.50%	0.00%	0.00%	0.00%	0.00%
Unid Green	0.50%	0.00%	0.00%	0.00%	0.50%
Yellow Mite	0	1	0	0	0

Transect	SIO1	SIO2	SIO3	SIO4	SIO5
Acanthinucella spirata	2	1	1	0	0
Anthopleura elegantissima	20.50%	37.50%	20.50%	10.00%	17.00%
Balanus glandula	0.50%	0.00%	0.00%	1.00%	1.00%
Bare rock	52.00%	236.50%	188.50%	292.00%	156.00%
Bugula neritina	0.00%	4.00%	0.00%	0.00%	0.00%
Caulacanthus ustulatus	320.00%	105.50%	136.00%	200.50%	256.50%
Chondracanthus canaliculatus	40.00%	0.50%	13.00%	0.50%	0.50%
Chthamalus fissus	96.50%	88.50%	109.00%	98.00%	180.00%
Combined limpets	20	4	12	13	17
Conus californicus	2	0	0	0	0
Corallina pinnatifolia	13.00%	20.00%	28.00%	4.00%	32.00%
Corallina vancouveriensis	4.50%	0.00%	0.50%	0.00%	0.00%
Corralline crust	1.00%	0.50%	0.00%	24.50%	0.50%
Endarachne binghamiae	0.00%	0.00%	0.00%	0.00%	0.50%
Eurystomella bilabiata	0.00%	0.00%	0.00%	0.50%	0.00%
Fissurella volcano	1	2	1	0	1
Gelidium sp.	12.00%	0.00%	0.00%	0.00%	0.00%
Jania crassa	4.00%	0.00%	0.00%	0.00%	0.00%
Laurencia pacifica	68.50%	16.00%	25.00%	0.50%	0.50%
Lepidochitona hartwegii	0	3	0	0	0
Littorina keenae	116	12	9	40	72
Littorina scutulata	3	28	39	6	18
Lottia gigantea	1	2	2	4	4
Macron lividus	0	1	0	2	0
Mazzaella leptorhyncos	1.00%	0.50%	5.00%	0.00%	0.00%
Mexicanthina lugubris	1	2	0	1	0
Mytilus californianus	96.00%	40.00%	60.00%	100.00%	100.00%
Nuttallina sp.	2	9	17	3	7
Petrospongium rugosum	0.00%	0.00%	0.50%	0.00%	0.00%
Phragmatopoma californica	4.00%	0.50%	2.50%	0.00%	1.00%
Policipes polymerus	0.00%	0.00%	0.00%	0.00%	0.50%
Porphyra sp.	0.00%	4.00%	28.00%	0.50%	0.50%
Pseudochama exogyra	148.00%	64.00%	68.50%	40.00%	88.50%
Ralfsia pacifia	69.00%	32.50%	113.00%	13.50%	25.50%
Ralfsia sp.	16.00%	164.00%	48.50%	24.50%	21.00%
Rhizoclonium sp.	0.00%	0.00%	0.00%	0.00%	0.00%
Rhodymenia sp.	1.50%	0.00%	0.00%	0.00%	0.00%
Roperia poulsoni	1	0	0	0	0
Selvetia compressa	0.00%	0.00%	0.50%	0.50%	0.00%
Septifer sp.	0.00%	0.50%	0.50%	0.50%	1.00%
Serpulids	0.00%	0.00%	0.50%	0.00%	0.00%
Tetraclita rubescens	0.50%	0.50%	1.00%	0.50%	0.00%
Ulva spp.	6.50%	33.50%	29.50%	33.00%	6.00%
Unid Brown	0.00%	0.00%	0.00%	0.50%	0.00%
Watersipora sp.	0.50%	0.00%	0.00%	0.00%	0.00%

Transect	SP1	SP2	SP3	SP4	SP5
Anthopleura elegantissima	0.00%	1.00%	8.00%	48.50%	40.00%
Balanus glandula	165.00%	180.50%	265.50%	229.00%	273.50%
Bare rock	356.00%	352.00%	260.00%	288.00%	204.50%
Bosiella orbigiana	4.00%	0.50%	0.00%	0.00%	0.00%
Calliarthron_tuberculosum	0.50%	0.00%	0.00%	4.00%	0.00%
Ceramium sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Chthamalus fissus	52.50%	124.00%	156.00%	80.00%	136.00%
Combined limpets	190	400	299	177	256
Corallina pinnatifolia	68.00%	12.00%	4.50%	20.50%	28.50%
Corallina vancouveriensis	16.50%	0.00%	0.00%	0.50%	0.50%
Corralline crust	1.00%	0.50%	1.00%	4.00%	24.50%
Cryptopleura.corallinara	0.00%	0.00%	4.00%	0.00%	0.00%
Diatoms	1.50%	1.50%	1.00%	0.00%	0.00%
Dictyopteris sp.	0.00%	0.00%	0.00%	4.00%	0.50%
Fissurella volcano	8	3	1	1	0
Gelidium sp.	0.50%	0.50%	0.00%	0.50%	0.50%
Hildenbrandia sp.	0.00%	1.50%	0.00%	0.00%	1.00%
Lithophyllum sp.	48.00%	0.00%	0.00%	0.00%	0.00%
Littorina keenae	0	6	32	8	9
Littorina scutulata	0	0	0	0	1
Lottia gigantea	4	2	5	5	0
Mazzalla affinis	0.00%	0.00%	1.50%	0.50%	1.00%
Megabalanus californicus	0.50%	1.00%	0.50%	0.00%	0.00%
Mytilus californianus	12.50%	1.50%	0.50%	0.50%	8.50%
Mytilus galloprovincialis	1.00%	0.50%	0.50%	1.50%	0.50%
Nemalion helminthes	0.00%	0.00%	0.50%	0.00%	0.00%
Nuttallina sp.	15	11	8	24	4
Phragmatopoma californica	0.00%	0.50%	0.00%	0.00%	0.50%
Policipes polymerus	52.00%	20.50%	0.50%	56.00%	40.00%
Polysiphonia sp.	0.50%	0.00%	0.00%	0.00%	12.00%
Prionitis lanceolata	16.50%	88.00%	76.00%	40.50%	36.50%
Pseudolithophyllum muricatum	0.00%	8.00%	12.00%	0.00%	0.50%
Ralfsia pacifia	4.00%	0.00%	0.50%	0.00%	0.00%
Rhodymenia sp.	0.50%	0.00%	0.00%	0.00%	0.00%
Schizoporella unicornis	0.00%	0.50%	0.00%	0.00%	0.00%
Serpulids	0.00%	1.00%	0.00%	0.00%	0.50%
Strongylocentrotus purpuratus	0	3	0	1	3
Tetraclita rubescens	5.50%	37.00%	49.00%	29.00%	17.00%
Ulva spp.	0.00%	0.00%	0.50%	0.00%	1.00%
Unid Brown	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Green Crust (Microalgae)	0.50%	0.50%	0.00%	0.00%	0.00%
Unid Grenn	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Brown Crust	1.00%	0.00%	0.50%	4.50%	1.00%
Unid Green	0.00%	0.00%	0.00%	0.00%	0.50%
Unid Green Crust	0.50%	0.50%	0.00%	0.00%	0.00%
Unid Brown	0.00%	0.00%	0.00%	0.00%	0.50%

Appendix B - A List of Species That Occurred On Tiles From Paired Monthly Time Periods

Mean abundance and standard errors are presented for each species on both granite and sandstone. Values are percentages. The number of tiles within each treatment is reported in parentheses after each rock type within each time period.

	1 & 2 Months					
	Granite (6)			Sandstone (6)		
Species	Mean		SE	Mean		SE
Green Algae						
Ulothrix sp.	0.1682	±	0.1682	0.410517	±	0.3288
Ulva sp.	24.4037	±	12.826	19.46071	±	7.5184
Brown Algae						
Endarachne binghamiae	3.2013	±	2.6874	8.604136	±	6.7505
Unknown algae	13.132	±	13.132			
Red Algae						
Goniotrichum alsidii	5.04091	±	4.5864	0.647188	±	0.417
Porphyra sp.	0.88598	±	0.3455	1.305834	±	0.6414
Unidentified red	0.03566	±	0.0357	0.121347	±	0.1213
Ascidians						
Molgula verrucifera				1.609163	±	1.6092
Barnacles						
Chthamalus fissus	0.14743	±	0.0937	0.826102	±	0.5289
Policipes polymerus	0.03277	±	0.0328	0.101618	±	0.1016

	3 & 4 Months					
	Granite (6)			Sandstone (6)		
Species	Mean		SE	Mean		SE
Green Algae						
Cheatomorpha linum				0.083333	±	0.0761
Cladophora sp.	0.08333	±	0.0833			
Ulothrix sp.				0.4708	±	0.3366
Ulva sp.	27.0879	±	13.704	30.98221	±	16.444
Brown Algae						
Endarachne binghamiae	9.3435	±	4.1923	30.77881	±	9.2739
Leathesia difformis	1.45119	±	1.4512	0.653066	±	0.5962
Ralfsia sp.	5.79304	±	4.6057	4.035951	±	2.8832
Red Algae						
Ceramium flaccidum	0.16667	±	0.1054			
Corallina crust	0.2624	±	0.1818	0.22031	±	0.2011
Endocladia muricata				0.143704	±	0.1312
Gelidium coulteri				0.083333	±	0.0761
Gelidium pusillum				0.173738	±	0.1532
Gelidium sp.	0.21617	±	0.2162			
Goniotrichum alsidii				0.845107	±	0.4913
Hydrolithon decipiens	0.08333	±	0.0833			
Jania crassa	0.08333	±	0.0833			
Laurencia lajolla	0.09847	±	0.0985			
Laurencia pacifica	7.06054	±	3.6691	0.758443	±	0.5716
Laurencia spectabilis var. *tenuis*	0.88949	±	0.8895	0.083333	±	0.0761
Lithothrix aspergillum	0.08333	±	0.0833			
Osmundea sinicola	0.18282	±	0.1163	0.083333	±	0.0761
Polysiphonia sp.	0.29772	±	0.1909	0.083333	±	0.0761
Pseudolithoderma nigra				0.111656	±	0.1019
Barnacles						
Balanus glandula	0.04917	±	0.0352	0.01808	±	0.0165
Chthamalus fissus	0.17865	±	0.091	0.2615	±	0.1145
Cyprids	0.19301	±	0.193	0.05303	±	0.0484
Megabalanus californicus				0.039997	±	0.0365
Policipes polymerus	0.31918	±	0.2681			
Tetraclita rubescens				0.044935	±	0.041
Bryozoans						
Bugula neritina	0.16667	±	0.1054			
Filicrisia fransiscana	0.08333	±	0.0833			
Membranipora tuberculata	0.08333	±	0.0833			
Unid Bryozoan				0.011277	±	0.0103
Cnidarians						
Stoloniferous hydroid	0.08333	±	0.0833			
Mollusks						
Mytilus sp.	0.01368	±	0.0137	0.113454	±	0.1036
Polycheates						
Phragmatopoma californica				0.494988	±	0.2858
Unidentified tube worm				0.083333	±	0.0761

Species	5 & 6 Months Summer Granite (6) Mean		SE	Sandstone (6) Mean		SE
Green Algae						
Cheatomorpha linum	0.00261	±	0.002611	0.083333	±	0.083333
Cladophora sp.	0.58397	±	0.396776	0.351419	±	0.18146
Green crust	0.16667	±	0.105409	0.890048	±	0.628827
Ulva sp.	7.63646	±	5.198036	19.89367	±	7.289935
Unid Green filament				0.083333	±	0.083333
Brown Algae						
Endarachne binghamiae	9.78457	±	5.365033	11.14032	±	6.872637
Leathesia difformis	0.02798	±	0.027975	0.02627	±	0.02627
Ralfsia pacifica	4.38961	±	2.952857			
Ralfsia sp.	3.17015	±	1.389681	1.961616	±	0.560716
Red Algae						
Centroceras clavulatum				0.253353	±	0.253353
Ceramium flaccidum	1.03044	±	0.579043	0.436882	±	0.314199
Corallina crust	0.2041	±	0.114018	1.239	±	0.619944
Corallina pinnatifolia	1.99002	±	0.892111	2.412039	±	1.826284
Corallina sp.	0.0061	±	0.006104	0.250556	±	0.250556
Corallina vancouveriensis				1.031385	±	1.031385
Cryptopleura crispa				0.083333	±	0.083333
Endocladia muricata	0.24675	±	0.167934			
Erythrocystis saccata	0.08333	±	0.083333			
Gelidium coulteri	0.08251	±	0.082508	2.724875	±	2.299811
Gelidium purpurescens				0.026904	±	0.026904
Gelidium pusillum	0.48577	±	0.313492	0.39183	±	0.345085
Gelidium robustum	0.09197	±	0.09197	0.083333	±	0.083333
Gelidium sp.	0.08333	±	0.083333	0.039923	±	0.025381
Goniotrichum alsidii	0.16667	±	0.105409	0.120341	±	0.084145
Halyptilon gracile	0.08333	±	0.083333			
Herposiphonia littoralis	1.45123	±	1.451227			
Hydrolithon decipiens	0.08487	±	0.084869	0.083333	±	0.083333
Jania crassa	0.03514	±	0.035138			
Jania tenella	0.08333	±	0.083333	0.083333	±	0.083333
Laurencia pacifica	2.21586	±	1.403612	2.022475	±	0.865043
Laurencia sp.	0.01248	±	0.01248			
Laurencia spectabilis var. *tenuis*	0.08333	±	0.083333	1.409698	±	1.409698
Lithothrix aspergillum	0.13117	±	0.08845	0.642892	±	0.50678
Mazaella leptorhynchos				0.689873	±	0.689873
Osmundea sinicola	0.30099	±	0.136181	0.540582	±	0.260537
Polysiphonia sp.	0.08333	±	0.083333	0.336595	±	0.191886
Pterocladiella caloglossoides	0.10868	±	0.08211	0.179739	±	0.113234
Pterosiphonia dendroidea	0.16667	±	0.105409	0.166667	±	0.105409
Unidentified red				0.174566	±	0.174566

	5 & 6 Months Summer Continued					
	Granite (6)			Sandstone (6)		
Species	Mean		SE	Mean		SE
Ascidians						
Molgula verrucifera	0.3975	±	0.247842	0.102904	±	0.065325
Barnacles						
Balanus glandula	0.04833	±	0.048329	0.083333	±	0.083333
Chthamalus fissus	0.37863	±	0.208384	1.101669	±	0.629014
Megabalanus californicus	0.29151	±	0.291511	0.980411	±	0.620143
Policipes polymerus	0.19606	±	0.138588	0.153715	±	0.116581
Tetraclita rubescens						
Bryozoans						
Bugula neritina	0.50078	±	0.409016	0.500728	±	0.408962
Filicrisia fransiscana	0.01456	±	0.014557	0.218669	±	0.101728
Hippodiplosia insculpta	0.2566	±	0.17661	3.333333	±	3.333333
Membranipora tuberculata	0.02273	±	0.022728			
Tricellaria occidentalis	0.08333	±	0.083333			
Cnidarians						
Juvenile anemone	0.02684	±	0.026839	0.092381	±	0.092381
Stoloniferous hydroid	0.08333	±	0.083333			
Mollusks						
Mytilus californianus				0.988753	±	0.988753
Pseudochama exogyra				0.037609	±	0.037609
Polycheates						
Phragmatopoma californica	3.2681	±	2.188813	6.056645	±	3.613714
Serpulid	0.00905	±	0.009048			
Unidentified tube worm				0.028356	±	0.028356
White sponge	0.02948	±	0.029481	0.017569	±	0.017569

	5 & 6 Months Winter					
	Granite (6)			Sandstone (5)		
Species	Mean		SE	Mean		SE
Green Algae						
Cheatomorpha linum	0.1667	±	0.1054	0.2000	±	0.1225
Cladophora sp.	0.0833	±	0.0833	0.1000	±	0.1000
Green crust	16.9167	±	10.3726	13.6000	±	11.7030
Ulva sp.	8.1667	±	7.1934	17.7000	±	7.1617
Brown Algae						
Endarachne binghamiae	0.3333	±	0.1054	3.3000	±	3.1765
Ralfsia sp.	2.0000	±	2.0000	2.5000	±	2.3770
Red Algae						
Ceramium flaccidum	0.0833	±	0.0833	0.2000	±	0.1225
Corallina crust	0.2500	±	0.1118	0.2000	±	0.1225
Corallina pinnatifolia	0.1667	±	0.1054	9.7000	±	6.3632
Cryptopleura corallinara				0.1000	±	0.1000
Cryptopleura crispa				0.1000	±	0.1000
Gelidium coulteri	0.0833	±	0.0833	6.5000	±	6.3757
Gelidium purpurescens				1.7000	±	1.5780
Gelidium pusillum	0.6667	±	0.6667	0.2000	±	0.1225
Gelidium robustum				0.1000	±	0.1000
Gelidium sp.	1.5000	±	1.3038	1.0000	±	0.7583
Goniotrichum alsidii	0.1667	±	0.1054	0.2000	±	0.1225
Herposiphonia littoralis				0.8000	±	0.8000
Hydrolithon decipiens	0.8333	±	0.6412	1.0000	±	0.7583
Laurencia pacifica	4.6667	±	4.6667	16.1000	±	14.9937
Lithothrix aspergillum	0.0833	±	0.0833	0.2000	±	0.1225
Polysiphonia sp.	0.0833	±	0.0833	0.1000	±	0.1000
Porphyra sp.	2.0000	±	2.0000	0.9000	±	0.7810
Pterocladiella caloglossoides	0.0833	±	0.0833	1.8000	±	1.5540
Pterocladiella capillacea				1.0000	±	0.7583
Pterosiphonia dendroidea				0.1000	±	0.1000
Barnacles						
Balanus glandula				0.1000	±	0.1000
Chthamalus fissus	0.3333	±	0.1054	0.1000	±	0.1000
Policipes polymerus	0.0833	±	0.0833			
Bryozoans						
Hippodiplosia insculpta	0.0833	±	0.0833	0.1000	±	0.1000
Tricellaria occidentalis	0.0833	±	0.0833	0.1000	±	0.1000
Cnidarians						
Stoloniferous hydroid				0.1000	±	0.1000
Mollusks						
Mytilus spat	0.0833	±	0.0833			
Polycheates						
Phragmatopoma californica	0.7500	±	0.6551	0.1000	±	0.1000

	7 & 8 Months					
	Granite (4)			Sandstone (6)		
Species	Mean		SE	Mean		SE
Green Algae						
Cheatomorpha linum	0.3750	±	0.1250	0.2500	±	0.1118
Cladophora sp.	1.1250	±	0.9656	0.1667	±	0.1054
Green crust	37.0000	±	15.0000	23.3783	±	11.9045
Ulva sp.	2.2500	±	1.9203	8.0633	±	2.6070
Brown Algae						
Endarachne binghamiae	9.2500	±	8.9174	3.5633	±	3.2950
Ralfsia pacifica	0.1250	±	0.1250	1.7150	±	1.7150
Ralfsia sp.	5.1250	±	2.9324	6.0833	±	5.2224
Red Algae						
Centroceras clavulatum						
Ceramium flaccidum	0.1250	±	0.1250	0.1667	±	0.1054
Corallina crust	7.0000	±	4.7258	4.2500	±	2.4520
Corallina pinnatifolia	7.0000	±	5.7446	6.2050	±	3.0411
Corallina vancouveriensis	3.0000	±	3.0000	0.0833	±	0.0833
Cryptopleura crispa	0.1250	±	0.1250			
Gelidium coulteri	1.0000	±	1.0000	0.2550	±	0.1752
Gelidium purpurescens	0.1250	±	0.1250	5.3900	±	4.5673
Gelidium pusillum	0.2500	±	0.1443	0.6667	±	0.6667
Gelidium robustum				0.3650	±	0.2773
Gelidium sp.	1.2500	±	0.9242	0.1667	±	0.1054
Goniotrichum alsidii	0.2500	±	0.1443	0.0833	±	0.0833
Halyptilon gracile	0.1250	±	0.1250			
Herposiphonia hollenbergii	3.0000	±	3.0000			
Herposiphonia littoralis	0.1250	±	0.1250	0.0833	±	0.0833
Hydrolithon decipiens	4.0000	±	2.8284			
Jania crassa				0.0833	±	0.0833
Laurencia lajolla	6.0000	±	6.0000			
Laurencia pacifica	4.0000	±	4.0000	18.0933	±	8.9161
Lithothrix aspergillum	0.2500	±	0.1443	1.4167	±	1.3192
Osmundea sinicola	0.1250	±	0.1250	0.2150	±	0.1011
Polysiphonia sp.	0.1250	±	0.1250	2.7500	±	2.6513
Porphyra sp.	0.2500	±	0.1443	0.0833	±	0.0833
Pterocladiella caloglossoides				0.1667	±	0.1054
Pterocladiella capillacea	0.1250	±	0.1250	0.7233	±	0.6577
Ascidians						
Molgula verrucifera	0.1250	±	0.1250			
Styela montereyensis	0.1250	±	0.1250			
Barnacles						
Chthamalus fissus	0.2500	±	0.1443	0.1667	±	0.1054
Bryozoans						
Hippodiplosia insculpta	0.1250	±	0.1250	0.0833	±	0.0833
Tricellaria occidentalis				0.0833	±	0.0833
Cnidarians						
Obelia sp.				0.0833	±	0.0833
Stoloniferous hydroid				0.0833	±	0.0833
Polycheates						
Phragmatopoma californica	1.0000	±	1.0000			
Serpulid	0.1250	±	0.1250	0.1667	±	0.1054

	9 & 10 Months					
	Granite (5)			Sandstone (5)		
Species	Mean		SE	Mean		SE
Green Algae						
Cheatomorpha linum	0.2000	±	0.1225	0.3000	±	0.1225
Cladophora sp.	0.9000	±	0.7810	0.2000	±	0.1225
Green crust	23.3000	±	16.3796	4.8000	±	2.9394
Ulva sp.	1.1000	±	0.7314	11.5000	±	10.1477
Brown Algae						
Endarachne binghamiae	9.7000	±	5.4120	10.6000	±	6.5677
Ralfsia pacifica	0.1000	±	0.1000			
Ralfsia sp.	3.5000	±	3.1265	3.5000	±	2.2305
Red Algae						
Ceramium flaccidum	0.1000	±	0.1000	0.8000	±	0.8000
Corallina crust	4.8000	±	2.3324	15.2000	±	13.2303
Corallina pinnatifolia	9.6000	±	5.1536	15.2000	±	8.0399
Corallina vancouveriensis	1.0000	±	0.7583	16.8000	±	8.4285
Cryptopleura crispa	0.1000	±	0.1000	0.2000	±	0.1225
Gelidium coulteri	0.1000	±	0.1000	0.2000	±	0.1225
Gelidium purpurescens	0.1000	±	0.1000	2.6000	±	1.5281
Gelidium pusillum	5.1000	±	4.7260	2.5000	±	1.5652
Gelidium robustum	0.1000	±	0.1000			
Gelidium sp.	1.0000	±	0.7583	0.9000	±	0.7810
Goniotrichum alsidii	0.2000	±	0.1225	0.4000	±	0.1871
Halyptilon gracile				0.2000	±	0.1225
Herposiphonia hollenbergii				1.6000	±	1.6000
Herposiphonia littoralis				0.2000	±	0.1225
Hydrolithon decipiens	1.2000	±	0.7000	0.2000	±	0.1225
Laurencia lajolla				2.5000	±	2.3770
Laurencia pacifica	0.9000	±	0.7810	2.5000	±	1.5652
Lithothrix aspergillum	0.3000	±	0.1225	1.1000	±	0.7314
Osmundea sinicola	0.1000	±	0.1000	0.8000	±	0.8000
Polysiphonia sp.	0.1000	±	0.1000	4.1000	±	2.4920
Porphyra sp.	0.1000	±	0.1000	0.2000	±	0.1225
Pterocladiella caloglossoides				2.6000	±	2.3527
Pterocladiella capillacea				1.6000	±	0.9798
Barnacles						
Chthamalus fissus	1.0000	±	0.7583			
Cyprids	0.0000	±	0.0000			
Megabalanus californicus	0.1000	±	0.1000	0.1000	±	0.1000
Policipes polymerus	0.1000	±	0.1000	0.1000	±	0.1000
Bryozoans						
Hippodiplosia insculpta				0.1000	±	0.1000
Cnidarians						
Stoloniferous hydroid	0.1000	±	0.1000	0.9000	±	0.7810
Mollusks						
Crepidula perforans	0.1000	±	0.1000			
Mytilus californianus	7.2000	±	7.2000			
Mytilus spat	0.1000	±	0.1000	0.2000	±	0.1225
Polycheates						
Phragmatopoma californica	3.2000	±	1.4967	0.9000	±	0.7810
Serpulid	0.1000	±	0.1000	0.1000	±	0.1000

	11 Months					
	Granite (14)			Sandstone (15)		
Species	Mean		SE	Mean		SE
Green Algae						
Cheatomorpha linum	0.6071	±	0.2682	0.2667	±	0.0667
Cladophora sp.	0.2143	±	0.0686	0.3247	±	0.1248
Green crust	16.4757	±	5.4428	20.6853	±	6.3453
Ulva sp.	4.8350	±	2.3703	4.7800	±	2.1315
Brown Algae						
Eisenia arborescens				1.0667	±	1.0667
Endarachne binghamiae	6.3929	±	2.4502	9.0673	±	4.5703
Ralfsia pacifica	4.3913	±	2.0147	4.9360	±	1.9697
Ralfsia sp.	4.4371	±	2.0507	5.1113	±	1.6573
Unknown algae						
Red Algae						
Ceramium flaccidum	0.1429	±	0.0626	0.5620	±	0.3132
Corallina crust	8.6236	±	3.2064	11.0960	±	3.1436
Corallina pinnatifolia	3.5357	±	2.2795	7.1713	±	2.7095
Corallina vancouveriensis	5.7857	±	2.5633	6.9813	±	3.5549
Cryptopleura corallinara	0.0357	±	0.0357			
Cryptopleura crispa	0.1071	±	0.0569	0.1667	±	0.0630
Endocladia muricata				0.0667	±	0.0454
Gelidium coulteri	0.0357	±	0.0357	0.3520	±	0.2648
Gelidium purpurescens	0.2857	±	0.2857	0.4340	±	0.2642
Gelidium pusillum	1.2143	±	0.6456	2.5000	±	1.4392
Gelidium robustum	0.6786	±	0.3802	0.4680	±	0.3303
Gelidium sp.	1.2500	±	0.4854	0.9667	±	0.4096
Goniotrichum alsidii	0.2143	±	0.0864	0.2333	±	0.0667
Halyptilon gracile	0.0357	±	0.0357	1.0667	±	0.7268
Hydrolithon decipiens	0.2500	±	0.0693	0.7333	±	0.5230
Jania tenella				0.1000	±	0.0535
Laurencia lajolla				0.0333	±	0.0333
Laurencia pacifica	3.2143	±	2.3718	7.1547	±	3.8752
Lithothrix aspergillum	1.2857	±	0.7626	0.7873	±	0.3584
Osmundea pacifica	0.2857	±	0.2857			
Osmundea sinicola				0.3667	±	0.2649
Osmundea spectabalis	0.0357	±	0.0357			
Polysiphonia sp.	0.1071	±	0.0569	1.2840	±	0.8191
Porphyra sp.	0.0357	±	0.0357	0.2833	±	0.0795
Pterocladiella caloglossoides	0.0357	±	0.0357	0.0667	±	0.0454
Pterocladiella capillacea	0.1071	±	0.0569	0.1000	±	0.0535
Pterosiphonia dendroidea	0.0714	±	0.0485	0.0333	±	0.0333
Rhodymenia californica	0.0357	±	0.0357			
Ascidians						
Molgula verrucifera	0.0357	±	0.0357			
Barnacles						
Balanus glandula	0.0357	±	0.0357			
Chthamalus fissus	0.1453	±	0.0623	0.1673	±	0.0629
Cyprids	0.0000	±	0.0000			
Megabalanus californicus	0.2857	±	0.2857	0.0333	±	0.0333
Policipes polymerus	0.3571	±	0.2843	0.0667	±	0.0454
Bryozoans						
Filicrisia fransiscana	0.0357	±	0.0357	0.0333	±	0.0333
Hippodiplosia insculpta	0.0714	±	0.0485	0.1000	±	0.0535
Tricellaria occidentalis	0.0357	±	0.0357			
Cnidarians						
Stoloniferous hydroid	0.0357	±	0.0357	0.1667	±	0.0630
Mollusks						
Crepidula perforans	0.0357	±	0.0357			
Mytilus californianus	0.2857	±	0.2857			
Mytilus spat	0.1071	±	0.0569	0.1333	±	0.0591
Pseudochama exogyra				0.0667	±	0.0454
Polycheates						
Phragmatopoma californica	4.6071	±	2.2860	2.7000	±	0.9230
Serpulid	0.1786	±	0.0664	0.1000	±	0.0535

Appendix C – An Illustration of Possible Invasive Species on Riprap Structures