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The flora and fauna of boulders in a kelp forest

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THE FLORA AND FAUNA OF BOULDERS IN A KELP FOREST

A Thesis

Presented to

the Faculty of Moss Landing Marine Laboratories

and the Department of Marine Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Vincent Christian

December 2006

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ABSTRACT

THE FLORA AND FAUNA OF BOULDERS IN A KELP FOREST

by Vincent Christian

The abundance and diversity of the flora and fauna were determined on the topsides and undersides of 60 randomly-selected boulders of various sizes in March-May and August-September 2004 within a kelp forest in central California. Two hundred twenty-two (222) taxa [12 algae, 9 attached invertebrates, 46 large mobile animals ($>0.5\text{mm}$), and 155 small mobile animals ($<0.5\text{mm}$)] were identified. The topsides hosted a completely different set of organisms than the undersides. The underside mobile fauna was almost twice as dense as the topside fauna, and had higher diversity. Abundance of attached organisms varied with boulder size and location while mobile organisms varied more by time of sampling. Topsides of small boulders had higher densities of total animals, the snail, *Lithopoma gibberosum*, and higher cover encrusting sponge than densities of large boulders. The undersides of small boulders had higher cover of encrusting coralline algae than large boulders.

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INTRODUCTION

Subtidal boulder fields are a common habitat within and near many reefs, and they may play an important role in determining the diversity of the reef. They are structurally complex and more susceptible to disturbance than the solid reef; both are important factors in determining the abundance and diversity of organisms. However, most of the research on marine boulder fields has been done in the intertidal zone (e.g., Sousa 1979, McGuinness and Underwood 1986, Guichard and Bourget 1998, Chapman 2002). The exception is Dunton and Schoenberg (2000) who found a very rich and diverse biological community (approximately 140 taxa from 11 phyla) living on boulders and in the sediments between boulders in an Alaskan subtidal boulder field.

As the structural complexity of a habitat increases, the number of microhabitats also increases, allowing more species to coexist (MacArthur 1972). Many researchers have explored the relationship between habitat complexity and community composition. Ojeda and Dearborn (1989) found invertebrates were more abundant, dense, and diverse within mussel beds than in the surrounding less rugose habitat. Hacker and Steneck (1990) found higher densities of amphipods on algae with more complex thallus structure. Habitats with very complex structure such as kelp holdfasts or articulated coralline algae mats are known to harbor a diverse assemblage of organisms. For example, Dearn (1987) found 178 species in articulated coralline algae mats, and that both species richness and organism abundances increased with the density of coralline branches. One of the reasons that complex habitats support high diversity may be that they provide shelter from storms and protection from predators. Studies focused on the

effects of shelter availability have found that it is very important in determining the community structure (see Table 1 for summary).

Disturbance, like habitat complexity, is also considered an important ecological factor. Historically, it was thought that local communities are in equilibrium, and the relative abundance of species remains relatively constant or undergoes regular cyclic oscillations over many generations (Sousa 1979). This equilibrium theory has been used to explain the maintenance of highly diverse communities because 1) each species is competitively superior to similar species in exploiting a particular subdivision of available resources (MacArthur 1972, Schoener 1974), 2) each species uses interference mechanisms to win over some competitors but loses to others, thus preventing any one species from becoming too abundant (Gilpin 1975, Jackson and Buss 1975), and 3) natural enemies or physical disturbance causes greater mortality to the more dominant species (Paine 1966).

This view of the relationship of disturbance to community structure has changed over the past few decades. Many investigators now think that natural communities are rarely in a state of equilibrium, and that disturbance is an important factor for maintaining diversity. In the absence of disturbance, local monopolization by dominant species may occur (Dayton 1975, Lubchenco and Menge 1978), thereby reducing diversity. Fossil records of marine invertebrates in encrusting limestone cobbles show a progression of community structure from a low-diversity pioneer assemblage to a high diversity stage and then returning to a low-diversity stable fauna stage (Wilson 1985). Several other investigators discovered a similar pattern. The highest level of diversity occurred at

intermediate levels of physical disturbance in intertidal algal assemblages (Sousa 1979), subtidal epifaunal communities (Osman 1977), and subtidal encrusting communities (Ayling 1981). Contrary to these findings, McGuiness (1987) found no significant effects of disturbance on algal assemblages on intertidal boulders. He speculated that this was because the dominant species were primarily thin encrusting species that are relatively unaffected by darkness and abrasion. Except for one common grazer, he did, however, find significant effects on the mobile invertebrate community: smaller boulders had fewer mobile invertebrates.

Severe disturbances can have vastly different effects on community structure depending on the state of the community before the disturbance. Ebeling and others (1985) found that after one severe storm in southern Californian, understory algae in a kelp forest were reduced because the storm had removed the kelp canopy and drift from the canopy (a primary food source for sea urchins), which caused overgrazing of the understory. Another severe storm two years later increased the understory algae by eliminating the exposed sea urchins and clearing rock surfaces for kelp settlement and growth. Marine environments that are disturbed regularly, such as some cobble beds, are typically dominated by encrusting species, probably because foliose species are abraded before they get established (Lieberman and Lieberman 1984, Davis and Wilce 1987a). Although these studies only looked at the attached community, the disturbance effects to these cobble beds following storms were not as severe as the surrounding habitats because the beds were dominated by encrusting organisms which are more adapted to frequent disturbance.

The degree of disturbance to a boulder field is related to the strength of the wave surge and the size and shape of the boulders (Sousa 1979, Davis and Wilce 1987b). Therefore, the disturbance experienced by a particular boulder field is likely to be unevenly distributed because the sizes and shapes of boulders are variable. That is, large boulders will be less disturbed than small boulders. The community structure on boulders of similar sizes should be similar. McGuinness and Underwood (1986) showed that this is true on a small scale for intertidal boulder communities. Guichard and Bourget (1998) studied the hydrodynamic effects of boulders, comparing flow velocities around boulders of various sizes to the communities living near them. While algal composition was not affected, invertebrate biomass decreased significantly downstream of boulders and diversity generally increased with boulder size. They also found that boulder size influenced flow velocity patterns. The down gradient side of the boulders had reduced flow velocities and this effect was more pronounced for larger boulders. This has significant implications on sedimentation rates and therefore food flux into this habitat, and may have caused the lower abundance of dominant species on the down gradient side of boulders.

At large scales, biological patterns tend to be variable and inconsistent (e.g., Foster 1990, Underwood and Chapman 1998). In fact, a large scale study of macroinvertebrates on intertidal boulders did not find any relationship between community composition and boulder size (Chapman 2002). This may be partially due to the patchy distribution of most species and to the nature of the habitat itself. Boulders can be considered as discrete patches of habitat, separated from other similar patches

(i.e., other boulders) by a different type of habitat such as open water and sand. This patchiness may obscure relationships between community composition and boulder size. Relationships between individual species abundances and boulder size may be particularly difficult to identify, but patterns for the community as a whole may be more apparent.

I examined the role boulder fields play in shaping the community structure of a kelp forest habitat by providing a detailed characterization of the flora and fauna on individual boulders (topside and underside) in a subtidal boulder field located in Stillwater Cove, Carmel Bay, California. This is primarily a descriptive study. My objective was to identify the biota in this habitat and see how it compares to the biota others found on the solid reef. My secondary objective was to determine if boulder size affects the most common species or the community composition. My hypothesis was that there is a difference in community composition, either in the density of individual species or on the community as a whole, among boulders of various sizes. I also tested the effects of season (spring and fall) and location within the study area because I wasn't able to control for these two factors in the sampling design. I didn't study the causes of the relationships I found, but these patterns can serve as the basis for future research.

STUDY SITE

Stillwater Cove is located in Carmel Bay, in central California, about 200 km south of San Francisco (Figure 1). This 1 km² southward facing cove, described by Foster and Schiel (1985), is relatively protected from northwest swells. The main topographic features are a group of islands in the center of the cove known as Pescadero Rocks, and a wash rock located at the outer western edge of the cove. Much of the cove's interior is relatively protected from southern swells as waves break on these barriers. Due to its interesting features and its accessibility, Stillwater Cove has been a popular site for many researchers and there is a plethora of background literature available to enable broad comparisons between habitats (e.g., Andrews 1945, Foster 1982, Reed and Foster 1984, Schiel 1985, Konar and Foster 1992, Edwards 1998, Clark and others 2004).

While Stillwater Cove has been characterized as a location with relatively low levels of physical and biological disturbance (Reed and Foster 1984), this site is at least occasionally disturbed during winter storms. I observed boulders up to 1m in diameter that had been overturned at depths up to 20m after the November/December 2002 storms. While these storms were larger than normal, I also observed boulder movement in February 2004 following a relatively mild winter.

The seafloor of the outer deeper portion of the cove (> 20m) is flat, consisting primarily of sand and cobbles. The inner portion is a mosaic of plateaus and pinnacles surrounded by relatively flat areas composed of various-sized boulders. The substrate consists of sandstone, conglomerate, and lava (Simpson 1972). This rocky reef area is dominated by dense stands of giant kelp *Macrocystis pyrifera* with some bull kelp

Nereocystis luetkeana. There are also dense stands of *Cystoseira osmundacea* and *Egregia menziesii* in the shallow areas north and west of Pescadero Rocks. The understory kelp, *Pterygophora californica*, is ubiquitous and very abundant creating a canopy layer about 1-2m above the seafloor. Geniculate coralline algae dominate the vegetation layer below the *P. californica* canopy, often forming dense mats that harbor an array of different organisms similar to those found in kelp holdfasts (Dearn 1987). *Calliarthron tuberculosum* and *Bossiella schmittii* are by far the most common geniculate species in Stillwater Cove, with less than 1% cover of *Calliarthron cheilosporioides* and *Corallina vancouveriensis* (Konar and Foster 1992). Konar and Foster (1992) found that *C. tuberculosum* was the most abundant geniculate species at all depths they studied, growing primarily on horizontal surfaces, while *B. schmittii* dominated vertical surfaces and cobbles. Within this geniculate coralline layer, there is a large variety of fleshy red and brown algae. Below this layer are small filamentous species, encrusting sponges, and encrusting coralline algae.

The study area was a boulder-lined channel, about 100m long and about 15m wide, cut about 3-5m into the reef. The channel is oriented approximately north/south with its center located at about N36° 33.650', W121° 56.890'. The depth at the northern end of the channel is about 10.5m and it gradually deepens at a slope of 0.05m/m to 16m at the southern end. The northern 1/3 of the channel has slightly different characteristics than the southern portion. To the north, the channel is less well defined, the boulder density is lower, and it is more densely covered with *P. californica*. Most boulders at the study site exhibit distinct zones (Figure 2) where the topsides are dominated by coralline

algae, and the undersides are dominated by sponge if not buried in sand, or completely bare if buried (pers. obs.).

MATERIALS AND METHODS

Sixty boulders of various sizes were sampled during two sampling events, 29 boulders in the spring (March - May) of 2004 and 31 boulders in the fall (September - October) of 2004. The sizes ranged from 0.003m^3 to 0.102m^3 (17.9-58.0 cm average diameter) and the distribution was approximately uniform (19 small boulders $<.02\text{m}^3$, 20 medium boulders $.02\text{-.}04\text{m}^3$, and 21 large boulders $>.04\text{m}^3$). The topsides (algae zone) and undersides (sponge and bare zones) were sampled separately. The disturbance caused by overturning boulders in the spring should not have significantly affect the fall sampling because the study area is large relative to the number of boulders sampled. Therefore, it was unlikely that any of the boulders sampled in the spring were the same boulders sampled in the fall. Even if the same boulder was sampled during both events, there should be sufficient recovery time between the two sampling events. Chapman and Underwood (1996) studied the effects of overturning boulders as a source of disturbance to intertidal communities. They found no significant differences in community assemblages between previously-overturned boulders and boulders that had not been overturned when the previously-overturned boulders were allowed 3-4 months to recover.

I used three different methods to characterize the community; one for the attached biota, one for large mobile animals, and one for small mobile animals. Algae and attached invertebrates were sampled using a Random Point Quadrat (RPQ) method. I draped a nylon cord with small fishing weights attached to each end over the boulder so that the cord lay flush against the boulder surface (see photo in Appendix E). The cord had 10 random marks. I recorded the taxa touching each mark, then randomly

repositioned the cord 2-5 times depending on the size of the boulder and repeated the process until I reached an adequate sampling density. I determined through a pilot study that 43 points/m² were required to adequately characterize the attached community (Figure 3). All boulders were over-sampled because the surface areas of the boulders were unknown at the time of sampling.

Mobile animals were sampled by either counting them in-situ or by collecting them with an air-lift sampler similar to that described by Chess (1978) and used by others (Dearn 1987, Benson 1989, Cobb and Clancy 1999; Figure 4). Large mobile animals (typically >7mm) were those visible to the naked eye and they were counted in-situ. Small mobile animals (typically 0.5-7mm) were collected with an air-lift sampler and they were identified under a dissecting microscope. The sampler was made from a 7.6cm diameter PVC tube with a port for injecting compressed air near the bottom end. The specific gravity of the air/water mixture is reduced and the outside water pressure forces the mixture out the top end of the tube, thus creating suction at the bottom. The major advantage of this method is that it collects small cryptic animals that are not easily seen in the field, and many fast-moving animals such as brittle stars that move away before they could otherwise be counted.

I refined the method for selecting boulders between the spring and fall sampling events. In the spring, I chose the closest boulders to the boat anchor dropped at a randomly selected GIS coordinate within the study area. One to five boulders were sampled during each of two dives per day (29 total boulders during 9 dive days). No boulders within 1m of a previously sampled boulder were selected. The anchor was

moved to a new randomly selected location within the boulder channel on each day. The anchor was not moved between dives on the same day, but boulders sampled on the second dive were at least 3m from the boulders sampled on the first dive. This method resulted in a clustered sampling pattern (Figure 5), so I changed the method in the fall to get a more uniform distribution throughout the study area. A transect line was laid along the approximate center of the boulder channel prior to sampling, and boulders were sampled at pre-selected random locations along the transect line.

Once I selected a boulder, I sampled it as follows:

1. Count fish – I visually inspected boulder for fish in direct contact with the boulder. Careful examination was required because sculpin and the kelpfish, *Gibbonsia montereyensis*, are well camouflaged. In fact, several small fish collected with the air-lift sampler were not observed during the visual inspection.
2. Assess topside mobile fauna – I counted the mobile animals visual to the naked eye in direct contact with the boulder, or collected them if the species was unknown. I sampled 10 boulders using the air-lift sampler to identify the smaller mobile invertebrates.
3. Measure boulder size – I measured the height, length, and width of the boulder using a 96cm aluminum caliper (see photo in Appendix E).
4. Assess algae and attached invertebrates – I counted the number of *P. californica* stipes and *M. pyrifera* holdfasts. I assessed the remaining attached biota using the RPQ method described above.

5. Assess underside mobile fauna – I turned the boulder over with the help of my dive buddy, then counted the large mobile animals if the species was known or collected them if the species was unknown. Brittle stars were counted first because they move away quickly after the boulder is turned over. I counted mobile animals in direct contact with the boulder, or in the approximate "footprint" where the boulder formerly rested. I sampled the same ten boulders in step 2 above with the air-lift sampler, although I wasn't able to turn over 3 of them.
6. Assess underside attached community – Several of the boulders were completely bare of any attached or encrusting organisms. Others had a mixture of bare rock, encrusting algae, encrusting sponge, and occasionally other attached invertebrates and geniculate coralline algae. RPQs were done as in step 4 above unless the underside was completely bare.

Sample Processing

Collected specimens required immediate processing for preservation. The contents of the collection bags were emptied into a plastic bucket. The bag was inverted and residual material sticking to it was washed into the bucket with filtered seawater. The water in the bucket was swirled around a few times and then quickly poured into a 0.5mm sieve. After a few repetitions, this process separated most of the lighter organisms poured into the sieve from the heavier sand retained in the bucket. Material retained in the 0.5mm sieve was put into a labeled glass jar, preserved in a 10% formalin solution, and transferred to isopropyl alcohol after 24 hours. Invertebrates were separated

from the sand and algae pieces under a dissecting microscope. Most invertebrates were identified to species, but many could only be identified to genus or family.

Analyses

I analyzed the topside and underside communities using cluster analyses and principle component analyses (PCA). I used the software program, Systat[®] 10, for both methods. The cluster analyses use a maximum likelihood method to cluster similar taxonomic groups together. The PCA analyses shows which relationships among the taxonomic groups (PCA axes) explained the most variability in community composition (Clark and Warwick 1994). For each significant PCA axis (explains at least 10% of the variability), I analyzed the PCA scores to see if boulder size, season, or depth/location explained the relationship. The location along the transect line was closely related to depth (Figure 6) due to the geometry of the boulder channel. Since these two factors are not independent, I used the location along the transect line for all depth/location analyses.

I also analyzed the most common taxa individually using a variety of statistical analyses depending on which assumptions were met by the data set (see below). For most analyses, boulders sizes were categorized into small ($<.03\text{m}^3$) and large ($>.03\text{m}^3$) boulders based on their volume. For the taxa richness analysis, I used three categories, small ($<.02\text{m}^3$), medium ($.02\text{-.}04\text{m}^3$) and large ($>.04\text{m}^3$), to see if there was an intermediate-size effect. There was a 91-day break between the spring and fall sampling events, so the temporal factor was divided into spring and fall categories. The location (or depth) factor was analyzed by separating boulders into northern boulders located

above the 70m mark on the transect line (or <35m depth) and southern boulders located below the 70m mark (>35m depth).

I used 3-factor ANOVAs to test for differences in the factors if the data met the assumptions for parametric analyses (i.e., equal variances and normal distributions). I used Zar (1999) as a reference and Systat[®] 10 to run the analyses for all parametric tests. I tested for equal variances using Cochran's test and normal distributions using Kolmogorov-Smirnov test. I used a Model I ANOVAs because all three factors were fixed.

Most of the distributions were not normal so I used randomization tests for differences. Randomization tests do not require normal distributions or equal variance. They work by using computer power to artificially increase sample replication using the actual sample distribution instead of an assumed normal distribution. For example, if I wanted to test if there was a difference in *Calliarthron tuberculosum* cover between spring and fall, I would make two sample matrices (one for spring and one for fall) of *C. tuberculosum* covers by taking random samples from the combined population and then repeated this process a large number of times (e.g., 1000) to get 1000 pairs of sample matrices. I would then calculate the difference between each matrix pair. The percentage of times each difference occurs represents the probability that the difference was due to chance alone. I then determined if season was important for *C. tuberculosum* cover by comparing the actual difference to a histogram of the sample matrix differences. If the actual difference occurred less than 5% (α) of the time, then it was likely that season had

an effect on *C. tuberculosum* cover. Appendix C provides the Resampling Stats[®] program used for the randomization tests and the results of each analysis.

I also tested if there were differences in the presence or absence of each taxon using chi-squared (χ^2) tests. The expected distributions for these tests were that the frequencies were equal between spring and fall boulders, or between small and large boulders. The powers and minimum detectable effect sizes were calculated for the parametric analyses whenever I failed to reject the null hypotheses.

RESULTS

I observed or collected 222 different taxa, including 21 attached taxa, 46 large mobile taxa (visible to the naked eye) counted in-situ, and 155 small taxa (0.5mm-7mm) collected with the suction sampler and identified under a dissecting microscope (Table 2).

No seasonal, boulder size, or location effects were found for the topside community using a cluster analysis, but analysis of the underside community showed an effect that may be related to boulder size or possibly to the location within the study area (Figure 7). As indicated by the Euclidean distances, there was a group of large boulders at the northern end of the study area that cluster together and therefore had a different community than the rest of the boulders.

ANOVAs on PCA scores showed significant effects on the community due to season, boulder size and location within the study area. For the topside community, two PCs explained 29.6% of the variability. PC1 scores were high when cover of *Calliartrion tuberculosum*, *Laurencia subopposita*, and *Plocamium cartilagineum* were high, and cover of encrusting corallines and *Bossiella schmittii* were low. PC2 scores were high when cover of *P. cartilagineum* and densities of molluscs *Tegula* spp. and *Tonicella lineata* were high, and the cover of *L. subopposita* was low. PC1 scores were higher for large boulders than small boulders, and PC2 scores were higher for spring boulders than fall boulders (Appendix D.1). Three PCs explained 58.9% of the variability in the underside community. PC1 was highest when encrusting coralline algae, sponge, and brittle stars were high and lowest when the bare rock and *T. montereyi* were low. PC1 scores differed significantly between seasons and location within the study area, but PC2

and PC3 scores did not differ significantly between levels of any of the factors. A t-test showed PC1 scores were higher in the fall than in the spring and a regression analysis showed high PC1 scores in the deeper southern end of the study area (Appendix D.2).

Attached Community

Similar to Sousa's (1979) findings on intertidal boulders, medium sized boulders had higher mean taxa richness (4.57 ± 1.08 taxa/boulder) than small boulders (3.68 ± 1.11 taxa/boulder) or large boulders (4.55 ± 1.36 taxa/boulder), but the differences were not significant (Table 3). To explore disturbance relationships further, I compared "recently-disturbed" boulders to "non-disturbed" boulders by separating them into two groups. The non-disturbed group consisted of 21 boulders that I could not flip over or were completely bare on the undersides, and the disturbed group consisted of 39 boulders that had encrusting organisms on the undersides. T-tests showed there were no significant differences in the taxa-richness between the two groups for any of the taxonomic groups (Table 4).

The attached taxa are listed in Table 5. The most common taxa on the topsides of boulders were encrusting coralline algae ($30.1 \pm 21.8\%$ cover), *B. schmittii* ($26.7 \pm 22.9\%$ cover), *C. tuberculosum* ($17.7 \pm 22.6\%$ cover), encrusting sponge ($8.8 \pm 9.6\%$ cover), and the fleshy red alga, *Plocamium cartilagineum* ($8.0 \pm 14.0\%$ cover). Table 6 summarizes the statistical analyses for all of the most common taxa. Season was not an important factor for any of the topside taxa, but boulder size was important for encrusting sponge and location was important for *B. schmittii* and encrusting sponge (Table 7). *B. schmittii* had higher cover in the northern end of the boulder channel ($33.5 \pm 22.7\%$ cover) than the

southern end ($21.2 \pm 20.4\%$ cover; Table 7). Encrusting sponge had higher cover on small boulders ($11.3 \pm 11.3\%$ cover) than on large boulders ($6.3 \pm 6.9\%$ cover), and it had higher cover in the northern end of the boulder channel ($12.0 \pm 10.4\%$ cover) than the southern end ($7.3 \pm 8.9\%$ cover).

The most common underside taxa (or substrate) were bare rock ($53.2 \pm 40.2\%$ cover), encrusting coralline algae ($21.7 \pm 28.8\%$ cover) and encrusting sponge ($18.8 \pm 22.8\%$ cover). There were significant differences in all three factors for bare rock and for encrusting coralline. Bare rock was much higher in the spring ($70.5 \pm 37.6\%$ cover) than in the fall ($37.0 \pm 36.1\%$), higher on large boulders ($64.0 \pm 40.0\%$) than on small boulders ($42.4 \pm 38.1\%$), higher in the north end of the channel (67.6 ± 35.2) than in the south end (37.4 ± 42.3). Boulders that were completely bare were more common in the spring (16 of 29) than in the fall (6 of 31; Table 8). Encrusting coralline algae had the opposite pattern of bare rock, where the cover was higher in the fall ($31.2 \pm 30.2\%$) than in the spring ($11.5 \pm 23.7\%$), higher on small boulders ($33.1 \pm 32.1\%$) than large boulders ($10.2 \pm 19.5\%$), and higher in the south end of the channel ($31.1 \pm 34.7\%$) than in the north end ($10.2 \pm 17.2\%$). There were also fewer boulders in the spring (9 of 29) with encrusting coralline algae than in the fall (22 of 31). While not significantly different ($p=0.08$), the mean fall cover of encrusting sponge ($23.4 \pm 23.4\%$) was almost twice that of the mean spring cover ($14.1 \pm 20.6\%$). The frequency of boulders with sponge present was less in the spring (12 of 29) than in the fall (24 of 31), and it was also greater for small boulders (21 of 30) than large boulders (15 of 30).

Large Mobile Animals

Table 9 provides the frequencies and densities for each large mobile taxa. I used animal density to express abundance rather than animals per boulder to normalize for boulder size. The relationship between the boulder surface area and the number of animals per boulder was linear ($p=0.002$, Figure 8), although the r^2 -value was only 0.149. The total large animal density on the topsides of boulders was $45.2\pm48.0/\text{m}^2$, and the most common taxa were the gastropod molluscs *Tegula* spp. ($14.3\pm26.0/\text{m}^2$) and *Lithopoma gibberosum* ($8.1\pm16.1/\text{m}^2$), and the hermit crabs *Pagurus* spp. ($5.9\pm12.2/\text{m}^2$). The mean fall density of topside animals was higher ($p=0.11$; Table 10) on small boulders ($55.9\pm60.9/\text{m}^2$) than on large boulders ($34.4\pm27.3/\text{m}^2$). For individual taxa, *L. gibberosum* was the only one with season or size effects. It was significantly more abundant on small boulders ($12.0\pm21.2/\text{m}^2$) than on large boulders ($4.2\pm6.8/\text{m}^2$), and more abundant in the fall ($11.1\pm20.8/\text{m}^2$) than in the ($5.0\pm7.8/\text{m}^2$) spring.

The total large animal density on the undersides ($81.5\pm63.4/\text{m}^2$) was almost twice that of the topsides ($45.2\pm48.0/\text{m}^2$) and statistically different ($p=0.001$). The dominant large invertebrates were the chiton *Stenoplax fallax* ($27.0\pm32.4/\text{m}^2$), the brittle stars *Ophiopteris papillosa* ($16.0\pm26.1/\text{m}^2$) and *Ophiothrix spiculata* ($6.2\pm17.8/\text{m}^2$), and hermit crabs *Pagurus* spp. ($11.1\pm22.3/\text{m}^2$). Neither boulder size nor location had significant effects on total animal densities (Table 6), but there was a seasonal effect where mobile animals were more abundant on spring ($110.0\pm64.6/\text{m}^2$) than in fall ($65.8\pm51.5/\text{m}^2$). *S. fallax* was more abundant in the spring ($35.2\pm31.4/\text{m}^2$) than in the fall ($19.5\pm32.0/\text{m}^2$). *Pagurus* spp. was more abundant in the spring ($17.1\pm28.4/\text{m}^2$) than in

the fall ($5.7 \pm 13.2/\text{m}^2$). Brittle stars were also more abundant at the south end of the channel.

In addition to having higher mobile densities, the undersides also had higher taxa richness (4.0 ± 2.7 taxa/boulder; Table 11) than the topsides (2.8 ± 1.9 taxa/boulder). The taxa densities were also higher (top: 24.1 ± 23.5 taxa/ m^2 , under: 32.3 ± 21.3 taxa/ m^2 , $p=0.05$). Mobile animal taxa-richness patterns were very different both seasonally and between the topside and underside communities (Figure 9). Boulder size was an important factor (small: 2.3 ± 1.7 taxa/boulder, medium: 2.3 ± 1.9 taxa/boulder, large: 3.6 ± 1.9 taxa/boulder, $p=0.058$) for the topside richness, but season was not. Conversely, season was important (spring: 5.0 ± 3.0 taxa/boulder, fall: 3.1 ± 1.9 taxa/boulder, $p=0.013$) for the underside taxa richness, but size was not.

Small Mobile Animals

Amphipods (55 taxa), gastropod molluscs (30 taxa), and polychaetes (23 taxa) accounted for most of the species diversity among the small mobile invertebrates (Table 12). Other contributors were bivalve mollusks (5 taxa), isopods (10 species), copepods (2 species), echinoderms (5 taxa), and decapod crustaceans (8 taxa). Many of these taxa are shown in Appendix E. PCA analyses of the small mobile animals didn't provide any useful results because each significant axis contained a very large number of important taxa.

Most species of amphipods were rare. Only six genera composed 73% of the 1880 amphipods (706 *Pontogeneia* spp., 321 *Aoroides* spp., 106 *Amphilocheus* spp., 113 *Aruga holmesi*, 76 *Elasmopus* spp., and 69 *Gammaropsis* spp.). The remaining 489

amphipods were distributed among 49 different genera. Amphipod density was not significantly different ($p=0.58$) between the topsides ($915\pm1075/\text{m}^2$) and undersides ($691\pm653/\text{m}^2$), but it was different ($p=0.06$) between spring ($540\pm614/\text{m}^2$) and fall ($1292\pm1110/\text{m}^2$).

Littorina sp. was the dominant gastropod mollusk with 303 (35.8%) of the total 847 gastropods. Other common gastropods had similar abundances to each other; 70 *Alia tuberculosum*, 66 *Cystiscus jewettii*, 58 *Barleeia* sp., 58 *Alvania* sp., and 54 *Amphissa versicolor*. Gastropods were more abundant ($p=0.02$) on the topsides ($603\pm497/\text{m}^2$) of the boulders than on the undersides ($162\pm133/\text{m}^2$), but they were not significantly different ($p=0.71$) between spring ($350\pm320/\text{m}^2$) and fall ($443\pm590/\text{m}^2$).

The most common polychaetes were in the families Hesionidae, Ophilliidae, and Syllidae. Total polychaete abundance was much less ($p=0.03$) on the topsides of boulders ($25.7\pm48.3/\text{m}^2$) than on the undersides ($331\pm369/\text{m}^2$), and polychaetes were also more abundant ($p=0.08$) in the spring ($262\pm364/\text{m}^2$) than in the fall ($54.3\pm76.3/\text{m}^2$).

DISCUSSION

The topside attached PC1 analysis indicated a positive relationship between the two most common fleshy red algae, *Plocamium cartilagineum* and *Laurencia subopposita*, and the geniculated coralline, *Calliarthron tuberculosum* (high PC1), but there was a negative relationship between these fleshy reds and the other common geniculate coralline, *Bossiella schmittii*, and encrusting corallines (low PC1). These relationships were affected by boulder size with high PC1 scores associated with large boulders and low PC1 scores associated with small boulders. None of these taxa were significantly related to boulder size when analyzed individually. Since Konar and Foster (1992) found *C. tuberculosum* primarily on horizontal surfaces while *B. schmittii* is more prevalent on vertical surfaces and cobbles (Konar and Foster 1992), I expected higher *C. tuberculosum* cover on large boulders and higher *B. schmittii* cover on small boulders. However, I didn't investigate surface slope or rocks in the cobble size range. It could be that slope is more important than size, or that there is a boulder size relationship outside of the range I sampled.

Downing (1995) found that both fleshy red species reproduced vegetatively in Stillwater Cove and fragments recruited more successfully in spatially-complex environments such as coralline mats. Since *Calliarthron tuberculosum* has longer fronds and is more spatially complex than *Bossiella schmittii*, it makes sense that *Plocamium cartilagineum* and *Laurencia subopposita* would have a stronger association with *C. tuberculosum* if they are recruiting more successfully in this habitat. Therefore, the PC1/boulder size relationship described above could be a combination of two effects; 1)

higher *C. tuberculosum*'s prevalence on large boulders and 2) higher recruitment of fleshy red algae in *C. tuberculosum* than *B. schmittii*.

The topside attached PC2 analysis indicated a relationship with both fleshy red algae and two primary grazers, *Tegula* spp. and *Tonicella lineata*, where PC2 scores were higher in the spring than in the fall. Again, none of these species were related to season when analyzed individually. The average cover of *Plocamium cartilagineum* was higher in the spring than in the fall, but not significantly. However, $p=0.16$ indicates a possible α -error. Downing (1995) found higher cover of *P. cartilagineum* in the spring than in the fall, but he speculated that it was caused by *Aplysia* sp. grazing as they were unusually abundant that year. *Tegula* spp. did not have seasonal differences, and *T. lineata* was not tested because they were rare. The species involved indicates that PC2 is related to grazing. It also indicates that the molluscs may prefer *P. cartilagineum* over *Laurencia subopposita* because they were positively associated with *P. cartilagineum*, but negatively associated with *L. subopposita*. There isn't enough information to speculate why PC2 was affected by season. Most likely, one or more of the species has a seasonal effect not detected in this study.

The underside PCA analysis revealed an interesting relationship among three attached taxa (encrusting coralline, encrusting sponge, and bare rock) and three mobile species (*Ophiopteris papillosa*, *Ophiothrix spiculata* and *Tegula* spp.). The brittle stars were more abundant when encrusting coralline and sponge were high, and *Tegula* spp. was more abundant when bare rock was high. I noticed in the field that when boulders were not completely bare, there was usually a high abundance of brittle stars. This

phenomenon is likely related to the degree of burial. Well-buried boulders were typically bare, and it is possible that *O. papillosa* and *O. spiculata* need sand-free space to thrive. It's difficult to explain why *Tegula* spp. was more abundant when bare rock was abundant. It's possible that *Tegula* spp. forages on algal detritus that gets trapped between boulders, and the spaces around buried boulders are more accessible than non-buried boulders.

The algal composition was consistent with that found in Stillwater Cove by Reed and Foster (1984), Dearn (1987), Konar and Foster (1992), Edwards (1998), and Foster (2006) except there was no *Desmarestia* spp. and there was not as many red fleshy algal species. Reed and Foster (1984) found seven fleshy red algal species that I did not find, although they were rare (<3% cover combined). I observed some of these species inside the boulder channel, but they were also rare. *Desmarestia ligulata* was abundant during the study on the solid reef outside the boulder channel and *Desmarestia kurilensis* was present in the deeper cobble beds to the south of the channel, but I didn't see either species in the channel. Since *D. ligulata* is annual and opportunistic (Edwards 1998), I would expect it to recruit in the boulder channel after winter storms free space and allow more light in. However, this didn't happen so there must be some mechanism that restricted recruitment. While not supported by this study, perhaps the overturning of boulders by storms reduces encrusting coralline cover, the primary substratum on which *D. ligulata* recruits (Edwards 1998).

While there were no significant differences between boulder sizes or sampling season in any of the attached taxa, the power was very low for most analyses. For

example, the power for *Calliarthron tuberculosum* was 26% when testing for seasonal differences. This is far too low to provide confidence that I didn't make a β -error. A sample size of approximately 350 boulders would be needed to increase the power to 80%, the generally accepted level (Cohen 1988). Unfortunately, such a large sampling effort was not practical with the available resources. While the powers were low, this concern is alleviated by the low detectable effect sizes. For the same test on *C. tuberculosum*, the detectable effect size was 11.6%. This means that if the difference in the mean cover of *C. tuberculosum* between spring and fall had been greater than 11.6%, it would have been detected even with the relatively low sample size.

There are few quantitative studies of large mobile invertebrates in Stillwater Cove, but the species I found were consistent with those found by Foster and Schiel (1985). The small mobile animals were also consistent with those found in Stillwater Cove by Andrews (1945) in kelp holdfasts and by Reed (1984) and Dearn (1987) in geniculate coralline mats. In addition to the animals found by others on solid reef in Stillwater Cove, I also found other organisms, such as *Stenoplax fallax* and *Ophiopteris papillosa*, with high abundances on the undersides of boulders. The abundance of *S. fallax* $27.0 \pm 32.4/\text{m}^2$ was similar to $46.4 \pm 10.0/\text{m}^2$ found by Battle (1991). The presence of these "underside only" species shows that boulder fields contribute to the overall diversity of the kelp forest, possibly by providing a unique microhabitat that is otherwise unavailable on the solid reef. The higher disturbance levels in the boulder field may also contribute to diversity by providing habitat to species that would otherwise be outcompeted by long-lived species in more protected areas.

The taxa-richness patterns did not display the high-diversity/intermediate-size pattern found by Sousa (1979), but this pattern is suggested for the attached biota. It is not surprising that mobile taxa did not have the pattern because they are not as susceptible to physical disturbance. While slow animals such as *S. fallax* probably have high mortality during severe storms, faster animals such as *O. papillosa* can move to more sheltered areas. Also, surviving animals can rapidly recolonize a disturbed boulder through immigration where attached organisms can only recolonize by growing from propagules.

I did not see any factors such as higher algal cover that would explain high taxa richness on large boulders, so it is likely related to factors not considered in this study. This may be due to the phenomenon that diversity increases with area (Rosenzweig 1995), which suggests that habitat area may be more important than habitat structure to overall diversity in this system. It is also possible that large boulders provide more refuge from predators than small boulders.

While there were no seasonal differences in the densities of the two most common topside mobile taxa (*Tegula* spp. and *Lithopoma gibberosom*) or for the total topside animal density, there were definite or possible boulder size effects for both of these taxa and for total animal density. Both *Tegula* spp. and *L. gibberosum* were more abundant on large boulders, but the total animal density was higher on small boulders. This indicates that large molluscs are behaving differently than other topside organisms. The algal cover was not different between boulder sizes so it's probably not related to food availability. More likely, it's possible that their large size and thick shells makes them

less vulnerable to predation by fish than smaller molluscs and crabs. If so, they could exploit algae on the tops large of boulders while more vulnerable organisms would forage on small boulders where there is less distance to refuge.

I counted only one fish in the spring, but several in the fall. This could be explained by the lower topside amphipod density ($p=0.06$) in the spring ($540\pm613/\text{m}^2$) than fall ($1292\pm1110/\text{m}^2$) since amphipods are a major prey item for the fish species counted during the fall. However, I observed several fish in the area during the spring so the low springtime abundance was more likely because I had not yet perfected my method for counting fish without scaring them away.

CONCLUSIONS

The high diversity and abundance of organisms in this boulder field is consistent with other studies of structurally complex habitats. The topsides hosted an entirely different community of organisms and the abundance of animals was less than the undersides. Most species showed a strong preference for either the topside or the underside of the boulder, although some species such as *Asterina miniata*, *Tegula* spp., and *Pagurus* spp. occurred in both habitats. This suggests a high degree of specialization of the community members. Topside organisms likely respond to the abundant algae while the underside organisms no doubt benefit from some aspect of undersides, such as increased protection from predators or availability of detritus.

Ophiopteris papillosa and *Stenoplax fallax* were particularly abundant under boulders. The average biomasses of these two species were approximately 0.2 and 0.1 kg/m², respectively. However, the lack of knowledge about these two species makes it difficult to speculate about the reason for their abundance. Much more needs to be known about their diets and behavior. Boulders buried in sand, or partially buried, negatively affected the presence of *O. papillosa*, but not *S. fallax* possibly due to its ability to burrow. This suggests that the sponge zone is more important to *O. papillosa* while the bare zone is more important to *S. fallax*. Brittle stars are normally detritus feeders, and the habitat of *O. papillosa* suggests that it relies on detritus falling from above. The food of *S. fallax* is more of a mystery. Chitons are normally grazers, but there little to graze in the sand zone. Perhaps they are grazing on meiofauna, microbes, or other biofilm constituents. They may migrate regularly to get food, or maybe they

feed on large pieces of detritus just above the sand zone. Much research is needed before we can begin to understand interactions among organisms in this complex community.

The study also suggests that disturbance may play an important role in structuring the attached community. I didn't measure disturbance directly so I don't know how strongly boulder size is related to disturbance at this location within the range of sizes studied. While the patterns didn't support the intermediate disturbance/high diversity relationship described by Sousa (1979), there were boulder size effects on certain individual taxa and on the topside community.

The community analyses showed that all the factors, boulder size, season, and location within the study area, were important. The strongest topside PC axis suggested an epiphytic relationship between geniculate corallines and fleshy red algae that was related to boulder size. Another strong topside PC axis suggested a grazing relationship between the most common molluscs and fleshy red algae that was related to season.

The strongest underside PC axis involved bare rock, encrusting coralline, encrusting sponge, brittle stars and *Tegula* spp. This PC axis was not affected by boulder size, but season and location within the study area. The impacted taxa suggest that the degree of burial in sand, another form of disturbance, may be important.

This study supports the development of additional research needed to determine what factors have the strongest effects on boulder communities since the composition and abundance of taxa living in this habitat have now been described.

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APPENDIX A
Tables

Table 1. Habitat Complexity and Shelter Studies

Study	Summary
Menge and Lubchenco (1981)	Performed predator exclusion experiments in a tropical rocky intertidal habitat, and found that the primary effect of predators was to restrict their prey to holes and crevices.
Witman (1985)	Studied New England mussel beds as a refuge for three prey species and found significantly higher predation rates for all three species outside the mussel beds.
Caddy and Stamatopoulos (1990)	Studied the effects of shelter size by providing blocks with holes of various diameters to refuge-seeking organisms. Their results indicate that shelter size can affect the population of various species and the structure of the whole community.
Hixon and Beets (1989)	Similar study to that of Caddy and Stamatopoulos (1990), but with tropical fish. Found similar results.
Wahle and Steneck (1992)	Found that juvenile lobsters prefer cobble habitats to gravel, sand and mud habitats.
Eggleston and Lipcius (1992)	Studied lobsters, examining their preference for shelter size as lobster density and predation risk varied. They found that when density and predation risk was low, lobsters resided in shelters scaled to their own body size; when density was high and predation risk was low, they preferred large shelters; when density was low and predation risk was high, they preferred small shelters; and when density and predation risk were both high, they shifted to gregarious habitation in small shelters.
Beck (1995)	Found that habitat complexity can increase abundance and size of stone crabs.
Roberts and Ormond (1987)	Found higher fish diversity with increased habitat complexity in coral reefs.
Anderson et al (1989)	Found that small fish are more dependent on shelter availability than large fish.
Gorman and Alevizon (1989)	Found much higher densities (about 3 times) of juvenile fish on concrete blocks fitted with "streamers" of polypropylene rope than on blocks without the streamers.

Table 2. Taxa Summary.

= the total number of animals. T= total number of taxa.

	Spring 2004		Fall 2004		Total Taxa
	Topside	Underside	Topside	Underside	
	# of Taxa n=29	# of Taxa n=27	# of Taxa n=31	# of Taxa n=29	
Attached Biota Using RPQ					
Rhodophyta	7	2	7	3	8
Phaeophyta	2	0	3	1	4
Invertebrates	4	4	2	6	9
Total	13	6	12	10	21

Large Animals Counted In-situ	Spring 2004				Fall 2004				Total #	Total Taxa
	Topside		Underside		Topside		Underside			
	# n=29	T	# n=27	T	# n=31	T	# n=30	T		
Crustaceans	29	6	99	8	35	3	23	4	186	9
Molluscs	123	11	204	15	112	12	137	8	576	19
Echinoderms	13	1	76	9	19	3	115	6	223	9
Annelids	0	0	20	4	0	0	5	2	25	4
Fish	1	1	0	0	15	5	0	0	16	5
Total	166	19	399	36	181	23	280	20	1026	46

Small Animals Collected with the Suction Sampler	Spring 2004				Fall 2004				Total #	Total Taxa
	Topside		Underside		Topside		Underside			
	# n=6	T	# n=7	T	# n=4	T	# n=3	T		
Amphipods	176	26	593	37	967	28	144	26	1880	55
Isopods	49	7	53	9	83	6	10	5	195	10
Crabs and Shrimp	57	8	81	7	134	6	36	4	308	13
Copepods/Cumaceans/ Ostracods	3	3	55	3	10	2	3	2	71	4
Molluscs	464	28	118	22	249	20	63	16	894	40
Echinoderms	4	3	30	2	4	2	20	1	58	5
Annelids	10	6	308	20	7	4	25	9	350	25
Fish	2	2	2	2	2	2	0	0	6	1
Other (pychnogonids & cnidarians)	1	1	8	1	3	2	0	0	12	2
Total	776	84	1248	103	1459	72	301	63	3774	155

Table 3. Analysis of Variance for the effects of season, size and location on the topside taxa richness.

Dep Var: RICHNESS N: 60

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON	4.433	1	4.433	3.268	0.077
SIZE	1.748	2	0.874	0.644	0.529
LOCATION	0.060	1	0.060	0.044	0.834
SEASON*SIZE	0.174	2	0.087	0.064	0.938
SEASON*LOCATION	0.022	1	0.022	0.016	0.900
SIZE*LOCATION	0.280	2	0.140	0.103	0.902
SEASON*SIZE*LOCATION	0.047	2	0.024	0.017	0.983
Error	65.107	48	1.356		

Power for Size:

$$f = \frac{\sqrt{\frac{\sum(x_i - \bar{x})^2}{k}}}{\sqrt{MSE}} = \frac{\sqrt{\frac{(3.68 - 4.27)^2 + (4.57 - 4.27)^2 + (4.55 - 4.27)^2}{3}}}{\sqrt{1.356}} = 0.1478$$

From Table 8.3.13 (Cohen):

POWER_(α=0.05, f=0.15, u=2, n=19) = 15%
Minimum detectable effect size = 19%

Power for Location:

$$f = \frac{\sqrt{\frac{\sum(x_i - \bar{x})^2}{k}}}{\sqrt{MSE}} = \frac{\sqrt{\frac{(3.28 - 4.27)^2 + (4.25 - 4.27)^2}{2}}}{\sqrt{1.356}} = 0.01$$

From Table 8.3.12 (Cohen):

POWER_(α=0.05, f=0.01, u=1, n=29) = 6%
Minimum detectable effect size = 16%

Table 4. Two-sample t tests comparing the cover of the most common topside attached taxa between the 21 “non-disturbed” boulders (i.e. boulders that were completely bare on the undersides) and the 39 “disturbed” boulders (boulders with attached organisms on the undersides).

	Not Disturbed n=21	Disturbed n=39	pooled variance t	p
Geniculate coralline algae			0.904	0.370
mean	47.61	42.49		
st. dev	22.38	20.20		
encrusting coralline algae			0.010	0.992
mean	30.52	30.46		
st. dev	21.56	22.10		
encrusting sponge			0.937	0.353
mean	7.76	10.26		
st. dev	7.73	10.78		
<i>Plocamium cartilagineum</i>			0.290	0.773
mean	8.00	7.02		
st. dev	13.65	11.70		

Table 5. Attached Biota.

F=frequency (number of boulders with taxa present). Percent cover equals the number of RPQ contact points divided by total number of RPQ contact points.

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	% cover	F n=27	% cover	F n=31	% cover	F n=30	% cover
Bare rock	5	3.5±10.4	25	61.3±44.4	2	0.5±1.8	30	34.9±34.7
Rhodophyta								
encrusting coralline	27	30.0±22.8	9	13.8±28.8	28	30.5±21.4	22	32.3±30.2
<i>Calliarthron tuberculosum</i> Postels & Ruprecht 1840	18	14.3±22.5	1	0.6±2.1	20	20.3±22.9	3	0.8±2.7
<i>Bosziella schmittii</i> Manza 1937	24	28.4±23.8	1	5.3±13.6	26	25.5±21.9	2	1.5±7.6
<i>Corallina vancouveriensis</i> Yendo 1922	1	0.2±1.0			1	0.1±0.6		
<i>Plocanium cartilagineum</i> Dixon 1967	14	9.7±18.2			13	5.8±8.2		
<i>Laurencia subopposita</i> Setchell 1914	2	1.0±3.8			8	4.5±8.8		
<i>Gelidium coulteri</i> Harvey 1853	1	0.3±1.7						
<i>Weeksia digitata</i> Abbott 1968					4	2.6±10.9		
Phaeophyta								
<i>Cystoseira osmundacea</i> Turner 1809	1	0.5±2.7						
<i>Dictyota binghamiae</i> Agardh 1894	1	1.2±6.5			3	1.4±5.2		
<i>Macrocystis</i> holdfast					1	0.5±1.9		
<i>Pterogophora</i> holdfast					1	0.5±2.6		
old degraded holdfast							1	1.4±7.9
Sponge								
<i>Hymenamphistra cyanocrypta</i> de Laubenfels 1930			1	0.5±2.4			5	1.8±5.1
other encrusting sponge	19	10.5±11.5	12	16.3±26.2	24	8.2±7.9	23	22.2±24.0
<i>Craniella arb</i> de Laubenfels 1930	1	0.1±0.7						
Tunicates								
<i>Metandrocarpa taylora</i> Huntsman 1912			2	1.2±5.0			2	0.6±1.5

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	% cover	F n=27	% cover	F n=31	% cover	F n=30	% cover
Worms								
<i>Serpulorbis squamigerus</i> Carpenter 1857			1	1.1±5.8			3	1.4±4.3
Barnacles								
<i>Balanus nubilus</i> Darwin 1854	1	0.1±0.8						
unknown barnacles			1	0.2±1.0				
Bryozoa								
unknown bryozoans							4	2.8±9.3
Cnidarians								
<i>Balanophyllia elegans</i> Verrill 1864	1	0.1±0.5			1	0.2±1.0	1	0.2±1.3

Table 6. Summary of Statistical Analyses.

No=no difference. **Bold**=season, size group, or end of boulder channel (north end or south end) that was highest.

Taxa	Means Different?			Data Normal?	Test	Power	Detectable Effect Size
	Season	Size	Location				
Topside Attached							
<i>C. tuberculosum</i> (17.7%)	No	No	No	No	randomization		
<i>B. schmittii</i> (26.7%)	No	No	North	Yes	3-factor ANOVA	9% for season 14% for size	11.8% for season 11.8% for size
Encr. coralline (30.1%)	No	No	No	Yes	3-factor ANOVA	2% for season 26% for size 26% for location	11.1% for season 11.1% for size 11.4% for location
Encr. sponge (8.8%)	No	Small	North	Yes	3-factor ANOVA ¹	62% for season	25% for season
<i>P. cartilagineum</i> (8.0%)	No	No	No	No	randomization		
Underside Attached							
Bare Rock (53.2%)	Spring	Large	North	No	randomization		
Encr. Coralline (21.7%)	Fall	Small	South	No	randomization		
Encr. Sponge (18.8%)	No ²	No	No	No	randomization		
Topside Mobile							
Total Density (45.2/m ²)	No	Small	No	Yes	3-factor ANOVA	5% for season 30% for location	24% for season 25% for location
<i>Tegula</i> spp. (14.3/m ²)	No	No ³	No	No	randomization		
<i>L. gibberosum</i> (8.1/m ²)	Fall	Small	No	No	randomization		
<i>Pogurus</i> spp. (5.9/m ²)	No	No	No	No	randomization		
Underside Mobile							
Total Density (81.5/m ²)	Spring	No	No	Yes	3-factor ANOVA	23% for size 33% for location	32% for size 32% for location
<i>S. fallax</i> (27.0/m ²)	Spring	No	No	No	randomization		
<i>O. papillosa</i> (16.0/m ²)	No	No	South	No	randomization		
<i>Pagurus</i> spp. (11.1/m ²)	Spring	No ⁴	No	No	randomization		
<i>O. spiculata</i> (6.2/m ²)	No	No ⁵	No ⁶	No	randomization		

¹ Data log-transformed to meet equal variance criteria² p=0.08. Mean cover higher in spring.³ p=0.11. Mean density higher on large boulders.⁴ p=0.10. Mean density higher on large boulders.⁵ p=0.11. Mean density higher on small boulders.⁶ p=0.09. Mean density higher on south end of channel

Table 7. 3-Factor Analysis of Variance tests for attached topside biota

<u>Season</u>	<u>Size</u>	<u>Location</u>
Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$	Ho: $\mu_{\text{small}} = \mu_{\text{large}}$	Ho: $\mu_{\text{north}} = \mu_{\text{south}}$
Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$	Ha: $\mu_{\text{small}} \neq \mu_{\text{large}}$	Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

Bossiaella schmittii

Dep Var: COVER N: 60 Multiple R: 0.314 Squared multiple R: 0.098					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON\$	135.894	1	135.894	0.273	0.604
SIZE\$	8.400	1	8.400	0.017	0.897
LOCATION\$	1941.696	1	1941.696	3.901	0.054
SEASON\$*SIZE\$	18.235	1	18.235	0.037	0.849
SEASON\$*LOCAT ION\$	0.110	1	0.110	0.000	0.988
SIZE\$*LOCATIO N\$	191.124	1	191.124	0.384	0.538
SEASON\$*SIZE\$ *LOCATION\$	99.629	1	99.629	0.200	0.656
Error	25881.880	52	497.728		

Encrusting Coralline

Dep Var: COVER N: 60 Multiple R: 0.253 Squared multiple R: 0.064					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON\$	84.452	1	84.452	0.171	0.681
SIZE\$	157.830	1	157.830	0.320	0.574
LOCATION\$	123.308	1	123.308	0.250	0.619
SEASON\$*SIZE\$	4.257	1	4.257	0.009	0.926
SEASON\$*LOCATION\$	461.193	1	461.193	0.935	0.338
SIZE\$*LOCATION\$	491.386	1	491.386	0.996	0.323
SEASON\$*SIZE\$*LOC ATION\$	92.850	1	92.850	0.188	0.666
Error	25647.260	52	493.217		

Encrusting Sponge

Dep Var: COVER N: 60 Multiple R: 0.427 Squared multiple R: 0.182					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON\$	205.717	1	205.717	2.339	0.132
SIZE\$	304.796	1	304.796	3.465	0.068
LOCATION\$	489.205	1	489.205	5.562	0.022
SEASON\$*SIZE\$	15.221	1	15.221	0.173	0.679
SEASON\$*LOCATION\$	278.956	1	278.956	3.172	0.081
SIZE\$*LOCATION\$	3.386	1	3.386	0.039	0.845
SEASON\$*SIZE\$*LOC ATION\$	5.520	1	5.520	0.063	0.803
Error	4573.647	52	87.955		

Table 8. Chi-squared analyses for attached underside biota. The expected number was determined by multiplying the percent of total boulders with the taxa present by the number of boulders in the sample.

Summary. No=no difference. **Bold**=season or size group that was highest

Taxa	Season	Size	Power	Effect Size
Bare Rock ⁷	Spring	No	52%	16%
Encrusting Coralline	Fall	No	64%	36%
Encrusting Sponge	Fall	Small		

Ho: $\text{Freq}_{\text{spring}} = \text{Freq}_{\text{fall}}$

Ha: $\text{Freq}_{\text{spring}} \neq \text{Freq}_{\text{fall}}$

$\text{Freq}_{\text{small}} = \text{Freq}_{\text{large}}$

$\text{Freq}_{\text{small}} \neq \text{Freq}_{\text{large}}$

$$\chi^2_{\text{crit}}(\alpha=0.05, v=1) = 3.841$$

Bare Rock

	Small	Large	Season Total	Expected	χ^2
Spring	4/13	12/16	16/29	10.63	2.23
Fall	3/17	3/14	6/31	11.37	2.09
Size Total	7/30	15/30	22/60		4.32
Expected	11	11			
$\chi^2 = \sum \frac{(\text{exp} - \text{obs})^2}{\text{exp}}$	1.11	1.11	2.22		

Encrusting coralline algae.

	Small	Large	Season Total	Expected	χ^2
Spring	6/13	3/16	9/29	15	2.02
Fall	13/17	9/14	22/31	16	1.89
Size Total	19/30	12/30	31/60		3.91
Expected	15.5	15.5			
χ^2	0.58	0.58	1.16		

Encrusting sponge

	Small	Large	Season Total	Expected	χ^2
Spring	8/13	4/16	12/29	12.57	0.00
Fall	13/17	11/14	24/31	13.43	7.55
Size Total	21/30	15/30	26/60		7.55
Expected	13	13			
χ^2	4.33	0.17	4.50		

⁷ Number of completely bare boulders tested

Table 9. Large Mobile Animals.

F=frequency (number of boulders with taxa present). D=density (#/m²).

Molluscs

Snails

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
<i>Calliostoma annulatum</i> Lightfoot 1786								
<i>Calliostoma ligatum</i> Gould 1849			2	1.4±3.3	2	2.0±8.2		
<i>Ceratostoma foliatum</i> Gmelin 1791	1	0.2±0.8				0.8±3.9		
<i>Fusitriton oregonensis</i> Redfield 1846					1	0.2±1.3		
<i>Homalopoma luridum</i> Dall 1885	1	0.3±1.7						
<i>Lithopoma gibberosum</i> Dillwyn 1817	13	5.2±7.8	1	1.1±4.1	20	10.8±20.7		0.6±2.1
<i>Margarites</i> sp.	1	0.5±2.5	2	0.2±1.3				
<i>Mitra idae</i> Melville 1893			1	0.6±3.1	4	1.0±2.7	3	0.7±2.0
<i>Tegula montereyi</i> Kiener 1850	20	17.6±28.0	10	6.2±14.0	11	9.9±22.8	2	0.4±1.9
unknown snails	2	0.7±2.7	7	4.4±9.9	2	1.2±4.7	5	4.5±14.3
Limpets								
<i>Acmaea mitra</i> Rathke 1833	5	1.6±4.0			3	1.1±3.9	1	0.3±1.5
<i>Collisella ochracea</i> Dall 1871	1	0.3±1.4						
<i>Collisella triangularis</i> Carpenter 1864			1	0.2±1.3				
<i>Crepidula adunca</i> Sowerby 1825	5	4.8±14.4	4	2.6±7.6				
unknown limpet					1	0.5±2.9		
Chitons								
<i>Cryptochiton stelleri</i> Middendorf 1847			1	0.6±3.3				
<i>Stenoplax fallax</i> Carpenter in Pilsbry 1892			23	34.3±30.0			15	18.5±31.9
<i>Tonicella lineata</i> Wood 1815	9	3.9±7.1	1	0.3±1.3	9	2.4±4.2	1	0.3±1.4
unknown chiton			2	1.0±3.9				

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
Nudibranchs								
<i>Hermisenda crassicornis</i> Eschscholtz 1831	3	1.0±3.5						
<i>Triopha catalinae</i> Cooper 1863			1	0.3±1.7				
<i>Doriopsilla albopuntata</i> Cooper 1863			2	0.3±1.7	1	0.3±1.9	1	0.4±2.1
Clam								
<i>Diplodonta orbella</i> Gould 1851			1	0.2±0.9				
Abalone								
<i>Haliotis walallensis</i> Stearns 1899			2	0.3±1.1			6	1.3±2.8

Molluscs cont.

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
Crabs								
<i>Cancer</i> sp.			2	0.5±1.7				
<i>Cancer anthoni</i> Rathbun 1879			1	0.2±0.8				
<i>Cryptolithodes sitchensis</i> Brandt 1853	3	0.7±2.1			1	0.2±1.3		
<i>Hapalogaster cavicauda</i> Stimpson 1859			3	1.5±4.7			3	0.9±2.0
<i>Loxorhynchus crispatus</i> Stimpson 1857	2	0.4±1.5	2	0.8±3.1				
<i>Pagurus</i> sp.	10	4.1±7.8	13	20.0±31.0	8	6.6±12.6	8	4.4±9.9
Porcellanidae			3	0.8±2.7				
<i>Pugettia producta</i> Randall 1839	1	0.2±0.8	2	0.8±3.0				
<i>Pugettia richii</i> Dana 1851	1	0.5±0.8	3	2.3±7.1	2	0.2±0.6	2	0.7±2.5
Shrimp								
<i>Heptacarpus</i> sp.			1	0.5±1.6	2	1.2±4.6	2	0.6±3.2

Crustaceans

Worms

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
<i>Diopatra ornata</i> Moore			1	0.6±2.3			1	0.1±0.3
Nemerteans							3	1.9±6.0
F. Sabellidae			2	0.3±1.2				
Sipunculids			3	0.6±1.7				
Unknown worms			6	2.9±6.8			1	0.2±

Echinoderms

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
Asteroidea	8	2.6±4.7	3	1.5±5.6	10	2.7±4.6	6	2.3±5.4
<i>Asterina miniata</i> Brandt 1835			1	0.6±3.2				
<i>Dermasterias imbricata</i> Grube 1857			1	0.2±0.9				
<i>Henricia leviuscula</i> Stimpson 1859			2	0.8±3.0			1	0.4±2.0
<i>Orthasterias koehleri</i> de Loriol			2	0.6±2.2			4	0.9±2.5
<i>Pycnopodia helianthoides</i> Brandt 1835								
Ophioroidea								
<i>Ophiothrix spiculata</i> Le Conte 1851			5	5.0±18.9	3	2.5±11.5	8	5.7±12.7
<i>Ophiopteris papillosa</i> Lyman 1875			11	12.3±20.4			14	16.8±26.5
unknown brittle stars			3	1.6±5.1				
Echinoidea								
<i>Strongylocentrotus purpuratus</i> Stimpson 1857			2	1.5±3.8	1	3.1±17.2	2	1.0±3.8

Fish	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=29	D	F n=27	D	F n=31	D	F n=30	D
<i>Sebastes</i> sp.					1	0.1±0.7		
<i>Oxylebius pictus</i> Gill					4	0.8±2.2		
<i>Rhinogobio nicholsii</i> Am. Fish. Soc. (2004)					2	0.4±1.4		
unidentified sculpin ⁸					5	1.4±3.5		
<i>Gibbonsia</i> sp.	1	0.2±1.3			1	0.1±0.7		

⁸ Most likely *Orthonopias triacis* Starks & Mann. It is a common sculpin in Carmel Bay at this depth (Calliet, G., per. com.).

Table 10. Analysis of Variance for total mobile animal density.

Topside

Dep Var: DENSITY N: 60

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON	115.399	1	115.399	0.051	0.822
SIZE	9109.850	1	9109.850	4.017	0.050
LOCATION	3556.998	1	3556.998	1.569	0.216
SEASON*SIZE	105.447	1	105.447	0.046	0.830
SEASON*LOCATION	2810.498	1	2810.498	1.239	0.271
SIZE*LOCATION	1405.481	1	1405.481	0.620	0.435
SEASON*SIZE*LOCATION	47.982	1	47.982	0.021	0.885
Error	117919.592	52	2267.684		

Size

Group	N	Mean	SD
large	30	35.813	26.466
small	30	55.733	60.379

Underside

Dep Var: DENSITY N: 57

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON	24445.806	1	24445.806	6.742	0.012
SIZE	2159.126	1	2159.126	0.595	0.444
LOCATION	2583.569	1	2583.569	0.713	0.403
SEASON*SIZE	1942.314	1	1942.314	0.536	0.468
SEASON*LOCATION	168.237	1	168.237	0.046	0.830
SIZE*LOCATION	844.480	1	844.480	0.233	0.632
SEASON*SIZE*LOCATION	15.437	1	15.437	0.004	0.948
Error	177667.008	49	3625.857		

Season

Group	N	Mean	SD
fall	30	65.780	51.149
spring	27	110.569	64.580

Table 11. T-tests for taxa richness (taxa/boulder) and taxa density (taxa/m²) to test for differences between the topsides and undersides of boulders.

Taxa Richness

Two-sample t test on taxa richness grouped by side

Group	N	Mean	SD
top	60	2.783	1.905
under	57	3.965	2.632

Separate Variance t = -2.769 df = 101.7 Prob = 0.007
 Difference in Means = -1.182 95.00% CI = -2.028 to -0.335

Pooled Variance t = -2.792 df = 115 Prob = 0.006
 Difference in Means = -1.182 95.00% CI = -2.020 to -0.343

Taxa Density

Two-sample t test on taxa density grouped by side

Group	N	Mean	SD
top	60	24.104	23.482
under	57	32.288	21.312

Separate Variance t = -1.976 df = 114.8 Prob = 0.051
 Difference in Means = -8.183 95.00% CI = -16.389 to 0.022

Pooled Variance t = -1.971 df = 115 Prob = 0.051
 Difference in Means = -8.183 95.00% CI = -16.409 to 0.042

Table 12. Small Mobile Animals. F=frequency (number of boulders with taxa present). D=density (#/m²).

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
<i>Alia carinata</i> Hinds 1844							1	2.9±5.1
<i>Alia gausapata</i> Carpenter 1864	1	9.2±22.5						
<i>Alia tuberosa</i> Gould 1850	6	58.1±31.7	5	9.7±14.6	3	22.7±29.2		
<i>Alvania</i> sp.	6	44.6±30.7		11.7±19.5	3	111±202	1	14.6±18.3
<i>Amphissa undata</i> Carpenter 1864	1	1.4±3.3	5				2	2.9±5.1
<i>Amphissa versicolor</i> Dall 1871	6	36.7±17.0		17.2±14.8	2	10.3±15.0		3.6±4.7
<i>Baleis</i> sp.	2	3.4±5.4			2	8.4±15.6		
<i>Barleeia</i> sp.	5	60.6±40.0	1	12.8±11.3	3	116±180	2	16.3±17.2
<i>Bittium</i> sp.	4	15.4±15.1		3.9±10.4	1	5.8±11.7		6.8±6.1
<i>Bittium munitum</i> Carpenter 1864	1	2.2±5.5						
<i>Cerithidea californica</i> Haldeman 1840					1	0.5±0.9		
<i>Cymakra</i> sp.			1	0.6±1.7				
<i>Cystiscus jewettii</i> Carpenter 1857	4	40.0±55.2	4	4.0±5.3	4	94.3±78.5	1	2.9±5.1
<i>Epitonium tinctum</i> Carpenter 1865	1	1.7±4.1	2	4.8±10.3				
<i>Fusinus luteopictus</i> Dall 1857	3	5.5±7.9	1	0.6±1.7	3	9.4±14.6	2	6.8±6.1
<i>Homalopoma luridum</i> Dall 1885	3	20.2±28.7	5	19.6±28.9	1	0.9±1.9	3	11.6±6.1
<i>Lacuna</i> sp.	2	2.3±3.7	3	11.9±20.2	2	2.7±4.2	2	6.8±6.1
<i>Littorina</i> sp.	6	164±146	7	13.3±8.2	4	178±121	3	78.2±101
<i>Margarites salmoneus</i> Carpenter 1864	2	3.8±7.3	4	7.3±9.8	1	8.0±15.9		
<i>Margarites</i> sp.	3	4.9±5.9	1	2.3±6.2	2	7.5±9.1		
<i>Nassarius mendicus</i> Gould 1849			1	3.9±10.4				
<i>Odostomia</i> sp.	3	7.2±9.5	1	0.8±2.2	1	15.9±31.8	1	5.9±10.2
<i>Odostomia stricta</i> Dall & Bartsch 1907	3	4.6±6.4	3	2.1±2.7	1	1.8±3.7		

Molluscs

Snails

Molluscs cont.

	Spring 2004						Fall 2004					
	Topside			Underside			Topside			Underside		
	F n=6	D	F n=7	D	F n=7	D	F n=4	D	F n=3	D	F n=3	D
Limpets												
<i>Acmaea mitra</i> Rathke 1833									1	2.9±5.1		
<i>Crepidula adunca</i> Sowerby 1824	4	18.6±15.7	4	8.0±10.4			4	37.9±59.7	1	1.2±2.1		
<i>Diodora aspera</i> Rathke 1833			1	0.6±1.7			1	8.0±15.9				
<i>Lottia gigantea</i> Sowerby 1834	1	1.1±2.5										
<i>Megatebennus bimaculatus</i> Dall 1871							1	2.9±5.9				
<i>Notoacmea scutum</i> Rathke 1833	1	1.4±3.3										
Nudibranchs												
<i>Phidiana hiltoni</i> O'Donoghue 1927	2	2.1±3.5										
Clams												
<i>Glans carpenteri</i> Lamy 1922	1	0.7±1.8										
<i>Leptopecten latiauratus</i> Conrad 1837			1	0.6±1.7								
<i>Nutricula</i> sp.	1	1.0±2.5										
<i>Nutricula ovalis</i> Dall 1902									1	2.9±5.1		
<i>Nutricula tantilla</i> Gould 1853	1	1.7±4.1										
Chiton												
<i>Ishnochiton radians</i>												
<i>Lepidozona mertensii</i>												
<i>Stenoplax fallax</i> Carpenter in Pilsbry 1892			2	3.6±3.9								
Scaphapod												
<i>Caecum californicum</i> Dall in Orcutt 1885	5	61.8±64.3	3	11.0±14.5								

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Worms								
Phylum Annelida								
Class Polychaeta								
F. Amphinomididae			3	12.1±26.1			1	2.9±5.1
F. Cirratulidae			5	16.0±26.1				
F. Euphrosinidae							1	3.9±6.8
F. Glyceridae			2	6.8±11.8				
<i>Haploscoloplos elongatus</i> Pettibone 1957			1	1.2±3.1				
F. Hesionidae			6	66.7±77.8				
F. Lumbrineridae		40.6±35.2	3	38.1±32.8				
F. Onuphidae			2	10.8±21.0	1	8.0±15.9		
F. Opheliidae	1	1.7±4.1	7	68.0±56.2	1	0.5±0.9	2	38.0±58.4
F. Orbiniidae			2	2.0±3.5				
F. Nereidae			4	7.5±9.1	1	8.0±15.9	1	7.8±13.5
F. Paraonidae			1	2.1±3.9				
F. Phyllodocidae	1	1.7±4.1	3	7.8±14.8				
F. Pilargiidae	1	1.0±2.5						
F. Polynoidae			4	10.3±10.9	3	27.3±45.8	3	20.2±16.9
F. Sabellidae							1	3.9±6.8
F. Sphaerodoridae	1	3.0±7.5	1	0.9±2.3				
O. Spionida			1	2.6±6.9				
F. Syllidae	3	6.4±10.7	7	124±226				
F. Terebellidae			1					
Class Oligochaeta				74.0±97.1			1	2.9±5.1
Phylum Nemertea			5	5.8			1	2.1±
Phylum Sipuncula	1	1.4±3.3	3	2.4±3.3			1	3.9±6.8

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Copepods								
<i>Calanus</i> sp.	1	4.6±11.2						
<i>Nebalia gerkenae</i> Haney & Martin 2000			3	26.7±43.2				
Cumacean								
<i>Cyclaspis nubila</i> Zimmer 1936	1	4.6±11.2	3	20.6±40.9	1	2.9±5.8	1	7.8±13.5
Amphipods								
<i>Americhelidium micropleon</i> Barnard 1977					2	5.2±6.1		
<i>Americorophium stimpsoni</i> Bousfield & Hoover 1997							1	11.8±20.4
F. Amphilochidae	2	10.1±15.7	6	25.1±23.2	4	213±149	2	39.1±35.9
<i>Aoroides</i> sp.	6	57.2±40.2	6	207±298	2	121±238	2	57.7±57.3
<i>Aoroides exilis</i> Conlan & Bousfield 1982	2	18.9±31.0	4	98.1±144	2	55.6±89.2	1	3.7±6.4
<i>Aoroides intermedia</i> Conlan & Bousfield 1982	1	3.4±8.3	5	15.0±12.7			1	3.9±6.8
<i>Apolochus barnardi</i> Hoover & Bousfield 2001					1	8.8±17.6		
<i>Apolochus litoralis</i> Stout 1912					1	1.4±2.8		
<i>Aruga holmesi</i> Barnard 1955	2	3.7±7.2	6	117±151				
<i>Caprella equilibra</i> Say 1818					1	0.5±0.9	1	0.6±1.1
<i>Chronopleustes oculatus</i> Holmes 1908	1	1.5±3.6			2	21.3±29.1	1	11.7±20.3
<i>Coboldus hedgpethi</i> Barnard 1969					1	2.2±4.4		
<i>Desdemelita</i> sp.			1	3.8±10.1				
<i>Desdimelita dentata</i> Kröyer 1842			2	22.7±42.6				
<i>Desdimelita desdichada</i> Barnard 1969			1	1.9±5.0				
<i>Elasmopus</i> sp.	1	3.0±7.5	3	14.9±19.2	3	23.8±20.1	1	5.9±10.2

Crustaceans

Crustaceans cont.

Amphipods cont.

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
<i>Elasmopus antennatus</i> Stout 1913	4	17.8±21.3	5	29.5±30.8	2	22.5±30.1		
<i>Elasmopus bampo</i> Barnard 1979			1	1.7±4.6			1	3.9±6.8
<i>Eobrolgus</i> sp.					1	0.5±0.9		
<i>Eusiroides monoculoides</i> Haswell 1879	1	1.0±2.5			2	10.9±12.7	1	2.5±4.3
<i>Foxiphalus obtusidens</i> Alderman 1936			4	13.7±19.6			3	23.0±30.9
<i>Gammaropsis</i> sp.			2	17.5±41.1			2	8.5±
<i>Gammaropsis martesia</i> Barnard 1964			3	38.5±72.9			1	2.1±
<i>Gammaropsis shoemakeri</i> Conlan 1983	2	12.1±24.3	1	1.5±2.6	3	29.6±27.3		
<i>Gammaropsis thompsoni</i> Walker 1898	1	1.0±	1	3.5±9.2	2	23.5±33.3		
<i>Gibberosus myersi</i> McKinney			1	0.8±2.2				
<i>Haliophasma geminata</i> Menzies & Barnard 1959					1	25.0±50.0		
<i>Hourstonius vilordes</i> Barnard 1962				1.4±3.8	1			
F. Isaeidae					1	0.5±0.9		
F. Ischyroceridae	2	4.4±8.1			3	17.7±18.4		
<i>Ischyrocerus</i> sp.	5	14.9±15.6	3	15.2±30.4				
<i>Lepidepecreum serraculum</i> Dalkey 1998	2	1.7±2.8	3	10.8±14.1			1	2.9±5.1
<i>Leucothoe alata</i> Barnard 1959							1	2.9±5.1
<i>Maera</i> sp.	2	2.4±4.1	6	46.1±49.5			2	9.6±12.2
<i>Melita nitida</i> Smith 1873			1	24.3±11.5				
<i>Melita sulca</i> Stout 1913	1	0.8±1.8						
<i>Microjassa litotes</i> Barnard 1954			1	0.9±2.3				
<i>Neoischyrocerus claustris</i> Barnard 1969	2	5.5±9.9					1	3.9±6.8

Crustaceans cont.

Amphipods cont.

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
<i>Netameliita cortada</i> Barnard 1962	1	4.6±11.2					1	2.9±5.1
<i>Pariphinotus escabrosus</i> Barnard 1962			1			0.5±0.9		
<i>Photis</i> sp.	3	6.8±11.8	4	19.2±30.9	4	39.6±37.5	1	3.9±6.8
<i>Photis brevipes</i> Shoemaker 1942			1	0.8±2.2				
<i>Photis californica</i> Stout 1913			1	11.8±31.2				
<i>Photis conchicola</i> Alderman 1936			1	1.6±4.5				
<i>Pleusirus secorrius</i> Barnard 1969			2	9.0±15.5	4	139±183		
<i>Pleusymples subglaber</i> Barnard & Given 1960			1	1.4±3.8			1	2.1±
<i>Podocerus</i> sp.	1	3.4±8.3	1	0.6±1.7				
<i>Podocerus cristatus</i> Thomson 1879	5	17.7±18.0	1	5.9±15.6	4	64.4±87.3	1	2.9±5.1
<i>Pontogeneia inermis</i> Kröyer 1838			1	0.6±1.7	4	172±155	1	7.8±13.5
<i>Pontogeneia intermedia</i> Gurjanova 1938	2	7.8±14.6	4	30.4±44.8	4	287±408	3	29.9±25.9
<i>Pontogeneia rostrata</i> Gurjanova 1938	3	10.2±12.0	5	20.1±38.2	4	564±285	3	146±183
<i>Protohyale</i> sp.			1	0.8±2.2	2	4.5±5.2		
<i>Rhepoxynius heterocuspoidatus</i> Bernard 1960			1					
<i>Thorlaksonius depressus</i> Alderman 1936	2	4.5±7.6	2	17.2±41.2	4	96.9±86.8	3	11.0±7.0
<i>Tiron biocellata</i> Barnard 1962	2	8.7±13.4	1	0.8±2.2	1	0.5±0.9	1	5.9±10.2
<i>Ventojassa ventosa</i> Barnard 1962	1	1.0±2.5						
Isopods								
<i>Ianiropsis montereyensis</i> Menzies 1952	1	3.0±7.3	3	32.5±71.3	1	2.2±4.4	1	3.9±6.8
<i>Ianiropsis tridens</i> Menzies 1952	1	9.2±22.5	3	7.1±10.4	3	35.4±61.4		
<i>Idotea rufescens</i> Fee 1926	1	0.8±1.8	3	4.2±5.7	1	1.4±2.8	1	2.9±5.1
<i>Janirallata occidentalis</i> Walker 1898			1	1.3±3.4				

Crustaceans cont.

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Isopods cont.								
<i>Joeropsis dubia</i> Menzies 1951	1	14.2±34.8	4	24.6±50.4	4	14.0±12.3	1	5.9±10.2
<i>Leptochelia dubia</i> Kröyer 1844			2	9.0±20.5				
<i>Paracerceis sculpta</i> Holmes 1904	5	31.3±40.2	6	13.1±9.5	4	274±433	2	16.6±14.5
<i>Paranthura elegans</i> Menzies 1951			1	0.9±2.3			1	2.1±
<i>Pentidotea stenops</i> Benedict 1898	1	0.7±1.8			1	0.5±0.9		
<i>Uromunna ubiquita</i> Menzies 1952	1	1.7±4.1	1	2.5±6.7				
Crabs								
<i>Cancer</i> sp					1	0.5±0.9		
<i>Hapalogaster cavicauda</i> Stimpson 1859	1	0.7±1.8						
<i>Loxorhynchus crispatus</i> Stimpson 1857			2	1.8±3.3	1	4.4±8.8		
<i>Pagurus</i> sp.	4	41.6±51.5	6	79.7±122	3	62.4±70.9	2	31.7±53.5
<i>Petrolisthes manimaculis</i> Glassell 1945			3	5.7±8.2			1	3.9±6.8
F. Porcellanidae	1	2.2±5.5	4	8.3±11.1			1	3.9±6.8
<i>Pugettia producta</i> Randall 1839			2	4.6±10.3				
<i>Pugettia richii</i> Dall 1851	3	12.0±17.0	4	10.3±12.4	2	66.4±126		
Shrimp								
<i>Acanthomysis californica</i> Murano & Chess 1987					1	2.9±5.8		
<i>Lebbeus lagunae</i> Schmidt 1921	1	4.1±9.9						
<i>Heptacarpus carinatus</i> Holmes 1900					1	0.5±0.9		
<i>Heptacarpus palpator</i> Owen 1839	3	11.2±11.2	4	27.3±39.5	4	288±423	3	62.9±46.6
<i>Spirontocaris prionota</i> Stimpson 1864	1	1.0±2.5				33.7±62.5	1	2.9±5.1
Ostracod								
<i>Podocopida ostracodes</i> Abe & Vannier 1995	1	1.0±2.5	3	3.1±4.1	3	16.6±14.0	1	3.9±6.8

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Echinoderms								
Asteroids								
<i>Asterina miniata</i> Brandt 1835			1	0.6±1.7				
<i>Pisaster giganteus</i> Stimpson 1862	1	0.7±1.8						
Juvenile asteroid					2	8.4±15.6		
Ophioroids								
<i>Amphiodia psara</i> Clark 1935	2	5.6±11.0	7	42.6±23.1	2	8.4±15.6		35.4±28.4
<i>Ophiothrix spiculata</i> Le Conte 1851				0.6±1.7				
Echinoids								
<i>Strongylocentrotus pupuratus</i> Stimpson 1857	1	0.7±1.8						

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	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Fish								
juvenile sculpin (Moser et. al. 1996)	1	1.0±2.5	1	1.4±3.8	2	8.0±15.9		

	Spring 2004				Fall 2004			
	Topside		Underside		Topside		Underside	
	F n=6	D	F n=7	D	F n=4	D	F n=3	D
Other								
Cnidarians			3	9.9±16.1	1	2.2±4.4		
Pychnogonids	1	1.4±3.3			1	4.4±8.8		

APPENDIX B Figures

Figure 1. Side-scan bathymetry map of Stillwater Cove, Carmel Bay, CA. (E. Sandoval)

Figure 2. Three Primary Biotic Zones of Boulder Habitat. **Algae Zone:** The tops of the boulders usually covered with algae, primarily non-geniculate and geniculate coralline. **Sponge Zone:** The underside of the boulder above the sand. Encrusting sponges dominate this zone, but it may contain patches of coralline algae or bare rock. The transition between the algae zone and the sponge zone may be gradual rather than abrupt depending on the orientation of the boulder. The sponge zone may be absent depending on the degree of burial. **Bare Zone:** This is the area under the sandy substrate. It is usually completely bare. The transition between the sponge zone and the bare zone is almost always abrupt.

N=29

Figure 3. RPQ Density Analysis. For each of the 29 spring topside boulders, I randomly selected a taxon from the population with replacement 21 times and recorded the cumulative number of taxa. The error bars represent the standard error for the 29 replications. The slope becomes asymptotic at about 18 points/boulder. To convert this to density, I dividing 18 points/boulder by the average surface area, 0.41m^2 , to get approximately 43 points/ m^2 .

Figure 4. Air-Lift Sampler

Figure 5. Sampling locations

Figure 6. Depth vs. Location Along Transect Line.

Figure 7. Cluster analysis for the underside community. For size: l=large boulders, sm=small boulders. For location: n=boulders located in the northern 1/3 of the channel, c= boulders located in the central 1/3 of the channel, so=boulders located in the southern 2/3 of the channel. For season: sp=spring, f=fall.

Figure 8. Boulder size vs. total mobile animal density. Spring and fall samples are combined.

Analysis of Variance
Dep Var: RICHNESS N: 60

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON	0.637	1	0.637	0.182	0.671
SIZE	20.933	2	10.466	2.997	0.058
SEASON*SIZE	0.020	2	0.010	0.003	0.997
Error	188.592	54	3.492

Analysis of Variance
Dep Var: RICHNESS N: 56

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SEASON	38.627	1	38.627	6.689	0.013
SIZE	24.421	2	12.210	2.114	0.131
SEASON*SIZE	21.752	2	10.876	1.883	0.163
Error	288.737	50	5.775		

Figure 9. Large Mobile Animal Taxa Richness.

APPENDIX C – Randomization Tests

The following program was used for all randomization tests using Resampling Stats[®]6.0.

<u>Command</u>	<u>Result</u>
data () factor1	Data set 1 (spring, small, or north boulders)
data () factor2	Data set 2 (fall, large, or south boulders)
mean factor1 mean1	Calculates average of factor1 population
mean factor2 mean2	Calculates average of factor2 population
subtract mean1 mean2 diff	Calculates difference between population means
repeat 1000	Run loop 1000 times
shuffle factor1 pop1	Shuffle factor1 population
shuffle factor2 pop2	Shuffle factor2 population
sample 29 pop1 spop1	Creates factor1 sample spop1 with 29 values ⁹
sample 31 pop2 spop2	Creates factor2 sample spop2 with 31 values
mean spop1 ave1	Calculates mean of factor1 sample pop
mean spop2 ave2	Calculates mean of factor2 sample pop.
subtract ave1 ave2 dif	Calculates difference between sample pops
score dif differ	Creates vector of the 1000 differences
end	End loop
histogram differ	Creates a histogram of the 1000 differences

Calliarthron tuberculosis - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Resampling Stats Output

Spring mean = 14.921

Fall mean = 19.955

Difference = -5.0341

Bin Center	Freq	%	Cum %
-18	3	0.3	0.3
-16	4	0.4	0.7
-14	8	0.8	1.5
-12	23	2.3	3.8
-10	32	3.2	7.0
-8	62	6.2	13.2
-6	83	8.3	21.5
-4	122	12.2	33.7
-2	123	12.3	
0	120	12.0	
2	120	12.0	
4	116	11.6	
6	69	6.9	
8	57	5.7	
10	34	3.4	
12	12	1.2	
14	8	0.8

⁹ Actual number depends on the factor being considered

The table above indicates the probability of getting a difference the less than the observed difference (-5.03) is about 27.6%. This is greater than α (5%), so I do not reject H_0 . There is no significant difference in percent cover of *C. tuberculosum* between spring and fall.

Randomization test for boulder size differences using Resampling Stats 5.0.3:
(see Appendix A for algorithm)

***Calliarthron tuberculosum* - size**

$H_0: \mu_{\text{small}} = \mu_{\text{large}}$

$H_a: \mu_{\text{small}} \neq \mu_{\text{large}}$

Small mean = 14.690

Large mean = 20.683

Difference = -5.993

Resampling Stats Output

Bin Center	Freq	%	Cum %
-20	1	0.1	0.1
-18	1	0.1	0.2
-16	5	0.5	0.7
-14	6	0.6	1.3
-12	16	1.6	2.9
-10	31	3.1	6.0
-8	47	4.7	10.7
-6	88	8.8	19.5
-4	125	12.5	
-2	117	11.7	
0	146	14.6	
2	116	11.6	
4	105	10.5	
6	87	8.7	
8	51	5.1	
10	33	3.3	
12	12	1.2	
14	8	0.8	
16	5	0.5

The table above indicates the probability of getting a difference the less than the observed difference (-5.99) is about 19.5%. This is greater than α (5%), so I do not reject H_0 . There is no significant difference in percent cover of *C. tuberculosum* between small and large boulders.

***Calliarthron tuberculosum* – location**

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 19.14

South mean = 16.16

Difference = 2.98

Resampling Stats Output

Bin Center	Freq	%	Cum %
-25	1	0.1	0.1
-15	18	1.8	1.9
-10	91	9.1	11.0
-5	213	21.3	32.3
0	346	34.6	66.9
5	221	22.1	89.0
10	88	8.8	97.8
15	19	1.9	99.7
20	2	0.2	99.9
30	1	0.1	100

The table above indicates the probability of getting a difference the less than the observed difference (2.98) is about 80%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in percent cover of *C. tuberculosum* between the north end and the south end of the channel.

***Plocamium cartilagineum* - season**

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 10.444

Fall mean = 5.668

Difference = 4.777

Resampling Stats Output

Bin Center	Freq	%	Cum %
-12	3	0.3	
-10	6	0.6	
-8	16	1.6	
-6	57	5.7	
-4	126	12.6	
-2	177	17.7	
0	236	23.6	
2	179	17.9	
4	119	11.9	21.0
6	56	5.6	9.1
8	22	2.2	2.5
10	3	0.3	0.3

The table above indicates the probability of getting a value greater than the observed difference (4.8) is about 16%. Do not reject Ho. There is no significant difference in percent cover of *P. cartilagineum* between spring and fall.

***Plocamium cartilagineum* - location**

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 5.60

South mean = 9.16

Difference = -3.56

Resampling Stats Output

Bin Center	Freq	%	Cum %
-12	2	0.2	0.2
-10	5	0.5	0.7
-8	12	1.2	1.9
-6	56	5.6	7.5
-4	131	13.1	20.6
-2	175	17.5	38.1
0	231	23.1	61.2
2	188	18.8	80.0
4	125	12.5	92.5
6	52	5.2	97.7
8	17	1.7	99.4
10	4	0.4	99.8
12	2	0.2	100

The table above indicates the probability of getting a difference the less than the observed difference (-3.6) is about 24%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in percent cover of *Plocamium cartilagineum* between the north end and the south end of the channel.

Underside Bare Rock- season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 70.514

Fall mean = 37.000

Difference = 33.514

Resampling Stats Output

Bin Center	Freq	%	Cum %
-30	3	0.3	
-25	10	1.0	
-20	28	2.8	
-15	63	6.3	
-10	110	11.0	
-5	173	17.3	
0	186	18.6	
5	188	18.8	
10	123	12.3	
15	79	7.9	
20	21	2.1	
25	13	1.3	
30	2	0.2	0.3
35	1	0.1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (33.5) is about 0.2%. This is less than α (5%), so reject Ho. Spring boulders had significantly higher "cover" of underside bare rock than fall boulders.

Underside Bare Rock - size

H₀: $\mu_{\text{small}} = \mu_{\text{large}}$

H_a: $\mu_{\text{small}} \neq \mu_{\text{large}}$

Small mean = 42.357

Large mean = 64.040

Difference = -21.683

Resampling Stats Output

Bin Center	Freq	%	Cum %
-30	3	0.3	0.3
-25	8	0.8	1.1
-20	30	3.0	4.1
-15	47	4.7	
-10	109	10.9	
-5	190	19.0	
0	200	20.0	
5	185	18.5	
10	115	11.5	
15	72	7.2	
20	28	2.8	
25	11	1.1	
30	2	0.2

The table above indicates the probability of getting a difference the less than the observed difference (-21.7) is about 3.5%. This is less than α (5%), so reject H₀. Large boulders had significantly higher "cover" of underside bare rock than small boulders.

Underside Bare Rock – location

H₀: $\mu_{\text{north}} = \mu_{\text{south}}$

H_a: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 69.90

South mean = 37.43

Difference = 32.48

Resampling Stats Output

Bin Center	Freq	%	Cum %
-35	1	0.1	0.1
-30	3	0.3	0.4
-25	12	1.2	1.6
-20	39	3.9	5.5
-15	78	7.8	13.3
-10	116	11.6	24.9
-5	160	16.0	40.9
0	172	17.2	58.1
5	178	17.8	75.9
10	118	11.8	87.7
15	62	6.2	93.9
20	43	4.3	98.2
25	15	1.5	99.7
30	3	0.3	100

The table above indicates the probability of getting the observed difference (32.5) is less than 0.3%. This is less than α (5%), so reject H₀. There is a significant difference in percent cover of bare rock between the north end and the south end of the channel.

Underside Encrusting Coralline - season

$$H_0: \mu_{\text{spring}} = \mu_{\text{fall}}$$

$$H_a: \mu_{\text{spring}} \neq \mu_{\text{fall}}$$

$$\text{Spring mean} = 11.875$$

$$\text{Fall mean} = 31.216$$

$$\text{Difference} = -19.341$$

Resampling Stats Output

Bin Center	Freq	%	Cum %
-25	2	0.2	
-20	9	0.9	
-15	30	3.0	
-10	105	10.5	
-5	201	20.1	
0	270	27.0	
5	227	22.7	
10	111	11.1	
15	35	3.5	4.5
20	8	0.8	1.0
25	2	0.2	0.2

The table above indicates the probability of getting a difference the less than the observed difference (-19.3) is about 1.1%. This is less than α (5%), so reject H_0 . Fall boulders had significantly more cover of encrusting coralline algae than spring boulders.

Underside Encrusting Coralline - size

$$H_0: \mu_{\text{small}} = \mu_{\text{large}}$$

$$H_a: \mu_{\text{small}} \neq \mu_{\text{large}}$$

$$\text{Small mean} = 34.283$$

$$\text{Large mean} = 10.200$$

$$\text{Difference} = 24.083$$

Resampling Stats Output

Bin Center	Freq	%	Cum %
-25	1	0.1	
-20	2	0.2	
-15	42	4.2	
-10	115	11.5	
-5	214	21.4	
0	243	24.3	
5	231	23.1	
10	101	10.1	
15	41	4.1	
20	7	0.7	1.0
25	3	0.3	0.3

The table above indicates the probability of getting a difference the less than the observed difference (24.1) is about 0.4%. This is less than α (5%), so reject H_0 . Small boulders had significantly more cover of underside encrusting coralline algae than large boulders.

Underside Encrusting Coralline – location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 11.72

South mean = 31.07

Difference = -19.34

Resampling Stats Output

Bin Center	Freq	%	Cum %
-25	2	0.2	0.2
-20	7	0.7	0.9
-15	32	3.2	4.1
-10	104	10.4	14.5
-5	235	23.5	38.0
0	245	24.5	62.5
5	209	20.9	83.4
10	117	11.7	95.1
15	36	3.6	98.7
20	11	1.1	99.8
25	2	0.2	100

The table above indicates the probability of getting the observed difference (-19.3) is less than 2%. This is less than α (5%), so reject Ho. There is a significant difference in percent cover of encrusting coralline between the north end and the south end of the channel.

Underside Encrusting Sponge - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 14.048

Fall mean = 24.157

Difference = -10.108

Resampling Stats Output

Bin Center	Freq	%	Cum %
-20	2	0.2	0.2
-15	13	1.3	1.5
-10	70	7.0	8.5
-5	239	23.9	
0	332	33.2	
5	248	24.8	
10	79	7.9	
15	16	1.6	
20	1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (-10.1) is about 8%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the cover of underside encrusting sponge between spring and fall.

Underside Encrusting Sponge – location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 17.17

South mean = 20.83

Difference = -3.67

Resampling Stats Output

Bin Center	Freq	%	Cum %
-20	4	0.4	0.4
-15	22	2.2	2.6
-10	93	9.3	11.9
-5	229	22.9	34.8
0	305	30.5	65.3
5	238	23.8	89.1
10	82	8.2	97.3
15	23	2.3	99.6
20	3	0.3	99.9
25	1	0.1	100

The table above indicates the probability of getting the observed difference (-3.7) is about 25%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in percent cover of encrusting sponge between the north end and the south end of the channel.

Topside *Tegula montereyi* - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 17.714

Fall mean = 11.171

Difference = 6.543

Resampling Stats Output

Bin Center	Freq	%	Cum %
-20	7	0.7	
-15	15	1.5	
-10	101	10.1	
-5	235	23.5	
0	302	30.2	
5	211	21.1	34.0
10	98	9.8	12.9
15	27	2.7	3.1
20	4	0.4	0.4

The table above indicates the probability of getting a difference the greater than the observed difference (6.5) is about 30%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in the density of *Tegula montereyi* between spring and fall.

Topside *Tegula montereyi* – location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

Resampling Stats Output

North mean = 11.31

South mean = 8.09

Difference = 3.22

Bin Center	Freq	%	Cum %
-16	1	0.1	
-14	1	0.1	
-12	2	0.2	
-10	19	1.9	
-8	45	4.5	
-6	76	7.6	
-4	119	11.9	
-2	152	15.2	
0	166	16.6	
2	164	16.4	41.9
4	109	10.9	25.5
6	68	6.8	14.6
8	44	4.4	7.8
10	24	2.4	3.4
12	4	0.4	1.0
14	1	0.1	0.6
16	3	0.3	0.5
18	2	0.2	0.2

The table above indicates the probability of getting the observed difference (3.2) is about 14%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the density of *Tegula montereyi* between the north end and the south end of the channel.

Topside *Lithopoma gibberosum* - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Resampling Stats Output

Spring mean = 5.766

Fall mean = 13.797

Difference = -8.031

Bin Center	Freq	%	Cum %
-14	2	0.2	0.2
-12	4	0.4	0.6
-10	9	0.9	1.5
-8	37	3.7	5.2
-6	55	5.5	
-4	137	13.7	
-2	165	16.5	
0	180	18.0	
2	198	19.8	
4	114	11.4	
6	54	5.4	
8	32	3.2	
10	8	0.8	
12	3	0.3	
14	1	0.1	
16	1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (-8.03) is about 5%. This is equal to α (5%), so reject Ho. The density of *L. gibberosum* is no significantly higher in the fall than in the spring.

Topside *Lithopoma gibberosum* – size

H₀: $\mu_{\text{small}} = \mu_{\text{large}}$

H_a: $\mu_{\text{small}} \neq \mu_{\text{large}}$

Small mean = 15.227

Large mean = 4.603

Difference = 10.624

Resampling Stats Output

Bin Center	Freq	%	Cum %
-14	1	0.1	
-12	2	0.2	
-10	12	1.2	
-8	40	4.0	
-6	67	6.7	
-4	139	13.9	
-2	162	16.2	
0	192	19.2	
2	160	16.0	
4	105	10.5	
6	63	6.3	
8	33	3.3	5.7
10	20	2.0	2.4
12	2	0.2	0.4
16	2	0.2	0.2

The table above indicates the probability of getting a difference the less than the observed difference (10.6) is about 3.4%. This is less than α (5%), so reject H₀. The density of *L. gibberosum* is no significantly higher on small boulders than in on large boulders.

Topside *Lithopoma gibberosum* – location

H₀: $\mu_{\text{north}} = \mu_{\text{south}}$

H_a: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 8.07

South mean = 5.72

Difference = 2.35

Resampling Stats Output

Bin Center	Freq	%	Cum %
-12	1	0.1	0.1
-10	4	0.4	0.5
-8	27	2.7	3.2
-6	70	7.0	10.2
-4	113	11.3	21.5
-2	189	18.9	40.4
0	207	20.7	61.1
2	167	16.7	77.8
4	119	11.9	89.7
6	56	5.6	95.3
8	27	2.7	98.0
10	14	1.4	99.4
12	5	0.5	99.9
14	1	0.1	100

The table above indicates the probability of getting the observed difference (2.3) is about 16%. This is greater than α (5%), so do not reject H₀. There is no significant difference in the density of *L. gibberosum* between the north end and the south end of the channel.

Topside *Pagurus* sp. - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 4.0897

Fall mean = 7.6839

Difference = -3.5942

Resampling Stats Output

Bin Center	Freq	%	Cum %
-10	2	0.2	0.2
-8	10	1.0	1.2
-6	35	3.5	4.7
-4	105	10.5	15.2
-2	204	20.4	35.6
0	254	25.4	
2	226	22.6	
4	116	11.6	
6	36	3.6	
8	11	1.1	
12	1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (-3.6) is about 19%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in the density of topside *Pagurus* sp. between spring and fall.

Topside *Pagurus* sp. - location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 5.40

South mean = 3.90

Difference = 1.50

Resampling Stats Output

Bin Center	Freq	%	Cum %
-7	4	0.4	0.4
-6	7	0.7	1.1
-5	23	2.3	3.4
-4	45	4.5	7.9
-3	71	7.1	15.0
-2	117	11.7	26.7
-1	149	14.9	41.6
0	172	17.2	58.8
1	135	13.5	72.3
2	119	11.9	84.2
3	77	7.7	91.9
4	42	4.2	96.1
5	18	1.8	97.9
6	14	1.4	99.3
7	5	0.5	99.8
8	1	0.1	99.9
9	1	0.1	100

The table above indicates the probability of getting the observed difference (1.5) is about 13%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the density of *Pagurus* sp. between the north end and the south end of the channel.

Underside *Stenoplax fallax* - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 35.233

Fall mean = 19.547

Difference = 15.687

Bin Center	Freq	%	Cum %
-25	5	0.5	
-20	13	1.3	
-15	39	3.9	
-10	124	12.4	
-5	205	20.5	
0	232	23.2	
5	211	21.1	
10	115	11.5	
15	43	4.3	5.6
20	10	1.0	1.3
25	3	0.3	0.3

The table above indicates the probability of getting a difference greater than the observed difference (15.7) is about 4.7%. This is less than α (5%), so reject Ho. Spring boulders had significantly higher density of *Stenoplax fallax* than fall boulders.

Underside *Stenoplax fallax* – size

Ho: $\mu_{\text{small}} = \mu_{\text{large}}$

Ha: $\mu_{\text{small}} \neq \mu_{\text{large}}$

Small mean = 23.648

Large mean = 30.425

Difference = -6.777

Bin Center	Freq	%	Cum %
-30	1	0.1	0.1
-25	5	0.5	0.6
-20	19	1.9	2.5
-15	78	7.8	10.3
-10	133	13.3	44.3
-5	207	20.7	72.9
0	286	28.6	
5	150	15.0	
10	88	8.8	
15	25	2.5	
20	1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (-6.7) is about 37%. This is greater than α (5%), so I do not reject Ho. There is **no significant difference** in the density of *Stenoplax fallax* between small and large boulders.

Underside *Stenoplax fallax* – location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 22.12

South mean = 19.19

Difference = 4.92

Bin Center	Freq	%	Cum %
-20	5	0.5	0.5
-15	29	2.9	3.4
-10	103	10.3	13.7
-5	217	21.7	35.4
0	269	26.9	62.3
5	229	22.9	85.2
10	94	9.4	94.6
15	39	3.9	98.5
20	12	1.2	99.7
25	3	0.3	100

The table above indicates the probability of getting the observed difference (4.9) is about 22%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the density of *Stenoplax fallax* between the north end and the south end of the channel.

Underside *Ophiopteris papillosa* - season

Ho: $\mu_{\text{spring}} = \mu_{\text{fall}}$

Ha: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

SPMEAN = 14.921

FMEAN = 19.955

DIFFERENCE = -5.0341

Bin Center	Freq	%	Cum %
-20	3	0.3	0.3
-15	35	3.5	3.8
-10	109	10.9	14.7
-5	251	25.1	39.8
0	268	26.8	
5	215	21.5	
10	93	9.3	
15	21	2.1	
20	4	0.4	
25	1	0.1

The table above indicates the probability of getting a difference the less than the observed difference (-5.03) is about 40%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in percent cover of *O. papillosa* between spring and fall.

Underside *Ophiopteris papillosa* – location

H₀: $\mu_{\text{north}} = \mu_{\text{south}}$

H_a: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 4.88

South mean = 15.66

Difference = -10.77

Bin Center	Freq	%	Cum %
-18	1	0.1	0.1
-16	2	0.2	0.3
-14	7	0.7	1.0
-12	6	0.6	1.6
-10	25	2.5	4.1
-8	49	4.9	9.0
-6	87	8.7	17.7
-4	103	10.3	28.0
-2	138	13.8	41.8
0	154	15.4	57.2
2	152	15.2	72.4
4	112	11.2	83.6
6	82	8.2	91.8
8	42	4.2	96.0
10	23	2.3	98.3
12	9	0.9	99.2
14	4	0.4	99.6
16	4	0.4	100

The table above indicates the probability of getting less than the observed difference (-10.8) is about 4%. This is less than α (5%), so reject H₀. There is a significant difference in the density of *Ophiopteris papillosa* between the north end and the south end of the channel.

Underside *Pagurus* sp. - season

H₀: $\mu_{\text{spring}} = \mu_{\text{fall}}$

H_a: $\mu_{\text{spring}} \neq \mu_{\text{fall}}$

Spring mean = 17.096

Fall mean = 5.740

Difference = 11.356

Bin Center	Freq	%	Cum %
-25	1	0.1	
-20	3	0.3	
-15	16	1.6	
-10	77	7.7	
-5	237	23.7	
0	335	33.5	
5	239	23.9	
10	76	7.6	9.2
15	15	1.5	1.6
20	1	0.1	0.1

The table above indicates the probability of getting a difference the greater than the observed difference (11.4) is about 8%. This is greater than α (5%), so I do not reject H₀. There is no significant difference in the density of underside *Pagurus* sp. between spring and fall.

Underside *Pagurus* sp. - size

Ho: $\mu_{\text{small}} = \mu_{\text{large}}$

Ha: $\mu_{\text{small}} \neq \mu_{\text{large}}$

Small mean = 7.643

Large mean = 14.981

Difference = -7.338

Bin Center	Freq	%	Cum %
-18	1	0.1	0.1
-16	4	0.4	0.5
-14	8	0.8	1.3
-12	6	0.6	1.9
-10	25	2.5	4.4
-8	37	3.7	8.1
-6	75	7.5	15.6
-4	119	11.9	
-2	136	13.6	
0	165	16.5	
2	143	14.3	
4	110	11.0	
6	61	6.1	
8	40	4.0	
10	32	3.2	
12	22	2.2	
14	10	1.0	
16	4	0.4	
18	2	0.2

The table above indicates the probability of getting a difference the less than the observed difference (-7.3) is about 10.7%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in the density of *Pagurus* sp. between small and large boulders.

Underside *Pagurus* sp. - location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

North mean = 5.69

South mean = 7.47

Difference = -1.78

Bin Center	Freq	%	Cum %
-10	4	0.4	0.4
-8	12	1.2	1.6
-6	59	5.9	7.5
-4	110	11.0	18.5
-2	200	20.0	38.5
0	241	24.1	62.6
2	186	18.6	81.2
4	112	11.2	92.4
6	53	5.3	97.7
8	19	1.9	99.6
10	4	0.4	100

The table above indicates the probability of getting the observed difference (-1.8) is about 20%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the density of *Pagurus* sp. between the north end and the south end of the channel.

Underside *Ophiothrix spiculata* - season

Ho: $\mu_{\text{small}} = \mu_{\text{large}}$

Small mean = 9.670

Ha: $\mu_{\text{small}} \neq \mu_{\text{large}}$

Large mean = 2.616

Resampling Stats Output

Difference = 7.054

Bin Center	Freq	%	Cum %
-20	1	0.1	
-14	1	0.1	
-12	4	0.4	
-10	20	2.0	
-8	28	2.8	
-6	67	6.7	
-4	137	13.7	
-2	149	14.9	
0	194	19.4	
2	150	15.0	
4	112	11.2	
6	68	6.8	14.7
8	43	4.3	7.9
10	18	1.8	3.6
12	4	0.4	0.8
14	3	0.3	0.4
16	1	0.1	0.1

The table above indicates the probability of getting a difference the greater than the observed difference (7.1) is about 11%. This is greater than α (5%), so I do not reject Ho. There is no significant difference in the density of *O. spiculata* between small and large boulders.

Underside *Ophiothrix spiculata* - location

Ho: $\mu_{\text{north}} = \mu_{\text{south}}$

North mean = 1.58

Ha: $\mu_{\text{north}} \neq \mu_{\text{south}}$

South mean = 5.87

Resampling Stats Output

Difference = -4.31

Bin Center	Freq	%	Cum %
-10	1	0.1	0.1
-9	2	0.2	0.3
-8	3	0.3	0.6
-7	8	0.8	1.4
-6	18	1.8	3.2
-5	26	2.6	5.8
-4	59	5.9	11.7
-3	77	7.7	19.4
-2	124	12.4	21.8
-1	145	14.5	46.3
0	132	13.2	59.5
1	128	12.8	72.3
2	103	10.3	82.6
3	69	6.9	89.5
4	47	4.7	94.2
5	28	2.8	87.0
6	16	1.6	98.6
7	8	0.8	99.4
8	1	0.1	99.5
9	4	0.4	99.9
10	1	0.1	100

The table above indicates the probability of getting less than the observed difference (-4.3) is about 9.9%. This is greater than α (5%), so do not reject Ho. There is no significant difference in the density of *Ophiothrix spiculata* between the north end and the south end of the channel.

APPENDIX D - PCA Results

APPENDIX D.1 - Topside PCA Results

PCA	1	2	3	4	5	6
Eigenvalue	2.293	1.561	1.395	1.298	1.203	1.045
Proportion	17.6	12.0	10.7	10.0	9.3	8.04
Cum. Prop.	17.6	29.6	40.4	50.4	59.6	67.7

PCA	Eigenvectors					
	1	2	3	4	5	6
Rock	-.161	-.208	-.190	-.481	-.013	.212
Encr. coralline	-.373	-.076	-.180	.134	.603	-.281
Bossiella	-.402	.086	.064	.342	-.454	.062
Calliarthron	.564	-.173	.139	-.010	.122	-.001
Sponge	-.089	.285	.331	-.572	-.019	.144
Laurencia	.326	-.448	-.096	.063	-.231	-.313
Plocamium	.350	.311	-.278	.019	-.269	.273
Pterygophora	-.0144	-.156	.234	.332	.005	.400
Lithopoma	.093	-.101	.478	.201	.246	.459
Tegula	.114	.396	-.360	.349	.050	.110
Asterina	.219	.145	.376	.162	.171	-.293
Tonicella	.121	.536	.025	-.053	.256	-.107
Pagurus	-.119	.187	.397	.014	-.362	-.446

PC1 – high scores characterized by low encrusting coralline, low bossiella, high calliarthron, high laurencia, high plocamium

Boulder Size

Analysis of Variance on PC1 scores

Dep Var: FACTOR(1) N: 60

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SIZES	14.055	2	7.027	3.304	0.044
Error	121.242	57	2.127

PC2 – high scores characterized by low laurenzia, high plocamium, high tegula, high tonicella

Season

PC2 scores

Group	N	Mean	SD
fall	31	-0.303	1.004
spring	29	0.324	1.414

t-test result

Separate Variance t = -1.967 df = 50.2 Prob = 0.055
 Difference in Means = -0.626 95.00% CI = -1.266 to 0.013

Pooled Variance t = -1.989 df = 58 Prob = 0.051
 Difference in Means = -0.626 95.00% CI = -1.257 to 0.004

APPENDIX D.2 - Underside PCA Results

PCA	1	2	3
Eigenvalue	2.431	1.453	1.419
Proportion	27.0	16.1	15.8
Cum. Proportion	27.0	43.1	58.9

PCA	Eigenvectors		
	1	2	3
Rock	-.577	-.063	.078
Encr. Coralline	.373	-.393	.171
Bossiella	.239	.305	.046
Sponge	.327	-.427	-.334
Ophiopteris	.319	-.007	-.230
Ophiothrix	.330	.389	.080
Stenoplax	-.200	.317	.500
Tegula	-.297	.388	-.458
pagurus	-.158	.404	-.576

PC1 – high scores characterized by low bare rock, high encrusting coralline, high sponge, high brittle stars, low tegula

Season:

Two-sample t test on PC1 scores grouped by season

Group	N	Mean	SD
fall	30	0.518	1.106
spring	27	-0.575	1.795

Pooled Variance $t=2.798$ $df=55$ Prob = **0.007**
 Difference in Means = 1.093 95.00% CI = 0.310 to 1.875

Location:

Regression analysis on PC1 scores grouped by location

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	33.641	1	33.641	18.048	0.000
Residual	102.520	55	1.864

APPENDIX E: Boulder Photographs - page 1 of 2

Aluminum caliper used to measure boulders

Weighted cord for RPQ sampling

Topside of boulder #F2

Underside of boulder #F2

Topside of boulder #F5

Underside of boulder #F5

Boulder Photographs – page 2 of 2

Topside of boulder #F8

Underside of boulder #F8

Topside of boulder #F18

Underside of boulder #F18

Topside of boulder #F20

Underside of boulder #F20

APPENDIX F – Large Invertebrates

Common Topside Mobile Animals

Lithopoma gibberosum

Pagurus sp.

Tegula sp.

Common Underside Mobile Animals

Ophiopteris papillosa

Ophiothrix spiculata

Stenoplax fallax

Pagurus sp.

Americhelidium micropleon

Americorophium stimpsoni

F. Amphilochoidea

Aoroides exilis female

Aoroides exilis male

Aoroides intermedia

Apolochus barnardi

Aruga holmesi

Chronopleustes oculatus

Coboldus hedgpethi

Desdimelita dentata

Elasmopus antennatus

Elasmopus bampo
scale marks are mm

Eusiroides mononucloides

Foxiphalus obtusidens

Amphipods – page 2 of 3

Gammaropsis marteia

Gammaropsis shoemakeri

Gammaropsis thompsoni

Gibberosus myersi

F. Isaeidae

Ischyrocerus sp.

F. Ischyroceridae

Lepidepcreum serraculum

Leucothoe alata

Maera sp.

Melita nitida

Melita sulca

Microjassa litoles
scale marks are mm

Neoischyrocerus claustris

Netamelita cortada

Pariphinotus escabrosus

Photis brevipes

Photis californica

Photis conchicola

Pleusirus secorrus

Pleusymptes subglaber

Podocerus cristatus

Pontogeneia inermis

Pontogeneia intermedia

Pontogeneia rostrata

Protohyle sp.

Rhepoxynius heterocuspoidatus

Thorlaksonius depressus
scale marks are mm

Tiron Biocellata

Ventojassa ventosa

APPENDIX G.2 - Isopods page 1 of 1

Ianiropsis montereyensis

Ianiropsis tridens

Idotea rufescens

Janiralata occidentalis

Joeropsis dubia

Leptochelia dubia

Paracerceis sculpta

Paronhura elegans

Pentidotea stenops

Uromunna ubiquita

scale marks are mm

APPENDIX G.3 - Other Crustaceans (Crabs, Shrimp, Copepods, Ostracod) page 1 of 1

Cancer anthoni

Cancer sp.

Loxorynchus crispatus

Pagurus hemphillia

Pagurus sp.

Petrolisthes manimaculis

F. Porcellanidae

Pugettia richii

Pugettia producta

Heptacarpus palpator

Spirontocaris prionota

Cyclapsis nubliah
scale marks are mm

Nebalia gerkenae

Podocopia ostracodes

APPENDIX G.4 - Annelids page 1 of 1

F. Cirratulidae

F. Glyceridae

F. Hesionidae

C. Oligochaeta

F. Onuphidae

F. Opheliidae

F. Orbiniidae

P. Nemertea

F. Nereidae

F. Paraonidae

F. Pillargiidae

F. Polynoidae

F. Sabellidae

F. Sphaerodoridae

F. Terebellidae

scale marks are mm

Alia carinata

Alia gausapata

Alia tuberosa

Alvania sp.

Amphissa undata

Amphissa versicolor

Baleis sp.

Barleeia sp.

Bittium sp.

Bittium munitum

Calliostoma ligatum

Cerithidea californica

Cystiscus jewettii
scale marks are mm

Epitonium tinctum

Fusinus luteopictus

Molluscs – page 2 of 2

Homalopoma luridum

Lacuna sp.

Littorina sp.

Margarites salmoneus

Odostomia sp.

Odostomia astricta

Diplodonta orbella

Glans carpenteri

Leptopecten latiauratus

Nutricula ovalis

Nutricula tantilla

Lepidozona mertensii

Crepidula adunca
scale marks are mm

Diodora aspera

Phidiana hiltoni

APPENIX G.6

Fish

Juvenile sculpin, most likely *Orthonopias triacis*

APPENDIX G.7

Echinoderms

Amphiodia psara

Amphiodia psara

Ophiothrix spiculata

Henricia leviuscula

Strongylocentrotus purpuratus

Pisaster sp.

scale marks are mm