Fall 2015

Motile Cryptofaunal Invertebrate Assemblages in Catalina Island's Rhodolith Beds in Relation to Physical Structure and Live Rhodoliths

Kristin Meagher Robinson
California State University, Monterey Bay

MOTILE CRYPTOFAUNAL INVERTEBRATE ASSEMBLAGES IN CATALINA ISLAND'S RHODOLITH BEDS IN RELATION TO PHYSICAL STRUCTURE AND LIVE RHODOLITHS

A Thesis

Presented to the

Faculty of the

Moss Landing Marine Laboratories

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Marine Science

---

by

Kristin Meagher Robinson

Fall 2015

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

Thesis of Kristin Meagher Robinson:

MOTILE CRYTOFAUNAL INVERTEBRATE ASSEMBLAGES IN CATALINA ISLAND'S RHODOLITH BEDS IN RELATION TO PHYSICAL STRUCTURE AND LIVE RHODOLITHS

Jonathan Geller, Chair
Moss Landing Marine Laboratories

Diana Steller
Moss Landing Marine Laboratories

Michael Graham
Moss Landing Marine Laboratories

Digitally signed by Dr. Kris Roney
Date: 2015.12.22 12:25:43 -08'00'

Kris Roney, Dean
Undergraduate and Graduate Studies

DEDICATION

This work is dedicated to the thousands of invertebrates that gave their lives for the advancement of science. Their sacrifice will be forever appreciated. To my Mom, who made me play outside as kid, and to my Dad, who taught me to ask questions.

ABSTRACT

Motile cryptofaunal invertebrate assemblages in Catalina Island's rhodolith beds in relation to physical structure and live rhodoliths.
by
Kristin Meagher Robinson
Master of Science in Marine Science
California State University Monterey Bay, 2015

Rhodoliths (Corallinaceae, Rhodophyta) are unattached, branching, calcareous red algae that are important foundation species in near shore marine systems. Aggregations, or beds, produce habitat that is a mixture of hard substrate and soft sediment supporting diverse assemblages of both crypto- and macrofauna. At Catalina Island, CA (33º44'55"N, 118º50'22"W), beds of relatively small rhodoliths were recently documented within several bays and coves. To better understand the associated community, this study describes the cryptofaunal invertebrate assemblages associated with live rhodolith (LR), dead rhodolith (DR) and sand (S) habitats within three sites (Cherry Cove, Isthmus Harbor, Avalon Harbor). Motile invertebrates (> 0.5 mm) were removed from sediment cores, identified to lowest certain taxonomic level and enumerated. Percent dry weight of eight size classes of sediment and percent dry weight of live rhodoliths were calculated. All three habitats had different sediment compositions with LR and DR habitats being more similar to each other than to S. Of the 184 morphotypes found across all habitats and sites, 142 were within LR, 109 within DR and 91 within S. LR hosted greater mean abundance of invertebrates (479.4 ± 42.0 ind./core) and greater mean taxonomic richness (43.3 ± 2.3 taxa/core) than either DR (226.5 ± 34.0 ind./core, 26.8 ± 1.2 taxa/core) or S (152.7 ± 17.3 ind./core, 24.3 ± 1.5 taxa/core) across all sites. Invertebrate community composition differed by habitat with LR and DR supporting slightly different communities that more strongly differed from S. Community composition differed significantly by site within S (ANOSIM, $R = 0.968$, $p < 0.001$) and weakly within the LR ($R = 0.702$, $p < 0.001$) and DR ($R = 0.534$, $p < 0.001$). Live rhodolith habitat was dominated by the gastropod *Amphithalamus* sp. (28.0%), the tanaid *Zeuxo* sp. (14.9%), an aorid amphipod (8.5%), and two species of ostracods (8.4% and 6.5%), while sand was dominated by the syllid *Exogon* sp. (40.1%) and other polychaete worms. Nematodes (27.6%) and oligochaetes (18.6%) were most abundant within the DR habitat. Abundance of intact rhodoliths (live + dead, > 4750 μm) in the substrate explained more variation in invertebrate abundance and taxonomic diversity than percent dry weight of live rhodolith material (live only, > 500 μm) suggesting that physical structure provided by intact rhodoliths has an influence on the associated invertebrate assemblages. This study demonstrates that despite their small size (< 2 cm) the rhodolith beds at Catalina Island support an abundant and diverse invertebrate community. Further research will help identify the mechanisms supporting the observed rhodolith associated invertebrate diversity identified in this study.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

PAGE

LIST OF FIGURES

PAGE

ACKNOWLEDGEMENTS

It definitely takes a village to write a thesis. This work would not be possible without the help of so many people. Thank you to my committee members for all your valuable feedback and support. Dr. Jonathan Geller, for never giving up on me, even after I sold my soul and started leading whale watching trips. Dr. Diana Steller, for exposing me to the mysterious world of rhodoliths and inducting me into the BCSES. Dr. Michael Graham, for reminding me that my sample size is not that big.

A special thanks to my Catalina partner in crime, Scott Gabara, for all those shared sampling trips and brainstorming sessions. For all those who helped in the field: Scott Gabara, Will Fennie, Sarah Jeffries, Diana Steller, Paul Tompkins, Michael Fox, Michelle Marraffini, Kelley & Dan van Hees, Alex Olson, and Everett Robinson. In exchange for beautiful diving conditions and great meals, everyone gave their all, endured frantic team leaders, multiple eighty minute dives, and late night sorting sessions.

Without my UROC intern, Imani Thomas, I would still be sitting in the wet classroom counting invertebrates. Thank you for all your help in sorting, counting, and keeping my spirits up during so many days of microscope work. Also, thank you to everyone who gave up an hour of their time to help sort and count: Sarah Jeffries, Marilyn Cruikshank, Kenji Soto, Gabi Navas, Alan Wood, Catherine Drake, Jennifer Keliher-Venegas, Jinchen "Martin" Guo, Sara Worden, and Michelle Marraffini. And a special thank you to Dr. Ivano Aiello and Dr. Scott Hamilton for answering my random geology and MDS questions.

I would like to acknowledge my funding sources: MLML Wave scholarships and the COAST travel grant so I could share my findings with the international rhodolith community. Dr. Geller and Dr. Simona Bartl, who hired me to work on their grants, and especially Richard Ternullo of Monterey Bay Boat Charters and Nancy Black of Monterey Bay Whale Watch for giving an invert girl a chance to brainwash a bunch a mammal lovers.

And finally, an emphatic thank you to the Invertebrate Lab and my friends for proofreading my thesis over and over again, while helping to keep me sane. My family,

especially my little sister, for all their encouragement and support. And to my husband, Everett Robinson, for making sure I was well fed.

INTRODUCTION

Physical structure of the marine environment can influence associated communities (e.g. soft-sediment versus rocky reef) (Gray 1974, Bell & McCoy 1991, Thrush *et al.* 2003, Anderson 2008). These structures influence biological (e.g. propagule retention) and environmental processes (e.g. water motion), and competitive interactions among species, which all influence the associated community (reviewed by Bertness *et al.* 2014). This is exemplified in soft-sediment habitats where species composition has a strong relationship with sediment size (Gray 1974, Thrush *et al.* 2003, Anderson 2008). Muddy sediments (particles < 0.05 mm diameter) generally support deposit feeders while sandy sediments (particles up to 1.0 mm in diameter) contain suspension feeders (Sanders 1958, McCall & Tevesz 1982, Byers & Grabowski 2014). Physical factors, such as sediment grain size, are not the only source of structure in a habitat, as the organisms themselves can provide structure and modify the physical parameters (Jones *et al.* 1994, Jones *et al*. 1997).

Habitat modifiers can transform a landscape from two to three dimensions thereby increasing biotic and structural complexity, promoting diversity (Rhoads & Young 1971, Jones *et al.* 1994, Bruno *et al.* 2003, Altieri & van de Koppel 2014). Three dimensionality can mitigate environmental stresses (Levine *et al.* 1999), provide refuge from predation (Kamenos *et al.* 2004b), increase food supply (Bruno & Bertness 2001), and provide retention of propagules and sediment (Bruno & Kennedy 2000). Some habitat modifiers are the most conspicuous organisms in a system, and they are considered foundation species when their effects are disproportionate to their biomass (*sensu* Dayton 1972).

Kelps, corals, and sea grasses are well-studied foundation species that serve important roles in creating three-dimensional habitats with increased functional diversity (McRoy & Helferrich 1977, Connell 1978, Foster & Schiel 1985). Comparisons of intact kelp forests to overly grazed areas (urchin barrens) show both higher abundances of associated species and greater species diversity within the kelp (Graham 2004). Andrews (1945) found that most of the animals within kelp holdfasts were larvae or juveniles of animals that inhabit kelp bed as adults, suggesting holdfasts might act as nursery grounds. Coral reefs increase propagule retention by altering water flow and providing chemical cues to larval recruits (Koehl *et al.* 2001, Reidenbach *et al.* 2009). Sea grass beds decrease mean water flow, resulting in seed retention and sediment stabilization (Bruno 2000). The collective literature is still small compared to kelps and corals, but aggregations of unattached calcified red algae (rhodolith beds) have been shown to support higher abundance and diversity of associated species (Steller *et al.* 2003), provide settlement cues to larvae (Steller and Caceres-Martinez 2009), and act as nursery habitat (Kamenos *et al.* 2004c); all features of a foundation species (Altieri & van de Koppel 2014).

Rhodoliths (Corallinaceae, Rhodophyta) are unattached, branching, calcareous red algae that are important foundation species in nearshore systems (Foster 2001, Steller *et al.* 2003, Nelson 2009). Rhodoliths can form massive aggregations (beds), found worldwide in tropical, temperate, and polar waters (Foster 2001), with new beds still being described in the northeastern Pacific (Konar *et al.* 2006, Parnell *et al*. 2006, Tompkins 2011). Like other coralline algae, rhodoliths have extracellular deposition of calcium carbonate, but do not require attachment to hard substrate (Nelson 2009). Most

rhodoliths have very slow growth rates only about 1-5 mm/yr. (Littler *et al.* 1991, Tompkins 2011). Beds generally form over what would otherwise be sandy habitat, and create a complex, three-dimensional structure (Foster 2001; Steller & Foster 1995).

On a geographic scale rhodolith beds are not uniform in size, shape or sediment composition (Keegan 1974, Bosence 1979, Steller & Foster 1995, Neill *et al.* 2015). Rhodoliths are fragile and prone to fragmentation (Marrack 1999, Hall-Spencer & Moore 2000, Kamenos *et al.* 2003, Nelsen 2009). In most cases, beds are a mosaic of large intact rhodoliths, rhodolith fragments, and fine calcium carbonate sand (Tanadjaja 2010). Some beds grow over areas of muddy sediment (Keegan 1974, Neill *et al.* 2015). Beds can be mixtures of multiple rhodolith species, with each species having different growth forms (foliose, fruticose; Riosmena-Rodriguez *et al.* 1999, Hinojosa-Arango & Riosmena-Rodriguez 2004, Amado-Filho *et al.* 2007, Villas-Boas *et al.* 2013). Differences in associated assemblages of both flora and fauna seem to coincide with differences in sediment characteristics (Keegan 1974, Bosence 1979, De Grave 1999) and rhodolith species (Hinojosa-Arango & Riosmena-Rodriguez 2004). Within a bed, larger rhodoliths support a high diversity and abundance of invertebrates than small fragmented ones (Steller *et al.* 2003, Foster *et al*. 2007, Teichert 2014).

Rhodoliths provide hard substrate for both algal epibionts and small (0.5 – 5.0 mm) cryptic invertebrates referred to as cryptofauna (Keegan 1974, Bosence 1979, Steller *et al*. 2003, Foster *et al*. 2007). These cryptofaunal organisms are found at lower abundances or absent from adjacent sand habitat lacking rhodoliths (Steller *et al.* 2003). It is theorized that the branching nature of rhodoliths creates microhabitats with decreased water flow, and retention of detritus and propagules (Keegan 1974, Bosence

1979, Steller *et al.* 2003; Foster *et al.* 2007; Nelson 2009). Their hard structure offers protection from predation to many cryptofaunal and algal species (Kamenos *et al.* 2004b, Kamenos *et al*. 2006), as well as nursery habitat to commercially important scallops (Kamenos *et al*. 2004c*;* Steller & Caceres-Martinez 2009). Within the cryptofauna, a mixture of organisms that prefer gravel, sand or hard substrate can be found within a single sample (Foster 2001, Nelson 2009).

Worldwide, cryptofauna represent a large proportion of the total invertebrate species found within rhodolith beds. In Baja California, rhodolith beds support over 100 species of cryptofaunal invertebrates (Hinojosa-Arango & Riosmena-Rodriguez 2004, Foster *et al.* 2007) at an average density of 14.4 individuals per cm^3 (Steller *et al.* 2003). Dominant taxa within these beds are crustaceans, annelids, and cnidarians (Steller *et al.* 2003; Hinojosa-Arango & Riosmena-Rodriguez 2004; Foster *et al*. 2007). Beds in temperate European waters support a greater diversity ranging from 180 to 466 taxa of invertebrates identified, with polychaetes and crustaceans as the most dominant taxa (Barbera *et al.* 2003, Bordehore *et al.* 2003; Grall *et al.* 2006). Cryptofaunal communities in Brazilian beds (depending on season) were also dominated by polychaetes (63%) or amphipods (70%), while mollusks (both bivalves and gastropods) constituted only about 5% of the fauna (Figueiredo *et al.* 2007). In comparison, beds off Alaska, Canada and Norway are dominated by chitons (Mollusca; Konar *et al.* 2006, Gagnon *et al.* 2012, Teichert *et al.* 2014). Some of the species found on or within these beds were previously undescribed (Clark 2000) and could be rhodolith-obligates. Because of the potential for new species and the high variability in diversity and bed

characteristics, communities of new beds need to be described before more complex interactions can be investigated.

Despite the potential importance of rhodolith beds as a habitat, standardized methods for sampling the associated fauna do not exist. In Baja California Sur, rhodoliths can grow to a size greater than 10 cm in diameter (Steller and Foster 1995), which allows for the collection of a single rhodolith to investigate cryptofaunal abundance. Other beds, such as the Abrolhos bank, Brazil (Berlandi *et al.* 2012) and Catalina Island, USA (Tompkins 2011), are composed of smaller rhodoliths (2-4 cm diameter), making selection of a single rhodolith impractical for cryptofaunal counts, resulting in use of cores for sampling. Berlandi *et al.* (2012) compared polychaete diversity between two Brazilian beds that required different collection methods (coring and quadrats) because of the bed characteristics. This complicated interpretation of results because cores included sediment-dwelling polychaetes, which inflated results. Without standardize methods, meaningful comparisons between beds become challenging, if not impossible.

Rhodolith beds were recently documented around Catalina Island, part of the Channel Island archipelago off southern California (Parnell *et al.* 2006, Tompkins 2011). Seven rhodolith beds have been described off Catalina Island, all located within coves or harbors on the leeward side of the island (Tompkins 2011). Five of the beds (Big Fishermen's, Isthmus, Cherry, and 4th of July Cove) are located close together within five miles of the town of Two Harbors, while Avalon Harbor and Emerald Cove are located at the far ends of the island (Fig. 1). All beds appear to be dominated by a single rhodolith species, *Sporolithon australe* (*sensu* R. Riosmena-Rodriguez) that averages 20-

50% live cover throughout the beds (Tompkins 2011). The rhodoliths are relatively small, with the majority of the individuals being 5 – 15 mm in diameter (Tompkins 2011). Beneath the rhodolith cover is a mixture of sandy sediment composed of both calcium carbonate and silicate materials (Tompkins 2011, Gabara 2014). While investigating nutrient flow and food webs within the rhodolith beds, Gabara (2014) found an average of 20.9 infauna taxa (cryptofauna + infauna) per 6.5 cm diameter core; however he did not identify organisms down to species or relate diversity to rhodolith size and percent cover.

In order to address major gaps in knowledge of a common coastal California benthic habitat, the objectives of this study were to:

1.) Identify the motile species of cryptofaunal invertebrates making up the assemblages of Catalina Island rhodolith beds.

2.) Describe patterns of cryptofaunal invertebrate assemblages between different habitat types (live rhodolith cover, dead rhodolith cover and no rhodolith cover) and sites at Catalina Island.

3.) Determine if motile cryptofaunal invertebrate abundance and taxonomic richness correlates with amount of live rhodolith material or amount of intact rhodoliths.

METHODS

Study Sites:

All live rhodolith beds studied herein were located on the northeast coast of Catalina Island, CA (33^{o} 44’50”N, 118^{o} 50’22”W; Fig. 1). Estimates of bed size, depth and amount of rhodolith cover were made by Tompkins (2011) in 2009 (Appendix A). Catalina rhodolith beds were found within sheltered bays and consisted of areas of live

rhodolith cover, interspersed amongst patches of dead or fragmented rhodoliths and sand (Tompkins 2011). Within all beds, the layer of live rhodolith material varied in depth, but was generally less than 5 cm. Below the rhodolith layer was a mixture of fine and coarse sediments. Mooring chain arrays located within these beds along with bioturbation by fishes and invertebrates are possible sources of the crushed rhodolith sand (Tompkins 2011, pers. obs.). The beds sampled for this study were located in Avalon Harbor (7.8 - 21 m depth), Isthmus Harbor (4.3 - 6.1 m depth), and Cherry Cove (5.8 - 7.3 m depth). These sites were selected because they were the three largest beds and had similar bed and rhodolith characteristics except for depth and total bed size (Appendix A, Tompkins 2011).

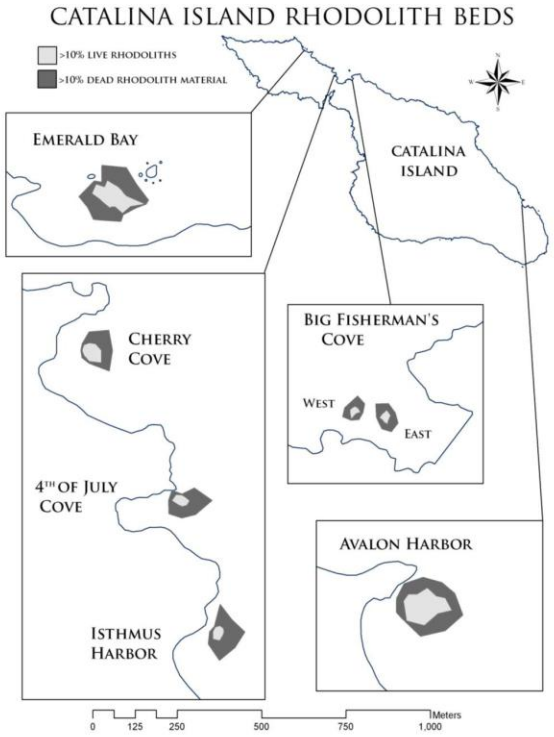

Figure 1. Seven rhodolith beds located around Catalina Island, southern California. Surveys conducted in 2009 documented beds within Emerald Bay, Cherry Cove, 4th of July Cove, Isthmus Harbor, Big Fishermen's Cove, and Avalon Harbor**.** Dark outside boundaries indicate >10% dead rhodolith cover while inner light boundaries indicate >10% live cover (reprinted with permission, Tompkins 2011).

Sample Collection:

Samples were collected on SCUBA from three different sites (Avalon Harbor, Isthmus Harbor, and Cherry Cove) during December 2013. Within each site, sampling was stratified between three sedimentary habitats distinguished by > 90% cover of live rhodolith (LR; rhodolith had pigmentation), > 90% cover of dead rhodolith (DR; rhodolith lacked pigmentation), or > 90% non-rhodolith sand (S; no observable rhodoliths/fragments). Cores of LR and DR were collected from within rhodolith beds, while S cores were collected from an adjacent non-carbonate sandy area at a similar depth. Six cores (5 cm in height and 7 cm in diameter) were haphazardly collected from each habitat type with at least 2 m between each core. Cores were transferred into plastic bags and sealed at depth.

All samples were transported back to Wrigley Marine Lab (Wrigley). Each sample was transferred to a glass jar and preserved by adding enough 37% formaldehyde to make a final concentration of 10% buffered formalin solution within each jar. Formalin did not remove pigmentation from rhodolith material, so rhodolith material that was alive at time of collection could be distinguished from dead rhodolith material based on the amount of visible pigmentation.

Processing of Samples:

Preserved samples were transported back to Moss Landing Marine Laboratories (MLML) and sat in formalin solution for 48 hours before processing. Samples were gently poured onto a 0.5 mm mesh screen and rinsed with fresh water. The resulting mixture of sediment and invertebrates greater than 0.5 mm were examined under a Leica dissecting microscope at 6.3x magnification; all motile invertebrates were removed and placed in 70% ethanol for further identification.

Motile invertebrate specimens were sorted into "morphotypes" based on shared visible morphological characteristics. Each morphotype was considered the equivalent of a "species" for statistical analysis. Individuals within each morphotype were enumerated with at least one individual selected as a voucher specimen and photographed for use in an informal identification guide. Each morphotype was identified to lowest taxonomic level for which the author was confident using invertebrate taxonomic keys by Carlton (2007) and Lissner & Blake (1998). Specimen identifications were refined and/or confirmed, when possible, by consulting museum collections at MLML and taxonomic experts (Amphipoda: A. Wood, Mollusca: J. Geller, Ostracoda: G. Hecht, Polychaeta: L. Harris, M. Marraffini, T. Phillips). Within the lowest taxonomic level reached, if multiple groups existed, as evidence by morphological characteristics, they were differentiated by numbers (e.g. gastropod 1, gastropod 2).

For each habitat type (LR, DR, S), any intact rhodoliths or rhodolith fragments that had ≥ 10% pigmentation were considered live rhodolith material and removed from other sediment. Dead rhodoliths (< 10% pigmentation) and dead rhodolith fragments were left mixed with other sediment such as shell fragments and clastic sediment. All sediment, including live rhodolith material, was sieved through a modified version of the Wentworth scale, resulting in eight size classes (Table 1; Wentworth 1922). After sieving, each fraction was dried at 60°C until all water evaporated and sediment remained at a constant weight. Each size class and live rhodolith fraction were weighed and compared based on percent weight of the total sample.

	Classification	
Sediment size fractions (μm)	Wentworth 1922	This study
> 4750	Pebble gravel	Intact rhodoliths
2000 – 4750	Granule gravel	
1000 – 2000	Very course sand	Rhodolith fragments
500 – 1000	Course sand	
250 – 500	Medium sand	
125 – 250	Fine sand	Sand
63 – 125	Very fine sand	
< 63	Silt	Silt

Table 1. Breakdown of sediment size classes and classification terms for analysis of sediment profiles. Modified from Wentworth 1922.

Statistical Analysis:

Only motile invertebrates were used for statistical analysis because encrusting sessile organisms were not found within the S group and are difficult to determine accurate abundance counts. As a result, this study potentially misestimates the degree of community differences. As noted above, each morphotype was treated as a species, which may result in an under-estimation of true species richness due to the potential for cryptic species or over-estimation in the case of intraspecific polymorphism. Abundance, taxonomic richness and percent dry weight of sediment were expressed as per core for statistical analysis.

Two-way analysis of variance (ANOVA) was used to compare the variables of mean invertebrate abundance, taxonomic richness, amount of intact rhodolith, and amount of live rhodolith material between habitats and across sites. Taxonomic richness and live material met test assumptions while total abundance and intact rhodoliths failed the assumption of equal variance, even after transformation of the data. However the ANOVAs were considered robust because of equal sample size and the assumption of normality was met. To test for a correlation between intact rhodoliths and live material

with invertebrate mean abundance and taxonomic richness, a simple linear regression was used. The data were tested to ensure all assumptions were met. All univariate calculations were done using software package SPSS 22 (IBM® SPSS® Statistics, 2013)

To compare composition of sediment profiles and associated motile invertebrates between habitats and sites, multi-dimensional scaling ordinations (MDS) were calculated. For sediment, Euclidian distance matrices were calculated to compare multivariate differences of the percent dry weight of each sediment size class per core. Since sediment was already standardized to percent dry weight, no transformation of the data was done before calculating the resemblance matrix. Bray-Curtis similarity matrices were used for invertebrate assemblage composition utilizing the abundance counts for all morphotypes after the data were square root transformed. A two-way analysis of similarity (ANOSIM) was used to test for differences in sediment size and invertebrate assemblages between sites and habitats. The similarity percentage analysis (SIMPER) was calculated to determine the taxa contributing the most to similarities within habitats and sites and the dissimilarities among different habitats and sites. All calculations were done using software package PRIMER-E (Plymouth Routines in Multivariate Ecological Research, 6.0)

RESULTS

Sediment Size by Habitat and Site:

Two-way ANOSIM test detected significant differences in sediment composition between habitat types across all sites ($R= 0.805$, $p < 0.001$) and between sites across all habitat types ($R= 0.517$, $p < 0.001$). Pairwise comparison of R values for both habitat type and site, indicated habitat type was a stronger contributor to the observed differences

between cores than site (Table 2). LR and DR habitats clustered more closely together in MDS plots than either clustered to S habitat, regardless of site (Fig. 2). However, some DR and LR cores were intermixed in MDS plots (Fig. 2), showing that the two "habitats" were not discrete with respect to sediment size.

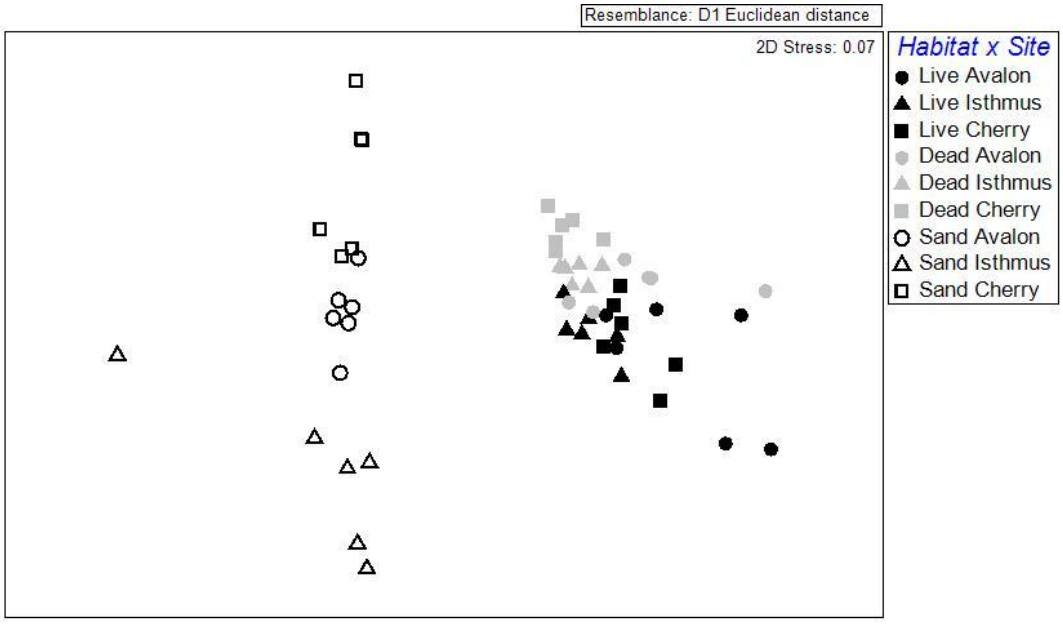

Figure 2. Comparison based on sediment size classes. Two-dimensional multidimensional scaling (MDS) plot comparing percent dry weight of the eight sediment size classes (> 4750 µm – < 63µm) from the fifty-four cores collected from Catalina Island, CA. Habitat type shown by color: Live Rhodolith (black), Dead Rhodolith (gray), and Sand (white). Sites indicated by shape: Avalon Harbor (circles), Isthmus Harbor (triangles), Cherry Cove (squares).

Table 2. Two-way ANOSIM values for sediment characteristics. Analysis based on percent dry weight of eight sediment size classes (> 4750 µm – < 63µm) with pairwise comparison by site and habitat type.

Sites	R	p
Avalon x Isthmus	0.517	0.001
Avalon x Cherry	0.557	0.001
Isthmus x Cherry	0.501	0.001
Global	0.517	0.001

Habitat	R	p
LR x DR	0.616	0.001
LR x S	0.947	0.001
DR x S	0.948	0.001
Global	0.805	0.001

To determine the sediment sizes driving the differences between the habitat types, sites were combined. All three habitat types had a different dominant sediment size class. S habitat was dominated by 125 - 250 µm size class (phi = 3), while the larger size classes (>1000 µm, phi < 0) dominated the rhodolith habitats (Fig. 3). The greatest difference between LR and DR sediment profiles was the amount of intact rhodoliths (> 4750 µm, Table 3).

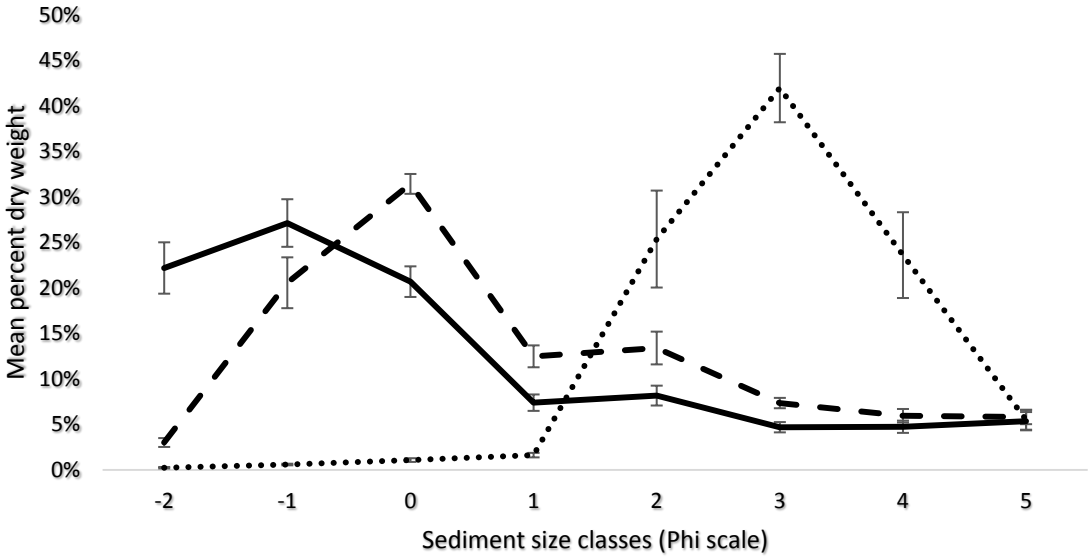

Figure 3. Sediment profiles by habitat type. Mean percent dry weight (± SE) of each sediment size class within each habitat type, all sites combined: Live Rhodolith (LR, solid line, n = 18), Dead Rhodolith (DR, dash line, n = 18), Sand (S, dotted line, n = 18). The sediment size classes were converted to the phi scale on the x-axis: -2 = > 4750 µm, 5 = < 63 µm.

Table 3. SIMPER pairwise comparison of dissimilarities between habitat types based on sediment size classes. Top number is average squared distance (dissimilarity) between compared habitat types followed by sediment size classes that contribute the most to the distance between the compared habitat types: Live Rhodolith (LR), Dead Rhodolith (DR), and Sand (S).

LR x DR		LR x S		DR x S	
0.10		**0.51**		**0.43**	
> 4750	49.18%	125 – 250	32.25%	125 – 250	33.70%
2000 - 4750	19.79%	2000 – 4750	16.06%	1000 – 2000	21.75%
1000 – 2000	17.67%	250 – 500	15.65%	63 – 125	15.68%
250 – 500	5.45%	63 – 125	13.70%	250 – 500	12.39%

No live rhodolith material was found within the S habitat type, but varying amounts of live rhodolith material (≥ 10% pigmentation) was found within LR and DR cores (Fig. 4). Between sites, there was no significant difference in percent live rhodolith material among LR habitat type but there was a significant difference among the DR (Fig.4; two-way ANOVA: Habitat $F_{1,30} = 41.268$, $p < 0.001$; Site $F_{2,30} = 7.245$, $p = 0.003$, Interaction $F_{2,30} = 1.755$, $p = 0.190$). *Post-hoc* analysis revealed that within DR habitat type, Avalon Harbor (18.8% live) had a significantly higher amount of live rhodolith material than the other sites (4.29% & 1.43% live), which was not significantly different from the LR habitat types (22.9% - 29.0% live). The interaction of site and percentage of live rhodolith material was not significant because in both habitat types, Avalon Harbor had the highest amount of live rhodolith material and Cherry Cove had the lowest amount.

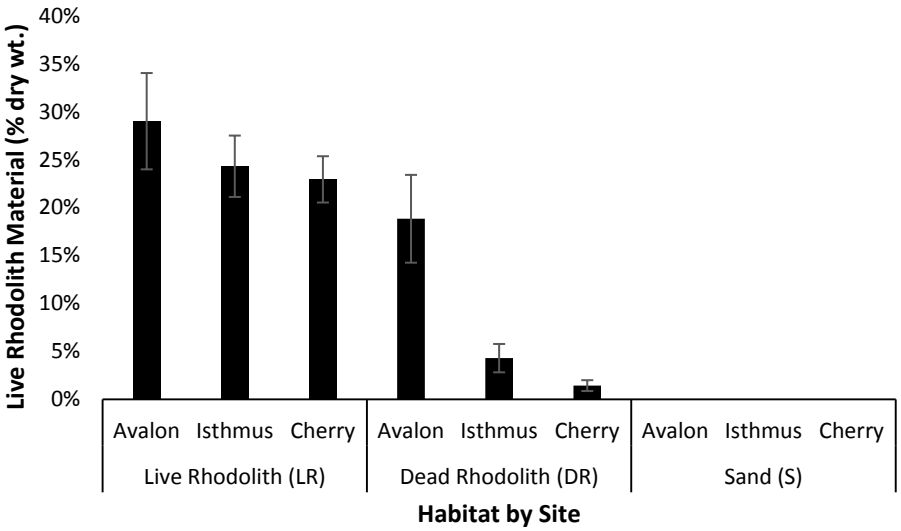

Figure 4. Mean percent dry weight (± SE) of live rhodolith material (≥ 10% pigmentation) by habitat type and site (n = 6).

Invertebrate Abundance and Taxonomic Richness:

Fifty-four cores from three habitat types from three sites at Catalina Island produced a total of 15,515 motile invertebrates that constituted 184 morphotypes within nine phyla (Appendix B). With all sites combined, there were 142 taxa located within the LR habitat, 109 taxa within the DR habitat, and 91 taxa within S. Overall the most abundant groups were crustaceans (39.3%), polychaetes (21.5%), and mollusks (17.2%), with crustaceans and polychaetes being the most specious groups with 48 and 63 morphotypes, respectively. Total abundance of cryptofaunal invertebrates varied between both habitats and sites (Table 4).

Table 4. Mean abundance of motile cryptofaunal invertebrates scaled to per m^2 densities by site and habitat type.

	Avalon Harbor	Isthmus Harbor	Cherry Cove	Average
Live Rhodolith	93,599	107,848	172,340	124,596
Dead Rhodolith	40,757	60,854	74,974	58,861
Sand (S)	57,259	18,278	43,572	39,703

When averaged across all sites, LR (479.4 ± 42.0 ind./core) had more than double the number of motile cryptofaunal invertebrates as DR (226.5 ± 34.1 ind./core) and more than three times the amount as S (152.8 ±17.4 ind./core). A two-way ANOVA confirmed that both site and habitat type were significant and revealed a significant interaction between site and habitat (Table 5). The significant interaction was driven by disproportionately higher abundance within S (220.3 ± 13.3 ind./core) relative to DR (156.8 ± 20.3 ind./core) at Avalon Harbor, while the other two sites had the lowest total abundances within the S habitat type (Fig. 5).

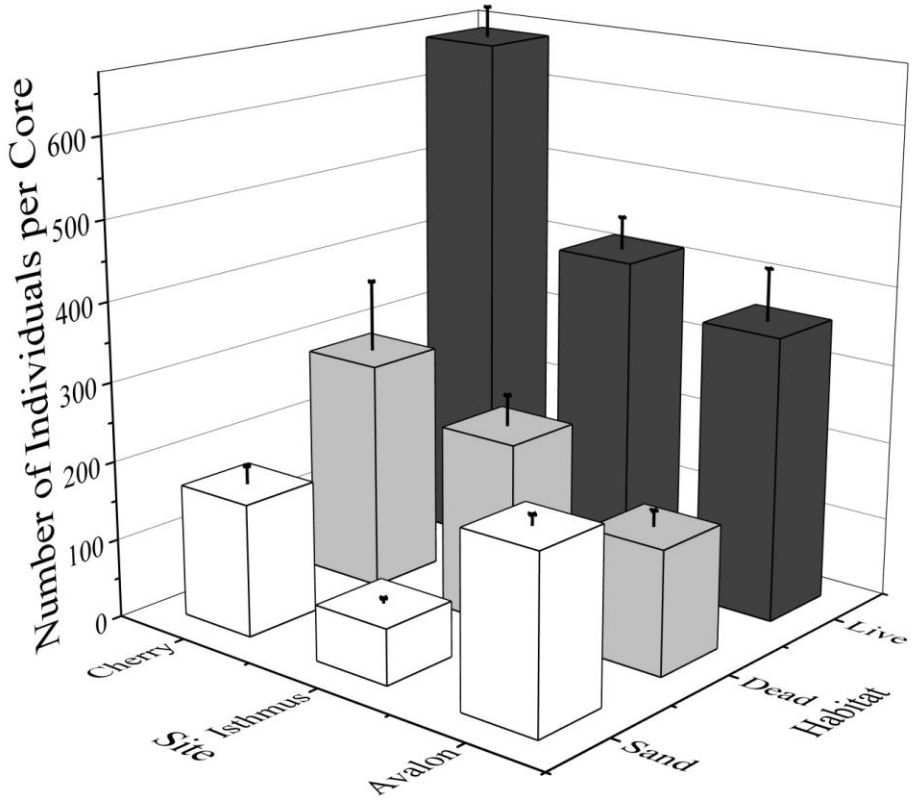

Figure 5. Mean motile cryptofaunal invertebrate abundance (± SE) per core relative to habitat and site. Arranged by habitat type: Live Rhodolith (Live), Dead Rhodolith (Dead), and Sand (Sand) and site: Avalon Harbor (Avalon), Isthmus Harbor (Isthmus), and Cherry Cove (Cherry), n = 6.

Table 5. Two-way ANOVA for total invertebrate abundance by site and habitat type with pairwise Tukey *post hoc* output.

Source	df	MS	F	p
Site	2	102036.241	8.309	0.001
Habitat	2	528380.907	43.029	< 0.001
Site*Habitat	4	57691.185	4.698	0.003
Error	45	12279.530		

Note. df = degrees of freedom, MS = Mean Square, alpha = 0.05

Habitat Type	p	Site	p
Live Rhodolith x Dead Rhodolith	< 0.0001	Avalon x Isthmus	0.986
Live Rhodolith x Sand	< 0.0001	Avalon x Cherry	0.003
Dead Rhodolith x Sand	0.125	Isthmus x Cherry	0.002

Note: alpha = 0.5

In general, taxonomic richness was almost double within LR habitat type (43.4 ± 2.3 taxa per core) than DR or S habitat type (26.9 ± 1.2 and 24.3 ± 1.3 taxa per core, respectively), when averaged across all sites. Two-way ANOVA revealed a statistically significant interaction ($p < 0.001$) between site ($p = 0.001$) and habitat type ($p < 0.001$), which were also significant factors. The significant interaction was driven by a higher taxonomic richness (54.5 ± 2.6 taxa/core) within LR from Cherry Cove compared to the LR from other sites (Isthmus Harbor = 38.3 ± 1.4 taxa/core, Avalon Harbor = 37.3 ± 3.2 taxa/core) and Isthmus Harbor had significantly lower taxonomic richness within its S (18.8 ± 1.5 taxa/core) than DR habitat type (28.0 ± 1.5 taxa/core; Fig. 6). There was no difference in taxonomic richness at the other two sites between DR (Avalon Harbor = 26.8 ± 2.4 taxa/core, Cherry Cove = 25.8 ± 2.6 taxa/core) and S (Avalon Harbor = 28.2 ± 1.6 taxa/core, Cherry Cove = 26.0 ± 1.9 taxa/core).

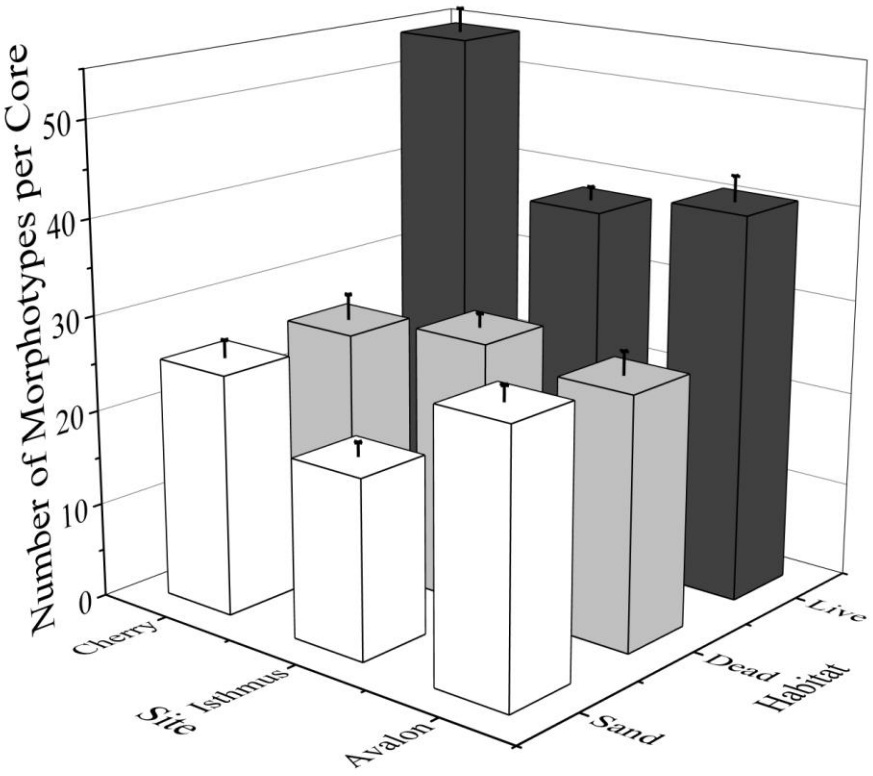

Figure 6. Mean taxonomic richness for motile cryptofaunal invertebrates (± SE) per core relative to habitat and site. Arranged by habitat type: Live Rhodolith (Live), Dead Rhodolith (Dead), and Sand (Sand) and site: Avalon Harbor (Avalon), Isthmus Harbor (Isthmus), and Cherry Cove (Cherry), n = 6.

Table 6. Two-way ANOVA for invertebrate taxonomic richness by site and habitat type with pairwise Tukey *post hoc* output.

Source	df	MS	F	p
Site	2	231.796	8.191	0.001
Habitat	2	1925.685	68.045	< 0.0001
Site*Habitat	4	237.741	8.401	< 0.0001
Error	45	28.300		

Note. df = degrees of freedom, MS = Mean Square, alpha = 0.05

Habitat Type	p
Live Rhodolith x Dead Rhodolith	< 0.0001
Live Rhodolith x Sand	< 0.0001
Dead Rhodolith x Sand	0.329

Site	p
Avalon x Isthmus	0.377
Avalon x Cherry	0.031
Isthmus x Cherry	0.001

Note: alpha = 0.05

Invertebrate Assemblages:

A two-way ANOSIM test indicated that there were significant differences between sites across all habitat types (R= 0.740, $p < 0.001$; Table 7A) and between habitat types across all sites (R= 0.945, $p < 0.001$; Table 7B). Pairwise comparisons of R values for site and habitat type indicate habitat type was a stronger contributor to observed differences between cores (Table 7). There were subtle differences in morphotype frequencies between individual cores, but overall the three habitat types clustered separately on a MDS plot with LR and DR being most similar (Fig. 7). Among S cores, each site was clustered, while LR and DR were not segregated by site (Fig. 7).

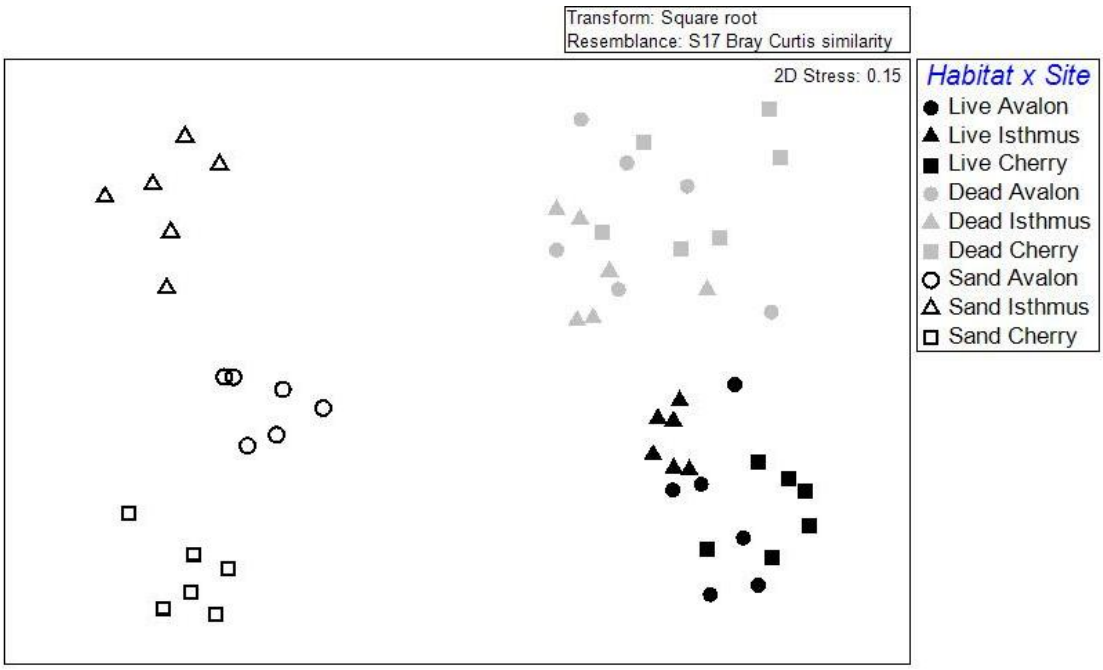

Figure 7. Comparison of cryptofaunal invertebrate assemblages based on the abundance of each morphotype. Two-dimensional multidimensional scaling plot of community composition based on total abundance of motile cryptofaunal invertebrates within 184 morphotypes from fifty-four cores collected from Catalina Island, CA. Habitat types: Live Rhodolith (black), Dead Rhodolith (gray), Sand (white). Sites: Avalon Harbor (circles), Isthmus Harbor (triangle), Cherry Cove (squares).

Table 7. Two-way ANOSIM pairwise comparisons based on community composition. A.) Sites: Avalon Harbor (Avalon), Isthmus Harbor (Isthmus) and Cherry Cove (Cherry) across all habitat types and B.) Habitat types: Live Rhodolith (LR), Dead rhodolith (DR) and Sand (S) across all sites.

A.)

Sites	R	p
Avalon x Isthmus	0.637	0.001
Avalon x Cherry	0.758	0.001
Isthmus x Cherry	0.876	0.001
Global	0.740	0.001

B.)

Habitat Type	R	p
LR x DR	0.888	0.001
LR x S	1.000	0.001
DR x S	0.988	0.001
Global	0.945	0.001

The more noticeable clustering of S cores by site compared to DR and LR, suggested a possible interaction between habitat type and site. To test this, one-way ANOSIM values were calculated for site within each habitat type. Within each habitat type, cores clustered by site (Table 8), but S had the highest R values (Table 8A), consistent with the separation by site seen in Figure 7 for S. For all three habitat types Cherry Cove and Isthmus Harbor had the greatest pairwise separation (Table 8).

Table 8. One-way ANOSIM values, testing the degree of separation between sites within a single habitat type: Live Rhodolith (LR), Dead Rhodolith (DR), and Sand (S).

A.)

S only	R	p
Avalon x Isthmus	0.989	0.002
Avalon x Cherry	0.996	0.002
Isthmus x Cherry	1.000	0.002
Global	0.968	0.001

B.)

DR only	R	p
Avalon x Isthmus	0.396	0.004
Avalon x Cherry	0.513	0.002
Isthmus x Cherry	0.717	0.002
Global	0.534	0.001

C.)

LR only	R	p
Avalon x Isthmus	0.504	0.002
Avalon x Cherry	0.765	0.002
Isthmus x Cherry	0.909	0.002
Global	0.702	0.001

Live rhodolith invertebrate assemblages were dominated by mollusks, crustaceans and polychaetes (Table 9). The gastropod *Amphithalamus sp.* was the most abundant invertebrate. It constituted over 20% of the invertebrate abundance per core and in some LR cores numbered over 300 individuals. This species was also found in DR cores but at lower abundances (3.5-11% abundance per core and averaging 12 individuals per core) and was absent from all S cores. Most of the other common taxa were located in all three habitat types but at varying abundances (Appendix B). The S habitat was dominated by the syllid polychaete *Exogon sp*. with average abundances constituting over 25% of each core (Table 9). This morphotype was also found in LR and DR at lower abundances.

Table 9. Morphotypes with the ten highest mean percent abundance (± SE) for each site within each habitat type. A = amphipod, B = bivalve, G = gastropod, I = isopod, O = ostracod, P = polychaete, T = tanaid

Live Rhodolith (LR)

Avalon		Isthmus		Cherry	
Amphithalamus sp., G	20.01% (4.04%)	*Amphithalamus* sp., G	20.65% (2.33%)	*Amphithalamus* sp., G	30.46% (5.32%)
Aoridae 1, A	10.96% (2.51%)	*Zeuxo* sp., T	13.66% (2.55%)	*Zeuxo* sp., T	18.34% (3.48%)
Zeuxo sp., T	9.80% (4.08%)	*Macrocypris* sp., O	10.61% (0.57%)	*Anatanis* sp. , T	7.47% (1.30%)
Macrocypris sp., O	9.76% (3.07%)	Aoridae 1, A	10.49% (2.18%)	Nematoda 1	5.24% (1.16%)
Neonesidea sp., O	6.22% (2.00%)	*Neonesidea* sp., O	8.83% (1.23%)	Aoridae 1, A	4.93% (1.48%)
Exogon sp., P	5.52% (0.91%)	Oligochaeta	5.88% (1.21%)	Spionidae 1, P	3.51% (1.05%)
Nematoda 1	4.25% (1.70%)	Phoxocephalidae 1, A	4.19% (3.01%)	*Neonesidea* sp., O	2.56% (0.50%)
Leptochelida sp. 1, T	2.80% (0.59%)	*Exogon* sp., P	3.11% (0.31%)	*Exogon* sp., P	2.50% (0.81%)
Oligochaeta	2.75% (1.10%)	Spionidae 1, P	3.04% (0.70%)	Oligochaeta	1.99% (0.59%)
Caprellidae 1, A	2.65% (0.38%)	Nematoda 1	3.00% (0.52%)	*Macrocypris* sp., O	1.54% (0.52%)

Dead Rhodolith (DR)

Avalon		Isthmus		Cherry	
Oligochaeta	15.28% (1.85%)	*Neonesidea* sp., O	23.31% (5.22%)	Nematoda 1	49.01% (9.92%)
Nematoda 1	13.86% (3.25%)	Nematoda 1	15.73% (3.75%)	*Exogon* sp., P	8.88% (3.07%)
Exogon sp., P	11.94% (1.37%)	Oligochaeta	15.12% (2.02%)	*Neonesidea* sp., O	8.16% (3.93%)
Neonesidea sp., O	11.72% (1.84%)	*Macrocypris* sp., O	9.06% (1.81%)	Oligochaeta	7.74% (1.53%)
Amphithalamus sp., G	9.79% (4.03%)	*Exogon* sp., P	6.09% (0.95%)	*Amphithalamus* sp., G	5.73% (1.80%)
Macrocypris sp., O	3.63% (1.50%)	*Amphithalamus* sp., G	4.45% (0.99%)	Polychaeta 19	2.36% (1.17%)
Spionidae 2, P	3.59% (2.44%)	Amphipoda 5	3.42% (1.30%)	Nematoda 2	1.93% (0.67%)
Scalibregmatidae, P	3.24% (2.95%)	Amphipoda 3	3.26% (1.94%)	Sipuncula 3	1.40% (0.62%)
Nematoda 4	2.29% (0.84%)	Spionidae 1, P	1.82% (0.59%)	Cumacea	1.14% (0.83%)
Apanthura californiensis, I	1.49% (0.54%)	Oweniidae, P	1.62% (0.67%)	Polychaete 47	1.03% (0.61%)

Sand (S)

Avalon		Isthmus		Cherry	
Exogon sp., P	34.02% (2.79%)	*Exogon* sp., P	30.86% (3.82%)	*Exogon* sp., P	25.39% (2.26%)
Polychaeta 11	12.03% (3.70%)	Myodocopida 1, O	22.04% (4.74%)	Amphipoda 3	12.85% (3.02%)
Nematoda 1	8.47% (1.23%)	Spionidae 1, P	6.36% (2.09%)	Phoxocephalidae 1, A	9.37% (1.37%)
Spionidae 1, P	5.46% (0.85%)	Lumbrineridae, P	6.18% (1.69%)	Myodocopida 1, O	8.85% (3.19%)
Nereididae 1, P	4.67% (0.69%)	Amphipoda 3	3.41% (1.53%)	Amphipoda 5	6.08% (1.62%)
Sabellidae, P	3.88% (0.62%)	*Tellina* sp., B	2.38% (0.78%)	Nereididae 1, P	4.29% (0.75%)
Phoxocephalidae 1, A	2.71% (0.88%)	Phoxocephalidae 1, A	2.30% (0.62%)	Polychaeta 11	4.07% (3.83%)
Maldanidae, P	2.55% (0.56%)	Terebellidae 1, P	2.20% (0.65%)	Sabellidae, P	2.89% (0.65%)
Nematoda 2	2.40% (1.67%)	*Neonesidea* sp., O	1.69% (1.69%)	Polychaeta 13	2.70% (0.57%)
Myodocopida 1, O	6.28% (1.82%)	Sabellidae, P	1.51% (0.61%)	Leptochelida sp. 1, T	2.48% (1.06%)

To evaluate which invertebrate groups were driving the assemblage differences between habitat types, all sites were pooled for SIMPER analysis. LR habitat was dominated by the gastropod *Amphithalamus* sp., the crustaceans *Zeuxo* sp., Aoridae 1, ostracods *Macrocypris* sp. and *Neonesidea* sp., the syllid *Exogon* sp. and Nematoda. DR habitat was dominated by Nematoda, Oligochaeta, *Neonesidea* sp. and *Exogon* sp., while sand was dominated by the polychaetes *Exogon* sp., Spionidae 1, Nereididae 1, and Sabellidae and the crustaceans Myodocopida 1, Phoxocephalidae 1, (Table 10). The SIMPER pairwise comparison revealed which morphotypes worked best as discriminators between the habitat types by presence or absence. Table 10 shows that most of the taxa accounting for the majority of the differences in habitat types were morphotypes found in either the LR or DR habitat and were absent from or at low abundances in the S habitat. The only S morphotype to make the top seven discriminators (Table 10) was the syllid polychaete *Exogon* sp., which is the most abundant taxa within S, but only qualified for comparing S to DR. The morphotypes listed as discriminators between LR and DR (Table 10) are found in both habitat types, but more were found in LR (Table 9)

Table 10. Similarity percentages (SIMPER) analysis of invertebrate morphotypes by habitat type. Top row gives percent similarity within each habitat type. Listed morphotypes contributed to 50% of the similarity within a given habitat type. Bottom portion shows pairwise percent dissimilarity between habitat types: Live Rhodolith (LR), Dead Rhodolith (DR) and Sand (S) and top seven morphotypes that contributed to the differences. R values are one-way ANOSIM values for habitat only.

Live Rhodolith		**Dead Rhodolith**		**Sand**	
63.53%		52.99%		59.54%	
Amphithalamus sp.	12.81%	Nematoda 1	16.53%	*Exogon* sp.	20.55%
Zeuxo sp.	9.01%	Oligochaeta 1	14.12%	Myodocopida 1	8.76%
Aoridae 1	7.50%	*Neonesidea* sp.	12.97%	Phoxocephalidae 1	7.19%
Macrocypris sp.	6.44%	*Exogon* sp.	11.06%	Spionidae 1	6.89%
Neonesidea sp.	6.04%			Nereididae 1	4.83%
Exogon sp.	4.98%			Sabellidae	4.75%
Nematoda 1	4.52%				

LR vs. DR		LR vs. S		DR vs. S	
60.2%		78.3%		75.4%	
Amphithalamus sp.	7.43%	*Amphithalamus* sp.	8.60%	Nematoda 1	7.58%
Zeuxo sp.	7.31%	*Zeuxo* sp.	6.07%	*Neonesidea* sp.	6.12%
Aoridae 1	5.96%	Aoridae 1	5.18%	Oligochaeta	5.70%
Nematoda 1	4.04%	*Macrocypris* sp.	4.25%	*Amphithalamus* sp.	4.04%
Macrocypris sp.	2.93%	*Neonesidea* sp.	3.83%	*Exogon* sp.	3.54%
Anatanais sp.	2.84%	Oligochaeta	2.81%	*Macrocypris* sp.	3.13%
Leptochelida sp. 1	2.60%	Nematoda 1	2.79%	Amphipoda 3	2.81%

Invertebrate assemblages can also be compared by the number and abundance of obligate species. There were 42 morphotypes of motile cryptofaunal invertebrates found solely within LR and 16 morphotypes found within the S (Appendix B). The unique morphotypes within LR were from several phyla, including Annelida, Arthropoda, Mollusca, and Echinodermata. Some notable "rhodolith-specific" invertebrates were one morphotype of sipunculid, small spider crabs, sea mites, chitons, limpets, sea stars, and sea urchins. *Leptochelida* sp. 2 (Tanaidacea) was the most abundant of the "rhodolith-specific" invertebrates at 6.0 ± 0.6 individuals per core in Cherry Cove. There were a

few taxa that were only found in the DR habitat, however these morphotypes were rare with most represented by one individual. It is possible that these morphotypes do live within the LR habitat type, but are so rare that the sample effort of this study was too small to detect them. The species unique to S were mostly polychaetes and bivalves with one species of sand-dwelling gastropod (Gastropoda 17).

Physical Structure Versus Live Material:

Within rhodolith habitat, there is a continuous gradient between what is subjectively called live rhodolith habitat and dead rhodolith habitat. The two substrate characteristics that offer the greatest difference between LR and DR habitats were the amount of intact rhodoliths and amount of live rhodolith material (Table 2, Fig. 4). Simple linear regression was used to compare these traits between all LR and DR cores versus total invertebrate abundance and taxonomic richness. This confirmed that total abundance (total abundance = 568.802*(percent sediment$_{> 4750\ \mu m}$) + 281.289, $F_{1,34}$ = 4.987, p = 0.032, r^2 = 0.128) and taxonomic richness (taxonomic richness = 48.431*(percent sediment$_{> 4750\ \mu m}$) + 29.035, $F_{1,34}$ = 14.369, p = 0.001, r^2 = 0.297) were positively correlated with percent dry weight of intact rhodoliths (Fig. 8A&C). Total invertebrate abundance per core ($F_{1,34}$ = 1.613, p = 0.213, r^2 = 0.045) was not correlated with percent dry weight of live rhodolith material while there was a weak but positive correlation with taxonomic richness (taxonomic richness = 36.2900*(percent live rhodolith material) + 29.045, $F_{1,34}$ = 6.750, p = 0.014, r^2 = 0.166; Fig. 8B&D). It appeared that intact rhodoliths (>4750 µm) explained more variation in the abundance and taxonomic richness per core for the associated invertebrates than percent live rhodolith material, but only accounted for about 12% to 30% of the variation.

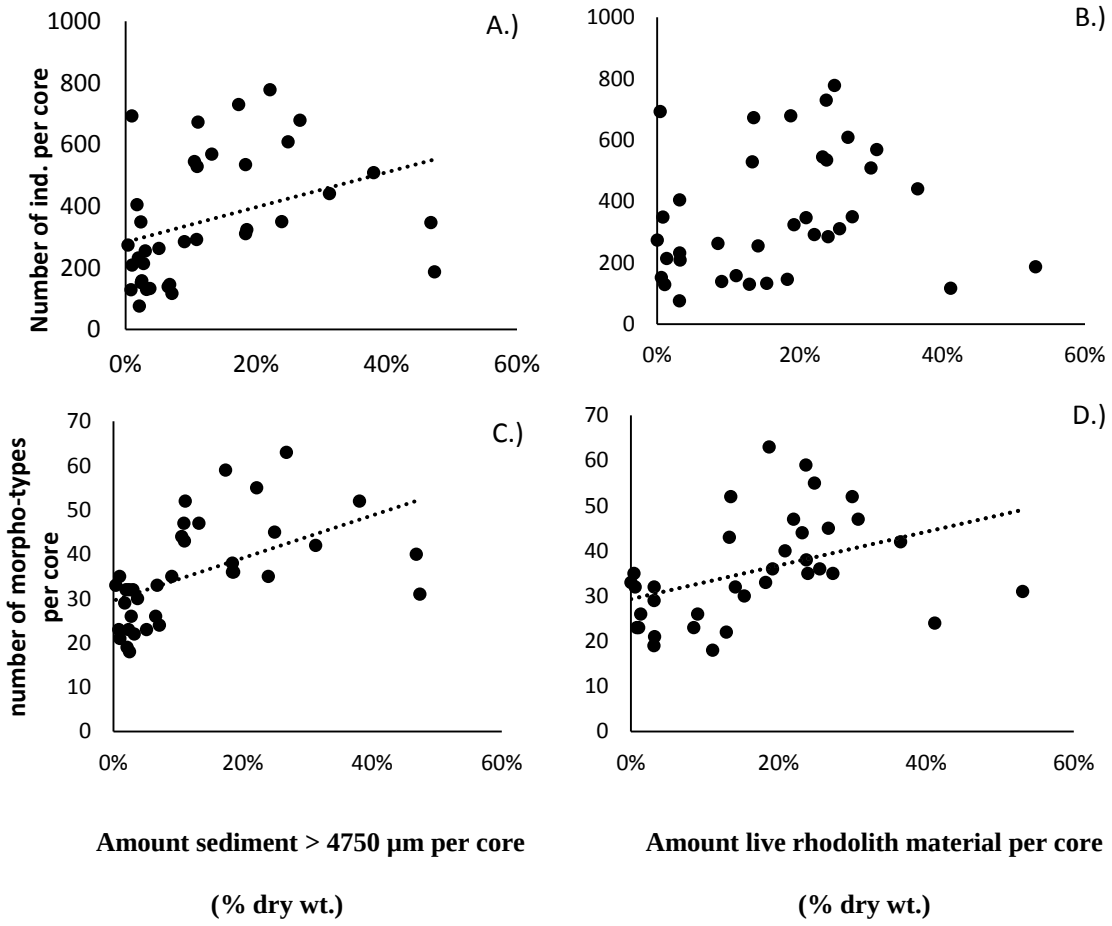

Figure 8. Total cryptofaunal invertebrate abundance and taxonomic richness relative to intact rhodoliths and live rhodolith material. Only counts from Live Rhodolith and Dead Rhodolith habitats used in graphs. A.) Percent dry weight of intact rhodoliths (> 4750 µm) against total invertebrate abundance per core ($p = 0.032$, $r^2 = 0.128$), B.) Percent dry weight of total live rhodolith material against total invertebrate abundance per core ($p = 0.213$, $r^2 = 0.045$), C.) Percent dry weight intact rhodoliths (> 4750 µm) against taxonomic richness per core ($p = 0.001$, $r^2 = 0.297$), D.) Percent dry weight of total live rhodolith material against taxonomic richness per core ($p = 0.014$, $r^2 = 0.166$).

DISCUSSION

This current study supports the growing body of evidence that the presence of rhodoliths support high abundance and diversity of invertebrates relative to other sedimentary benthic habitats (Steller *et al.* 2003, Figueiredo *et al.* 2007, Foster *et al.* 2007, Gagnon *et al*. 2012, Neill *et al.* 2015). The live rhodolith habitat at Catalina Island

supported greater motile cryptofaunal invertebrate abundance, taxonomic richness, and number of "obligates" than adjacent dead rhodolith or sand habitats. The relatively high abundance and diversity of polychaetes and crustaceans found in Catalina rhodolith habitats is consistent with other habitat modifiers, such as kelp holdfasts (Andrew 1945, Foster & Schiel 1985), and was consistent with other rhodolith invertebrate communities (De Grave 1999, Steller *et al.* 2003, Foster *et al.* 2007, Berlandi *et al.* 2012). However, the high abundance of a single genus of gastropod (*Amphithalamus* spp.; 20,000-50,000 ind./m^2) seems to be unique to the Catalina Island rhodolith beds. This gastropod genus is known to associate with attached coralline algae and gravel along the California coast (Carlton 2007, J. Pearse, personal communication). By documenting the associated cryptofaunal invertebrate assemblages of Catalina Island rhodolith beds, this study was a first step towards understanding this understudied coastal ecosystem.

The rhodolith beds at different sites at Catalina Island appear to support similar invertebrate assemblages. The site related differences in taxonomic richness between live rhodolith sites seem to be driven by the presence of different rare morphotypes and varying abundances of the dominant morphotypes. Studies of other rhodolith bed invertebrate assemblages either remove rare species from their analyses (De Grave 1999, Gabara 2014) or do not sort to species level (Gagnon *et al*. 2012). Rare species are important for understanding the ε-diversity (absolute diversity) for a habitat and should not be overlooked during diversity studies (Zajac *et al*. 2013). These species can account for 30-40% of the total species found in some rhodolith beds (Reira *et al.* 2012, Neill *et al.* 2015) and in this study they account for 24.6% of taxa found in live rhodolith habitat. More sampling is needed to determine if site differences are merely patch differences

within the same larger community or if these rare species are indicative of unique communities.

Invertebrate assemblages, in this study, strongly clustered by site in sand habitat while invertebrate communities only loosely clustered by site in rhodolith habitats, suggesting rhodoliths might mitigate site differences. Environmental factors can influence the sediment profiles of soft-sediment that in turn influence the associated invertebrate communities (e.g. Gray 1974, Thrush *et al.* 2003, Anderson 2008, Byers & Grabowski 2014). If environmental factors are driving the differences between sand habitats at the different sites, it is possible that rhodolith (live and dead) presence has a unifying effect on invertebrate assemblages. This facilitation has been studied in other systems. Mussel beds have been shown to mitigate the environmental stresses impacting different sites, resulting in greater similarity in the associated invertebrate communities between mussel plots across sites than between plots lacking mussels across sites (van der Zee *et al.* 2015). Other possible mechanisms for the observed differences in community assemblages is that rhodolith branches can increase the amount of detritus retained, thus increasing the amount of available food (Grall *et al.* 2006, Gabara 2014). Further research is needed to identify the possible mechanisms for this unification of associated invertebrates due to the presence of rhodoliths.

Even though site differences were subtle, various abiotic factors might influence these differences. Avalon Harbor is geographically further away from the other sites and the bed is located twice as deep as the other beds. However, Avalon Harbor had similar abundance and taxonomic richness values as Isthmus Harbor, while Cherry Cove had the highest invertebrate abundances and number of rare morphotypes compared to the other

sites within live rhodolith habitat. Cherry Cove did have the lowest amount of silt (< 63 μm) for each habitat. The amount of silt could have negative impacts on the structure and function of invertebrates associated with rhodolith beds (Grall & Glémarec 1997) and should be considered in future investigations.

Avalon Harbor provided an unexpected insight into the importance of rhodoliths as physical structure versus living substratum. The invertebrate community in the dead rhodolith habitat at Avalon Harbor was similar to the other dead rhodolith sites. However, the size classes that contain rhodolith fragments (500 – 4750 μm) contained similar amounts of percent dry weight live rhodolith material as the live rhodolith habitat. If living tissue was a strong factor for habitat selection by motile cryptofaunal invertebrates, then Avalon Harbor's dead rhodolith habitat should have clustered with the live rhodolith habitat instead of the other dead rhodolith habitat sites, but this was not observed in the present study. Across all sites, percent live material did not correlate with the total abundance while the largest size class of sediment (i.e. intact rhodoliths) did positively correlate. Figueiredo *et al.* (2007) found that when rhodolith sizes were similar, there was no statistical difference in the motile invertebrate community between recolonized live and dead rhodoliths. However, the presence of live rhodolith material has been found to be an important factor to recruiting of planktonic larvae (Steller & Caceres-Martinez 2009). I hypothesize that the motile invertebrates in this study were attracted to the intact rhodolith, because of physical structure rather than living surface.

Replication of studies can strengthen hypotheses and illuminate possible errors in methods or presence of unknown factors (Underwood 1990). Another Catalina Island rhodolith community study, recorded 20.9 taxa per core and a mean abundance of 25,915

ind./m^2 of the cryptofaunal invertebrates within live rhodolith habitat (Gabara 2014). The two-fold greater taxonomic richness and the five-fold greater mean abundance reported in this study may be due to methodological differences. Though both studies collected samples during December 2013, Gabara (2014) also collected cores during April 2013. Gabara (2014) density estimates were from 24 cores (6.5 x 10 cm) taken in areas of > 50% pigmented rhodoliths while this study took 18 cores (7 x 5 cm) from areas of > 90% pigmented rhodolith. As a consequence, both studies recorded different amounts of intact rhodoliths (> 4750 µm; Gabara 2014 = 4.3% -7.3%, this study >20%). Invertebrates were also sorted to different levels of taxonomic resolution. Gabara (2014) sorted to higher taxonomic levels (e.g. gammarid, gastropod, ostracod, polychaete), while the present study attempted to sort to species level, as inferred from distinct morphotypes. However, even accounting for these differences, a major difference was the lack of gastropods detected by Gabara (2014) within the cryptofauna. In this study, *Amphithalamus* sp. was the most abundant animal within live rhodolith habitat and was still noticeable within the dead rhodolith habitat. It is possible that *Amphithalamus* sp. has a very patchy distribution within the bed, and random chance resulted in Gabara (2014) sampling areas of low abundance, while this study sampled areas of high abundance.

Differences in collection methods and substrate and faunal definitions make comparisons to other sites within the rhodolith literature challenging. Studies from Bahía Concepción, Baja California Sur, consistently reported between 104-118 taxa within the cryptofauna (Medina-Lopez 1999, Hinojosa-Arango and Riosmena-Rodriguez 2004, Foster *et al.* 2007), which are lower numbers than found in this study (142 taxa).

However, in these previous studies rhodoliths were collected by hand instead of coring. The inclusion of near-surface infauna into the cryptofaunal assemblages by coring is probably inflating the Catalina Island diversity. Neill *et al.* (2015), using cores, found 197 invertebrate taxa within two New Zealand rhodolith beds and Sciberras *et al.* (2009) found 244 faunal taxa in Malta. Higher latitude beds have reported lower diversity with only 61 taxa found in Norwegian beds (Teichert *et al.* 2014). However, not all the northern studies identified invertebrates down to the species level causing possible underestimation of diversity (Konar *et al.* 2006, Gagnon *et al.* 2012). European rhodolith beds have some of the highest reported diversities with the Atlantic and Mediterranean having over 450 species of invertebrates. These studies failed, however, to differentiate between different faunal types (e.g. infauna vs cryptofauna), size classes, or substrate conditions (Barbera *et al.* 2003). Even when faunal type is taken into consideration, comparisons are still challenging because of the lack of universal conformity of definitions and methods.

Using definitions from previous studies (Steller *et al.* 2003, Foster *et al.* 2007), some of the associated invertebrates identified in this study, could be classified as epifauna (living on top of the rhodolith) or infauna (living within the sediment below rhodoliths) instead of cryptofauna (living within the rhodolith). However, due to the small size of the rhodoliths at Catalina Island (Tompkins 2011), differentiating these groups was nearly impossible. Also, given the potential for cryptofaunal invertebrates to be found on the outside of large rhodoliths (Gagnon *et al.* 2012) or within the sediment (Steller *et al.* 2003), I suggest that all future work involving associated invertebrates use cores or grabs large enough to sample several rhodoliths. This method will ensure that

invertebrates using the spaces between interlocking rhodoliths are not excluded from the cryptofauna. Cores and grab sampling allows for densities to be calculated in either m^3 or cm^3, and comparisons could then be made between beds of different rhodolith sizes. If necessary, a division by size could be made between large invertebrates that are easily observed versus smaller, more cryptic, organisms that require investigation under a dissecting scope. Standardization of methods and terms in future studies would allow communities to be compared across biogeographical scales and among different rhodolith species.

While this study concludes that Catalina Island rhodolith beds support higher species richness and abundances than adjacent sand habitat, the mechanisms driving these patterns are unclear. Observations from this study support the hypothesis that rhodolith structure is the main driver determining invertebrate diversity and abundance. Further research is needed, along with standardized methods, to better understand the ecology of the associated invertebrates and the benefits rhodoliths provide as a foundation species worldwide.

REFERENCES

Altieri, A. H. & van de Koppel, J. (2014). Foundation species in marine ecosystems. In: *Marine Community Ecology and Conservation*, Bertness, M.D., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. eds. (Sinauer, Sunderland). 37-56.

Amado-Filho, G. M., Maneveldt, G., Manso, R. C. C., Marins-Rosa, B. V., Pacheco, M. R. & Guimaraes S. M. P. B. (2007). Structure of rhodolith beds from 4 to 55 meters deep along the southern coast of Espirito Santo State, Brazil. *Ciencias Marinas* 33, 399-410.

Anderson, M. J. (2008). Animal-sediment relationships re-visited: characterizing species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *J. Exp. Mar. Bio. Eco. 366*, 16-27.

Andrews, H. L. (1945). The kelp beds of the Monterey region. *Ecology 26*, 24-37.

Barbera, C., Bordehore, C., Borg, J. A., Glemarec, M., Grall, J., Hall-Spencer, J. M., De La Huz, Ch., Lanfranco, E., Lastra, M., Moore, P. G., Mora, J., Pita, M. E., Ramos-Espla, A. A., Rizzo, M. Sanchez-Mata, A., Seva, A., Schembri, P. J., & Valle, C. (2003). Conservation and management of northeast Atlantic and Mediterranean maerl beds. *Aquatic Conserv: Mar. Freshw. Ecosyst. 13,* S65-S76

Bell S. S., & McCoy E. D. (1991). Habitat structure: the evolution and diversification of a complex topic. In: *Habitat Structure: the Physical Arrangement of Objects in Space*. Bell S. S., McCoy E. D. & Mushinsky, H. R. eds. (Chapman and Hall, California) 3-27.

Berlandi, R. M., Figueiredo M. A., & Paiva P. C. (2012). Rhodolith morphology and the diversity of polychaetes off the southeastern Brazilian coast. *Journal of Coastal Research 28*, 280-287.

Bertness, M. D., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. eds. (2014) *Marine Community Ecology and Conservation.* (Sinauer Associates, Inc., Sunderland) pp 566.

Bertness, M. D., Leonard, G. H., Levine, J. M., Schmidt, P. R., & Ingraham, A. O. (1999). Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology 80*, 2711-2726.

Bordehore, C., Ramos-Espla, A. A., & Riosmena-Rodiquez, R. (2003). Comparative study of two maerl beds with different otter trawling history, southeast Iberian Peninsula. *Aquat. Conserv: Mar. and Freshw. Ecosys. 13*, S43-S54.

Bosence, D. W. (1979). Live and dead faunas from coralline algal gravels, Co. Galway. *Palaeontology 22,* 449-478.

Bruno, J. F. (2000). Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology 81*, 1179-1192.

Bruno, J. F., & Bertness, M. D. (2001). Habitat modification and facilitation in benthic marine communities. in: *Marine Community Ecology,* Bertness, M. D., Gaines S. D., & Hay M. E. eds. (Sinauer, Sunderland). 201-218.

Bruno, J. F., & Kennedy, C. W. (2000). Patch-size dependent habitat modification and facilitation and New England cobble beaches by *Spartina alterniflora. Oecologia 122*, 98-108.

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *TRENDS in Ecology and Evolution 18,* 119-125.

Byers, J. E. & Grabowski, J. H. (2014). Soft-Sediment Communities. In: *Marine Community Ecology and Conservation*, Bertness, M.D., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. eds. (Sinauer, Sunderland). 227-249.

Carlton, J. T., ed. (2007) *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon.* University of California Press, Berkeley.

Clark, R. N. (2000). The chiton fauna of the Gulf of California rhodolith beds (with descriptions of four new species). *Nemouria – Occasional Papers of the Delaware Museum of Natural History 43*: 1-20.

Connell, J. H. (1978) Diversity of tropical rainforests and coral reefs. *Science. 199*, 1304–1310.

Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of eSichments to the benthos at McMurdo Sound, Antarctica. *Proceedings of colloquium on conservation problems in Antarctica*. 81-96.

De Grave, S. (1999). The influence of sedimentary heterogeneity on within maerl bed differences in infaunal crustacean community. *Estuarine, Coastal and Shelf Science 49*, 153-163.

Dutertre, M., Hamon, D., Chevalier, C., & Ehrhold, A. (2013). The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES Journal of Marine Science 70*, 294-308.

Figueiredo, M. A., Santos-de Menezes, K., Costa-Paiva, E. M., Paiva, P. C., & Ventura, C. R. R. (2007). Experimental evaluation of rhodoliths as living substrata for infauna at the Abrolhos Bank, Brazil. *Ciencias Marinas 33,* 427-440.

Foster, M. S., & Schiel, D. R. (1985). The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife Service.

Foster, M. S. (2001). Rhodoliths: between rocks and soft places. *J. Phycol. 37*, 659-667.

Foster, M. S., McConnico, L.M., Lundsten, L., Wadsworth, T., Kimball, T., Brooks, L. B., Medina-Lopez, M., Riosmena-Rodriguez, R., Hernandez-Carmona, G., Vasquez-Elizondo, R. M., Johnson, S., & Steller, D. L. (2007). Diversity and natural history of a *Lithothamnion muelleri-Sargassum horridum* community in the Gulf of California. *Ciencias Marinas. 33*, 367-384.

Gabara, S. S. (2014). Community structure and energy flow within rhodolith habitats at Santa Catalina Island, CA. Thesis, San Jose State University.

Gagnon, P., Matheson, K., & Stapleton, M. (2012). Variation in rhodolith morphology and biogenic potential of newly discovered rhodolith beds in Newfoundland and Labrador (Canada). *Botanica Marina 55*, 85-99.

Grall, J., & Glémarec, M. (1997). Using biotic indices to estimate microbenthic community perturbations in the Bay of Brest. *Estuarine, Coastal and Shelf Science 44 (Supplement A),* 43-53.

Grall, J., Le Loc'h, F., Guyonnet, B., & Pascal, R. (2006). Community structure and food web based on stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) analysis of a North Eastern Atlantic maerl bed. *J. Exper. Mar. Bio. Ecol. 338,* 1-15.

Graham, M. H. (2004). Effects of local deforestation on the diversity and structure of southern California Giant kelp forest food webs. *Ecosystems. 7*, 341-357.

Gray, J. S. (1974). Animal-sediment relationships. *Oceanogra. Mar. Biol. Annu. Rev. 12*, 223-261.

Hall-Spencer, J. M., & Moore, P. G. (2000). Scallop dredging has profound, long-term impacts on maerl habitats. *ICES Journal of Marine Science*. *57,* 1407-1415.

Hinojosa-Arango, G., & Riosmena-Rodriquiez, R. (2004). The influence of rhodolith species and growth-form on cryptofaunal assemblages of rhodolith beds in the central-west Gulf of California, Mexico. *PSZN Mar. Ecol. 54*, 234-244.

Hinojosa-Arango, G., Maggs, C. A., Johnson, M. P. (2009). Like a Rolling Stone: The mobility of maerl (Corallinaceae) and the neutrality of the associated assemblages. Ecology 90, 517-528.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos 69,* 373-386.

Jones, C. G., Lawton, J. H., Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology 78*, 1946-1957

Kamenos, N. A., Moore, P. G., & Hall-Spencer, J. M. (2003). Substratum heterogeneity of dredged vs un-dredged maerl grounds. *J. Mar. Biol. Ass. U.K. 83*, 411-413

Kamenos, N. A., Moore, P. G., & Hall-Spencer, J. M. (2004a). Attachment of the juvenile queen scallop (*Aequipecten opercularis* (L.)) to maerl in mesocosm conditions: juvenile habitat selection. *J. Exp. Mar. Bio. Eco. 306*, 139-155

Kamenos, N., Moore, P., & Hall-Spencer, J. (2004b). Maerl grounds provide both refuge and high-growth potential for juvenile queen scallops (L.). *J. Exp. Mar. Bio. Ecol. 313,* 241-254

Kamenos, N., Moore, P., & Hall-Spencer, J. (2004c). The nursery area function of maerl grounds for juvenile queen scallops (*Aequipecten opercularis*) and other invertebrates. *Mar. Ecol. Prog. Ser. 274*, 183-189

Kamenos, N. A., Calsoi, P., & Moore, P. G. (2006). Substratum-mediated heart rate responses of an invertebrate to predation threat. *Anim. Behav. 71*, 809-813

Keegan, B. F. (1974). The macrofauna of maërl substrates on the west coast of Ireland. *Cah. Biol. Mar. 4*, 513-530

Koehl, M. A., Hadfield, M. G., Reidenbach, M., & Koseff, J.R. (2001). Behavioral responses to instantaneous patterns of water-borne chemical cues encountered by microscopic larvae in turbulent wave-driven flow affect larval settlement. *EOS*, Transactions, American Geophysical Union 82.

Konar, B., Riosmena-Rodriguez, R., & Iken, K. (2006) Rhodolith bed: a newly discovered habitat in the North Pacific Ocean. *Botanica Marina 49*, 355-359.

Levine, J. M., Bruno, J. F., Leonard, G. H., & Bertness, M. D. (1999). Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. *Oecologia 120*, 446–450

Lissner, A. L., & Blake, J. A. eds. (1998) *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel: final report.* (U.S. Dept. of the Interior, Minerals Management Service, Camarillo, CA)

Littler, M. M., Littler, D. S., Hanisak, M. D. (1991). Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *J. Exp. Mar. Biol. Ecol. 150,* 163-182

McCall, P. L., & Tevesz, M. J. S. eds. (1982). *Animal-Sediment Relations.* (Plenum Press, New York)

McRoy, C. P., & Helferrich, C. eds. (1977). *Seagrass Ecosytems: a scientific perspective* (Dekker, New York).

Marrack, E. C. (1999). The relationship between water motion and living rhodolith beds in the southwestern Gulf of California, Mexico. *PALAIOS 14*, 159-171.

Medina-López, M. A. (1999). Estructura de la criptofauna asociada a mantos de rodolitos en el suroeste del Golfo de California, México. Tesis, Universidad Autónoma de Baja California Sur, La Paz, México.

Neill, K. F., Nelson, W. A., D'Archino, R., Leduc, D., & Farr, T. J. (2015). Northern New Zealand rhodoliths: assessing faunal and floral diversity in physically contrasting beds. *Mar. Biodiv. 45*, 63-75.

Nelson, W. A. (2009). Calcified macroalgae – critical to coastal ecosystem and vulnerable to change: a review. *Mar. Fresh. Res. 60*, 787-801.

Parnell, E., Miller, K.A., & Dayton, P.K. (2006). Santa Catalina Island: reclaiming a national treasure. A report to the Ralph M. Parson's Foundation. Scripps Institution of Oceanography Technical Report, Scripps Institution of Oceanography, University of California, San Diego.

Peña, V. & Bárbara, I. (2007). Maërl community in the northwestern Iberian Peninsula: a review of floristic studies and long-term changes. *Aquat. Conserv.: Mar. Freshw. Ecosyst. 17*, 1-28

Reidenbach, M. A., Koseff, J. R., & Koehl, M. A. R. (2009). Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnology and Oceanography. 54*, 318-330.

Rhoads, D. C., & Young, D. K. (1971). Animal-sediment relations in Cape Cod Bay, Massachusetts II. Reworking by *Molpadia oolitica* (Holothuroidea). *Marine Biology 11*, 255-261.

Riera, R., Delgado, J., Rodríquez, M., Monterrose, O., & Ramos, E. (2012). Macrofaunal communities of threatened subtidal maërl seabeds on Tenerife (Canary Islands, north-east Atlantic Ocean) in summer. *Acta Oceanologica Sinica. 31(1)* 98-105.

Riosmena-Rodriguez, R., Woelkerling, W. J., & Foster, M. S. (1999). Taxonomic reassessment of rhodolith-forming species of *Lithophyllum* (Corallinales, Rhodophyta) in the Gulf of California, Mexico. *Phycologia 38*, 401-417.

Sanders, H. L. (1958). Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships. *Limnology and Oceanography 3*, 245-258.

Sciberras, M., Rizzo, M., Mifsud, J. R., Camilleri, K. Borg, J.A., Lanfranc, E., Schembri, P. J. (2009). Habitat structure and biological characteristics of a maerl bed off the northeastern coast of the Maltese Islands (central Mediterranean). *Mar Biodivers 39*, 251-264.

Steller, D. L., & Foster, M. S. (1995). Environmental factors influencing distribution and morphology of rhodoliths in Bahia Concepcion, B.C.S., Mexico. *J. Exp. Mar. Bio. Ecol. 194,* 201-212.

Steller, D. L., Riosmena-Rodriguez, R., Foster, M. S., & Roberts, C. A. (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. *Aquat. Conserv. Mar. Fresh. Ecosyst. 13,* 5-20.

Steller, D. L., & Caceres-Martinez, C. (2009). Coralline algal rhodoliths enhance larval settlement and early growth of Pacific calico scallop *Argopecten ventricosus*. *Mar. Ecol. Prog. Ser. 396*, 49-60.

Tanadjaja, E. D. (2010). The roole of mechanical and chemical processes in rhodalgal sediment production and implications for ocean acidification (Baja California, Mexico). Thesis, Fresno State University.

Teichert, S. (2014). Hollow rhodoliths increase Svalbard's shelf biodiversity. *Scientific Reports 4:6972,* 1-5.

Teichert, S., Woelkering, W., Ruggeberg, A., Wisshak, M., Piepenbury, D., Meyerhofer, M., Form, A., & Freiwald, A. (2014). Arctic rhodolith beds and their environmental controls (Spitsbergen, Norway). *Facies 60*, 15-37.

Thrush, S. F., Hewitt, J. E., Norkko, A., Nicholls, P. E., Funnel, G. A., & Ellis, J. I. (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Mar. Ecol. Prog. Ser. 263*, 101-112.

Tompkins, P. A. (2011). Distribution, growth, and disturbance of Catalina Island rhodoliths. Thesis, San Jose State University.

Underwood, A. J. (1990). Experiments in ecology and management: their logics, function and interpretations. *Aust. J. Ecol. 15*, 365-389.

van der Zee, E. M., Tielens, E., Holthuijsen, S., Donadi, S., Eriksson, B., van der Veer, H., W., Piersma, T., Olff, H., & van der Heide, T. (2015). Habitat modification drives benthic trophic diversity in an intertidal soft- bottom ecosystem.

Villas-Boas, A. B., Riosmena-Rodriguez, R., Figueiredo, M., (2014). Community structure of the rhodolith-forming beds on the central Brazilian continental shelf. *Helgol. Mar. Res. 68,* 27-35.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology. 30*, 377-392.

Wilson, S., Blake, C. Berges, J. A. Maggs, C. A. (2004). Environmental tolerances of free-living corralling algae (maerl): implications for European marine conservation. Biological Conservation 120, 279-289.

Zajac, R. N., Vozarik, J. M., Gibbons, B. R. (2013). Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscapes structure. *PLOS One 8,* e65823.

APPENDIX A

LOCATION, DEPTH, AND SIZE OF CATALINA ISLAND RHODOLITH BEDS SAMPLED (MODIFIED FROM TOMPKINS 2011).

Site	Latitude (N)	Longitude (W)	Live Cover (m^2)	Dead Cover (m^2)	Depth Range (m)	
					Min.	Max.
Avalon Harbor	33.3477	118.3246	9,765	4,093	7.8	21
Isthmus Harbor	33.4441	118.4982	1,148	7,939	4.3	6.1
Cherry Cove	33.4515	118.5022	2,627	5,543	5.8	7.3

Appendix A. Location, depth, and size of Catalina Island rhodolith beds sampled for cryptofauna in this study. Data based on surveys conducted in 2009 (modified from Tompkins 2011).

APPENDIX B

MEAN ABUNDANCE OF MOTILE INVERTEBRATES BASED ON HABITAT AND SITE FOR CATALINA ISLAND RHODOLITH BEDS COLLECTED DECEMBER 2013

	Live Rhodolith						Dead Rhodolith						Sand					
	Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry	
Platyhelminthes																		
Turbellaria 1	0.67 ±	0.42			1.83 ±	0.54	0.17 ±	0.17	0.17 ±	0.17	0.17 ±	0.17			0.17 ±	0.17		
Turbellaria 2			0.17 ±	0.17	0.50 ±	0.50					0.50 ±	0.22						
Turbellaria 3	0.17 ±	0.17	0.33 ±	0.33	1.67 ±	1.17	0.17 ±	0.17							0.17 ±	0.17		
Turbellaria 4	0.33 ±	0.21	0.17 ±	0.17	1.17 ±	0.31	0.17 ±	0.17										
Nematoda																		
Nematoda 1	17.00 ±	6.16	12.83 ±	3.03	35.83 ±	8.51	23.00 ±	6.40	37.50 ±	9.11	178.33 ±	78.33	19.00 ±	3.26	1.00 ±	0.37		
Nematoda 2	1.00 ±	0.26			1.83 ±	1.05	1.83 ±	0.70	2.33 ±	1.05	3.83 ±	1.10	6.00 ±	4.41			0.17 ±	0.17
Nematoda 3			1.00 ±	0.26	1.33 ±	0.71	1.67 ±	1.09	0.33 ±	0.21	1.67 ±	0.71	1.50 ±	0.96				
Nematoda 4							3.17 ±	1.11	0.83 ±	0.54								
Sipunculida																		
Sipunculida 1	0.17 ±	0.17	0.33 ±	0.21	0.33 ±	0.33	0.50 ±	0.22	1.17 ±	0.48			1.83 ±	0.54	0.33 ±	0.21	0.33 ±	0.21
Sipunculida 2			0.17 ±	0.17	2.17 ±	1.97	0.50 ±	0.34	0.17 ±	0.17			0.50 ±	0.22			0.17 ±	0.17
Sipunculida 3	0.33 ±	0.33	1.17 ±	0.40	6.67 ±	1.69	0.50 ±	0.22	1.50 ±	0.56	2.00 ±	0.68	0.17 ±	0.17	0.17 ±	0.17		
Sipunculida 4													0.17 ±	0.17	0.67 ±	0.33		
Sipunculida 5	0.17 ±	0.17	0.17 ±	0.17	0.33 ±	0.21	1.00 ±	0.68	0.50 ±	0.34					0.17 ±	0.17		
Sipunculida 6	0.17 ±	0.17	0.17 ±	0.17	0.67 ±	0.21	0.17 ±	0.17										
Sipunculida 7	0.33 ±	0.21	0.83 ±	0.40	0.67 ±	0.33												
Sipunculida 8							0.50 ±	0.34							0.17 ±	0.17		
Sipunculida 9	1.33 ±	0.67	0.17 ±	0.17			0.17 ±	0.17			0.17 ±	0.17	0.33 ±	0.21				
Annelida																		
Oligochaeta	12.17 ±	5.56	24.17 ±	5.02	13.00 ±	4.13	23.17 ±	2.91	36.67 ±	8.17	17.17 ±	3.48	1.33 ±	0.61	1.00 ±	0.63		
Polychaeta																		
Cossura sp.	0.17 ±	0.17					0.83 ±	0.40										
Maldanidae	0.50 ±	0.34	0.33 ±	0.21	1.33 ±	0.56	0.83 ±	0.40			1.00 ±	0.52	5.67 ±	1.28				
Polyophthalmus pictus	3.50 ±	2.38	0.17 ±	0.17	1.00 ±	0.26					0.17 ±	0.17	0.67 ±	0.42	0.17 ±	0.17		
Oribiniidae			0.33 ±	0.33	0.33 ±	0.21	0.17 ±	0.17	0.67 ±	0.21	0.33 ±	0.21	1.67 ±	0.76	1.00 ±	0.52		
Paraonidae	0.50 ±	0.22	1.00 ±	0.63	0.83 ±	0.31	1.50 ±	1.15	0.83 ±	0.40	0.67 ±	0.49						
Scalibergmatidae	2.00 ±	1.03					3.83 ±	3.45										
Lumbrineridae	0.33 ±	0.33	2.67 ±	0.42	2.50 ±	1.02	1.00 ±	0.68	1.67 ±	0.76	0.33 ±	0.21	1.00 ±	0.45	4.00 ±	1.03		
Oenonidae			0.17 ±	0.17	0.17 ±	0.17							2.50 ±	0.72	0.17 ±	0.17		
Dorvillea sp. 1					1.00 ±	0.68					1.67 ±	1.28						
Dorvillea sp. 2	0.00 ±				0.17 ±	0.17			0.17 ±	0.17								
Harmothoe sp.	0.17 ±	0.17													0.50 ±	0.22		
Halosydna sp.	0.17 ±	0.17	0.33 ±	0.33														
Sigalionidae									0.33 ±	0.21							0.17 ±	0.17
Chrysopetalidae	1.67 ±	0.61	0.17 ±	0.17	0.50 ±	0.22												
Hesionidae	1.00 ±	0.37			1.00 ±	0.63											0.33 ±	0.33
Nereididae 1													10.50 ±	1.91			6.83 ±	1.22
Nereididae 2	0.50 ±	0.34	0.50 ±	0.50	1.67 ±	0.42	0.17 ±	0.17	0.17 ±	0.17					0.33 ±	0.21		
Nereididae 3			0.17 ±	0.17														
Platynereis bicanaliculata	0.50 ±	0.50			0.83 ±	0.54							0.67 ±	0.49				
Exogone sp.	21.00 ±	5.80	12.83 ±	1.54	16.67 ±	5.58	17.83 ±	1.62	14.50 ±	3.78	23.00 ±	7.72	74.33 ±	7.77	22.00 ±	4.13	43.83 ±	9.33

	Live Rhodolith						Dead Rhodolith						Sand					
	Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry	
Syllidae					1.00 ±	0.82	1.50 ±	0.62	0.67 ±	0.33	0.33 ±	0.21	0.67 ±	0.67				
Phyllodocidae					0.50 ±	0.22			0.17 ±	0.17			0.67 ±	0.49	0.33 ±	0.21	0.33 ±	0.21
Oweniidae	1.00 ±	0.37	1.17 ±	0.31	1.00 ±	0.63	2.17 ±	0.95	3.33 ±	1.12	0.67 ±	0.33	1.33 ±	0.49			0.17 ±	0.17
Sabellariidae																	0.33 ±	0.21
Sabellidae	3.67 ±	1.17	1.17 ±	0.17	3.17 ±	1.19			0.00 ±		0.33 ±	0.21	8.83 ±	1.89	1.17 ±	0.48	4.83 ±	1.35
Spoinidae 1	1.83 ±	0.60	12.67 ±	3.23	21.83 ±	4.90	0.67 ±	0.33	4.67 ±	1.99	1.67 ±	0.84	11.83 ±	1.76	4.50 ±	1.65	4.33 ±	1.20
Spionidae 2	1.67 ±	0.56	5.17 ±	1.05			5.50 ±	3.86	0.50 ±	0.50							0.17 ±	0.17
Spionidae 3							0.17 ±	0.17										
Cirratulidae 1	0.50 ±	0.34	0.17 ±	0.17	0.33 ±	0.33	1.33 ±	0.61	0.67 ±	0.42			0.33 ±	0.33				
Cirratulidae 2					0.17 ±	0.17			0.17 ±	0.17	0.33 ±	0.21	0.33 ±	0.33				
Flabelligeridae	1.00 ±	0.52	1.00 ±	0.26	0.33 ±	0.33	0.17 ±	0.17	0.83 ±	0.48			0.17 ±	0.17	0.17 ±	0.17		
Pista sp.	0.17 ±	0.17	0.50 ±	0.34	5.83 ±	2.04	0.50 ±	0.34	0.33 ±	0.33							0.33 ±	0.21
Terebellidae 1					0.17 ±	0.17							0.33 ±	0.21	1.67 ±	0.49		
Terebellidae 2	0.50 ±	0.34																
Terebellidae 3	0.33 ±	0.33																
Polychaeta 11													26.17 ±	7.99	0.17 ±	0.17	10.17 ±	9.97
Polychaeta 13	0.17 ±	0.17	0.67 ±	0.49	0.33 ±	0.33			0.17 ±	0.18	0.17 ±	0.17	1.00 ±	0.63	0.17 ±	0.17	5.00 ±	1.53
Polychaeta 16			0.17 ±	0.17														
Polychaeta 19	0.83 ±	0.65	0.33 ±	0.33	7.33 ±	2.89	0.83 ±	0.65	0.17 ±	0.17	4.00 ±	1.26	0.17 ±	0.17				
Polychaeta 23			0.50 ±	0.34	1.00 ±	0.82	0.50 ±	0.50	0.17 ±	0.17								
Polychaeta 25	5.67 ±	1.65			0.33 ±	0.21	0.33 ±	0.21										
Polychaeta 28	2.00 ±	0.52					0.17 ±	0.17										
Polychaeta 29													0.17 ±	0.17			3.17 ±	0.75
Polychaeta 30					0.33 ±	0.33	0.33 ±	0.21			1.00 ±	0.82					0.67 ±	0.33
Polychaeta 34					0.17 ±	0.17			1.00 ±	0.68			0.50 ±	0.50	0.33 ±	0.21		
Polychaeta 38					0.17 ±	0.17												
Polychaeta 40					0.50 ±	0.34												
Polychaeta 41					0.17 ±	0.17												
Polychaeta 42	1.50 ±	1.50			1.00 ±	0.37					0.17 ±	0.17						
Polychaeta 43	0.17 ±	0.17			0.33 ±	0.21												
Polychaeta 44					0.17 ±	0.17												
Polychaeta 47	0.33 ±	0.33									3.00 ±	1.90						
Polychaeta 48											0.50 ±	0.22						
Polychaeta 50											0.17 ±	0.17						
Polychaeta 51															0.33 ±	0.21		
Polychaeta 53			0.17 ±	0.17					0.33 ±	0.33								
Polychaeta 55			0.17 ±	0.17					0.00 ±									
Polychaeta 56									0.17 ±	0.17								
Polychaeta 57									0.17 ±	0.17								
Polychaeta 58									0.17 ±	0.17								
Polychaeta 59	0.17 ±	0.17																
Polychaeta 60	0.17 ±	0.17																
Polychaeta 63											0.17 ±	0.17	1.50 ±	0.81	0.17 ±	0.17		
Arthropoda																		
Chelicerata																		
Acari			0.17 ±	0.17	0.17 ±	0.17												

	Live Rhodolith						Dead Rhodolith						Sand					
	Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry	
Pycnogonida					0.83 ±	0.31			0.17 ±	0.17	0.17 ±	0.17			0.17 ±	0.17	0.33 ±	0.21
Crustacea																		
Copepoda																		
Copepoda 1					0.50 ±	0.34							0.17 ±	0.17				
Copepoda 2					0.17 ±	0.17												
Ostracoda																		
Ostracoda 1	0.50 ±	0.34	1.17 ±	0.48	0.33 ±	0.21	1.00 ±	1.00	2.00 ±	0.86	0.17 ±	0.17	0.33 ±	0.21	0.67 ±	0.49		
Asteropella sp.					0.17 ±	0.17					0.17 ±	0.17	1.83 ±	0.54			0.50 ±	0.34
Myodocopida 1	1.00 ±	0.52	2.33 ±	0.61	0.17 ±	0.17	2.00 ±	0.82	3.67 ±	1.63	0.33 ±	0.21	14.83 ±	5.18	15.83 ±	3.53	1.33 ±	0.49
Myodocopida 2			1.00 ±	1.00	1.83 ±	1.17			0.33 ±	0.21	0.67 ±	0.67			0.17 ±	0.17		
Myodocopida 3											0.33 ±	0.21	0.83 ±	0.31			11.83 ±	2.40
Neoesidea sp.	19.33 ±	4.95	37.50 ±	7.99	17.33 ±	3.98	18.00 ±	2.73	58.00 ±	18.59	15.00 ±	4.29	0.33 ±	0.21	1.17 ±	1.17	0.33 ±	0.33
Macrocypris sp.	35.00 ±	10.11	43.83 ±	4.39	10.50 ±	3.74	7.00 ±	3.92	22.17 ±	6.75	1.17 ±	0.48	0.50 ±	0.34			0.33 ±	0.21
Rutidera sp.	0.17 ±	0.17	0.17 ±	0.17													1.00 ±	0.82
Radimella sp.			0.83 ±	0.83														
Tanaidacea																		
Leptochelida sp. 1	10.00 ±	2.74	9.83 ±	1.82	6.17 ±	3.54			0.67 ±	0.49	0.33 ±	0.21			0.17 ±	0.17	4.50 ±	1.84
Leptochelida sp. 2	2.50 ±	1.57	1.83 ±	1.28	6.00 ±	1.34												
Psuedotanais sp.	0.83 ±	0.65	1.50 ±	0.56	1.00 ±	0.45	0.33 ±	0.21										
Zeuxo sp.	37.33 ±	14.83	53.50 ±	9.20	123.33 ±	26.92	0.50 ±	0.22	0.67 ±	0.21	0.50 ±	0.50			0.33 ±	0.33	1.83 ±	0.65
Anatanais sp.	8.00 ±	4.16			49.50 ±	9.79			0.17 ±	0.17	0.50 ±	0.34	0.17 ±	0.17			0.67 ±	0.33
Decapoda																		
Loxorhynchus sp.	0.17 ±	0.17	0.17 ±	0.17	0.50 ±	0.22												
Mysida																		
Mysidae 1			1.50 ±	0.56	0.50 ±	0.34											0.17 ±	0.17
Mysidae 2					0.17 ±	0.17												
Pseudomma sp.			0.17 ±	0.17														
Mysidae 4					0.33 ±	0.21												
Amphipoda																		
Caprellidae 1	9.33 ±	1.63	7.33 ±	1.58	4.17 ±	1.35	0.50 ±	0.34	0.17 ±	0.17					0.17 ±	0.17	0.17 ±	0.17
Caprellidae 2	0.17 ±	0.17			1.83 ±	1.22	0.17 ±	0.17							0.33 ±	0.21	0.67 ±	0.67
Caprellidae 3							0.00 ±		0.00 ±				3.33 ±	1.33				
Caprellidae 4					0.33 ±	0.33	0.00 ±		0.00 ±									
Phoxocephalidae	3.67 ±	1.05	5.67 ±	1.61	4.33 ±	2.29	1.17 ±	0.48	0.50 ±	0.34	0.17 ±	0.17	5.67 ±	1.54	1.50 ±	0.34	14.83 ±	2.30
Aoridae 1	43.50 ±	13.06	55.50 ±	9.18	35.00 ±	11.64	0.33 ±	0.21	1.00 ±	0.45	0.33 ±	0.21			0.33 ±	0.33	0.67 ±	0.49
Amphipoda 3			0.67 ±	0.49	1.17 ±	0.60			7.17 ±	4.21	0.17 ±	0.17	1.33 ±	1.33	2.67 ±	1.38	21.17 ±	5.16
Amphipoda 4	0.67 ±	0.49	0.83 ±	0.40					0.00 ±				1.00 ±	0.45	0.67 ±	0.33	1.50 ±	1.31
Amphipoda 5			1.67 ±	0.67	1.00 ±	0.63			7.00 ±	2.72	1.17 ±	0.65	0.83 ±	0.54	0.50 ±	0.34	10.00 ±	2.89
Amphipoda 6			0.17 ±	0.17					0.00 ±								0.83 ±	0.54
Amphipoda 7	2.33 ±	1.23					0.17 ±	0.17	0.17 ±	0.17			0.33 ±	0.21				
Pariphinotus sp.	1.33 ±	0.76			2.67 ±	0.99	0.33 ±	0.33			0.33 ±	0.21						
Amphipoda 9																	0.83 ±	0.31
Amphipoda 10					1.50 ±	1.50											1.17 ±	0.40
Amphipoda 11					0.50 ±	0.34												

	Live Rhodolith			Dead Rhodolith			Sand		
	Avalon	Isthmus	Cherry	Avalon	Isthmus	Cherry	Avalon	Isthmus	Cherry
Isopoda									
Isopoda 1									0.33 ± 0.33
Apanthura californiensis	3.00 ± 0.68	3.17 ± 0.60	2.50 ± 1.15	2.33 ± 0.84	2.00 ± 1.03	3.83 ± 2.50	0.17 ± 0.17		0.50 ± 0.50
Asellota	0.33 ± 0.21			0.50 ± 0.34	0.17 ± 0.17				
Isopoda 4	1.67 ± 0.67	0.83 ± 0.40	1.50 ± 0.76						
Isopoda 5	2.17 ± 1.80		7.33 ± 3.66						
Paranthura sp.	0.50 ± 0.34		0.17 ± 0.17	0.50 ± 0.50					
Isopoda 7	0.17 ± 0.17								
Isopoda 8					0.33 ± 0.33				
Munna sp.	0.67 ± 0.33		0.50 ± 0.22			0.33 ± 0.21			
Cumacea	4.17 ± 1.40	1.50 ± 0.62	7.83 ± 2.02	0.67 ± 0.49	0.67 ± 0.21	1.83 ± 0.75	1.00 ± 0.52		0.33 ± 0.21
Leptostraca	0.83 ± 0.40	0.17 ± 0.17				0.50 ± 0.34			
Mollusca									
Bivalvia									
Parvilucina		0.17 ± 0.17			0.67 ± 0.33			0.17 ± 0.17	0.33 ± 0.21
Cryptomya californica	0.17 ± 0.17	0.17 ± 0.17	0.17 ± 0.17	0.17 ± 0.17		0.17 ± 0.17		0.33 ± 0.33	
Modiolus sp.	0.83 ± 0.48	0.17 ± 0.17	0.50 ± 0.22	0.17 ± 0.17					
Crenella descussata	0.17 ± 0.17	2.00 ± 0.52	0.83 ± 0.31	0.50 ± 0.34	1.83 ± 0.79	0.33 ± 0.21	0.17 ± 0.17		0.33 ± 0.33
Americardia biangulata					0.17 ± 0.17	0.17 ± 0.17			
Psammobiidae			0.17 ± 0.17						
Tellina sp.					0.17 ± 0.17		0.17 ± 0.17	1.50 ± 0.43	0.83 ± 0.31
Veneroida 1			1.83 ± 1.14		0.33 ± 0.33				
Veneroida 2							0.17 ± 0.17	0.33 ± 0.21	0.50 ± 0.22
Bivalvia 10							1.50 ± 0.85	1.00 ± 0.63	
Bivalvia 11							1.17 ± 0.31		
Bivalvia 12								0.33 ± 0.21	
Polyplacophora									
Polyplacophora 1		0.17 ± 0.17							
Polyplacophora 2		0.17 ± 0.17	0.50 ± 0.34						
Gastropoda									
Pyriscus sp.						0.17 ± 0.17			
Turbinidae 1						0.17 ± 0.17			
Turbinidae 2	0.17 ± 0.17	0.50 ± 0.34		0.17 ± 0.17					
Megastraea	0.17 ± 0.17								
Calptraeidae		0.17 ± 0.17	0.33 ± 0.21		0.17 ± 0.16				
Limpet 2		0.17 ± 0.17							
Amphithalamus sp.	80.00 ± 23.70	88.67 ± 16.81	198.83 ± 32.79	17.33 ± 9.18	9.67 ± 2.23	10.17 ± 3.16			
Caecum californicum	0.50 ± 0.34	0.50 ± 0.22	1.00 ± 0.37	0.50 ± 0.34	0.17 ± 0.17				
Caecum crebricinctum	0.17 ± 0.17		0.50 ± 0.34	0.50 ± 0.34	0.17 ± 0.17	0.33 ± 0.33			

	Live Rhodolith						Dead Rhodolith						Sand		
	Avalon		Isthmus		Cherry		Avalon		Isthmus		Cherry		Avalon	Isthmus	Cherry
Alvania sp.					0.67 ±	0.33									
Rissoidae					0.17 ±	0.17	0.17 ±	0.17							
Cystiscus sp.	4.00 ±	1.44	0.33 ±	0.21	3.17 ±	1.11	1.00 ±	0.63	0.17 ±	0.17					
Opistobranchia											0.17 ±	0.17			
Gastropoda 5					0.83 ±	0.83									
Gastropoda 8	0.17 ±	0.17			0.17 ±	0.17									
Gastropoda 17													0.33 ± 0.33		
Gastropoda 18			0.17 ±	0.17											
Chaetognatha															
Spadella bradshawi	4.67 ±	1.28	2.17 ±	1.38	7.50 ±	1.70	1.67 ±	1.28	0.17 ±	0.17	1.33 ±	0.42			
Echinodermata															
Asteroidea															
Pteraster tesselatus	0.17 ±	0.17			0.17 ±	0.17									
Echinoidea															
Lytechinus pictus	0.33 ±	0.33			0.67 ±	0.33									
Dendraster sp.															0.17 ± 0.17
Ophiuroidea															
Ophiuroidea 1	0.50 ±	0.22	1.17 ±	0.48	3.17 ±	1.92			0.17 ±	0.17	0.50 ±	0.50	0.17 ± 0.17		
Ophiuroidea 2					3.00 ±	0.68	0.33 ±	0.21			0.33 ±	0.33		0.17 ± 0.17	
Ophiuroidea 3					0.17 ±	0.17	0.00 ±								
Ophiuroidea 4			0.17 ±	0.17	0.17 ±	0.17	0.00 ±								
Ophiuroidea 5	0.17 ±	0.17			0.33 ±	0.21	0.00 ±								
Ophiuroidea 6	0.33 ±	0.33	0.17 ±	0.17	1.17 ±	1.17	0.50 ±	0.50			1.67 ±	1.48	0.17 ± 0.17		
Ophiuroidea 7					0.50 ±	0.50	0.00 ±								
Ophiuroidea 8							0.00 ±						0.17 ± 0.17		
Ophiuroidea 9							0.00 ±				0.33 ±	0.33			
Holothuroidea															
Holothuroidea 1	0.83 ±	0.54			0.17 ±	0.17	0.50 ±	0.34	0.17 ±	0.17	0.17 ±	0.17	1.50 ± 0.62		3.50 ± 1.23
Leptosynapta sp.	0.50 ±	0.34	0.33 ±	0.33	1.67 ±	1.12	0.00 ±				0.50 ±	0.34		0.17 ± 0.17	
Holothuroidea 3	0.17 ±	0.17					0.33 ±	0.21							
Chordata															
Hemichordata			0.17 ±	0.17			0.17 ±	0.17					0.33 ± 0.21	0.67 ± 0.49	0.33 ± 0.21