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# Vertical stratification in the distribution of demersal fishes along the walls of the La Jolla and Scripps submarine canyons, California, USA



CONTINENTAL SHELF RESEARCH

Joshua G. Smith<sup>a,\*</sup>, James Lindholm<sup>a</sup> <sup>a</sup> Institute for Applied Marine Ecology at California State University, Monterey Bay. 100 Campus Center Drive, Seaside, CA, United States

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# ABSTRACT

The geographic distributions of many coastal marine fish assemblages are strongly driven by habitat features, particularly among demersal fishes that live along the seafloor. Ecologists have long recognized the importance of characterizing fish habitat associations, especially where spatial management is under consideration. However, little is known about fish distributions and habitat suitability in unique demersal habitats such as submarine canyons. The active continental margin of the California coast is cut by eight submarine canyons, several of which extend from the shore to the deep abyssal plain. We sampled the demersal fish assemblages in two of those canyons: (1) the Scripps submarine canyon in the San-Diego-Scripps State Marine Conservation Area (SMCA) and (2) the La Jolla canyon in the Matlahuayl State Marine Reserve (SMR) to gain insight into both the distributions and habitat associations of demersal fishes in canyons. A remotely operated vehicle was used to conduct 21 vertically oriented transects along the canyon walls in depths ranging from 20 to 300 m. Species composition was assessed in three depthstratified zones (100 m per zone) along the canyon walls. Species richness, abundance, and attributes of the surrounding canyon habitat structure (slope and benthic terrain ruggedness) were quantified. Three distinct assemblage groupings were identified, which comprised 35 species of demersal fishes from 17 families. Among all factors analyzed in this study, depth, slope, and ruggedness were strong explanatory variables of patterns of species richness and abundance; however, the relationship between depth and assemblage structure was non-linear. The greatest number of species was observed in the mid depthstratified zone. These trends suggest that variation in canyon dynamics across depth strata may facilitate distinct assemblage groupings of demersal fishes, which can in turn be used to better manage these unique habitats.

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# 1. Introduction

The geographic distributions of many coastal marine fish assemblages are strongly driven by habitat features and associations with those features, particularly among demersal (seafloor-oriented) fishes that live along the seafloor. Key attributes of the environment such as depth, relief, rugosity, and substratum type (e.g., rock, cobble, sand, mud) facilitate both viable habitat and fish residency (e.g., Greene et al., 1999; Auster et al., 2003; Anderson and Yoklavich, 2007; Grober-Dunsmore et al., 2008). While associations between habitat structure and faunal composition have recently gained much attention for management practices (Genin, 2004; Bosley et al., 2004; De Leo et al., 2010; Starr et al., 2010; Currie et al., 2012; Carr et al., 2013), the distributions of fishes in submarine canyons are comparatively less understood than those of near shore coastal environments. Mounting evidence suggests that submarine canyons channel high levels of productivity and provide natural refugia (Yoklavich et al., 2000), thereby increasing local geographic biomass (Macquart-Moulin and Patriti, 1996). As such, submarine canyons may support unique fish assemblages that are compositionally distinct from those of the surrounding shelf environment (Allen et al., 2001).

Submarine canyons are steep sided valleys in the seafloor that cut into the continental slope. These distinct underwater topographies share several physical characteristics with terrestrial river gorges (Liu et al., 2002). For example, submarine canyons are erosional features often associated with large river extensions or geologic faults (Seilacher, 2006). Active fault lines and oceanic currents facilitate the exposure of older sediments in the canyon walls. Sediment deposits from currents, storms, earthquakes, tidal fluctuations, and flooding rivers accumulate on the axes of active submarine canyons and create underwater landslides that deposit

<sup>\*</sup> Correspondence to: Present address: University of California at Santa Cruz, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA, United States. *E-mail address:* JogSmith@ucsc.edu (J.G. Smith).

nutrient-rich sediment on the canyon floor (Greene et al., 1988). The dynamic and rapid rate of sediment turnover in canyons may facilitate increased nutrient input capable of supporting complex fish assemblages.

The active continental margin of the California coast is cut by eight submarine canyons, several of which extend from the shore to the continental shelf break (Yoklavich et al., 2000). The La Jolla Canyon in southern California is unique from other submarine canyons in that it is the main branch of a canyon network that extends from the deep sea virtually into the beach. The second main canyon of the network is the Scripps canyon, which intercepts the La Jolla canyon one kilometer offshore. These canyons are abruptly steep, lined with high vertical walls and overhangs that extend below 1,000 m near the continental shelf (Francis and Neil, 1969). Historic evidence suggests each canyon head is unstable and shifting towards the shore at a rate of nearly one inch per year (Shepard and Dill, 1966).

The distributions of many organisms found within submarine canyons are not exclusive to canyons alone, but extend to other similar depths and habitats outside of canyons (Stefanescu et al., 1994). Demersal fishes, for example, aggregate near rocky outcrops along canyon walls, which provide shelter and essential habitat (Demestre et al., 2000). Because canyon topography spans a wide range from near shore to deep sea environments, they generate complex water circulations that result in higher local productivity (Macquart-Moulin and Patriti, 1996; Greene et al., 1998; Allen et al., 2001; Bosley et al., 2004). Although small micronekton are susceptible to offshore advection by variable flows in canyons, vertically migrating macronekton and macrozooplankton can maintain themselves in position within a canyon's flow field (Macquart-Moulin and Patriti, 1996; Allen 1996; Mackas et al., 1997; Allen et al., 2001). These aggregations of macronekton are consumed by many resident fish species (Smith et al., 2001).

Among the demersal fish species in canyons are highly harvested commercial species. One group of fishes in particular is rockfishes, Sebastes spp. (Love, 2002). Rockfish compose one of the most valuable fisheries on the temperate California coast and are often associated with rocky substratum found in submarine canyons (Love et al., 1991). Most rockfish species have some economic value that contributes to the state's annual \$17.8 million groundfish fishing industry (CDFW [California Department of Fish and Wildlife], 2013). Rockfish are long lived and slow to mature, making their populations extremely susceptible to overfishing. Southern California has historically received high fishing pressure. Consequently, rockfish abundances were sharply reduced between 1990 and the year 2000 (Love et al., 1998). To compensate for the loss in near shore rockfish catch, fishing fleets are continuously extending their range to deeper water. Although fishing fleets are shifting their focus to deeper areas, the steep walls of the La Jolla and Scripps canyons make this area particularly difficult to fish with the imminent risk of gear entanglement.

Challenges associated with surveying deep subtidal ecosystems have limited the amount of research conducted in these areas. Specifically, detailed analyses of these locations have been impossible until now due to a lack of effective technological sampling equipment (McClain and Barry, 2010). Common traditional methods include traps, trawls, grabs, and hook and line (Barry and Baxter, 1993). Each of these approaches provides a general understanding of fish habitat associations, but it is now clear that they do not capture fine scale accuracy that is achievable with modern techniques. Additionally, few studies have been conducted on submarine canyons because traditional sampling gear is subject to entanglement on high relief outcrops (Chuenpagdee et al., 2003; Freiwald et al., 2004).

Imagery based approaches to collecting information in the deep subtidal marine environment (e.g., remotely operated vehicles, human occupied submersibles, towed camera sleds) have a long history (Grassle et al., 1975; Uzmann et al., 1977; Ballard, 1993). These approaches provide detailed insight for understanding the fine scale habitat associations, diversity, depth distribution, relative abundance, and behavior of demersal fish species (Yoerger et al., 2000; Trenkel et al., 2004; Costello et al., 2005). Underwater camera systems mounted on these devices provide photo- and video-graphic imagery of sea floor habitat and the habitat-associations of benthic and mobile organisms. On-board Global Positioning Systems (GPS) provide detailed spatial scales to within two-meter resolution that is not obtainable through the use of conventional trawling methods. Additionally, conductivity, temperature, and depth (CTD) gauges provide detailed chemical properties associated with each marked observation (Lindholm et al., 2015).

Here we examine the vertical stratification of demersal fish assemblages along the walls of the La Jolla and Scripps submarine canyons. The ultimate objectives of our study were two-fold: (1) characterize observed patterns in the vertical stratification of demersal fish assemblage structure along the steep walls of the La Jolla and Scripps submarine canyons, and (2) identify attributes of the environment (including canyon-related factors) influencing observed patterns in assemblage structure. While near shore environments have been heavily studied, we are just beginning to understand those beyond the depth limits of SCUBA (greater than 30 m). The La Jolla and Scripps canyons provide a unique opportunity to assess the influence of canyon topographic effects (e.g., variation in slope, ruggedness, and orientation) on the distribution of demersal fishes, and to investigate spatial variation in fish assemblages across two adjacent canyon heads. Our study was intended to improve current knowledge of fish habitat associations and assemblage structure inside submarine canyons and to demonstrate a novel approach for surveying canyons using a remotely operated vehicle.

# 2. Methods

# 2.1. Study Site

The La Jolla canyon is comprised of two main branches, which extend from the shore to the open ocean. The northern portion of the canyon (32°52'N, 117°16'W) is located in the San Diego-Scripps Coastal State Marine Conservation Area (SMCA), and the southern portion (32°51'N, 117°16'W) in the Matlahuayl State Marine Reserve (SMR) (Fig. 1). The northern portion extends southward from the mainland. The southern portion of the canyon extends for nearly 53 km seaward in a southwest direction and is intersected by the northern branch approximately one kilometer offshore. The habitat contained within this site is managed under both state and federal jurisdiction. The study site included a very large depth range with the axes of canyon walls extending from 20 m deep to over 300 m. Substrate type across the study region was generally composed of hard rocky outcrops along steep canyon walls, with a relatively even mixture of loose cobble and soft substrate.

## 2.2. Data collection

Video and still imagery of the canyon walls were collected using a Vector L4 ROV (Deep Ocean Engineering and Marine Applied Research Exploration) equipped with three geo-referenced cameras (forward- and down-looking video, and digital still images), two Quartz halogen Hydrargyum Medium-arc Iodide (HMI) lights, paired forward- and down-looking lasers, and a strobe for still photo enhancement. The ROV was also equipped with an altimeter and forward-facing multi-beam sonar. The position of the ROV along the canyon walls was maintained using Trackpoint III<sup>®</sup>



Fig. 1. Study site within the La Jolla and Scripps canyons. Transect lines are drawn in orange (2011) and yellow (2012). The San Diego-Scripps SMCA is outlined in blue and the Matlahuayl SMR in red.

acoustic positioning system (ORE Offshore, West Wareham, MA) with the resulting coordinates logged into Hypack<sup>®</sup> navigational software (HYPACK, INC, Middletown, CT).

Primary video imagery was collected using the forward-facing color camera. A second up-looking video camera, oriented at 45 degrees above the forward-facing camera, was used for identification support (i.e., increase accuracy of identification estimates) and to observe fishes stationed above the ROV that may have moved out of frame during transit. In addition to the two continuous video cameras, a third camera captured still photos. This camera recorded time, depth, heading, range, screen width, and temperature for every second spent in transit (See 'ROV heads up display' in supplementary material). Collectively, the cameras captured habitat features (e.g., substrate type, canyon slope) and associated fauna of the canyon environment.

## 2.3. Survey design

Vertically-oriented ROV transects were conducted along the La Jolla and Scripps submarine canyon walls. The ROV was positioned facing the canyon walls and 'flown' at a distance of 0.9 m from the walls at a speed approximately 0.67 knots (Fig. 2A). Transect length depended on the distance from the floor of the canyon to its upper axes (Fig. 2B), but generally covered a distance of 200–300 m between 20 and 300 m seawater depth. A total of 21 transects were completed across two expeditions in the years 2011 and 2012. Each expedition was scheduled for early November and all transects were conducted mid-day.

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#### 2.4. Data extraction from video

Video transects were observed for the presence of demersal fish species. An initial viewer recorded the following data from the ROV imagery: *time of occurrence, identification* (to the lowest taxonomic group possible), *identification quality*, and *fish size*. Scaling lasers spaced 10 cm apart were used to approximate fish size to the nearest 5 cm. Identification quality was assessed on a scale from one to five (1=uncertain and 5=certain) and represented our measure of confidence for all observations. To ensure identification quality control, all identifications were confirmed by second and third reviewers. Only species with identification levels greater than or equal to three were used in subsequent analyses to improve predictive capacity and increase the accuracy of our models.

ArcGIS (ESRI Geographic Information Software) was used to pair fish observations with associated habitat attributes and to undertake all calculations of habitat ruggedness and canyon slope. Habitat features and bathymetry data were obtained from a California statewide seafloor mapping project. These data were used to calculate both canyon slope and ruggedness of the benthic environment for all ROV transects. Benthic terrain ruggedness and canyon slope were calculated as the variation in three-dimensional orientation of the nearest neighbor grid cells, and are accurate to within 2 m resolution (Hobson, 1972). Calculated slope and ruggedness values were then paired with GPS coordinates logged by the ROV to link biological observations with associated slope and ruggedness values.



**Fig. 2.** 3D rendition of multi-beam bathymetry from CSUMB's Seafloor Mapping Lab profiling the headward portion of each canyon's geomorphology for A) Scripps Canyon and B) La Jolla Canyon. Transect lines are drawn in orange (2011) and yellow (2012). The color gradient was scaled to 20 m intervals for visualization of natural contours. See 'Canyon animation' in supplementary material.

#### 2.5. Analytical approach

Prior to all analyses, depth profiles were categorized into three stratified zones of 100 m (hereafter referred to as shallow, mid, and deep) to correct for unequal sampling effort applied at different depth strata. Richness and abundance were standardized as the number of species or individuals, respectively, per square meter per depth zone. Sampling effort was determined by calculating the distance of the geospatial hypotenuse traveled by the ROV along the canyon walls within each depth zone. Total species richness and abundance per depth zone were divided by this parameter to correct for unequal sampling effort applied between zones. Relationships between depth, temperature, slope, ruggedness, richness, and abundance were subsequently tested using Pearson correlations.

Relationships between the number of species (*S*) and sampling effort (*I*) per depth zone were projected and fitted using the Michaelis-Menten (M-M) species accumulation curve (Keating and Quinn, 1998):

$$S = \frac{S_{max}*I}{b+I}$$

where  $S_{max}$  and b are constants calculated from a maximum likelihood ratio test. This allowed us to compare our estimates of richness across depth zones and to evaluate the likelihood of accurately measuring richness based on sampled area. An overall  $R^2$ description of each model was calculated as the sum of squared deviations of observed points from the fitted M-M model prediction, divided by the total sum of squares.

Spatial variation in demersal fish assemblage structure across depth strata and between canyons were further analyzed using Bray-Curtis (B-C) dissimilarity measures (Faith et al., 1987) in the computer package PRIMER (Plymouth Marine Laboratory). Squareroot transformations were applied to decrease the influence of particularly abundant species and increase the importance of less abundant species. Multi-dimensional scaling (MDS) ordination plots were used to visualize discontinuities in assemblage structure and differences were mapped using hierarchical agglomerative clustering. Significant differences between canyons and depth zones were subsequently tested using a two-way permutational analysis of variance (PERMANOVA). Similarity percentages (SIMPER) were then performed to determine which taxa were most important in structuring assemblage composition between and within depth zones.

Generalized Linear Models (GLMs) were used to determine the best predictors of species richness and abundance across depth, temperature, slope, and ruggedness gradients using a Poisson error structure defined as: Richness, Abundance =exp  $[\mu + \beta_0^*(depth) + \beta_1^*(temperature) + \beta_2^*(slope) + \beta_3^*(ruggedness) + \epsilon]$ where  $\mu$ =model intercept,  $\beta_x$ = regression coefficient (i.e., re-

where  $\mu$  = hour intercept,  $h_x$  = regression connecting (i.e., relative influence of treatment), and

 $\epsilon$  = unexplained model error.

The Poisson error structure was used to account for zero-inflated distribution of our presence-absence observational data and because the variance was proportional to the square of the mean. Significant models for species richness and abundance were chosen by forward-selecting terms within each model and using Akaike's Information Criterion (AIC; Bozdogan, 1987) to choose the models with the lowest scores.

# 3. Results

# 3.1. Composition of demersal fishes

Demersal fish assemblages comprised 35 species from 17 families (Table 1) and contained many key species of economic and ecological interest (Lea et al., 1999; Love, 2002; Starr et al., 2010; Carr et al., 2013). Family Sebastidae was the most speciose family (15 species), followed by Hexagrammidae (3 species) and Pleuronectidae (2 species). In general, aurora/splitnose and vermilion rockfish were observed at high densities within narrow depth ranges (Fig. 3 and Table 1). Halfbanded rockfish and California lizardfish densities were evenly distributed across the depth gradient. Blackeye goby and hundred-fathom codling exhibited clear inverse relationships between their respective densities and depth. Densities of blackeye goby decreased along a depth gradient from 20 to 170 m. Conversely, hundred-fathom codling densities steadily increased from 170 to 270 m.

## 3.2. Assemblage structure

Three distinct demersal fish assemblages were identified from multi-dimensional scaling (MDS) ordination plots and cluster analyses set at the five percent significance level. Shallow (20–100 m) and mid (100–200 m) depth assemblages were represented at 40% similarity between the La Jolla and Scripps canyons, and were highly similar (60%) within individual canyons (Fig. 4). These shallow and mid depth assemblages were primarily dominated by members from the genus *Sebastes* spp. (15 species; SIMPER: Cum. Percent = 50). Other members found at shallow and mid depths included (Table 1): lingcod (*Ophiodon elongates*), senorita (*Oxyjulis californica*), blackeye goby (*Rhinogobiops nicholsii*), pink surfperch (*Zalembius rosaceus*), combfish (*Zaniolepis* spp.),

# Table 1

Densities (number of individuals  $\times 10^4$  per m<sup>2</sup>) of fishes observed in the La Jolla and Scripps canyons across three depth stratified zones.

Family	Species	Location					
		La Jolla			Scripps		
		Shallow	Mid	Deep	Shallow	Mid	Deep
Agonidae Bathymasteridae Cottidae	Poacher (family Agonidae)	3.65	36.51	_	5.69	6.82	_
	Ronquil (family Bathymasteridae)	10.96	-	_	-	-	-
	Sculpin (family Cottidae)	-	-	-	-	1.36	-
Embiotocidae	Pink Surfperch (Zalembius resaceus)	7.30	-	-	1.90	-	-
Gobiidae	Blackeye Goby (Rhinogobiops nicholsii)	76.70	1.52	_	36.05	2.73	-
Hexagrammidae	-	36.52	25.86	9.17	11.39	2.73	-
	Lingcod (Ophiodon elongatus)	7.30	1.52	-	-	1.36	-
	Longspine Combfish (Zaniolepis latipinnis)	-	15.21	3.06	11.39	1.36	-
	Shortspine Combfish (Zaniolepis frenata)	29.22	9.13	6.11	9.49	-	-
Merluccidae	Pacific Hake (Merluccius productus)	_	_	15.29	_	_	_
Moridae Ophidiidae Paralichthyidae Pleuronectidae	Hundred-fathom Codling (Physiculus rastrelliger)	_	10.65	45.86	-	-	-
	Spotted Cusk Eel (Chilara taylori)	-	3.04	-	-	-	-
	Pacific Sanddab (Citharichthys sordidus)	10.96	-	-	-	-	_
	_	_	3.00	3.10	1.90	8.20	_
	Dover Sole (Microstomus pacificus)	-	3.04	-	1.90	8.19	_
	Slender Sole (Lyopsetta exilis)	-	-	3.06	-	-	-
Sebastidae	_	1760.41	717.98	64.20	593.93	147.38	81.52
	Aurora/Splitnose Rockfish (Sebastes aurora/diploproa)	_	112.56	_	_	1.36	_
	Blackgill Rockfish (Sebastes melastomus)	_	1.52	_	_	_	_
	Chilinenner Rockfish (Sebastes goodei)	_	1.52	_	_	_	_
	Flag Rockfish (Sebastes rubrivinctus)	10.96	_	_	_	_	_
	Greenblotched Rockfish (Sebastes rosenblatti)	_	3.04	_	_	136	_
	Greenspotted Rockfish (Sebastes chlorostictus)	3 65	4 56	_	190	_	_
	Greenstriped Rockfish (Sebastes elongatus)	_	7.61	_	_	1.36	_
	Halfbanded Rockfish (Sebastes semicinctus)	1639.88	579 56	58.09	552.18	131.00	81 52
	Honeycomb Rockfish (Sebastes umbrosus)	3 65	-	_	190	_	_
	Rosy Rockfish (Sebastes rosaceus)	3.65	_	_	_	_	_
	Squarespot Rockfish (Sebastes honkinsi)	21.91	_	_	13 28	_	_
	Starry Rockfish (Sebastes constellatus)	3 65	_	_	190	_	_
	Sehastomus	730	7.61	611	11 39	12.28	_
	Strinetail Rockfish (Sebastes saxicola)	_	-	_	190	-	_
	Vermilion Rockfish (Sebastes miniatus)	65.74	-	-	9.49	_	-
Scorpaenidae	California Scorpionfish (Scorpaena guttata)	36.52	152	_	190	136	_
Stichaedidade	Bluebarred Prickleback (Plectobranchus evidus)	_	13.69	_	-	5.46	_
Stromateidae Synodontidae	Pacific Butterfish (Penrilus similimus)	_	6.08	917	_	_	_
	California Lizardfish (Synodus luciocens)	51 13	44 11	27.51	81 59	12 28	_
			913	39.74	-	12.20	_
Louitiuat	Bigfin Felpout (Incodes cortizianus)	-	152	18 3/	-	-	-
	Folpout (Lycodes spp.)	-	7.52	21 40	-	-	-
	Ecipour (Lycones spp.)	-	7.01	21.40	-	-	-



HFBD - Halfbanded Rockfish Sebastes semicinctus

CALD - California Lizardfish Synodus lucioceps

AUSN - Aurora/Splitnose Rockfish

Sebastes aurora/diploproa

**BEGD - Blackeye Goby** Rhinogobiops nicholsii

VERM - Vermilion Rockfish Sebastes miniatus

HFCD - Hundred Fathom Codling Physiculus rastrelliger

SQSP - Squarespot Rockfish Sebastes hopkinsi

CASC - California Scorpionfish CASC Scorpaena guttata

Fig. 3. Relative densities (number of individuals per m<sup>2</sup>) of the eight most abundant species observed across 21 vertical transects in the La Jolla and Scripps canyons.



Fig. 4. MDS ordination (a) and cluster dendrogram (b) of demersal fish assemblages in three depth-stratified zones at the La Jolla and Scripps submarine canyon heads.

poacher (family Agonidae), and ronquil (family Bathymasteridae).

Assemblages in the deep zones (depths greater than 200 m) showed no significant similarity with other groupings. These deep assemblages were highly independent of each other and the shallow and mid depth assemblages between the Scripps and La Jolla canyons (Fig. 4b; PERMANOVA: df=2, P=0.001). The La Jolla canyon deep assemblage comprised members from genera *Lycodes* spp., *Synodus* spp., *Zaniolepis* spp., *Merluccius* spp., *Physiculus* spp., and *Peprilus* spp. These members were relatively uniformly represented in the La Jolla deep assemblage grouping (one to two species observed per genus). Two species of demersal fishes unique to the La Jolla deep zone included: (1) hundred-fathom codling (*Physiculus rastrelliger*), and (2) northern pacific hake (*Merluccius productus*). Only a single species was observed in the Scripps deep canyon, halfbanded rockfish (*S. semicinctus*), which made it independent from other assemblage groupings.

# 3.3. Vertical patterns in richness and abundance

Abundance and richness (number of species per depth zone) were correlated and represented similar spatial patterns in shallow and mid depths (Fig. 5); however, abundance and richness showed a clear divergence at depths greater than 200 m. It should also be noted that abundance and richness co-varied with each other and were independently strongly correlated with depth. Michaelis-Menten projections of species-area relationships

revealed the mid depth (100–200 m) zone comprised the most species (31 species; Fig. 6 and Table 2). The deep zone asymptotic projection was 28 species, and the shallow zone at 29.

Generalized linear models showed that depth, slope, and ruggedness were significant predictors of species richness and abundance (Table 3). In both models, temperature did not significantly contribute to any variation in species richness or abundance.

# 4. Discussion

We hypothesized that marked differences in richness and abundance between the two canyons were correlated with canyon related differences in orientation and topography. Our expedition was scheduled to precede the implementation of the Matylahual State Marine Reserve. Therefore, we do not attribute any differences in assemblage composition between the two canyon heads to a reserve-effect. Several studies have described distinct relationships between canyon related upwelling and centralized primary productivity (Hill and Cota, 2002; Ryan et al., 2005; Rennie et al., 2009; Wei et al., 2010). Many deep sea demersal fish assemblages are dependent upon rich sources of organic matter in the upper photic zone (Smetacek, 1984; Smith et al., 2001). Stefanescu et al. (1994) investigated the influence of a Mediterranean submarine canyon on the distribution of fishes and found greater



Fig. 5. Pearson correlation coefficients between treatment variables: depth, richness, temperature, slope, ruggedness, and abundance. Significant correlations are denoted at the \*5% level.

abundance inside the canyon compared to the adjacent slope. Trophic resources inside the canyon were identified as the primary factor facilitating patterns of increased abundance and biomass inside the Mediterranean canyon. Our observations of greater species richness and abundance in the La Jolla canyon provided compelling evidence of connectivity between topography and nutrient input. The La Jolla canyon is the main branch of the canyon system in our study area. After intersecting the smaller Scripps canyon approximately one-kilometer offshore, the La Jolla canyon continues seaward beyond the continental shelf. This main canyon channel may focus upwelling from the deep sea to the subtidal, providing a flux of nutrient-rich water. Conversely, the Scripps canyon is disconnected from the main canyon's flow-field and thus may not act as a conduit favoring nutrient input (Fig. 7). In addition to broad oceanographic processes, several studies have highlighted the importance of fine-scale habitats influencing the distribution of fishes (Carr, 1994; Levin 1994; Lindholm et al., 2004; Stone 2006; D'Onghia et al., 2011). While canyon slope and ruggedness were calculated to within two-meter accuracy for each fish observation, they failed to be positive predictors of species richness and abundance. Other studies have found slope to be a strong predictor of fish distribution (Wigand, 2012) and that the abundance of many species is positively related to benthic ruggedness (Yoklavich et al., 2000). Our slope and ruggedness calculations were performed using multibeam bathymetry data extracted from a statewide monitoring study that were later paired with our fish observations. It is likely that mismatches in the scale of paired observations did not accurately capture the fine-scale



**Fig. 6.** Number of species observed per unit area (points) per zone (shallow, mid, deep) and Michaelis-Menten species-area curve projections (lines). Although 21 vertically-oriented transects were conducted during this study, the M-M projections are depicted to the asymptotic level at 39 transects.

#### Table 2

Species accumulation models based on Michaelis-Menten projections.

Zone	Model	R <sup>2</sup>	Observed Species	Projected number of species
Shallow	29.37 * Number of transects 11.03 + Number of transects	0.997	22	29
Mid	31.12 * Number of transects 11.55 + Number of transects	0.999	24	31
Deep	28.89 * Number of transects 15.12 + Number of transects	0.998	12	28

#### Table 3

Regression coefficients from GLM's for richness and abundance. Note: shallow depth was set at the GLM's categorical reference level and is not displayed.

Response	Treatment	Estimate	$\mathbf{Pr}$ ( $>$ z)
Richness	Mid Depth (100–200 m)	5.25	0.35
	Deep Depth ( > 200 m)	16.8	0.03
	Slope	- 0.01	0.01
	Ruggedness	- 9.52	0.03
	Temperature	0.14	0.75
Abundance	Mid Depth (200–300 m)	8.99	< 0.0001
	Deep Depth ( > 300 m)	5.7	0.01
	Slope	- 0.03	< 0.0001
	Ruggedness	- 30.38	< 0.0001
	Temperature	- 0.09	0.5

\* Indicates significant (p < 0.05)



Fig. 7. Theoretical nutrient flow based on canyon orientation and topography.

habitat associations of demersal fishes inside the canyons. Future analyses and fine-scale habitat associations at a resolution more accurate than two meters would require directly extracting paired fish-habitat observations from ROV video.

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.csr.2016.07.001.

In our analyses of physical and environmental parameters influencing richness and abundance, depth was identified as the strongest and only positive predictor variable. However, depth should not be considered an independent factor influencing vertical stratification in the distribution of fishes. This is because several chemical and physical properties co-vary with depth. For example, salinity and dissolved oxygen change with depth and play key roles in the distribution of fishes (Cyrus et al., 1992; Castillo et al., 1996; Abookire et al., 2000). Our observations of distinct assemblage groupings across depth strata may be associated with other environmental parameters not recorded here.

The La Jolla and Scripps canyons were comparatively low in demersal fish species richness (35 species) when compared to the surrounding shelf environment. For example, an eleven-year submersible study in similar depths (19-365 m) found greater than 137 species on the continental shelf (Love et al., 2009). These researchers attributed patterns of species richness to selective fishing pressure. Selecting for large adult fish could enhance the success of other smaller species, creating a positive effect on overall species richness (e.g., Loos, 1989 described an angler's fishing experience and selectivity in the Scripps canyon). The regionally low species richness observed in our study may be due to selective fishing pressure, which could be naturally mediated by the physical steepness of the canyon walls (e.g., Stefanescu et al., 1994; Farrugio, 2012; Tecchio et al., 2013). Natural refugia could allow larger species to thrive, thereby increasing local geographic biomass and decreasing species richness (Yoklavich et al., 2000). It is also possible that selected fishes responded to the presence of the ROV by avoiding it, resulting in a lower observed richness. Given the vertical orientation of our transects, fishes that escaped laterally may not have been captured in the field of view of the forward- or above-facing cameras. However, ROV avoidance alone is not likely to explain the considerable difference in richness relative to the adjacent non-canyon environments.

The absence of juveniles in the canyons suggests that the La Jolla and Scripps canyons may provide important adult refuge, but do not serve as a nursery ground for juvenile fishes. This hypothesis is consistent with the findings reported by Yoklavich et al. (2011) in the Soquel Canyon, which is comparable in depth and size to the La Jolla and Scripps canyons. In contrast, Stefanescu et al. (1994) and Brodeur (2001) found canyons provided critical nurserv areas for species near continental margins. Another study conducted by Schlacher et al. (2009) found some species preferentially spawned inside submarine canyons. It is possible that our sampling periods did not coincide with the timing of recruitment inside the canvons. It is also possible the absence of juvenile fishes may have been an artifact of the ROV sampling limitations described above. However, the fact that we have observed juvenile fishes frequently with the ROV elsewhere along the shelf and slope suggests that sampling limitations alone do not explain the absence.

To date, our finite understanding of recruitment processes impairs our ability to understand the replenishment of stock to submarine canyons. The complex physical dynamics occurring in canyons are known to act as conduits that channel organic matter, sediments, and nutrients that support spawning and recruitment for bentho-fauna (D'Onghia et al., 2015). Our results highlight the fact that any future sampling occur within an experimental framework that integrates the local and regional dynamics of recruitment with our understandings of fish populations and communities. Such efforts will provide resource managers with greater accounts of standing stock and more accurate forecasts of stock replenishment.

# 5. Conclusions

Three distinct fish assemblages identified along the walls of the La Jolla and Scripps canyons reveal the existence of vertical stratification in demersal fish distribution in which depth, canyon orientation and topography, and habitat structure are important factors in assemblage differentiation. Faunal assemblage structure by depth and canyon can be described as a La Jolla canyon deep assemblage (> 300 m), a Scripps canyon deep assemblage (> 300 m), and a "transitional" assemblage between canyons at shallow (< 100 m) and mid depths (200–300 m). Hecker (1990) found that deep water assemblages changed along a gradient of 100 m between groupings and described a deep water transitional zone where important assemblage groupings overlap. Our investigation revealed a similar transition zone at mid-depths, where the greatest number of species observed was probably due to overlap in shallow and deep assemblage groupings.

Our study supports the importance of both broad physical oceanographic processes and fine-scale habitat attributes as mechanisms that influence the distributions of demersal fishes. Mesoscale oceanographic processes such as upwelling, for example, provide crucial nutrient input into near shore marine systems. We suspect that benthic topographies found outside of submarine canyons along the continental shelf may perform similar functions in channeling organic nutrients. Thus, estimates of broad physical processes (e.g., nutrient input trajectory and timing) are important components of effective spatial and temporal management regimes (DeMartini, 1993; Nowlis and Roberts 1999). Continued analyses of biological, physical, and topographic factors affecting the distributions of fishes in submarine canyons, and along the continental shelf, are necessary to develop effective spatial management strategies. Furthermore, long-term monitoring is essential to assess the responsiveness of fish communities to existing management practices.

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