ROV's Video Recordings as a Tool to Estimate Variation in Megabenthic Epifauna Diversity and Community Composition in the Guaymas Basin

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Patterns in benthic megafauna diversity in littoral and intertidal zones in the Gulf of California have been associated with both habitat heterogeneity and substrate type. Current knowledge of invertebrate communities in hard bottom habitats at depths > 200 m in the Gulf is poor due to the methodological limitations inherent in sampling deep habitats. Using video imagery of benthic habitats coupled with environmental data from the Remotely Operated Vehicle *Doc Ricketts*, we documented variation in the diversity and community composition of the benthos from 849 to 990 m depth in the NW limit of the Guaymas Basin, in relation to dissolved oxygen and substrate characteristics. This depth range overlaps an oxygen minimum zone where oxygen drops to levels < 0.5 ml L^{-1} and strong gradients in a narrow depth range occur. Dissolved oxygen varied along our benthic survey from 0.200 to 0.135 ml L^{-1}. We observed high taxonomic richness across an area of rocky outcrops through the lower transition zone. This megafaunal pattern differs from reports from other oxygen minimum zones characterized by a great abundance of a few species. Taxonomic richness diminished at depths with reduced dissolved oxygen in the lower boundary of the oxygen minimum zone with increasing soft sediment cover. We found that rocky outcrops and structure-forming organisms such as corals, sponges, and oyster aggregations supported a higher diversity (H' = 0.8) than soft sediment (H' = 0.7) as have been observed in other habitats such as seamounts. Environmental variables that explained most of the megafaunal variation were substrate type (18.4%), depth (1.14%) and temperature (0.9%). Salinity (0.45%) and dissolved oxygen (0.3%) were less important factors to explain the megafaunal composition variance. Substrate type played a key role in the diversity and composition of benthic megafauna. These results broaden our understanding concerning the potential roles of substrate characteristics in the community composition of the deep-sea benthic megafaunal assemblages in the Gulf of California and oxygen minimum zones in general.

Keywords: Sonoran Margin, megafauna, bathyal, substrate, structural complexity, continental slope, Guaymas Basin, Gulf of California

INTRODUCTION

Habitat is defined by the space and abiotic factors in which an organism, population or species assemblage lives (Norse, 1993; Davies et al., 2004; Tapia de la Yossellin, 2018). The Gulf of California (GoC), hosts a wide variety of shallow-water habitats (e.g., coral reefs at the southern end in both margins, rocky habitats in the peninsular shore and sandy beaches in continental shore) (Lluch-Cota et al., 2007) in which biological diversity is thought to vary with substrate heterogeneity (Brusca and Hendrickx, 2010). However, biological patterns of invertebrate communities and processes are perhaps known better in littoral and intertidal zones than in hard bottom habitats at depths greater than 200 m in the GoC (Brusca and Hendrickx, 2010) due to the methodological limitations inherent in sampling deep habitats, such as the time and cost required to deploy equipment at great depths or the effectiveness of the samplers.

In the last three decades, the development of imaging methods coupled with the use of submersibles and remotely operated vehicles (ROV's) to obtain high resolution video images of the deep seabed, has allowed a more extended overview of the habitats and faunal communities, as well as the possibility of doing long-term studies (Pilgrim et al., 2000; Méndez, 2007; Cuvelier et al., 2012; Ayma et al., 2016). ROV video surveys have been used more commonly for hard, steep, and rugged substrate and in areas of cold-water corals (CWC's) (Du Preez and Tunnicliffe, 2012; Ayma et al., 2016). Traditional methods of sampling, such as dredge and sledges are difficult to use in hard and rugged substrate and cannot be used in areas inhabited by delicate and vulnerable structure forming-organisms (Tyler et al., 2016). Therefore, the analysis of images recorded by ROVs has become a non-invasive and complementary method (to conventional methodologies) for sampling deep water fauna in all habitats and substrate types (Cuvelier et al., 2012; Ayma et al., 2016; Tyler et al., 2016).

Preliminary data collected mainly by sledges, dredges and box cores indicate that the southeast GoC has an abundant and diverse deep-sea benthic fauna dominated by polychaetes, decapod crustaceans, echinoderms, and mollusks (Hendrickx, 2006; Lluch-Cota et al., 2007; Méndez, 2007; Zamorano et al., 2007; Zamorano and Hendrickx, 2012; Hendrickx and Serrano, 2014; Hendrickx et al., 2014; Hernández-Alcántara et al., 2014; Mejía-Mercado et al., 2014; Papiol and Hendrickx, 2016).

Many physical variables are known to be important factors associated with patterns of community composition and diversity (McArthur et al., 2010; Anderson et al., 2011). For example, substrate characteristics, structural complexity, sediment composition, organic matter, oxygen, among others, have been identified sources of heterogeneity and important descriptors of biological patterns (Gooday et al., 2010; Ramirez-Llodra et al., 2010; Anderson et al., 2011). Several studies conducted in submarine canyons, such as Schlacher et al. (2010), revealed that structural complexity enhances benthic diversity and biomass. Structural complexity refers to the physical heterogeneity of the habitat related to the rugosity of the seabed

substrate and the complex architecture of biogenic aggregations (Laguionie-Marchais et al., 2015; Bartholomew et al., 2016; Ferrari et al., 2016). Increased habitat heterogeneity provides refugia, sites for settlement, feeding, predation, and parasitism of organisms (Buhl-Mortensen et al., 2010; Storlazzi et al., 2016). Consequently, substrate type and structural complexity have been identified as important descriptors of biological patterns (Anderson et al., 2011; Du Preez and Tunnicliffe, 2012). High structural complexity likely contributes to the high taxonomic wealth observed in the GoC funds is precisely a reflection of their structural complexity.

On the other hand, previous studies have documented changes in the abundance, density, and diversity of bathyal macrofauna and megafauna in habitats worldwide where the Oxygen Minimum Zone (OMZ) impinges the seafloor (Levin and Gage, 1998; Rogers, 2000; Levin et al., 2001; Levin, 2003). Macrofaunal and megafaunal densities decreased dramatically in the cores of most OMZ's where bottom-water dissolved oxygen (DO) is < 0.15 ml l^{-1} (Levin, 2003). In the GoC several oceanographic processes, including wind-induced upwelling, tidal mixing, regional circulation and global thermohaline circulation (Roden, 1958; Santamaría-del-Angel et al., 1994; Álvarez-Borrego, 2010), contribute to the development of an OMZ in the southern GoC, where DO concentrations are < 0.5 ml l^{-1} (Levin, 2003). In the southern Gulf the OMZ has been reported from 82 to 1300 m depth and in the central Gulf from 232 to 1705 m depth, decreasing in thickness and eventually disappearing to the northern region (Hendrickx and Serrano, 2014).

In the GoC, low bottom water DO is strongly associated with the density or diversity of a range of taxa, such as Polychaeta (Méndez, 2007), Bivalvia (Zamorano et al., 2007; Zamorano and Hendrickx, 2012) and Decapoda (Hendrickx and Serrano, 2014; Papiol and Hendrickx, 2016). Nevertheless, these studies also document that other factors (e.g., temperature, depth and sediment composition) also influence deep-sea macrofaunal assemblages. The distribution and diversity of deep water polychaetes from the GoC are correlated with depth and temperature; diversity of polychaetes increased with depth and reached a maximum value at 1270 m depth, while higher density and diversity are found between 2.5 and 4.0°C (Méndez, 2007). Species richness of mollusks from the southern GoC decreases with depth, but reaches a maximum value between 1000 and 1300 m depth (Zamorano et al., 2007). Studies of decapod crustaceans in the southeastern GoC also indicate highest species richness between 1000 and 1380 m depth, suggesting that the availability of food, nature of substrate, currents, or other factors could affect their distribution (Hendrickx, 2006). While these water quality factors show strong relationships with bathyal faunal patterns, the influence of substrate type and structural complexity in a fine scale on deep-sea benthos in the GoC has received little study.

In this study, we aim to document the variation in the diversity, composition and coverage of epibenthic megafauna in relation to DO and habitat quality at bathyal depths from 849 to 990 m in the Guaymas Basin by using benthic imagery recorded on video coupled with environmental data from the ROV *Doc Ricketts*. These two factors in particular – substrate heterogeneity and DO concentration - are expected to play a large role in

deep-sea benthic communities. Thus, we hypothesize that the taxonomic richness of megabenthos would be highest in rocky benthic habitats with the greatest structural complexity, and that soft sediment habitats will be the least diverse.

MATERIALS AND METHODS

Study Area

The GoC is divided into semi-isolated basins (separated from each other by transverse ridges) which become deeper to the south (Lonsdale, 1989). The Guaymas Basin (**Figure 1**) in the central Gulf province is the largest depression within the Gulf (Rusnak et al., 1964; Bischoff and Henyey, 1974), with a maximum depth of 2100 m (Brusca et al., 2005; Mejía-Mercado et al., 2014). This basin is characterized by its rapid deposition of organic-matter rich sediments, particularly where the OMZ impinges on the seafloor (Bischoff and Henyey, 1974; Lonsdale, 1989; Kluesner, 2011; Kurnosov and Blinova, 2015; Teske et al., 2016). The seafloor in Guaymas Basin is mainly composed of fine-grained mud turbidites (Bischoff and Henyey, 1974), though basaltic rocks have been dredged from widespread outcrops on the southern wall of the basin (Lonsdale, 1989).

The Sonoran Margin, the northernmost physiographic province in the basin, extends from the distal portion of the continental shelf adjacent to the state of Sonora to ca. 1300 m depth, has a gentle slope (1.7°) and is characterized by a flat and regular bathymetric relief (Figueroa Albornoz, 2013). The transitional zone from the Sonoran Margin to the floor of Guaymas Basin is affected by different tectonic processes, as well as erosion and gravitational instability (Lonsdale, 1989; Figueroa Albornoz, 2013).

The thermohaline structure of the water column in this region comprises several water masses, principally the Pacific Intermediate Water (PIW) (1200–500 m depth with salinities of 34.50 to 34.80 psu and temperature from 4 to < 9°C) and OMZ waters protruding into the southern and central regions (Álvarez-Borrego and Schwartzlose, 1979; Páez-Osuna et al., 2016).

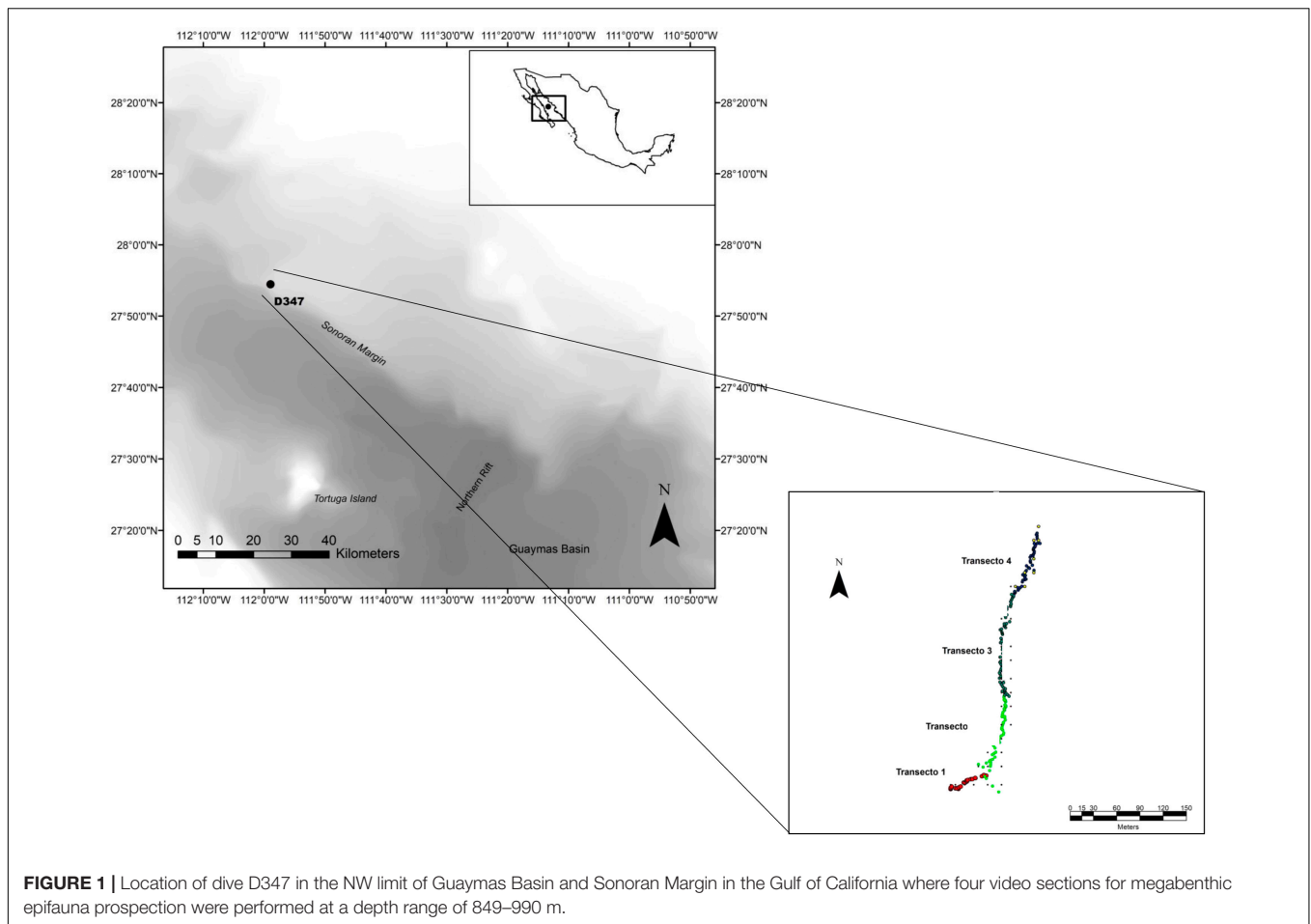### Visual Survey of Benthic Megafauna and Data Collection

Benthic video transects were performed using the ROV *Doc Ricketts* operated from the R/V *Western Flyer* by the Monterey Bay Aquarium Research Institute. The ROV survey sites were determined during the "2012 Gulf of California Expedition" on the basis of maps created with the sonar data gathered previously by the *D. Allan B.* autonomous underwater vehicle (AUV) on board of the R/V *Zephyr*. Transects were located (dive D347, March 2012) in an unexplored area in NW limit of Guaymas Basin and the Sonoran Margin (27.91° N, 111.982° W) (**Figure 1**). Overall, a total of four seabed video transects (**Table 1**) corresponding to 51 min and 0.436 km of seabed length were performed. ROV *Doc Ricketts* has a maximum operation depth of 4000 m and was equipped with a high definition camera (1080 × 1920 resolution) with 10× zoom, an illumination system of six 17700 Lumen LED lights and four 250 W incandescent

lights and navigation instrumentation allowing determination of ROV location to ca. 1 m of dive depth, science tools (e.g., suction sampler, swing arm and manipulators) and a CTD equipped with a transmissometer and oxygen sensor. During video transects, the ROV *Doc Ricketts* moved at an altitude of ∼2 m above the seafloor and a constant speed 0.14 m s^{-1} and the focal axis of the camera was kept tilted downward and zoomed to view a ca. 1 m wide portion of the seabed near the ROV. Visibility in seawater was appropriate enough for image analysis. Thus two-parallel lasers mounted 29 cm apart projected red dots on the seafloor to serve as a spatial scale. ROV position was determined by an ultrashort baseline acoustic tracking systems, coupled to the ship's GPS system. Navigation information for the ROV were logged along with near-bottom environmental parameters (depth, temperature, salinity and bottom-water DO) throughout the survey.

Video and Image Analysis

Benthic images extracted from video recorded along transects during ROV dive D347 were edited using Corel Video Studio Pro X5©. Transect images of the seafloor were selected manually at 15 s intervals, equivalent to 1 image per 1.4 m along the video transect, based on the average ROV speed over the bottom and the mobility, size and behavior of the organisms related to the field of view of the camera (Bakus, 2007; Clark et al., 2012). Furthermore, this distance avoids any overlap between successive images.

For each of the images, all epibenthic megafauna > 3 cm were counted and identified to the lowest possible taxon. In cases where organisms could not be assigned to a determinate taxon, they were defined as distinct morphospecies in relation to the available taxonomic information. The identity of organisms was determined using general and specialized literature (Gage and Tyler, 1992; Ruppert and Barnes, 1996; Marshal and Richer de Forges, 2004; Solís-Marín et al., 2005, 2014; Hendrickx et al., 2007, 2014, 2016; Roberts et al., 2009; Álvarez et al., 2014; Hendrickx and Serrano, 2014; Mejía-Mercado et al., 2014; Villalobos Vazquez de la Parra, 2014), as well as specialized databases to validate the taxonomic identification (Brusca and Hendrickx, 2008; Jacobsen Stout et al., 2015; NOAA Office of Ocean Exploration and Research, 2018; WoRMS Editorial Board, 2018; OBIS, 2019). To aid the identification we supplemented these sources with a previous study that identified specimens of taxa collected during dive D347 (Villalobos Vazquez de la Parra, 2014). Additionally, to maximizes the comparability of our results with other studies, we grouped specimens and coverage data of sponges recorded in each benthic images into one of the following morphotypes categories based on the criteria proposed by Boury-Esnault and Rützler (1997) and Kazanidis et al. (2019): amorphous, tubular and clavate ("club-shaped") (see the sponge morphotype examples provide as **Supplementary Material**). Taxonomic richness described the total number of morphospecies per image. Occurrences of morphospecies on each substrate type was recorded in each transect image. The cover of epibenthic megafauna (m^2) was measured on-screen with Image J© software, by tracing the surfaces covered by the sessile and motile fauna visible in each transect image. We

FIGURE 1 | Location of dive D347 in the NW limit of Guaymas Basin and Sonoran Margin in the Gulf of California where four video sections for megabenthic epifauna prospection were performed at a depth range of 849–990 m.

included fauna with low motility (demersal fishes, decapods, holothurians), completely passive taxa, those swimming slowly over the bottom, as well as fauna exhibiting no raction to ROV motion or lights (Lorance and Trenkel, 2006). Several studies that compared ROV observations with sampling methods, have revealed that estimations of the presence and/or abundance of motile megafauna, particularly fishes, decapod crustaceans and mollusks, are more accurate based on imagery than sampling, since the mobile fauna tend to escape during sampling (Spanier et al., 1994; Lorance and Trenkel, 2006; Cuvelier et al., 2012; Gates et al., 2012; Porteiro et al., 2013; Ayma et al., 2016). Moreover, imagery analysis has a high acccuracy in assessing surface areas, epibenthic faunal coverage and the presence of associated fauna in different habitats, such as cold-water corals (Guinan et al., 2009; Cuvelier et al., 2012; Du Preez and Tunnicliffe, 2012). Therefore, coverage (m²) of substrata also was estimated for each transect image using Image J© software.

Habitat was visually classified on the basis of substrate type (soft and hard) (Greene et al., 1999; van den Beld et al., 2017) and its structural complexity followed the rugosity criteria (Ferrari et al., 2016; Storlazzi et al., 2016; De la Torriente et al., 2018). For fine-scale habitat characteristics, we assigned seabed sub-habitats based on their composition (e.g., soft sediments and rocky outcrops), structure-forming organisms (e.g., corals,

sponges and oyster aggregations that are used by other species as substrate for attachment or feeding) (Buhl-Mortensen et al., 2010) and associated biological assemblages (Greene et al., 1999). Environmental variables (depth, temperature, salinity and DO) and ROV location data (geographic coordinates) registered during dive D347 were coupled to each video transect image.
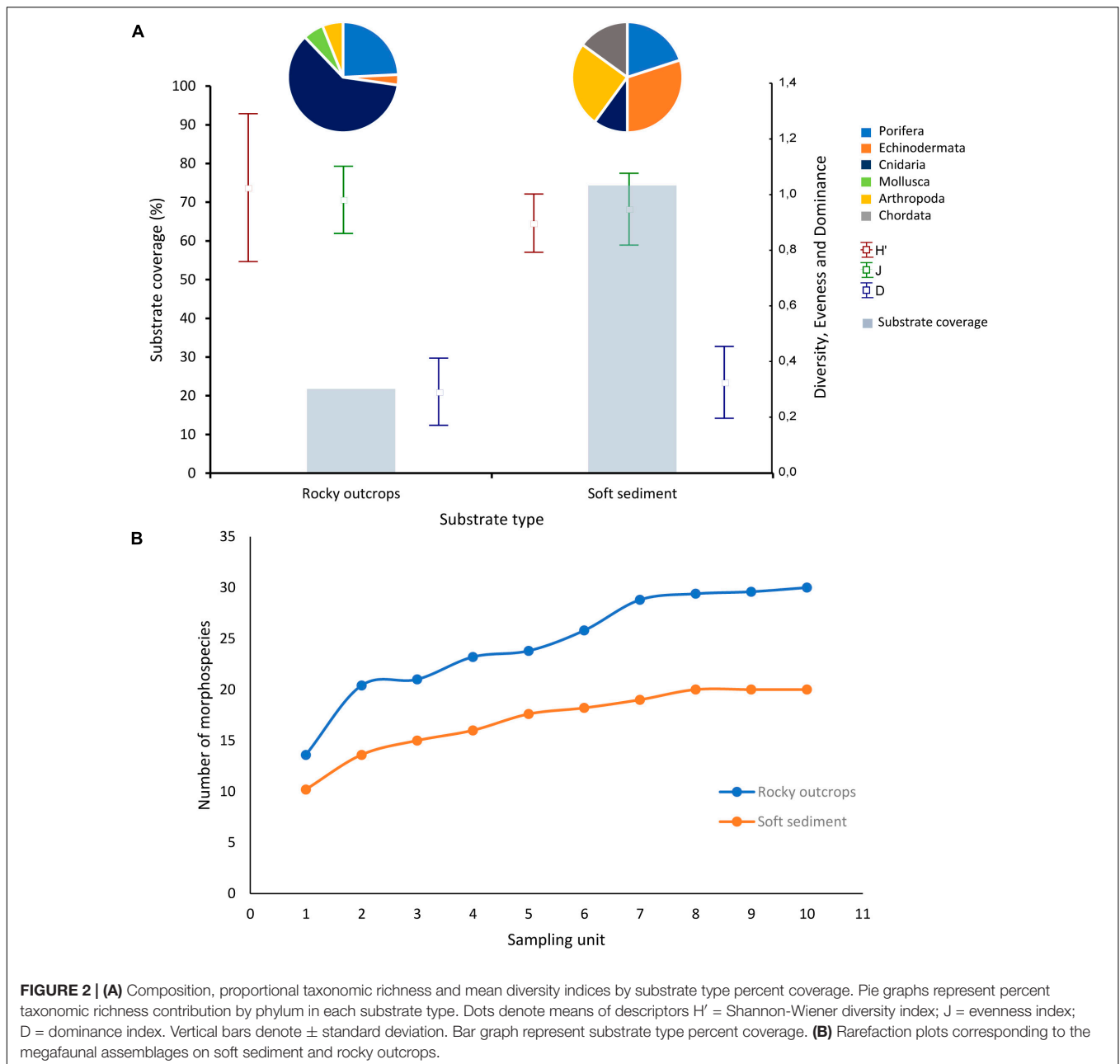
Statistical Analyses

To assess the adequacy of megabenthos sampling, we plotted species-area curves following criteria from several studies (Estacio, 1996; Krebs, 1999; Bianchi et al., 2004; Underwood,

TABLE 1 | Transects performed with the ROV *Doc Ricketts* during 2012 Gulf of California Expedition.

Transect No.	Depth (m)	Number of images sampled	Distance covered (m)	Total area (m²)
1	990.0–984.5	24	50.0	15.9
2	984.3–940.8	62	128.8	41.4
3	940.2–890.7	79	164.5	50.9
4	889.9–848.6	35	76	20.19
Total		200	419.3	128.39

TABLE 2 | Taxonomic list in the NW limit of Guaymas Basin and the Sonoran Margin (849–990 m) inhabiting soft and hard substrate.

Phylum	Class	Order	Family	Genus/Morphospecies
Porifera				sp1(Porifera)
				sp2(Porifera)
				sp3(Porifera)
				sp4(Porifera)
				sp5(Porifera)
				sp6(Porifera)
				sp7(Porifera)
				sp8(Porifera)
				sp9(Porifera)
				sp10(Porifera)
				sp11(Porifera)
				sp34(Porifera)
Echinodermata	Asteroidea			sp1(Asteroidea)
				sp2(Asteroidea)
				sp3(Asteroidea)
				sp4(Asteroidea)
	Ophiuroidea			sp1(Ophiuroidea)
				sp10(Ophiuroidea)
	Holothuroidea	Elasipodida	Laetmogonidae	*Pannychia* Théel, 1882
Cnidaria				sp1 (Cnidaria)
	Anthozoa	Actiniaria		sp1(Actiniaria)
				sp2(Actiniaria)
				sp3(Actiniaria)
				sp4(Actiniaria)
				sp7(Actiniaria)
			Actinoscyphiidae	*Actinoscyphia* Stephenson, 1920
		Ceriantharia		sp1(Ceriantharia)
				sp2(Ceriantharia)
		Pennatulacea		sp1(Pennatulacea)
		Antipatharia		sp1(Antipatharia)
				sp2(Antipatharia)
				sp3(Antipatharia)
				sp4(Antipatharia)
				sp5(Antipatharia)
				sp6(Antipatharia)
			Antipathidae	*Stichopathes* Brook, 1889
		Alcyonacea		sp1(Alcyonacea)
				sp2(Alcyonacea)
				sp3(Alcyonacea)
			Primnoidae	*Narella* Gray, 1870
	Hexacorrallia		Corallimorphidae	sp1(Corallimorphidae)
Mollusca	Bivalvia	Ostreida	Pectinidae	sp1(Pectinidae)
				sp2(Pectinidae)
Arthropoda				sp1(Arthropoda)
	Malacostraca	Decapoda		sp1(Decapoda)
				sp2(Decapoda)
			Galatheidae	sp1(Galatheidae)
				sp3(Galatheidae)
			Chirostylidae	*Gastroptychus* Caullery, 1896
			Lithodidae	*Paralomis* White, 1856
Chordata	Actinopterygii	Gadiformes	Macrouridae	sp1(Macrouridae)
				sp2(Macrouridae)
		Lophiiformes	Ogcocephalidae	*Dibranchus* Peters, 1876

FIGURE 2 | (A) Composition, proportional taxonomic richness and mean diversity indices by substrate type percent coverage. Pie graphs represent percent taxonomic richness contribution by phylum in each substrate type. Dots denote means of descriptors H′ = Shannon-Wiener diversity index; J = evenness index; D = dominance index. Vertical bars denote ± standard deviation. Bar graph represent substrate type percent coverage. **(B)** Rarefaction plots corresponding to the megafaunal assemblages on soft sediment and rocky outcrops.

2006; Bakus, 2007; Clark et al., 2012). Species accumulation curves included data from all extracted images from transects T1 and T2, removing all species that appeared only once among all images. We repeated species accumulation curves for an area of soft sediment (where no rocks were present) between a field of rocky outcrops on soft sediment. A minimum sampling area (with a mean of 0.7 m²/image) was defined as the number of images (selected randomly) analyzed before no new taxa were added with an additional image sampled. The minimum sampling area determined for the area of rocky outcrops was 14 m², corresponding to 20 video images. For sediment dominated habitat, the minimum sampling area was 7 m² or 10 benthic images. Sample size for comparisons between

rocky outcrops and soft sediment were then standardized to 20 benthic images (with a mean of 0.7 m²/image) and $n = 10$. Images for integrate samples were selected randomly. Sample size for comparisons between OMZ zones were standardized to 20 benthic images (selected randomly and with a mean of 0.7 m²/image) and $n = 3$ for each OMZ zone.

Morphospecies rarefaction curves (Sanders, 1968) were obtained using the Biodiversity Professional© V.2 program and plotted per rocky outcrops and soft sediment. The cover data for each morphospecies at the two substrata (soft sediment and rocky outcrops) in each sample was used to calculate diversity indices. Diversity and related indices were estimated with the Biodiversity Professional© V.2 program. Shannon-Wiener diversity index is

TABLE 3 | Environmental variables recorded near the seafloor during the ROV dive D347 in the NW limit of Guaymas Basin and the Sonoran Margin.

Dive	Depth (m)	Temperature (°C)	Salinity(psu)	Bottom-water DO (mL L^{-1})
D347	849–990	4.920–4.480	34.536–34.547	0.135–0.200

herein expressed as:

$$H' = - \sum_{i=1}^{s} (Pi)(\log(10)\ Pi)$$

The evenness index is expressed as:

$$J = \frac{H'}{H'\ max}$$

The dominance index was calculated as the complement of evenness:

$$D = 1 - J$$

A Shannon-Wiener diversity index was calculated for each sample and the results pooled by soft sediment and rocky outcrops. Means and standard deviations were plotted. To test for differences in Shannon-Wiener diversity index between soft sediment and rocky outcrops, we used a Kruskal–Wallis non-parametric analysis of variance. Kruskal–Wallis test was performed with software Statistica© V.8.

Redundancy analysis (RDA) was used to assessed environmental factors that were most correlated with changes in the composition of benthic assemblages. This analysis was performed in R studio software. A Hellinger transformation was applied to morphospecies cover data for images (Borcard et al., 2011; Legendre and Legendre, 2012). Environmental variables (substrate, depth temperature salinity and bottom-water dissolved oxygen) were log-transformed and then standardized to a zero mean to obtain a z-scores data matrix (Borcard et al., 2011). Water mass was interpreted on the basis of depth, temperature and salinity gathered during the survey and those from the published hydrology of the region (Álvarez-Borrego and Schwartzlose, 1979; Lavín and Marinone, 2003; Álvarez-Borrego, 2010).

RESULTS

Benthic Megafaunal Composition

A total of 200 transect images were selected from the video transect recordings to be used for benthic megafauna and substrate analyses. The video sequences covered a depth range from 849 to 990 m and a linear distance of 0.419 km that include soft sediments with no visible rocks and a field of rocky outcrops on soft sediment. A total of 53 benthic taxa (or morphospecies) belonging to 6 phyla (Porifera, Echinodermata, Cnidaria, Mollusca, Arthropoda and Chordata) were identified in the analysis (**Table 2**). 12 sponges morphospecies, 7 echinoderm morphospecies, 22 cnidarian morphospecies, 2 bivalve morphospecies, 7 crustaceans morphospecies and 3
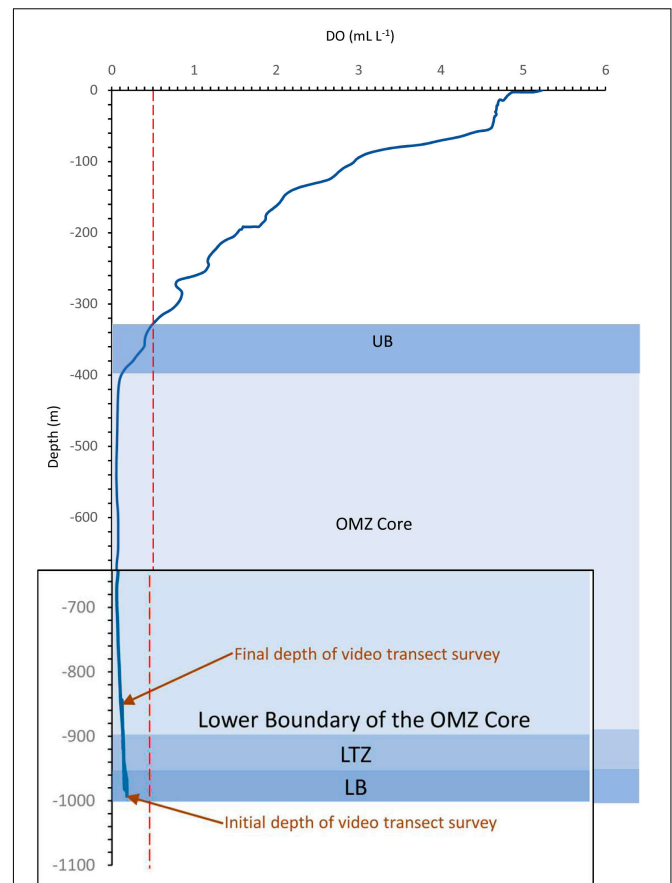

FIGURE 3 | Dissolved oxygen profile during dive D347 in the NW limit of Guaymas Basin and the Sonoran Margin. Oxygen minimum zone (OMZ) where dissolved oxygen (DO) is < 0.5 mL L^{-1}; red dotted line represents the limit where DO = 0.5 mL L^{-1}; LB = lower OMZ boundary; LTZ = lower OMZ transitional zone; UB = upper boundary of the OMZ. Note the magnifying over OMZ survey zones.

Actinopterygii morphospecies. Cnidaria was the most diverse phylum with 22 morphospecies including structure-forming cold-water corals (CWC's) (e.g., antipatharians, zoanthids and alcyonarians) (**Table 2**).

Physical Environment

The substrate along the survey was dominated by soft sediment that constituted 74.4% of the total area analyzed in all benthic images (**Figure 2A**). Rocky outcrops covered 25.6% of the total sampled area (**Figure 2A**).

Environmental sensors documented variation in near-bottom temperature (T = 4.920–4.480°C) and salinity (S = 34.536–34.547) during ROV dive D347 (**Table 3**). These data indicates the influence of the Pacific Intermediate Water between 1200 and 500 m depth (Álvarez-Borrego and Schwartzlose, 1979; Álvarez-Borrego, 2010; Páez-Osuna et al., 2016) in the study area. DO levels were very low (DO < 0.5 ml L^{-1}) in the OMZ at these depths (**Table 3**). Changes in DO levels across this depth range allowed us to identify zonation in the OMZ, including the
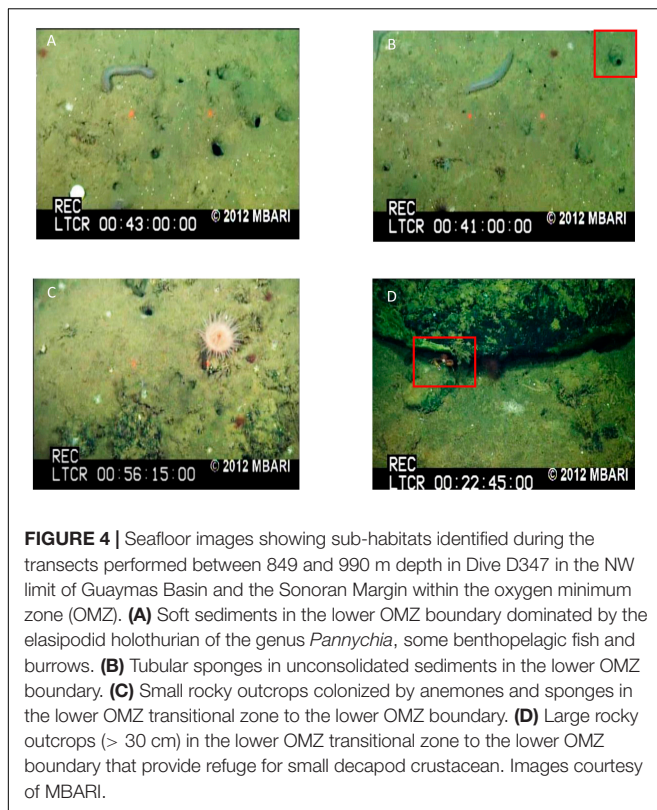
FIGURE 4 | Seafloor images showing sub-habitats identified during the transects performed between 849 and 990 m depth in Dive D347 in the NW limit of Guaymas Basin and the Sonoran Margin within the oxygen minimum zone (OMZ). **(A)** Soft sediments in the lower OMZ boundary dominated by the elasipodid holothurian of the genus *Pannychia*, some benthopelagic fish and burrows. **(B)** Tubular sponges in unconsolidated sediments in the lower OMZ boundary. **(C)** Small rocky outcrops colonized by anemones and sponges in the lower OMZ transitional zone to the lower OMZ boundary. **(D)** Large rocky outcrops (> 30 cm) in the lower OMZ transitional zone to the lower OMZ boundary that provide refuge for small decapod crustacean. Images courtesy of MBARI.
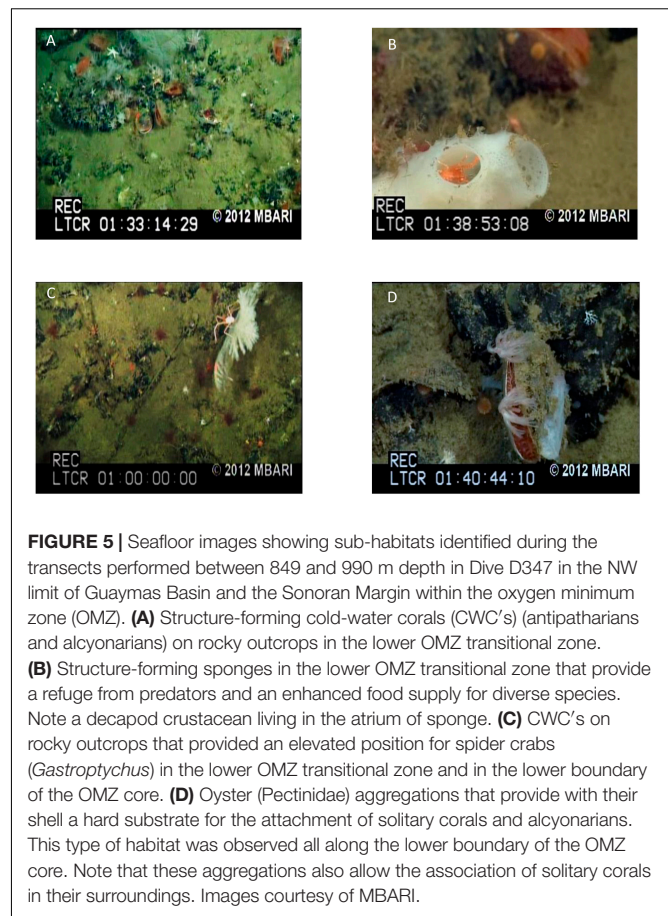

FIGURE 5 | Seafloor images showing sub-habitats identified during the transects performed between 849 and 990 m depth in Dive D347 in the NW limit of Guaymas Basin and the Sonoran Margin within the oxygen minimum zone (OMZ). **(A)** Structure-forming cold-water corals (CWC's) (antipatharians and alcyonarians) on rocky outcrops in the lower OMZ transitional zone. **(B)** Structure-forming sponges in the lower OMZ transitional zone that provide a refuge from predators and an enhanced food supply for diverse species. Note a decapod crustacean living in the atrium of sponge. **(C)** CWC's on rocky outcrops that provided an elevated position for spider crabs (*Gastroptychus*) in the lower OMZ transitional zone and in the lower boundary of the OMZ core. **(D)** Oyster (Pectinidae) aggregations that provide with their shell a hard substrate for the attachment of solitary corals and alcyonarians. This type of habitat was observed all along the lower boundary of the OMZ core. Note that these aggregations also allow the association of solitary corals in their surroundings. Images courtesy of MBARI.

lower boundary of the OMZ core (849–901 m), the lower OMZ transitional zone (LTZ) (901–954 m), and the lower boundary (LB) of OMZ (955–990 m) (**Figure 3**).

Fine-Scale Habitat Characterization

Images analysis showed in the fine scale the presence of ten distinct sub-habitats associated to rocky outcrops and soft sediments (**Figures 4**, **5** and **Table 4**). Rocky outcrops typically had more structure-forming taxa such as CWC's and sponges which provide a variety of habitats for decapod crustaceans (*Gastroptychus*) and other alcyonarians (Primnoidae). In comparison, the diversity of sub-habitats decreased considerably in soft sediment habitats (**Figures 4**, **5** and **Table 4**).

Megafaunal Patterns Among Major Habitat

Taxonomic richness was greater in rocky outcrops (33 taxa, including structure-forming organisms), than on soft sediment (20) (**Table 5**). The morphospecies list in table showing the occurrence of each morphospecies in each substrate is shown in **Table 5**. Structure-forming organisms (corals, sponges and oyster aggregations) were common on rocky outcrops and providing additional substrata for a variety of taxa such as sponges, ophiuroids, decapod crustaceans, alcyonarians, and corallimorpharians (**Table 5**). The variety of sponge morphotypes that occurred on rocky outcrops including amorphous, tubular and clavate, whereas sponges morphotypes occurring on soft sediments were tubular and clavate.

The composition of megafaunal assemblages differed among rocky outcrops and soft sediment (**Figure 2A** and **Table 6**). Cnidaria (particularly diverse habitat-forming CWC's species) and Porifera were far more diverse on rocky outcrops, whereas Echinodermata and Arthropoda had peak taxonomic richness on soft sediment (**Figure 2A** and **Table 5**).

Relative coverage of epibenthic megafauna taxa was greater on rocky outcrops (68.8%) where Cnidaria, Mollusca and Porifera dominated, compared to soft sediment (31.2%) where Echinodermata and Arthropoda were most dominant (**Figure 6A**). Taxa that contributed to differences among the total coverage on rocky outcrops were structure-forming organisms such as CWC's, oyster aggregations and sponges, whereas a sea cucumber (*Pannychia* sp.) and galatheids dominated soft sediment (**Figure 6A**). The dominant sponge morphotypes on rocky outcrops and soft sediments were clavate (**Table 7**).

Morphospecies rarefaction curves for rocky outcrops showed a general tendency to increase above the soft substrate curve (**Figure 2B**). These graphic results are in agreement with the significant differences (Kruskal–Wallis, $H_{(1;19)} = 6.4123$; $p = 0.0113$) of mean Shannon-Wiener diversity index (H') observed between rocky outcrops and soft sediment (**Table 6**). The mean Shannon-Wiener diversity index for rocky outcrops ($H' = 0.8$) was higher than measured for the megafaunal assemblages on soft sediment ($H' = 0.7$) (**Figure 2A** and **Table 6**).

TABLE 4 | Fine-scale epibenthic habitat characterization.

Habitat	Sub-habitat	Depth range (m)	DO zone	Associated biological assemblages
Soft sediment	Soft sediment	967–990	LB	elasipodid holothurian of the genera *Pannychia*, ceriantharians, tubular sponges, some benthopelagic fish and characterized by burrow areas of a possible arthropod
	Tubular sponges in soft sediment	967–990	LB	
Rocky outcrops	Small rocky outcrops	849–968	LB/LTZ	anemones and sponges attached to the surface
	Large rocky outcrops (> 30 cm)	849–968	LB/LTZ	small decapod crustaceans that live under these rocks
	Antipatharians and alcyonarians on rocky outcrops	849–968	LTZ	fauna in their surroundings like sponges, galatheids, sea stars, among others.
	Oyster aggregations on rocky outcrops	849–968	Lower Boundary of the OMZ core/LTZ	solitary corals and sponges in their surroundings
	Sponges on rocky outcrops	849–968	Lower Boundary of the OMZ core/LTZ	galatheids in their surroundings
	Antipatharians and alcyonarians that provide a hard substrate for an elevated position of other species	849 to 901	Lower Boundary of the OMZ core/LTZ	specimens of *Gastroptychus* sp., *Narella* sp. and ophiuroids on the surface of habitat-forming species
	Sponges that provide a refuge for predation and an enhanced food supply for other fauna	849 to 901	LB	decapod crustaceans living in the atrium of sponges
	Shells of oyster aggregations that provide hard substrate for the attachment of other fauna	849 to 901	Lower Boundary of the OMZ core/LTZ	anemones, solitary corals and alcyonarians attached to the shell of oyster (Pectinidae) aggregations.

There were no significative differences in the mean evenness index (Kruskal–Wallis, $H_{(1;19)} = 0.1667$; $p = 0.6831$) or mean dominance index (Kruskal–Wallis, $H_{(1;19)} = 0.1667$; $p = 0.6831$) of megafaunal assemblages among substrata (**Figure 2A**).

Megafaunal Patterns and DO

Taxonomic richness in the LTZ and in the lower boundary of the OMZ core was greater than in the LB (**Table 8**). Taxonomic richness within the LB decreased with decreasing DO conditions and where soft sediments dominated. Although the taxonomic richness of OMZ assemblages varied with DO, their taxonomic composition showed little variation among OMZ zones (**Figure 7**). Cnidaria, Porifera, Echinodermata and Arthropoda were the most diverse taxa through all three OMZ zones (**Figure 7**).

Megafaunal Composition and Environmental Variables

The RDA analysis indicated that 21.15% of the variation in megafaunal abundance was explained by environmental variables (substrata type, depth, temperature, salinity and DO). A permutation test (with 999 permutations) indicated that global model ($p = 0.001$) was significant. Environmental variables that explained the most megafaunal variation were substrate type (18.4%), depth (1.14%) and temperature (0.9%). Salinity (0.45%) and DO (0.3%) were less important factors to explain the megafaunal composition variance. The triplot (**Figure 6B**) showed that substrate type, temperature and depth were correlated with megafaunal morphospecies. As illustrated by the triplot in **Figure 6B**, most morphospecies are bunched together with short projections at the centroid oriented toward rocky outcrops, temperature and soft sediment, but away from most of the environmental variables. We interpret this to indicate that megafaunal patterns are related to muliple explanatory variables.

DISCUSSION

The principal aim of our study was to document variation in the diversity and composition of epibenthic megafauna in relation to DO and habitat characteristics at bathyal depths from 849 to 990 m in the Guaymas Basin in the GoC. Our data indicates a diverse fauna of Cnidaria, Porifera, Arthropoda and Echinodermata common on rocky outcrops and soft sediments in the NW limit of Guaymas Basin and the Sonoran Margin. Similarly, in the southern to central region of the Gulf (between 438 and 3747 m depth) Hinojosa-Corona (2014) found a diverse fauna of antipatharians, gorgonians and sponges on scarps and other deep-sea hard bottoms habitats. Patterns of benthic megafaunal diversity in littoral and intertidal zones in the GoC have been widely reported in relation to habitat and substrate type (Brusca and Hendrickx, 2010). These patterns are little known in the GoC at > 200 m depth, particularly for hard bottom habitats that are not easily sampled using traditional methods.

This study spans a narrow bathymetric range (849–990 m) where a strong gradient in DO levels occurred and crosses distinct OMZ zones defined on the basis of DO criteria (Hendrickx, 2006; Hendrickx and Serrano, 2014; Papiol and Hendrickx, 2016) for the southern and central regions in the GoC. We observed a great

TABLE 5 | Rocky outcrops and soft sediment morphospecies in the NW limit of Guaymas Basin and the Sonoran Margin (849–990 m).

| Phylum	Morphospecies	Rocky outcrops	Soft sediment
Porifera	sp1(Porifera)	0	1
	sp2(Porifera)	0	1
	sp3(Porifera)	0	1
	sp4(Porifera)	1	0
	sp5(Porifera)	0	1
	sp6(Porifera)*	1	0
	sp7(Porifera)*	1	0
	sp8(Porifera)*	1	0
	sp9(Porifera)	1	0
	sp10(Porifera)	1	0
	sp11(Porifera)	1	0
	sp34(Porifera)	1	0
Echinodermata	sp1(Asteroidea)	0	1
	sp2(Asteroidea)	0	1
	sp3(Asteroidea)	0	1
	sp4(Asteroidea)	0	1
	sp1(Ophiuroidea)	0	1
	sp10(Ophiuroidea)*	1	0
	Pannychia Théel, 1882	0	1
Cnidaria	sp1 (Cnidaria)	1	0
	sp1(Actiniaria)	1	0
	sp2(Actiniaria)	1	0
	sp3(Actiniaria)	1	0
	sp4(Actiniaria)	1	0
	Actinia Linnaeus, 1767	1	0
	Actinoscyphia Stephenson, 1920	1	0
	sp1(Ceriantharia)	0	1
	sp2(Ceriantharia)	0	1
	sp1(Pennatulacea)	1	0
	sp1(Antipatharia)	1	0
	sp2(Antipatharia)	1	0
	sp3(Antipatharia)	1	0
	sp4(Antipatharia)	1	0
	sp5(Antipatharia)	1	0
	sp6(Antipatharia)	1	0
	Stichopathes Brook, 1889	1	0
	sp1(Alcyonacea)	1	0
	sp2(Alcyonacea)	1	0
	sp3(Alcyonacea)*	1	0
	Narella Gray, 1870*	1	0
	sp1(Corallimorphidae)*	1	0
Mollusca	sp1(Pectinidae)	1	0
	sp2(Pectinidae)	1	0
Arthropoda	sp1(Arthropoda)	0	1
	sp1(Decapoda)	0	1
	sp2(Decapoda)*	1	0
	sp1(Galatheidae)	0	1
	sp3(Galatheidae)	0	1
	Gastroptychus Caullery, 1896*	1	0
	Paralomis White, 1856	0	1
Chordata	sp1(Macrouridae)	0	1
	sp2(Macrouridae)	0	1
	Dibranchus Peters, 1876	0	1
	Total	**33**	**20**

*0 = Absence; 1 = Presence. *Morphospecies observed also using structure-forming organisms as substrate.*

taxonomic richness through the LTZ across an area with rocky outcrops. This megafaunal pattern observed is different to that reported in other OMZs where they are characterized by a great abundance of a few species (Levin et al., 2000; Gooday et al., 2010; Papiol and Hendrickx, 2016). For instance, previous studies conducted in the southeast GoC, showed that soft sediments between 800 and 1000 m depth in the LTZ were dominated by a galatheid (*Munidopsis depressa*) (Papiol and Hendrickx, 2016). In Volcano 7 in the eastern tropical Pacific, the Oman margin in the Arabian Sea, and off central California, was observed high densities of crustaceans and echinoderms near the LB of the OMZ (Levin, 2003). DO appears to be an important factor that controls the diversity in the core regions of OMZs (Levin and Gage, 1998; Gooday et al., 2010). However, as DO starts to rise below the OMZ core and the potential stress related to hypoxia diminishes, other environmental factors could influence on diversity patterns (Levin and Gage, 1998; Levin, 2003; Gooday et al., 2010; Papiol and Hendrickx, 2016). Among these factors, hard substrate in the LTZ where food is not a limiting factor could allow the colonization of species (e.g., filter and suspension feeders) that already tolerate hypoxic conditions, resulting in an increase of taxonomic richness.

On the other hand, low taxonomic richness of megabenthic fauna was observed at depths with reduced DO and greater cover of soft sediment in the LB of the OMZ. Several studies in this region (Méndez, 2007; Zamorano et al., 2007; Zamorano and Hendrickx, 2012; Hendrickx and Serrano, 2014; Hinojosa-Corona, 2014; Hendrickx et al., 2016; Papiol and Hendrickx, 2016) have reported that the OMZ is coupled closely to the diversity, composition, abundance and distribution of megafauna inhabiting the water column and the benthos. Differences in the tolerances of megafauna to OMZ conditions very likely influence the shift in the species composition of communities in the LTZ (Levin, 2003; Gooday et al., 2010). However, it should be noted that in our study the distribution of a field of soft sediments with no visible rocks overlaps almost totally with the LB of the OMZ. Under these conditions, the influence of the OMZ on the composition of the megafauna is hard to interpret and our results are limited by the collinearity of substrate and DO.

We found that environmental variables under study are responsible for some of the megafaunal variation. Although, the global model explain only 21.15% of the faunal variation, this result is consistent with variation explained by environmental variables in a study realized in Seco de los Olivos seamount (De la Torriente et al., 2018). However, our model results are probably related somewhat to the spatial scale of the sampling and collection of environmental variables. We speculate that on a larger environmental scale (e.g., if the transects crossed all zones of the OMZ and more), the role of environmental factors may have been larger.

Our results indicate that variation in megafaunal composition was mostly explained by substrate type. Thus, substrate characteristics very likely play a key role in regulating community patterns. The composition of megafaunal assemblages on rocky outcrops differed from those on soft sediments. We found an abundant and diverse fauna of CWC's (antipatharians, alcyonarians) and sponges, attached to volcanic rocky outcrops
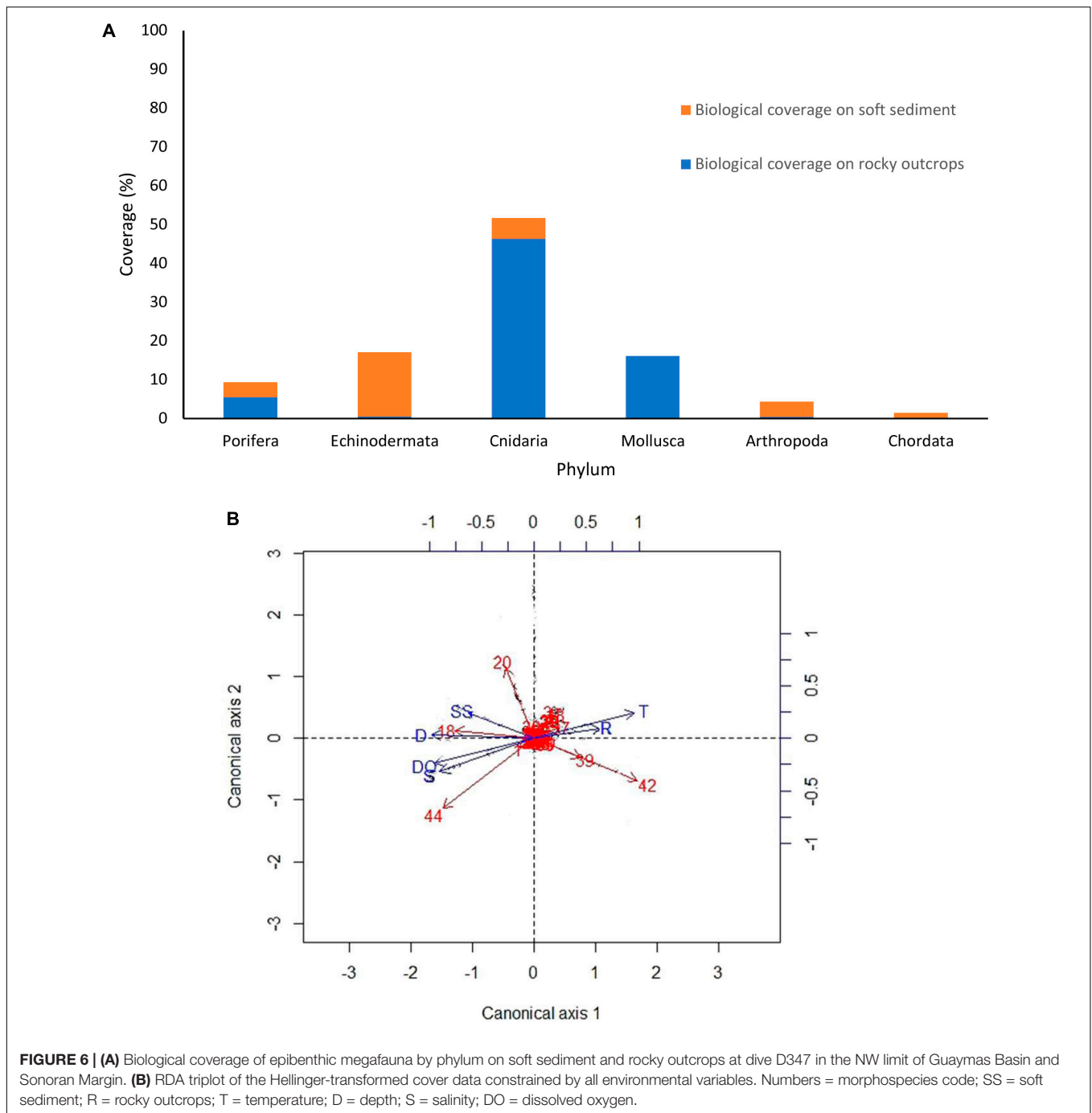
FIGURE 6 | (A) Biological coverage of epibenthic megafauna by phylum on soft sediment and rocky outcrops at dive D347 in the NW limit of Guaymas Basin and Sonoran Margin. **(B)** RDA triplot of the Hellinger-transformed cover data constrained by all environmental variables. Numbers = morphospecies code; SS = soft sediment; R = rocky outcrops; T = temperature; D = depth; S = salinity; DO = dissolved oxygen.

through the LTZ and LB of OMZ. Hard substrate within an OMZ are often formed by materials such as phosphorite, carbonate and volcanic materials (Levin et al., 2010). In comparison, studies realized in the seamount Volcano-7 in the eastern Pacific that protrude into the OMZ have shown a dense aggregation of sponges and serpulid polychaetes attached to basalt substrate and manganese crust (Gooday et al., 2010). Several studies of benthic megafauna have also reported higher species richness on hard substrata than on soft sediments. Canyons in the Gulf of Gioia (Pierdomenico et al., 2016;

van den Beld et al., 2017; De la Torriente et al., 2018), the Bay of Biscay (800–1200 m) as well as in the seamount Seco de los Olivos (< 700 m) are sites where hard substrata (including structure-forming organisms) were shown to have higher species richness and diversity than soft sediments. Here, the higher diversity, taxonomic richness and cover of megafauna that we observed on rocky outcrops was because the species associated with hard substrate occur attached to the surface of rocky outcrops and structure-forming organisms, within or around the three-dimensional complex structures constituted by rocky outcrops

TABLE 6 | Shannon-Wiener diversity index (H′), evenness (J) and dominance calculated for each sample and per substrate.

Sample ID	Rocky outcrops			Soft sediment		
	H'	*J*	*D*	*H'*	*J*	*D*
1	0.282	0.937	0.063	0.660	0.66	0.34
2	–	–	–	0.554	0.656	0.344
3	0.817	0.856	0.144	0.664	0.596	0.404
4	0.817	0.785	0.215	0.689	0.689	0.311
5	0.916	0.761	0.239	0.704	0.676	0.324
6	0.907	0.723	0.277	0.751	0.787	0.213
7	0.94	0.82	0.18	0.878	0.878	0.122
8	0.779	0.68	0.32	0.746	0.826	0.174
9	0.988	0.759	0.241	0.687	0.882	0.118
10	0.803	0.617	0.383	0.718	0.795	0.205
x̄	0.805	0.771	0.229	0.705	0.745	0.256
σ	0.209	0.095	0.095	0.082	0.101	0.101

TABLE 7 | Composition of sponge morphotypes found at the NW limit of Guaymas Basin and the Sonoran Margin (849–990 m).

Substrate type	Amorphous (mean coverage ± SD) (m^2) $n = 10$	Clavate (mean coverage ± SD) (m^2) $n = 10$	Tubular (mean coverage ± SD) (m^2) $n = 10$
Rocky outcrops	0.018 ± 0.040	0.044 ± 0.072	0.011 ± 0.017
Soft sediment	0	0.022 ± 0.018	0.016 ± 0.036

TABLE 8 | Taxonomic richness by OMZ strata and its dissolved oxygen concentration range.

Phylum	Lower boundary of the OMZ core (DO < 0.15 ml L^{-1}; Depth = 849–901 m); $n = 3$	LTZ (DO = 0.15 - 0.18 ml L^{-1}; Depth = 901–954 m); $n = 3$	LB (DO > 0.18– 0,5 mL/L^{-1}; Depth = 955–990 m); $n = 3$
Porifera	8	8	4
Echinodermata	4	6	4
Cnidaria	15	18	10
Mollusca	2	1	0
Arthropoda	5	5	5
Chordata	2	2	3
Total	36	40	26

FIGURE 7 | Composition and proportional taxonomic richness by phylum through the oxygen minimum zones during dive D347 in the NW limit of Guaymas Basin and Sonoran Margin.

and habitat-forming organisms and in crevices. More species were also recorded on soft sediment between rocks. Habitats with hard substrate and three-dimensional complex structures, generally supported a higher epibenthic megafauna diversity in comparison with more uniform substrate habitats, such as soft bottom plains (Schlacher et al., 2007; Buhl-Mortensen et al., 2012; Rowden et al., 2016; Åström et al., 2018). Structural habitat complexity was positively related to the local species diversity of sessile and mobile species (Buhl-Mortensen et al., 2010; Matias et al., 2010; Bartholomew et al., 2016; Ferrari et al., 2016; Storlazzi et al., 2016). The underlying substratum and habitat-forming organisms provide a significant proportion of three-dimensional
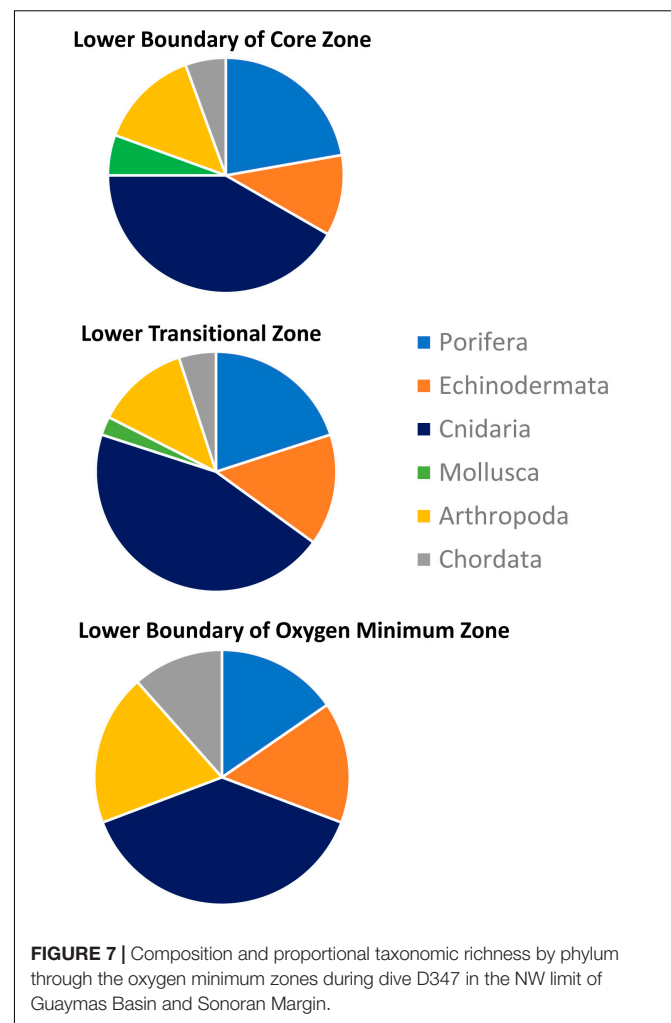
habitat in marine communities (Ferrari et al., 2016). Numerous studies have documented that structure-forming organisms such as sponges and CWC′s play a key structural and functional role in the marine benthos, because they can modified physical properties of the sea floor and influence composition, abundance and distribution of epibenthic megafauna (Schlacher et al., 2007; Beazley et al., 2013; Howell et al., 2016; Huvenne et al., 2016; van den Beld et al., 2017; Kazanidis et al., 2019).

Taxa identified in the NW limit of Guaymas basin and Sonoran Margin span several trophic levels including filter and suspension feeders, deposit feeders and carnivorous benthophages (Sokolova, 2000). Among filter-feeding fauna we found that clavate sponge morphotypes were dominant on rocky outcrops and soft sediment habitats. These results are different to the results found by Kazanidis et al. (2019) in the northeast Atlantic (∼500 m depth), where sponges aggregations on rock and sand substrate were mainly composed of massive and flabellate sponges. Several studies have shown that environmental and anthropogenic factors, such as hydrography or trawling respectively, have an influence in the sponge morphotypes inhabiting in an specific area (Cryer et al., 2008;

Kazanidis et al., 2019). For example, a study realized by Bell and Barnes (2000) showed that encrusting forms were more abundant on high flow areas. At a local scale the morphology of structure-forming organisms can also vary with local hydrodynamic patterns and create microhabitats differing in flow and the transport or settlement of particles (Buhl-Mortensen et al., 2010). Furthermore, the evolutionary origin of the fauna may account for the differences observed. Most invertebrate fauna of the Gulf of California were derived from the Caribbean Sea, the temperate shores of California and from the tropical Indo-west Pacific (Brusca and Hendrickx, 2010).

The findings of this study support the hypothesis that taxonomic richness in the NW limit of Guaymas Basin are highest in rocky benthic habitats with the greatest structural complexity in comparison with soft sediment habitats, but also, we found that diversity, composition and cover of benthic megafauna vary among soft sediment and rocky outcrops.

In our study we found that depth and temperature were also important environmental factors related to variation in the composition of benthic megafauna as reported in other studies of the southern and central regions in the GoC (Hendrickx, 1996, 2006; Méndez, 2007; Zamorano et al., 2007; Zamorano and Hendrickx, 2012). However, multiple interacting factors ranging from hydrographic (DO, water masses) to food supply and interactions act in synergy with DO and substratum type to influence the structure of these communities.

CONCLUSION

The present study documented that diversity, taxonomic richness, composition and cover of benthic megafauna within the OMZs from 849 to 990 m depth in the NW limit of the Guaymas Basin varied among rocky outcrops and soft sediments. Variation in megafaunal composition was highly correlated with substrate type (rocky outcrops and soft sediments) depth and temperature. Salinity and DO had a minor role in explaining variation in the composition of megafaunal assemblages. We found high taxonomic richness through the LTZ across an area with rocky outcrops, in contrast with some previous reports from other OMZ habitats where a high abundance of few species has been observed. We documented that taxonomic richness diminished at depths with reduced DO in the LB of OMZ with increasing soft sediment cover, however, the relative influence on the observed pattern is limited by the collinearity of DO and substrate. Taxonomic richness and diversity of megabenthos in the NW limit of Guaymas Basin and Sonoran Margin were positively correlated with the increase in structural habitat complexity and heterogeneity of rocky outcrops and structure-forming organisms in the lower boundary of OMZ core and LTZ of the OMZ. These results broaden our understanding concerning the potential roles of substrate characteristics in the community composition of the deep-sea benthic megafaunal assemblages in the GOC and OMZs in general. Our results also contribute to the information required by decision-makers for Marine Protected Areas and design of habitats conservation.

DATA AVAILABILITY STATEMENT

The dataset analyzed for this study can be found in the UNINMAR repository at: http://metadata.icmyl.unam.mx/handle/20.500.12201/10238, http://metadata.icmyl.unam.mx/handle/20.500.12201/10239, http://metadata.icmyl.unam.mx/handle/20.500.12201/10240, http://metadata.icmyl.unam.mx/handle/20.500.12201/10241, http://metadata.icmyl.unam.mx/handle/20.500.12201/10242.

AUTHOR CONTRIBUTIONS

PL-G coordinated the study, elaborated the manuscript, responsible for the integration of datasets, and carried out the analysis and results presented in this article. JB chief scientist of leg 3 of MBARI's 2012 Gulf of California Expedition, and responsible for data collection and editing of the manuscript. JG-G collaborated with the design of the method for video and images analysis, as well as the results analysis, and reviewed the manuscript. EE-B collaborated with the theoretical framework of the study, contributed as the international counterpart during the 2012 MBARI Gulf of California Expedition, assisted in the results analysis, and reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00154/full#supplementary-material

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