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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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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;

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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