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The effects of tectonic deformation and sediment allocation on shelf habitats and megabenthic distribution and diversity in southern California

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ABSTRACT

Landscape and seascape structures are typically complex and manifest as patch mosaics within characteristic biomes, bordering one another in gradual or abrupt ecotones. The underlying patch structure in coastal shelf ecosystems is driven by the interaction of tectonic, sedimentary, and sea level dynamic processes. Animals and plants occupy and interact within these mosaics. Terrestrial landscape ecological studies have shown that patch structure is important for ecological processes such as foraging, connectivity, predation, and species dynamics. The importance of patch structure for marine systems is less clear because far fewer pattern-process studies have been conducted in these systems. For many coastal shelf systems, there is a paucity of information on how species occupy shelf seascapes, particularly for seascapes imbued with complex patch structure and ecotones that are common globally due to tectonic activity. Here, we present the results of a study conducted along a myriameter-scale gradient of bottom and sub-bottom geological forcing altered by tectonic deformation, sea level transgression and sediment allocation. The resulting seascape is dominated by unconsolidated sediments throughout, but also exhibits increasing density and size of outcropping patches along a habitat patch gradient forced by the erosion of a sea level transgressive surface that has been deformed and tilted by tectonic forcing. A combination of sub-bottom profiling, multibeam bathymetry, and ROV surveys of the habitats and the demersal megafauna occupying the habitats indicate (1) significant beta diversity along this gradient, (2) biological diversity does not scale with habitat diversity, and (3) species occupy the patches disproportionately (non-linearly) with regard to the proportional availability of their preferred habitats. These results indicate that shelf habitat patch structure modulates species specific processes and interactions with other species. Further studies are needed to examine experimentally the mechanics of how patch structure modulates ecological processes in shelf systems. Our results also provide further support for including multiple spatial scales of patch structure for the application of remote habitat sensing as a surrogate for biological community structure.

1. Introduction

One of the most fundamental topics in ecology is that of understanding the dynamics of patches. All ecosystems exist in patches in time and space, and the description of patch structure has occupied ecologists since the late 1800's (Haeckel, 1890). The creation and maintenance of patches touches upon most dominant ecological topics including dispersal, recruitment, disturbance, succession, and foraging. Patterns of underlying habitat structure are closely linked to biological patch structure in both terrestrial and aquatic biomes (Turner, 1989; Bostrom et al., 2011).

The importance of spatial habitat pattern on ecological processes is well established for terrestrial biomes (Wiens, 1995), and has become an increasing focus of study in marine systems which are inherently more difficult to study especially at deeper shelf depths (>30 m). Recent studies of coastal shelf and slope species indicate that multi-scale habitat patch structure is important for ecological patterning as smaller-scale patch structure interacts with broader-scale seascape to contextualize species-specific patterns of habitat utilization and biodiversity (Hewitt et al., 2005;

Anderson and Yoklavich, 2007; Kendall et al., 2011; Parnell, 2015). This underscores the need for a refined understanding of (1) how shelf ecological processes are modulated by, and interact with, multi-scale habitat patchiness (Turner, 1989; Anderson et al., 2005, 2009), and (2) how these processes manifest as emergent patterns of biodiversity and trophic structure. Such refinement is also warranted for increasing the precision of estimating megabenthic species and community structure based on fine-scale digital elevation models (Wedding et al., 2011; Anderson et al., 2009).

Continental shelf habitats are highly heterogeneous as a result of multiple structuring processes (Shepard, 1948). Oceanographic and sedimentary processes, sea level change, and tectonic deformation control the geomorphology and the thickness and distribution of sediments along continental shelves (Ryan et al., 2007; Pratson et al., 2007). The relative importance of these processes varies globally and regionally, resulting in a continuum of characteristic patch types and spatial scales. Tectonically deformed coastal shelves are common, exhibiting highly complex seascapes and patch structure. Tectonic deformation structures shelf geomorphology through (1) the deformation of transgressive surfaces (Le Dantec et al., 2010; Hogarth et al., 2012; def., regional unconformities formed by wave erosion as sea level rose following the last glacial maximum, manifesting as boundaries between lithified Pleistocene deposits below and Holocene sediments above), and (2) subsequent effects on patterns of sediment deposition and erosion (Le Dantec et al., 2010). Thus, tectonic deformation controls the distribution and patch structure of unconsolidated sediments and emergent hard ground both directly and indirectly (Hogarth et al., 2007). Sediment deposition and erosion patterns are affected by the interaction of the underlying geomorphology with grain size, and surface and internal wave energy (Emery, 1956; Cacchione and Drake, 1986; Cacchione et al., 2002). The geomorphology of tectonically deformed shelves therefore is dominated by habitat gradients ranging from thick sediments to outcropping hardground and gradational mixed patch structure in between, all dependent on the dip of the underlying transgressive surface. The spatial distribution and shape of these patches can be dynamic over ecological time scales where unconsolidated sediments are thin and subject to redistribution by surface and internal waves, or near submarine canyons, river mouths (Shepard et al., 1974), or where human use alters the supply and erosion of sediments (Thrush et al., 2004).

In this study, we utilized a myriameter-scale transgressive surface gradient as a natural laboratory to investigate the effects of such gradients on habitat patch structure and how this patch structure affects habitat utilization by megabenthos. Specifically, we hoped to (1) utilize seismic sub-bottom profiling to visualize gradational patch structure and sediment thicknesses along a transgressive surface gradient, (2) relate habitat structure and length scales to patterns of megabenthic abundance and diversity, and (3) gage how species distributional and community diversity patterns scale with habitat composition across common geologically-forced shelf habitat gradients. The latter addresses how animals respond differently to habitat patch structure at different spatial scales, thus supporting a refined understanding of how benthic habitat affects community structure and diversity. This study was intended as a first step to support subsequent pattern-process studies wherein the patches identified in this study will be used to stratify studies of ecological patch processes. The study was conducted off San Diego County (California, USA) where the shelf is dominated by multiple faults (Hogarth et al., 2007) resulting in complex transgressive surface gradients.

2. Methods

Compressed high intensity radar pulse (CHIRP) seismic data and multibeam sonar data were used to define shelf habitats (30–120 m depths) off La Jolla and Del Mar, CA (USA). Video surveys were conducted using a remotely operated vehicle (ROV) to ground truth CHIRP (seismic) and multibeam data, and to quantify the occupying megabenthos at fine spatial scales. Specifically, (1) fine-scale relationships between the spatial distribution of benthos with substratum texture and thickness were examined using CHIRP and multibeam data and ROV video recorded along the CHIRP transects, (2) these relationships were characterized graphically and statistically for the most commonly observed species and taxonomic groups, (3) links between geological processes and habitat patterns important for the reef and sedimentary biological communities were examined, and (4) patterns of megafaunal diversity and abundance were examined in relation to this geologically-forced habitat structural gradient.

2.1. Geological setting

The study region consisted of the La Jolla/Del Mar shelf where the topography and bathymetry has been greatly altered by the active Rose Canyon strike-slip fault (Fig. 1). Complex geomorphic features include the La Jolla Submarine Canyon (LJSC), Mt. Soledad (uplifted ~150 m), and a 'popup' feature off Del Mar (Hogarth et al., 2007 - Del Mar Popup Feature − DMPF), which shoals north of the LJSC (Fig. 1). Tectonic uplift and deformation of ancient and modern sediments is evident from sub-bottom profiles of sedimentary sequences north of the LJSC, which are spatially related to offsets of the Rose Canyon fault system (Fig. 1; Le Dantec et al., 2010). The study area was chosen to span the shoaling hard sub-bottom horizon along the soft-sediment dominated shelf (Henry, 1976).

2.2. Geophysical surveys

High resolution swath bathymetry and compressed high intensity radar pulse (CHIRP) seismic data were acquired in the nearshore marginal shelf from Torrey Pines State Reserve to Penasquitos Lagoon (Fig. 1) in 2002, 2003, and 2015. Swath bathymetric surveys were conducted using an interferometric swath bathymetric sonar. Sub-bottom profiles were acquired using a modified CHIRP system consisting of a dual-transducer sonar with an ADSL link between the towfish and topside computers. The CHIRP sonar swept with a frequency of 1−5.5 kHz yielding submeter resolution. CHIRP survey procedures are described in detail in Le Dantec et al. (2010) and Hogarth et al. (2007, 2012).

2.3. ROV surveys

Three ROV transects were conducted along the alongshore CHIRP transects that best covered the full extent of the shoaling transgressive surface. ROV survey tracks followed CHIRP transects as closely as possible (CHIRP lines 3, 5, and 7 - Fig. 1). The resulting survey area encompassed much of the DMPF from the ~30 m−120 m contours (cross-shore distances ranged from ~3200 to 3700 m). Surveys were conducted 14 August (CHIRP 7), and 21 October (CHIRP3), 2013 and 25 January, 2014 (CHIRP 5).

A SeaBotix LBV-150 equipped with a SeaBird SBE 37 MicroCAT CTD, 2 external LED lights (1080 lumen, 140° beam angle), and red scaling lasers (5 cm separation) was used to survey the bottom for composition and megabenthos. The ROV was deployed from a small surface vessel (8 m length) cruising at a velocity of ~0.75 m s^{-1}. A 25 kg clump weight, positioned above and in front of the ROV, was used to stabilize the ROV at depth and maneuver it as a semi-towed vehicle. ROV navigation was determined by wire angle and wire out in relation to a topside GPS receiver (Hemisphere V110GPS). Cross-referencing features observed in both the CHIRP and ROV provided
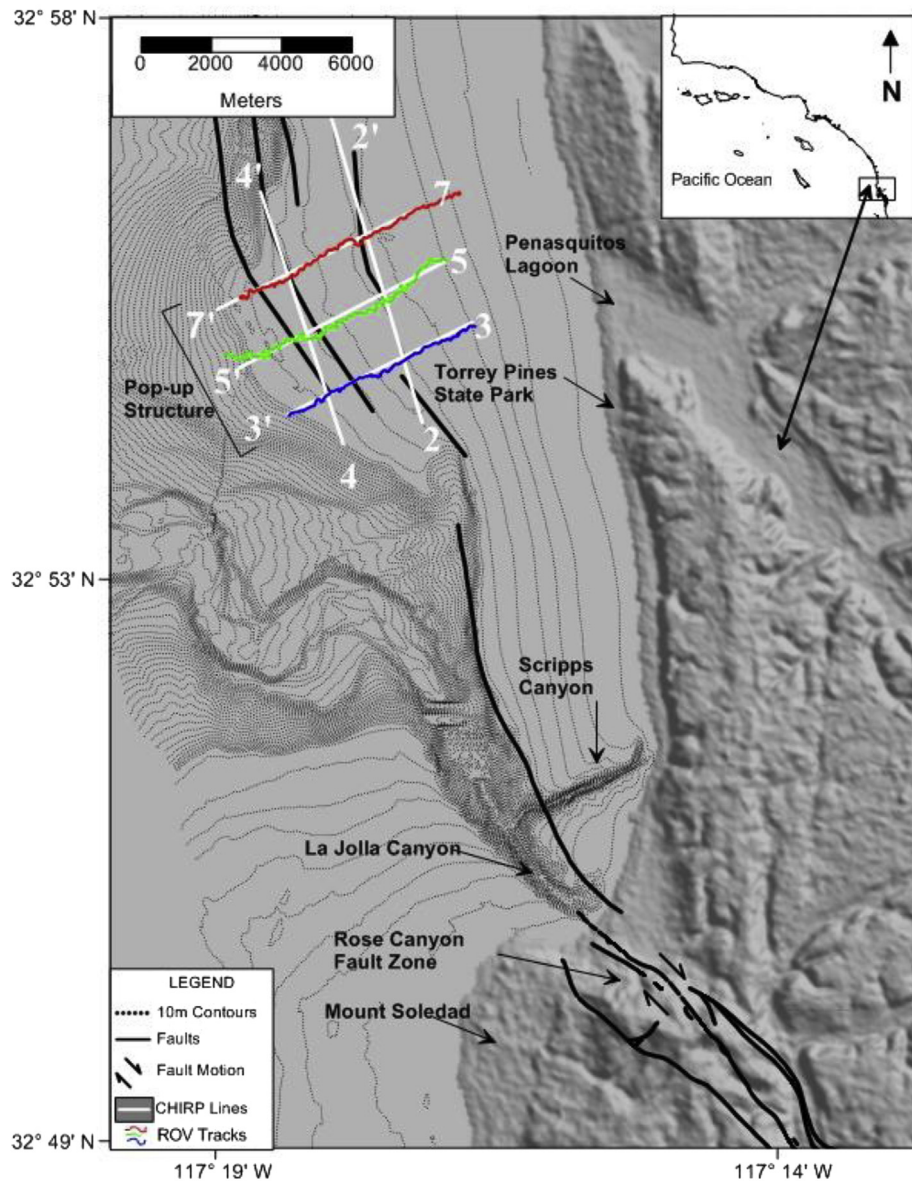
Fig. 1. Map of the Rose Canyon Fault Zone and the Del Mar pop-up feature where CHIRP and ROV transects were conducted. CHIRP transects 2, 3, 4, 5 and 7 are indicated by white lines. ROV tracks are indicated in color along CHIRP 3 (blue), CHIRP 5 (green), and CHIRP 7 (red). Black lines indicate known faults.

additional constraints on ROV navigation. Such navigational approaches often are employed in geophysical surveys (e.g., Hill et al., 2004; Hogarth et al., 2012). Pre-planned routes along the CHIRP transects were navigated, and positional tracks were recorded at 5 m intervals. High resolution (0.5 m horizontal resolution) shaded relief maps, created from previous multi-beam survey data were projected underneath the vessel track on a laptop as a real time check for concordance between bottom features and the real-time ROV video feed. The main ROV video camera (520 line, dynamic range 90 mm to infinity, color, 0.1 lux) provided a composite NTSC signal that was converted from analog to digital format using a Canopus ADVC110 converter (720×480 resolution, 29.97 frames s^{-1}) and recorded on a second laptop computer. A GoPro Hero 2 camera housed in a Golem Gear LCD_150 housing, was mounted on the side of the ROV and recorded high definition video (1280×960 resolution, 48 frames s^{-1}) to aide animal identification in the main video.

2.4. Video sampling

ROV transect videos were analyzed in 5 s bin intervals along each survey transect to identify bottom characteristics and quantify megabenthos. Bottom characteristic factors included composition (levels = 'Boulders' [>1 m largest dimension], 'Rocks With Sand', 'Sediment Veneer', and 'Soft'), slope (levels = 'Flat' [~<5°], and 'Sloped' [>5°]), grain size (levels = 'Coarse'[>2 mm], 'Fine'[0.063–2 mm], 'Mud'[<0.063 mm], and 'None'), and bedform (levels = 'Hatched Ripples', 'Outcrop', 'Smooth'). All megafauna (finfish and invertebrates) on or near the bottom were enumerated to the lowest possible taxonomic level. Avoidance of underwater vehicles by mobile species is known to be problematic for estimating animal densities (Lorance and Trenkel, 2006). However, we assumed avoidance for individual species would be consistent among the CHIRP lines since the focus of our study was to estimate relative densities and diversity among the CHIRP lines.

2.5. Analysis

Data analysis consisted of (1) characterizing habitat features (bottom composition and morphology) and habitat length scales among the CHIRP lines, (2) associating species assemblages with habitats, (3) characterizing beta diversity and species rank abundance along the transgressive surface gradient, and (4) gaging potential non-linear dependencies of species abundance along the transgressive surface gradient. Only demersal species known to be resident on or near the benthos as adults were included in the analyses to avoid seasonal bias. All data analyses were conducted using R (R Core Team, 2014) including the 'vegan' (Oksanen et al., 2013), 'multcomp' (Hothorn et al., 2008), 'MASS' (Venables and Ripley, 2002), 'rgdal' (Bivand et al., 2014), 'sp' (Bivand et al., 2013), 'cluster' (Maechler et al., 2015), and 'plotrix' (Lemon, 2006) libraries.

Bottom features were characterized using multiple correspondence analysis (MCA) to generate derived quantitative orthogonal habitat factors (hereafter 'MCA factors') from the categorical bottom characteristic factors derived from the ROV video. MCA analysis (Greenacre and Blasius, 2006) is a categorical analog of principal component analysis (PCA). MCA scores were then used to develop habitat clusters (hereafter 'PAM clusters') using partitioning around medoids (PAM). PAM utilizes medoids representing distinctive characteristic habitat clusters which are constructed in a divisive fashion using an objective function that minimizes the sum of the dissimilarities between each observation and the set of medoids (Reynolds et al., 1992). Seven PAM clusters were chosen based on the first large difference in silhouettes (average cluster dissimilarity) with increasing numbers of clusters. Results of the MCA and PAM analyses were used to estimate length scales of contiguous habitat and habitat diversity (Renyi entropy – Kindt and Coe, 2005), respectively. Renyi entropy is calculated as a function of the scaling parameter α that yields differential sensitivity to rare and abundant habitats. Patch length was calculated by differencing along-track distances where habitat transitions occurred using the R 'sp' library. Positions were ascertained by time matching ROV observations with ROV track. Significance testing for differences in habitat-patch length among CHIRP transects was conducted using Tukey's honest significance difference method (Miller, 1981).

Species rank abundance and cumulative percent dominance were modeled for each CHIRP transect using the 'radfit' function in 'vegan' (Wilson, 1991), and the best fitting models (log-normal models, link function = log, family = Poisson) were plotted. Redundancy analysis (RDA) was used to characterize the association of bottom habitats to megafaunal abundances estimated from the ROV video. Redundancy analysis is the multivariate response variable analog of multiple regression (Legendre and Legendre, 1998). RDA's were conducted for unconditioned data, and data conditioned by CHIRP line. Permutation testing (999 permutations each) was used to test for the significance of (1) the overall unconditioned model, (2) the conditioned model, and (3) comparison of the two models (Legendre and Legendre, 1998). The latter was conducted to determine the significance of the effect of conditioning the RDA by CHIRP line, thus effectively gaging the importance of the differing degrees of community-wide habitat occupancy and diversity among the lines. Significance of the permuted comparison of models indicates significant beta diversity (Legendre et al., 2005) along the transgressive surface gradient. Additionally, non-linear habitat occupancy among CHIRP lines for individual species was examined for the most commonly observed species. Individual species abundance was first modeled as a function of the MCA-derived variables (to avoid collinearity issues; Graham, 2003) using linear multiple regression. Only significant

factors ($p < 0.05$) and factor levels were included in each species model. Residuals from the individual species models were then compared among CHIRP lines using Tukey's all pair comparisons. Shannon diversity (Hill, 1973) and evenness (Pielou, 1969) were calculated for each CHIRP transect. Finally, Renyi taxonomic diversity was calculated for each CHIRP line as previously discussed for habitats.

3. Results

3.1. Geophysical surveys

CHIRP profiles exhibit three distinct geological features (Fig. 2) – the transgressive surface, basal lag deposits, and modern Holocene deposits. The transgressive surface, which shoals northward, exhibits pronounced truncation formed by surface wave and subaerial erosion during multiple cycles of Pleistocene sea level fluctuation (Figs. 2 and 3). The mid to outer shelf region of the transgressive surface is overlain by a basal lag deposit that is likely a result of the most recent Pleistocene sea level transgression (Le Dantec et al., 2010) and whose thickness covaries with the shoaling of the underlying transgressive surface. The modern Holocene subunit overlays both the transgressive surface and the basal lag deposit, and comprises the majority of sediment covering the transgressive surface. Its thickness varies considerably both along and across the margin. A cross-shore depocenter is evident as a wedge shaped profile 10–20 m thick (Fig. 3), and its alongshore thickness ranges from ~10 m in the south thinning systematically northward until it virtually disappears near CHIRP 7 where there is less sediment between 40 and 70 m due to uplift along the Rose Canyon Fault. Visibility observed in the ROV videos was reduced to 2–3 m at depths between 60 and 80 m along all three transects indicating the potential role of internal waves forcing the deeper edge of the depocenter through resuspension (Cacchione and Drake, 1986).

3.2. Habitats

Habitat composition and patch length scales varied greatly among the CHIRP lines. Forcing of habitats by the northward shoaling transgressive surface and sediment depocenter is evident in the differential habitat types and diversity observed among the CHIRP transects. Four factors accounted for ~82% of the overall variability in the MCA analysis of ROV bottom characteristic factors (cumulative variances and factor loadings are listed in Table 1).

MCA factor loadings characterize the most important bottom characteristic factor for each MCA factor. MCA factor 1 consists of soft bottom dominated by muds exhibiting a flat bedform. Boulders, slope, and a lack of sediment characterize MCA factor 2. MCA factor 3 habitats include rocks interspersed with soft sediment (mostly muds) also lacking in bedform rugosity, whereas MCA factor 4 is dominated by coarse sand. A plot of bottom characteristic factors among the first two MCA factors (whose area indicates the degree of flat soft bottom on the abscissa and flat to sloped bare hard ground on the ordinate) characterizes CHIRP 3 as mainly flat and unconsolidated while CHIRP 5 and 7 are increasingly composed of hard sloped boulders and outcrops (Fig. 4).

A histogram of PAM clusters, which represent combinations of the most important bottom characteristic factors (listed in Table A.1), indicates that CHIRP 5 has the greatest diversity of PAM clusters (Fig. A.1). All seven PAM clusters were common along CHIRP 5, which displayed much greater habitat diversity across the range of common to rare habitats than CHIRP 3 and 7 (Fig. 5 top panel). Outcropping features, sediment veneers and boulders were most abundant along CHIRP 7 (Fig. A.1). Habitat diversity along CHIRP 7 was greater than CHIRP 3 at $\alpha < 3$ and was similar for $\alpha > 3$
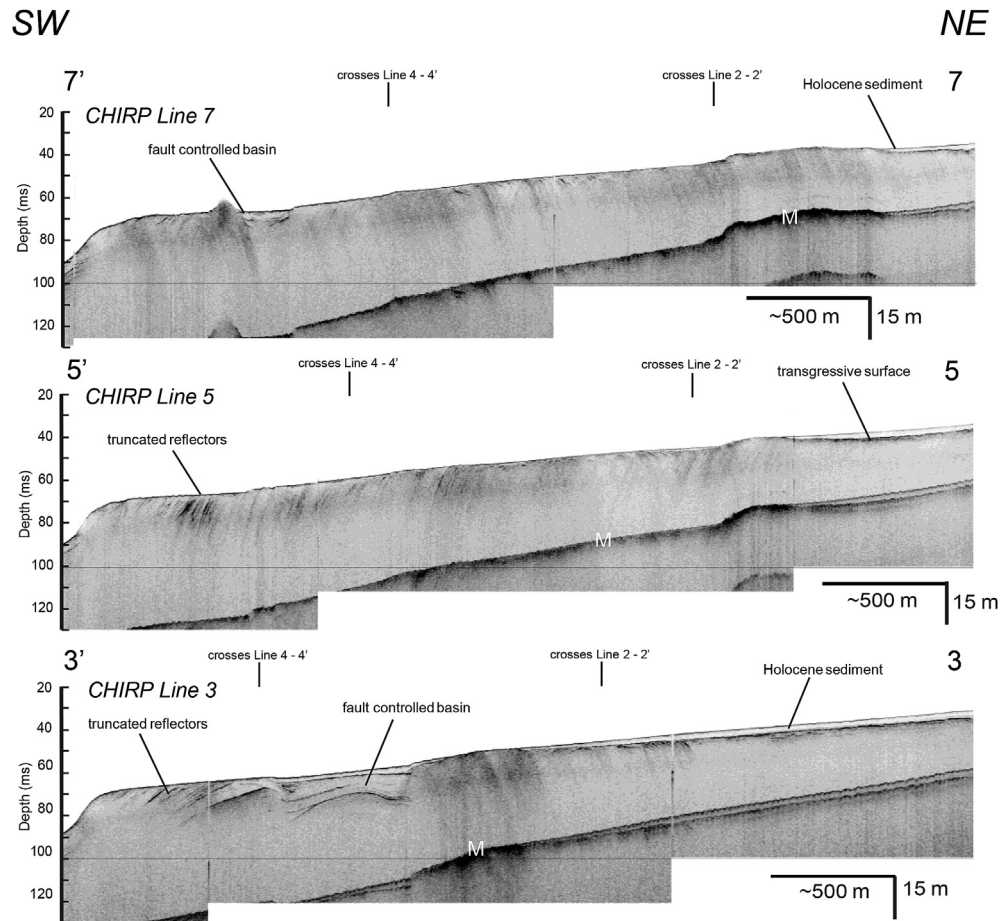
Fig. 2. CHIRP profiles (CHIRP 7, CHIRP 5, and CHIRP 3) run cross-shore and image the shoaling of the transgressive surface from south to north (CHIRP 3 to CHIRP 7). Refer to Fig. 1 for locations of CHIRP profiles.
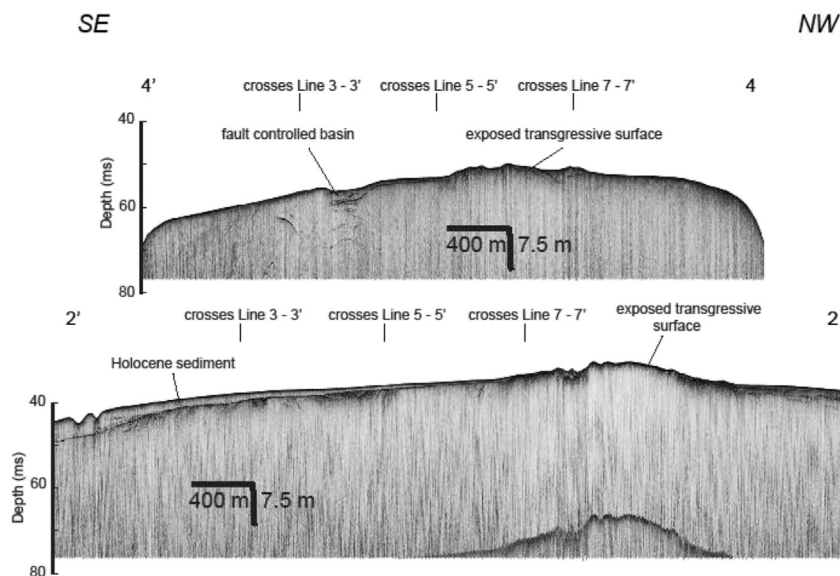

Fig. 3. Alongshore CHIRP profiles (CHIRP 2 and CHIRP 4) run along the strike of the Rose Canyon Fault closely paralleling the shoreline. CHIRP 2 and 4 demonstrate the shoaling of the transgressive surface and thinning of the modern Holocene sediments to the north from the Scripps Canyon to the Del Mar pop-up feature. Locations of intersection with cross-shore CHIRP ROV transects are also indicated. Refer to Fig. 1 for locations of CHIRP profiles.

indicating that the diversity of common habitats along CHIRP 7 was greater, and the diversity of rarer habitats was similar between the two CHIRP lines. Despite their similar diversity profiles, both MCA factors (Fig. 4) and PAM clusters (Fig. A.1) were quite different for

Table 1
MCA factor loadings for bottom characteristic factors. Scaled values >0.25 standard deviations are highlighted in bold. The 4 MCA factors accounted for ~82% of total variability.

Factor	Level	MCA 1	MCA 2	MCA 3	MCA 4
Composition	Boulder	−0.0351	**0.0259**	−0.0050	0.0040
	Rocks with sand	−0.0099	−0.0253	**0.0727**	−0.1059
	Sediment veneer	−0.0141	−0.0378	0.0028	0.0109
	Soft	**0.0188**	0.0101	−0.0048	0.0012
Slope	Flat	0.0008	−0.0013	0.0001	0.0002
	Slope	−0.0816	**0.1367**	−0.0123	−0.0252
Grain	Coarse	−0.0044	−0.0060	0.0151	**0.0934**
	Fine	0.0012	−0.0095	−0.0146	−0.0048
	Mud	**0.0151**	0.0093	**0.0387**	−0.0105
	None	−0.0505	**0.0574**	−0.0036	−0.0046
Bedform	Hatched ripples	**0.0158**	−0.0013	−0.0791	−0.0402
	Outcrop	−0.0219	−0.0118	0.0055	−0.0014
	Smooth	**0.0193**	0.0119	0.0066	0.0076
Percent cumulative variance		25.4%	46.0%	64.5%	81.9%

CHIRP 3 and 7. Thus, forcing by the allocation of sediment along the shoaling transgressive surface has resulted in (1) a low diversity soft-bottom dominated habitat in the south with a few rocky outcrops to (2) a diverse mix of soft and hard bottom habitats with abundant sediment veneers and low relief outcrops along CHIRP 5 to (3) a sharply contrasting soft bottom interspersed with larger and higher relief outcrops along CHIRP 7.

Median habitat patch length scales also varied along this habitat gradient with decreasing median patch length scales from south to north (65, 35, and 30 m for CHIRP 3, 5, and 7 respectively – see Fig. 6) indicating that habitat patch core areas decrease, and patch density and interspersion increase northward. Multiple comparisons of patch lengths along the CHIRP lines indicate that patch lengths along CHIRP 3 were significantly greater than CHIRP 5 and CHIRP 7 ($p < 0.001$ for CHIRP 3 vs. CHIRP 5 and CHIRP 3 vs. CHIRP 7). However, patch lengths were not significantly different between CHIRP 5 and 7 ($p = 0.940$).

3.3. Species and community habitat utilization patterns

Sixty-three megafaunal species/taxa were discriminated in the ROV video along the pooled CHIRP transects. Of these, 37 species were observed in ≥1% of all ROV observations (Table A.2). Species/taxa richness increased northward as 28, 42, and 52 species were observed along CHIRP 3, 5, and 7 respectively. Shannon diversity also increased northward (2.12, 2.35, 2.91 for CHIRP 3, 5, and 7 respectively). Species evenness was greatest along CHIRP 7 (0.741), whereas evenness was similar between CHIRP 3 (0.64) and CHIRP 7 (0.63). Plots of species rank abundance and cumulative percent dominance (Fig. 7) illustrate that megafaunal abundance was much greater along CHIRP 5 and 7 compared to the less speciose CHIRP 3 transect, and an increasingly greater number of species contributed to rank abundance from north to south, thus indicating beta diversity along the shoaling transgressive surface (compare to Fig. 5 bottom panel).

Habitat occupancy for species observed in ≥1% of the ROV sample observations (37 species, see Table A.2) is shown in a plot of the RDA results of the pooled unconditioned RDA (Fig. 8). The most habitat selective species are located furthest from the origin in Fig. 8 and include (1) all hard-bottom sessile megafauna including
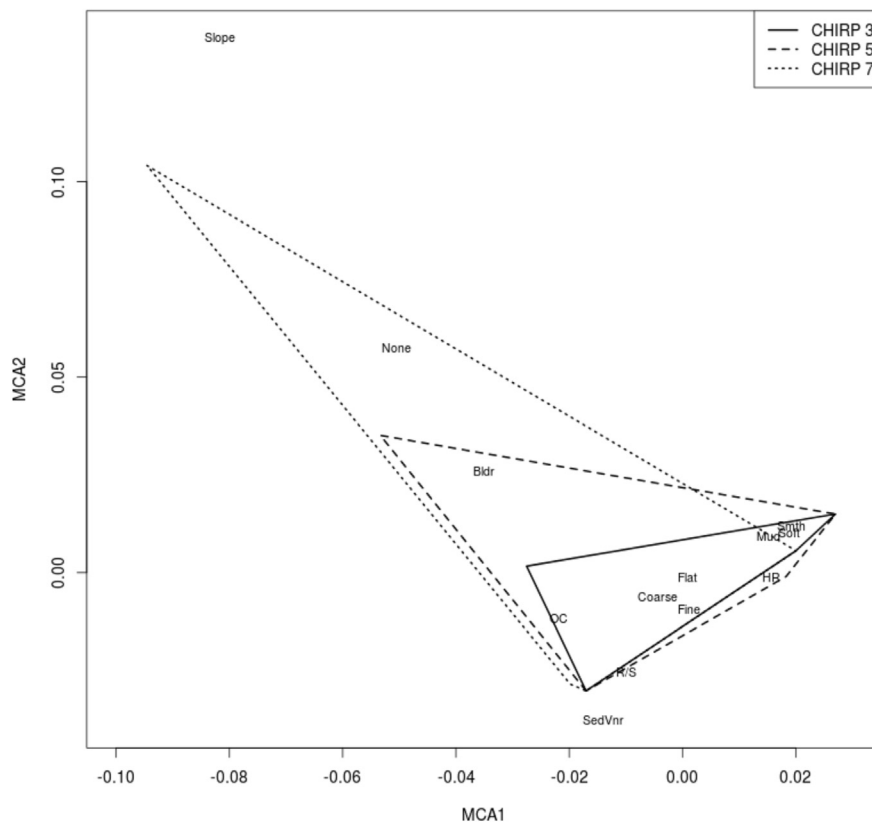

Fig. 4. Plot of the first two MCA factors describing bottom characteristic factors (Composition factors include 'Bldr' = boulder, 'R/S' = rocks mixed with soft sediment, 'SedVnr' = thin veneer of sediments, 'Soft' = soft bottom; Relief Angle factors include 'Flat', 'Slope'; Grain size factors include 'Coarse', 'Fine', 'Mud', and 'None' [consolidated outcrop]'; Bedform factors include 'HR' = hatched ripples, 'OC' = outcrop, 'Smth' = smooth unconsolidated sediment. See text for full description of habitat factors and levels. Triangles indicate range of habitats observed on each CHIRP transect.
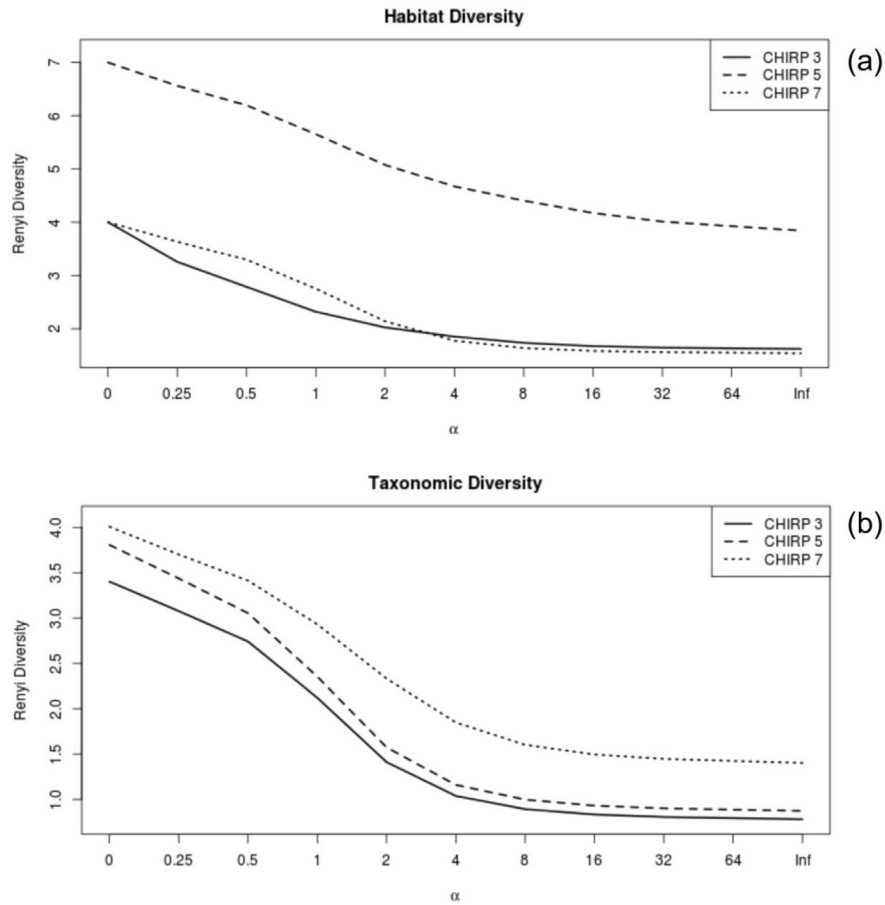
Habitat Diversity

Taxonomic Diversity

Fig. 5. Renyi diversity (entropy) as a function of scaling parameter (α) for habitats (a) and taxa (b) observed along CHIRP transect lines. Increasing values of α represent increasingly rarer habitats/taxa.
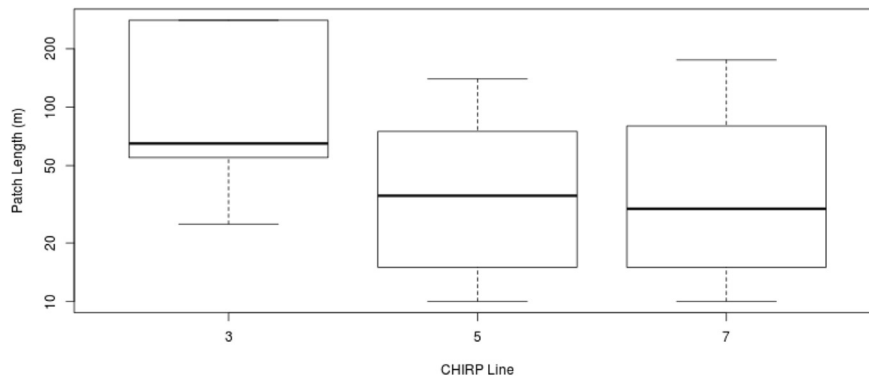

Fig. 6. Boxplots of contiguous habitat patch lengths for CHIRP transects. Boxes indicate 25th and 75th percentiles, whiskers indicate 5th and 95th percentiles. Bold lines indicate medians.

gorgonians, the encrusting sponge (*Toxadocia* spp.), *Florometra serratissima*, and cup corals, (2) mobile unconsolidated bottom and sediment veneer species including *Thesea* spp., infaunal ophiuroids, *Lytechinus* spp., *Parastichopus californicus*, *Diopatra* spp., and (3) schooling fishes including *Chromis punctipinnis* and *Sebastes paucispinis*.

The constrained components of the unconditioned RDA (Table 2) accounted for ~28% of the total inertia, and the permutation test was highly significant (p << 0.001). Conditioning the RDA by CHIRP line gained 3% more of total model inertia and was also significant (permutation test p < 0.001). Permutation testing to

compare the two models was highly significant (p < 0.001) indicating that beta diversity along the shoaling transgressive surface is significantly related to bottom morphology. Thus, forcing of beta diversity by tectonic forcing and sediment allocation is unambiguous.

Several species exhibited non-linear habitat occupancy among the CHIRP transects based on among-CHIRP comparisons of multiple regression residuals. Seventy-three percent of abundant species observed on all three CHIRP lines and that were significantly related to particular habitats clearly occupied their preferred habitats differently among the CHIRP lines. In effect, these species were
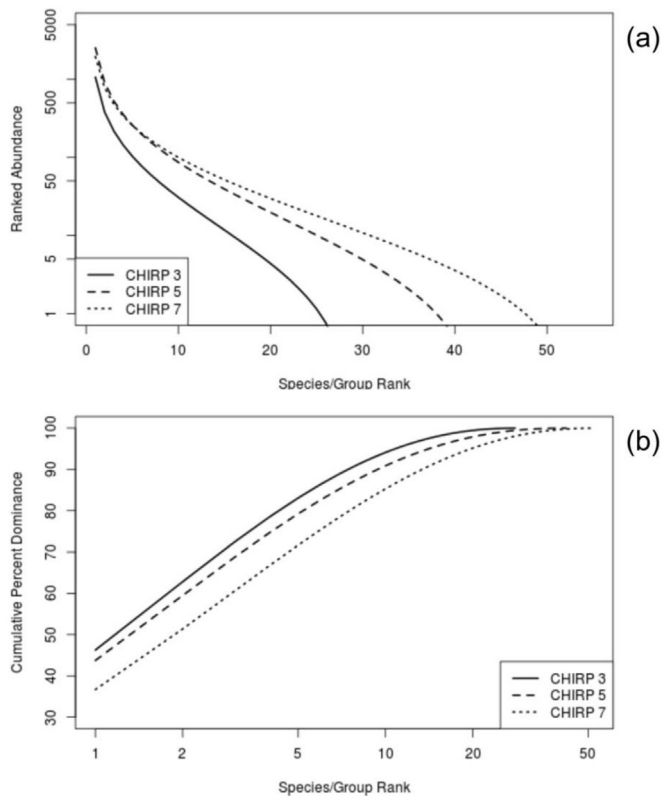
Fig. 7. Modeled rank abundance (a) and cumulative percent dominance (b) by species/group rank for CHIRP lines 3, 5, and 7. Rank abundance and percent dominance was modeled using generalized linear models of species/group counts along each transect (log link function, Poisson error distribution).

either more or less abundant than would be expected, given the proportional habitat composition observed along a given CHIRP line (Table 3).

The only exceptions were (1) small encrusting species including the cup coral *Paracyathus stearnsii*, and the sponge *Toxadocia* spp., and (2) the suspension-feeding cnidarian *Thesea* sp. Along CHIRP 3, infaunal ophiuroids, the sea cucumber *Parastichopus californicus*, and the gorgonian *Adelogorgia phyllosclera* were observed in greater abundances, and the sea urchin *Lytechinus* spp. was observed in significantly lower abundances than would be expected based on habitat composition. The abundance of the tubiculous polychaete worm, *Diopatra* spp., was significantly greater and abundances of the gorgonians *Eugorgia rubens* and *Lophogorgia chilensis* and infaunal ophiuroids were significantly less than expected along CHIRP 5. *Lophogorgia chilensis* and the gobiid *Rhinogobiops nicholsii* were observed at significantly greater abundances than expected and *Adelogorgia phyllosclera* and infaunal ophiuroids were observed less than expected along CHIRP 7.

4. Discussion

The results of this study indicate that species abundance and diversity patterns are clearly related to the gradational habitat structure resulting from tectonic and sedimentary processes (sensu Hogarth et al., 2007). The juxtaposition of the northward shoaling transgressive surface, the tectonically-controlled Holocene depocenter, and the surface-wave energy climate has created a texturally complex seascape that is differentially occupied by shelf megabenthos. While the entire region is dominated by unconsolidated sediments, there is a clear gradient of small scale (decameter)

patches nested within a larger-scale (myriameter) alongshore habitat gradient trending from soft to hard bottom. In response, the shelf community exhibits significant beta diversity along the transgressive surface gradient, and the habitat structure along the shoaling transgressive surface exerts complex low level control of species abundance and distribution patterns that are disproportionate for several species. These results indicate that habitat patch characteristics and distribution affect how species occupy and likely interact within this seascape in a complex manner. Sediment thicknesses thin and emergent hardbottom extent and profile increase northward along the gradient resulting in differential characteristic patch lengths and a decreasing potential for hardground sediment burial disturbance. These results have important implications for contextualizing and scaling ecological process studies and for the efficacy of acoustic remote sensing as a surrogate of species abundance, diversity, and community composition. In this soft-bottom dominated coastal shelf system, megafaunal biodiversity does not scale with habitat diversity unlike the generally accepted dogma for many other biomes (Simpson, 1949; MacArthur and Wilson, 1967; Tews et al., 2004), and patterns of abundance appear dependent on the underlying characteristic patch mosaic for many species (see also Anderson and Yoklavich, 2007; Anderson et al., 2009; Hunter-Thomson, 2011). Our results concur with previous studies of shallow benthos diversity that have also shown areas with the greatest taxonomic diversity do not necessarily coincide with the greatest habitat diversity (e.g., Parnell et al., 2006; Messmer et al., 2011), and that habitat effects on biodiversity are likely scale dependent (Hewitt et al., 2005; Anderson et al., 2009).

4.1. Patterns of diversity

Environmental heterogeneity including habitat complexity is generally thought to increase species richness (Huston, 1994; Statzner and Moss, 2004). This was clearly observed in our study in which species richness was greatest along CHIRP 7 where bottom complexity (patchy outcrops, boulders and sloped bottom nested within a larger area of unconsolidated sediments) was greatest. However, the greatest habitat diversity was observed along CHIRP 5 (Fig. 5, top panel), where taxonomic diversity was intermediate between CHIRP 7 and CHIRP 3 (Fig. 5, bottom panel). These observations indicate that structural complexity is a more important driver of species diversity than habitat diversity in this shelf system. Habitat complexity and diversity are implicitly characterized at different spatial scales and therefore affect taxonomic diversity differently across spatial scales (Anderson and Yoklavich, 2007). Habitat complexity is locally-scaled, whereas habitat diversity, by definition, is inclusive of multiple patches of characteristic habitat types. The distribution, composition, and sizes of characteristic patches therefore must be considered when characterizing taxonomic diversity (Anderson and Yoklavich, 2007; Hunter-Thomson, 2011). In our local shelf system and in many shelf systems globally, patch structure is forced by the superposition of unconsolidated sediments on the underlying hardground whose morphology records the interaction of tectonic deformation and sea level changes.

The patch structure of the DMPF is dominated by the transgressive surface gradient, which manifests as an ecotone with significant beta diversity. The gradation in habitat patch structure is subtle and is only observable at the appropriate scale, identified by seismic sub-bottom profiling, yet has produced a robust biological gradient. Factors that likely contribute to the observed beta diversity include gradients of patch size, habitat fragmentation, sediment burial disturbance (associated with sediment thickness), species-area relationships, edge effects, and biotic interactions
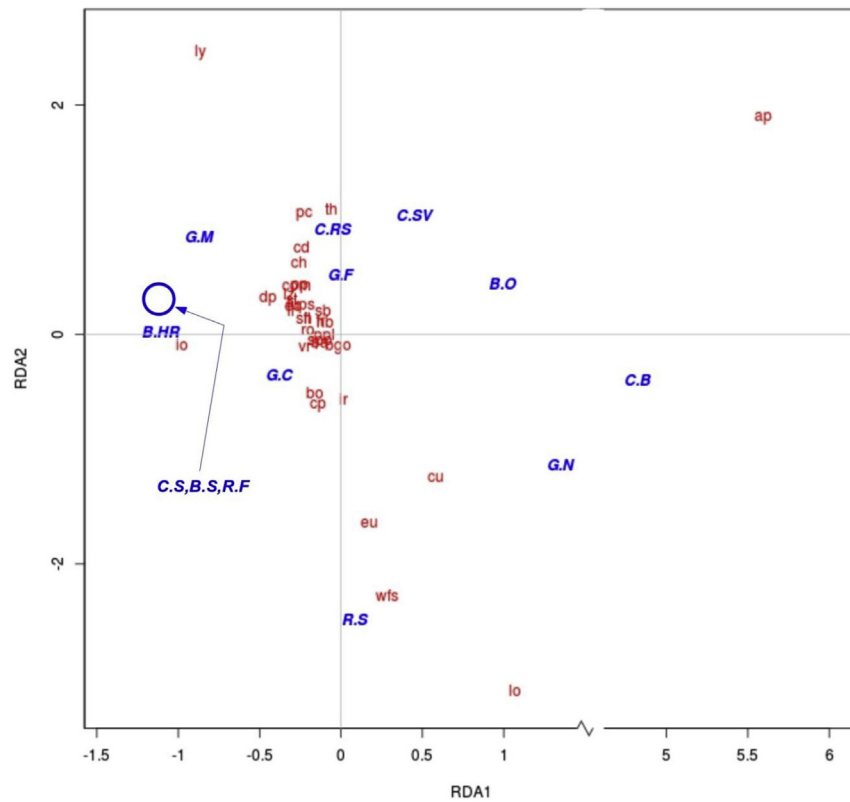
Fig. 8. Plot of species affinities to bottom characteristic factors resulting from RDA analysis. See Table A.1 for a list of species/taxa acronyms. Bottom characteristic factors included: 'C.S' = composition.soft, 'C.RS' = composition.rock/sand, 'C.SV' = composition.sediment veneer, 'C.B' = composition.boulder, 'G.C' = grain.coarse, 'G.F' = grain.fine, 'G.M' = grain.mud, 'G.N' = grain.none, 'R.S' = relief angle.sloped, 'R.F' = relief angle.flat,'B.S' = bedform.smooth, 'B.O' = bedform.outcrop, 'B.HR' = bedform.hatched.ripples.

(Hewitt et al., 2005). Many of these factors have been shown to be important drivers in landscape ecological studies (Wu and Loucks, 1995), and in the emerging field of seascape ecology (Pittman and Brown, 2011), in which most studies thus far have been conducted in estuarine, intertidal, or shallow subtidal systems.

The present work extends the question of the importance of fine

Table 2
Results of RDA analysis and permutation tests for full unconditioned model of species and habitat variables (top), RDA conditioned by CHIRP transect line (middle), and permutation significance test comparing the two models (bottom).

RDA not conditioned by CHIRP line						
	Inertia (variance)	Inertia proportion	Rank			
Total	33.90	1.00				
Constrained	9.52	0.28	7			
Unconstrained	24.39	0.72	37			
Eigenvalues	RDA1 = 8.78, RDA2 = 1.26, RDA3 = 0.22, …					
	PC1 = 17.24, PC2 = 1.19, PC3 = 0.85, …					
Permutation test	Component	d.f.		Variance	F	p	Permutations
	Model	7		9.52	32.66	**0.001**	999
	Residual	586		24.39			

RDA conditioned by CHIRP line						
	Inertia (variance)	Inertia proportion	Rank			
Total	33.90	1.00				
Conditional	1.030	0.03	8			
Constrained	10.44	0.31	7			
Unconstrained	22.43	0.66	37			
Eigenvalues	RDA1 = 9.75, RDA2 = 1.27, RDA3 = 0.19, …					
	PC1 = 15.58, PC2 = 1.21, PC3 = 0.737, …					
Permutation test	Component	d.f.		Variance	F	p	Permutations
	Model	7		10.44	38.84	**0.001**	999
	Residual	584		22.43			

Permutation test of conditioned and unconditioned RDA models						
Model	Residual d.f.	Residual variance	d.f.	Variance	F	p	Permutations
Unconditioned	586	24.39	2	1.95	25.43	**0.001**	999
Conditioned	584	22.43					

Significance (p < 0.05) is indicated by boldface.

Table 3
Results of (1) linear regression models of species abundance as a function of environmental variables in which CHIRP transect was included, and (2) simultaneous general linear hypothesis tests of residuals of linear regression models which excluded CHIRP transect (see text).

Species	Species code[a]	p	CHIRP 3[b]	CHIRP 5[b]	CHIRP 7[b]
Cnidarians					
Adelogorgia phyllosclera	ap	<0.001	**3.20**, 2.06, 4.34	0.17, −0.39, 0.73	**−1.11**, −1.72, −0.500
Eugorgia rubens	eu	0.005	0.11, −0.05, 0.27	**−0.09**, −0.17, −0.01	0.07, −0.012, 0.16
Lophogorgia chilensis	Lo	0.013	−0.02, −0.31, 0.27	**−0.26**, −0.40, −0.12	**0.31**, 0.15, 0.47
Paracyathus stearnsii	Cu	0.513	0.08, −0.13, 0.29	0.01, −0.09, 0.11	−0.03, −0.14, 0.08
Thesea sp.	th	0.711	0.05, −0.08, 0.18	0.002, −0.06, 0.07	−0.02, −0.09, 0.05
Echinoderms					
Infaunal ophiuroids	io	<0.001	**0.80**, 0.56, 1.04	**−0.25**, −0.37, −0.13	**0.15**, 0.02, 0.27
Lytechinus spp.	ly	<0.001	**−0.46**, −0.70, −0.22	0.03, −0.09, 0.14	0.10, −0.03, 0.23
Parastichopus californicus	Pc	<0.001	**0.37**, 0.23, 0.51	**−0.08**, −0.15, −0.02	−0.004, −0.08, 0.07
Annelids					
Diopatra spp.	dp	0.027	−0.08, −0.28, 0.12	**0.21**, 0.11, 0.31	0.03, −0.08, 0.13
Porifera					
Toxadocia spp.	wfs	0.371	0.14, −0.09, 0.36	−0.09, −0.20, 0.02	0.06, −0.06, 0.18
Fish					
Rhinogobiops nicholsii	bgo	<0.001	−0.06, −0.17, 0.04	−0.01, −0.06, 0.04	**0.03**, −0.03, 0.08

[a] Species code refers to codes used in RDA analysis (Fig. 8).
[b] Values in CHIRP columns indicate estimated expectation, lower and upper 95% family-wise confidence levels. Significantly different estimated expectation values are indicated in bold.

to mesoscale seascape modulation of diversity and species assemblages to continental shelf depths. Previous work at shelf and deeper depths has mainly focused on animal–habitat associations (e.g., Kostylev et al., 2001; Vierling et al., 2008) in which habitats are defined at larger scales, and habitats are differentiated with lower categorical resolution (e.g., deep reefs, unconsolidated sediments, etc.). In such a classification system, the DMPF would be considered a sand plain with scattered outcrops wherein the gradients of animal and habitat diversity would not have been resolved. This would be problematic for the application of digital elevation models as proxies for patterns of megabenthic species abundance, and could mask species–habitat associations in so called pattern–pattern studies in which spatial patterns of species abundance are tested for correlation with seascape features (Bostrom et al., 2011).

4.2. Patch structure and species occupancy

The tectonically forced patch structure of the DMPF is closely related to individual species abundance patterns as evidenced by significant differences among the CHIRP transect regression residuals (Table 3). These are likely driven by ecological processes associated with seascape patch structure such as edge effects (Jelbart et al., 2006), predator foraging patterns (Rilov and Schiel, 2006) and density (Stier et al., 2014), prey refugia (Wcisel et al., 2015), and movement corridors for mobile species (Appeldoorn et al., 2009). Species occupancy patterns observed in this study provide a starting point from which to design and conduct pattern-process studies focused on developing a mechanistic understanding of species abundance and diversity patterns forced by seascape patch structure. The shoaling transgressive surface provides a natural laboratory to conduct more detailed observational and experimental studies.

The results of regression model residuals for species common to all 3 CHIRP transects indicated that these species were not distributed among transects in relative proportion to their preferred habitats. The underlying causes of these distributional differences are not clear at present, and include patterns that may be forced solely by biological processes or by biological interactions modulated by physical patch structure (e.g, Hovel and Lipcius, 2001; Stier et al., 2014). The holothuroid, *Parastichopus californicus* is common in southern California trawl samples (Stull et al., 1999) and is a habitat generalist with least affinity to boulders and rocky outcrops (Woodby et al., 2000). Therefore, its

preferential distribution along CHIRP 3, where unconsolidated sediments were most dominant, may be behavioral or related to its detrital food source, which may not be as greatly utilized by edge foraging species. Predation is not likely since there are few known predators of adult *P. californicus*, but commercial fishing could affect habitat occupancy. However, the commercial fishery for *P. californicus* off San Diego has thus far been mainly conducted by divers within kelp forests. Similarly, the gobiid *Rhinogobiops nicholsii* was observed at a disproportionately greater abundance along CHIRP 7. *R. nicholsii* is a structural and edge species specialist (Love, 2011), and CHIRP 7 exhibits the most structural edge habitat. Similarly, the tubiculous polychaete *Diopatra* spp. (pooled *D. ornata* and *D. splendidissima*) was observed at disproportionately greater abundances along CHIRP 5 where its preferred habitat was most abundant. The preferred habitat of *Diopatra* spp. consists of a mixture of unconsolidated fine sediments, gravel, shell hash and rubble (Abbott and Reish, 1980) since soft sediments are a necessity for burrowing and these species attach larger-grained particles and rubble to their outer tube for protection from predation. The habitat occupancy patterns for *P. californicus*, *R. nicholsii*, and *Diopatra* spp., therefore appear to be enhanced in areas where their preferential habitats are located, and appear to scale non-linearly with percentage of favorable habitat.

In contrast, greater habitat diversity along CHIRP 5 appears related to disproportionate reductions in relative abundance for the gorgonians *Eugorgia rubens* and *Lophogorgia chilensis* and for pooled infaunal ophiuroids. Such disproportionate or non-linear habitat occupancy for these species is quite possibly related to patterns of patch size, interspersion, adjacency, and edge density. Further observation and experimental work are needed to develop a mechanistic understanding. On the other hand, some species did not exhibit nonlinear habitat occupancy. These included the sponge *Toxadocia* spp. and the cup coral *Paracyathus stearnsii*, both small sessile organisms with limited dispersal capability. Another species exhibiting a linear occupancy pattern was the suspension feeding octocoral, *Thesea* sp., whose movement is limited and which is mainly associated with thinly-layered soft sediments and is common in southern California trawls (Stull et al., 1999).

4.3. Implications and linking patterns to processes

Patterns of linear and non-linear occupancy observed in this study appear robust and are ecologically important in this coastal

shelf system. Results of previous shelf studies have indicated that linking multiple habitat scales is important for a fuller understanding of species distributional patterns (e.g., Anderson et al., 2009). Using a combination of seismic, acoustic, and ROV data we have identified the larger seascape scale that forces patch structure in this soft-sediment dominated shelf and how the megabenthos occupy this structure. The next step is to utilize these scales and patches of habitat for the design and stratification of patch specific studies of species occupancy and interaction.

These results have important implications for conservation planning (Collinge, 1996; Rhodes et al., 2008). Associated with habitat fragmentation and patch structure are local patch extinction risks, connectivity, and colonization potential, which increase complexity and affect the ecological functioning of the seascape mosaic for supporting metapopulations and biodiversity at the desired scales of conservation planning (Bascompte and Solé, 1996; Tilman et al., 1994). These results also have implications for the efficacy of remotely-sensed habitats as surrogates for species abundance and diversity (Anderson et al., 2005; Harris and Baker, 2012) in coastal shelf communities. Habitat-species abundance relationships established in a particular seascape are not likely transferrable to other seemingly similar seascapes especially when their patch structure and characteristic length scales vary as they do for the tectonically forced shelf habitats off La Jolla and Del Mar.

Acknowledgments

Appendix A

Table A.1 Characterization of PAM clusters resulting from partitioning around medoids (PAM) cluster analysis. Defining bottom characteristic factors dominant for each PAM cluster are listed.

PAM cluster	Defining bottom characteristic factors
1	Soft, Flat, Fine, Smooth
2	Soft, Flat, Mud, Smooth
3	Sediment Veneer, Flat, Fine, Outcrop
4	Boulder, Flat, Fine, Outcrop
5	Boulder, Flat, None, Outcrop
6	Soft, Flat, Fine, Hatched Ripples
7	Rocks with Sand, Flat, Mud, Outcrop

Table A.2 List of megafaunal species/taxa included in RDA analysis (observed in ≥1% of video sampling) along with density means and standard deviations along pooled CHIRP transects. Frequency indicates fraction of total observations each species/taxa was observed.

| Code	Species/taxa	Common name	Phylum/subphylum	Major group	Frequency	Density $\bar{x}$ (m^{-2})	Density s.d.
ap	*Adelogorgia phyllosclera*	Orange Gorgonian	Cnidaria	Gorgoniid	0.365	0.317	0.666
ly	*Lytechinus* spp.	White Sea Urchin	Echinodermata	Asteroid	0.296	1.040	2.985
io	*Multi-Species Complex*	Infaunal Ophiuroids	Echinodermata	Ophiuroid	0.204	1.251	3.768
lo	*Lophogorgia chilensis*	Red Gorgonian	Cnidaria	Gorgoniid	0.175	0.064	0.169
cu	*Paracyathus stearnsii, Balanophyllia elegans*	Cup Corals	Cnidaria	Caryophylliid	0.174	0.791	2.647
pc	*Parastichopus californicus*	California Sea Cucumber	Echinodermata	Holothuroidea	0.113	0.020	0.067
dp	*Diopatra* spp.	Parchment Tubeworm	Annelida	Polychaeta	0.103	0.535	2.117
eu	*Eugorgia rubens*	Purple gorgonian	Cnidaria	Gorgoniid	0.101	0.024	0.083
wfs	*Toxadocia* spp.	White Finger Sponges	Porifera	Demospongiae	0.098	0.030	0.119
th	*Thesea* sp.	Yellow Sea Twig	Cnidaria	Muriceid	0.095	0.019	0.064
bgo	*Rhinogobiops nicholsii*	Blackeye Goby	Chordata	Gobiid	0.074	0.014	0.054
lz	*Synodus lucioceps*	California Lizardfish	Chordata	Synodontid	0.046	0.007	0.029
ch	*Paralichthus californicus*	California Halibut	Chordata	Paralichthyid	0.039	0.007	0.040
ba	*Patiria miniata*	Bat Star	Echinodermata	Asteroid	0.031	0.006	0.037
ppl	*Polyclinum planum*	Elephant Ear Tunicate	Tunicata	Polyclinid	0.029	0.009	0.057
ir	*Mazzaella flaccida*	Irridescent Algae	Rhodophyta	Gigartinacea	0.026	0.011	0.077
spo	*Encrusting Sponges*	Pooled Encrusting sponges	Porifera	Demospongiae	0.026	0.005	0.034
st	*Stylatula elongata*	Slender Sea Pen	Cnidaria	Virgulariid	0.024	0.004	0.029
cp	*Chromis punctipinnis*	Blacksmith	Chordata	Pomacentrid	0.023	0.058	0.527
hb	*Sebastes semicinctus*	Halfbanded Rockfish	Chordata	Scorpaenid	0.023	0.009	0.058
ol	*Sebastes serranoides*	Olive Rockfish	Chordata	Scorpaenid	0.021	0.003	0.021
fl	*Sebastes rubrivinctus*	Flag Rockfish	Chordata	Scorpaenid	0.021	0.003	0.020
lu	*Luidia foliolata*	Light Sand Star	Echinodermata	Asteroid	0.021	0.003	0.024
cd	*Florometra serratissima*	Feather Star	Echinodermata	Crinoid	0.019	0.005	0.038
eo	*Ophiura luetkeni*	Brokenspine Brittlestar	Echinodermata	Ophiuroid	0.019	0.006	0.089
fr	*Muricea fruticosa*	Brown Gorgonian	Cnidaria	Gorgoniid	0.018	0.005	0.044
pp	*Parastichopus parvimensis*	Warty Sea Cucumber	Echinodermata	Holothuroidea	0.018	0.003	0.020
com	*Zaniolepis* spp.	Combfish	Chordata	Zaniolepid	0.016	0.003	0.022
ps	*Zalembius rosaceus*	Pink Seaperch	Chordata	Embiotocid	0.014	0.012	0.152
sh	*Semicossyphus pulcher*	California Sheephead	Chordata	Labrid	0.013	0.002	0.014
vr	*Sebastes miniatus*	Vermillion Rockfish	Chordata	Scorpaenid	0.013	0.002	0.020
bo	*Sebastes paucispinis*	Bocaccio	Chordata	Scorpaenid	0.013	0.005	0.054
ro	*Sebastes rosaceus*	Rosy Rockfish	Chordata	Scorpaenid	0.013	0.002	0.025
as	*Astropecten* sp.	Sand Star	Echinodermata	Asteroid	0.010	0.005	0.032
ii	*Luidia sarsi*	Dark Sand Star	Echinodermata	Asteroid	0.010	0.004	0.040
unksf	*Sebastes* spp. (schooling)	Pooled Schooling Rockfish	Chordata	Scorpaenid	0.010	0.196	1.282
sb	*Sebastes dallii*	Calico Rockfish	Chordata	Scorpaenid	0.010	0.005	0.059
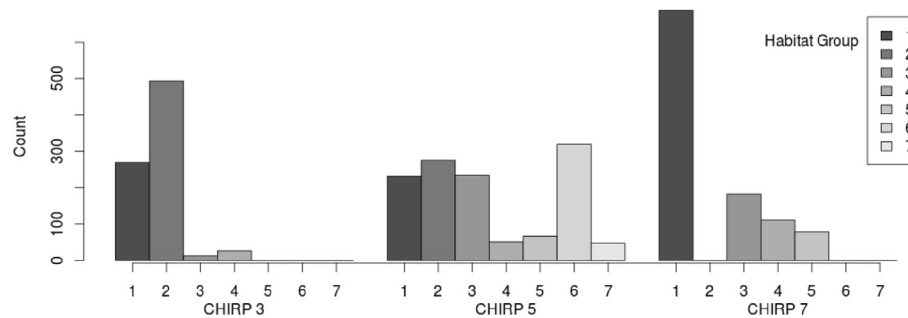
Fig. A.1. Distribution of PAM clusters (medoid groups) among the CHIRP transects. See Table A.1 for list of habitat features for each group.

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