RIPPLED SCOUR DEPRESSIONS ADD ECOLOGICALLY SIGNIFICANT HETEROGENEITY TO SOFT SEDIMENT HABITATS ON THE CONTINENTAL SHELF

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by

Todd Russell Hallenbeck

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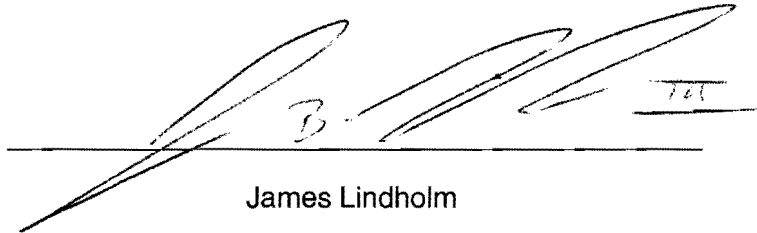
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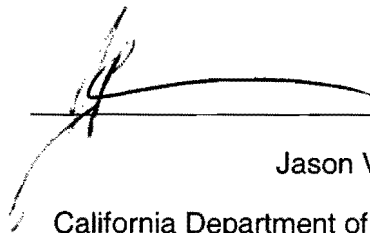HETEROGENEITY TO SOFT SEDIMENT HABITATS ON THE CONTINENTAL
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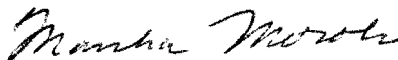California State University, Monterey Bay

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DEDICATION

I dedicate this work to my family for encouraging me to dream and to the oceans for giving me something to dream about.

ABSTRACT

RIPPLED SCOUR DEPRESSIONS ADD ECOLOGICALLY SIGNIFICANT
HETEROGENEITY TO SOFT SEDIMENT HABITATS ON THE
CONTONENTAL SHELF

By

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Master of Science in Coastal and Watershed Science and Policy

California State University Monterey Bay, 2011

Comprehensive high-resolution seafloor mapping of California's state waters have revealed rippled scour depressions (RSD) to be one of the most abundant and widespread habitats of the inner continental shelf. These sharply delineated elongate features range in size from 100's to 1000's of m^2 in aerial extent and are characterized by 30 to 50 cm deep depressions of coarser sediments and longer period bedforms than found on the surrounding seabed. Although RSDs have been identified on many of the world's continental margins, previous studies focused on their geomorphology and dynamics, leaving the ecological influence and associated biological communities of RSDs unexplored. Here we test the hypothesis that there are ecologically important differences in the density and richness of benthic fish and invertebrate groups inside and outside RSDs. A small remotely operated vehicle (ROV) was used to survey twenty RSDs in three depth zones (shallow [<15 m], intermediate [15 to 30 m], deep [>30 m]) within Monterey Bay, California. Sediment grab samples taken inside and outside of RSDs confirmed the mean grain size was significantly larger inside RSDs (0.5 to 0.9 mm) than outside (0.15 to 0.4 mm). As predicted from known species/grain size relationships, mean density of combined trophic groups was lower inside RSDs in the shallow, intermediate, and deep zones (0.03, 0.16, 0.21 ind m^{-2} respectively) than outside (0.04, 0.31, 0.45 ind m^{-2} respectively). Richness of trophic groups was also lower inside RSDs in each depth zone (0.03, 0.10, 0.14 taxa m^{-2} respectively) than outside RSDs (0.03, 0.17, 0.25 taxa m^{-2} respectively). Surprisingly, RSDs did contain significantly more young of the year (YOY) rockfish (especially ESA threatened canary rockfish, *Sebastes pinniger*) and small flatfish than adjacent fine sediments, suggesting a possible nursery function for these otherwise depauperate coarse-grained habitats. This study illustrates the utility of high-resolution habitat mapping data in refining our understanding of seafloor landscape heterogeneity and species habitat relationships specifically in the context of adaptive management in marine spatial planning.

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Introduction

Rippled scour depressions (RSDs, Fig.1) have been identified and physically described in small scale studies on many of the world's continental shelves (Bellec et al. 2010, Garnaud et al. 2005, Gutierrez et al. 2005, Iacono & Guillen 2008). These elongate shallow depressions (0.3 to 1 m, in depth), oriented normal to the general trend of the isobaths, are characterized by long crested bedforms (0.5 to 1 m wavelength), coarse sediment (0.3 to 1 mm), and abundant shell hash. RSDs have been found in water depths of 15 to 150 m and reported dimensions of 30 to 250 m wide, and 100 to 1000 km long (Cacchione et al. 1984, Bellac et al. 2010, Phillips 2007). The sediments surrounding RSDs are typically of finer grain size (0.05 to 0.3 mm), shorter period bedforms, with a sharp edge delineating the coarser-grained RSDs (Diesing et al. 2006, Goff et al. 2005, Green et al. 2004). Although previous studies provide detailed information on the physical characteristics of RSDs within narrowly defined study sites, regional assessment of RSD distribution and abundance was not possible. Now with the near completion of the California Seafloor Mapping Project (CMSP), comprehensive high-resolution multibeam bathymetric maps of the seafloor reveal RSDs cover approximately 180 km^2 of 7700 km^2 mapped thus far, representing the most prominent and widespread soft-bottom feature within the low-relief unconsolidated sediments of California's continental shelf (Davis et al. in prep).

Hypothesized mechanisms for the formation of RSDs include tidal scour (Bellac et al. 2010), cross shore currents (Cacchione et al. 1984), storm generated downwelling (Garnaud et al. 2005), and alongshore currents (Murray & Thieler 2004). Bottom currents have been measured as high as 60 cm s^{-1} inside RSDs (Bellec et al. 2010), compared to currents speeds of 20 cm s^{-1} outside RSDs (Green et al. 2004). It is these strong currents which scour away fine sediment and create large bedforms. The bedforms then help to maintain the

RSD by disrupting the laminar flow of water and creating a localized turbulence which resuspends fine sediment. While RSDs have been described from many parts of the world and are an abundant habitat type of the inner continental shelf the majority of research has focused on the physical character and geomorphic dynamics of these habitat features (Bellec et al. 2010, Garnaud et al. 2005, Gutierrez et al. 2005, Iacono & Guillen 2008). As a result, little is known about the biological communities associated with or ecological importance of RSDs. However, knowledge of their physical properties can be combined with natural history associations to make predictions about the likely influence of RSDs on the distribution, diversity, and abundance of soft-bottom benthic organisms commonly found on the continental shelf.

The role of water depth, temperature, and substrate in the large-scale distribution and abundance of benthic communities has been well described (Warwick & Davies 1977, Langton & Watling 1990, Barry & Dayton 1991, Snelgrove & Butman 1999, Whitman 2004). Typically, abundance of fish and invertebrates increase with depth in soft sediment habitats on the continental shelf (Kostylev et al. 2001, Allen & Moore 1996). At smaller scales, the distribution of benthic organisms is mediated by a variety of factors, including fine scale habitat attributes such as grain size (Snelgrove et al. 1999, Brown & Collier 2008, Butman et al. 1988), hydrodynamic forces (Aller 1996, Pillay et al. 2007), bedform type (Auster et al. 2003a, Lindholm et al. 2004), and biogenic structure (Woodin 1978, Auster et al. 1991, Auster et al. 2003b, Lindholm et al. 2007, Stoner et al. 2007). For example, Kostylev et al. (2001) categorized benthic communities on the Scotian shelf according to sediment characteristics, water depth, and dominant benthic associations using multibeam sonar and bottom photography. Similarly, Brown and Collier (2008) used side scan sonar to map various sediment types (sand, mud, coarse, mixed) and found the highest diversity of infaunal invertebrate communities in heterogeneous sedimentary environments. Additionally, studies have shown fish size is related to sediment

grain size (Gibson & Robb 1992) and bedform period and amplitude (Auster et al. 2003a, Gerstner 1998).

Here we use inferences from species/habitat association studies to test *a priori* predictions about the influence of RSDs on the distribution and abundance of benthic species and assemblages commonly found in the soft bottom habitats of the California continental shelf. Fish assemblages include *Paralichthydae* (left eyed flatfish) species such as *Paralichthys californicus* (California halibut), *Platichthys stellatus* (starry flounder), *Eopsetta jordani* (petrale sole), and *Pleuronectidae* (right eyed flatfish) species such as *Citharichthys sordidus* (Pacific sanddab), as well as *Ophiodon elongatus* (Lingcod). Invertebrate assemblages include *Cancer magister* (Dungeness crab), *Pagurus* spp. (hermit crabs), *Nassarius* spp. (Mud snails), *Octopus rubescens* (red octopus), *Luidia foliolata (sand star), Asterina miniata* (bat star), *Pycnopodia helianthoides* (sunflower star), *Dendraster extentricus* (Western sand dollar), *Ptilosarcus gurneyi* (sea pen), *Ophiothrix spiculata* (spiny brittle stars), *Urechis caupo* (Fat Innkeeper worm), and *Callinassidae spp.* (Ghost shrimp). All are species or species groups found over sandy or muddy habitat on the continental shelf from depths of 10 m to 300 m (Allen 2006, Lenihan & Micheli 2001, Kvitek et al. 2008). Many of these species actively choose to associate with finer sediment types, which can facilitate ease of burial for refuge (Gibson & Robb 1992, Tanada 1990, Burke et al. 1991) and typically support higher abundances of infaunal prey items than coarser sediments (Brown & Collier 2008, Abookhire & Norcross 1998). Additionally, the presence of strong bottom currents and turbulence induced by flow over the higher RSD bedforms thought to be required for the maintenance of RSDs through the resuspension and transport of fine sediments (Green et al. 2004) could negatively impact the density and diversity of benthic communities inside RSDs by limiting settlement and recruitment of organisms (Kaiser & Spencer 1996, Aller 1996, Jumars & Nowell 1984) or interfering with the filter feeding apparatus of some benthic invertebrates (Pillay et al. 2007, Rhoads &

Young 1970). However, the halo of resuspended organic material just outside the RSDs may be a beneficial mechanism for bringing detritus to filter feeding benthic organisms that create biogenic habitat for demersal fish species (Woodin 1978). The physical characteristics of RSDs, especially at their boundaries, are likely to influence the ecological role of these habitats and allow us to make predictions about the benthic communities likely associated with RSDs.

In a management context, coastal and marine spatial planning is emerging as the dominant paradigm for the allocation of human activities in the marine environment (Pauly et al. 2002, Browman & Stergiou 2004, Pikitch et al. 2004, Gleason 2010). At the state, regional, and federal levels resource management agencies are using best available science to develop spatial planning frameworks to balance the conflict of human use with the mandate to restore ecosystem health by protecting representative habitats (CDFG 2008, NOP 2010). California has adopted this approach through the implementation of the Marine Life Protection Act (MLPA) mandating the creation of North America's first statewide network of marine protected areas (MPA). The MLPA requires this network be comprised of representative habitat types found within state waters including; rocky reefs, intertidal zones, submerged pinnacles, kelp forests, submarine canyons, seagrass beds, and soft bottom habitats (CDFG 2008). Representative habitat was classified by large-scale (50 to 100 km) features like substrate type, depth, and bathymetric features but did not consider fine scale features like grain size or bedforms type in maintaining diversity or ecosystem function as that data largely did not exist. However, these plans call for an adaptive approach to allow for refinements in both the design and implementation of spatial plans as better knowledge of ocean ecosystems becomes available (CDFG 2008). Critical to effective marine spatial plans is a clear understanding of habitat associations of ecologically and economically important organisms and the functional role of habitats over multiple spatial scales (COST 2010). This is especially true for the unconsolidated sedimentary

environments in which RSDs occur comprising over 80% of California's continental shelf (Allen 2006) and supporting ecologically and economically important fish species (Starr & Yoklavich 2008). Given the abundant and widespread nature of RSDs, if they have a significant influence on the distribution and abundance of benthic communities they may have a profound influence on the performance of marine spatial plans and may need to be incorporated into their design and evaluation.

The goal of this study was to determine the ecological role of RSDs and inform the on-going refinement of California's marine spatial planning and evaluation efforts through the identification of key soft sediment habitats. We evaluated the general hypothesis that there are differences in the distribution and abundance of benthic communities within and adjacent to RSDs based on physical differences inside and outside RSDs. Specifically, we predicted density and richness of benthic organisms would be lower inside RSDs because coarse sediments generally support less diverse and less abundant communities (Brown & Collier 2008, Snelgrove et al. 1999, Abookhire & Norcross 1998). The biological differences between habitats should increase with depth because the physical differences between habitats will also increase with depth along the disturbance gradient created by hydrodynamic scouring (Green et al. 2004, Kostylev et al. 2001, Allen & Moore 1996). Additionally, we hypothesize there will be larger fish inside RSDs because fish length has been correlated with bedform size and RSDs create and maintain larger bedforms than the surrounding fine sediment (Auster et al. 2003a, Gerstner 1998).

Methods

The locations of six distinct RSD fields were identified in the Monterey Bay, CA from multibeam and side scan sonar data collected in 2001, 2004, and 2010 by the California State University, Monterey Bay, Seafloor Mapping Lab

(SFML) and used in the California Seafloor Mapping Project (Fig. 2). A survey cruise was conducted from 06 to 09 July 2009 aboard the *RV Macginitie* to characterize the sediments and benthic communities associated with RSDs and adjacent areas along transects in these six study sites (Fig. 2).

Analysis of sediment grain size

Sediment grabs (n = 32) were conducted opportunistically along transects, using a sediment sampler modeled after a Kahlsico Scoopfish, deployed from the vessel to verify expected sediment differences inside and outside of RSDs in Monterey Bay. Samples were only taken in locations where both multibeam imagery and video footage verified habitat type. Coarse fraction analysis was conducted following the methods of Poppe et al. (2000) and mean grain size was estimated for each sample. Welch's Two Sample t-test was performed to detect differences in the mean grain size between the two habitat types.

ROV transects

Video transects were conducted using a small acoustically tracked remotely operated vehicle (ROV) (LBV 200L, Seabotix Inc.) equipped with a digital color camera (560 line wide dynamic range, 0.3 lux), external LED lights, and 5 cm paired scaling lasers. Each transect was conducted at a speed over ground of 0.5 to 1 knots at an altitude of 0.5 to 1 m above the seafloor with a downward pointing camera angle of 45°. The position of the ROV was recorded every 0.5 s using an ultra short baseline (USBL) acoustic tracking system with ± 3° accuracy (Micronav, Tritech Inc.) and converted to real world geographic coordinates. The geographic position of ROV and a universal time code were stamped on the audio and video track to facilitate matching observations with real world locations and against side scan and multibeam imagery.

A total of thirty ROV transects (10 to 50 m water depth) were conducted to collect continuous video imagery inside RSDs ("Inside") and outside RSDs

("Outside") (Fig. 2). Transects were stratified by depth and start locations were haphazardly selected in the study area to ensure adequate sampling inside, outside, and across RSD boundary within three depth zones (shallow [<15 m], intermediate [15 to 30 m], deep [>30 m]). We ran transects across boundaries to investigate if the distance from the boundary influenced biological communities. Transect lengths ranged from 90 to 1260 m depending on vessel drift and extent of RSD habitat.

Analysis of Video Imagery

ROV video was collected continously throughout each transect. Data on the density and richness of benthic organisms were extracted from approximately 15 hours of ROV video using a frame-by-frame approach in which successive non-overlapping video frames were treated as individual quadrats. All fish and macro invertebrates that occurred within each sampling frame were counted and identified to the lowest taxonomic level possible. Organisms were then binned into one of three trophic groups; suspension feeders ("Suspension"), invertebrate predators ("Invertebrates"), and benthic fish predators ("Fish"). The density and richness of combined trophic groups ("Total") was also analyzed as a measure of the entire community abundance and richness. A fourth group added *post hoc* was comprised of young of the year (YOY) *Sebastes* spp. and analyzed separately. Paired lasers were used to estimate bedform period and amplitude, total length (TL) of each fish observed, and the width of the sampling frame to facilitate calculation of total area covered by each transect. Fish smaller than 2 cm or that occurred only partially in frame were not counted. Additionally, for three groups of macro invertebrates that were often too numerous in frames to count as individuals (*D. exentricus*, *U. caupo* and *Callinassidae* spp. burrows, and *Ophiuroid* spp.) percent cover was measured using a 100 point contact grid for sampling each frame. *U. caupo* and *Callinassidae* spp. are infaunal invertebrates that co-occur on the Monterey Bay shelf (Kvitek et al. 2008) and create distinct "volcano" burrow openings.

Physical parameters including substrate, relief, bedform type, and water depth were recorded for each sampling frame. Habitat type (Inside, Outside) was determined using combinations of the physical parameters. Criteria used to define inside RSD habitat included coarse sediment substrate, bedform period >0.5 m, and amplitude >0.25 m. Outside RSD habitat was defined as unconsolidated fine sediment substrate, bedform period <0.5 m, and amplitude <0.25 m. Data QA/QC was conducted by randomly re-analyzing 1.5 hours of video imagery. All organism identifications were verified prior to analysis.

Variogram analysis of abundance data was used to identify the optimal scale for sub sampling transects following the methods of Camerero and Gutierrez (2002). Transects within each habitat type were subsampled *post hoc* into samping units based on the spatial scales suggested by the variogram analysis. Data collected from individual sampling frames was aggreagated into these larger sampling units. Density and richness of benthic biota were calculated for each sampling unit as measured by the linear distance traveled by the ROV multiplied by 0.87 m, the average width of the sampling frame. This width was determined by averaging the width of 100 randomly selected sampling frames, as estimated by the paired lasers.

Two way ANOVAs were used to test for significant differences in the mean density and richness of combined trophic groups between habitat and water depth. Multivariate analysis of variance (MANOVA) was performed in the R stats package (R Development Core Team 2010) to simultaneously estimate the response (e.g. mean density and richness) of individual trophic groups to habitat and depth. MANOVAs were more appropriate than simple ANOVA because they simultaneously estimated covariance between groups and no adjustment of the alpha level was needed. Eigen values were calculated that represented the linear combination of all dependent variables, which were used to estimate the test statistic. Roy's greatest root is the first discriminant function and was used

because it is the most amenable to *post hoc* pair wise tests of interaction effects between response variables. Tukey HSD *post hoc* analysis were performed on the groups that exhibited significant interaction affects.

$$(X_{1ij} X_{2ij}) T \mu + T_i + E_{ij}$$

Where $(X_{1ij} X_{2ij})$ = a vector of densities of trophic group 1 and trophic group 2 of the jth replicate in the ith treatment, T = vector transpose, μ = grand mean, T_i = deviations from the grand mean due to the ith treatment, and E_{ij} = the deviation of the jth individual from the mean of the ith treatment.

Data were tested for normality and equal variance to meet the assumptions of ANOVA. Density data were right skewed (i.e. Poisson distribution) and a square root transformation was performed prior to statistical analysis.

Results

In total, 2953 observations of 28 different fish and invertebrate taxonomic groups were derived from the 20 rippled scour depressions examined. Within each of three depth zones (shallow [<15 m], intermediate [15 to 30 m], and deep [>30 m]), totals of 59, 2034, and 860 individuals were identified belonging to 13, 25, and 18 separate taxonomic groups, respectively. A total of 32 sediment grab samples from inside (n = 12) and outside (n = 20) RSDs were collected and analyzed for mean grain size.

Sediment grain size Inside and Outside RSDs

Grain size analysis of sediment samples revealed consistent differences in mean grain sizes found inside and outside of RSDs across all depth zones (Fig. 3). As expected, mean sediment grain size from inside RSDs (0.70 ± 0.05 SE mm, n = 12) was significantly coarser than samples collected outside RSDs (0.21 ± 0.04 SE mm, n = 20, Welch's two sample t-test, p < 0.001).

Analysis of Spatial Scale

Variogram analysis revealed significant clustering of organism abundance at spatial scales of 10, 20, and 40 m. Video transects were therefore broken into quantitative sampling units based on these three sampling scales and analyzed separately. However, all significant effects present at the 10 m scale were also present at the 20 and 40 m scale, with the exception of fish density and richness, which were significant at the 10 m but not the 20 and 40 m scale. The overall relationship between density and richness with habitat and depth was preserved across all sampling scales, therefore only the results from the 10 m scale are presented here.

Effects of RSD habitat on density and richness

One-way ANOVA revealed the mean density of combined trophic groups outside RSDs (0.26 ± 0.01 ind m^{-2}, SS = 9.46, Df = 1, F = 22.16, p < 0.001) was greater than inside RSDs (0.17 ± 0.01 ind m^{-2}) and the mean richness of combined trophic groups outside RSDs (0.15 ± 0.01 ind m^{-2}, SS = 8.38, Df = 1, F = 21.37, p < 0.001) was greater than inside RSDs (0.11 ± 0.01 ind m^{-2}). Density of individual trophic groups was greater outside RSDs, suspension feeders (0.02 ± 0.00 ind m^{-2}, SS = 0.447, Df = 1, F = 12.43, p < 0.001), invertebrate predators (0.06 ± 0.00 ind m^{-2}, SS = 2.66, Df = 1, F = 32.17, p < 0.001), and fish (0.18 ± 0.01 ind m^{-2}, SS = 1.25, Df = 1, F = 4.063, p = 0.04) than inside RSDs (0.01 ± 0.00, 0.03 ± 0.00, 0.13 ± 0.01 ind m^{-2} respectively). Mean richness was greater outside RSDs for suspension feeders (0.01 ± 0.00 ind m^{-2}, SS = 0.947, Df = 1, F = 9.51, p = 0.002), invertebrate predators (0.05 ± 0.00 ind m^{-2}, SS = 10.18, Df = 1, F = 29.97, p < 0.001), and fish (0.09 ± 0.00 ind m^{-2} SS = 1.51, Df = 1, F = 4.84, p = 0.03) than inside RSDs (0.01, 0.03, 0.08 ± 0.00 ind m^{-2} respectively).

In addition to the differences in the relative abundance, the composition of biological communities (based on the relative ranking of the top five most abundant taxa within each depth zone) differed inside and outside of RSDs

(Tables 1 and 2). This community difference was most pronounced in the shallow zone where *Paralichthyidae* spp. and *Pychnopodia* spp. were abundant inside RSDs but not outside (*Pychnopodia* spp. were never observed outside RSDs). *Cancer* spp. and *Nassarius* spp. were abundant outside shallow zone RSDs but not inside (*Nassarius* spp. were never observed inside RSDs). Unlike the shallow zone, the intermediate zone community was similar between habitats but the ranked abundance of taxonomic groups differed inside and outside RSDs. One notable exception was YOY *Sebastes* spp., which were the second most abundant taxonomic group inside RSDs and only the fifth most abundant group outside RSDs. In the deep zone four of the five most abundant groups were similar between habitats. However, *Ophiuroid* spp., the most abundant outside RSDs, were virtually absent inside RSD.

Effects of RSD habitat and depth on density and richness

At all sampling scales, density of combined trophic groups was greater outside RSD in the intermediate and deep zones (Fig. 4). Multivariate ANOVAs indicated the interaction of habitat and water depth had a significant effect on density and richness of combined trophic groups for all sampling scales except 40 m. Pair-wise comparisons of interaction terms on combined and individual trophic groups were performed *post hoc* using Tukey Honestly Square Differences (HSD). There were no detectable differences in either the density or richness of trophic groups between habitats in the shallow zone.

Interaction of depth and habitat were significant for density and richness of suspension feeders and invertebrate predators ($p < 0.001$, Fig. 4). Density of suspension feeders was greater outside RSDs only in the deep zone ($p < 0.001$) but richness was greater outside in both the intermediate and deep zones ($p = 0.01$ and $p < 0.001$, respectively). Density and richness of invertebrate predators was greater outside in the intermediate and deep zones for all sampling scales but 40 m ($p < 0.001$). Density of fish was greater outside RSDs in the

intermediate zone (p < 0.001) and richness of fish predators was significantly greater outside RSDs in the intermediate zone for the 10 and 20 m sampling scale.

Several invertebrates groups (*D. exentricus, U. caupo/Callinassidae* spp. burrows, and *Ophiuroid* spp.) occurred in dense patches and percent cover was used to estimate their relative density. Because *U. caupo* and *Callinassidae* spp. burrows could not be readily distinguished from video imagery they were necessarily treated as a single group. MANOVA revealed significant interaction of depth and habitat for *D. exentricus, U. caupo/Callinassidae spp.* burrows, and *Ophiuroid* spp. (Table 1). At all sampling scales, mean percent cover of *D. exentricus* was greatest inside RSDs in the shallow zone (p < 0.001). Mean percent cover of *U. caupo/Callinassidae spp.* burrows was greater outside RSDs in the shallow zone (p < 0.001) for all scales and intermediate zone (p < 0.001) at the 10 m scale. Mean percent cover of *Ophiuroid* spp. was greatest outside RSDs in the deep zone (p < 0.001) for all sampling scales.

Fish size and abundance

Two-way ANOVA revealed significant differences in the mean size of flatfish inside and outside of RSDs at all sampling scales (Fig. 5). Mean total length of all flatfish inside and outside RSD was 5.61 ± 0.20 cm and 7.54 ± 0.30 cm, and mean size tended to increase with depth. Mean total length of combined flatfish was greater outside RSD in the intermediate and deep zones (p = 0.003 and p < 0.001).The mean size of individual taxonomic groups was not significantly different, except in the deep zone (p < 0.001). *Paralichthyidae* spp. tended to be larger than *Pleuronectidae* spp., which had the potential to skew differences in fish size inside and outside RSDs. However, a paired T-Test revealed there were not significant differences in the abundance of these two groups across habitats (Table 1).

Interestingly, YOY *Sebastes* spp. were not found in the shallow zone but occurred in greater densities inside RSDs in both the intermediate and deep zones (Fig. 6). Two way ANOVA revealed significant interaction of habitat and depth on mean density of YOY in the intermediate zone ($p < 0.001$). Inside RSDs, YOY density ranged from 0.28 ± 0.06 ind m^{-2} in the intermediate zone to 0.10 ± 0.02 ind m^{-2} in the deep zone. Outside RSDs, YOY density ranged from 0.02 ± 0.00 ind m^{-2} in the intermediate zone to 0.07 ± 0.01 ind m^{-2} in the deep zone. While species identification was difficult for every individual, the distinctive dorsal spots on 45% of the 605 YOY observations allowed them to be positively identified as *S. pinniger* (canary rockfish). Additionally, YOY *S. miniatus* (vermillion rockfish), *S. saxicola* (stripetail rockfish), and *S. mystinus* (blue rockfish), and *S. melanops* (black rockfish) were also positively identified. Generally, YOY *Sebastes* spp. were found within approximately 10 m of the boundary and a third habitat class was created and analyzed *post hoc* to represent this "transition zone." The transition zone was defined (as per the variogram analysis) as a 20 m buffer situated over the boundary. Tukey's pairwise comparisons were performed to compare the density of YOY between the three habitat types (Inside, Transition, Outside). The densities of YOY at the Transition for both the intermediate and deep zones (0.23 ± 0.15 ind m^{-2} and 0.17 ± 0.12 ind m^{-2} respectively) were significantly higher than for outside RSD (0.02 ± 0.00 and 0.07 ± 0.02 ind m^{-2}, $p < 0.001$) but not Inside RSD (0.21 ± 0.04 and 0.09 ± 0.02 ind m^{-2} respectively).

Discussion

This study determined that rippled scour depressions (RSD) found in Monterey Bay, CA are physically representative of RSDs described from other parts of the world and that the biological communities associated with these RSDs are significantly different from those found in the adjacent soft sediments.

Specifically, RSDs sampled in this study had sharply defined boundaries separating their coarser grain sediments and longer period bedforms from the 0.3 to 0.5 m higher adjacent fine sediment plateau. These physical characteristics are consistent with the presence of strong hydrodynamic currents acting inside RSDs to scour away fine sediment and maintain bedforms. As predicted, these coarse sediments tended to support less dense and less diverse biological communities and the density and richness of most trophic groups was lower inside RSDs (Fig. 4). Also as predicted, the relative difference of biological communities inside and outside RSDs increased with depth; a finding consistent with a disturbance gradient declining less rapidly with depth inside RSDs likely due to the stronger currents and greater turbulence found within these features. However, the prediction that larger bedforms would support larger fish was not borne out and the opposite was true; smaller flatfish were found inside RSDs.

The finding that the density of suspension feeders, invertebrate predators, and fish as well as the richness of suspension feeders and invertebrate predators was significantly greater outside RSDs is consistent with our a priori predictions that RSDs are relatively depauperate habitats. This hypothesis was based on physical descriptions of RSDs as coarse sediment depressions found on fine sediment plateaus (confirmed, Fig. 3), combined with the well-established negative correlation between increasing grain size and epifaunal species density and diversity (Snelgrove et al. 1999, Brown & Collier 2008). This negative relationship has been documented for many fish and invertebrates known to actively settle on sediments of a specific grain size (Chia & Crawford 1973, Kurihara 1999, Stoner & Ottoman 2003), preferring finer sediments for ease of burying (Stoner & Ottoman 2003), abundance of infaunal organisms (Brown & Collier 2008, Abookhire & Norcross 1998), or to maintain associations with other benthic organisms (Lindholm et al. 2004). While this work highlights the physical and biological differences inside and outside of RSDs, future work should investigate the possibility of a halo or ecotone effect on the density and diversity

benthic communities at the RSD boundary where physical conditions are dynamic.

Grain size alone does not determine the density or diversity of benthic communities (Snelgrove & Butman 1999) and as predicted, the effect of depth on this relationship was found to be significant as well. The relative difference in density and richness of benthic communities inside and outside of RSDs increased with depth and significant differences were observed in the intermediate and deep zones that were not observed in the shallow zone (Fig. 4). Again, this prediction was based on the physical descriptions of RSDs as chronically disturbed by hydrodynamic currents (Green et al. 2004, Murray & Thieler 2004, Sternberg 1972). On the continental shelf, grain size decreases with depth as the frequency and magnitude of wave/current disturbance rapidly decreases (Allen 2006, Lenihan & Micheli 2001). However, the presence of RSDs out to 150 m water depth indicate that disturbance inside RSDs is maintained over a broader depth range thus amplifying the physical differences between habitats as depth increases (Green et al. 2004, Goff et al. 2005). This disturbance has a strong effect on the physical and biological characteristics of RSDs. In particular, hydrodynamic resuspension of sediments may have a negative impact on filter feeding invertebrate species, whose feeding apparatus may be clogged with suspended sediments (Rhoads & Young 1970, Pillay et al. 2007). Indeed, suspension feeders were generally less dense and less rich inside RSDs (Table 1). Additionally, hydrodynamic scouring may inhibit the settlement of infaunal organisms (Jumars & Nowell 1984) which serve as food for many fish and invertebrate species (Edgar & Shaw 1995, Quammen 1984). While the diversity and abundance of infaunal organisms was not addressed here, the very strong and well documented influence of grain size on the structure of infaunal communities (Brown & Collier 2008, Abookhire & Norcross 1998, Hall and Harding 1997) suggests that RSDs will likely have an even greater influence on infaunal distributions. Explorations of these differences offer

a way to examine hypotheses of food availability as a mechanism for the epifaunal differences described here. Indeed, the more turbulent flow generated by even weak currents moving over the RSD bedforms during non-storm periods could be sufficient to suspend small invertebrate prey in greater abundance than found in the water column over otherwise richer non-RSD sediments, thereby actually increasing prey availability to small fish in the RSDs. The differences in disturbance gradients with depth inside and outside RSDs may partially account for the physical and biological differences we observed, but should be investigated beyond the depths examined here (10 to 50 m) to determine how the distribution and abundance of biological communities changes over the full depth range in which RSDs are found. For example, along the California coast many RSD fields extend out to the 130 m shelf break (Davis et al. in prep).

There were also differences with respect to dominant taxonomic groups found between habitats and depth zones. This was especially true for the suspension/deposit feeding groups of *D. exentricus, U. caupo/Callinassidae* spp. burrows, and *Ophiuroid* spp., which had significant differences in percent cover for the depth zone for which they were most abundant (Table 1). *U. caupo/Callinassidae* spp. burrows dominated outside RSDs in both the shallow and intermediate zones and *Ophiuroid* spp. dominated outside RSD in the deep zone. The dominance of these organisms outside RSDs is especially relevant to the density and diversity of benthic communities as both *U. caupo/Callinassidae* spp. and *Ophiuroid* spp. have been shown to create habitat for other fish and invertebrate species (Piepenberg & Juterzenka 1994, Macginitie 1934). Moreover, the spatial distribution of these organisms within habitats might contribute to the biological differences observed between habitats in the intermediate and deep zones, especially in relation to the RSD boundary.

While the strong interaction of habitat and depth on the density of organisms and diversity of benthic communities has been well established

(Warwick & Davies 1977, Barry & Dayton 1991, Snelgrove & Butman 1999, Whitman 2004) no previous work had examined the distribution and abundance of benthic communities associated with RSDs. This work offers a first look at the ecological role of these abundant habitats and our results show RSDs conform to the general understanding of how benthic communities respond to fine scale physical differences in soft sediment habitats (i.e. grain size, bedforms, hydrodynamic disturbance). However, many questions remain as to the larger scale significance of RSDs, including how RSD size, configuration, and latitudinal distribution mediate the biological relationships observed in this study and ultimately the significance of RSDs with respect to marine spatial planning.

Most surprising and of potentially great significance for marine spatial planning, was the counter intuitive use of RSDs by fish. While differences in fine scale physical variables allowed us to make reliable predictions about the overall distribution of benthic communities with respect to RSDs, we did not anticipate finding small flatfish and abundant Young of the Year (YOY) *Sebastes* spp. inside RSDs. This study revealed flatfish were significantly smaller inside RSDs (Fig. 5). We had predicted, based on the larger size of bedforms inside RSDs, to find larger fish. This is likely a result of a combination of physical and biological interactions. The large bedforms inside RSDs, created by the strong currents that form RSDs, can act as a refuge for fish small enough to tuck into their lee (Gerstner 1998). As the size of the organism increases, its ability to benefit from refuge between bedforms may diminish. Furthermore, the main predators of juvenile flatfish are larger fish (Gibson & Robb 1996), which were found to be more abundant outside RSDs. While the mechanism and seasonality of this relationship needs to be investigated further, these physical and biological factors may create an incentive for small fish to seek out RSDs despite potentially harsh physical conditions. This finding suggests a potential ecological role of RSDs as previously undescribed nursery habitat, which has important implications for the design of marine spatial plans.

The significantly greater density of YOY *Sebastes* spp. inside RSDs at the intermediate depth zone was a surprising discovery (Fig. 6). While many species of rockfish are known to recruit in the late summer to early fall (Johnson et al. 2001, Love et al. 1991) to a variety of habitats including kelp canopy (Nelson 2001, Holbrook et al. 1990), high relief hard substrate (Carlson and Straty 1981), and shallow surfgrass beds (Guido et al. 2007) the importance of soft substrata for the young of deep dwelling rockfish species is relatively unknown (Johnson et al. 2001, Love et al. 1991). The intermediate depth zone RSDs investigated here, supported densities of YOY *Sebastes* comparable to densities found in artificial reefs (West 1994) and kelp canopies (Holbrook et al. 1990). Indeed, RSDs may serve similar functions as these better known nursery habitats, with the larger bedforms generating turbulent flow that provides a rich source of suspended organic material and small prey lifted off the bottom, as well as offering refuge from predators or currents. Simple bedload and benthic plankton traps along with direct observations of fish feeding behavior could be used to test these hypotheses.

The potential importance of RSDs as previously undescribed nursery habitat is underscored by the fact that many of the identified YOY were canary rockfish (*S. pinniger*), some populations of which are currently listed as threatened under the Endangered Species Act (NOAA 2010). Given the large aerial extent of RSD habitat now documented for the California continental shelf and the fact that these features typically occur offshore of rocky reefs (Davis et al. 2011, in prep), RSDs may have important implications for the replenishment of adult rockfish on those adjacent reefs and therefore the performance of marine protected areas (MPA) in terms of faster than expected population recovery rates. Additionally, the widespread and abundant distribution of RSDs along the California coast may serve as conduits for gene flow between widely spaced reefs, thereby increasing the connectivity of rockfish populations on the west coast (Miller and Shanks 2004, Hyde and Vetter 2009). This has explicit

implications for marine spatial planning, like California's Marine Life Protection Act (MLPA) in which MPAs were designed to function as a network to specifically take into account connectivity of populations through larval dispersal and ontogenetic migrations (CDFG 2008). The timing of this study (July) was fortuitous for observing YOY rockfish, but efforts should be made to sample these habitats seasonally to determine if they serve as nurseries for other species throughout the year.

Recently collected high-resolution seafloor maps of the California continental shelf reveal RSDs to be abundant, making soft bottom habitats much more heterogeneous than previously thought (Morissey et al. 1992, Kostylev et al. 2001, Brown & Collier 2008, Davis et al. in prep). Now, with the results presented here, it is also clear that this RSD-generated heterogeneity adds a significant and previously undescribed level of ecologically important patchiness to neashore soft sediment communities, challenging the common paradigm within marine resource management that soft sediments can be treated as homogenous habitats. Marine spatial plans, like the MLPA, seek to use best available science to protect representative habitat and biodiversity (CDFG 2008). Moreover, in the adaptive management context called for in these plans, the identification of previously undescribed and ecologically significant habitats could be incorporated in order to address mandated goals of habitat representation and population connectivity. For example, RSDs represent ~5% of the total area on the continental shelf but account for 0-26% of available habitat inside the various marine protected areas designated under the MLPA (Davis et al., in prep). At the state and federal level, as efforts to implement spatial planning frameworks and evaluate the effectiveness of these strategies progress, spatially explicit information about the distribution and functional role of finer scale nearshore habitat distinctions, like RSDs, becomes critical (Gleason 2010, Pauly et al. 2002, Browman & Stergiou 2004, Pikitch et al. 2004). The discovery of the ecological significance of rippled scour depressions on the distribution and

abundance of benthic invertebrates and groundfish illustrates the importance of high-resolution habitat mapping data in refining our understanding of heterogeneity in benthic habitats specifically in the context of adaptive management in marine spatial planning.

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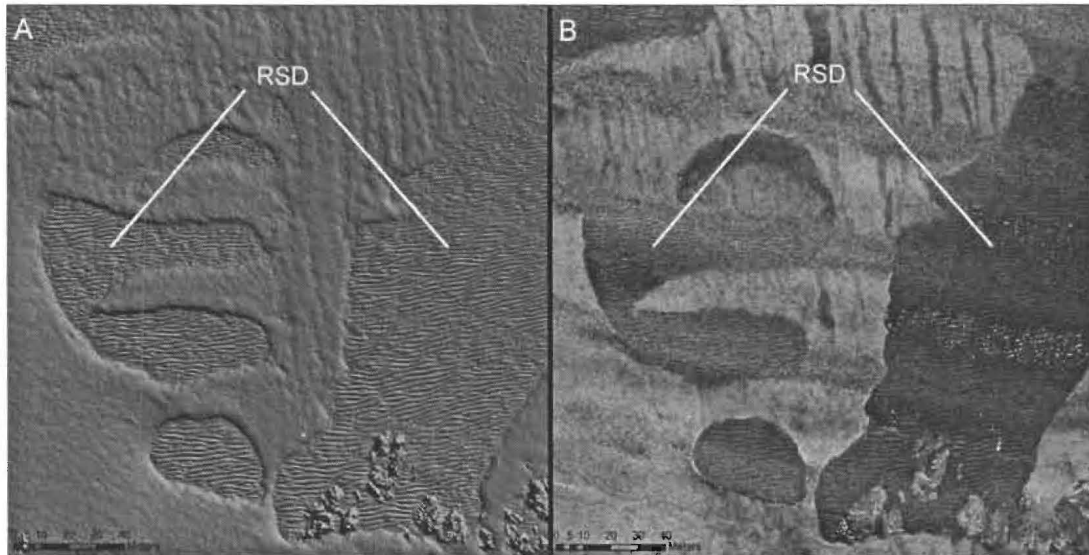
Figure 1: Physical characteristics of rippled scour depressions (RSD) and adjacent fine sediment. High-resolution multibeam (A) and side scan (B) sonar images are presented from the same site in Monterey Bay, CA. Multibeam bathymetry in shaded relief shows distinct bedforms inside RSDs. Side scan image shows the higher reflectivity of coarser sediments (dark colors) inside RSDs.
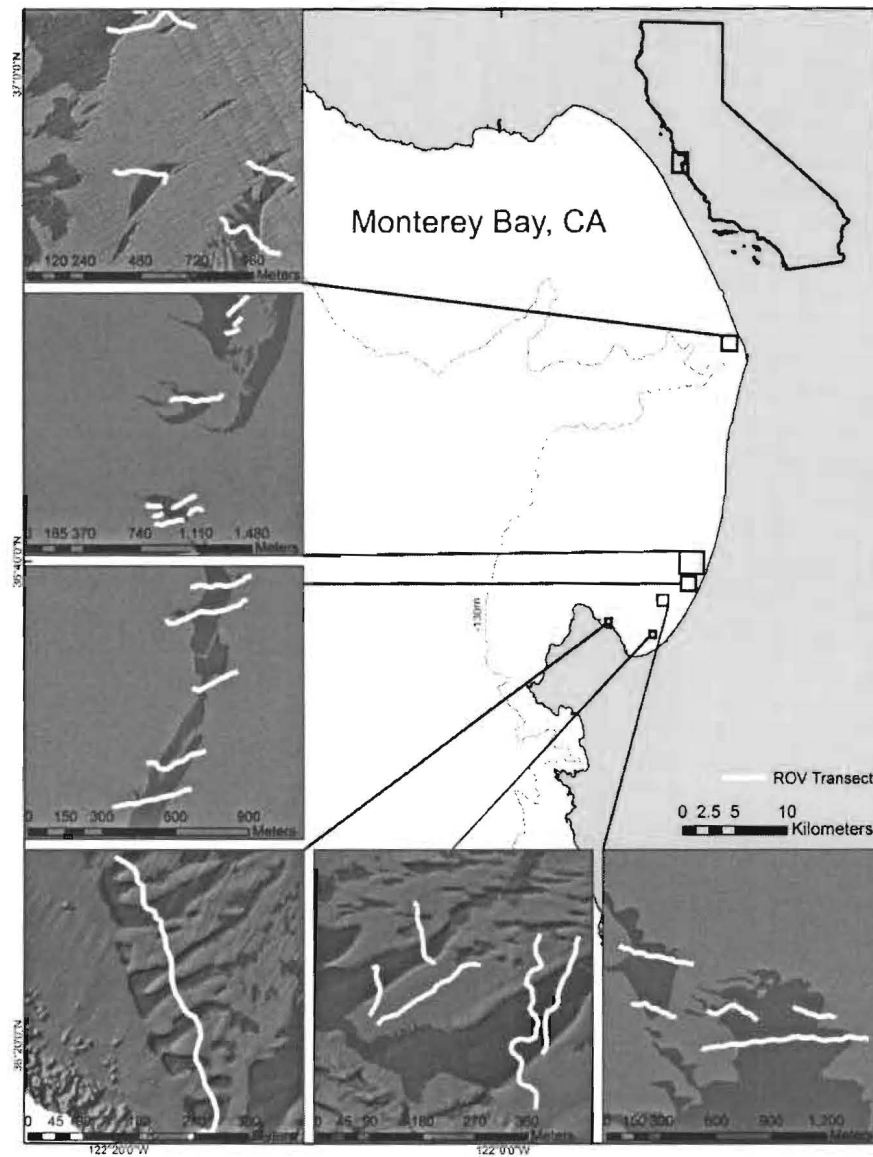
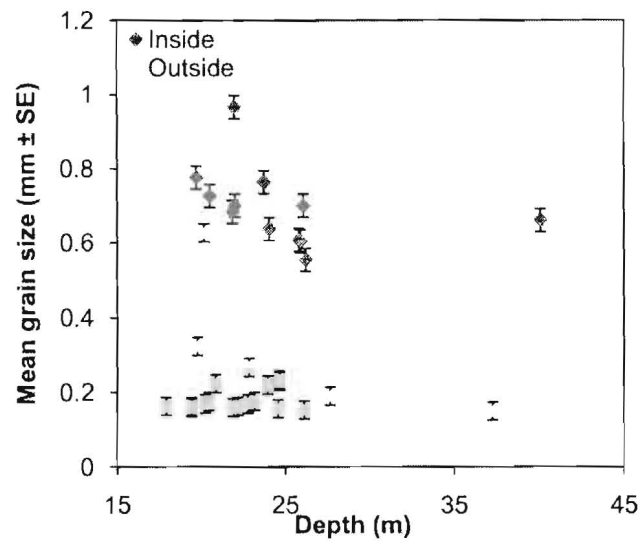**Figure 2:** Map of study region showing RSDs and the locations of ROV transects.

Figure 3: Mean grain size (mm ± SE) versus water depth of sediment samples collected inside (n = 12) and outside (n = 20) RSDs.
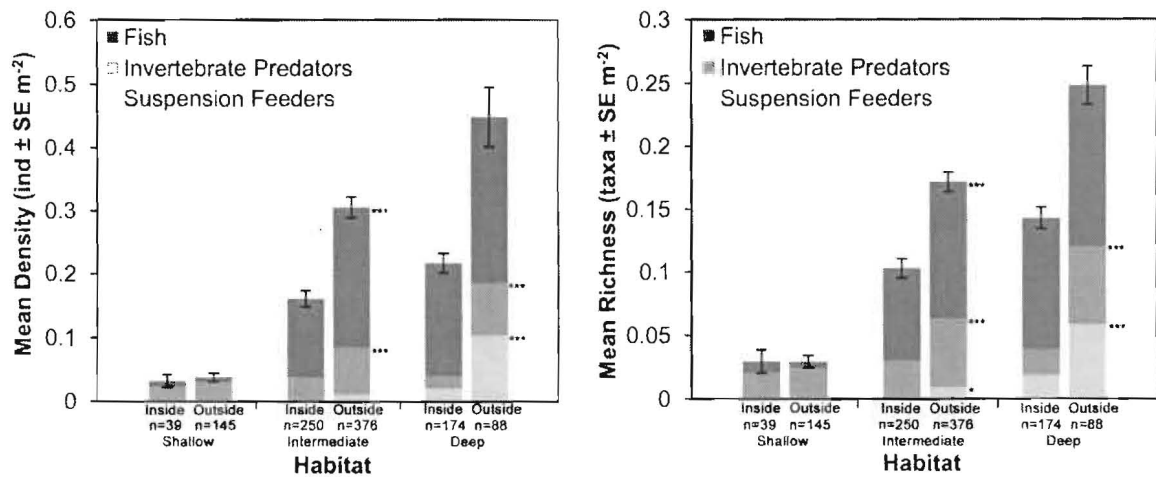

Figure 4: Density and richness of the three trophic groupings inside and outside of RSDs for the three depth zones ([< 5 m], [15 to 30 m], [>30 m]) at the 10 m scale. Error bars represent the standard error about the combined mean for all three groups, asterisks denote p values (0.01*, 0.001**, < 0.001***) of the relationship with habitat, and sample sizes (n) are given.
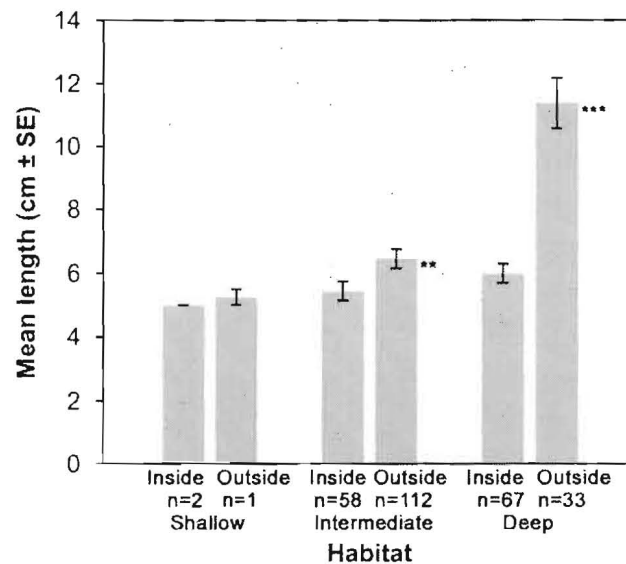
Figure 5: Mean total length of combined flatfish groups (*Pleuronectidae* ["right eyed"], *Paralichthyidae* ["left eyed"]) inside and outside of RSD by depth zone. Error bars represent the standard error, asterisks denote p values (0.01*, 0.001**, < 0.001***) of the relationship with habitat, and sample sizes (n) are given.

Figure 6: Mean density of YOY *Sebastes* spp. inside and outside of RSDs by depth. Error bars represent the standard error, asterisks denote p values (0.01*, 0.001**, < 0.001***) of the relationship with habitat, and sample sizes (n) are given.
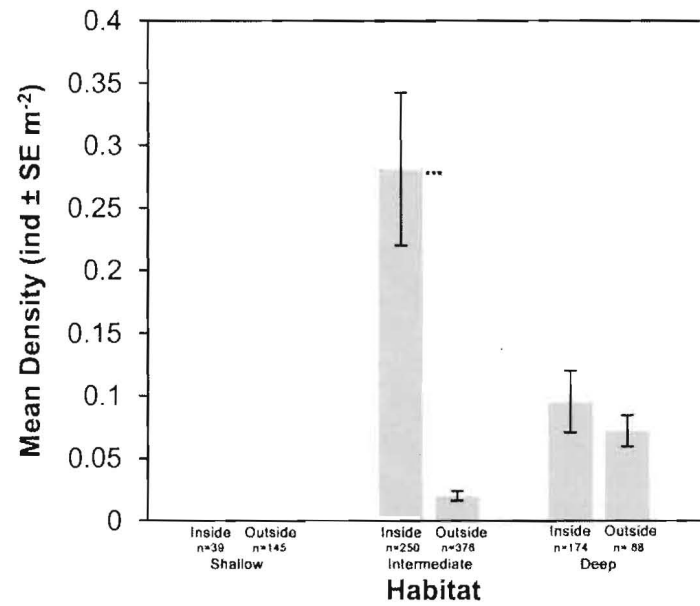
APPENDIX A

Sediment Analysis

```
Grain<-read.csv(file.choose(), header=T, sep=",")
str(Grain)
t.test(Grain$Mean.GS..mm~Grain$Habitat)
```

Variogram Analysis

```
library(gstat)
RSD<-read.csv(file.choose(), header=T, sep=",")
attach(RSD)
names(RSD)
str(RSD)
coordinates(RSD) = ~X+Y
variog<-variogram(TOTAL~1, RSD, width=5, alpha = c(0, 34, 90, 135), cressie=
T)
model.variog<-vgm(psill=1,model="Gau", nugget=1, range=60)
fit.variog<-fit.variogram(variog, model.variog)
plot(variog, model=fit.variog)
plot(variog, type="b", main = "Variogram: All")
detach(RSD_all)  #splancs
```

MANOVA

```
Density<-read.csv(file.choose(), header=T, sep=",")
str(Density)
TOTAL.sqrt<-sqrt(Density$TOTAL_WO_YOY+1)
```

```
suspension.sqrt<-sqrt(Density$Suspension+1)

Invert.sqrt<-sqrt(Density$Invert_Preds+1)

Fish.sqrt<-sqrt(Density$Fish_Preds+1)

YOY.sqrt<-sqrt(Density$YOY+1)


Total.aov<-aov(Fish.sqrt~Density$Substrate, Data=Density)

summary(Total.aov)

print(TukeyHSD( Total.aov)    )

Epifaunal.density<-aov(cbind(Burrows_pe, Dendrast_1,
Ophiuroid_)~Substrate*Depth, data=Density)

summary(Epifaunal.density, test="Roy")

Tukey<-TukeyHSD(Epifaunal.density)

yoy.density<-aov(Density$YOY~Substrate*Depth, data=Density)

summary(yoy.density)

Tukey<-TukeyHSD(yoy.density)

print(Tukey)
```